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Edited by
Colette C. C. Wabnitz and Carie Hoover

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A Research Report from the Fisheries Centre at UBC

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DIRECTOR'S FOREWORD

This report summarizes the existing knowledge on three ecosystems: Hudson Bay, Canada, Kaloko-Honokōhau, Hawai'i, and the Antarctic Peninsula, Antarctica. Through the construction of ecosystem models representing these three regions, research from numerous aspects of each ecosystem are pieced together to present a holistic story. While we live in a rapidly changing world, it is important to remember there are many regions where we are still gaining an understanding of basic knowledge.

Research on these ecosystems, from the Arctic to the tropics to the Antarctic, presents different levels of our knowledge. For the Arctic (Hudson Bay) the focus is identifying changes known to be occurring for certain species, and addressing the reasons for those changes in addition to the greater implications to the rest of the ecosystem. In the tropics (Hawai'i) the construction of a model allows insight into structure and function of the ecosystem focusing on the role of an endangered species, the green sea turtle, and provides a baseline to assess potential future impacts on the ecosystem from coastal development. In the Antarctic (Antarctic Peninsula) ecosystem, environmental changes are explored as they impact a key link in the food web.

While the models presented address localized issues relating to very different regions of the world, the ultimate goal is the same; to increase our understanding of ecosystems as a whole and the different stressors related to each region. With this knowledge, we can formulate better questions for future research, assist in informing managers, and hopefully gain greater insights and understanding of the likely impact of future stressors.

U. RASHID SUMAILA
Director and Professor
UBC Fisheries Centre
December 2012

AN ECOSYSTEM MODEL OF HUDSON BAY, CANADA WITH CHANGES FROM 1970-2009[1]

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ABSTRACT

An ecosystem model was created for the Hudson Bay region, Canada, for 1970-2010, aiming to identify the threats of global warming to marine mammals. The model presented in detail here includes 40 functional groups and provides estimates for previously unknown parameters such as biomass of fish species, given ecosystem constraints, using the Ecopath with Ecosim modeling framework. The model is tuned to all catch data known for the region. In addition to providing a comprehensive overview of the trophic dynamics within the system, temporal simulations driven by declines in sea ice mimic the changes known to occur to the region. The 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.

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 (Arctic Climate Impact Assessment 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.

Hudson Bay (HB) is a unique ecosystem. While in location it is considered sub-Arctic, between 50-70˚N, the climate of this system is atypical reflecting high Arctic climate and biogeography, especially when considering higher trophic level animals. For example, polar bears, one of the most famous examples, 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).

While surface temperatures in Hudson Bay have increased 0.5-1.5˚C during 1955-2005 2005 (Hansen *et al.* 2006), sea ice decreased by 2000±900 km^2 $year^{-1}$ between 1978 and 1996 (Parkinson *et al.* 1999). These changes combined with a longer ice free season (Gagnon and Gough 2005) have unknown consequences for the marine ecosystem. There is a greater need than ever to utilize the available data to discover new information within HB and other polar regions.

HB, being relatively unstudied compared to other parts of the Arctic and Antarctic, became the focus for an ecosystem model as part of the Global Warming and Arctic Marine Mammals (GWAMM) project as funded by IPY (International Polar Year) and DFO (Department of Fisheries and Oceans). The aim of the ecosystem model presented in this report is to gain a deeper understanding of the trophic links within the Hudson Bay, particularly those impinging on marine mammals, and to understand how the ecosystem structure might change due to future climate change.

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[1] Cite as: Hoover, C., Pitcher, T.J., and Christensen, V. (2012) An Ecosystem Model of Hudson Bay, Canada and Changes from 1970-2009, p. 2-68. *In*: Wabnitz, C.C.C. and Hoover, C. (eds.) From the tropics to the poles: Ecosystem models of Hudson Bay, Kaloko-Honokōhau, Hawai'i, and the Antarctic Peninsula. Fisheries Centre Research Reports 20(2). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

MATERIALS AND METHODS

Ecosystem Overview

The Hudson Bay ecosystem has been an integral part of Canadian history, most notably in the 18th century with the expansion of the fur trade by Hudson's Bay Company (Stewart and Lockhart 2005). Prior to this Thule and Dorset cultures had survived for thousands of years by hunting marine mammals. Presently, Inuit and Cree populations inhabit the coast of Hudson Bay, along with additional communities further north in the Canadian archipelago. The majority of Inuit and Cree reside in Nunavut and the Nunavik portion of Quebec (which represents the top third of the province, and is comprised of First Nations).

The greater HB complex often includes Hudson Bay, James Bay (JB), Foxe Basin (FB) and Hudson Strait (HS) (figure 1). This system is one of 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 chokepoint for Hudson Bay, ultimately determining which marine species have access to the region (Higdon and Ferguson 2009).

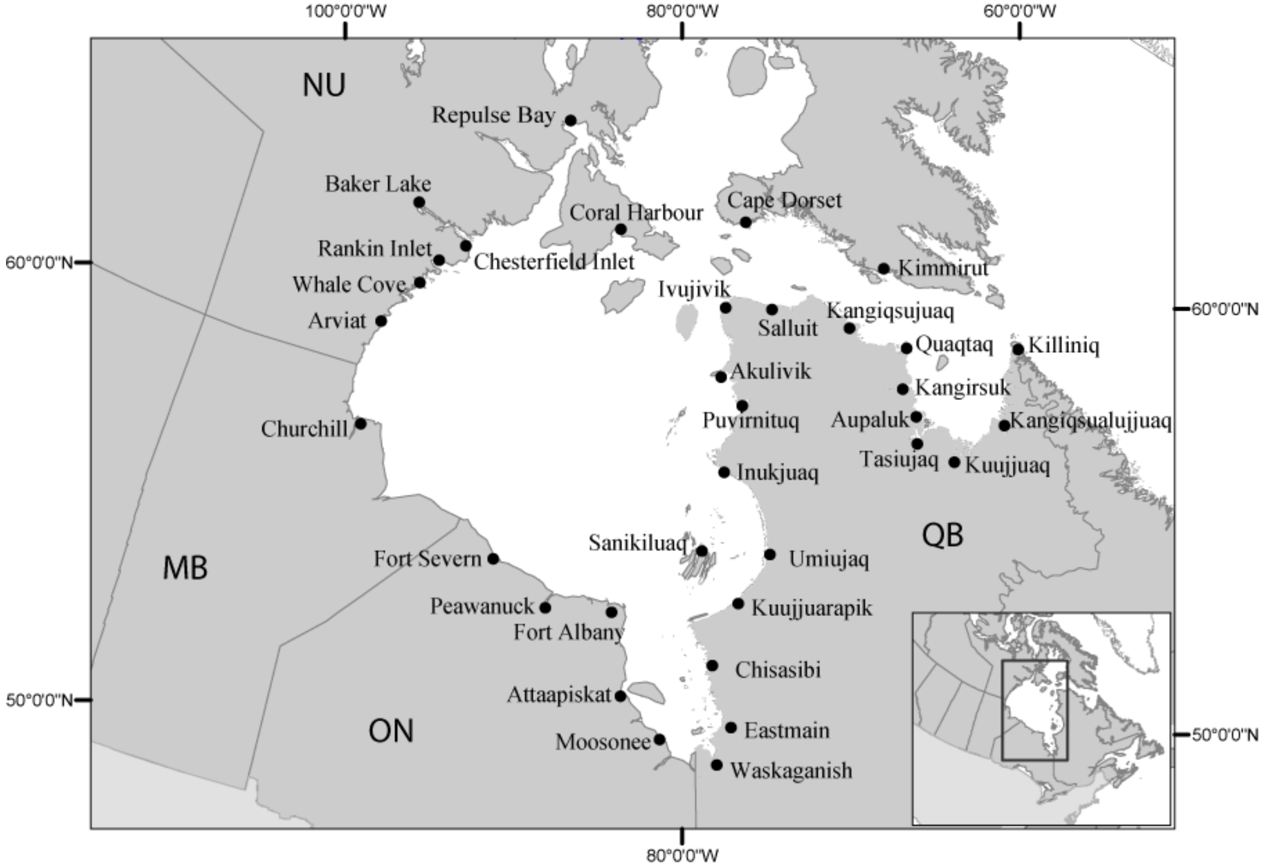

Figure 1: Greater Hudson Bay region and associated communities.

There is a large gradient regarding the types of lower trophic level species found from the north to southern HB, although marine mammals are able to utilize the whole region. Selection of the model area was based on use patterns of marine mammals as their data is more prevalent compared to fish and plankton species, and because modelling aims to focus on the impact of climate change on marine mammal species. James Bay was included in the model area due to its similarity to southern HB. Belugas from two of the three stocks found within HB reside in or near JB in the summer months; therefore this region was believed to be important. Hudson Strait and Foxe Basin were excluded from the model area, as the model area was already quite large and incorporation of these areas was not believed to be essential to understanding the dynamics within HB. For the remainder of this paper, referral to Hudson Bay will include James Bay.

The time period for the model was selected to be 1970. This was chosen as few studies were completed prior to the 1960s regarding estimates of marine species. In addition decreases in sea ice and rising temperatures have been recorded over the last 50 years (Gagnon and Gough 2005), thus making for an interesting time to examine the ecosystem. Finally, there was a lack of data pre-1970, indicating no additional information regarding the ecosystem would be gained by expanding the modelling temporally.

Model Equations

The basic Ecopath model requires various parameters as input; biomass, production, consumption, and ecotrophic efficiency (Christensen *et al.* 2005). Production and consumption values are entered as a ratio to the biomass of a species group (i.e. production/consumption). The master equations (eq. 1-3) to this modelling method are:

(1) Production=predation + fishery+ biomass change+ net migration+ other mortality

(2) Consumption= production + unassimilated food + respiration

(3) EE= 1- other mortality

Biomasses for all groups, where available, were based on the abundance of individual species or species groups multiplied by an average weight per individual and divided among the model area. For Hudson Bay and James Bay the estimated area was nearly 900,000 km^2 (Legendre *et al.* 1996).

For each functional group (or species group) one parameter may be left missing to be solved by the program. Through the use of linear equations, and trophic links, these missing parameters may be solved for. Trophic links are incorporated in the model through the use of the diet matrix.

Temporal simulations are then generated in Ecosim using equation 4;

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \quad (4)$$

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. Vulnerabilities are set within the model with values =2 indicating a mixed interaction between predator and prey, >2 resulting in a bottom up interaction, and <2 resulting in a top down interaction. Vulnerabilities are estimated through an automated search routine (Fit to time series), and user determined values.

Monte Carlo simulations were run on the fitted model, using a pedigree ranking, whereby input parameters are assigned a coefficient of variation (CV) based on the quality of input data from the pedigree ranking from Ecopath with Ecosim version 5 (Christensen *et al.* 2005). 1000 simulations were run to estimate ranges of biomass and P/B values of all functional groups.

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 listed in table 1).

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 1.). 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 5 (Hunt *et al.* 2000; Guénette 2005);

$$E = aM^{0.75} \tag{5}$$

where E in 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 Cauffopé and Heymans (2005).

Table 1: Input parameters for marine mammal functional groups

Species	Pop Size	Source	Mean Weight (Kg)	Source	Longevity (Years)	Source	Mortality (calculated)	Hunting Mortality	Model P/B	Calculated 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	2.080
Polar Bear SHB	1000	(Lunn et al. 2002)	300	(Stirling and Parkinson 2006)	25	(Stirling 2002)	0.096	0.058	0.154	3.109	2.080
Polar Bear Foxe	3000	(Aars et al. 2005)	300	(Stirling and Parkinson 2006)	25	(Stirling 2002)	0.096	0.024	0.120	2.849	2.080
Killer Whale†	20	(Higdon and Ferguson 2009)	4689	(Ford 2002)	80	(Ford 2002)	0.048	0.051	0.151	4.998	4.998
Narwhal†	2710	(Richard 1991)	1300	Heide-Jørgensen 2002)	115	(Garde et al. 2007)	0.083	0.008	0.084	18.696	26.182
Bowhead†	64	Higdon 2009 unpublished data	31076	(Trites and Pauly 1998)	200	(George et al. 1999)	0.018	0.003	0.021	5.475	5.475
Walrus N	2500	(Mansfield and St Aubin 1991) 1976 estimate	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	29.560	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 Pauly 1998)	0.123	0.002	0.125	18.612	18.612
Ringed Seal	600,000	(Smith 1975)	42.5	(Trites and Pauly 1998)	43	(Miyazaki 2002)	0.15	0.008	0.158	16.050	17.272
Harp seal	8000	Assumed (Ferguson pers. Comm)	130	(Lavigne 2002)	30	(Lavigne 2002)	0.112	0.014	0.126	15.660	15.660
Belgua E†	4200	(Hammill 2001 ; Gosselin 2005 ; Hammill et al. 2009a)	725	(DFO 2002b; NAMMCO 2005b)	50	(Harwood et al. 2002; Stewart et al. 2006)	0.044	0.032	0.066*	21.448	21.448
Belgua W†	50,000	(COSEWIC 2004a; NAMMCO 2005b)	725	(DFO 2002b; NAMMCO 2005b)	50	(Harwood et al. 2002; Stewart et al. 2006)	0.0587	0.005	0.064	16.713	16.713
Beluga James†	1842	(Gosselin et al. 2002)	725	(DFO 2002b; NAMMCO 2005b)	50	(Harwood et al. 2002; Stewart et al. 2006)	0.057	0.019	0.087*	16.623	16.623

† Narwhal, Killer whale, bowhead, and all beluga biomasses were adjusted to 50% to account for roughly 50% of their time spent in the model area

* The 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 (figure 2). 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 form 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.

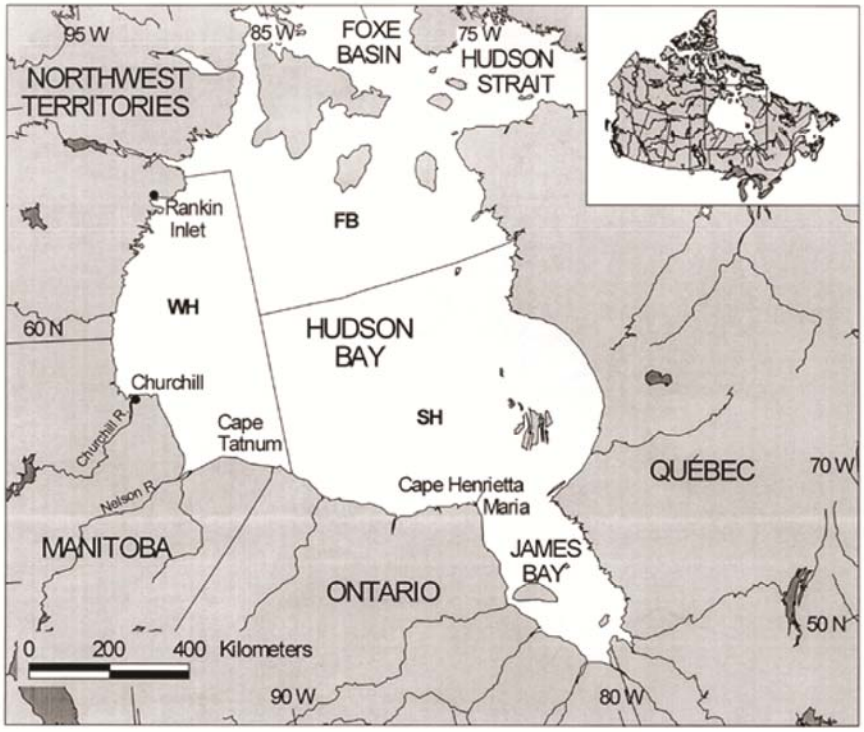

Figure 2: Delineation of the Western Hudson Bay (WHB), Southern Hudson Bay (SHB), and Foxe Basin (FB) populations of polar bears within Hudson Bay. Reprinted from Stirling *et al.* (1999).

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).

1. 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 t·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.

2. 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 t·km^{-2} for the entire region. As 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% harbour 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.

3. 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 t·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 t·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% harbour 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 t·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 that 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% harbour 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/zoarcids, 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 0.103 year^{-1}. This combined with the natural mortality led to a P/B of 0.151 year^{-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 2004b). 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 2004b). 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-Jørgensen 2002; COSEWIC 2004b; 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 54000kg up to 68,000 kg 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 t·km^{-2}.

The diet of bowhead whales is believed to consist primarily of copepods and euphausiids with other zooplankton (mysids, gammerid 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 (figure 3) 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 2002a; COSEWIC 2006). There are no complete stock assessments for any of the four walrus stocks, however estimates are presented for each of the HB stocks (DFO 2002a). These stocks were split into two functional groups as they are hunted by different communities, and have different dietary habits.

Figure 3: Ranges of Atlantic Walrus stocks reprinted from (Stewart 2008). Modeled stocks include the walrus N functional group (stock #3 on map) the Northern Hudson Bay-Davis Strait stock and the walrus S (stock #2 on map) known as the Southern and Eastern Hudson Bay stock. No other walrus stocks are used in the model.

1. 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 0.00274 t·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.

2. 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 2002a), indicating a declining population. The biomass was set to 0.001 t·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; Muir *et al.* 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 t·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 fisheries section).

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 adult 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*)

Harbour seals in Hudson Bay are known to reside in the marine environment as well as lakes which drain into HB (Mansfield 1967a; 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 harbour 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). Harbour seals are thought to be one of the least abundant seals in HB therefore the abundance was set to 1000 seals or 0.001 $t{\cdot}km^{-2}$ (Ferguson pers. comm.).

The diet of harbour 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 2009) representing only a small portion of the model area. Densities estimated varied from 0.97±0.06 seals km^{-2} in 2007 to 0.49±0.04 seals 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 450000 and 900000 seals. 1975 estimates from projected population at 61000 seals for James Bay and 455000 from Hudson Bay (Smith 1975). The population for the 1970s was set to 600000 seals, or 0.0469 $t{\cdot}km^{-2}$.

In general ringed seals feed primarily on Arctic cod and other pelagic fish along with amphipods (DFO 2009). 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 south eastern 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 700000 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 1967b). For the model the population within HB was estimated to be 8000 (Ferguson pers. comm.) or 0.001 $t{\cdot}km^{-2}$.

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 invertebrates (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 2005b), 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 Sanikiluaq 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 3 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 modelling 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 6 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.* 1998). 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-Jørgensen 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).

1. 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 2005b). The eastern HB population winters in northern Labrador and makes it migration past Ungava Bay and down the eastern coast of HB to its summer location ranging from Kuujjuaraapik 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 2004a).

Areal transect surveys have shown varying trends in the population (Gosselin 2005; Gosselin *et al.* 2009), however the general trend from surveys and modelling is the population has declined from roughly 4000 whales in 1985 to 2000-3100 whales in 2008 (Hammill 2001; Gosselin 2005; NAMMCO 2005b; 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 2004a). 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 2004a).

The biomass for the 1970s population was set to 0.00207 t·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.

2. 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 2004a). This population appears to be relatively abundant, although surveys have been sporadic (i.e. 1987 and 2005). COSEWIC (2004a) 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 2004b). 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 2004a;

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 t·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.

3. 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 2004a), although closer to eastern HB in proximity. Traditional knowledge indicates that there are some whales that 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 2005). 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 form the Sanikiluaq (Belcher Island) community, as no harvest occurs within James Bay (COSEWIC 2004a). 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 artefact of survey coverage, and seasonal movements (COSEWIC 2004a). 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 0.00147 t·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 2) 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 t·km^{-2}. A P/B value of 0.113 year^{-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 0.005 year^{-1} was calculated. The combined P/B value of 0.118 year^{-1} was too low for the model and had to be increased to 0.37 year^{-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 levelled 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.* 2009a; Gaston *et al.* 2009b). The diet of thick-billed murres has demonstrated shifts from Arctic cod to capelin (Gaston *et al.* 2003) (figure 4). 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

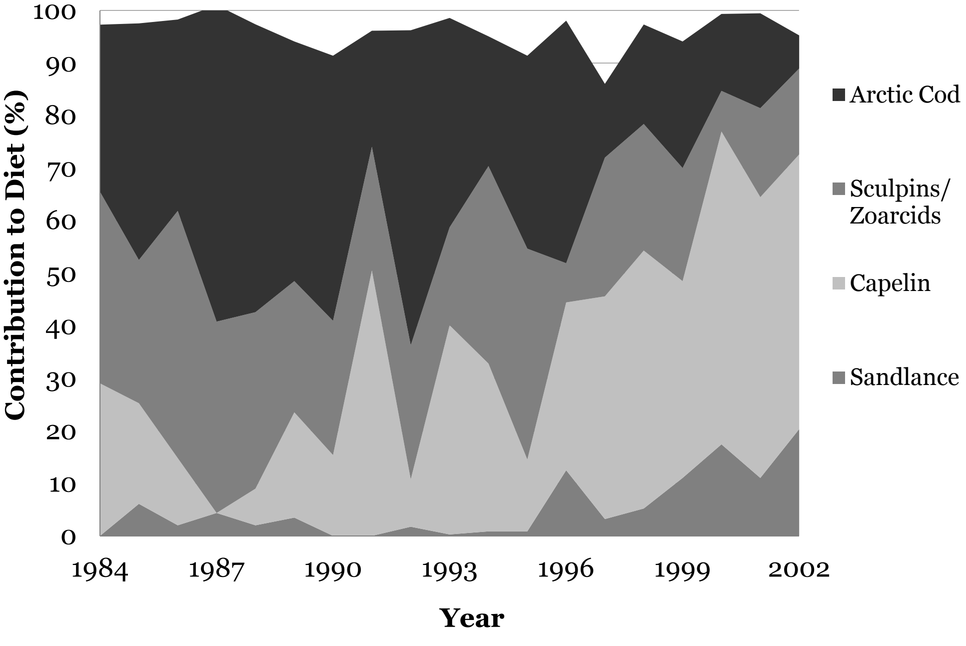

Figure 4: Changes in diet of thick-billed murres at Coats and Diggs Islands from 1984-2002. Graph reproduced from data in Gaston *et al.* (2003).

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 3.

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 (table 2) and natural mortality, with the natural mortality being calculated using the life history tool page in Fishbase (Froese and Pauly 2008), which provides equation 6, where M is the natural mortality, L_∞= the maximum length of the fish, and T is the temperature of the water in degrees Celsius (Pauly 1980; Froese and Pauly 2008). As little information is known about fish in Hudson Bay, 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 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; British Atmospheric Data Centre 2010).

$$(6) \quad M = 10^{(0.566-0.718*Log(L_\infty)+0.02*T)}$$

Values for natural mortality (M), Equation 6, was 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 no commercial fisheries operating in the model area at present, with only a few brief attempts in the past (Stewart and Lockhart 2005). Recreational fishery information is only available for Arctic char from 1988-1997 through DFO harvest records (DFO 1990; DFO 1991; DFO 1992; DFO 1993; DFO 1994; DFO 1995; DFO 1996; DFO 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 per person year^{-1} was estimated for 1970. Underreporting is believed to occur therefore the upper estimate of 120 kg per person year^{-1} was believed to be more accurate.

Table 2. Fishing mortality based on per capita consumption rate of 120kg per person·year^{-1}.

Species group	% of total catch	Catches (Tonnes)	Hunting Mortality
Arctic Char	35	421.614	6.334E-04
Atlantic Salmon	1	12.046	3.900E-05
Gadiformes	20	240.923	2.665E-04
Sculpins/ Zoarcids	20	240.923	6.604E-04
Capelin	10	120.461	1.823E-04
Sandlance	3	36.138	6.151E-05
Sharks/Rays	0	0	0
Other Marine Fish	5	60.231	9.137E-05
Brackish Fish	2	24.092	3.967E-04

Based on a population size of 10033 (see fishing section for community population estimates) this would yield a total catch of 1204.6 T 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 2, and include the estimated hunting mortality.

Consumption rates were calculated using equation 7 from Palomares and Pauly (1998):

$$(7) \qquad \log Q/B = 7.964 - 0.204 logW_{\infty} - 1.965T' + 0.083A + 0.532h + 0.398d$$

where W_{∞} (infinity) 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 modelling program to estimate biomass parameters. Previous modelling 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 (Christensen pers. Comm. 2006). Parameters calculated for all fish species are presented in table 3.

Arctic Char

The Arctic Char *(Salvelinus alpinus)* group consists of only one species. Char 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, char are hunted by subsistence and recreational hunters (Stewart and Lockhart 2005). Arctic char 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), molluscs, 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 (molluscs, crustaceans, and small fish), while adults have been known to prey on fish (capelin, sandlance, and small cod) (Froese and Pauly 2008). For the model the diet was set to: 1% Arctic char, 1% Atlantic salmon, 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 murres 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.

Table 3: Calculated input parameters for all fish groups within the model.

Group	Species	Common Name	L∞	Average Temp °C	Mortality at Average Temp	M at 0.5 °C	Q/B at 0.5 °C
Arctic Char	*Salvelinus alpinus*	Arctic Char		1.5	0.10	0.10	1.7
Atlantic Salmon	*Salmo salar*	Atlantic Salmon	156	9	0.30	0.25	7.14
Gadiformes	*Arctogadus glacialis*	Polar cod	34	8	0.55	0.46	2.3
	Boreogadus saida	Arctic cod	31.3	1	0.31	0.30	2.5
	Gadus ogac	Greenland cod	79.5	1	0.22	0.22	1.3
Sculpins/ Zoarcids	*Gymnocanthus tricuspis*	Arctic staghorn	31.5	1	0.30	0.29	2.2
	Icelus bicornis	twohorn sculpin	16.6	1	0.51	0.50	3.6
	Icelus spatula	spatulate sculpin	22.1	3	0.35	0.33	3
	Myoxocephalus quadricornis	fourhorn sculpin	33.1	1	0.32	0.32	2.1
	Myoxocephalus scorpioides	Arctic sculpin	23.2	1	0.32	0.39	2.9
	Myoxocephalus scorpius	shorthorn sculpin	21.9	9.3	0.79	0.64	2.7
	Triglops murrayi	moustache sculpin	21.1	10	0.65	0.42	3.1
	Triglops pingelli	ribbed sculpin	27.3	10	0.35	0.28	3
	Gymnelus viridis	fish doctor	58.1	1	0.28	0.28	1.6
	Lycodes pallidus	pale eelpout	27.3	1	0.41	0.35	2.6
	Lycodes reticulatus	Arctic eelpout	37.6	1.3	0.30	0.28	2.2
Capelin	*Mallotus villosus*	capelin	16.9	4.3	0.85	0.78	3.9
Sandlance	*Ammodytes dubius*	northern sand lance	26.2	2	0.45	0.44	3.8
	Ammodytes hexapterus	stout sand lance	31.5	10	0.47	0.38	2.4
Sharks/Rays	*Somniosidae*	sleeper sharks			0.04		0.5
	Rajidae	skates			0.18		2
Other Marine Fish	*Leptagonus decagonus*	alligator poacher	22.1	1	0.45	0.41	3
	Ulcina olriki	Atlantic alligatorfish	9.2	1	1.03	0.77	5.3
	Cyclopterus lumpus	lumpfish	55	5	0.19	0.17	1.3
	Eumicrotremus derjugini	leatherfin lumpsucker	NA				4.7
	Eumicrotremus spinosus	Atlantic spiny lumpsucker	NA				4
	Careproctus reinhardti	sea tadpole	31.5	3	0.57	0.32	2.4
	Liparis fabricii	gelatinous snailfish	21.1	8	0.94	0.42	3.1
	Liparis gibbus	dusky snailfish	54	1	0.33	0.21	1.7
	Liparis tunicatus	kelp snailfish	16.9	1	0.98	0.49	3.5
	Anisarchus medius	stout eelblenny	31.5	1	0.26	0.32	2.4
	Eumesogrammus praecisus	fourline snakeblenny	23.2	1	0.35	0.39	2.9
	Leptoclinus maculatus	daubed shanny	21.1	1	0.38	0.42	3.1
	Pholis fasciata	banded gunnel	31.5	1	0.49	0.32	2.4
	Clupea harengus	Atlantic Herring	30.4	9	0.48	0.39	10.1
Brackish Fish	*Lumpenus fabricii*	slender eelblenny	38.1	1	0.28	0.28	2.2
	Stichaeus punctatus	Arctic shanny	14.5	12	0.94	0.55	3.9
	Hippoglossoides platessoides	Canadian plaice	70.4	1.4	0.19	0.18	1.7

NA indicates parameter could not be calculated due to missing information required for calculations.

Sculpins/Zoarcids

Sculpins (Family: Cottidae) and zoarcids or eelpouts (Family: Zoarcidae) were combined to form one functional group and include: Arctic eelpout (*Lycodes reticulates*), Arctic sculpin (*Myoxocephalus scorpioides*), Arctic staghorn (*Gymnocanthus tricuspis*), fish doctor (*Gymnelus viridis*), fourhorn sculpin (*Myoxocephalus quadricornis*), moustache sculpin (*Triglops murrayi*), 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 Pauly 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 Pauly 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 Pauly 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 Pauly 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 radiate)* 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 Pauly 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), lumpfishs (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 Pauly 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 Pauly 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 28.1 $g \cdot m^{-2}$. Original samples were presented in dry weight (0.52 to 5.62 $g \cdot m^{-2}$), but converted to wet weight using a conversion factor of 5 (DW:WW) for zooplankton (Cushing *et al.* 1958; Cauffopé 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 5-10 $g \cdot m^{-2}$ for HB samples, although biomasses were higher for Hudson Strait, up to 20 $g \cdot m^{-2}$ for macro-zooplankton, and 110 $g \cdot m^{-2}$ 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 that more than one species is found within HB. This combined with the diets of predators led to the belief that cephalopods are present within the model area, and they 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 6.9 year^{-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 5 year^{-1} for P/B and Q/B respectively. 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 5-10 g·m^{-2}. A value of 7.5 g·m^{-2} or t·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 1.5 year^{-1} depending on the season, and Q/B ratios ranged from 0.33 to 5 year^{-1} (Okey and Pauly 1999). P/B for HB was set to 1 and Q/B set to 3 year^{-1} based on the values from Prince William Sound. Chaetognaths were the most abundant species in this group, with a diet focused on copepods (Tönnesson 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 *Thysanhoessa rachii* and other unidentified species. Based on the 1993 samples euphausiids contributed on average 2.14 g·m^{-2} or t·km^{-2} to the zooplankton biomass. The P/B for this group was set to 3 year^{-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 meso-zooplankton 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 4.015 g·m^{-2} or t·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 5 year^{-1} (Okey and Pauly 1999). Other zooplankton groups show higher P/B values ranging from 5.8 to 36.3 year^{-1} for the Aleutian Islands (Heymans 2005) or 10.7 to 24 year^{-1} for the Kerguelen Islands (Pruvost *et al.* 2005). A P/B of 16 year^{-1} was used for the HB model. A P/Q of 0.25 was assumed to give a Q/B value of 64 year^{-1} when balancing the model. Copepods are primarily grazers, with a strong link to ice algae identified in HB (Runge and Ingram 1987; Runge and Ingram 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 1.05 $g{\cdot}m^{-2}$ 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 0.45 $g{\cdot}m^{-2}$ 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 1.8 $g{\cdot}m^{-2}$ was used for the model. P/B for various crustacean plankton for Prince William Sound ranged from 2-8 $year^{-1}$ (Okey and Pauly 1999). P/B for benthos ranged from 0.7 $year^{-1}$ for benthic crustaceans in the Weddell Sea (Jarre-Teichmann *et al.* 1997) to 2.1 $year^{-1}$ for benthic invertebrates for the Aleutian Islands (Heymans 2005). A P/B value of 3.6 $year^{-1}$ was used along with a P/Q ratio of 0.25 to give a Q/B ratio of 14.4 $year^{-1}$.

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 $g{\cdot}m^{-2}$. The P/B was set to 10 $year^{-1}$ 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 40 $year^{-1}$. 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 36 $year^{-1}$ and a Q/B of 112 $year^{-1}$ (Heymans 2005). Herbivorous zooplankton from the Kerguelen Islands were estimated to have a P/B of 24 $year^{-1}$ and a Q/B of 96 $year^{-1}$ (Pruvost *et al.* 2005). Okey and Pauly (1999) state a P/B of 15 $year^{-1}$ for small zooplankton in Prince William Sound. For the HB model the P/B was set to the lower range of 15 $year^{-1}$ and a Q/B of 45 $year^{-1}$ 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, 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 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 0.18 to 0.55 year^{-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.

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 4 year^{-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 lilies), Echinoidea (sea urchins), Holothuroidea (sea cucumbers), and Ophuiroidea (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 0.63 year^{-1} (Jarre-Teichmann *et al.* 1997). However, these values were too low to balance the model, so they were increased to 0.3 and 1 year^{-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 0.57 and 6.33 year^{-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.

Table 4: Parameters for benthic functional groups from high latitude Ecopath models

Functional Group	Model Area	Year of Model	B ($t \cdot km^{-2}$)	P/B (year)	Q/B (year)	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)

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 2.5 $year^{-1}$, and the Q/B was set to 12.5 $year^{-1}$. 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.* 1997). The first survey in 1993 yielded estimates of 0.36-133.5 $t{\cdot}km^{-2}$ (based on chl *a* samples of 1.2-145 $mg{\cdot}m^{-2}$)[2], and the second survey estimated 7.5-75 $t{\cdot}km^{-2}$ (based on chl*a* samples of 25-250 $mg{\cdot}m^{-2}$).

Pelagic Production

Pelagic production was sampled at 0.33-129 $t{\cdot}km^{-2}$ (1.1-431 mg Chl*a* m^{-2}) in 1993 (Harvey *et al.* 1997), although this was during the ice free season, so a biomass of 8 $t{\cdot}km^{-2}$ 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 0.03-4.2 $t{\cdot}km^{-2}$ (0.1-14 mg Chl*a* m^{-2}) in 1993 (Harvey *et al.* 1997), 0.003-6 $t{\cdot}km^{-2}$ for values ranging 1978-1990 (Legendre *et al.* 1996), and 0.03-3.6 $t{\cdot}km^{-2}$ 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 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 0.6gC 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 $t{\cdot}km^{-2}$ (Pauly and Christensen 1995)[3]. The biomass for HB was set to 3.5 $t{\cdot}km^{-2}$.

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 8 (Pauly *et al.* 1993):

$$(8) \qquad \mathrm{Log_{10}D} = -2.41 + 0.954\ \mathrm{Log_{10}PP} + 0.863\mathrm{Log_{10}10E}$$

where D is the standing stock of detritus (g C m^{-2} $year^{-1}$), PP is primary productivity (g C m^{-2} $year^{-1}$), and E is the euphotic depth (in meters).

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[2] Wet weight (t·km-2) was calculated using the conversion Chl*a*=1.5% of ash free dry weight (AFDW) (Farabee 2001), 1g carbon=2g AFDW (Cauffopé and Heymans 2005), and 1gC=9g wet weight (Pauly and Christensen 1995).
[3] Using the conversion for phytoplankton where 1g Carbon=9g wet weight.

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 an ice detritus biomass of 0.009 t·km^{-2}.

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 t·km^{-2}.

Ecosim Parameters

Fisheries

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 was then continued through the temporal simulations in Ecosim. Catches for the first year, and subsequent years are presented.

Polar bear Hunting

1. 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.

2. 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.

3. 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 modelling 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

Killer whales are not generally targeted, however they are occasionally hunted in HB (Ferguson pers. comm.). Table 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 ¼ of a whale was used as a starting value.

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

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

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; Chesterfiled 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 5, 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 of 40% of total catch (Roberge and 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 5.

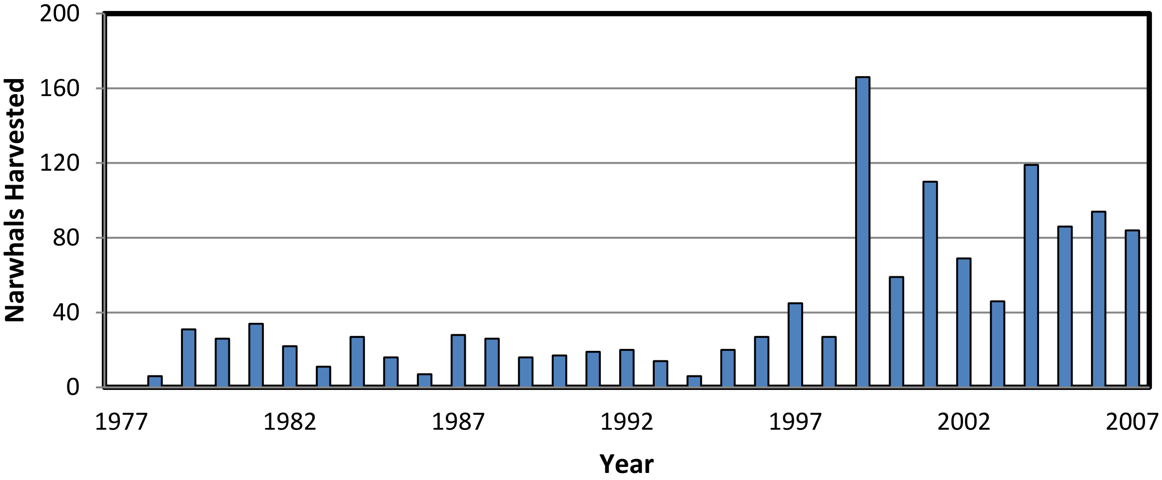

Figure 5: Reported catches of narwhal from 1977-2007 for Repulse Bay, Chesterfiled Inlet, Coral Harbour, Ranklin Inlet, Whale Cove, and Cape Dorset (DFO 1990; DFO 1991; DFO 1992; DFO 1993; DFO 1994; DFO 1995; DFO 1996; DFO 1997; Stewart and Lockhart 2005). Figure does not incorporate a struck and loss rate.

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.

1. 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.

2. 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 Puvirnituq. 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

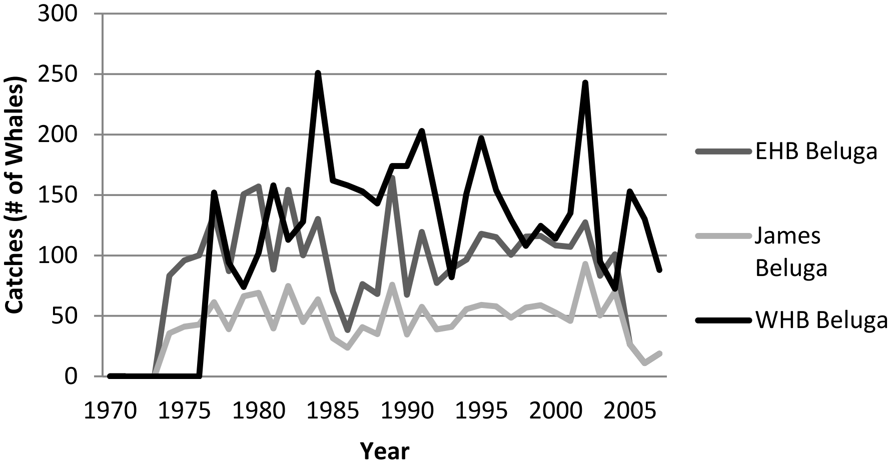

Figure 6: Catches of Beluga whales form 1970-2007 as aggregated by stock.

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 6 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 2009).

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

1. Beluga East

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

2. Beluga West

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

3. 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 7). 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 7), 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.

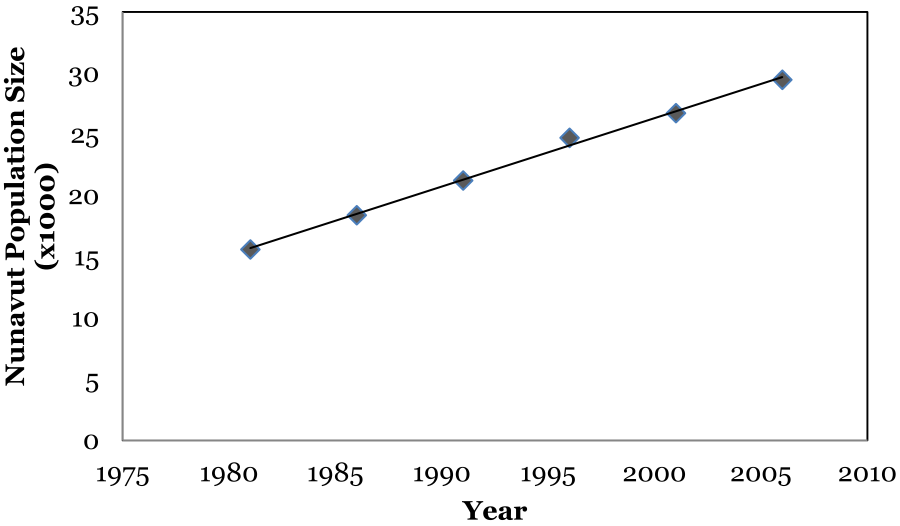

Figure 7: Regression of community population size in Nunavut (all communities) from 1981-2006.

1. 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 seals per person 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% harbour 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.

2. 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.

3. Fishing

Fishing rates were based on a per capita rate of 120kg per person year^{-1}. See Fishing mortality (table 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.

Fitting the Model to Data

Time series data (table 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[4] (figure 7).

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 8 uses data from the HadISST[5] (Hadley Centre Sea Ice and Sea Surface Temperature data set) model (British Atmospheric Data Centre 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

Table 6: Name and type of time series data used to fit the HB model

Time Series Data	Type of 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

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[4] Human population was scaled to 1 for 1970.

[5] The HasISST dataset has replaced the Global sea Ice and Sea Surface Temperature (GISST) dataset. HasISST data is generated from other datasets in addition to sea ice algorithm, and passive satellite data http://hadobs.metoffice.com/hadisst/

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 rescaled 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 8 shows the annual SST average for HB by month, with 95% CI. Again, data was rescaled to positive values with a mean value of 1 for 1970.

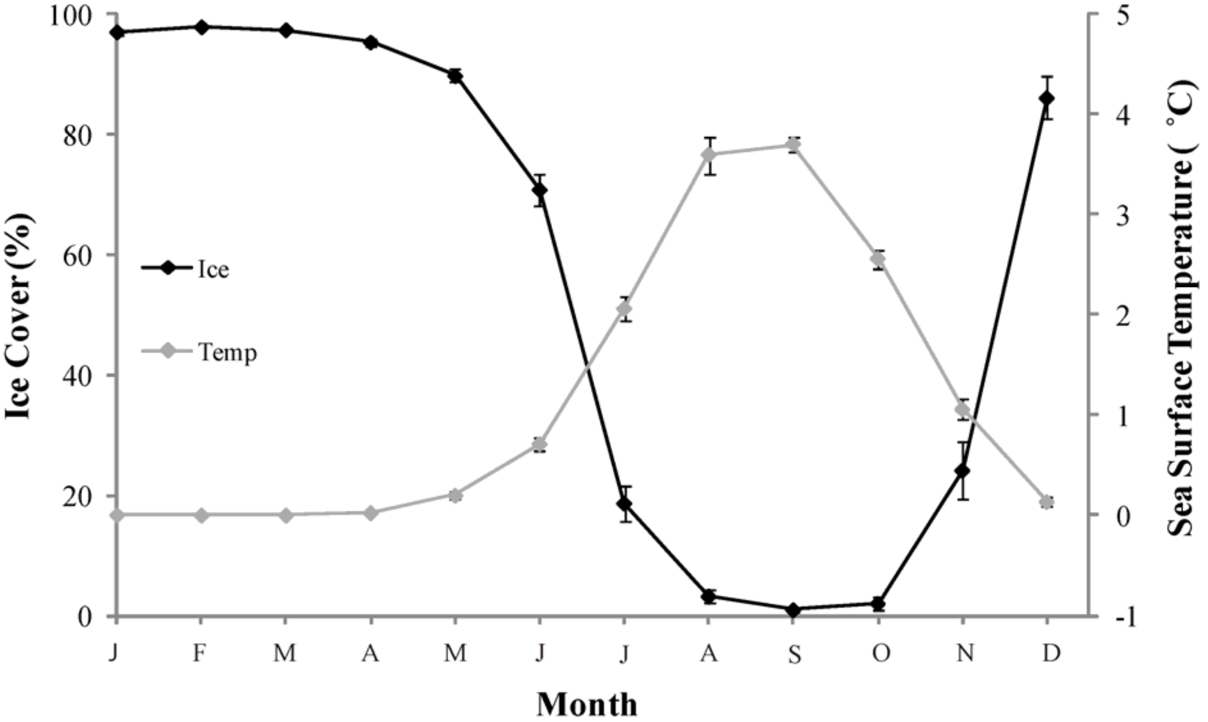

Figure 8: Monthly SST and ice cover with 95% CI for 1970-2009. Values were taken from the HadISST model.

Mediation Functions

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 (figure 9). 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.

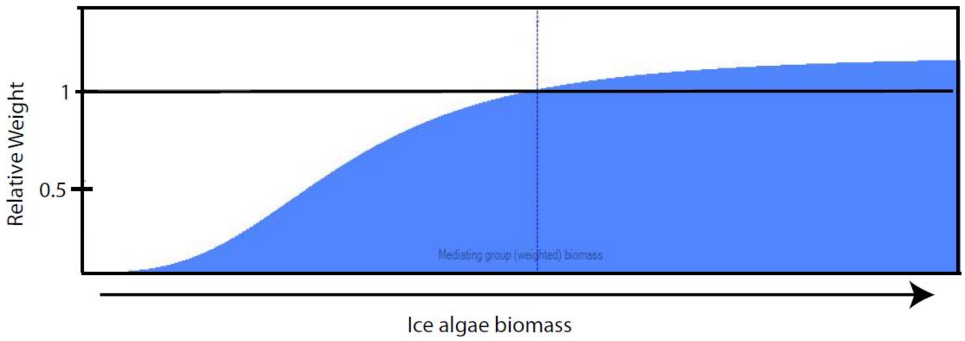

Figure 9: Polar Bear Mediating Function with ice algae as the mediating group (x- axis). Y axis shows the relative weight of polar bears, starting at y=1 (Ecopath value).

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; Hammill et al 2009b), 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% year^{-1} was necessary to fit the observed declines of EHB belugas. This led to an increased biomass accumulation of 1% year^{-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 year^{-1}, and JB beluga P/B was increased from 0.0673 to 0.0873 year^{-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% year^{-1} was initially used, however this value was later lowered to 0.7% year^{-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 harbour 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; Christensen *et al.* 2007).

Vulnerabilities

Vulnerabilities were first estimated using the automated fit to time series routine in Ecosim (Buszowski *et al.* 2007). 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 4.

RESULTS

Balancing the Model

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 7.

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 5, as output from the mixed trophic impact table in Ecopath.

Table 7: Balanced model with parameters estimated by the model in bold

Group Name	Trophic Level	Biomass $(t\cdot Km^{-2})$	P/B $(Year^{-1})$	Q/B $(Year^{-1})$	EE	P/Q
WHB Polar Bear	4.857	0.0005	0.129	2.080	**0.414**	**0.062**
SH Polar Bear	4.906	0.0004	0.154	2.080	**0.506**	**0.074**
Polar Bear Foxe	4.927	0.0002	0.121	2.080	**0.304**	**0.058**
Killer Whale	4.872	0.0000	0.151	4.998	**0.265**	**0.030**
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	0.0010	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	0.0010	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	0.0010	0.126	15.660	**0.688**	**0.008**
Beluga E	3.694	0.0021	0.066	21.448	**0.220**	**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	0.0650	0.370	**17.258**	0.950	**0.021**
Arctic Char	3.300	**0.412**	0.200	1.500	0.950	**0.133**
Atlantic Salmon	3.450	**0.148**	0.520	7.150	0.950	**0.073**
Gadiformes	3.235	**0.853**	0.470	1.850	0.950	**0.254**
Sculpins/ Zoarcids	3.188	**0.382**	0.700	3.269	0.950	**0.214**
Capelin	3.132	**0.488**	1.700	4.800	0.950	**0.354**
Sandlance	3.128	**0.705**	0.850	3.450	0.950	**0.246**
Sharks/Rays	4.033	**3.18E-06**	0.220	1.250	0.950	**0.176**
Other Marine Fish	2.948	**0.374**	0.932	3.018	0.950	**0.309**
Brackish Fish	3.216	**0.055**	3.500	5.798	0.950	**0.604**
Cephalopods	3.645	**0.227**	1.500	5.000	0.950	**0.300**
MacroZooplankton	2.711	7.5000	1.000	3.000	**0.278**	**0.333**
Euphausiids	2.787	2.1480	3.300	**13.200**	**0.800**	0.250
Copepods	2.050	4.0150	16.000	**64.000**	**0.472**	0.250
Crustaceans	2.410	1.8000	3.600	**14.400**	**0.584**	0.250
Other MesoZooplankton	2.336	1.2100	10.000	**40.000**	**0.556**	0.250
MicroZooplankton	2.000	**2.235**	15.000	45.000	0.950	**0.333**
Marine Worms	2.275	**5.930**	0.600	4.000	0.950	**0.150**
Echinoderms	2.575	**8.708**	0.300	1.000	0.950	**0.300**
Bivalves	2.148	**5.942**	0.570	6.300	0.950	**0.091**
Other Benthos	2.091	**3.139**	2.500	12.500	0.950	**0.200**
Pelagic Production	1.000	8.0000	**46.865**	0.000	0.800	-
Ice Algae	1.000	3.5000	**46.197**	0.000	0.650	-
Ice Detritus	1.000	0.0090	-	-	**0.904**	-
Detritus	1.000	0.3300	-	-	**0.224**	-

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

	Functional Group	Biomass (CV)	Lower Limit	Mean Biomass	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

Monte Carlo Results

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 6 for all CV values and appendix 7 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 8.

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 endeavours 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 t·km^{-2} compared to 4.32 t·km^{-2} in the Antarctic Peninsula (Hoover unpublished data), 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 t·km^{-2} appears to fall within the ranges of observed samples. Harvey *et al.* (2006), estimated macro and meso-zooplankton from >1 to 6 g DW m^{-2} for central HB, while a few samples from Harvey *et al.* (2001) reached close to 10 g DW m^{-2} in northern HB. Using the conversion of DW:WW of 5 (Cushing *et al.* 1958), this would indicate values of zooplankton biomass from 5-30 g·m^{-2} within Hudson Bay and up to 50 g·m^{-2} for Hudson Strait. However these high values were obtained from late summer values, and are likely not representative of an annual value.

Fitting Results

Results of time series fitting, including effort and mediation are presented in figure 10. 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 data and the model are not the same, the trend appears to be similar, with catches decreasing and levelling 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.

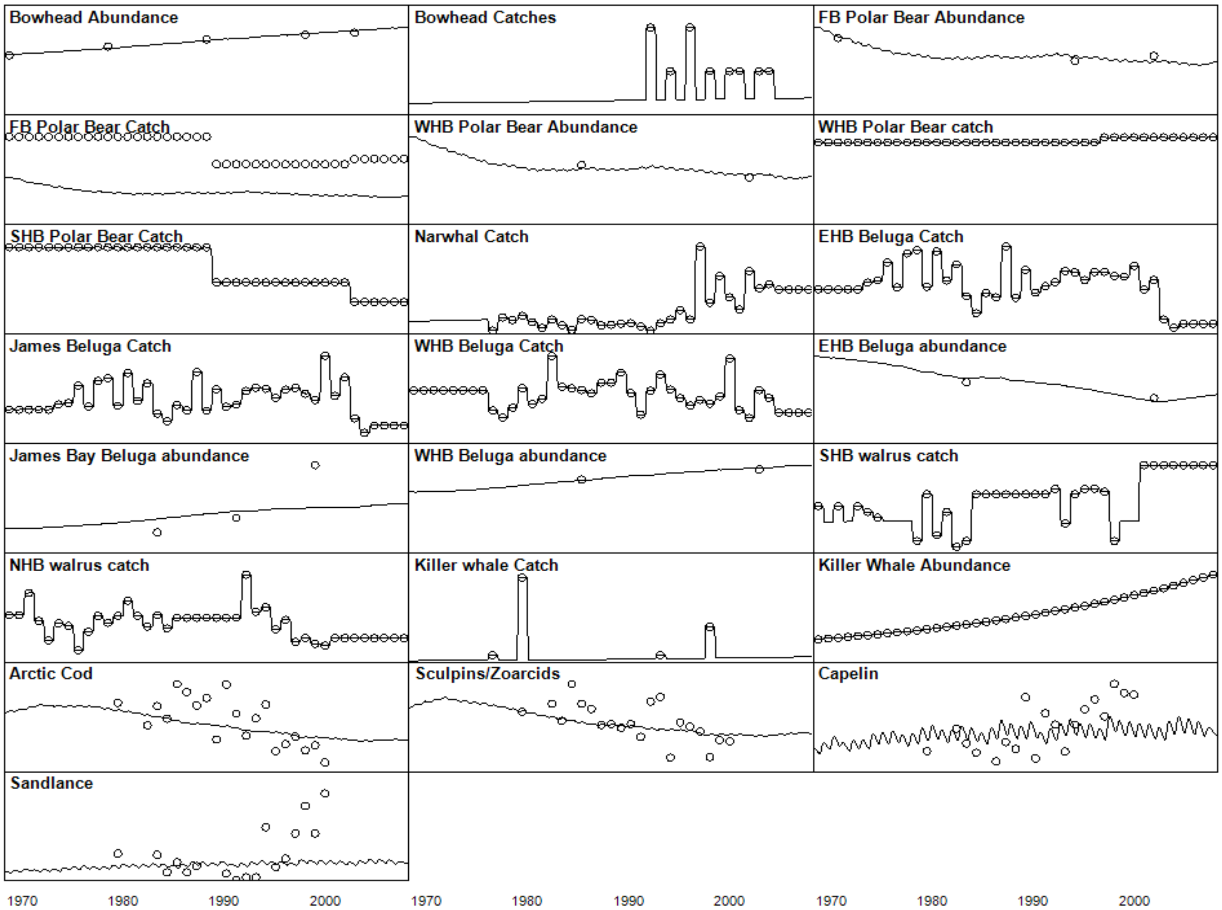

Figure 10: Time series data (open dots) with abundance and catch trends (lines) from model output.

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.

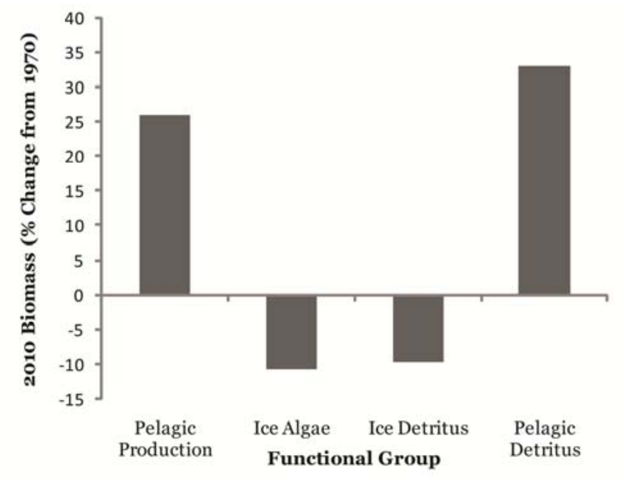

Figure 11: Model end biomass for 2010 presented as percentage change from starting biomass for producers and detritus.

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.

Starting from the bottom of the food web, shifts caused by forcing functions can be identified. Figure 11 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 levels, as shown in figure 12 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.

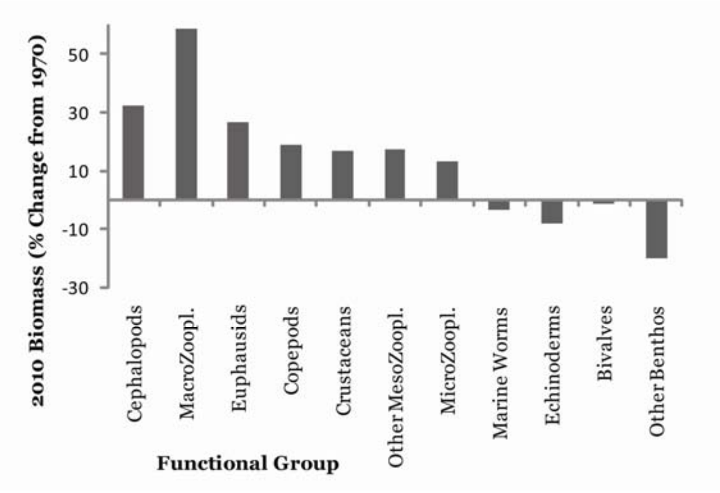

Figure 12: Model ending biomass for 2010 presented as percentage change from the starting biomass for zooplankton and benthic groups

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 13). Gadiformes and sculpins/zoarcids decreased in the diet of thick-billed murres an average of 68 and 57%, respectively (Gaston *et al.* 2003)[6]. Pelagic based fish show increases, with the largest being capelin and sandlance. Fitting of time-series data (figure 10) 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 these groups show substantial increases with capelin increasing over 70% of their original biomass, with

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[6] When comparing the average contribution to the diet of thick billed murres as the average value for the first and last 3 years of the diet study.

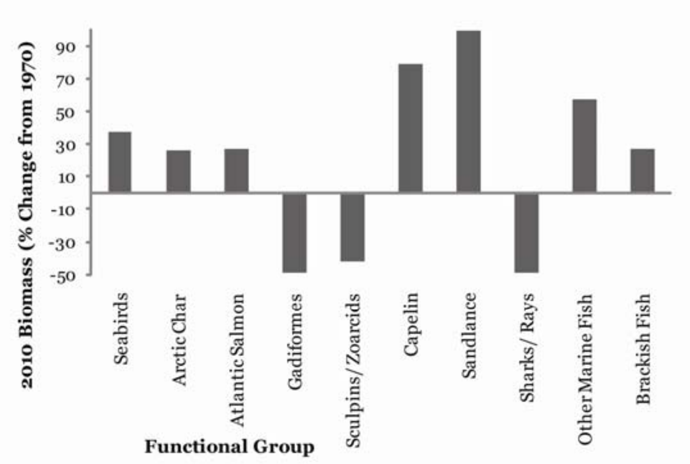

Figure 13: Model ending biomass for 2010 presented as percentage change from starting biomass for fish and seabirds.

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 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 14); 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 8). Removal of catches in the model identifies an increase in narwhal biomass

Bearded seals also appear to decline due to hunting mortality (figure 14). For bearded seals, hunting 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 harbour seals show low hunting mortality throughout the simulation, indicating the populations are large enough to sustain the effort levels used in the model fitting.

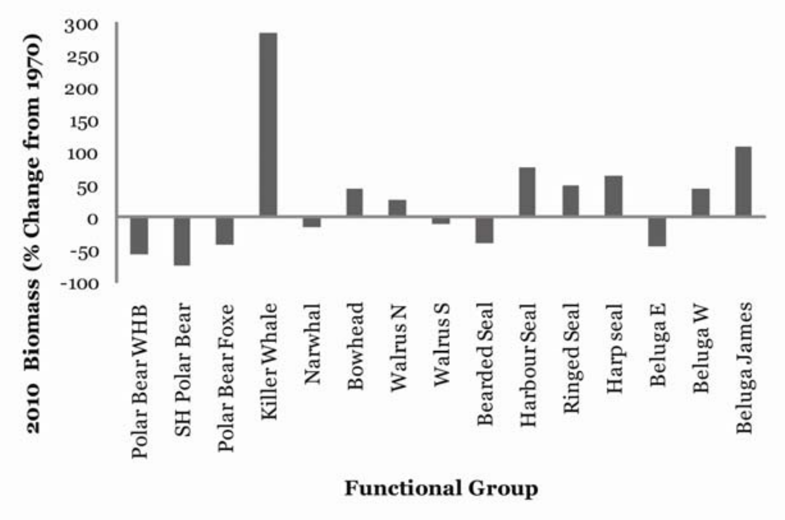

Figure 14: Model ending biomass for 2010 presented as percentage change from starting biomass for marine mammals.

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

DISCUSSION

There are many dynamics expected to alter Arctic ecosystems presently and in the future; climate change, environmental contaminants, off-shore oil and gas activities, shipping, hunting, and commercial fisheries (Huntington 2009). While there are no models large enough to capture the dynamics of Arctic ecosystems including all of these potential threats, this model brings us closer through the inclusion of climate dynamics, and hunting. There are most certainly more dynamics shaping the Hudson Bay ecosystem than included in this model, however there is much to be learned before we move on to incorporating more influences.

Parkinson *et al.* (1999) found a slight (although not significant) negative trend in sea ice from 1979-1996, along with positive ice thickening trends in Hudson Bay. Although the timing of the spring melt has moved earlier in the year -0.49-1.25 days year^{-1}, and freeze-up has shifted later 0.32-0.55 days year^{-1} (Gagnon and Gough 2005). Gough *et al.* (2004) showed a decrease in Arctic summer ice extent has decreased 15-30% in the last 30 years. This model captures a 10% decrease in ice algae biomass, assuming a linear relationship between ice algae and extent of sea ice, however this decline is not as large as the Arctic summer average decline of 15-30%. As ice declines in HB have shown to be less intense than other Arctic areas, the declines used to force the model (and the ice algae group) appear to be within range of observed changes; less than the Arctic average, but still showing declines. If sea ice declines escalate to be on par with high Arctic areas, it is likely biomass changes observed in the model would be exaggerated.

Bentho-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 runoff flushing algal cells 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 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). This would indicate changes in the HB sea ice could have a strong impact on the benthic community. It should be noted that the timing of ice melt generally coincides with the pelagic bloom, making for a complex dynamic in bentho-pelagic coupling (Smith *et al.* 2006). Decreases in benthic groups were observed in the model. These decreases in benthos were impacted by declining ice, yet there are certainly other 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 bentho-pelagic coupling was disrupted, it would allow for restructuring of the ecosystem where pelagic species would dominate lower trophic levels. In fact we see increases in zooplankton biomasses, as they benefit from increased spring blooms.

Zooplankton may not continue to thrive under increasingly warming conditions. As temperature increases, so will river runoff and freshwater inputs to the system, causing both increased nutrients and increased stratification in the water column. However, the impacts to the zooplankton community as a whole remain unknown.

As thick-billed murre diets indicated, there was a shift from Arctic to sub-Arctic fish composition; from cod, sculpins, and zoarcids to capelin and sandlance (Gaston *et al.* 2003). Although it appears that trends were not fully captured (figure 10) large changes in biomass (figure 13) indicate substantial changes in biomass have occurred. As there is a gross lack of data on fish populations in this region, diets of birds was the only indication of fish abundance. Because the data are based on the northern edge of the region, it is questionable as to the capacity to be extrapolated to the entire region. Fish in southern HB are likely to be impacted differently with large freshwater inputs from rivers, causing different environmental conditions. These possibilities need to be explored along with basic comprehensive surveys in order to provide more accurate modelling of fish groups.

Hunting and fishing data is important in understanding the human impacts upon species. Significant under-reporting is likely to have occurred throughout the region, especially in the unregulated catches of seals, birds, and fish. While in the model the mortality inflicted on these groups is nearly negligible, in reality the subsistence harvest is almost certainly an important contribution to the mortality of most groups. The exception will most likely be ringed seals, as the biomass in the region is large and less likely to be impacted by the number of human inhabitants. Ultimately, better estimates of subsistence hunting would lead to better overall indication of the pressures upon marine mammals, fish, and birds.

Marine mammal results provide insight as to potential reasons for changes in abundance, because trends are already known. James Bay beluga increases were not fully captured within the model, even with migration from the EHB beluga population. If the JB population is a mixture of eastern and western HB beluga population, migration from WHB belugas could potentially contribute enough migration to simulate the increase. Another possibility is the reported increase is a factor of survey methods (or survey coverage) rather than actual increases. However, this will likely never be revealed, so at present the increase is believed to be occurring, yet not fully explained by the model.

The narwhal of HB, once believed to be part of a larger population, are under growing hunting pressure, with catches increasing in recent years. As identified in the model, larger harvests are already causing declines in the population, with catches increasing since 2000.

Declines in polar bear populations were difficult to simulate through trophic interactions and hunting harvests. However, the inclusion of a mediating function based on sea ice was key to capturing these declines. This information was necessary to improve the model, however because it is well documented (Stirling and Derocher 1993; Stirling *et al.* 1999; Stirling and Parkinson 2006) we were able to incorporate the indirect effect of sea ice. What remains unknown are the other potentially important interactions between species and their habitat which have yet to be studied, most notable the lower trophic levels.

Future research on the HB ecosystem should focus on expanding our understanding of lower trophic level organisms such as zooplankton and fish. While zooplankton have been sampled in the past, HB is lacking any formal surveys of fish populations. In addition, increased samples will start to identify temporal and spatial trends of these species. Diets of lower level organisms are poorly understood, and the basis of the food web is contingent upon this understanding. More research is needed to better understand the impacts changes in the food web have on higher trophic level species (marine mammals), and to improve the model. If in fact changes to fish populations are occurring at the same rate in the ecosystem as they are in the diets of birds, then the issue of bentho-pelagic coupling should be explored with fish and zooplankton in mind. There will ultimately be consequences to top predators, however if we wait to identify these changes at higher trophic levels, it is almost certain large scale shift will have occurred throughout the system.

CONCLUSIONS

The Hudson Bay ecosystem model summarizes the information known about the species which inhabit the region. Through the exercise of creating a model and fitting it to data, important linkages in the system are identified or validated if previously known. A well-documented linkage further validated by the model is that sea ice is an essential factor in determining the abundance of polar bears. Bentho-pelagic coupling of sea ice to benthos via the spring melt is identified as a potentially vital link in determining the future of Hudson Bay as a benthic or pelagic dominated ecosystem. However, our general lack of knowledge for lower trophic level species (benthos, zooplankton, and fish) may be the greatest hindrance in terms of modelling and expanding our knowledge on this ecosystem.

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APPENDIX 1 : MARINE MAMMAL MORTALITY CALCULATIONS

Mortality for marine mammal functional groups was calculated based on life history information and estimates of longevity, using equation 1 to estimate the probability of survivorship from birth to age x, with information from equations 2-4, and parameters in table A1.

$$eq.(1) \qquad L(x) = L_j(x) \cdot L_c(x) \cdot L_s\,(x)$$

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

$$eq.(3) \qquad L_c(x) = \; exp[-a_2 \cdot x/\Omega]$$

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

Table A1: Parameters for equations 1-4

$L_j(x)$	Mortality due to juvenile factors
$L_c(x)$	Constant mortality experienced by all age classes
$L_s(x)$	Mortality due to senescent factors
$a_1, a_{2,} a_3, b_1, b_3$	Allow flexibility in shape of survivorship curve
Ω	Longevity

For all pinniped groups survivorship curve parameters from northern fur seals were used to estimate survivorship (table A2). Human survivorship parameter were used for killer whales, as there are few to zero predators on this group, likely causing lowered juvenile mortality. Baleen whale (bowhead whales) and beluga whale 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 survivorship. Mortality was calculated as 1- the survivorship for each year of longevity, and averaged over all ages (x) to give the P/B value.

Table A2: Survivorship curve parameters based on life histories of fur seals, monkeys, and humans.

Species group	$\boldsymbol{a_1}$	$\boldsymbol{a_2}$	$\boldsymbol{a_3}$	$\boldsymbol{b_1}$	$\boldsymbol{b_3}$
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

Appendix 2 : Bird species found within the Hudson Bay model area by family, as reported from Stewart and Lockhart (2005).

Family Gaviidae: Loons

red-throated loon	*Gavia stellata* (Pontoppidan, 1763)
Pacific loon	*G. pacifica* (Lawrence)
common loon	*G. immer* (Brünnich)
yellow-billed loon	*G. adamsii* (Gray) *

Family Podicipedidae: Grebes

pied-billed grebe	*Podilymbus podiceps* (Linnaeus) *
horned grebe	*Podiceps auritus* (Linnaeus)

Family Procellariidae: Fulmars

northern fulmar	*Fulmarus glacialis* (Linnaeus) *

Family Hydrobatidae: Storm-petrels

Leach's storm-petrel	*Oceanodroma leucorhoa* (Viellot) *

Family Pelecanidae: Pelicans

American white pelican	*Pelecanus erythrorhynchos* (Gmelin) *

Family Sulidae: Gannets

northern gannet	*Sula bassanus* (Linnaeus) *

Family Phalacrocoracidae: Cormorants

double crested cormorant	*Phalacrocorax auritus* (Lesson)

Family Ardeidae: Herons and Bitterns

American bittern	*Botaurus lentiginosus* (Rackett)
great blue heron	*Ardea herodias* (Linnaeus)
snowy egret	*Egretta thula* (Molina) *
little blue heron	*E. caerulea* (Linnaeus) *
tricolor heron	*E. tricolor* (Müller) *
black-crowned night heron	*Nycticorax nycticorax* (Linnaeus) *

Family Anatidae: Geese, Swans, and Ducks

greater white-fronted goose	*Anser albifrons* (Scopoli)
snow goose	*Chen caerulescens* (Linnaeus)
Ross's goose	*C. rossii* (Cassin)
Canada goose	*Branta canadensis* (Linnaeus)
Brant	*B. bernicla* (Linnaeus)
trumpeter swan	*Cygnus buccinator* (Richardson) *
tundra swan	*C. columbianus* (Ord)
gadwall	*Anas strepera* (Linnaeus) *
Eurasian widgeon	*A. penelope* (Linnaeus) *
American widgeon (baldpate)	*A. americana* (Gmelin)
American black duck	*A. rubripes* (Brewster)
mallard	*A. platyrhynchos* (Linnaeus)
blue winged tea l	*A. discors* (Linnaeus)
northern shoveler	*A. souchet* (Linnaeus)
northern pintail	*A. acuta* (Linnaeus)
green-winged teal	*A. crecca* (Linnaeus)
canvasback	*Aythya valisineria* (Wilson) *

APPENDIX 2 (CONTINUED) : BIRD SPECIES FOUND WITHIN THE HUDSON BAY MODEL AREA

Family Anatidae: Geese, Swans, and Ducks (Continued)

redhead	*A. americana* (Eyton) *
ring-necked duck	*A. collaris* (Donovan)
greater scaup	*A. marila* (Linnaeus)
lesser scaup	*A. affinis* (Eyton)
king eider	*Somateria spectabilis* (Linnaeus)
common eider	*S. mollissima* (Linnaeus)
harlequin ducks	*Histrionicus histrionicus* (Linnaeus)
surf scoter	*Melanitta perspicillata* (Linnaeus)
white-winged scoter	*M. fusca* (Linnaeus)
black scoter (common scoter)	*M. nigra* (Linnaeus)
long-tailed duck (oldsquaw)	*Clangula hyemalis* (Linnaeus)
bufflehead	*Bucephala albeola* (Linnaeus) *
common goldeneye	*B. clangula* (Linnaeus)
Barrow's goldeneye	*B. islandica* (Gmelin) *
hooded merganser	*Lophodytes cucullatus* (Linnaeus) *
common merganser	*Mergus merganser* Linnaeus
red-breasted merganser	*M. serrator (*Linnaeus)
ruddy duck	*Oxyura jamaicensis* (Gmelin) *

Family Accipiteridae: Ospreys, Eagles, Hawks, and Allies

osprey	*Pandion haliaetus* (Linnaeus)
bald eagle	*Haliaeetus leucocephalus* (Linnaeus)
northern harrier (marsh hawk)	*Circus cyaneus* (Linnaeus)
northern goshawk	*Accipter gentilis* (Wilson) *
sharp-shinned hawk	*A. striatus (*Vieillot)
rough-legged hawk	*Buteo lapopus* (Gmelin)
golden eagle	*Aquila chrysaetos* (Linnaeus) *

Family Falconidae: Falcons

merlin	*Falco columbarius (*Linnaeus)
peregrine falcon	*F. peregrinus (*Tunstall)
gyrfalcon	*F. rusticolus (*Linnaeus)
prairie falcon	*F. mexicanus (*Schlegel) *

Family Rallidae: Rails, Gallinules, and Coots

yellow rail	*Coturnicops noveboracensis* (Gmelin)
sora	*Porzana carolina* (Linnaeus)
American coot	*Fulica americana* Gmelin

Family Gruidae: Cranes

sandhill crane	*Grus canadensis* (Linnaeus)

Family Charadriidae: Plovers

black-bellied plover	*Pluvialis squatarola* (Linnaeus)
American golden-plover	*P. dominica* (Muller)
semipalmated plover	*Charadrius semipalmatus (*Bonaparte)
killdeer	*C. vociferus (*Linnaeus)

Family Scolopacidae: Sandpipers, Phalaropes, and allies

greater yellowlegs	*Tringa melanoleuca* (Gmelin)
lesser yellowlegs	*T. flavipes* (Gmelin)
solitary sandpiper	*T. solitaire (*Wilson)
spotted sandpiper	*Actitis macularia* (Linnaeus)

APPENDIX 2 (CONTINUED) : BIRD SPECIES FOUND WITHIN THE HUDSON BAY MODEL AREA

Family Scolopacidae: Sandpipers, Phalaropes, and allies (Continued)

whimbrel	*Numenius phaeopus* (Linnaeus)
Hudsonian godwit	*Limosa haemastica* (Linnaeus)
marbled godwit	*L. fedoa* (Linnaeus)
ruddy turnstone	*Arenaria interpres* (Linnaeus)
red knot	*Calidris canutus* (Linnaeus)
sanderling	*C. alba* (Pallas)
semipalmated sandpiper	*C. pusilla* (Linnaeus)
little stint	*C. minuta* (Leisler)*
least sandpiper	*C. minutilla* (Vieillot)
white-rumped sandpiper	*C. fuscicollis* (Vieillot)
Baird's sandpiper	*C. bairdii* (Coues)
pectoral sandpiper	*C. melanotos* (Vieillot)
purple sandpiper	*C. maritima* (Brunnich)
dunlin	*C. alpina* (Linnaeus)
stilt sandpiper	*C. himantopus* (Bonaparte)
buff-breasted sandpiper	*Tryngites subruficollis* (Vieillot)
short-billed dowitcher	*Limnodromus griseus* (Gmelin)
Wilson's snipe	*Gallinago delicata* (Ord)
Wilson's phalarope	*Phalaropus tricolor* (Vieillot)
red-necked/northern phalarope	*P. lobatus* (Linnaeus)
red phalarope	*P. fulicaria* (Linnaeus)

Family Laridae: Jaegers, Gulls, and Terns

Pomeranian jaeger	*Stercorarius pomarinus* (Temminick)
parasitic jaeger	*S. parasiticus* (Linnaeus)
long-tailed jaeger	*S. longicaudus* (Vieillot)
laughing gull	*Larus atricilla* (Linnaeus) *
Franklin's gull	*L. pixican* (Wagler)*
little gull	*Larus minutus* (Pallas)
black-headed gull	*L. ridibundus* (Linnaeus) *
Bonaparte's gull	*L. philadelphia* (Ord)
mew gull	*L. canus* (Linnaeus) *
ring-billed gull	*L. delawarensis* (Ord)
California gull	*L. californicus* (Lawrence) *
herring gull	*L. argentatus* (Pontoppidan)
Iceland gull	*L. glaucoides* (Meyer)
lesser black-backed gull	*L. fuscus* (Linnaeus) *
glaucous -winged gull	*L. glaucescens* (Naumann) *
glaucous gull	*L. hyperboreus* (Gunnerus)
great black-backed gull	*L. marinus* (Linnaeus) *
black-legged kittiwake	*Rissa tridactyle* (Linnaeus)
Ross's gull11	*Rodostethia rosea* (MacGillivray)
Sabine's gull	*Xema sabini* (Sabine)
ivory gull12	*Pagophila eburnea* (Phipps) *
Caspian tern	*Sterna caspia* (Pallas)
common tern	*S. hirundo* (Linnaeus)
Arctic tern	*S. parasisaea* (Pontoppidan)
Forster's tern	*S. forsteri* (Nuttall) *
white-winged tern	*Chlidonias leucopterus* (Temminck) *
black tern	*C. niger* (Linnaeus)

Appendix 2 (Continued) : Bird species found within the Hudson Bay model area

Family Alcidae: Auks, Murres, and Puffins

Dovekie	*Alle alle* (Linnaeus)
thick-billed murre	*Uria lomvia* (Linnaeus)
black guillemot	*Cepphus grylle* (Linnaeus)

Family Strigidae: Typical owls

snowy owl	*Nyctea scandiaca* (Linnaeus)
short-eared owl	*Asio flammeu*s (Pontoppidan)

Family Alcedinidae: Kingfishers

belted kingfisher	*Ceryle alcyon* (Linnaeus)

Family Corvidae: Crows and Ravens

American crow	*Corvus brachyrhynchos (*Brehm)
common raven	*C. corax (*Linnaeus)

Family Alaudidae: Larks

horned lark	*Eremophila alpestris*

Family Motacillidae: Pipits

American pipit	*Anthus rubescens* (Tunstall)

*Indicates the species is rare in its distribution within the model area as classified by Stewart and Lockhart (2005).

APPENDIX 3: FISH FUNCTIONAL GROUPS AND SPECIES INCLUDED IN EACH GROUP

Arctic Char:

Salvelinus alpinus	Arctic Char

Atlantic Salmon:

Salmo salar	Atlantic Salmon

Gadiformes:

Arctogadus glacialis	polar cod
Boreogadus saida	Arctic cod
Gadus ogac	Greenland cod

Sculpins/ Zoarcids:

Gymnocanthus tricuspis	Arctic staghorn
Icelus bicornis	twohorn sculpin
Icelus spatula	spatulate sculpin
Myoxocephalus quadricornis	fourhorn sculpin
Myoxocephalus scorpioides	Arctic sculpin
Myoxocephalus scorpius	shorthorn sculpin
Triglops murrayi	moustache sculpin
Triglops pingelli	ribbed sculpin
Gymnelus viridis	fish doctor
Lycodes pallidus	pale eelpout
Lycodes reticulatus	Arctic eelpout

Other Marine Fish:

Stichaeus punctatus	Arctic shanny
Lumpenus fabricii	slender eelblenny
Pleuronectidae sp.	righteye flounder
Hippoglossoides platessoides	Canadian plaice

Capelin:

Mallotus villosus	Capelin

Sandlance:

Ammodytes dubius	northern sand lance
Ammodytes hexapterus	stout sand lance

Sharks/Rays:

Somniosidae	sleeper sharks
Rajidae	skates

Other Marine Fish:

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

Appendix 4: Vulnerabilities used to fit the model

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13
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	2
19	Gadiformes				10	1		10	2	2	10	10	2	1
20	Sculpins/ Zoarcids				10	1		2	2	1	10	10	1	1
21	Capelin					1				10	2	1	1	2
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			2
26	Cephalopods			2	10	1				1	2	2		2
27	MacroZooplankton			2		1	2			1	2	2		
28	Euphausids			2		1	2				2	2		2
29	Copepods			2			2							2
30	Crustaceans			2		1	2	10	10	1	2	2	1	2
31	Other MesoZooplankton			2			2							
32	MicroZooplankton			2			2							
33	Marine Worms			2			2	10	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			10
37	Primary Production	2	2	2										
38	Ice Algae			2										
39	Ice Detritus			2										
40	Pelagic Detritus		2	2										

APPENDIX 4 (CONTINUED): VULNERABILITIES USED TO FIT THE MODEL

	Prey \ predator	**14**	**15**	**16**	**17**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
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						2			2
18	Atlantic Salmon	2	2	2	1					2			2
19	Gadiformes	10	2	2	2	2				1			10
20	Sculpins/ Zoarcids	2		2	2		2			1			10
21	Capelin	2	1	2	1	10	10			10	1	2	1
22	Sandlance	2		2	1	10	10			10		2	1
23	Sharks/Rays									2			
24	Other Marine Fish	2		2	1	10	10			2			2
25	Brackish Fish	2		2	1					2		1	
26	Cephalopods	2	1	2					1	2	1	1	2
27	MacroZooplankton	2		2	1			1	1	2	1	1	1
28	Euphausids	2	2	2	1			2	2	2	1	1	1
29	Copepods	2	2	2	1			2	2		1	1	1
30	Crustaceans	2	2		1	2	2	2	2	2	1	1	1
31	Other MesoZooplankton			2	1			2	2		1	1	1
32	MicroZooplankton				1			2	2		1	1	1
33	Marine Worms	10	10	10	10	10	10			10	10	10	
34	Echinoderms			10	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	2	2				1	1	
39	Ice Detritus					2	2						
40	Pelagic Detritus			1				1	1		1	1	

APPENDIX 4 (CONTINUED): VULNERABILITIES USED TO FIT THE MODEL

	Prey \ predator	**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										
18	Atlantic Salmon										
19	Gadiformes										
20	Sculpins/ Zoarcids										
21	Capelin										
22	Sandlance										
23	Sharks/Rays										
24	Other Marine Fish										
25	Brackish Fish										
26	Cephalopods										
27	MacroZooplankton		1					1			1
28	Euphausids	2	1		2	1		2	2		
29	Copepods	2	1		1	1		1	2	1	
30	Crustaceans	2	1		1	2		2	2		
31	Other MesoZooplankton	2	1		2	1		1	2	1	1
32	MicroZooplankton	2	1	2	2	1		1	2	1	1
33	Marine Worms				10			10	10		10
34	Echinoderms				10			10	10		10
35	Bivalves				10				10		10
36	Other Benthos				10			10	10		10
37	Primary Production	1	1	1	1	1	1	1	1	1	1
38	Ice Algae	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				

APPENDIX 5: MIXED TROPHIC IMPACT RESULTS FROM THE BALANCED ECOPATH MODEL

	Impacting / Impacted	Polar Bear WHB	SH Polar Bear	Polar Bear Foxe	Killer Whale	Narwhal	Bowhead	Walrus N	Walrus S	Bearded Seal	Harbour Seal	Ringed Seal
1	Polar Bear WHB	-0.53	-0.0237	-0.0328	-0.0255	0.0138	0.0035	-0.0133	0.0095	-0.0635	0.0009	-0.0607
2	SH Polar Bear	-0.0123	-0.52	-0.0152	-0.017	0.005	0.0024	0.0007	-0.094	-0.0648	-0.0163	-0.0228
3	Polar Bear Foxe	-0.0138	-0.0111	-0.515	-0.0123	0.0057	0.0017	0.0004	0.0045	-0.0528	-0.184	-0.0226
4	Killer Whale	0.0047	0.0052	0.0036	-0.508	-0.063	-0.0726	-0.0109	-0.0937	-0.0161	-0.103	0.026
5	Narwhal	-0.0006	-0.0005	-0.0007	0.021	-0.442	-0.0031	-0.0002	-0.0043	-0.0031	-0.0053	-0.0007
6	Bowhead	8E-06	2E-05	-7E-06	0.007	-0.001	-0.427	-0.0002	-0.0013	-0.0003	-0.0016	0.0002
7	Walrus N	0.0012	-0.0002	-0.0003	0.0073	-0.0021	-0.0012	-0.477	-0.0037	-0.0017	-0.0023	0.0002
8	Walrus S	-0.0593	-0.0585	-0.0543	-0.0119	0.0179	0.0009	0.0004	-0.294	0.0513	0.0931	-0.212
9	Bearded Seal	0.0417	0.042	0.0752	0.0464	-0.0057	-0.007	-0.0021	-0.0177	-0.105	-0.0922	-0.0385
10	Harbour Seal	-0.0007	-0.0007	0.0037	0.0063	-0.0022	-0.0009	-0.0001	-0.0013	-0.0025	-0.0057	-0.003
11	Ringed Seal	0.194	0.197	0.172	0.067	-0.0671	-0.007	-0.0035	-0.041	-0.314	-0.309	-0.276
12	Harp seal	0.0113	0.0112	0.0157	0.0114	-0.0018	-0.0016	-0.0007	-0.0046	-0.0137	-0.0158	-0.0068
13	Beluga E	-0.0003	0.001	-0.0004	0.0021	-0.0016	-0.0004	0.0001	-0.0006	-0.0011	-0.0009	-0.0006
14	Beluga W	0.0282	-0.0095	0.0194	0.0481	-0.0267	-0.0073	-0.0008	-0.0107	-0.0342	-0.0306	-0.0172
15	Beluga James	-0.0013	0.0255	-0.0015	0.0189	-0.0033	-0.0028	-0.0004	-0.0088	-0.0053	-0.0062	-0.0018
16	Seabirds	-0.0019	0.0102	-0.0025	-0.0018	-0.0149	0.0007	-0.0044	-0.0073	-0.017	-0.0259	-0.0108
17	Arctic Char	-0.0009	-0.0024	-0.0004	0.0008	-0.0018	-0.0006	-1E-04	-0.0012	0.0195	-0.0138	-0.0115
18	Atlantic Salmon	-0.0058	-0.006	-0.0057	-0.0039	-0.0167	0.0003	0.0024	0.0019	3E-06	-0.0221	-0.0174
19	Gadiformes	0.022	0.0181	0.0237	0.0325	0.0955	-0.0038	-0.013	0.0138	0.0979	-0.0229	0.0482
20	Sculpins/ Zoarcids	0.0068	0.0059	0.0061	0.0125	0.0574	-0.0012	-0.0089	-0.0153	-0.0002	0.0074	0.0268
21	Capelin	0.0566	0.0644	0.0603	0.0523	0.0412	-0.0131	0.0002	-0.0188	0.0609	0.0854	0.117
22	Sandlance	0.0601	0.0606	0.0555	0.0243	-0.0197	-0.0101	-0.0015	-0.0122	-0.0557	0.0973	0.215
23	Sharks/Rays	1E-05	2E-05	3E-06	0.0023	-0.0008	-0.0003	-5E-05	-0.0004	-0.0001	-0.0005	0.0001
24	Other Marine Fish	0.0147	0.0132	0.0146	0.0165	0.049	-0.0037	0.0149	0.0292	0.0147	0.062	0.0408
25	Brackish Fish	0.0002	-0.0002	0.0007	0.0024	0.0058	-0.0002	7E-06	-0.0008	0.0135	0.0497	-0.0069
26	Cephalopods	-0.0129	-0.0122	-0.0135	-0.0046	0.0182	0.0024	0.0036	0.0016	-0.0191	-0.0116	-0.0382
27	MacroZoopl.	0.0044	0.0058	0.0042	0.0043	0.0235	-0.0113	0.0035	0.0005	0.0005	0.0151	0.0072
28	Euphausids	0.0178	0.0185	0.0169	0.0182	0.022	0.072	0.003	-0.0028	0.0022	0.0299	0.039
29	Copepods	0.0125	0.0133	0.0117	0.0118	-0.0064	0.196	-0.0045	-0.011	-0.0237	0.0114	0.0405
30	Crustaceans	0.0281	0.0282	0.0346	0.0269	0.0683	-0.0015	-0.0746	-0.0722	0.145	0.0441	0.0765
31	Other MesoZoopl.	-0.0128	-0.0126	-0.0138	-0.0135	-0.0239	-0.0624	0.0227	0.0259	-0.0348	-0.0175	-0.0307
32	MicroZoopl.	0.0017	0.0029	0.0018	0.0009	-0.0014	-0.0023	0.0113	0.0094	-0.012	0.0129	0.0063
33	Marine Worms	-0.0124	-0.0063	-0.0046	0.0036	0.0081	-0.0028	0.0247	0.0427	0.008	0.0173	-0.0092
34	Echinoderms	0.0012	0.006	0.0067	0.0032	0.0047	-0.0027	0.0779	0.0336	0.0618	0.0111	-0.0149
35	Bivalves	-0.014	-0.007	-0.0081	0.0027	0.023	0.0072	0.154	0.213	0.0224	0.0208	-0.0548
36	Other Benthos	0.0354	0.013	0.0135	0.011	0.0121	0.0212	-0.0155	-0.028	0.0363	0.0176	0.0089
37	Primary Production	0.0325	0.0351	0.0331	0.0274	0.0233	0.113	0.0062	-5E-05	0.0147	0.0649	0.0873
38	Ice Algae	0.0151	0.0121	0.0131	0.0149	0.0329	0.0335	0.0183	0.0236	0.0378	0.0253	0.0218
39	Ice Detritus	0.0109	0.0064	0.0082	0.0179	0.0474	0.0158	0.136	0.162	0.0882	0.0455	-0.032
40	Pelagic Detritus	0.0094	0.0106	0.01	0.0082	0.0117	0.0075	-0.0046	-0.0055	0.0129	0.0198	0.0248
41	SH Polar Bear	0.009	-0.352	0.0111	0.0125	-0.0037	-0.0018	-0.0005	0.069	0.0475	0.0119	0.0167
42	WHB Polar Bear	-0.287	0.0145	0.02	0.0155	-0.0084	-0.0022	0.0081	-0.0058	0.0387	-0.0005	0.0371
43	FB Polar Bear	0.0099	0.0079	-0.347	0.0088	-0.0041	-0.0012	-0.0003	-0.0032	0.0377	0.131	0.0162
44	Killer whale	-0.0047	-0.0052	-0.0036	-0.492	0.063	0.0726	0.0109	0.0937	0.0161	0.103	-0.026
45	Bowhead	-6E-06	-1E-05	5E-06	-0.0052	0.0007	-0.425	0.0001	0.001	0.0002	0.0012	-0.0002
46	Narwhal	0.0005	0.0004	0.0005	-0.0162	-0.431	0.0024	0.0001	0.0034	0.0024	0.0041	0.0006
47	N Walrus	-0.0011	0.0001	0.0002	-0.0066	0.0019	0.001	-0.473	0.0033	0.0016	0.0021	-0.0002
48	S Walrus	0.0259	0.0256	0.0237	0.0052	-0.0078	-0.0004	-0.0002	-0.308	-0.0224	-0.0407	0.0926
49	Beluga E	0.0003	-0.0009	0.0003	-0.0018	0.0014	0.0003	-0.0001	0.0005	0.001	0.0007	0.0005
50	Beluga W	-0.0082	0.0028	-0.0057	-0.014	0.0078	0.0021	0.0002	0.0031	0.0099	0.0089	0.005
51	Beluga S	0.0002	-0.0049	0.0003	-0.0037	0.0006	0.0005	7E-05	0.0017	0.001	0.0012	0.0003
52	Sealing	-0.0401	-0.0406	-0.0497	-0.0268	0.0112	0.0036	0.0013	0.012	-0.247	-0.135	-0.0788
53	Bird Hunting	3E-05	-0.0002	4E-05	3E-05	0.0002	-1E-05	7E-05	0.0001	0.0003	0.0004	0.0002
54	Fishing	0	0	0	0	0	0	0	0	0	0	0

Appendix 5 (continued): Mixed Trophic Impact results

	Impacting / Impacted	Harp seal	Beluga E	Beluga W	Beluga James	Seabirds	Arctic Char	Atlantic Salmon	Gadi-formes	Sculpins/ Zoarcids	Capelin	Sand-lance
1	Polar Bear WHB	-0.113	0.0065	-0.15	0.0273	0.0038	0.0405	0.0142	0.0451	0.0226	0.021	0.0162
2	SH Polar Bear	-0.111	-0.0252	0.0103	-0.284	0.0003	-0.0019	0.0018	0.0106	0.0079	0.009	0.0077
3	Polar Bear Foxe	-0.0682	0.0027	-0.0474	0.012	0.0015	0.0133	0.005	0.0173	0.0096	0.0085	0.0072
4	Killer Whale	-0.0261	-0.0089	-0.0381	-0.0383	0.0003	0.0106	0.0041	-0.0007	-0.0047	0.0008	-0.0105
5	Narwhal	-0.0007	-0.002	-0.0038	-0.0022	-0.0008	-0.001	-0.0026	-0.0148	-0.013	8E-05	0.0052
6	Bowhead	-0.0006	-0.0003	-0.0007	-0.0008	-0.0001	0.0002	-0.0001	4E-05	-4E-05	-0.0003	-0.0003
7	Walrus N	-0.0001	-0.0004	-0.0015	-0.0002	-0.0004	0.0005	4E-05	-0.0045	-0.0034	0.001	0.001
8	Walrus S	0.089	0.0104	0.0409	0.0481	0.0041	-0.013	-0.0042	0.0664	0.0629	0.023	0.0755
9	Bearded Seal	-0.0765	-0.003	-0.0274	-0.0278	0.0003	-0.0111	-0.0087	-0.0032	0.0063	0.0028	0.0143
10	Harbour Seal	-0.0034	-0.0007	-0.0019	-0.0014	-0.0008	0.0007	0.0002	-0.0037	-0.005	-0.0029	-0.0045
11	Ringed Seal	-0.291	-0.0363	-0.138	-0.164	-0.0142	0.0469	0.0156	-0.24	-0.217	-0.0757	-0.255
12	Harp seal	-0.0252	-0.0013	-0.0084	-0.0135	-0.0008	0.0033	-0.003	0.0029	0.0016	-0.0145	0.0027
13	Beluga E	-0.0013	-0.464	-0.001	-0.0017	-0.0004	0.0016	-0.0062	-0.0033	-0.0075	-0.0013	0.0022
14	Beluga W	-0.0537	-0.0102	-0.271	-0.025	-0.0107	-0.191	-0.0609	-0.0933	-0.0091	-0.0491	0.0293
15	Beluga James	-0.0164	-0.0025	-0.0026	-0.184	-0.0008	0.0019	-0.0019	-0.0011	0.0012	-0.0114	0.0014
16	Seabirds	-0.0496	-0.0101	-0.0271	-0.0331	-0.521	-0.152	-0.166	0.0036	-0.0152	-0.0533	0.0004
17	Arctic Char	-0.0123	-0.0036	0.0307	-0.0045	0.0083	-0.01	-0.0801	-0.0156	-0.019	-0.0118	-0.0112
18	Atlantic Salmon	-0.0092	-0.0008	-0.0072	-0.0106	-0.0077	-0.0948	-0.112	-0.0163	-0.0314	-0.035	0.0024
19	Gadiformes	-0.101	0.0284	0.0634	-0.0131	-0.0061	-0.0245	-0.0002	-0.141	-0.0629	-0.0903	-0.138
20	Sculpins/ Zoarcids	-0.0664	0.0413	-0.0037	-0.0345	0.0044	-0.0049	0.0037	-0.0438	-0.114	-0.0689	-0.106
21	Capelin	0.71	0.0377	0.0971	0.333	0.0555	-0.0491	-0.025	-0.0247	-0.0115	-0.0906	-0.0592
22	Sandlance	-0.108	-0.0132	-0.0388	-0.0639	0.0073	0.0301	0.0131	-0.0206	-0.0092	-0.0419	-0.0898
23	Sharks/Rays	-0.0005	-4E-05	-0.0002	-0.0002	2E-06	5E-05	2E-05	1E-05	-1E-05	1E-05	-5E-05
24	Other Marine Fish	-0.0116	-0.0061	0.0136	-0.033	0.0127	0.0073	0.0019	0.0364	0.0211	-0.0483	-0.0245
25	Brackish Fish	-0.0142	0.0081	0.0245	-0.0084	0.0439	-0.0041	0.0047	-0.0011	0.0007	-0.0157	-0.006
26	Cephalopods	-0.0497	0.0087	0.0102	0.0117	0.0305	-0.14	-0.101	-0.0988	-0.161	-0.0718	-0.0645
27	MacroZoopl.	0.0413	-0.015	0.0009	0.0035	0.0658	0.0123	0.0489	-0.0103	-0.0262	0.0551	-0.0313
28	Euphausids	0.0836	0.0657	0.065	0.101	0.0299	-0.0719	0.0614	-0.0038	-0.0012	0.12	0.039
29	Copepods	0.0325	0.0422	0.0403	0.0589	-0.0014	0.113	-0.0582	-0.0336	-0.0207	0.0579	0.134
30	Crustaceans	0.0502	0.0572	0.0395	0.0565	-0.0063	0.0417	0.138	-0.137	-0.0784	0.0517	0.0109
31	Other MesoZoopl.	-0.0434	-0.0464	-0.0391	-0.0581	-0.001	0.0552	-0.0626	0.0283	0.0091	-0.0556	0.0095
32	MicroZoopl.	0.0155	-0.0108	-0.0019	-0.002	0.0196	0.0265	0.0872	-0.0123	-0.023	0.0246	0.0545
33	Marine Worms	-0.0112	0.0158	0.0179	0.0084	-0.003	0.0059	-0.0119	0.065	0.0619	-0.0221	-0.018
34	Echinoderms	-0.0204	-0.0149	-0.0116	-0.0245	0.0044	0.0143	-0.0122	0.0832	0.0449	-0.0129	-0.0118
35	Bivalves	0.0218	0.0018	0.0096	0.0042	0.039	-0.039	0.0017	0.0762	0.0648	0.0045	-0.004
36	Other Benthos	-0.0418	0.0752	0.0566	0.0481	-0.0024	0.0019	-0.0118	0.0637	0.0701	-0.0286	-0.0164
37	Primary Production	0.142	0.0326	0.0497	0.0872	0.0463	0.156	0.114	-0.0558	-0.0499	0.2	0.218
38	Ice Algae	-0.0064	0.0317	0.0336	0.0194	0.0165	0.0444	0.0437	0.0974	0.0602	-0.0013	0.01
39	Ice Detritus	-0.0332	0.0654	0.0564	0.0314	0.0253	-0.0139	-0.0047	0.185	0.226	-0.0399	-0.0444
40	Pelagic Detritus	0.0394	0.0075	0.011	0.0201	0.0353	0.0036	0.0109	-0.0148	-0.0117	0.0522	0.035
41	SH Polar Bear	0.0816	0.0185	-0.0075	0.208	-0.0002	0.0014	-0.0013	-0.0077	-0.0058	-0.0066	-0.0056
42	WHB Polar Bear	0.069	-0.004	0.0918	-0.0167	-0.0023	-0.0247	-0.0086	-0.0275	-0.0138	-0.0128	-0.0099
43	FB Polar Bear	0.0487	-0.0019	0.0338	-0.0086	-0.0011	-0.0095	-0.0036	-0.0123	-0.0068	-0.0061	-0.0052
44	Killer whale	0.0261	0.0089	0.0381	0.0383	-0.0003	-0.0106	-0.0041	0.0007	0.0047	-0.0008	0.0105
45	Bowhead	0.0004	0.0002	0.0005	0.0006	8E-05	-0.0001	9E-05	-3E-05	3E-05	0.0002	0.0002
46	Narwhal	0.0005	0.0015	0.0029	0.0017	0.0006	0.0008	0.002	0.0114	0.0101	-6E-05	-0.004
47	N Walrus	9E-05	0.0004	0.0013	0.0002	0.0004	-0.0005	-3E-05	0.004	0.0031	-0.0009	-0.0009
48	S Walrus	-0.0389	-0.0045	-0.0179	-0.021	-0.0018	0.0057	0.0018	-0.029	-0.0275	-0.01	-0.033
49	Beluga E	0.0011	-0.462	0.0008	0.0015	0.0003	-0.0014	0.0053	0.0028	0.0065	0.0011	-0.0019
50	Beluga W	0.0156	0.003	-0.212	0.0073	0.0031	0.0556	0.0177	0.0271	0.0027	0.0143	-0.0085
51	Beluga S	0.0032	0.0005	0.0005	-0.158	0.0002	-0.0004	0.0004	0.0002	-0.0002	0.0022	-0.0003
52	Sealing	-0.0951	0.006	0.0284	0.0325	0.002	-0.0031	0.0013	0.0322	0.0266	0.0118	0.0286
53	Bird Hunting	0.0008	0.0002	0.0004	0.0005	-0.0079	0.0025	0.0027	-6E-05	0.0003	0.0009	-7E-06
54	Fishing	0	0	0	0	0	-6E-06	0	0	-1E-06	0	0

Appendix 5 (continued): Mixed Trophic Impact results

	Impacting / Impacted	Sharks /Rays	Other Marine Fish	Brackish Fish	Cephalo-pods	Macro Zoopl	Euph-ausids	Copepods	Crust-aceans	Other MesoZoopl	Micro Zoopl	Marine Worms
1	Polar Bear WHB	0.0348	0.0013	0.00764	0.0118	-0.00699	-0.000107	0.000067	-0.000571	0.000405	0.000927	-0.00146
2	SH Polar Bear	0.0169	0.0011	-0.000756	0.00204	-0.00191	-0.000517	0.000146	-0.000137	0.00008	0.000171	-0.000514
3	Polar Bear Foxe	0.0152	0.0012	0.00358	0.0041	-0.00268	-0.000186	0.000058	-0.000221	0.000185	0.000336	-0.000614
4	Killer Whale	-0.442	-0.0006	0.0034	0.00242	-0.000434	0.000964	-0.000157	0.000329	-0.000016	0.000134	0.000286
5	Narwhal	-0.0176	-0.0017	-0.00206	-0.0094	0.000082	-0.000294	0.00006	-0.000287	-0.00032	-0.000063	0.000938
6	Bowhead	-0.0064	-7E-05	-0.000079	-0.00003	-0.00062	-0.00157	0.000278	-0.000333	0.00025	-0.000041	-0.000076
7	Walrus N	-0.0084	-0.0047	0.000275	0.000006	-0.000319	-0.000392	0.000153	-0.000691	0.0013	0.000028	0.00112
8	Walrus S	0.0338	0.0067	-0.00558	0.00747	-0.00606	-0.00418	0.000731	-0.00214	0.000625	0.000487	-0.00381
9	Bearded Seal	-0.0331	0.0033	-0.000227	0.00245	-0.00063	-0.000185	0.000021	-0.00214	-0.000432	0.000101	0.000505
10	Harbour Seal	-0.0078	-0.0034	-0.00641	-0.000618	0.00084	0.000261	-0.000056	0.000193	-0.00006	-0.000079	0.000192
11	Ringed Seal	-0.143	-0.0305	0.0195	-0.0259	0.02	0.0136	-0.00225	0.00645	-0.000522	-0.00164	0.0139
12	Harp seal	-0.0007	-0.0013	0.00205	0.00102	0.00237	0.000436	-0.000271	0.000759	-0.0002	-0.000159	-0.000197
13	Beluga E	-0.0034	0.0026	-0.00164	-0.0033	0.000822	-0.000635	0.000132	-0.000683	-0.000166	-0.000165	-0.000068
14	Beluga W	-0.0706	0.008	-0.0408	-0.0419	0.0203	-0.0055	0.000837	0.000288	-0.00132	-0.00324	0.000181
15	Beluga James	-0.0175	0.0009	0.00111	-0.00285	0.00219	-0.000008	-0.000103	0.000073	-0.000149	-0.000226	-0.000251
16	Seabirds	-0.0299	-0.0327	-0.236	-0.114	0.0152	-0.0017	-0.00008	0.0183	0.00509	-0.00135	-0.000659
17	Arctic Char	0.0341	-0.0256	-0.0647	0.0129	-0.0183	0.00363	-0.00232	-0.00415	-0.00454	0.00489	-0.0015
18	Atlantic Salmon	-0.0081	-0.0387	-0.154	-0.128	-0.0393	0.00315	0.00268	-0.0253	0.00336	0.00216	0.00671
19	Gadiformes	0.0508	-0.256	-0.00137	0.0455	0.0292	0.00605	-0.000659	0.0111	0.00944	-0.00283	-0.0238
20	Sculpins/ Zoarcids	0.0882	-0.131	-0.00446	0.0431	0.0189	0.00561	-0.000275	-0.00769	0.00824	-0.00157	-0.0202
21	Capelin	-0.0161	-0.0219	-0.0474	0.0177	-0.146	-0.0277	0.0155	-0.0388	0.0101	0.0109	0.00666
22	Sandlance	0.035	-0.0399	0.000597	-0.0891	-0.0386	-0.0346	0.00327	-0.0133	-0.0172	0.00279	0.00344
23	Sharks/Rays	-0.0495	0	0.000016	0.000019	-0.000003	0.000004	-0.000001	0.000002	0	0.000001	0
24	Other Marine Fish	0.0417	-0.0374	-0.0205	-0.0359	-0.0149	0.00507	-0.00259	-0.0509	0.00377	0.00434	-0.00679
25	Brackish Fish	0.0295	-0.0072	-0.0487	-0.0357	-0.0193	0.0039	0.000597	-0.00699	0.00122	0.00154	0.000378
26	Cephalopods	-0.0059	0.0435	0.0158	-0.109	-0.06	0.0206	-0.00206	-0.00334	-0.00398	0.00996	0.00791
27	MacroZoopl.	0.045	0.0223	0.0648	0.0915	-0.0561	-0.197	0.00774	-0.0666	-0.12	-0.143	0.0172
28	Euphausids	-0.0014	-0.0224	0.0445	-0.019	-0.0601	-0.108	-0.322	0.00371	-0.0605	0.197	0.0104
29	Copepods	-0.0102	0.0303	-0.116	-0.0116	-0.147	0.332	-0.375	-0.0674	-0.168	-0.46	0.0016
30	Crustaceans	-0.0327	0.177	0.0907	0.0509	0.0256	-0.0682	-0.0194	-0.0531	0.0397	-0.00509	-0.166
31	Other MesoZoopl.	0.0131	-0.0423	-0.0191	0.0513	0.0154	-0.37	0.00929	-0.224	-0.0614	-0.151	0.0389
32	MicroZoopl.	0.0183	-0.0271	0.126	0.0719	0.16	-0.0289	-0.0932	-0.091	-0.0557	-0.137	0.0204
33	Marine Worms	0.0417	0.0041	-0.0126	-0.00539	-0.0413	-0.0104	0.000428	-0.0321	-0.0303	0.0019	-0.0851
34	Echinoderms	0.0944	-0.0644	0.00627	0.011	0.0338	-0.0276	0.009	-0.0813	0.0519	-0.00984	-0.171
35	Bivalves	0.0125	0.009	-0.0238	-0.0118	0.0267	0.0689	-0.0202	0.0605	-0.205	0.00149	-0.149
36	Other Benthos	0.0049	-0.011	0.0296	-0.0114	-0.149	0.0276	-0.00383	0.0606	0.0298	0.0173	-0.125
37	Primary Production	0.0265	0.119	0.116	0.0789	0.191	0.111	0.321	0.0412	0.231	0.257	0.00847
38	Ice Algae	0.0332	0.0772	0.0237	0.0335	0.069	0.0318	0.0802	0.0762	0.137	0.0249	0.0343
39	Ice Detritus	0.0836	-0.0305	0.00629	-0.00335	-0.0852	0.0428	-0.0147	0.124	-0.116	0.00883	0.282
40	Pelagic Detritus	0.0037	0.0783	0.0494	0.00488	0.0439	0.0128	0.0105	0.0643	0.0302	0.0396	-0.0117
41	SH Polar Bear	-0.0124	-0.0008	0.000555	-0.0015	0.0014	0.000379	-0.000107	0.000101	-0.000058	-0.000125	0.000377
42	WHB Polar Bear	-0.0212	-0.0008	-0.00466	-0.00723	0.00426	0.000065	-0.000041	0.000349	-0.000247	-0.000566	0.00089
43	FB Polar Bear	-0.0109	-0.0008	-0.00256	-0.00293	0.00192	0.000133	-0.000042	0.000158	-0.000133	-0.00024	0.000439
44	Killer whale	0.442	0.0006	-0.0034	-0.00242	0.000434	-0.000964	0.000157	-0.000329	0.000016	-0.000134	-0.000286
45	Bowhead	0.0047	5E-05	0.000059	0.000022	0.00046	0.00117	-0.000206	0.000247	-0.000186	0.00003	0.000056
46	Narwhal	0.0136	0.0013	0.00159	0.00725	-0.000064	0.000227	-0.000047	0.000222	0.000247	0.000049	-0.000724
47	N Walrus	0.0076	0.0043	-0.000248	-0.000005	0.000288	0.000354	-0.000138	0.000624	-0.00117	-0.000025	-0.00101
48	S Walrus	-0.0148	-0.0029	0.00244	-0.00326	0.00265	0.00183	-0.000319	0.000934	-0.000273	-0.000213	0.00166
49	Beluga E	0.0029	-0.0023	0.00142	0.00285	-0.000709	0.000548	-0.000114	0.00059	0.000143	0.000142	0.000058
50	Beluga W	0.0205	-0.0023	0.0119	0.0122	-0.00589	0.0016	-0.000243	-0.000084	0.000384	0.000942	-0.000053
51	Beluga S	0.0034	-0.0002	-0.000216	0.000553	-0.000425	0.000001	0.00002	-0.000014	0.000029	0.000044	0.000049
52	Sealing	0.0308	0.0038	-0.00143	0.0025	-0.00292	-0.00181	0.000338	-0.000297	0.000252	0.000219	-0.00196
53	Bird Hunting	0.0005	0.0005	0.00389	0.00187	-0.00025	0.000028	0.000001	-0.000302	-0.000084	0.000022	0.000011
54	Fishing	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 5 (CONTINUED): MIXED TROPHIC IMPACT RESULTS

*H indicates harvest of a species or group

	Impacting / Impacted	Marine Worms	Echino -derms	Bivalves	Other Benthos	Primary Production	Ice Algae	Ice Detritus	H: SH Polar Bear	H: WHB Polar Bear	H: FB Polar Bear
1	Polar Bear WHB	-0.00146	-0.00474	-0.00213	0.000225	-0.000194	0.000011	0.00115	-0.0237	0.47	-0.0328
2	SH Polar Bear	-0.000514	-0.000941	-0.000333	-0.000068	-0.000105	-0.00003	0.000275	0.48	-0.0123	-0.0152
3	Polar Bear Foxe	-0.000614	-0.00182	-0.000929	0.00007	-0.000089	-0.000002	0.000497	-0.0111	-0.0138	0.485
4	Killer Whale	0.000286	0.000445	0.000462	0.000048	0.000048	0.000002	-0.000265	0.00521	0.0047	0.00359
5	Narwhal	0.000938	0.00203	0.000961	0.000139	-0.000001	-0.000028	-0.000635	-0.000523	-0.000615	-0.000707
6	Bowhead	-0.000076	0.000026	0.00007	-0.000092	-0.000133	-0.000087	0.000033	0.000015	0.000008	-0.000007
7	Walrus N	0.00112	-0.00566	-0.00505	0.000927	-0.000138	-0.000009	0.00157	-0.000164	0.00118	-0.00025
8	Walrus S	-0.00381	-0.00912	-0.00588	0.000031	-0.00042	0.000076	0.00322	-0.0585	-0.0593	-0.0543
9	Bearded Seal	0.000505	-0.000473	0.000655	0.000257	0.000042	0.000064	-0.000333	0.042	0.0417	0.0752
10	Harbour Seal	0.000192	0.000272	0.000358	-0.000005	0.00004	0.000005	-0.000173	-0.000704	-0.000728	0.00371
11	Ringed Seal	0.0139	0.0286	0.0137	0.00111	0.00124	-0.000289	-0.00912	0.197	0.194	0.172
12	Harp seal	-0.000197	-0.000625	-0.000255	-0.000058	0.00017	0.000107	0.000149	0.0112	0.0113	0.0157
13	Beluga E	-0.000068	0.000994	0.000532	-0.000105	-0.000016	-0.000008	-0.000149	0.001	-0.000331	-0.000359
14	Beluga W	0.000181	0.00979	0.00388	-0.00165	0.000181	-0.000035	-0.00124	-0.0095	0.0282	0.0194
15	Beluga James	-0.000251	0.000057	0.000058	-0.000099	0.000104	0.000062	0.000058	0.0255	-0.00128	-0.00153
16	Seabirds	-0.000659	-0.0114	-0.0135	-0.00209	-0.000438	-0.000382	0.00562	0.0102	-0.00194	-0.00253
17	Arctic Char	-0.0015	0.000075	0.00347	0.000516	0.000817	0.00119	-0.00094	-0.00239	-0.000871	-0.000433
18	Atlantic Salmon	0.00671	0.0146	0.00669	0.00328	-0.00136	-0.00113	-0.00464	-0.00597	-0.00578	-0.00566
19	Gadiformes	-0.0238	-0.0756	-0.0248	-0.00416	0.000182	0.000152	0.0178	0.0181	0.022	0.0237
20	Sculpins/Zoarcids	-0.0202	-0.0349	-0.0216	-0.00201	0.000212	0.000765	0.0131	0.0059	0.00682	0.00614
21	Capelin	0.00666	0.0192	0.00843	0.00289	-0.01	-0.00575	-0.00487	0.0644	0.0566	0.0603
22	Sandlance	0.00344	0.00754	0.00346	0.00203	-0.000642	0.00147	-0.0025	0.0606	0.0601	0.0555
23	Sharks/Rays	0	0	0.000001	0	0	0	-0.000001	0.000015	0.000012	0.000003
24	Other Marine Fish	-0.00679	0.0191	-0.00496	0.00804	0.0014	0.00104	0.0011	0.0132	0.0147	0.0146
25	Brackish Fish	0.000378	0.000828	0.00153	-0.000634	-0.000453	-0.000078	-0.000188	-0.0002	0.000173	0.000691
26	Cephalopods	0.00791	0.0183	0.00747	0.000939	-0.000135	0.000357	-0.00501	-0.0122	-0.0129	-0.0135
27	MacroZoopl.	0.0172	0.0235	0.00188	0.0192	0.0287	0.0151	-0.00961	0.00581	0.00442	0.00418
28	Euphausids	0.0104	0.0149	0.00241	0.0176	0.136	0.112	-0.0101	0.0185	0.0178	0.0169
29	Copepods	0.0016	0.0178	-0.00916	-0.0331	-0.248	-0.213	0.0163	0.0133	0.0125	0.0117
30	Crustaceans	-0.166	-0.393	-0.166	-0.127	-0.0114	-0.007	0.123	0.0282	0.0281	0.0346
31	Other MesoZoopl.	0.0389	0.089	0.0684	0.02	-0.0257	-0.0646	-0.0357	-0.0126	-0.0128	-0.0138
32	MicroZoopl.	0.0204	0.0534	0.0353	-0.00803	-0.157	-0.0898	-0.0131	0.00286	0.00173	0.00175
33	Marine Worms	-0.0851	-0.0163	-0.00349	-0.305	0.00233	0.00545	-0.07	-0.00625	-0.0124	-0.00459
34	Echinoderms	-0.171	0.0119	-0.193	-0.042	-0.0036	0.00449	0.0713	0.006	0.00123	0.0067
35	Bivalves	-0.149	-0.052	-0.179	-0.109	0.0198	0.00427	-0.226	-0.00703	-0.014	-0.00809
36	Other Benthos	-0.125	-0.148	-0.236	-0.143	-0.00725	-0.0593	-0.191	0.013	0.0354	0.0135
37	Primary Production	0.00847	0.00831	0.027	-0.0259	-0.28	-0.23	-0.0039	0.0351	0.0325	0.0331
38	Ice Algae	0.0343	0.00388	0.019	0.115	-0.069	-0.074	-0.0575	0.0121	0.0151	0.0131
39	Ice Detritus	0.282	0.225	0.318	0.273	0.00791	-0.0316	0	0.00642	0.0109	0.00821
40	Pelagic Detritus	-0.0117	-0.026	-0.0111	-0.0117	-0.0209	-0.0167	0.00944	0.0106	0.00944	0.00999
41	SH Polar Bear	0.000377	0.00069	0.000244	0.00005	0.000077	0.000022	-0.000202	-0.352	0.00904	0.0111
42	WHB Polar Bear	0.00089	0.00289	0.0013	-0.000137	0.000118	-0.000007	-0.000703	0.0145	-0.287	0.02
43	FB Polar Bear	0.000439	0.0013	0.000664	-0.00005	0.000064	0.000001	-0.000355	0.00793	0.00989	-0.347
44	Killer whale	-0.000286	-0.000445	-0.000462	-0.000048	-0.000048	-0.000002	0.000265	-0.00521	-0.0047	-0.00359
45	Bowhead	0.000056	-0.000019	-0.000052	0.000068	0.000098	0.000065	-0.000025	-0.000011	-0.000006	0.000005
46	Narwhal	-0.000724	-0.00157	-0.000742	-0.000107	0.000001	0.000022	0.00049	0.000404	0.000475	0.000546
47	N Walrus	-0.00101	0.00512	0.00456	-0.000838	0.000125	0.000009	-0.00142	0.000148	-0.00106	0.000226
48	S Walrus	0.00166	0.00398	0.00257	-0.000014	0.000183	-0.000033	-0.0014	0.0256	0.0259	0.0237
49	Beluga E	0.000058	-0.000857	-0.000459	0.000091	0.000014	0.000007	0.000128	-0.000867	0.000285	0.000309
50	Beluga W	-0.000053	-0.00284	-0.00113	0.000478	-0.000053	0.00001	0.00036	0.00276	-0.0082	-0.00565
51	Beluga S	0.000049	-0.000011	-0.000011	0.000019	-0.00002	-0.000012	-0.000011	-0.00494	0.000248	0.000298
52	Sealing	-0.00196	-0.00347	-0.002	-0.000215	-0.000209	-0.000002	0.00129	-0.0406	-0.0401	-0.0497
53	Bird Hunting	0.000011	0.000188	0.000221	0.000034	0.000007	0.000006	-0.000092	-0.000168	0.000032	0.000042
54	Fishing	0	0	0	0	0	0	0	0	0	0

APPENDIX 5 (CONTINUED): MIXED TROPHIC IMPACT RESULTS

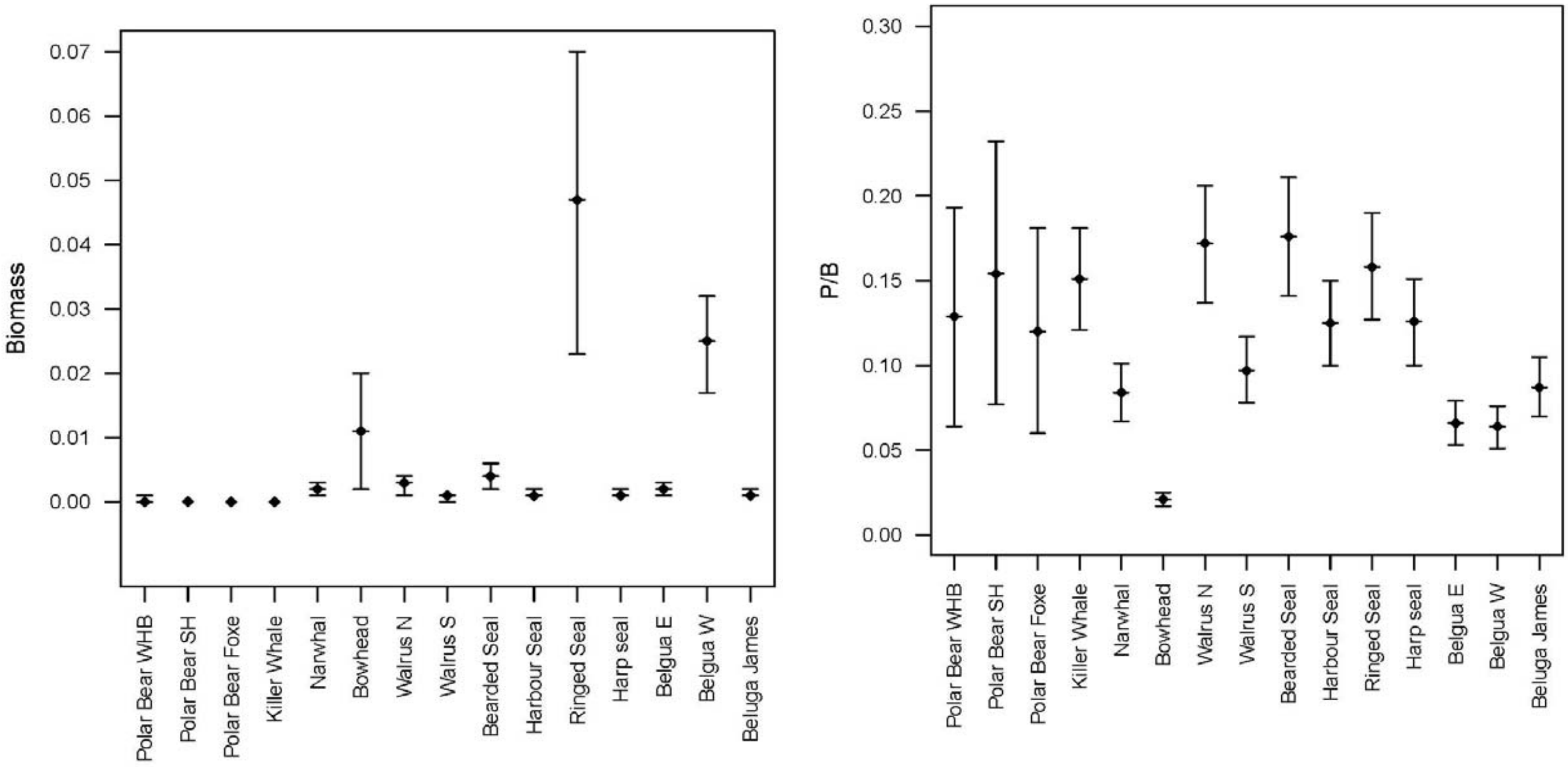
*H indicates harvest of a species or group

	Impacting / Impacted	H : Killer Whale	H: Bowhead	H: Narwhal	H: N Walrus	H: S Walrus	H: Beluga W	H: Beluga S	H: Sealing	H: Bird Hunting	H: Fishing
1	Polar Bear WHB	-0.0255	0.00353	0.0138	-0.0133	0.00945	-0.15	0.0273	-0.0626	0.00376	0.0319
2	SH Polar Bear	-0.017	0.0024	0.00503	0.000669	-0.094	0.0103	-0.284	-0.0371	0.000305	0.00439
3	Polar Bear Foxe	-0.0123	0.0017	0.00572	0.000446	0.00449	-0.0474	0.012	-0.033	0.00148	0.0117
4	Killer Whale	0.492	-0.0726	-0.063	-0.0109	-0.0937	-0.0381	-0.0383	0.0121	0.000251	0.00259
5	Narwhal	0.021	-0.00312	0.558	-0.000182	-0.00434	-0.00378	-0.00221	-0.00144	-0.000815	-0.00615
6	Bowhead	0.007	0.573	-0.000999	-0.000159	-0.00133	-0.000719	-0.000799	0.000061	-0.000109	0.000025
7	Walrus N	0.00733	-0.00115	-0.00212	0.523	-0.00368	-0.00145	-0.000176	-0.000349	-0.000407	-0.00156
8	Walrus S	-0.0119	0.000889	0.0179	0.000386	0.706	0.0409	0.0481	-0.127	0.00405	0.0271
9	Bearded Seal	0.0464	-0.00696	-0.00565	-0.00211	-0.0177	-0.0274	-0.0278	0.231	0.00034	-0.00259
10	Harbour Seal	0.00629	-0.000867	-0.00219	-0.000111	-0.00134	-0.00193	-0.00139	0.000641	-0.000755	-0.00232
11	Ringed Seal	0.067	-0.00701	-0.0671	-0.00352	-0.041	-0.138	-0.164	0.395	-0.0142	-0.095
12	Harp seal	0.0114	-0.0016	-0.00175	-0.000682	-0.00461	-0.00837	-0.0135	0.0151	-0.000761	0.000638
13	Beluga E	0.00213	-0.000386	-0.00159	0.00014	-0.000562	-0.000965	-0.00173	-0.000778	-0.000393	-0.00168
14	Beluga W	0.0481	-0.00732	-0.0267	-0.000766	-0.0107	0.729	-0.025	-0.0231	-0.0107	-0.0964
15	Beluga James	0.0189	-0.00277	-0.00325	-0.000371	-0.0088	-0.00262	0.816	-0.00317	-0.000805	-0.00038
16	Seabirds	-0.00177	0.000689	-0.0149	-0.00439	-0.00732	-0.0271	-0.0331	-0.0136	0.479	-0.0718
17	Arctic Char	0.000833	-0.00061	-0.00183	-0.000096	-0.00116	0.0307	-0.00452	-0.00251	0.00826	0.349
18	Atlantic Salmon	-0.00393	0.000338	-0.0167	0.00241	0.00186	-0.00724	-0.0106	-0.0122	-0.00774	-0.044
19	Gadiformes	0.0325	-0.00378	0.0955	-0.013	0.0138	0.0634	-0.0131	0.0587	-0.00607	0.13
20	Sculpins/Zoarcids	0.0125	-0.00124	0.0574	-0.00893	-0.0153	-0.00373	-0.0345	0.0167	0.00436	0.156
21	Capelin	0.0523	-0.0131	0.0412	0.000176	-0.0188	0.0971	0.333	0.115	0.0555	0.0651
22	Sandlance	0.0243	-0.0101	-0.0197	-0.00152	-0.0122	-0.0388	-0.0639	0.128	0.00725	0.0269
23	Sharks/Rays	0.00232	-0.000342	-0.000778	-0.000051	-0.000439	-0.000171	-0.00017	0.00003	0.000002	0.000017
24	Other Marine Fish	0.0165	-0.00374	0.049	0.0149	0.0292	0.0136	-0.033	0.032	0.0127	0.0586
25	Brackish Fish	0.00242	-0.000235	0.00578	0.000007	-0.00075	0.0245	-0.00841	-0.000973	0.0439	0.0161
26	Cephalopods	-0.00463	0.00242	0.0182	0.00362	0.00163	0.0102	0.0117	-0.0329	0.0305	-0.113
27	MacroZoopl.	0.00427	-0.0113	0.0235	0.00348	0.000501	0.000905	0.00347	0.0061	0.0658	0.00467
28	Euphausids	0.0182	0.072	0.022	0.00303	-0.00278	0.065	0.101	0.0294	0.0299	-0.0131
29	Copepods	0.0118	0.196	-0.00637	-0.00448	-0.011	0.0403	0.0589	0.0216	-0.00135	0.0388
30	Crustaceans	0.0269	-0.00153	0.0683	-0.0746	-0.0722	0.0395	0.0565	0.0955	-0.00634	-0.0114
31	Other MesoZoopl.	-0.0135	-0.0624	-0.0239	0.0227	0.0259	-0.0391	-0.0581	-0.0322	-0.001	0.0192
32	MicroZoopl.	0.000926	-0.00227	-0.00139	0.0113	0.00944	-0.00188	-0.00196	0.00122	0.0196	0.0087
33	Marine Worms	0.00361	-0.0028	0.00807	0.0247	0.0427	0.0179	0.00843	-0.00416	-0.00297	0.0255
34	Echinoderms	0.00324	-0.00272	0.00472	0.0779	0.0336	-0.0116	-0.0245	0.00726	0.00441	0.0268
35	Bivalves	0.00269	0.0072	0.023	0.154	0.213	0.00961	0.00415	-0.0303	0.039	0.0155
36	Other Benthos	0.011	0.0212	0.0121	-0.0155	-0.028	0.0566	0.0481	0.0156	-0.00242	0.025
37	Primary Production	0.0274	0.113	0.0233	0.00623	-0.000046	0.0497	0.0872	0.0675	0.0463	0.0724
38	Ice Algae	0.0149	0.0335	0.0329	0.0183	0.0236	0.0336	0.0194	0.0258	0.0165	0.0541
39	Ice Detritus	0.0179	0.0158	0.0474	0.136	0.162	0.0564	0.0314	0.00311	0.0253	0.0736
40	Pelagic Detritus	0.00815	0.00745	0.0117	-0.00455	-0.00547	0.011	0.0201	0.0217	0.0353	0.00754
41	H: SH Polar Bear	0.0125	-0.00176	-0.00369	-0.000491	0.069	-0.00754	0.208	0.0272	-0.000224	-0.00322
42	H: WHB Polar Bear	0.0155	-0.00215	-0.00844	0.00814	-0.00577	0.0918	-0.0167	0.0382	-0.00229	-0.0195
43	H:FB Polar Bear	0.00876	-0.00122	-0.00409	-0.000319	-0.00321	0.0338	-0.00857	0.0236	-0.00106	-0.00839
44	H: Killer whale	-0.492	0.0726	0.063	0.0109	0.0937	0.0381	0.0383	-0.0121	-0.000251	-0.00259
45	H : Bowhead	-0.0052	-0.425	0.000741	0.000118	0.000989	0.000534	0.000593	-0.000045	0.000081	-0.000018
46	H : Narwhal	-0.0162	0.00241	-0.431	0.00014	0.00335	0.00292	0.0017	0.00111	0.000629	0.00475
47	H : N Walrus	-0.00662	0.00104	0.00192	-0.473	0.00332	0.00131	0.000159	0.000315	0.000368	0.00141
48	H : S Walrus	0.00522	-0.000388	-0.00784	-0.000169	-0.308	-0.0179	-0.021	0.0556	-0.00177	-0.0119
49	H : Beluga E	-0.00183	0.000333	0.00137	-0.00012	0.000485	0.000832	0.00149	0.000672	0.000339	0.00145
50	H : Beluga W	-0.014	0.00213	0.00776	0.000223	0.0031	-0.212	0.00727	0.00671	0.00311	0.028
51	H : Beluga S	-0.00366	0.000537	0.000632	0.000072	0.00171	0.000509	-0.158	0.000615	0.000156	0.000074
52	H : Sealing	-0.0268	0.00359	0.0112	0.00127	0.012	0.0284	0.0325	-0.128	0.00199	0.0134
53	H : Bird Hunting	0.000029	-0.000011	0.000245	0.000072	0.00012	0.000445	0.000545	0.000223	-0.00787	0.00118
54	H : Fishing	0	0	0	0	0	0	0	0	0	-0.000003

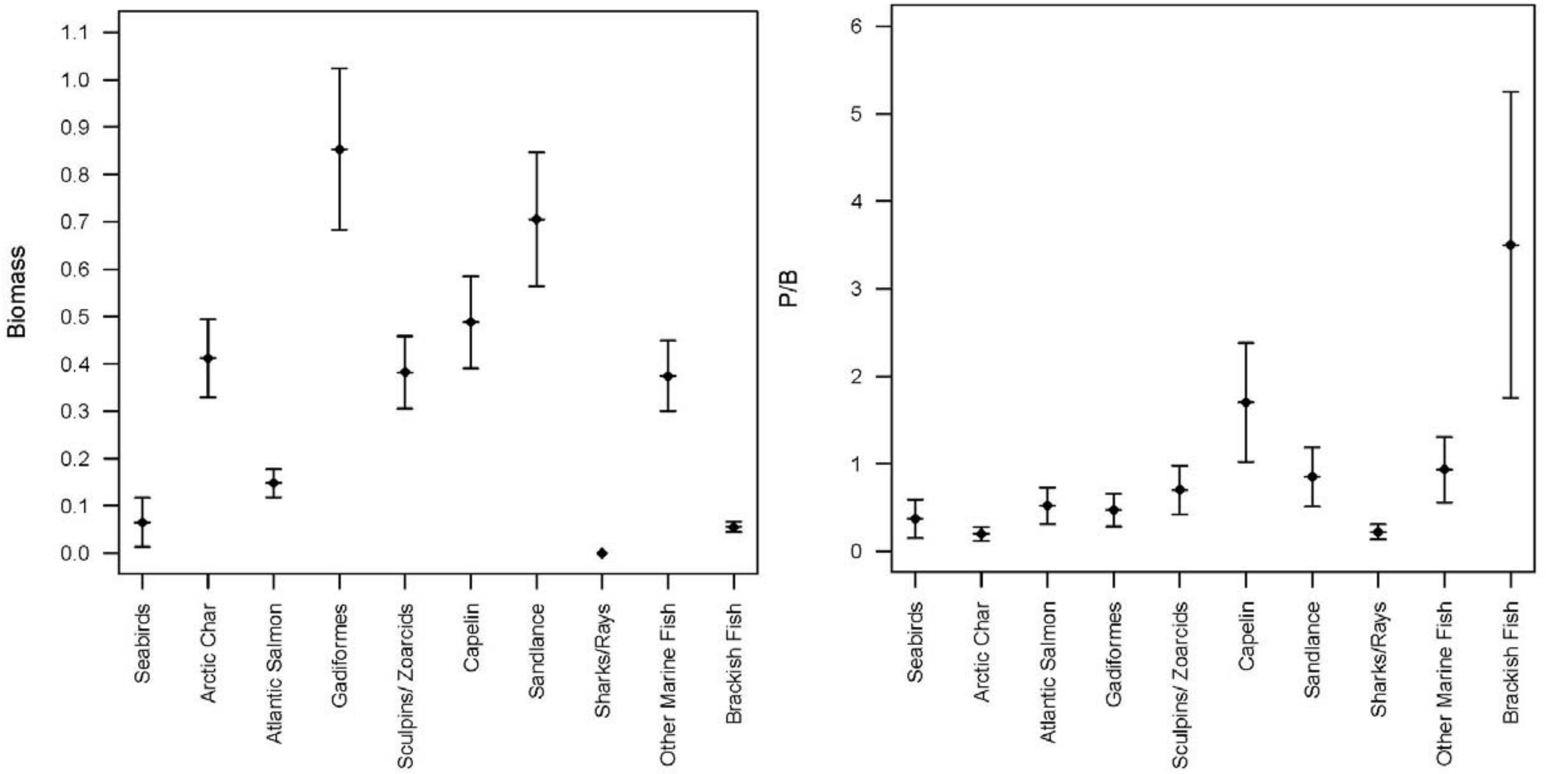
APPENDIX 6: COEFFICIENT OF VARIATION (CV) VALUES USED FOR MONTE CARLO ROUTINE

	Functional Group	Biomass (CV)	P/B (CV)	EE (CV)	BA (CV)
1	Polar Bear WHB	0.15	0.25	0.1	0.05
2	SH Polar Bear	0.15	0.25	0.1	0.05
3	Polar Bear Foxe	0.15	0.25	0.1	0.05
4	Killer Whale	0.15	0.1	0.1	0.05
5	Narwhal	0.15	0.1	0.1	0.05
6	Bowhead	0.4	0.1	0.1	0.15
7	Walrus N	0.25	0.1	0.1	0.05
8	Walrus S	0.25	0.1	0.1	0.05
9	Bearded Seal	0.25	0.1	0.1	0.05
10	Harbour Seal	0.25	0.1	0.1	0.05
11	Ringed Seal	0.25	0.1	0.1	0.05
12	Harp seal	0.25	0.1	0.1	0.05
13	Beluga E	0.15	0.1	0.1	0.15
14	Beluga W	0.15	0.1	0.1	0.15
15	Beluga James	0.15	0.1	0.1	0.05
16	Seabirds	0.4	0.3	0.1	0.05
17	Arctic Char	0.1	0.2	0.1	0.05
18	Atlantic Salmon	0.1	0.2	0.1	0.05
19	Gadiformes	0.1	0.2	0.1	0.05
20	Sculpins/ Zoarcids	0.1	0.2	0.1	0.05
21	Capelin	0.1	0.2	0.1	0.05
22	Sandlance	0.1	0.2	0.1	0.05
23	Sharks/Rays	0.1	0.2	0.1	0.05
24	Other Marine Fish	0.1	0.2	0.1	0.05
25	Brackish Fish	0.1	0.25	0.1	0.05
26	Cephalopods	0.25	0.3	0.1	0.05
27	MacroZooplankton	0.25	0.2	0.1	0.05
28	Euphausids	0.15	0.2	0.1	0.05
29	Copepods	0.15	0.2	0.1	0.05
30	Crustaceans	0.15	0.2	0.1	0.05
31	Other MesoZooplankton	0.15	0.2	0.1	0.05
32	MicroZooplankton	0.25	0.35	0.1	0.05
33	Marine Worms	0.1	0.25	0.1	0.05
34	Echinoderms	0.1	0.25	0.1	0.05
35	Bivalves	0.1	0.25	0.1	0.05
36	Other Benthos	0.1	0.25	0.1	0.05
37	Primary Production	0.15	0.1	0.1	0.05
38	Ice Algae	0.15	0.1	0.1	0.05

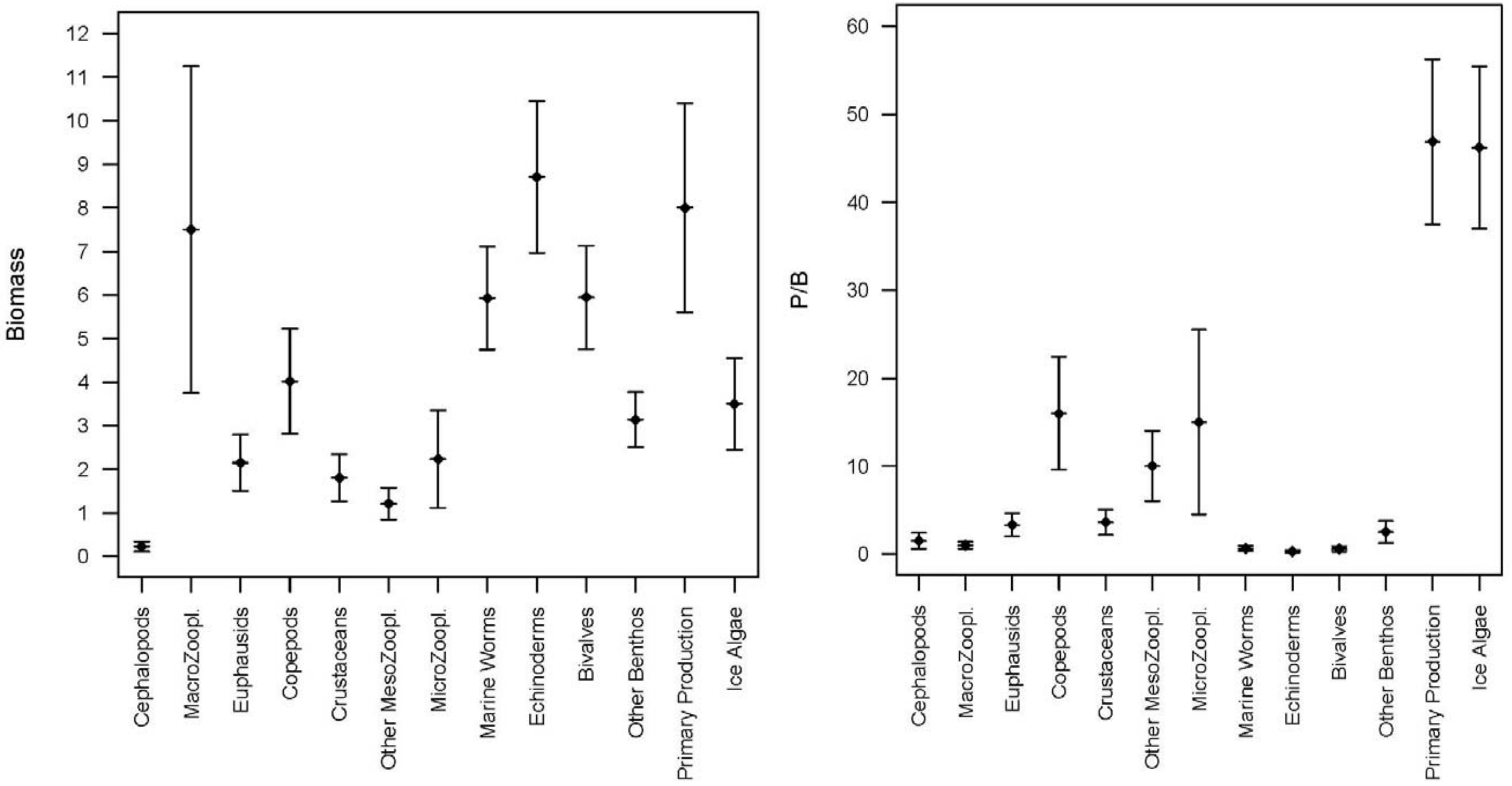
APPENDIX 7: MONTE CARLO RESULTS FOR ESTIMATES OF BIOMASS ($T \cdot KM^{-2}$) AND P/B ($YEAR^{-1}$)



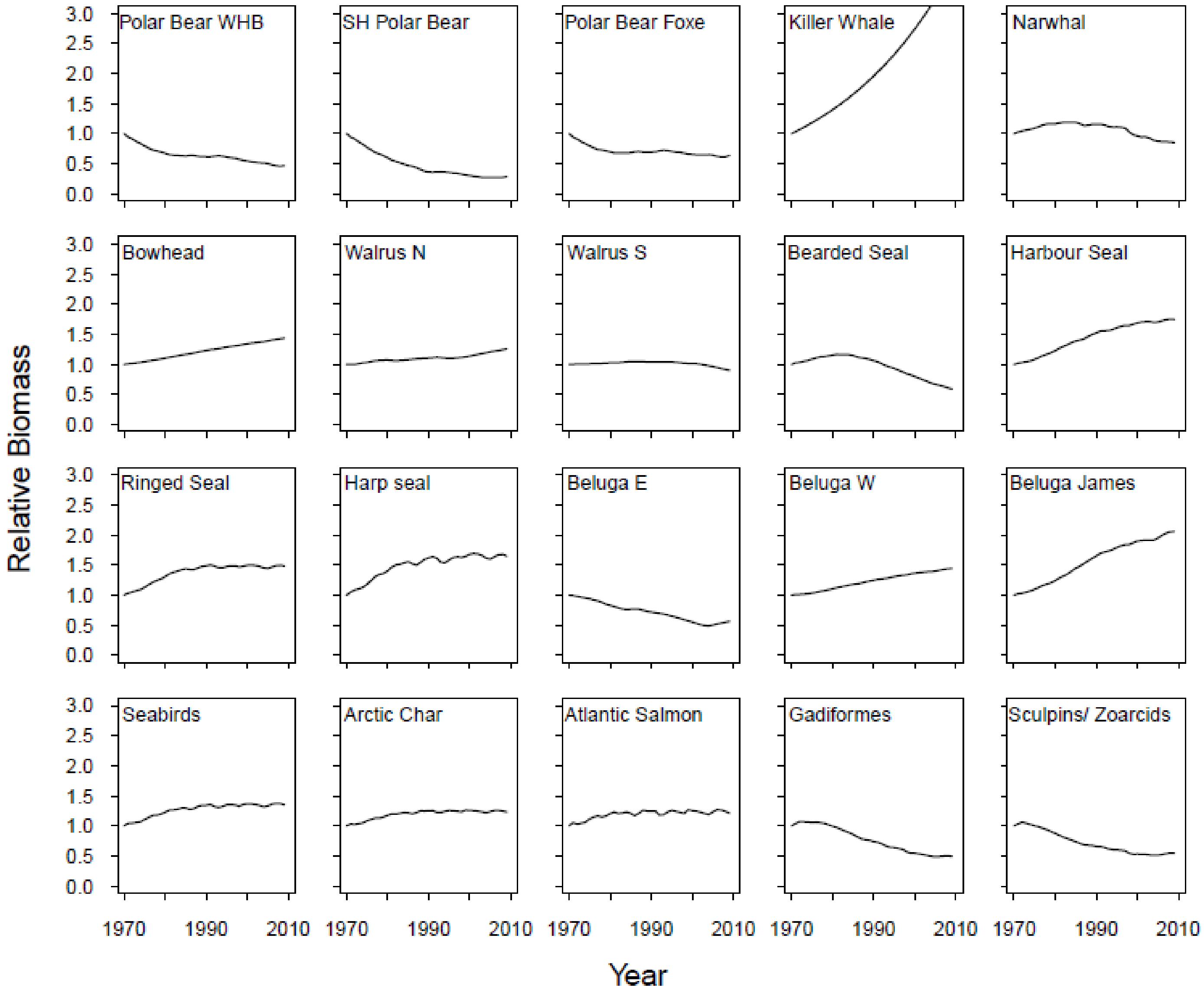
APPENDIX 7 (CONTINUED): MONTE CARLO RESULTS FOR ESTIMATES OF BIOMASS (T·KM^{-2}) AND P/B (YEAR^{-1})



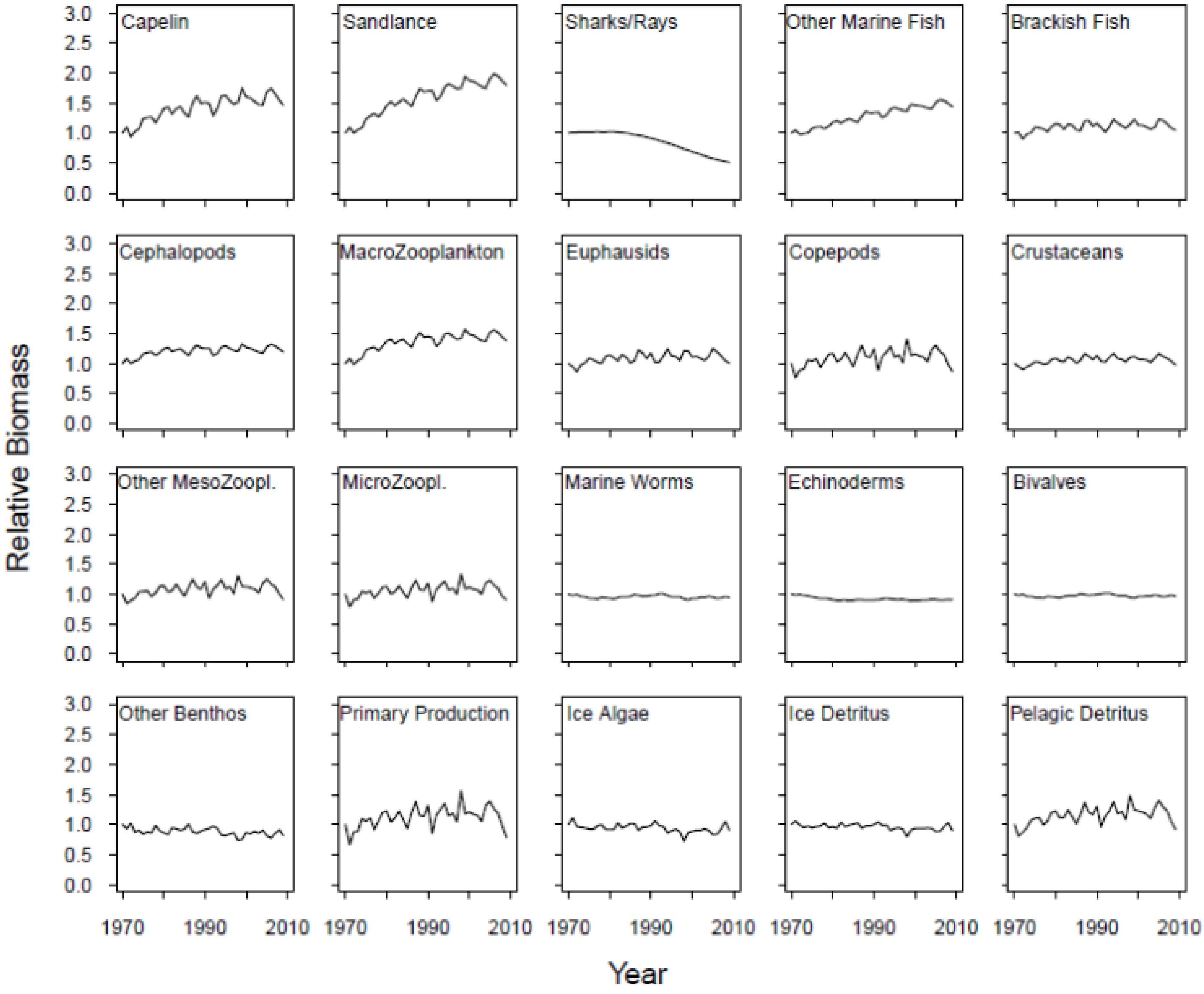
APPENDIX 7 (CONTINUED): MONTE CARLO RESULTS FOR ESTIMATES OF BIOMASS ($T \cdot KM^{-2}$) AND P/B ($YEAR^{-1}$)



APPENDIX 8: ECOSIM OUTPUT BIOMASS TRENDS FROM 1970-2010 AS SCALED TO 1970 BIOMASS VALUE.



APPENDIX 8 (CONTINUED) ECOSIM OUTPUT BIOMASS TRENDS FROM 1970-2010 AS SCALED TO 1970 BIOMASS VALUE.



BASELINE TROPHIC RELATIONSHIPS IN KALOKO-HONOKŌHAU, HAWAIʻI [7]

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ABSTRACT

The formal protection of the Hawaiian green turtle (*Chelonia mydas*) in the 1970s has led to significant increases in the number of individuals recorded throughout the archipelago. However, reduced growth rates and poor body condition of individuals at a number of foraging sites, including Kaloko-Honokōhau National Historical Park (Kaloko, Big Island), suggest that some aggregations have reached carrying capacity. To better understand the ecological structure and processes of the reef system at the park, an ecosystem model was developed that synthesized available data on Kaloko for the year 2005 and included 26 groups, spanning the entire trophic web. Model results showed that the combined grazing pressure by the different herbivorous functional groups (i.e., reef fish, sea urchins and green turtles) matched overall algal production. Sea urchins exerted the strongest control over algal resources, partly because of their large biomass within park waters. Results confirmed that the Kaloko green turtle aggregation has reached carrying capacity. Green turtles help maintain low algal cover, and thus resilience of reefs in the face of disturbance and should be explicitly included in studies of ecosystem dynamics on reefs. The model also serves as a 'current-condition' baseline for Kaloko, and provides a valuable tool for the assessment of the future marine ecosystem impacts of projected urban expansion plans around the park.

INTRODUCTION

Grazing by macroherbivores is one of the major processes structuring benthic coral reef communities. Studies which have highlighted the role of herbivores in promoting reef resilience and recovery to coral-dominated states where disturbance has led to increased algal biomass (e.g., Bellwood *et al.* 2004), have focused almost exclusively on fish and sea urchins (Hay 1984a; Hay1984b; Carreiro-Silva and McClanahan 2001; Mumby *et al.* 2006a; Paddack *et al.* 2006; Albert *et al.* 2008). Numerous reefs in the Caribbean have transitioned from coral to algal-dominated states (Gardner *et al.* 2003). This shift has been attributed to either a dramatic reduction in fish stocks, shown to limit the distribution, abundance and production of algae (Ogden and Lobel 1978; Hay 1981; Lewis 1986) or the region-wide loss to disease of an important echinoid herbivore (*Diadema antillarum*) in systems that had seen a shift from fish-dominated to echinoid-dominated herbivory (Lessios 1988; Mumby *et al.* 2006b). At some locations, increased anthropogenic nutrient loading has further exacerbated the abundance of primary producers (Burkepile and Hay 2006; Littler and Littler 2007). The majority of reefs in Hawaiʻi are not as severely impacted as those throughout the Caribbean region (Brainard *et al.* 2002; Waddell and Clarke 2008). However, a number of locations are showing increasing signs of stress as a result of mounting anthropogenic pressures on the coastal zone through development and runoff, tourism and recreation activities, and overfishing (Grigg 1994; Hunter and Evans 1995; Friedlander *et al.* 2008; Williams *et al.* 2008).

Few studies have focused on the role of sea turtles in maintaining coral reef resilience. In the context of the Caribbean this is understandable given that green turtles (*Chelonia mydas*) in this region mostly forage on seagrass (Bjorndal 1980; Mortimer 1981; Thayer *et al.* 1984) and thus have predominantly an indirect impact on the trophodynamics of reef systems (Valentine *et al.* 2002; Heck and Valentine 2006). Moreover, populations of the green turtle have been subject to a long history of human exploitation for eggs, turtle meat and shells (Parsons 1962), and in some Caribbean locations still suffer high harvest rates (Campbell and Lagueux 2005). As a consequence their numbers have been so dramatically reduced that they probably no longer perform their functional role as grazers within local seagrass systems (Jackson

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[7] Cite as: Wabnitz,C.C.C. 2012. Baseline Trophic Relationships in Kolako Honokōhau, Hawaiʻi, p.69-107. *In*: Wabnitz, C.C.C. and Hoover, C. (eds.) From the Tropics to the Poles: Ecosystem Models of Hudson Bay, Kaloko- Honokōhau, Hawaiʻi, and the Antarctic Peninsula Fisheries Centre Research Reports 20(2). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

1997; Bjorndal and Bolten 2003; Bjorndal and Jackson 2003). In Hawaiʻi, however, green turtles feed primarily on algal species that commonly occur on the reef (McCutcheon *et al.* 2003; McDermid *et al.* 2007; Arthur and Balazs 2008; Russell and Balazs 2009) and may therefore play a direct role in maintaining the resilience of coral ecosystems in this region. Observations of green turtles actively feeding on *Acanthophora* spp. and *Hypnea* spp., both non-native algae on a number of Hawaiian reefs (Russell and Balazs 1994; Arthur and Balazs 2008; Russell and Balazs 2009) further highlight their contribution to the promotion of reef resilience.

Since turtle harvesting ended in the late 1970s (Witzell 1994), an approximately linear increase in abundance of nesting females has been observed at French Frigate Shoals, Northwestern Hawaiian Islands (Balazs and Chaloupka 2004a; Balazs and Chaloupka 2006), which accounts for > 90% of all nesting within the Hawaiian Archipelago (Balazs 1980). This increase in abundance is interpreted as a recovery trend because the Hawaiian green nesting population is one of several sea turtle stocks that has been continuously monitored using dependable methodology for several decades (Balazs and Chaloupka 2004a; Chaloupka *et al.* 2008) and is considered 'self-contained' (Dutton et al. 2008). Population trends at a number of foraging grounds that have been also subject to long term monitoring seem to mirror this trajectory (Chaloupka and Balazs 2007). The significant increase in green turtle abundance within the archipelago over the last 10–20 years has been associated with a significant decrease in somatic growth rates suggesting that the carrying capacity for a number of foraging grounds may have been reached (Balazs and Chaloupka 2004b).

The role of green turtles in maintaining algal communities in a low biomass/cropped state, at least in Hawaiʻi, may be equally important to that of other grazers. An understanding of the ecological role of green turtles as grazers on reefs requires a process-oriented approach that assesses the relative contributions of all herbivorous functional groups (i.e., fish, urchins and green turtles). Such an approach is currently lacking, though it may provide significant insights into the need for, and consequences of, improved turtle conservation and management.

Ecological modeling has developed ways to mathematically describe the complexity and non-linear behavior of ecological systems. Ecopath with Ecosim is a freely available, widely used software for describing the structure of ecosystems and their food webs. It was recently named as one of the 10 major scientific breakthroughs in the 200 year history of the US National Oceanographic and Atmospheric Administration (NOAA; see http://celebrating200years.noaa.gov/breakthroughs/welcome.html). Rather than providing outputs at the population level of biological organization, typical of many models, the Ecopath with Ecosim approach provides outputs at the ecosystem level, reflecting food-web linkages, energy cycling, and changes in biomass of each species group defined in the model (Christensen 2008). Although determining carrying capacity of a system has been highlighted as one of the uses of this software, few studies have explored this aspect (but see Christensen and Pauly 1998).

An Ecopath trophic model was developed to investigate the role that green turtles play in the coral reef ecosystem of Kaloko-Honokōhau National Historical Park (Kaloko). Located on the west coast of Hawaiʻi Island (the 'Big Island'; figure 1), the park supports a healthy and relatively diverse coral habitat with little evidence of non-native species of macroalgae or diseased coral (Gibbs *et al.* 2007). It has low fish biomass, but high fish diversity (Parrish *et al.* 1990, Beets *et al.* 2010). The park also has a resident foraging population of immature green turtles that has been the subject of a mark–recapture study by the NOAA National Marine Fisheries Service and the US National Park Service since 1999 (G. Balazs, Pacific Islands Fisheries Science Center, and S. Beavers, U.S. National Park Service, pers. comm., 2007). Three lines of evidence suggest that this foraging population has reached carrying capacity: (1) The significant increase in green turtle abundance throughout the archipelago over the last 10 to 20 years has been associated with a significant decrease in somatic growth rates at many foraging grounds around the Main Hawaiian Islands, including the west coast of the Big Island (Balazs and Chaloupka 2004), possibly the result of density dependence (Bjorndal *et al.* 2000); (2) Field measurements of body volume and mass as an index of body condition have shown that turtles at foraging locations near Kaloko have lower body condition indices than green turtles at other sites on the island of Hawaiʻi (Kubis *et al.* 2008); and (3) recent necropsy reports cite emaciation as a probable contributor in the death of a number of green turtles found stranded at foraging locations along the west coast of the Big Island (or Kona coast) (Work 2007; Work 2008a; Work 2008b).

The trophic model is also intended as a 'baseline' of ecosystem state for Kaloko prior to major developments projected for areas around the park. Concern has been expressed over the future health of Kaloko's coastal resources given proposed plans for the development of lands adjacent to the south boundary of the park, including a 300% expansion of a small-boat harbor, and construction of hotels, condominiums, and a light industrial park (Gibbs *et al.* 2007). Expected impacts include a reduction in groundwater flow, an important feature at Kaloko, with a concomitant increase in groundwater loads of sediment, nutrient, and chemical pollutants (Oki *et al.* 1999; Paytan *et al.* 2006; Knee *et* al. 2008; Johnson *et al.* 2008).

The goals of this study were therefore threefold: (1) to develop an ecosystem model of the marine portion of the park to synthesize available data and describe the ecological structure and processes of the reef system at Kaloko; (2) to ascertain whether Kaloko green turtles are at carrying capacity, by determining whether grazing by green turtles and other reef herbivores matches overall algal production; and (3) to provide the management community with a tool that can simulate the effects of increased urban development in the Kaloko area, and compare the outcomes of a range of potential management scenarios.

MATERIALS AND METHODS

Study Area

Kaloko-Honokōhau National Historical Park was established in 1978 "to provide a center for the preservation, interpretation, and perpetuation of traditional native Hawaiian activities and culture, and to demonstrate historic land use patterns, as well as to provide a needed resource for the education, enjoyment, and appreciation of such traditional native Hawaiian activities and culture by local residents and visitors". The legislative boundary of the park covers a total of 5.17 km^2, 2.48 km^2 of which are marine (Gibbs *et al.* 2007). The terrestrial portion encompasses a number of anchialine pools and wetland complexes, two large ponds modified for fish production by early Hawaiians, and a fish trap (Kaloko, Aimakapā and 'Ai'ōpio respectively; figure 1). The coastal waters and reefs of Kaloko are within the West Hawaii Fisheries Management Area and managed by the State of Hawaii. The National Park Service and the State are currently discussing a joint management agreement (S. Beavers, pers. comm., 2009). The legislated park boundary extends offshore for about 1,000 m at the widest point and to maximum depths of ca. 70 m (Parrish *et al.* 1990). Past this boundary the seabed quickly drops off to depths > 180 m. Approximately 73% of the study area is hardbottom. The remaining 27% comprises unconsolidated sediment and artificial/historical features. Most of the hardbottom area has 10% to < 50% coral cover, and ~ 12% exhibits moderately high (50% to <90%) to high (90% to 100%) coral cover (Gibbs *et al.* 2007). Overall, benthic habitats are considered relatively healthy with no signs of diseased corals or non-native algal species (Marrack *et al.* 2009; Weijerman *et al.* 2009). Low sedimentation rates and the presence of relatively high coral cover in protected locations, suggest that currently, the reef habitat in Kaloko is primarily controlled by natural wave-induced stresses (DeVerse 2006).

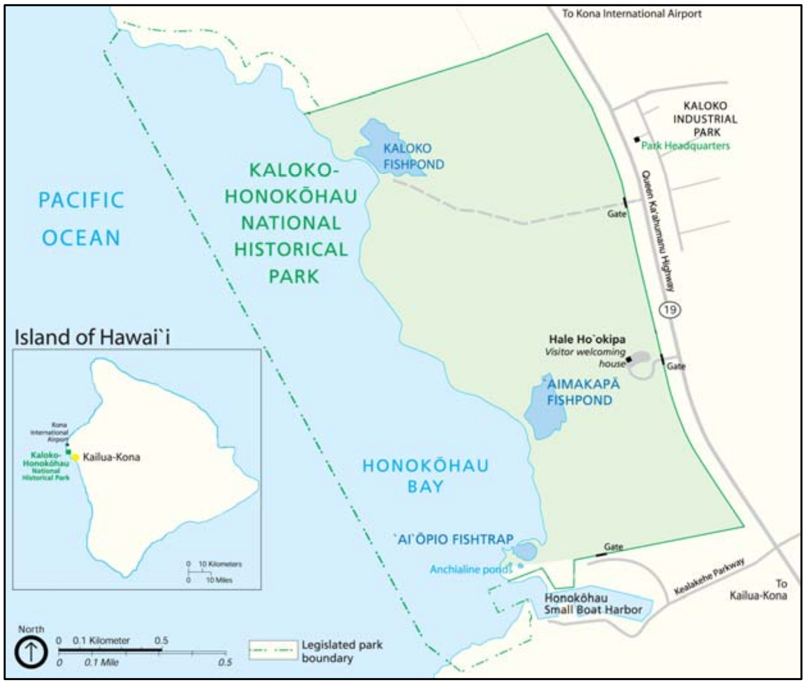

Figure 1: Map of Kaloko-Honokōhau National Historical Park (Kaloko).

Modeling Approach

Ecopath and Ecosim (EwE) version 5.1.208 was used for all modelling work (Christensen *et al.* 2005, http://www.ecopath.org). The Ecopath component of any EwE model provides a quantitative representation of the studied ecosystem for a defined time period. In other words it is a snapshot of the resources in an ecosystem and their interactions, represented by trophically linked mass-balanced biomass 'pools' (Polovina 1984; Christensen and Pauly 1992). The biomass pools, hereafter referred to as functional groups, consist of a single species, or species groups representing ecological guilds. The basic idea behind the mass-balance approach is that "at any time within the system, and within the elements of that system, the amounts of matter that flow in must balance the amount that goes out plus the change in biomass" (Pauly and Christensen 2002 / p. 215). Ecopath therefore operates under two main assumptions:

1. That biological production within a functional group equals the sum of mortalities, i.e., on an annual basis, biomass and energy in an ecosystem are conserved (Walters *et al.* 1997; Walters and Martell 2004). This relationship can be expressed as follows:

   $$B_i \cdot (P/B)_i = \sum_{j=1} B_j \cdot (Q/B)_j \cdot DC_{ij} + Y_i + E_i + BA_i + B_i (P/B)_i \cdot (1 - EE_i)$$

   where B_i and B_j are biomasses of prey (i) and predator (j) respectively; $(P/B)_i$ is the production to biomass ratio - equivalent to total mortali*ty (Z)* under most circumstances (Allen 1971); $(Q/B)_j$ is the food consumption per unit biomass of (j); DC_{ji} is the fraction of prey (i) in the average diet of predator (j); Y_i is the total fishery catch rate of group (i); E_i is the net migration rate (emigration – immigration); BA_i is the biomass accumulation rate of group (i); and EE_i is the ecotrophic efficiency, defined as the fraction of production that is consumed within the system or caught by fishers; and

2. That consumption within a group equals the sum of production, respiration, and unassimilated foods. This relationship can be expressed as follows:

   $$B \cdot (Q/B) = B \cdot (P/B) + (1 - GS) \cdot Q - (1 - TM) \cdot P + B(Q/B) \cdot GS$$

   where GS is the proportion of unassimilated food; and TM is the trophic mode expressing the degree of heterotrophy of groups represented within the system, with 0 representing autotrophs, 1 heterotrophs, and intermediate values facultative consumers.

Ecopath then uses a set of algorithms to simultaneously solve n linear equations of the form of the first equation, where n is the number of functional groups. For each functional group, three of the basic parameters: B_i, $(P/B)_i$, $(Q/B)_i$ or EE_i must be known, in addition to the fisheries yield (Y_i) and the diet composition. Units of the model are expressed in t·km^{-2}·year^{-1} wet weight organic matter for flows and t·km^{-2} for biomasses. Production per unit biomass (P/B) and consumption per unit biomass (Q/B) have the dimension year^{-1}. For a review of EwE's capabilities and limitations see Christensen and Walters (2004), Plaganyi and Butterworth (2004), and Plaganyi (2007).

To balance the model, changes were first made to the diet matrix, as diet compositions represent only snapshots of the feeding habits of individual species and are likely to be relatively variable based on location and time periods of data collection. The model required only minor adjustments and was considered balanced when: (i) the model produced realistic ecotrophic efficiencies ($EE<1$); (ii) values of the production to consumption ratio (P/Q) for functional groups were between 0.05 and 0.35, with the exception of groups with fast growth rates (higher ratios), and top predators (lower values) (Christensen *et al.* 2005).

Model Parameters and Functional Groups

The model represented an annual average situation of ecosystem conditions in the marine portion only (i.e., to the exclusion of the anchialine pools, fish ponds, and fish traps) of Kaloko in 2005. A total of 26 groups were defined, eight of which were fish, spanning the main trophic components of the ecosystem (including detritus; table 1, figure 2). The eight fish groups represent 106 species, recorded during underwater visual census (UVC) studies, which were primarily aggregated into functional groups based on ecological and biological similarities (e.g., diet, size, habitat, mortality) (Appendix 1).

Biomass estimates for individual species were based on values derived from field studies or from the literature. For species with data reported only for select habitats (e.g., fish), biomass values from these specific habitats were extrapolated to the entire park by calculating an area-weighted biomass for each species relative to the proportion each benthic habitat category covers within park waters, following Gibbs *et al.* (2007). For instances where P/B was equal to only natural mortality, estimates were taken directly from the literature or derived using the empirical formula of Pauly (1980). For exploited species, the fishing mortality was assumed to be proportional to M depending on the fishing pressure exerted (see below). Where possible, the consumption of each group was obtained through field studies; otherwise it was estimated from empirical equations such as those available in Fishbase (www.fishbase.org) for all finfish. The diet matrix was constructed using data from studies in Hawai'i (preferentially the Kona Coast); where no such data were available, the matrix was complemented with diet data obtained from the literature for the same species in similar ecosystems.

Table 1 : Trophic parameters for all functional groups of the balanced Kaloko model. Outputs from the balanced model are presented in bold. B = biomass; TL= Trophic level; P/B= Productivity biomass ratio; Q/B = consumption to biomass ratio; EE= Ecotrophic efficiency; P/Q Production to consumption ratio or gross efficiency; P/R= Production to respiration ratio. MIF = Mobile Invertebrate Feeders; SIF = Sessile Invertebrate Feeders; Zoo = Zooplanktivorous fish; CCA = Crustose Coralline Algae

		TL	B	P/B	Q/B	EE	P/Q	P/R	Catches
	Group name		(t/km²)	(/year)	(/year)				(t/km²/year)
1	Spinner dolphins	**3.21**	2.7400	0.151	11.519	**0.007**	**0.013**	**0.017**	
2	Monk seals	**3.89**	0.1790	0.121	11.508	**0.033**	**0.011**	**0.013**	
3	Sea birds	**3.17**	0.0024	0.127	76.515	**0.012**	**0.002**	**0.002**	
4	Rays	**3.15**	4.2330	0.200	3.100	**0.002**	**0.065**	**0.065**	
5	Sharks and jacks	**3.53**	0.0700	1.058	5.100	**0.453**	**0.207**	**0.350**	0.030
6	Hawksbill sea turtles	**3.18**	0.0540	0.100	3.500	**0.066**	**0.029**	**0.029**	
7	Green sea turtles	**2.00**	1.5910	0.109	6.764	**0.039**	**0.016**	**0.021**	
8	Reef fishes - piscivores	**3.39**	1.7295	0.615	6.121	**0.527**	**0.100**	**0.144**	0.003
9	Reef fishes - herbivores	**2.02**	20.3350	1.400	27.149	**0.205**	**0.052**	**0.069**	0.162
10	Reef fishes - corallivores	**2.60**	0.5417	2.100	12.918	**0.547**	**0.163**	**0.255**	
11	Reef fishes - detritivores	**2.00**	2.2598	1.900	32.272	**0.282**	**0.059**	**0.079**	0.018
12	Reef fishes - MIF	**3.13**	9.7610	0.950	8.108	**0.394**	**0.117**	**0.172**	0.130
13	Reef fishes - SIF	**2.84**	0.5440	1.700	9.581	**0.224**	**0.177**	**0.285**	
14	Reef fishes - Zoo	**2.85**	3.0460	1.450	13.378	**0.585**	**0.108**	**0.157**	0.004
15	Urchins	**2.00**	280.0000	0.484	8.547	**0.056**	**0.057**	**0.076**	
16	Crown of thorns	**2.59**	0.1170	0.411	9.000	**0.007**	**0.046**	**0.061**	
17	Benthic Invertebrates	**2.18**	42.5381	2.910	15.250	**0.950**	**0.191**	**0.313**	
18	Corals	**1.58**	130.0000	0.140	2.100	**0.594**	**0.067**	**0.075**	
19	Octocoral	**2.07**	2.9000	0.200	4.630	**0.484**	**0.043**	**0.054**	
20	Macroalgae	**1.00**	22.6910	9.824	-	**0.925**	**-**	**-**	
21	CCA	**1.00**	37.8180	1.770	-	**0.358**	**-**	**-**	
22	Turf algae	**1.00**	128.7800	19.000	-	**0.942**	**-**	**-**	
23	Turf algae_lava bench	**1.00**	3.0650	25.000	-	**0.921**	**-**	**-**	
24	Zooplankton	**2.02**	1.2400	219.000	949.000	**0.979**	**0.231**	**0.625**	
25	Phytoplankton	**1.00**	3.2900	325.458	-	**0.984**	**-**	**-**	
26	Detritus	**1.00**	100.0000	-	-	**0.694**	**-**	**-**	

Fisheries

Archaeological evidence reveals that seafood, particularly species encountered on coral reefs, was part of the traditional diet of the earliest human inhabitants of the Hawaiian Archipelago (Smith 1993). Kaloko's waters were designated as a Fisheries Management Area (FMA) on December 31, 1999 (HAR §13-60.3-14), effectively banning collection of fish for the aquarium trade in park waters, in response to declines of species targeted by collectors (Tissot *et al.* 2004). Baseline surveys conducted prior to FMA closure, comparing aquarium collection sites (including Kaloko) and 'control sites', showed a significant depletion in aquarium species compared to non-target species. Surveys conducted subsequent to the FMA designation recorded significant increases in the overall abundance of fish targeted by collectors (Tissot *et al.* 2004). However, at Kaloko specifically, post-closure surveys showed no significant change in the abundance of yellow tangs (*Zebrasoma flavescens*), the most sought-after species. The lack of response may have been due to the small size of the Kaloko FMA and the relatively small amount of suitable habitat compared to other FMAs included in the analysis (Hoover and Gold 2005). In the years since the surveys, biomass may well have responded to the closure, and because fishing pressure has been removed, P/B was set to M for all formerly collected species.

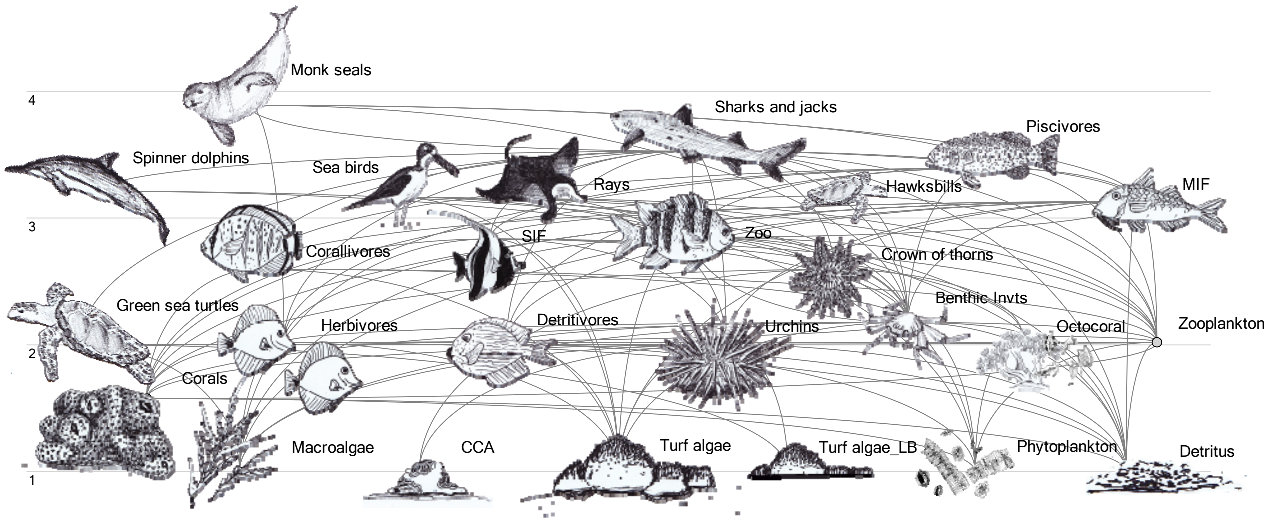

Figure 2 : Graphical representation of trophic flows within the Kaloko reef ecosystem. Each functional group is identified here by an illustration (© M. Bailey); where relevant, an image of a species representative of its guild is depicted. Images are not drawn to scale or proportional to the group's biomass. The light grey horizontal lines and associated numbers represent trophic levels; lines connecting individual functional groups represent trophic links. Zoo = Zooplanktivorous fish; MIF = Mobile Invertebrate Feeding fish; SIF = Sessile Invertebrate Feeding fish; Turf algae_LB = turf growing on the lava bench area; CCA = Crustose Coralline Algae; Benthic Invts = Benthic invertebrates

From a food-fish perspective, the park is a popular location for subsistence fishing and shoreline gathering, traditional activities that are permitted as long as they are consistent with state law and park mandates (i.e., with legal fishing gear for personal consumption DeVerse 2006). Harvesting is done primarily from shore using a variety of methods, such as throw nets, spear, and pole fishing. Gill, or "lay" netting, a serious threat to marine resources including marine mammals and sea turtles, was restricted within park waters in August 2005 to locally constructed, handmade nets of natural fibers. The state of Hawai'i does not have recreational and subsistence permitting or reporting requirements (Friedlander and Parrish 1997), despite surveys in the late 1980s indicated that 19-35% of human residents fish (Smith 1993) and recent studies concluding that total take of coral reef fish species by recreational fishers is far greater than commercial catches (Zeller *et al.* 2005), with shore-based fishing representing a much larger part of total fishery take than boat-based fishing for nearly all targeted species (Williams *et al.* 2008). Results from a recent study show that fish biomass of several target species groups was negatively correlated with local human population density and concluded that fishing was the prime driver of those trends (Williams *et al.* 2008). Of the 18 coral reef locations included in the study for comparison and widely spread throughout the Main Hawaiian Islands, none were located on the west coast of Hawai'i Island. Tissot *et al.* (2004) and Tissot *et al.* (2009) reported on the effectiveness of community-based co-management and an MPA network along the western Kohala-Kona Coast of Hawai'i Island as means to increase productivity of species targeted for the aquarium trade specifically. However, data are lacking to quantitatively assess patterns and trends relating to species targeted by commercial as well as recreational and subsistence fisheries along the western shores of the Big Island.

Hawai'i's Department of Aquatic Resources (DAR) conducts regular surveys at 14 sites in West Hawai'i, including one within Kaloko adjacent to the Honokōhau harbor, focusing on 'resource fish' (DAR unpublished data, in Weijerman *et al.* 2009). Results show that among these 14 sites, the one located in Kaloko has the lowest biomass. However, as this site is located just outside of the harbor, this low biomass may be due partly to its accessibility to spear fishers. More generally fish in park waters do not appear as grossly depleted as in some coastal waters of the state (Parrish *et al.* 1990; Beets *et al.* 2010, S. Beavers, pers. comm., 2008).

Of the few existing case studies documenting catch levels, results show landings to be either representative of fishers targeting specific species, or proportional to species' biomass on the reef. In 1997, Friedlander and Parrish (1997) measured standing stock and quantitatively estimated catch and effort of a small recreational/subsistence fishery at Hanalei Bay, Kauai, Hawai'i. In the absence of catch or effort data specific to Kaloko, it was assumed that catch data to standing stock proportions in the park would be comparable to those in Hanalei Bay (Friedlander and Parrish 1997); with values adjusted to reflect species known to be targeted at Kaloko. For example, although corallivores featured in the catch at Hanalei Bay, they are not target species at Kaloko. As no data were available on macroinvertebrates in Kaloko (with the exception of urchins), nor information regarding whether fishing occurs on those groups in the park, no catch was allocated to the 'benthic invertebrates' functional group.

The existing fisheries were divided into two 'fleets', one targeting sharks and jacks specifically and a recreational/subsistence fishery representing fishers operating mainly from shore using pole, spear, and line, and targeting small reef fish. The ratio of catch to standing stock was calculated for fish families targeted by fishers from Friedlander and Parrish (1997), and doubled given that fishing pressure is likely to be higher now than it was in 1997 (DAR unpublished data in Weijerman *et al.* 2009). In the absence of other information these indices were applied to fish families known to be harvested in Kaloko (E. Brown, unpublished data). For species groups targeted in Kaloko, but for which data were not available from the Friedlander and Parrish (1997) study, the same values were applied as for fish families in the same functional group. Fishing mortality for functional groups, and by extension individual species, was subsequently calculated using F = catch/biomass.

Functional Groups

Spinner dolphins

Hawaiian spinner dolphins belong to a stock that is separate from those involved in the tuna purse-seine fishery in the eastern tropical Pacific (NOAA 2005a). A 2002 shipboard line-transect survey of the entire Hawaiian Islands Exclusive Economic Zone resulted in an abundance estimate of 2,805 spinner dolphins (Barlow 2006). Only a fraction of this number is likely to be considered resident within Kaloko waters and to feed there regularly. Norris (1994), in his intensive study of spinner dolphins of the Kona Coast of Hawai'i, suggests that the waters surrounding this island may have a large, relatively stable 'resident' population with a minimum of 960 animals regularly frequenting the shore of the Big Island. Based on sightings information provided by National Park Service staff, an average of one hundred 68-kg dolphins were assumed to utilize park waters on a regular basis, a biomass of 2.74 $t \cdot km^{-2}$.

The P/B value was assumed to be equal to M (natural mortality) and was derived from a life history table model (Barlow and Boveng 1991) that estimates survivorship and mortality according to the longevity of a given species. Spinner dolphins live on average to be 20 years old (NOAA 2003; NOAA 2005a) and P/B was therefore set at 0.151 $year^{-1}$.

Consumption per unit of biomass (Q/B) was first calculated using an empirical equation for daily ration $R=0.1 \cdot W^{0.8}$, as modified from Innes *et al.* (1987) in Trites and Heise (1996), where W is body weight in kg and R the daily ration in $kg \cdot day^{-1}$ (Method 1). Hunt *et al.* (2000) describe energy requirements using the equation $E = a \cdot W^{0.75}$ where E is the energy requirement per day ($kcal \cdot day^{-1}$), W the mean body weight (kg) and a is a coefficient varying with the group of mammals (a=320 for otariids, 200 for phocids, 192 for mysticetes, 317 for odontocetes, and 320 for sea otters). The coefficient of 0.75 is intended to apply to mammals in general and was changed to 0.714 following Hunter (2005) who estimated a more precise coefficient for marine mammals (Method 2). Benoit-Bird (2004) found the daily maintenance energy needs of a spinner dolphin to range between 2,430 kcal and 4,050 kcal (measured on a stranded animal and large adult males respectively), with an estimate of 3,520 kcal for an average adult (Method 3). Using an average weight of 68 kg for an individual spinner dolphin resulted in Q/B estimates of 15.70 year^{-1}, 12.2 year^{-1}, and 6.66 year^{-1} for methods 1, 2, and 3 respectively. The average of 11.519 year^{-1} was used.

Spinner dolphins in Hawai'i have been observed to rest during the day and feed at night, as many of their prey species, small mesopelagics (< 20 cm), are organisms that rise from deep water to the surface near dusk (Norris and Dohl 1980; Norris *et al.* 1994; Benoit-Bird and Au 2003). The Hawaiian spinner populations are also known to take bottom dwelling, and small numbers of surface dwelling species, as well as crustaceans (Perrin and Gilpatrick 1994; Würsig *et al.* 1994; Perrin 1998).

Monk Seals

Counts at the six main Northwest Hawaiian Islands (NWHI) subpopulations of monk seal (*Monachus schauinslandi*), an extrapolation of counts at Necker and Nihoa Islands, and counts at the Main Hawaiian Islands (MHI) led to a best estimate of a total population size for Hawai'i of 1,202 individuals in 2006 (NMFS 2007). A 2001 aerial survey determined a minimum abundance of 52 individuals in the MHI and remains the most recent available estimate (Baker and Johanos 2004). However, occasional sighting reports from the area may not reflect the actual rate of park shoreline habitat use by monk seals. Rather, they represent the minimum shoreline usage because sightings are opportunistically collected and heavily biased by reporting effort. From existing data, monk seals found to haul out in the park cannot be assumed to utilize the parks' near shore resources as foraging habitat (i.e., have the resources contribute to their diet). Thus, although these animals may utilize the park's waters for foraging, they may well derive a greater portion of their diet from surrounding waters. In light of the paucity of data concerning monk seal usage of the area, our biomass estimate included two individuals (partly based on data presented by Baker and Johanos (2004)) of an average mass of 187.5 kg (NOAA 2005b; NMFS 2006) (i.e., B=0.179 t·km^{-2}) (T. Wurth, Pacific Islands Fisheries Science Center, pers. comm., 2007). These values are meant to serve as a placeholder until more information becomes available.

The net productivity rate for monk seals, based on overall declines of this species in Hawai'i, is currently assumed to be -0.019 year^{-1}, although stock assessment data highlight that population trends vary considerably among the six main subpopulations (Baker and Johanos 2004). Although the MHI monk seal population may be on the rise (Baker and Johanos 2004), this increase remains unconfirmed and abundance estimates appear to be too low to strongly influence current total stock trends. Application of the MHI overall population productivity trend, Barlow and Boveng's (1991) life history table model, and a longevity estimate of 25 years, led to a P/B estimate of 0.121 year^{-1}.

Consumption per unit of biomass was calculated according to methods 1 and 2 introduced above for spinner dolphins. Using an average monk seal mass of 187.5 kg, and two estimates of average caloric prey-content calculated from data presented in Goodman-Lowe *et al.* (1999a) and Goodman-Lowe *et al.* (1999b), resulted in Q/B values ranging from 10.27 year^{-1} to 12.82 year^{-1}, with the average of 11.508 year^{-1} being used for the model. These values are much lower than the estimate of Polovina (1984) or Massicot (2006), who assumed, respectively, that monk seals must consume, on average, 45 or 36.5 times their weight in food per year.

Based on the analysis of identifiable hard parts found in regurgitate and fecal material, Goodman-Lowe (1998) reported that fish comprised the grestest proportion of monk seal diets, with typical prey species including marine eels (Congridae, Muraenidae, and Ophicthidae), and various reef fish such as wrasse (Labridae), squirrelfish and soldierfish (Holocentridae), as well as triggerfish (Balistidae). The remainder of the diet was comprised of cephalopods and crustaceans (Longenecker *et al.* 2006).

Birds

Most Hawaiian lowland waterbirds, thought here to include waterfowl, rails, shorebirds, and waders (K. Uyehara, pers. comm., 2007), tend to be found in and around traditional fishponds (Morin 1994), which are not included in this model. Two of the most important fishponds along the Kona Coast, 'Aimakapa and Kaloko, lie within park boundaries. In addition to fishponds, the park offers a range of habitats, including sandy and rocky intertidal shoreline, anchialine pools, brackish water wetlands with some mudflats, coastal strand vegetation, all of which are known to attract a wide variety of bird species (Morin 1994).

The only indigenous resident birds remaining in Kaloko-Honokōhau are three endemic, endangered waterbird species: the Hawaiian stilt (*Himuntopus mexicanus knudseni*), the Hawaiian coot (*Fulica alai*), and the indigenous black-crowned night heron (*Nycticorax nycticorax hoactli*). Despite predominantly utilizing fishpond habitats, the endangered Hawaiian stilts, the black-crowned night-herons, and all of the waterbirds use the rocky intertidal beach areas for feeding, especially during low tides (Morin 1994). This usage was also confirmed by K. Uyehara, S. Waddington, and S. Beavers (pers. comm., 2008), and therefore the Hawaiian stilt, sanderling (*Calidris alba*), ruddy turnstone (*Arenaria interpres*), wandering tattler (*Heteroscelus incanus*), Pacific golden-plover (*Pluvialis fulva*), and black-crowned night-heron were included in the Kaloko model.

Biomass estimates were based on sighting surveys conducted in an area of about 0.02 km^{-2}, and these were subsequently extrapolated to the 0.1 km^{-2} portion of the park available for birds to forage in (S. Waddington, Cyanotech Corporation, pers. comm., 2007). Individual species' weight data were extracted from a number of sources (e.g., Anonymous 1996a; Anonymous 1996b; Reed *et al.* 1998; Nettleship 2000; Gill *et al.* 2002; MacWhirter *et al.* 2002). Biomass calculations were weighted by individual species biomass' contribution within the group and total bird biomass was estimated to be 0.0024 t·km^{-2}.

Very little information was found to guide estimates of P/B values for waterbirds found in Kaloko. Polovina (1984) used a value of 5.4 year^{-1} for birds in French Frigate Shoals (FFS). However, bird species at FFS are mostly pelagic seabirds, which typically suffer higher mortality rates than the coastal waterbirds encountered in Kaloko. Hence the overall P/B value used here (0.127 year^{-1}) was computed from survivorship rates found in a number of publications (e.g., Reed *et al.* 1998; Nettleship 2000; Gill *et al.* 2002) and weighted by individual species' biomass contribution to the overall group.

Q/B was determined by first calculating the ration for each species using the empirical formula derived by Nilsson and Nilsson (1976, in Wada 1996):

$$\log R = -0.293 + 0.85 \cdot \log W$$

where R is the daily ration in g per day, and W is body weight also in g. The values were then averaged across species based on biomass contributions by individual species and resulted in a group Q/B estimate of 76.515 year^{-1}.

Hawaiian stilts are opportunistic feeders that eat a variety of invertebrates and vertebrates found in shallow water and mudflats, such as polychaete worms, small crabs, aquatic insects, and small fish (Mitchell *et al.* 2005; U.S. Fish and Wildlife Service 2005). Sanderlings' diet are known to markedly change between seasons, consisting almost exclusively of insects during the breeding season, and small crabs, isopods, insects, amphipods, polychaetes, and small mollusks in winter (Perez Hurtado *et al.* 1997; Tsipoura and Burger 1999; Petracci 2002; Anonymous 2005a; Nuka *et al.* 2005). Pacific golden plovers feed primarily on terrestrial insects, but are also known to forage in the intertidal areas and opportunistically prey on aquatic invertebrates (Kato *et al.* 2000; Anonymous 2005b). Outside of the breeding season, ruddy turnstones are known to prey on crustaceans, mollusks, polychaetes, and small fish (Tsipoura and Burger 1999; Nettleship 2000; Anonymous 2005c). The diet of wandering tattlers varies with season and in winter tends to consist of invertebrates such as marine worms, aquatic insects, mollusks, crustaceans, and small fish (Gill *et al.* 2002; Anonymous 2005d). The black-crowned night heron is an opportunistic feeder, whose diet consists mainly of fish, though it will occasionally feed on other items such as earthworms, and aquatic and terrestrial insects (Wolford and Boag 1971). It has also been observed to feed on crayfish, mussels, squid, amphibians, lizards, snakes, and plant material (Davis 1993).

Rays

The spotted eagle ray (*Aetobatus narinari*) and the manta ray (*Manta birostris*) are both known to transit through park waters. Manta rays are the focus of commercial night diving and research activities in and near Kaloko waters. Relatively few quantitative data are available for this functional group within the park. A biomass estimate of 4.233 t·km^{-2} was assigned to the group overall, based on the subjective species level abundance rankings and use of park waters for feeding activities, as well as estimates of individuals' biomass provided by T. Clark (University of Hawai'i, unpublished data).

The group's P/B ratio (0.2 year^{-1}) was estimated by averaging individual species' natural mortality rate using Pauly's formula (1980). Very little is known about foraging patterns and rates of mantas or spotted eagle rays. Our estimate of Q/B (3.1 year^{-1}) was based on values for individual species derived from Fishbase as well as parameters presented in Olson and Watters (2003).

Rays as a functional group were assumed to feed on benthic invertebrates as well as zooplankton (Olson and Watters 2003; Wetherbee and Cortes 2004). Manta rays are known to mostly feed outside of park waters, but spotted eagle rays have been seen to regularly forage in the Honokōhau channel (T. Clark, unpublished data).

Sharks and Jacks

Sharks are sighted offshore relatively frequently (S. Beavers, unpublished data), and in recent years tiger sharks have been repeatedly sighted within, and near the mouth of Honokōhau harbor (DLNR 2001; Thompson 2005; Meyers *et al.* 2009). Based on park data, tiger sharks (*Galeocerdo cuvier*) and whitetip reef sharks (*Triaenodon obesus*), as well as other top predators such as bluefin trevally (*Caranx melampygus*), bigeye trevally (*Caranx sexfasciatus*), mackerel scad (*Decapterus macarellus*), golden trevally, (*Gnathanodon speciosus*), doublespotted queenfish (*Scomberoides lysan*), bigeye scad (*Selar crumenophthalmus*) and greater amberjack (*Seriola dumerili*) are only rarely spotted in Kaloko waters. A biomass estimate of 0.07 t·km^{-2} was assigned to the group overall, based on findings in Friedlander and DeMartini (2002), the subjective species level abundance rankings offered on the park's website (http://www.nps.gov/kaho/), and by Parrish *et al.* (1990).

The group's P/B ratio (1.058 year^{-1}) was estimated by averaging individual species natural mortality rates using Pauly's formula (1980) and fishing mortality estimates based on Friedlander and Parrish (1997). Consumption rate was estimated at 5.1 year^{-1} and represents the average of values derived for individual species based on data derived from Fishbase.

In Hawai'i, tiger sharks have a broad diet. As sharks increase in size, prey diversity and frequency of occurrence of large prey items increase. Teleost fish make up a large proportion of the diet of all size classes of sharks, and marine mammals and sea turtles are relatively uncommon, even in large sharks (Lowe *et al.* 1996). For most other species, diet data was derived from Fishbase.

Hawksbill turtles

Individually identified hawksbills are seen at specific sites within Kaloko, on a regular basis (S. Beavers, unpublished data). Although a number of them just travel through, hawksbill turtles have been filmed feeding and attempting to mate in park waters. It was assumed for three turtles to be 'resident' in Kaloko (G. Balazs and S. Beavers, unpublished data). Each turtle was assumed to weigh about 45 kg, resulting in a total biomass of 0.054 t·km^{-2}.

Few estimates of hawksbill survival rates exist, thus the P/B value was based on Crouse (1999) and set to 0.109 year^{-1}. As no data were available regarding foraging rates at Kaloko, the Q/B was set to be equal to 3.5 year^{-1}.

Hawksbill turtles primarily feed on sponges and benthic invertebrates (Bjorndal 1997). In Hawai'i, sponges are not abundant, and limited information gained through necropsies and visual observations indicate that hawksbill turtles appear to feed on sea cucumbers, fireworms, and red algae (S. Beavers and S. Hargrove, unpublished data).

Green Turtles

Data on green turtle sightings and measurements were obtained from the NOAA National Marine Fisheries Service's (NMFS) Marine Turtle Research Program (G. Balazs and S. Hargrove, unpublished data), and the National Park Service (NPS) (S. Beavers, unpublished data). The sum of the maximum mass for all 58 individual juvenile turtles caught in 2005 amounted to a total biomass of 1,600 kg. Turtles that were captured more than once in a year were only counted once and maximum mass for that individual was used in calculations. In instances where specific mass data were not available the following assumptions were made: (i) where size was available, mass was calculated using a length-weight relationship based on previous captures; and (ii) where size was not available, individuals were given an average value as derived from all turtles measured that year. Based on recapture rates since 2003, biomass outside the sampling area was estimated at ~25% of the biomass of individuals tagged within the study area, leading to a total green turtle biomass estimate of 0.806 $t{\cdot}km^{-2}$ within Kaloko. However, NPS resighting data suggest that the number of turtles tagged under the NMFS long-term turtle monitoring program is an underestimate of the total number of individuals that regularly use park waters. Based on weekly surveys and NPS mark and recapture data, 143-161 out of 196 turtles associated with Kaloko show high site fidelity, and can thus be considered Kaloko 'resident' (S. Beavers, NPS unpublished data). Using the average green turtle weight in 2005 of 27.6 kg, which is not significantly different from the average for all other years, led to an average green turtle biomass for Kaloko of 1.591 $t{\cdot}km^{-2}$. The model was run with this latter estimate.

In Hawai'i, green turtles have benefited from effective protection under the U.S. Endangered Species Act since 1978 (43 Federal register 32808). It therefore seems fair to assume that natural mortality rate represents a good estimate of green turtles' P/B ratio. Bjorndal *et al.* (2003) calculated true annual survival probability for green turtles protected from human induced mortality at Union Creek, Bahamas, to be equal to 0.891 $year^{-1}$. Although predation rates are likely to be higher in Hawai'i due to a greater natural abundance of tiger sharks (Witzell 1987), green turtles at Kaloko have generally been observed to show high site fidelity and not to migrate much. Indeed, individuals spend a significant portion of daytime hours, when tide height is sufficiently high, in very shallow waters or in the intertidal zone foraging on a dense mat of turf algae growing on a 'lava bench' (G. Balazs, pers. comm., 2008 and S. Beavers, NPS unpublished telemetry data). Therefore, the higher estimate, derived by Bjorndal *et al.* (2003), was used here (P/B=0.109 $year^{-1}$).

No estimates of consumption rates were available for the resident green turtle population at Kaloko and, overall, very few data are available on natural consumption rates of green turtles, particularly for algal environments. Weekly surveys conducted by NPS staff do however indicate that the primary activity of turtles observed is feeding (S. Beavers, NPS unpublished data). The Q/B ratio for green turtles was estimated at 6.764 $year^{-1}$ based on an average body mass intake of 1.8% per day. This proportion was recalculated from Brand *et al.* (1999) using the length weight relationship in Arthur *et al.* (2006), as the original study was conducted in Australia. It should be noted that both of these studies were conducted in seagrass environments. Our estimate is within the lower range of consumption rates estimated from seagrass intake rates in the Caribbean (Bjorndal *et al.* 2000). Data from a recent study conducted off the coast of Colombia suggest that consumption rates can be much lower (i.e., 1.9 $year^{-1}$ (Amorocho and Reina 2008)). However, Amorocho and Reina's (2008) findings were based on an experimental set up that involved moving animals into the laboratory every three days to be fed the equivalent of 1-2% body mass, a ratio considered to be a maintenance diet (Higgins 2003). Therefore, these consumption estimates may not be consistent with feeding rates observed in the wild.

Over 275 species of marine algae and two seagrass species have been reported from green turtle crop and stomach samples in the Hawaiian Islands (Balazs 1980; Balazs *et al.* 1987; Russell *et al.* 2003; Russell and Balazs 2009). A study examining diets of immature green turtles at seven sites in the MHI showed that despite variations among foraging grounds, overall, individuals' diets were dominated by red algae, with *Acanthophora spicifera* (an introduced species), *Hypnea* sp., *Pterocladiella* sp., and *Cladophora* sp. being prominent (Arthur and Balazs 2008). In the same study, all turtles appeared to have a base diet of algal turf, enhanced with desirable monogeneric stands when available. Hawaiian 'turf algae' are comprised of multiple species of compact, often filamentous, red and green algae with a canopy height of only a few millimeters. Given the high cover of turf algae and the low availability of macroalgae at Kaloko (Marrack *et al.* 2009; Weijerman *et al.* 2009), turf algae constitutes the primary dietary component of green turtles within park waters (G. Balazs and S. Beavers, pers. comm., 2009).

Reef Fish

The Park Certified Species list comprises 203 species of reef fish, not all common however (NPS unpublished data), making Kaloko host to the greatest number of fish species of the four national parks surveyed in Hawai'i (Hobson 1974). Beets *et al.* (2010) collected UVC transect data for three habitat classes: unconsolidated sediment [sand] (UCS), colonized hard bottom (CHB), uncolonized hardbottom (UCH) from mean low water to 30-m depth. Unconsolidated sediments were excluded from the analysis.

Although it represents one of the largest habitat classes in the study area, much of it is probably below 30 m depth, and it is unclear what proportion occurs at shallower depth, precluding reliable extrapolations from transect data to the entire park. In any event, few fish were recorded along transects on UCS and its exclusion therefore had a negligible effect on overall biomass estimates. A single species, *Malacanthus brevirostris*, was documented to occur only on UCS. Beets *et al.*'s (2010) fish biomass values for CHB and UCH were extrapolated to the entire park by calculating an area-weighted biomass for each species relative to the proportion of each benthic habitat category within park waters. According to Gibbs *et al.* (2007) CHB represents 60.73% and UCH 11.74% of park substrate. To facilitate data comparisons with ongoing monitoring studies, and to ensure greater transferability and relevance of results to existing efforts on the ground, fish species were grouped according to the same functional groups used by Beets *et al.* (2010). These were corallivores, detritivores, herbivores, mobile invertebrate feeders (MIF), piscivores, sessile invertebrate feeders (SIF), and zooplanktivores (Zoo) (see Appendix 1 for species list).

P/B rates were derived from natural mortality estimates, based on Pauly (1980), and fishing mortality estimates based on the catch data outlined in the fisheries section above. Functional group estimates were weighted by individual species biomass contribution within their respective group.

Q/B rates for each functional group were estimated based on information derived from Fishbase for individual species and using diet information (outlined below) to classify individual species as herbivores or detritivores. As was done for P/B values, Q/B estimates for a given guild were weighted according to individual species' biomass contributions within their respective groups.

A diet matrix was developed from a detailed analysis of food habits of some teleost fish along the Kona Coast (Hobson 1974) as well as from information gleaned from Fishbase and a large number of published studies (e.g. Bruggemann *et al.* 1994; Guiasu and Winterbottom 1998; Choat *et al.* 2002; DeFelice and Parrish 2003; Paddack *et al.* 2006; Dierking *et al.* 2009). Recent evidence from studies conducted in Australia shows that fish nominally considered as herbivores may actually feed on a number of items other than algae, especially detritus, and that, as such, explicitly herbivorous taxa are a minority (Crossman *et al.* 2001; Choat *et al.* 2002; Choat *et al.* 2004; Crossman *et al.* 2005). For continuity and comparative purposes the same functional groups as those used for monitoring activities in Hawai'i were retained, but for the relevant species these new findings were taken into consideration when assembling the diet composition matrix.

Urchins

Sea urchins are highly abundant at Kaloko and were examined separately from benthic invertebrates in more general terms due to their substantial contribution to grazing. Biomass estimates were based on surveys conducted at 10 m depth in 2006 by Marrack *et al.* (2009) and Weijerman *et al.* (2009). The most frequently encountered urchins during surveys were *Echinometra mathaei*, *Echinothrix* spp. (i.e., *Echinothrix diadema* and *Echinothrix calamaris*), *Heterocentrotus mammilatus* and *Tripneustes gratilla*. Test size for *Echinothrix* spp., *T. gratilla*, *E. mathaei*, and *H. mammilatus* were recorded on the reef by local researchers (M. Weijerman, U.S. National Park Service, pers. comm., 2008; H. Jessop, University of Hawai'i, pers. comm., 2008) and converted to biomass based on published test size-weight relationships (Dotan 1990; McClanahan and Kurtis 1991; Rahman *et al.* 2001; Rahman *et al.* 2004; Muthiga and Jaccarini 2005). Biomass survey data were extrapolated to the whole park by calculating an area-weighted biomass for all species based on the assumption that urchins chiefly occur on colonized substrate with at least 10% coral cover (M. Weijerman, pers. comm., 2008). Total biomass was reduced from an estimated total of 294 t·year^{-1} to 280 t·year^{-1} to account for likely reduced densities of urchins in deeper areas of the park compared to surveyed depths (F. Parrish, NOAA, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, pers. comm., 2008).

P/B rates were calculated for each species using the functional relationships for mortality developed by Brey (2001). The group's overall P/B rate was weighted according to individual species' biomass contributions to the guild and estimated at 0.484 year^{-1}.

Q/B estimates for *T. gratilla* were based on feeding experiments conducted on *T. gratilla* using averages for three species of algae employed in trials (M. Deagle, University of Hawai'i, pers. comm., 2007), and on *T. gratilla* and *Echinothrix* sp. using *Gracilaria* only (H. Jessop, pers. comm., 2007). Values of 14.72 year^{-1} and 13.9 year^{-1} for these two studies respectively, corroborate the findings of Stimson *et al.* (2007) who conducted food preference trials on T. *gratilla*. As no data were available for *E. mathaei* for Hawai'i, Q/B for this species was set at 4.44 year^{-1} based on data from Carreiro-Silva and McClanahan (2001) and McClanahan and Kurtis (1991). This value is much lower than the estimate of 16.51 year^{-1} derived by Hiratsuka and Uehara (2007) from laboratory feeding trials. Their estimate is based on feeding sea urchins ad libitum a diet prepared from turf algae and agar over a 7-day period. For *Echinothrix* sp. the Q/B was set at 7.86 year^{-1}. This represents the average of values reported by Carreiro-Silva and McClanahan (2001) and those obtained from feeding trials by H. Jessop (pers. comm., 2007). Consumption rates determined under laboratory conditions are frequently higher than those derived under natural conditions. In the absence of data for *H. mammilatus*, this species was assigned the same Q/B rate as *Echinothrix* sp. (intermediate between *E. mathaei* and *T. gratilla*). The guild's overall Q/B of 8.547 year^{-1} was calculated by weighting individual species' Q/B by their respective biomass contributions.

Although echinoids can show feeding preferences (de Ridder and Lawrence 1982), they are typically opportunistic feeders with their diets varying according to habitat and season. Observations at Kaneohe Bay, Oahu, Hawai'i, by Stimson *et al.* (2007) show that *T. gratilla*'s diet composition typically reflects reef algal distribution, with individuals observed feeding on a variety of macroscopic algae, coralline algae, endolithic algae, and turfs. Based on these findings, the proportion of different algae groups encountered at Kaloko was applied to *T. gratilla*'s diet. In Hawai'i, *E. calamaris* has been observed feeding on coralline algae, filamentous algae, brown algae (Castro, 1971 in de Ridder and Lawrence 1982). *Echinothrix diadema* is known to forage on algae and encrusting organisms (Mortensen, 1940 in de Ridder and Lawrence 1982). *Heterocentrotus mammilatus* has been seen to graze algae from bare substrate or the coral surface (Mortensen, 1943b and Dart, 1972 in de Ridder and Lawrence 1982). Although a number of studies have looked at the palatability and consumption rates of different algal species by sea urchins in laboratory conditions, few have looked at the proportion of macrophytes in sea urchins' guts from the field in Hawai'i. It was therefore assumed that *Echinothrix* sp. and *H. mammilatus* had diets comparable to that of *T. gratilla*, but the proportion of crustose coralline algae (CCA) was increased in the latter species based on the findings above and those by Regis and Thomassin (1983). *Echinometra mathaei* is a generalized herbivore, feeding on a variety of macrophytes (McClanahan and Muthiga 2001), and preferentially on turf growing on the surface of dead coral or pavement, which explains why calcium carbonate sediments are usually the largest fraction of the gut content of *Echinometra* (Odum and Odum 1955; McClanahan and Kurtis 1991). These findings were corroborated by results in Black *et al.* (1984) and Mills *et al.* (2000) who found that inorganic material constituted 73% of gut contents.

Crown of Thorns Starfish

The crown of thorns starfish (*Acanthaster planci*) is a large, predatory asteroid, which feeds almost exclusively on scleractinian corals. It affects coral reef communities to a far greater extent than most other species of coral reef animals (Birkeland and Lucas 1990). Population outbreaks of *A. planci* throughout the Pacific have raised concern amongst both the public and scientific communities due to the resultant extensive coral mortality and subsequent long-lasting impacts on the health of the coral reef community (Pearson 1981; Moran 1986). As a consequence of the potential impacts of this corallivore, *A. planci* was included here as a separate functional group.

Based on surveys conducted at 10 m depth in 2006, both Marrack *et al.* (2009) and Weijerman *et al.* (2009) recorded a total of two individuals on all transects within Kaloko. Assuming that an individual weighs on average 466 g (Branham *et al.* 1971), and that *A. planci* only occurs in areas with > 50% coral cover, a biomass estimate of 0.117 t·km^{-2} was derived for Kaloko.

The P/B ratio was calculated based on Brey's (2001) linear regression where maximum age was set to eight years (Zann *et al.* 1990) and maximum weight was derived from Branham *et al.* (1971). This led to an estimate of 0.411 year^{-1}.

The Q/B ratio was derived based on information provided in Moran (1990), Keesing and Lucas (1992), Reyes-Bonilla and Caldero-Aguilera (1999), and Scandol (1999) and ranged between 5.969 year^{-1} and 12.065 year^{-1}. An average of 9 year^{-1} was used here.

Adult *A. planci* feed mainly on hermatypic scleractinian corals, and preferentially on acroporids (Birkeland and Lucas 1990).

Benthic Invertebrates

Uncertainty in estimates of invertebrate biomass is likely, as these groups are the least studied and the most under-represented in the coral reef literature. Very little qualitative or quantitative data are available on benthic invertebrates for the island of Hawai'i. The cryptic nature and nocturnal patterns of many benthic invertebrates, as well as the rugosity of benthic cover on coral reefs, combine to make accurate sampling of many benthic invertebrates extremely difficult (Klumpp and Pulfrich 1989; Sorokin 1993). Based on the national park's website, the majority of species are listed as uncommon to rare, with the exception of the white-spotted cucumber (*Actinopyga mauritiana*), snapping shrimp (*Alpheus crassimanus*), the helmet urchin (*Colobocentrotus atratus*), and the lightfoot crab (*Grapsus tenuicrustatus*), which are all listed as common. In surveys conducted two decades ago, Parrish *et al.* (1990) identified a number of invertebrates in the park, but listed only a few species as common: the lightfoot crab, sea cucumbers (*Holothuria* sp.), the black purse shell (*Isognomon californicum*), black nerite (*Nerita picea*) (freshwater, brackish), banded coral shrimp (*Stenopus hispidus*), nerita snail (*Theodoxus neglectus*) (freshwater, brackish), white spotted sea cucumber (*Actinopyga mauritiana*), helmet urchin, and the cushion star (*Culcita novaeguineae*). Based on Parrish *et al.* (1990), the largest and most conspicuous invertebrates at Kaloko were sea urchins (echinoids) (dealt with here as a separate group, see above), followed by sea cucumbers (especially *Actinopyga mauritiana* and *Holothuria atra*), and sea stars. The authors also reported that ophiuroids are probably abundant, but that due to their nocturnal behavior, they are probably underestimated by census data, while a few species of mollusks (e.g., *Isognomom californicum*, *Theodoxus neglectus, Nerita picea*) and crustaceans (most notably the lightfoot crab *Grapsus tenuicrustatus*) were widespread and common to abundant (as per Parrish *et al.* 1990) in the intertidal. Although not surveyed, it seems reasonable to assume that polychaetes would constitute a significant proportion of the benthic invertebrate functional group. Benthic invertebrates overall constitute an important source of food for some fish and large invertebrates (Hobson 1974). Given the absence of quantitative data for benthic invertebrates in Kaloko, Ecopath was allowed to estimate the biomass of this group for all model runs based on the assumption that EE ~0.95.

In the absence of more detailed information, the P/B and Q/B ratios were adopted from Tudman (2001) and estimated at 2.910 year^{-1} and 15.250 year^{-1} respectively.

The diet of this group was set to consist chiefly of zooplankton, phytoplankton, and detritus (Brey 2001).

Corals

In two benthic habitat studies for Kaloko, average coral cover at 10 m depth ranged between 30.70% ±8.13% and 70.10% ±6.64% at the northern end (Marrack *et al.* 2009), and 31.4% ±7.4% to 58.3% ±5.5% in the southern portion of the park (Weijerman *et al.* 2009). Both these studies targeted areas with some coral cover (Marrack *et al.* 2009; Weijerman *et al.* 2009). Wide variability in coral cover depending on location within park waters was also reported by Gibbs *et al.* (2007) who found that 1.3 km^2 of available hardbottom were covered with a minimum of 10% coral. Areas of moderately high to high coral cover (50% to 90% and 90% to 100% coral cover respectively) are found at depth and in sections of the park that are protected from high wave energy (Gibbs *et al.* 2007). Based on average coral cover from the categories outlined above, it was assumed that about 0.5 km^2 of Kaloko was covered with 100% coral.

Based on the published literature, a wide variety of means exist to calculate coral biomass from coral cover (e.g., Odum and Odum 1955; Martinez-Estalella and Alcolado 1990; Crossland *et al.* 1991; McClanahan 1995). Calculated coral biomass for Kaloko varied markedly depending on the method applied, ranging from 10.342 t·km^{-2} to 8,000 t·km^{-2}, reflecting the immense range (three orders of magnitude) in actual coral tissue biomass between different species (M. Hardt, Blue Ocean institute, pers. comm., 2008). Considering the estimates of Odum and Odum (1955) for *Lobophyllia* sp., biomass of heterotrophic tissue (polyps) and zooxanthellae in polyps were assumed to range between 0.021 g and 0.0038 g dry weight·cm^{-2} of coral skeleton. Based on coral cover calculated above, total coral biomass was estimated at 130 t·km^{-2}. Values published in Atkinson and Grigg (1984) were used for dry to wet weight conversions.

Porites spp., the dominant genus on the reef at Kaloko have massive hemispherical growth forms characterized by reproduction during a short period each year and slow growth. Given the paucity of information on population dynamics in most species of scleractinian the P/B was set to 0.14 year^{-1}, based on information gleaned from Babcock (1991), who derived life history characteristics for 3 species of corals with relatively similar life characteristics to *Porites* spp.. This value is lower than those derived by Crossland *et al.* (1991) (1.095 year^{-1}) or Arias Gonzalez *et al.* (1998) (21.68 year^{-1}), and may in part reflect large differences recorded in the turnover time for different species of corals (Chadwick-Furman *et al.* 2000; Goffredo and Chadwick-Furman 2003).

Consumption rates were found to vary widely between species, partly a reflection of location, depth, how much of a facultative consumer particular corals are, whether experiments were conducted *in situ* or in the laboratory, flow velocity, and the abundance of food particles. Hence, the Q/B of individual reefs is likely to differ markedly based on species composition. Corals possess symbiotic zooxanthellae in their polyp tissues (Odum and Odum 1955), and are therefore considered to be partly autotrophic. It was assumed here that autotrophic carbon contributed ~ 60% to animal respiration, based on findings from a study conducted on coral species that included *Porites lobata* and *Porites compressa* (Palardy *et al.* 2008), the most common species at Kaloko. *Porites lobata* feeding rates observed *in situ* (Johannes and Tepley 1974), combined with the biomass value, resulted in an estimate of Q/B equal to 5.84 year^{-1}. However, this value was reduced to 2.1 year^{-1} based on the proportion of energy the species derives from heterotrophic feeding and evidence of patchy distribution of zooplankton over reefs (Palardy *et al.* 2006).

Coral diets included chiefly zooplankton, followed by detritus and phytoplankton (e.g., Anthony 1999; Rosenfeld *et al.* 1999; Ribes *et al.* 2003; Palardy *et al.* 2008).

Octocoral

Octocorals, represented here chiefly by *Sarcothelia edmonsoni* (also commonly spelled *Sarcothelia edmondsoni*), were included as a separate group as they are locally abundant (Beets *et al.* 2006; Marrack *et al.* 2009) and their sensitivity to water quality (Fabricius 2005) make them potentially important indicators of deteriorating conditions at Kaloko. Indeed, studies on the Great Barrier Reef suggest that *Sarcothelia edmonsoni* may be more strongly affected by declining water quality than hard corals (Fabricius 2005). Results from monitoring studies show significant variability in abundance between sites within Kaloko, with average cover estimated at 3.83% (range 0.7% ± 0.7% to 7.1% ± 5%) for surveys centered around 10 m depths (Marrack *et al.* 2009), and 10.1% in a study by Beets *et al.* (2010) that included shallower transects. Based on these findings, octocoral biomass was estimated to range between 1.62 t·km^{-2} and 4.22 t·km^{-2} and set at 2.9 t·km^{-2}.

Sarcothelia edmonsoni is a zooxanthellate octocoral, unlike most species of soft corals that do not contain symbiotic dinoflagellates in their tissue and therefore rely solely on heterotrophic nutrition. Despite benefiting from photosynthetic products produced by its endosymbionts, *S. edmonsoni* may derive a significant proportion of its carbon through suspension feeding of particulate and dissolved organic matter from the surrounding environment (Fabricius *et al.* 1995; Fabricius *et al.* 1998). It was therefore assumed that heterotrophically acquired carbon contributes about 80% of animal respiration. No studies have investigated the production or consumption rate of *S. edmonsoni* and published turnover rate values range widely depending on species (Chadwick-Furman *et al.* 2000). P/B was set to 0.2 year^{-1} based on a study by Goffredo and Lasker (2008), which calculated life history parameters for an octocoral as part of an adaptive management approach to a fishery on the species.

Data presented in Sorokin (1991) and Ribes *et al.* (2003a) led to a Q/B estimate of 9.25 year^{-1}, which was reduced to 4.63 year^{-1} for the same reasons outlined for the functional group "corals" above.

Studies on tropical and Mediterranean gorgonians and soft corals have shown octocorals to capture detrital particulate organic matter (Ribes *et al.* 1999; Ribes *et al.* 2003a), small zooplankton prey (Coma *et al.* 1994; Rossi *et al.* 2004), and phytoplankton (Ribes *et al.* 1998; Picciano and Ferrier-Pages 2007). Evidence suggests that zooxanthellae-free soft corals in tropical reef environments are mainly herbivorous (Fabricius *et al.* 1995; Fabricius *et al.* 1998). In the absence of more detailed information, it was assumed that *S. edmonsoni* shows trophic opportunism with respect to sources of feeding and its diet included primarily phytoplankton, followed by detritus, and zooplankton (e.g., Orejas *et al.* 2003; Ribes *et al.* 2003; Tsounis *et al.* 2006).

Algae

As turf (≤ 1 cm canopy height or frond extension) and macroalgae (> 1 cm canopy height or frond extension) are often used as indicators for nutrient availability and grazing pressure (Littler and Littler 1984), they were kept as separate functional groups. In addition, as green turtles predominantly feed on turf algae growing on the lava bench that spans the shallow subtidal/intertidal area, a separate functional group was created to represent their forage. Crustose coralline algae (CCA) were also included as a separate group. Surveys by Marrack *et al.* (2009) and Weijerman *et al.* (2009) showed that turf cover was equal to 33.13%, CCA cover 10.46%, and macroalgal cover 0.62%; corroborating findings by Beets *et al.* (2010). Turf samples from Kaloko-Honokōhau consisted of 20 different algal genera (McDermid *et al.* 2007). Other algae included *Asparagopsis taxiformis*, *Caulerpa serrulata*, *Dictyota* spp., *Liagora* sp., *Sargassum* sp., *Turbinaria ornata*, red gelatinous algae, and some geniculate corallines. Although no alien species were recorded by Marrack *et al.* (2009), the presence of *Acanthophora spicifera* has been documented on the west coast of Hawai'i at three sites, including within Kaloko fishpond (C. Squair, University of Hawai'i, pers. comm., 2008; Smith *et al.* 2002). *Acanthophora spicifera* has not been found on the reefs of Kaloko during dedicated surveys, or incidentally during coral cover surveys (S. Beavers, pers. Comm., 2008).

No direct biomass estimates were made at Kaloko for any of the algae groups; but every effort was extended to ensure that values used were based on communities most similar to those found at Kaloko. Biomass estimates were derived based on data published by Smith *et al.* (2001) and those kindly provided by T. Sauvage (University of Hawai'i, unpublished data) from experiments conducted in 2003 and 2004 in Waikiki; and estimates of percentage cover recorded within the park for each algae group (Beets *et al.* 2010; Marrack *et al.* 2009; Weijerman *et al.* 2009). Since intertidal turf communities are often much denser, a higher biomass estimate provided by J. Smith (unpublished data) was applied to the area encompassed by this habitat. Green turtles in Kaloko concentrate their foraging activities on turf algae growing on a shallow lava bench and intertidal area in Honokōhau Bay, the surface area of which was derived based on data presented in Gibbs *et al.* (2007) (0.026 km^2). Calculations resulted in a biomass estimate for turf algae within Kaloko of 128.78 $t \cdot km^{-2}$ and 3.065 $t \cdot km^{-2}$ for turf algae restricted to the lava bench on which turtles feed. Macroalgae biomass at Kaloko was set to 22.691 $t \cdot km^{-2}$ and estimated based on data provided by T. Sauvage (unpublished data) from his experimental plots at Waikiki. CCA biomass was calculated based on Smith *et al.* (2001) and set at 37.818 $t \cdot km^{-2}$.

The P/B ratio for turf algae was estimated at 19 $year^{-1}$ based on Payri (2000) and falls within the range of values (12.5 $year^{-1}$ - 30.8 $year^{-1}$) provided by Polovina (1984), Klumpp and McKinnon (1992), Arias-González (1994), and Bozec *et al.* (2004) for coral reefs in the Pacific region. The productivity of $turf_{LB}$ was set higher (25 $year^{-1}$) as shallow dense turf is known to register higher productivity rates than deeper reef turf (T. Sauvage, pers. comm., 2008). Naturally nutrient-rich groundwater that discharges in this area probably further contributes to elevated productivity rates. P/B for CCA and macroalgae were also calculated based on Payri (2000), and set at 1.777 $year^{-1}$ and 9.824 $year^{-1}$ respectively. Where necessary, conversion rates between gC, dry mass (DM) and wet weight (WW) were taken from Atkinson and Grigg (1984).

Zooplankton

The only data available for zooplankton biomass were taken from a station 150 m outside of Honokōhau Harbor (Bienfang 1980; Bienfang 1983). In all instances, samples were dominated by copepods (Bienfang 1983; Table 2 in Hoover and Gold (2005). Zooplankton biomass (g ww) for the entire park area was derived by integrating the mean tow biomass (44.96 mg m^{-3}) over an average water column depth weighted by the surface area of each of 12 habitats, as listed in Gibbs *et al.* (2007) (27.58 m). This resulted in an estimate of 1.24 $t \cdot km^{-2}$.

A review of the literature yielded a wide range of production rate estimates for zooplankton species, based in part on the ecosystem's temperature, season, the zooplankton's size fraction, diet, and the method used to infer production. The P/B was set to 219 $year^{-1}$ based on the average of a range of production rates presented in Calbet *et al.* (2000). This value is comparable to the P/B value of 238 $year^{-1}$, which was derived from production rates of the mesozooplankton fraction found at Uvéa atoll, New Caledonia (Le Borgne *et al.* 1997). Only the mesozooplankton fraction was used for comparative purposes given the 200 μm mesh size used for zooplankton sampling at Honokōhau (Bienfang 1980).

Consumption rates for zooplankton vary depending on whether the zooplankton is mostly carnivorous or herbivorous with rates typically increasing with the herbivorous fraction of the zooplankton. Based on limited information, it was assumed here that copepods encountered in Kaloko are mostly herbivorous (Bienfang 1980; Bienfang 1983). Consumption rates presented in Calbet *et al.* (2000) were used to guide estimates and the Q/B was set at 949 year^{-1}. Our estimate falls within the range of values found in or calculated from the literature: 269.29 year^{-1} as derived by Arias-González *et al.* (1997) for the Tiahura reef sector in French Polynesia; 550 year^{-1} based on estimates presented in Frost (1972); and 1,239.905 year^{-1} for the mesozooplankton fraction for an atoll community in Uvéa, whose taxonomic configuration is similar to that at Kaloko (Le Borgne *et al.* 1997).

Phytoplankton

Phytoplankton biomass values within park waters are considered to be low, ranging from ~ 0.14 mg chl*a* m^{-3} to 0.16 mg chl*a* m^{-3} (Bienfang and Johnson 1980). Although the reason for the low biomass has been hypothesized to chiefly be attributable to control by zooplankton grazing (Oceanic Foundation 1975, in Hoover and Gold 2005), Bienfang and Johnson (1980) suggest that limited nutrient availability and other phenomena, such as hydrology, may be exerting stronger control over phytoplankton activity than zooplankton grazing. To estimate biomass the average value of measurements made in 1980 at 1.5 m and 5 m depth at the oceanic station 150 m outside of Honokōhau Harbor was used (0.1475 mg chl*a* m^{-3}). Values observed in the park between 1994 and 1996 and in 2000, at sites 100 m to 200 m offshore of Kaloko and ‘Aimakapa ponds (Brock and Kam 1997; Marine Consultants 2000 in Hoover and Gold 2005), fall within the range of the earlier studies. Following the same protocol as described above for zooplankton, phytoplankton biomass was set at 3.295 t·km^{-2}. This value is identical to that derived by Polovina (1980) for French Frigate Shoals, but substantially higher than that calculated by Arias-González *et al.* (1997) for Moorea, French Polynesia (0.32 t·km^{-2}).

Phytoplankton productivity rates were set at 325.458 year^{-1}, based on measurements made by Bienfang and Johnson (1980) outside the harbor. This value is somewhat lower than the P/B of 475 year^{-1} derived for the Great Barrier Reef (Furnas *et al.* 1990). For Uvéa atoll, New Caledonia, Le Borgne (1997) estimated P/B to range between 716 year^{-1} and 511 year^{-1}, depending on the C: Chl *a* ratio used. C: Chl *a* ratios in the literature are highly variable, e.g., 84 (Charpy and Blanchot 1998), 60 (Yahel *et al.* 1998; Barbosa *et al.* 2001), 20 to 160 (Taylor *et al.* 1997). It is likely that a higher ratio is more appropriate for Kaloko, with values as high as 200 applicable to open ocean oligotrophic environments (Gasol *et al.* 1997), and was set to 90.

All basic input parameters for the 26 groups included in the model are presented in table 1.

Model analysis, indices, and uncertainty around input data

Total trophic flows within the ecosystem in terms of consumption, production, respiration, exports and imports, and flow to detritus (t·km^{-2}·year^{-1}) were quantified. Ecological indices as obtained through Ecological Network Analysis (ENA) were then used to describe the ecosystem structure. ENA is a modeling technique used for understanding the structure and flow of material between components of an ecosystem, as modeled (Ulanowicz 1997). It is descriptive in nature and is most commonly used for evaluating food webs (Wulff *et al.* 1989; Christensen and Pauly 1993). It is integrated into Ecopath and allows for the calculation of ecosystem macro-descriptors, which quantify trophic structure, organic matter recycling, and ecosystem size and organization. These descriptors include total system throughput (T), Ascendency (A), Development Capacity (C), and the relative overhead (O/C). Throughput describes the size of a system and represents a measure of its metabolism (Christensen and Pauly 1993). Ascendency integrates both size and organization of a given system (Christensen 1995). The Development Capacity quantifies the upper limit to Ascendency whilst the system’s overhead (O) is complementary to the Ascendency and measures to which degree particular links can be considered ‘redundant’ (Heymans 2003). The O/C ratio was proposed by Heymans (2003) as an index of the resilience of the system (i.e., it can be seen as an index of the system’s ability to withstand disturbance (Ulanowicz 1997)). ENA further allows the derivation of Transfer Efficiencies (TE), summarizing the proportion of consumption that is passed up a food web. The TE is obtained by calculating the ratio between the production of a given trophic level and the preceding trophic level (Pauly and Christensen 1995). Finally, the mixed trophic impact (MTI) analysis (Ulanowicz and Puccia 1990), or ecological input-output, was run. MTI describes how any functional group impacts, directly and indirectly (i.e., both predatory and competitive interactions), all other functional groups within the food network. In other words, this analysis provides a first-order quantification of the beneficial and negative impacts of one group on another (scaled between -1 and 1). The MTI for living groups is calculated by constructing an n x n matrix, where the interactions between the impacting group (*j*) and the impacted group (*i*) is represented as follows (Christensen and Walters 2004):

$$MTI_{ji} = DC_{ji} - FC_{ij}$$

where DC_{ji} as previously defined, is the diet composition term expressing how much (*i*) contributes to the diet of predator (*j*), and FC_{ij} is a host composition term giving the proportion of the predation on (*i*) that is due to (*j*). For detritus groups, the DC_{ji} term in the MTI analysis is set to 0.

Addressing Uncertainty

Any ecosystem model realisation requires acknowledging the large amount of data required in its development, and the difficulty in quantifying the flows between the food web's individual functional groups. Functional group dynamics can be verified by fitting model data to actual population trends over time. Such time series data do not exist for Kaloko. To address model uncertainties, probability distributions for all Ecopath input parameters (including the diet compositions matrices) were entered through the 'pedigree' function (Funtowicz and Ravetz 1990) of Ecopath (Pauly *et al.* 2000). Using a Monte Carlo re-sampling routine, the 'Ecoranger' module of Ecopath draws random input variables within the confidence intervals defined for each parameter type in the pedigree tables and uses these as prior probability distributions for all input data. This approach leads to a large number of model realizations that are evaluated for their conformity to user-defined criteria as well as physiological and mass-balance constraints. The results include probability distributions for the estimated parameters along with distributions of parameters in the accepted model realizations. This routine can be run for the model overall, as pedigrees were associated with all input parameters. However, given the primary goal of this study to determine whether green turtles are at carrying capacity at Kaloko, the focus was placed on sources of uncertainty associated with: estimates of green turtle biomass, P/B and Q/B; the proportion of sea urchins' diet that was derived from turf algae growing on the nearshore lava bench ($turf_{LB}$); and variability associated with $turf_{LB}$ biomass and P/B.

RESULTS

Trophic parameters for the 26 groups of the final balanced model for Kaloko are presented in table 1 (outputs are in bold). Trophic flows between all functional groups are depicted in figure 2. Sea urchins (*Tripneustes gratilla, Echinometra mathaei, Heterocentrotus mammilatus,* and *Echinothrix* spp.) accounted for the largest proportion of total living biomass in the system (40%) (figure 3). Green turtles and reef fish groups, including 'sharks and jacks', only represented 0.2% and 5.5% of total biomass respectively (figure 3). Reef fish functional groups were dominated by herbivorous and mobile invertebrate feeding species. Not surprisingly, consumption by sea urchins had the biggest impact (45%) on available resources at Kaloko; whereas fish accounted for 14.4% and green turtles 0.2% of total consumption. Total fisheries catches represented less than 1 % of the total fish biomass (table 1). 'Sharks and jacks' were caught in larger quantity compared with their relatively low biomass in the assemblage. Mean trophic level of the total fisheries catch was 2.59 (table 2).

Ecotrophic efficiency (EE) values (the proportion of the production used within the system) were lowest for some of the highest trophic levels, including 'spinner dolphins', 'monk seals', and 'sea birds', as well as for 'crown of thorns starfish', 'hawksbill turtles', 'green turtles', 'urchins', and 'corals'. For the first three groups, this valuation is due to these species deriving a significant proportion of their food from outside park waters. They were included in the model chiefly for purposes of representation (i.e., to acknowledge that these species occur in the park, and may at some point in the future suffer from indirect effects of park development, even if they do not feed exclusively or primarily in park waters). For the five other groups, the low EE values are a result of low predation and fishing pressure being exerted on these species. Fish groups, overall, also had relatively low EE values, with higher values registered by those species pools that were subject to higher fishing mortality. This valuation suggests that the system generates a reasonable amount of surplus secondary production. Indeed, the largest component of the mortality coefficients within the system at Kaloko was due to predation mortalities, with the exception of 'sharks and jacks' for which the fishing mortality rate was greater than predation mortality explained within the system. In contrast, most of the production by the macro- and turf algal groups, 'zooplankton', 'benthic invertebrates', and 'phytoplankton' was accounted for through consumption by other trophic groups within the model (EE > 90%). In other words, urchins, herbivorous fish, and green turtles maintained all algae at Kaloko in a cropped state. Reef building corals, octocorals, benthic invertebrates and zooplanktivorous fish were the main predators of zooplankton, whilst zooplankton consumed most of the phytoplankton production in the system. Benthic invertebrates were predated upon mostly by MIF reef fish and species within the benthic invertebrate group itself.

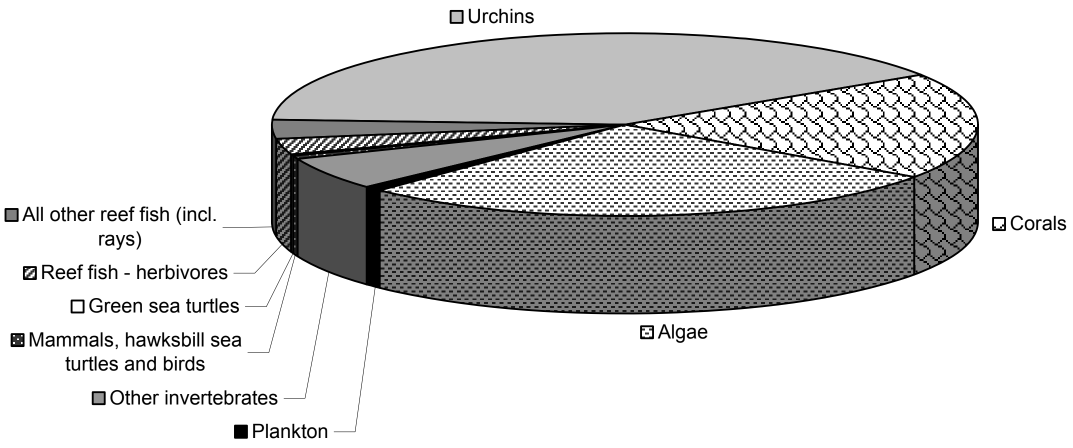

Figure 3: Proportions (%), in terms of biomass ($t \cdot km^{-2}$) of aggregated functional groups at Kaloko.

Throughput (total flows) values for each functional group highlighted the importance of turf algae, zooplankton, phytoplankton and sea urchins in system structure. The high EEs attained for all algal groups indicated that the system was at carrying capacity with respect to grazing, including for green turtles. The primary producers' high EEs were also reflected in the low production/respiration ratio of 1.12 for the system overall (table 2).

Table 2: Summary of outputs from the Ecological Network Analysis

Sum of all consumption	5,332.03	t/km²/year
Sum of all exports	520.07	t/km²/year
Sum of all respiratory flows	3,477.31	t/km²/year
Sum of all flows into detritus	1,700.15	t/km²/year
Total system throughput	11,030.00	t/km²/year
Calculated total net primary production	3,895.09	t/km²/year
Total primary production/total respiration	1.12	
Total biomass (excluding detritus)	699.53	t/km²
Total catches	0.35	t/km²/year
Mean trophic level of the catch	2.59	
Throughput cycled (excluding detritus)	54.52	t/km²/year
Finn's cycling index	6.13	% of total throughput
Ascendency	31.50	%
Relative overhead (O/C)	68.50	%

Focusing on green turtles, urchins, and herbivorous reef fish in the system only, the Mixed Trophic Impact (MTI) routine underlined the competition for resources both within and among the three groups (figure 4). Sea urchins were responsible for the largest among-group effect, impacting negatively on both herbivorous reef fish and green turtles, and overall had the largest impact on algal and detritus resources (not shown). Given green turtles' feeding preference on $turf_{LB}$, they were the group most impacted by changes in turf algae.

When accounting for the uncertainty around parameters affecting productivity and consumption of $turf_{LB}$, EE values of $turf_{LB}$ in successfully balanced model runs ranged between 0.416 and 0.998.

The mean Transfer efficiency (TE) in the ecosystem as a whole was 4.6%, with a value of 4.5% for flows originating from primary producers and 4.7% from the detritus. This was primarily due to poor transfer efficiencies at the higher trophic levels. This low efficiency was underlined by consumption dominating total system throughput for the lower trophic levels whereas respiration and flow to detritus dominated the higher trophic levels in the model (figure 5). This result would be expected in a system with low biomasses at the highest trophic levels. Some upper trophic level species such as trevally (also locally known as 'ulua' or 'jacks') are highly vagile. Thus, although they might not be heavily fished directly in park waters, their abundance may still be depressed due to high fishing pressure on this group along the remainder of the Kona Coast. Ascendancy was estimated at 31.5% of capacity and relative overhead was 68.5% (table 2), 46% of which was attributable to internal flows indicating that the system at Kaloko contains a number of 'redundant' trophic linkages. These observations are consistent with a system exhibiting relatively high resilience to perturbation with respect to energy flows, or a high system stability sensu Odum (1971).

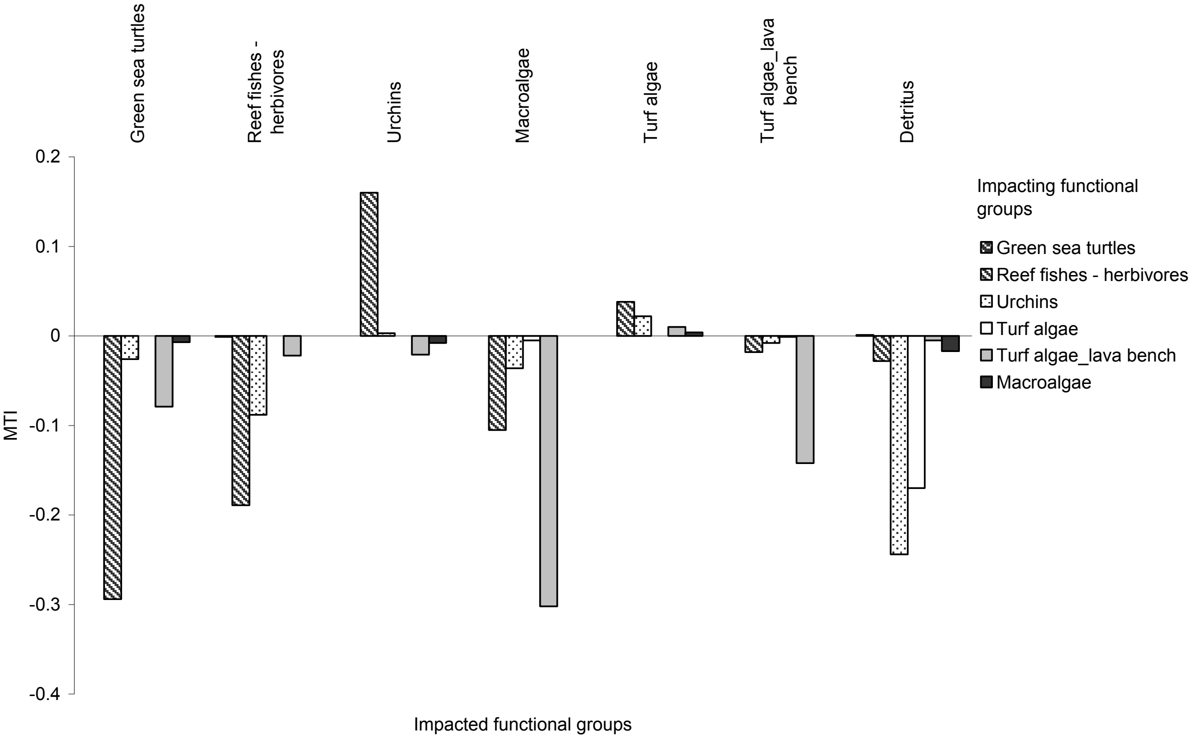

Figure 4: Mixed trophic impact analysis for herbivores at KAHO. Impacts of increases in the biomass of a particular group (impacting) on another (impacted), resulting in an increase in the latter's biomass, are recorded as a positive on the y-axis. Impacts resulting in a decline of the impacted group are recorded as a negative value. Group names along the x-axis represent the impacting groups, whilst the legend provides color codes for the impacted groups.

Net primary productivity was 3,895 t·km^{-2}·year^{-1} and was accompanied by a high flow to the detritus pool (table 2). Turf algae (including turf$_{LB}$) and phytoplankton accounted for 57% and 24% of total production in the system, or 65% and 27% of total primary production respectively. Sea urchins (38%) were the major contributors to the detrital pool, followed by by zooplankton, while the combined fish groups (mainly herbivores) contributed 11% of all flows to the detritus. The ratio between primary production and respiration (PP/R) indicates that the system is at a low developmental stage sensu Odum (1969; 1971). This finding was corroborated by the low Finn's cycling index, showing that only a small fraction of the throughput (including detritus) gets recycled (6%; table 2). The proportion of flows originating from the detritus was 0.27%.

The overall pedigree index of the model (0.539) was relatively high in comparison to 50 previously constructed models for which pedigree values ranged between 0.164 and 0.676 (Morissette 2007).

DISCUSSION

Description of the Kaloko-Honokōhau System

Quantitative descriptions of the flux of matter and energy can provide significant insights into the fundamental structure of ecosystems. The Kaloko system is dominated by primary production (PP), 27% of which is contributed by phytoplankton and 65% by algal turfs, which is slightly lower than other published estimates for primary producers in tropical systems (e.g., Wanders 1976; Adey and Steneck 1985; Adey and Gotmiller 1987). The trophic networks at Kaloko were dominated by grazing, with herbivores accounting for 43% of all living biomass within the system (figure 3), of which 93% was sea urchins. This grazer dominance was further highlighted by the high ecotrophic efficiencies achieved for the main PP functional groups, including phytoplankton. Results from rapid assessment surveys throughout the state confirm that sea urchins in particular, and herbivorous fish, are common on reefs in Hawai'i (Rodgers *et al.* 2004). In contrast, relatively low EEs of higher trophic functional groups indicate that the foraging activities of herbivores are not limited by predation pressure, as demonstrated by our analysis of total system throughput (figure 5). Indeed, few predators commonly occur in the park, and fewer still have been observed feeding in the park. Therefore, as highlighted by the model's average TE of 4.6%, much lower than the mean of 10% obtained for various other ecosystems (Christensen and Pauly 1993), only a small proportion of production is being transferred up the food chain. Comparison between two sets of underwater visual census data (E. Brown and NPS, unpublished data) showed a 5-fold increase in piscivore biomass between 2005 and 2007. This inter-annual differences may have been due to real differences between the two datasets, possibly reflecting the restrictions on gillnetting in park waters implemented in August 2005. Differences in species biomass and composition may also reflect either variability in survey accuracy due to some species displaying vagile (e.g., *Caranx melampygus*) or cryptic behavior (e.g., *Gymnothorax flavimarginatus*, *Gymnothorax meleagris*, *Cephalopholis argus*), or seasonal changes (Friedlander and Parrish 1998; Vitousek *et al.* 2009) as the 2005 and 2007 datasets were collected in April and October respectively. Future surveys should therefore focus on good intra-annual coverage to provide data that are representative of, and integrate, seasonal variation.

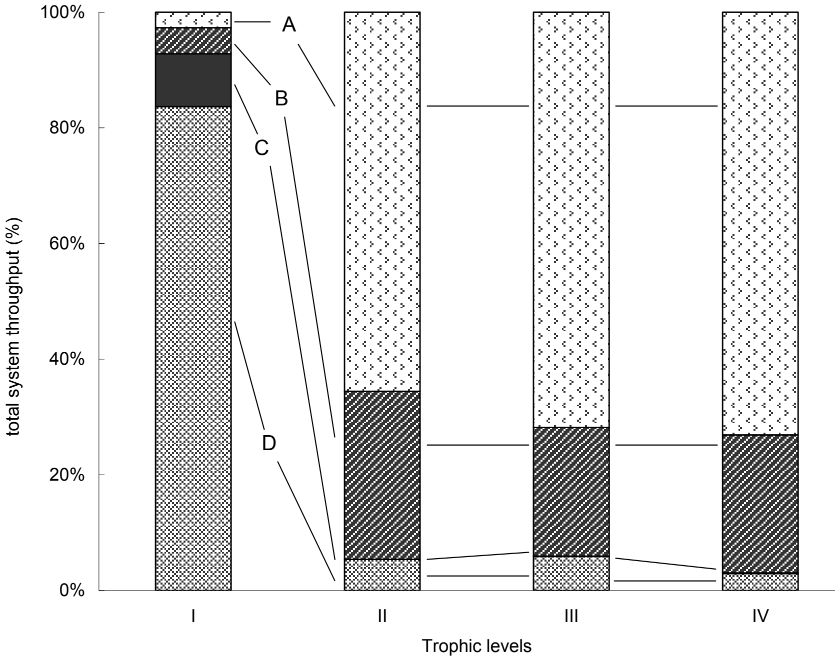

Figure 5: Fate of total system throughput (A = Respiration, B = Flow to detritus, C = Export, D = Consumption by predator) in percentage-per-integer trophic level.

Phytoplankton and zooplankton had some of the highest EEs. The waters around Hawai'i are generally oligotrophic (Bienfang *et al.* 2009), and consequently low biomass of phytoplankton and zooplankton groups is to be expected. Reef environments along the Kona coast are close to the deep slope of the Pacific and subject to strong wave action and currents along the shore (Presto *et al.* 2007). Therefore, it was assumed that zooplanktivores on the reef actually derive a substantial portion of their diet from open-ocean plankton. A further assumption was made: that ocean plankton also contributes to the energy intake of benthic invertebrate feeders and other functional groups that rely on plankton for a portion of their diet. Experiments should be conducted to ascertain, quantitatively, the proportion of ocean plankton in the diet of reef organisms at Kaloko, or other similar systems in Hawai'i.

At 42.54 t·km^{-2}, the model's benthic invertberate (excluding sea urchins) biomass was similar to estimates provided for models in Raja Ampat, Indonesia (51.68 t·km^{-2}; Ainsworth *et al.* 2007), and GBR, Australia (61.41 t·km^{-2}; Tudman 2001), but substantially lower than biomass estimates for the Moorea barrier reef and fringing reefs, French Polynesia (B = 198.26 t·km^{-2} (Arias-González 1994) and 322.8 t·km^{-2} (Arias-González *et al.* 1997) respectively). Few studies have investigated the composition of benthic invertebrates on reefs, yet they are an important prey for certain groups of reef fish (e.g., Hobson 1974), and can represent an important fishery (Friedlander and Parrish 1997). Given that benthic invertebrates accounted for 6% of total system biomass, species composition and their relative contribution to total group biomass of the invertebrate community at Kaloko should be determined.

Sea urchin densities at Kaloko (~ 5 individual per m^{-2} for *E. mathaei* and < 1 individual per m^{-2} for all other species) were comparable to sea urchin densities recorded on reefs throughout the state of Hawai'i (Rodgers *et al.* 2004) and similar to, or lower than, those reported from other locations (e.g., up to 5 to 6.8 individuals per m^{-2} (chiefly *E. mathaei* and *T. gratilla*) at La Réunion (Naim *et al.* 1997) and 2 to 4 individuals per m^{-2} (*Echinometra* sp.) in Fiji (Appana and Vuki 2006). Current sea urchin densities at Kaloko are also similar to those recorded in a study conducted in the 1970s (Ebert 1971). These similarities suggest that high urchin densities are natural and do not represent a release from predation pressure due to increased fishing pressure in the last 30 years, as noted in a number of locations along the coast of Kenya (Muthiga and McClanahan 1987; McClanahan 1998).

Given sea urchins' primary role in maintaining algae closely cropped on the reef and therefore their contribution to ecosystem resilience, future survey efforts should focus on obtaining more detailed data for urchin species, including:

1. Biomass for all reef zones - It is important to note that the sea urchin biomass was derived from survey data collected at randomly selected sites of relatively high coral cover at 10 m depth (Marrack *et al.* 2009; Weijerman *et al.* 2009), thought to be representative of sea urchin abundances throughout the park on similar hard bottom composition (M. Weijerman pers. comm., 2008). Complementary macroinvertebrate-focused surveys recording test size for individuals of the different sea urchin species recorded along all transects, with surveys conducted at all depths, would considerably help refine values used here. Different sized sea urchins from all species should be selected and a species-specific length-mass relationship established. Surveys should also ensure to cover both subtidal and intertidal zones as urchin community structure can differ substantially between them (Ebert 1971). For example, the shingle urchin (*Colobocentrotus atratus*) was recorded as one of the most common herbivores in the intertidal habitat in 1990 (Parrish *et al.* 1990). No data for this species were available for inclusion here as they were not targeted by recent surveys. Moreover, other studies have reported sea urchins to be patchily distributed and therefore, the averages used here and extrapolated to the entire hardbottom reef area (with ≤10% coral cover) may overestimate (or underestimate) actual sea urchin abundance;

2. P/B in the wild;

3. Q/B in the wild – most of the available data on consumption rates are confounded by the use of different methods for estimating (i) gut turnover (some echinoids feed only during the night, whilst other species eat continuously through 24h); and (ii) feeding rates in the field versus laboratory conditions where individuals are fed ad libitum. Additional variation in published information may stem from how individual researchers measure wet weight biomass of different urchin species. Depending on time of the day and state of gut evacuation, for example, mass of individual sea urchins may vary considerably which in turn may impact consumption rate calculations (Carreiro-Silva and McClanahan 2001); and

4. Dietary preferences in the different habitat zones based on abundance of food items – Surveys on reefs in Hawai'i indicate that certain algae species seem to be favored over others (Birkeland 1989; Stimson *et al.* 2007). In particular, attention should be paid to the proportion of turf algae to macroalgae consumed by sea urchins. Surveys should be conducted seasonally and include night-dives as published evidence indicates that echinoid species differ in foraging behaviors, with some feeding both day and night, while others are nocturnal (Vaitilingon *et al.* 2003). Note that some species are known to fill a large proportion of their gut with reef framework material ($CaCo_3$) (e.g., *Echinothrix* sp. and *E. mathaei*) (Bak 1990; Mills *et al.* 2000; Carreiro-Silva and McClanahan

2001). However, as sea urchins do not derive energy from this material, this impact is not considered under the current modeling scenario.

Turtles at Carrying Capacity

Green turtles are at carrying capacity at Kaloko - based on (i) their biomass estimates and consumption rates, (ii) estimates of turf_{LB} as well as the algae's primary production rates, and (iii) the high degree to which sea urchins feed on the turtles' main food resource. Balanced model outputs under Ecoranger, taking into account the uncertainty surrounding these input parameters, showed that the EE of turf_{LB} could range between 0.416 and 0.998. Specifically, it reflects the wide range in estimates for biomass and mass-specific productivity rates found in the published literature for turf algae. For example, biomass was found to vary between 230 $g{\cdot}m^{-2}$ (T. Sauvage pers. comm., 2008) and 600 $g{\cdot}m^{-2}$ (Smith *et al.* 2001) in Hawai'i alone, 78 $g{\cdot}m^{-2}$ in the Solomon Islands (Albert *et al.* 2008), and 850 $g{\cdot}m^{-2}$ in the Caribbean (Bruggemann *et al.* 1994). Even greater ranges in productivity have been recorded for the different algal groups that constitute 'turf', particularly according to depth and seasonal cycles (Payri 2000). An evaluation of algal turf productivity and consumption rates by green turtles at Kaloko would help refine the estimates presented here.

Results from the MTI analysis clearly highlighted the strong competition for the same resource between urchins, herbivorous reef fish, and green turtles. Grazing pressure exerted by herbivorous fish does not occur uniformly on a reef, but rather may be reduced in places where reef structure affords little refuge from predation (Lewis 1986). This may not be a significant factor at Kaloko where overall predation pressure is limited due to the low abundance of piscivores. Foraging efficiency may also be reduced on shallower portions of the reef due to relative high wave intensity and potential exposure of animals when water levels are low. It was therefore assumed that grazing by fish at Kaloko chiefly occurred on reef turf algae rather than turf_{LB} specifically. Recent evidence from the South Pacific demonstrates that few of the species previously classified as herbivorous are indeed exclusively herbivorous (Choat *et al.* 2002; Cvitanovic *et al.* 2007). Many appear to predominantly feed on detritus instead of algae, only incidentally removing turf from the reef in the process (Crossman *et al.* 2001; Crossman *et al.* 2005). Much of the energy derived from plant material may therefore reach 'grazing' consumers only indirectly, through detrital pathways. Data on the extent of algae removed but not consumed are needed to correct the current assumption that all algal material removed by herbivorous fish was ingested. Interestingly, these observations on reef herbivores stand in stark contrast to new findings for seagrass ecosystems, which show that despite the long held assumption that most seagrass production entered the foodweb via the detrital pathway (Duarte and Cebrián 1996; Duarte and Chiscano 1999), most of it is consumed directly by herbivores (Valentine and Heck 1999; Kirsch *et al.* 2002; Valentine and Duffy 2006). MTI results reflected resource competition between green turtles and fish primarily for macroalgae, which appeared 'magnified' as macroalgae biomass overall in the park is low. As sea urchins occur in the shallows (M. Weijerman pers. comm., 2008, L. Marrack, U.S. National Park Service, pers. comm., 2008), probably emerging at night to feed (Mills *et al.* 2000, Vaitilongon *et al.* 2003), a small proportion of turf_{LB} was included in the echinoids' diet matrix. Quantification in the field of this overlap and the extent to which relative densities of the three herbivore functional groups may change with time would help refine carrying capacity estimates for green turtles. Clarification of the extent to which urchins feed on turf_{LB} also has implications for their role in maintaining low algal biomass levels in the face of increased nutrient input due to urban development activities around the park (see below).

Observations that Kaloko turtles appear unusually 'skinny' (Kubis *et al.* 2008) and exhibit low growth rates (Balazs and Chaloupka 2004) compared to turtles at other Hawaiian foraging grounds off Maui and Oahu, support input parameters within the range used in the model (table 1). A key difference between individual Hawaiian foraging sites that may be contributing toward differences in observed growth rates is that green turtles at Kaloko forage on turf, the dominant algae on the central west coast of Hawai'i, whereas other foraging grounds have macroalgae available as forage. Recent observations have indicated a behavioral shift in the turtles' foraging patterns. Fewer turtles are utilizing the area in the summer months than they did up to about 2006 and they appear to be moving around more (S. Beavers, unpublished data). More interactions with humans as a result of increased visitor use in recent years partly may be responsible for greater movement of green turtles than previously observed (S. Beavers, unpublished data). However, greater turtle movement away from Kaloko further strengthens the case for carrying capacity having been reached at Kaloko because of limited available forage and poor forage quality. Indeed, nutritional composition analysis of turf samples collected from Kaloko indicate that ash content was higher, and mean protein and crude lipid content lower, than most marine plants consumed by green turtles at other foraging sites around the Hawaiian archipelago (McDermid *et al.* 2007). The year-round availability of turf algae at Kaloko partly may compensate its nutritional quality (McDermid *et al.* 2007). Interestingly, although *A. spicifera*, a non-native species, represents a main component of green turtle diets at other locations in Hawaiʻi (Russell and Balazs 2009), and is absent at Kaloko, the species does not show any notably high nutritional values. Green turtles at those sites may thus simply select it due to its extreme abundance throughout much of the range of the Hawaiian green turtle or because of its succulence, texture, or taste compared to other available species.

Turf algae growing on the lava bench close to shore and intertidal area was included in the model as a separate functional group, as resident turtles at Kaloko have typically been seen to concentrate their foraging to this portion of the park (G. Balazs and S. Beavers, pers. comm. 2009). Such focused foraging behavior may occur for three reasons. Firstly, by focusing their feeding activities to shallow portions of the reef, individuals exert less effort foraging as the lava-bench supports a dense algal mat that is highly productive from repeated grazing and can grow unrestricted by space competition with live coral. Were turtles to forage on deeper sections of the reef, for a similar intake of algae, animals would have to roam over wider areas and pick algae from in an around coral heads, resulting in greater energy expenditure. More energy would also have to be expended by animals in having to come to the surface to breathe. Results, which were corroborated by local observations of turf algae throughout the park being closely cropped (F. Parrish pers. comm., 2008), indicated that the system was also close to carrying capacity for overall turf algae, making foraging behavior by green turtles in deeper reef sections even less energy efficient. 'True' carrying capacity of turf algae on the reef may actually be realized at lower EE values, because where turf algae are laden with sediment, much of the algae may effectively not be available to grazers. Secondly, green turtles may prefer to forage on the lava bench because of the protection afforded by the shallows against predation by tiger sharks. Sharks are regularly sighted at Kaloko (e.g., see www.state.hi.us/dnlr/chairpio/HtmlNR/01-46.htm and http://starbulletin.com/2005/07/01/news/index5.html) and a log of necropsies performed on turtles at Kaloko indicates that shark attacks were responsible for the death of 4 turtles since 1992 (obviously attacks that resulted in the ingestion of turtles by sharks cannot be monitored) (G. Balazs, pers.comm., 2009). Thus, the distribution of turtles, and the algae they consume, may be affected by differential vulnerability of green turtles to shark predation in different habitats (Heithaus *et al.* 2002, 2006). Nutritionally profitable microhabitats at Kaloko also appear to be low risk from a predation perspective. Lastly, the repeatedly grazed turf$_{LB}$ may also be more palatable to green turtles than algae growing on deeper sections of the reef. The area where turtles aggregate to feed is located close to Aiopio Fishtrap, an area of considerable groundwater discharge (Johnson *et al.* 2008). As groundwater is the only conduit for nutrients into the coastal zone, the nutritional content of algae in this specific location may be significantly different from algae on the remainder of the reef.

Potential Threats Due to Urban Development

On many coral reefs near human population centers or adjacent to coastal strips subject to urban expansion projects, benthic community composition has shifted from coral dominance to macroalgal dominance (Hughes 1994; Hunter and Evans 1995; McClanahan and Mangi 2001). These shifts, often termed 'phase shifts' (Done 1992), have been attributed to increased anthropogenic nutrient input (e.g., Lapointe 1997) and to reductions in the abundance of herbivores (e.g., Hay 1984). Studies investigating changes in grazing intensity at sites that have undergone such phase shifts (e.g., Kāneʻohe Bay, Hawaiʻi), have focused primarily on the role of herbivorous reef fish, and to a lesser extent small, often invertebrate, herbivores (Cheroske *et al.* 2000) and sea urchins (Hunter and Evans 1995, Stimson *et al.* 2001, Smith *et al.* 2008). As results clearly demonstrate, future studies need to explicitly consider green turtles because of their important role as herbivores. Their consumption of non-native algae, including *Gracilaria salicornia* (Russell and Balazs 2009), abundant at a number of locations across Hawaiʻi, including Kāneʻohe Bay, further highlights their role in promoting reef resilience.

Ongoing and planned urban development activities and associated population growth around Kaloko will likely have significant and diverse impacts to the condition of the nearby reefs. Expected impacts include: (i) a reduction in groundwater discharge quality (i.e., increased nutrient loading), which could lead to increased macroalgal growth and subsequently a deterioration in the health of corals (e.g., Fabricius 2005; Smith and Smith 2006), particularly if combined with a reduction in the urchin population; and (ii) an increase in fishing pressure and a resulting decrease in the herbivore fish population, which could lead to an increase abundance of macroalgae on the reef (Stimson *et al.* 2001; Williams *et al.* 2007).

One of the goals of assembling all available data and information into an ecosystem model was to provide a 'current condition' snapshot of trophic relationships prior to major urban development around Kaloko. Investigating the potential impacts of such developments on Kaloko's ecosystem structure and function goes beyond the remit of this study. However, based on findings, some key points emerge that should be taken into account if dynamic simulations of various 'impact scenarios' are run in the future.

Increased nutrient input and higher fishing pressure may lead to an increase in the proportion of macroalgal cover at Kaloko and potential forage for resident herbivores. In 2008, the NPS initiated a long-term marine water quality monitoring program (quarterly sampling), which includes optical chlorophyll sampling (S. Beavers, pers. comm., 2009). Additionally, plans are underway through a partnership between the NPS and the US Geological Survey to use stable isotope tracers to identify sources of nutrient inputs to park groundwater. The NPS, in partnership with the University of Hawai'i at Hilo, recently also initiated a pilot fisheries harvest monitoring program to identify and quantify fishing pressure within the park (S. Beavers, pers. comm., 2009); this should be a long-term initiative. Nutrient levels and fisheries' catch time series in conjunction with regular monitoring of algal cover within the different habitats at Kaloko, and the Ecopath model developed herein, may help to determine the impacts of such changes at the ecosystem level. Based on the model, the following responses to two scenarios can be expected:

(i) Increased nutrient delivery to the reef system without changes in fishing pressure. Under conditions of nutrient enrichment and intense herbivory, algal productivity may be high while biomass remains low (Hatcher and Larkum 1983). Results demonstrate that current rates of herbivory, sea urchins, fish, and green turtles maintain all algal groups closely cropped and may therefore be able to consume increases in algal production. This grazing disturbance in turn limits the establishment of macroalgae (Lewis 1986, Williams *et al.* 2001, Paddack *et al.* 2006), implying that the current system is relatively resilient to change (as indicated by Kaloko's O/C ratio). Indeed, it is the synergy of these 3 herbivorous functional groups that makes Kaloko an interesting case study. The 'redundancy' in herbivory at Kaloko stands in contrast to areas of the Caribbean, where sea urchin biomass remains low 20 years after the region-wide loss of the key echinoid herbivore to disease (Mumby *et al.* 2006b), and where, due to high fishing pressure, the ability of herbivorous fish to maintain a high proportion of reef area free of macroalgae may be limited. Some evidence suggests that even robust herbivorous reef fish populations may be capable of maintaining only 50 to 65% of the substratum in a cropped state (Williams *et al.* 2001). Although herbivorous fish may be capable of increasing their grazing rates and/or population sizes in response to higher algal production, evidence for this in the published literature is limited (McClanahan *et al.* 1999, Williams *et al.* 2001, Garpe *et al.* 2006). Moreover, herbivorous reef fish, with the exception of *Naso* spp. (Choat et al. 2002), all prefer turf algae over other algal resources, and frequently avoid macroalgae (Bellwood and Choat 1990, Bruggemann *et al.* 1994). Green turtles and sea urchins, on the other hand, commonly feed on macroalgae, highlighting their respective roles in maintaining reef resilience (Nystrom and Folke 2001; Nystrom 2006).

(ii) Increased nutrient delivery to the reef system with increase in fishing pressure. Herbivorous fish and sea urchins play different and complementary roles in maintaining low algal cover on reefs in the face of disturbance (e.g., Morrison 1988). Under a scenario of higher fishing pressure, model parameterization indicates that sea urchin abundance may increase as a direct response to more abundant forage on the reef and reduced predation pressure due to harvesting of the urchins' predators. Sea urchins, when abundant, can have a considerable impact on benthic ecology. Healthy populations of sea urchins have been associated with reductions in macroalgal cover and increased coral recruitment (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006). Typically, sea urchins will consume a greater diversity of algae than herbivorous reef fish and, as such, they will be more effective than the latter at controlling algal growth in the event of increased nutrient levels. Alternatively, as some species of echinoids can remove a large amount of calcium carbonate while foraging (Hutchings 1986, Carreiro-Silva and McClanahan 2001), an overabundance of sea urchins can lead to rapid erosion of the reef framework (McClanahan and Kurtis 1991, Bak 1994, Mapstone et al. 2007). For example, *Echinothrix diadema* and *Echinometra mathaei* typically erode 20% of the calcium carbonate accreted (Carreiro-Silva and McClanahan 2001). However, the relative contributions of grazing and bioerosion are species-dependent. Tripneustes gratilla predominantly browses on macroalgae, suggesting that this species would have less of an impact on the reef framework (Mills *et al.* 2000). Currently, sea urchin densities are greatest in the shallows, while reef fish dominate grazing processes at depth (F. Parrish and M. Weijermann pers. comm., 2009). Higher fishing pressure may reduce fish grazing intensity on deeper reef sections. In response to reduced predation, competition, and increased forage availability, sea urchins could increase in abundance at greater depths. Similarly, green turtles may also displace some of their foraging activities to deeper reef areas to take advantage of increased algal biomass (i.e., profitable, high-risk microhabitat sensu Heithaus *et al.* 2007). Increases in algal biomass would further be exacerbated if mixing carries nutrients to those deeper sections of reef.

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APPENDIX 1: SPECIES INCLUDED UNDER EACH REEF FISH FUNCTIONAL GROUP AND THAT WERE RECORDED DURING THE 2005 UNDERWATER VISUAL CENSUS SURVEYS (BEETS *ET AL.* 2006)

FUNCTIONAL GROUP	**2005 SURVEY DATA**
CORALIVORES	*Arothron meleagris*
	Cantherhines dumerilii
	Chaetodon multicinctus
	Chaetodon ornatissimus
	Chaetodon quadrimaculatus
	Plectroglyphidodon johnstonianus
DETRITIVORES	*Ctenochaetus hawaiiensis*
	Ctenochaetus strigosus
HERBIVORES	*Abudefduf sordidus*
	Acanthurus blochii
	Acanthurus dussumieri
	Acanthurus leucopareius
	Acanthurus nigrofuscus
	Acanthurus nigroris
	Acanthurus olivaceus
	Acanthurus triostegus
	Calotomus carolinus
	Canthigaster jactator
	Cantherhines sandwichiensis
	Centropyge fisheri
	Centropyge potteri
	Chlorurus sordidus
	Cirripectes vanderbilti
	Melichthys niger
	Melichthys vidua
	Naso lituratus
	Naso unicornis
	Scarus psittacus
	Scarus rubroviolaceus
	Stegastes fasciolatus
	Zebrasoma flavescens
	Zebrasoma veliferum
MOBILE INVERTEBRATE FEEDERS	*Bodianus bilunulatus*
	Coris gaimard
	Coris venusta
	Diodon hystrix
	Echidna nebulosa
	Forcipiger longirostris
	Gomphosus varius
	Halichoeres ornatissimus
	Lutjanus kasmira
	Malacanthus brevirostris
	Macropharyngodon geoffroy
	Monotaxis grandoculis
	Mulloidichthys flavolineatus
	Paracirrhites arcatus
	Parupeneus bifasciatus
	Parupeneus multifasciatus
	Parupeneus pleurostigma

MOBILE INVERTEBRATE FEEDERS (CONT’D)	*Plectroglyphidodon imparipennis*
	Pseudojuloides cerasinus
	Pseudocheilinus evanidus
	Pseudocheilinus octotaenia
	Pseudocheilinus tetrataenia
	Rhinecanthus aculeatus
	Rhinecanthus rectangulus
	Sebastapistes coniorta
	Stethojulis balteata
	Sufflamen bursa
	Sufflamen fraenatus
	Thalassoma duperrey
	Thalassoma trilobatum
	Xyrichtys aneitensis
PISCIVORES	*Aphareus furca*
	Aulostomus chinensis
	Cephalopholis argus
	Fistularia commersonii
	Gymnothorax flavimarginatus
	Labroides phthirophagus
	Oxycheilinus unifasciatus
	Parupeneus cyclostomus
	Paracirrhites forsteri
	Plagiotremus ewaensis
	Plagiotremus goslinei
SESSILE INVERTEBRATE FEEDERS	*Chaetodon auriga*
	Chaetodon lineolatus
	Chaetodon lunula
	Forcipiger flavissimus
	Ostracion meleagris
	Zanclus cornutus
ZOOPLANKTIVORES	*Abudefduf abdominalis*
	Abudefduf vaigiensis
	Acanthurus thompsoni
	Chromis agilis
	Chromis hanui
	Chaetodon miliaris
	Chromis vanderbilti
	Chromis verater
	Dascyllus albisella
	Heniochus diphreutes
	Hemitaurichthys thompsoni
	Myripristis berndti
	Myripristis kuntee
	Naso hexacanthus
	Xanthichthys auromarginatus

THE ANTARCTIC PENINSULA MARINE ECOSYSTEM MODEL AND SIMULATIONS: 1978-PRESENT[8]

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ABSTRACT

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. Through the use of environmental drivers; sea surface temperature, the southern oscillation index and ice cover used as forcing and mediation functions, past trends were able to be captured within the model. Krill (*Euphausia superba*), the central link in the food web was included in four life stages with different environmental factors affecting each life stage in the model. Declines in krill and increases in salps (*Salpa thompsoni*) were re-created based on past data trends. While the southern oscillation index aligned with past salp trends better, using sea surface temperature to drive warmer water species provided an overall better fit to the model, with a lower sum of squares value. Large increases in penguin colonies were unable to be captured by the model indicating they are driven by forces outside the model capability, with more recent data supporting this theory. Overall, past 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.

INTRODUCTION

The Antarctic Peninsula is located on the northernmost part of the Antarctic continent, with the tip extending outside of the Antarctic Circle. Because of its location, temperatures are generally milder here than the rest of the continent. Yet, 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), with the warming trend considerably higher than mean global values (Anisimov *et al.* 2001; Hansen *et al.* 2006). Polar areas are a major concern for environmentalists as warming will affect ice dynamics, an important feature of high latitude ecosystems. In areas of the Arctic, it is believed that a doubling in CO_2 could lead to a 60% reduction in sea ice (Anisimov *et al.* 2001).

Since the 1980s there have been many changes to the peninsula region, with the collapse of ice shelves as a result of warming in the area. In addition to the breakup of five ice shelves, warming temperatures have caused glacial retreat of some 244 glaciers over the last 50 years (Doake and Vaughan 1991) indicating a large warming trend. Antarctic ecosystems have a high number of endemic species (Kock 1992), so their fate in relation to climate change could be serious. Pole ward migration is not an option for this region as land barriers prevent movement to higher latitudes. This is of major concern to the ecology of the region, as many species are adapted to the cold temperatures and will be unable to move or adapt to the new thermal ranges.

Different species of seals, whales, penguins and other birds spend varying amounts of time in this region, but are all present in the summer months when productivity is highest. All of these top predators are dependent upon Antarctic krill (*Euphausia superba*) at some point during the year, generally 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.* 1998; Brierley and Reid 1999;

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Tamura and Konishi 2005). Krill attract 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. In addition, krill from the Antarctic Peninsula are believed to be a source to krill populations around the Scotia Sea (Atkinson *et al.* 2004), suggesting that krill are important not only in its immediate area, but to surrounding areas, and also to predators at those locations (Hofmann *et al.* 1998; Brierley *et al.* 1999; Atkinson *et al.* 2004). Therefore changes to the krill population at the peninsula have the implication to impact predators locally and across the Scotia Sea.

The 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 (primarily: *Phaeocystis antarctica, Fragilariopsis cylindrus,* and *Fragilariopsis curta*) are an important food source for over-wintering krill and recruits in the spring, when more 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, decreasing protection, and making them more vulnerable to predators.

Although krill are very important in the ecosystem, they can be outcompeted in certain years by salps (*Salpa thompsoni*) (Loeb *et al.* 1997; Atkinson *et al.* 2004), gelatinous tunicates whose abundance is believed to be determined by lower sea ice extent and productivity (Nicol 2006). In cooler years there is an increased abundance of sea ice, and therefore ice algae available over the winter for krill to graze on, while in warmer years there is less ice algae available throughout winter, and smaller spring blooms lead to poor krill 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 the surface and rerouting it to the benthos as faecal pellets (Dubischar *et al.* 2006), while krill are consumed by predators 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).

Krill are also harvested commercially from the region with a large majority of catches in the Southern Ocean obtained from the Antarctic peninsula (FAO area 48.1) along with the South Orkney Islands (FAO area 48.2) and South Georgia (FAO area 48.3) (CCAMLR 2008). Commercial fisheries for fish stocks have existed in the past, with the finfish fishery open from 1978-1989 targeting *Champsocephalus gunnari, Chaenodraco wilsoni*, and *Notothenia rossi,* with bycatch species *Notothenia gibberifrons, Chaenocephalus aceratus*, and *Chionodraco rastrospinosus* (Kock 1998). With the establishment and regulation of the Antarctic resources by CCAMLR, there have been many regulations and closures placed on fisheries in area 48.1, as well as other Antarctic areas. Since the closure, there has been some exploratory fishing for these species in the 48.1 area, but no re-opening of commercial finfish fisheries.

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 entire Scotia Sea[9], and while a quota of 625,000 tonnes has been allocated to each subarea, in reality only about 100,000 tonnes are harvested each year for subarea 48.1 (Hewitt *et al.* 2002). The krill quota is set taking into account uncertainty in krill abundance, survival, growth, and mortality, in addition to predator demands. In reality, survival of fledging penguin chicks and Antarctic fur seals is lower in years of low krill abundance (Brierly and Reid 1999), suggesting that although this quota is thought to be conservative, krill is not always available to predators. Results from one spatial model (Marín 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 spatial competition to predators (Hewitt *et al.* 2002; Hewitt *et al.* 2004).

The establishment of 15 small scale management units (SSMUs) within area 48 to further divide the krill catches and to prevent concentrated fishing within small regions has been considered to

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[9] In the context of the paper by Hewitt *et al.* (2002), the Scotia Sea is defined as containing the South Shetland Islands, the South Orkney Islands, the South Sandwich Islands, and South Georgia (areas 48.1, 48.2, and 48.3).

ensure there is enough krill available for predators (Hewitt *et al.* 2004). Current recommendations to CCAMLR include incorporation of SSMUs into catch allocation, however at present the quota has not been further divided based on these smaller areas (Flores *et al.* 2011).

METHODS

An Ecosystem model was constructed for the Antarctic peninsula region (FAO area 48.1 in figure 1) using the Ecopath with Ecosim software (Christensen *et al.* 2005) to gain perspective into the changes in the ecosystem and the causes. This software employs a mass balance modelling approach starting with a static Ecopath model, before temporal simulations are utilized through the Ecosim portion of the software. The model was fit to past data trends before being used to test the impact of harvest and environmental factors on the ecosystem.

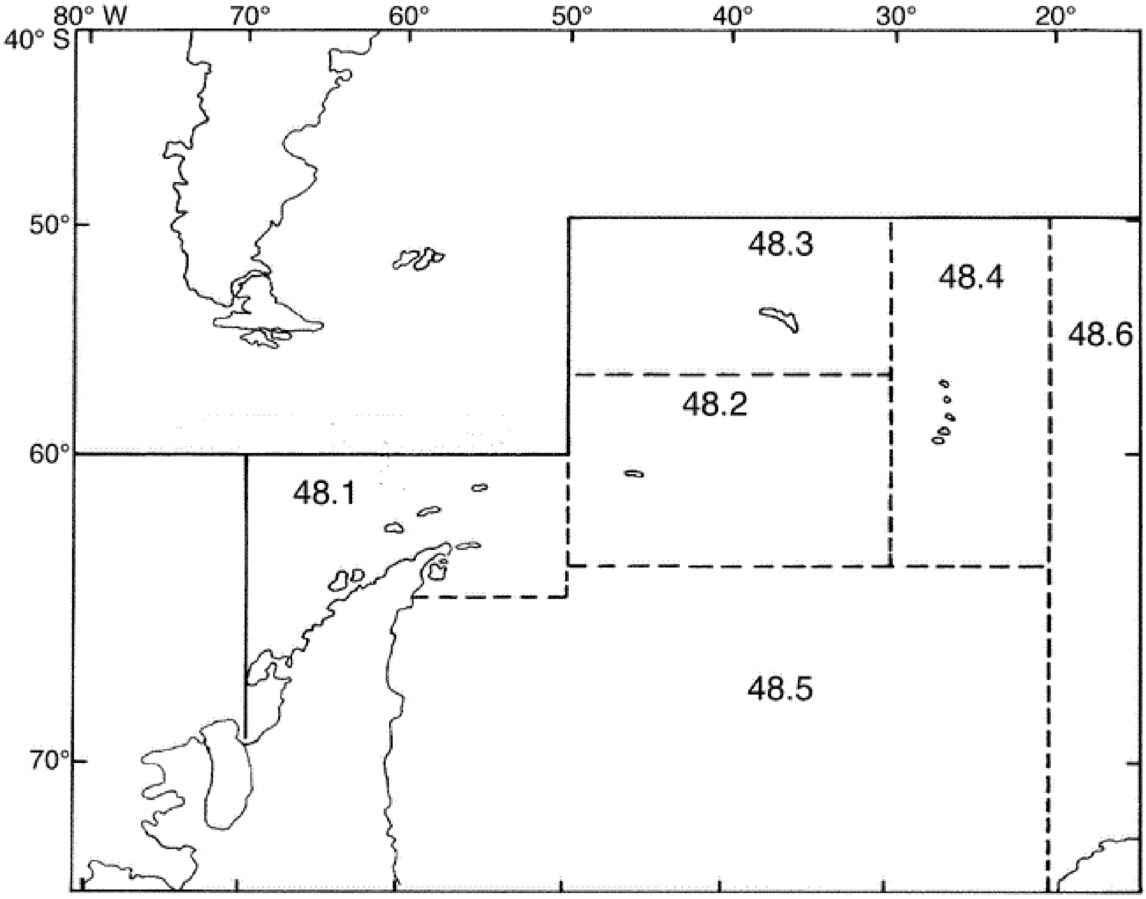

Figure 1: Map of Antarctic Peninsula (area 48.1) and surrounding areas. Other areas include south Orkney (48.2), South Georgia (48.3), South Sandwich (48.4), Weddell Sea (48.5) and Bouvet (48.6). The Scotia Sea represents areas 48.1, 48.2, and 48.3 combined.

Model Equations

The Ecopath portion of the model requires the following input parameters; biomass (in wet weight), production, consumption, ecotrophic efficiency, diets, and fisheries catches. For each functional group (or species group) one parameter may be left missing to be solved by the program. Through the use of linear equations and trophic linkages, these missing parameters may be solved through trophic linkages represented in the diet matrix. The production of each group (equation 1) is expressed as:

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

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 by trophic interactions and fishing) for prey i. Equation 1 can be re-written to incorporate the impacts of individual predators as :

$$B_i \cdot (P/B)_i = \sum_j B_j \cdot (Q/B)_j \cdot DC_{ji} + Y_i + E_i + BA_i + B_i \cdot (P/B)_i \cdot (1 - EE_i) \qquad (2)$$

Where B_i and P_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 i per unit biomass, 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 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.

Once the model is balanced in Ecopath, meaning there is enough prey produced within the first time step (static) to satisfy the needs of the predators and fisheries, temporal simulations care generated using equation 3;

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \qquad (3)$$

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 $B_i \cdot (\cdot e_i - I_i)$ 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. Vulnerabilities are set within the model with values =2 indicating a mixed interaction between predator and prey, >2 resulting in a bottom up interaction, and <2 resulting in a top down interaction. Vulnerabilities are estimated through an automated search routine (fit to time series), and user determined values.

Once the model was fitted to data, Monte Carlo simulations were run using an assigned Coefficient of Variation (CV) value as assigned based on the pedigree ranking within the program (Christensen *et al.* 2005) based on the source of the parameter used. 1000 simulations were run to estimate ranges on input parameters for the model for all functional groups using equation 4 to determine the best fitting model which provided the lowest sum of squares value when comparing time series data (predicted) with model results (observed).

$$L_{xi} = \bar{x}_i \pm 2 \cdot CV \cdot \bar{x}_i \qquad (4)$$

Where L_x is the limits (upper and lower) of the biomass for group i. The mean biomass $\bar{x}_i$ is taken as the Ecopath starting value.

Species Groups

Functional groups were created with a focus on krill, salps, and the top predators 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

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 Pauly (1998), compared to distribution and abundance information for each species. Southern Ocean abundance of cetacean species are found in table 1 as summarized by Branch and Butterworth (2001).

Table 1: Estimates of cetaceans from three 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

Mortality rates were calculated for each species using the life table from Barlow and Boveng (1991), where life history patterns and longevity were used to calculate natural mortality (full equations are available in appendix 1 of the Hudson Bay Ecosystem Model chapter, with longevity listed in table 2 of this section). 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.

Table 2: Published and calculated marine mammal parameters used in the model

Group	Species	Mean Weight (Kg)[1]	Longevity (Years)	Reference	Natural Mortality	Model P/B	Q/B[2]	Model Q/B
1	Killer Whales	2280.5	50	(Trites and Pauly 1998)	0.057	0.05	7.39	11.00
2	Leopard Seal	464	26	(Australian Antarctic Division 2008)	0.102	0.12	9.95	8.10
3	Ross seal	145.5	24	(Skinner and Klages 1994)	0.125	0.13	15.30	15.30
4	Weddell seal	158	13.5	(Trites and Pauly 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 Pauly 1998)	0.175	0.175	33.18	25.00
7	Elephant Seals	435	15	(Trites and Pauly 1998)	0.165	0.165	10.37	10.37
8	Sperm Whales	18518.5	69	(Trites and Pauly 1998)	0.043	0.034	7.33	7.33
9	Blue Whales	102736.5	100	(Trites and Pauly 1998)	0.032	0.032	3.53	3.53
10	Fin Whales	55590	98	(Trites and Pauly 1998)	0.035	0.035	4.12	4.12
11	Minke Whales	6566	47	(Trites and Pauly 1998)	0.064	0.064	6.34	6.34
12	Humpback Whales	30408	75	(Trites and Pauly 1998)	0.04	0.04	4.54	4.12

[1] Mean weight from Trites and Paul (1998) as averaged for males and females. Natural mortality was calculated from Barlow and Boveng (1991). [2]Q/B was calculated using equation 5.

Consumption (Q/B) was calculated using an empirical equation (equation 5) from Hunt *et al.* (2000), where E in the energy required per day (Kcal/day), M is the mean body weight (in Kg) and 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 (Cauffopé and Heymans 2005), in order to get the Q/B ratio. Table 2 compares calculated values, published values from literature, and values used in the model

$$E = aM^{0.75} \quad (5)$$

Killer Whales *(Orcinus orca)*

Recently in the Antarctic, three ecotypes have been identified which appear to be similar to the ecotypes of 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; *Dissostichus 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 Thiels 1997). Based on surveys in table 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 0.057 $year^{-1}$, but was lowered to 0.05 $year^{-1}$ to balance the model. The Q/B ratio was set to 11 $year^{-1}$, which is higher than the calculated transient Orca value in Guénette (2005). However, this value was used based on the majority of whales sighted in the area have been reported to feed 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% Adélie), 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 $seals \cdot km^{-2}$ for the Amundsen and Bellingshausen Seas (Gilbert and Erickson 1977). The biomass for the model was set to 0.00576 $t \cdot km^{-2}$. This is lower than other areas, as leopard seals are highly 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 $year^{-1}$ to account for killer whale predation, and the Q/B value was lowered slightly to 8.1 $year^{-1}$ 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% adélie penguins, 4% flying birds, 15% cephalopods, 2% other icefish, 1% large notothenoids, 1% small notothenoids, 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; Siniff and Stone 1985; Skinner and Klages 1994; 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 diving (Skinner and Klages 1994; Ackley *et al.* 2003). They are mostly found in interior pack ice zones in places such as the Ross Sea with concentrations of 0.6 animals $\cdot km^{-2}$ (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 0.0042 $t \cdot km^{-2}$. The P/B ratio was set to the calculated value 0.13 $year^{-1}$, and the calculated value of 15.3 $year^{-1}$ was used for Q/B.

The diet for Ross seals was set to: 46% cephalopods, 1.5% other icefish, 4.5% large notothenoids, 1% small notothenoids, 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% cnidaria, 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 0.005 $t \cdot km^{-2}$ (Laws 1977), and 0.021 to 0.12 $t \cdot km^{-2}$ for the Amundsen and Bellingshausen Seas for the 1970s and 1994 respectively (Gilbert and Erickson 1977; Gelatt and Siniff 1999). The biomass was set to 0.021 t·km-2 for the model. The P/B was increased from the calculated value to 0.17 $year^{-1}$ to account for predation by killer whales, and the Q/B was set to the calculated value of 13.88 $year^{-1}$.

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 Notothenoids, 1.5% small notothenoids, 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 Amundsen and Bellingshausen Seas are as high as 3.32 $seals \cdot km^{-2}$ in 1994 (Gelatt and Siniff 1999), with estimates on pack ice averaging 0.76 $seals \cdot km^{-2}$ 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 $seal \cdot km^{-2}$ (Van Franeker *et al.* 1997). A density of 0.8 $seals \cdot km^{-2}$ or 0.164 $t \cdot km^{-2}$ was used for the Antarctic Peninsula. The P/B for crabeater seals was increased from the calculated value of 0.083 to 0.09 $year^{-1}$ to balance the model, and the Q/B was set to the calculated value of 15.86 $year^{-1}$.

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; Bredesen 2003; Efran and Pitcher 2005).

Antarctic Fur Seals *(Arctocephalus gazella)*

There are 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) or 0.028 $t \cdot km^{-2}$. The same value was used for the model biomass. The P/B ratio used as calculated from the life table, 0.175 $year^{-1}$, was comparable to the estimate 0.16 $year^{-1}$ for northern fur seals (Wikens and York 1997; Guénette 2005). The calculated Q/B of 33.18 $year^{-1}$ was lowered to 25 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 estimates 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 notothenoids, 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 which is mostly comprised of cephalopods (McConnell *et al.* 1992). The 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 0.0026 $t \cdot km^{-2}$, 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 $t \cdot km^{-2}$, 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 0.165 and 10.37 $year^{-1}$ 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 notothenoids 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 notothenoids, 8% myctophids, 1% other pelagics, 2% P. antarcticum, 7.9% mollusca, 1% arthropod crustaceans, 3% adult krill, and 2% sub-adult krill.

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 $whales \cdot km^2$ for 1999 and 2000 respectively (Leaper *et al.* 2000), leading to a biomass of 0.0024 to 0.0035 $t \cdot km^2$. Biomass was assumed to be higher at the peninsula than South Georgia due to cooler deeper waters and was set to 0.005 $t \cdot km^2$ for the start of the model. The P/B was lowered from the calculated value of 0.043 $year^{-1}$ to 0.034 $year^{-1}$ to balance the model. The calculated Q/B value of 7.33 $year^{-1}$ 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.* 1998). 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% cnidaria, 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 the local 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 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 in the summer months. The biomass of the baleen whales has been adjusted to be 75% of their peak summer biomass to indicate 75% of yearly food intake coming from the model area.

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 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 biomass[10] for blue whales is 0.0005 $t \cdot km^{-2}$. The P/B and Q/B were set to the calculated values in table 2.

Blue whale diets consist 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-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 0.003 $t \cdot km^{-2}$. The calculated P/B and Q/B values from table 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. The 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 $whales \cdot km^{-2}$ 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 0.011 $t \cdot km^{-2}$ or 1500 whales present during the summer. This value was increased slightly to give a biomass of 0.065 $t \cdot km^{-2}$ in order to balance the model, as a large component of killer whales in the area feed on minke whales. The calculated P/B and Q/B values were used for the model from table 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.

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[10] Assuming 75% of the biomass for 5 whales

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 whales 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 0.02 $t \cdot km^{-2}$, based on 600 whales residing in the model area for the summer months. The calculated P/B of 0.04 $year^{-1}$ was used, however the Q/B was decreased slightly from 4.54 $year^{-1}$ to 4.12 $year^{-1}$ 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 adélie, gentoo, chinstrap, emperor, and macaroni penguins. The emperor and adélie penguins have a circumpolar distribution, while gentoo, macaroni and chinstrap penguins are found on sub-Antarctic islands, with the peninsula being 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 adélie penguins were known to inhibit the region. Adélie 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 (Quintana and Cirelli 2000). 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) dataset has been incorporated into the model (figure 2).

Surveys of various penguin rookeries at the south Shetland islands estimate populations of adélie, gentoo, and chinstraps at 65300, 12600, and 625000 breeding pairs respectively for the early 1980s (Trivelpiece *et al.* 1987)[11]. These were considered conservative estimates, as the surveys did not cover the entire model area. A more comprehensive survey for adélie penguins identified higher abundance within inshore zones in 1986; up to 3.5 $animals \cdot km^{-2}$ (Whitehouse and Viet 1994). Abundances of macaroni and emperor penguins were assumed based on their relative abundance compared to other penguin species, primarily adélie penguins.

P/B ratios were assumed for most species, based on survival rates of adélie penguins and taking into account other factors such as size and longevity. An average mortality rate of 0.29 $year^{-1}$ was used based on adélie penguin survivorship from 1968-1976 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 adélie penguins, with nearly the same lifespan, the P/B of both groups was set slightly higher at 0.3 $year^{-1}$. Emperor penguins have higher annual adult survival rates of 0.9 to 0.95 $year^{-1}$ (Bried *et al.* 1999; Croxall and Davis 1999). As these were for adult survival, the population P/B was assumed to be 0.15 $year^{-1}$. Gentoo penguins fall between emperor and adélie penguins in size, therefore their P/B was assumed to be 0.2 $year^{-1}$.

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[11] It should be noted that Trivelpiece *et al.* (2011) identifies declines of all three species of penguins studied: Adélie, Chinstrap and Gentoo in a recent study. Implications to the model are provided in the discussion.

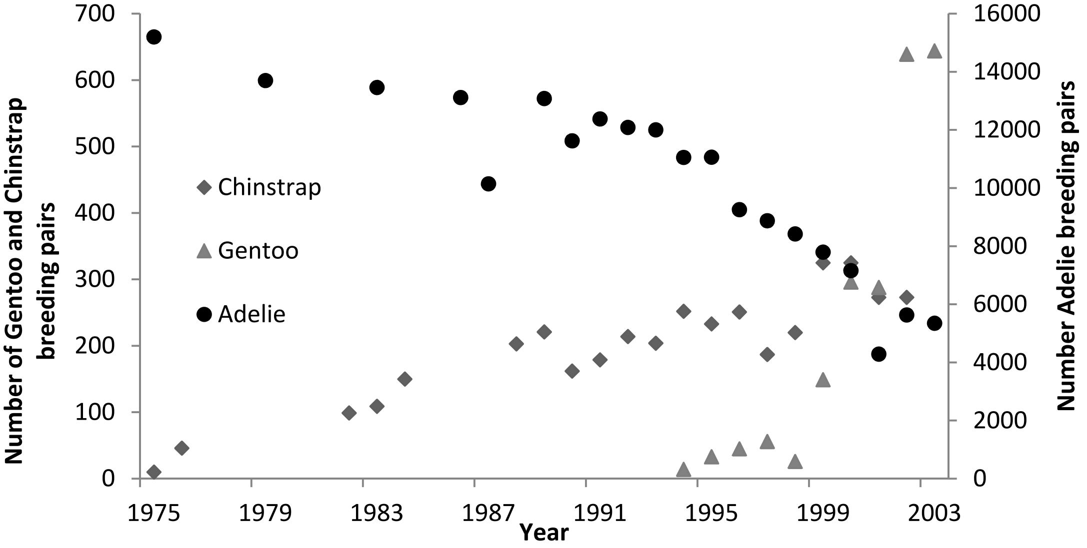

Figure 2: Number of breeding pairs for Chinstrap, Gentoo, and Adélie penguins from surveys at PALMER station, Anvers Island, Antarctic Peninsula (Fraser 2006).

Consumption was calculated using two general equations (6 and 7) to calculate the basal metabolic rate (BMR) and field metabolic rate (FMR) for Sphenisciformes (Ellis and Gabrielsen 2002) cited in (Karpouzi 2005).

$$BMR = 1.775 \cdot m^{0.768} \tag{6}$$

$$FMR = 21.33 \cdot m^{0.626} \tag{7}$$

Where Basal and Field Metabolic Rates are given in kJ/ day and m=mass of the bird in grams. These metabolic rates were then applied to the number of breeding and non breeding days (table 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 3: Number of breeding and non-breeding days per year. Q/B values were calculated using equations 6 and 7. Data for number of breeding, non-breeding days per year, and weight from Karpouzi (2005).

Species	Non-breeding days	Breeding days	Calculated Q/B (year^{-1})	Model Q/B (year^{-1})	Weight (Kg)	P/B (year^{-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
Adélie 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. Biomass was estimated to be roughly 10% of adélie penguin numbers (Ainley *et al.* 1994) or 0.0013 t·km^{-2}, but was increased to 0.005 t·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; Pütz 1995). The diet was set to 22% cephalopods, 1% other icefish, 3% Large notothenoids, 3% small notothenoids, 20% P. antarcticum, 0.1% arthropod crustaceans, 29.9% adult krill, and 21% sub-adult krill (Green 1986; Klages 1989; Pütz 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 gentoo penguins do not fast, however their ability to make deeper dives than adélie 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 t·km^{-2}. However this had to be increased to 0.0065 t·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 0.22 year^{-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 included (Volkman *et al.* 1980; Croxall *et al.* 1988; Coria *et al.* 2000; Clausen and Pütz 2003; Lescroël *et al.* 2004; Clausen *et al.* 2005). The diet was set to 32% cephalopods, 1% other icefish, 4% large notothenoids, 4% small notothenoids, 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% cnidaria, 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 (Fraser *et al.* 1992; Knox 1994). 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 0.003t·km^{-2} for areas with and without sea ice, respectively (Van Franeker *et al.* 1997). The biomass was assumed to be similar to the Weddell Sea and was set to a midrange value of 0.0053 t·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 (fig 2) 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 0.33 year^{-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 adélie 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 notothenoids, 1% small notothenoids, 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% cnidaria, 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 t·km^{-2}, however this was too low for the model, and the biomass was increased to 0.0135 t·km^{-2}, or nearly 15% of the biomass of other bird species in order to balance the model.

Fish in the diet consists primarily of myctophids, icefish, and Nothothenioids, 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 notothenoids, 2% small notothenoids, 0.5% deep demersals small, 2% myctophids, 1% other pelagics, 2% C. gunnari, 1% P. antarcicum, 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).

Adélie Penguins *(Pygoscelis adeliae)*

Adélie penguins are the most abundant penguins over the entire peninsula with estimates ranging from 3.5 animals·km^{-2} for inshore areas to less than 1 animal·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 animals·km^{-2} yielded a biomass of 0.016 t·km^{-2}, however this was too low and considering estimates from the Shetland Islands, the biomass was increased to 0.034t·km^{-2} to balance the model. Densities in the Weddell Sea reach 8 animals·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 adélie penguins in the peninsula region.

Fish, cephalopods and krill were the most important prey items to adélie 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 gigcialoides*), Antarctic petrel (*Thalassoica antarctica*), Snow Petrel (*Pagodroma nivea*), Dominican Gull (*Larus dominicanus*), Grey headed Albatross (*Diomedea chrysostoma*), Light-mantled Sooty Albatross (*Phoebetria 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 Albartoss (*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 Sheathbill (*Chionis alba*), Brown Skua or subantarctic skua (*Catharacta skua*), South Polar Skua (*Catharacta maccormicki*), Antarctic 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 Franker *et al.* (1997) provided a biomass for 15 species in the Weddell Sea region of 0.087 $t \cdot km^{-2}$, while Whitehouse and Viet (1994) identified the biomass of 21 species at the Antarctic Peninsula to be 0.199 $t \cdot km^{-2}$. The latter value was used for the model biomass. 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 $year^{-1}$. 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% adélie penguins, 2.1% flying birds, 21.6% cephalopods, 1% other icefish, 0.1% large notothenoids, 2% small notothenoids, 2% myctophids, 1.6% other pelagics, 1.8% P. antarcticum, 0.1% N. gibberifrons, 3.2% mollusca, 5% salps, 0.5% cnidaria, 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, Galiteuthis 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 $t \cdot km^{-2}$ 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 $year^{-1}$ for small and large cephalopods, respectively. Q/B was initially set to 2.5 $year^{-1}$ considering values of 2 and 3 $year^{-1}$ for large and small cephalopods; however this value was too high and was lowered to 2 to balance the model.

The diet of cephalopods was set to 1% cephalopods, 0.1% other icefish, 0.05% toothfish, 0.1% large notothenoids, 0.5% small notothenoids, 1% myctophids, 1% other pelagics, 7.5% P. antarcticum, 1% mollusca, 4.25% salps, 0.4% urochordata, 0.5% cnidaria, 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; Knox 1994; Lu and Williams 1994; Rodhouse and Nigmatullin 1996).

Fish

Fish species were separated into groups 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 groups. Factors taken into account for selecting groups 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 and known ranges for each species, before being 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; Kock *et al.* 2004; Kock and Jones 2005; Froese and Pauly 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. Two methods using different equations were used to calculate and compare natural mortality values: equation 8 (Pauly 1980; Froese and Pauly 2008) and equation 9 (Jensen 1997) with the results in table 4.

$$M = 10^{(0.566-0.718\cdot\log(L_\infty)+0.02\cdot T)} \tag{8}$$

$$M = 1.5k \tag{9}$$

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; FAO 1985b; Kock 1992; Frolkina *et al.* 1998; Arana and Vega 1999; Kock *et al.* 2000; Kock *et al.* 2004; Kock and Jones 2005; Froese and Pauly 2008). Although equation 8 is based on 175 fish stocks, it underestimates the mortality for polar species (Pauly 1980), so a second equation (Eq. 9) 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 10 (Palomares and Pauly 1998);

$$\log(Q/B) = 7.964 - 0.204\log W_\infty - 1.965T + 0.083A + 0.532h + 0.398d \tag{10}$$

Where W_∞ is the weight a fish would reach if it grew to $L\infty$, 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 1.82-14.6 year^{-1}. This indicates equations from Palomares and Pauly (1998) may be underestimating consumption of polar species.

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 notothenoids, 3.5% small notothenoids, 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% cnidaria, 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 0.165 year^{-1} in order to balance the model. The diet was set to: 17.4% cephalopods, 20% other icefish, 6% large notothenoids, 15% small Nototheniods, 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 (García de la Rosa *et al.* 1997; Arana and Vega 1999).

Large Notothenioids

Large Notothenioids were classified as fish in the family Nototheniidae with an average length over 30 cm. This included *Notothenia coriiceps, Notothenia neglecta, Notothenia rossii, Pagothenia (Trematomus) hansoni* and *Notothenia squamifrons*. The P/B ratio was increased to 0.37 year^{-1} to balance the model, and the diet was set to: 0.5% large notothenoids, 1.5% small notothenoids, 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 notothenoids were classified as fish from the family Nototheniidae 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% Ophiuoidea, 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 0.75 year^{-1} to balance the model, and diet was set to: 7.5% molluscs, 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 notothenoids, 4% small notothenoids, 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 notothenoids, 0.5% shallow demersals, 1% deep demersals small, 4% myctophids, 4% other pelagic, 8% P. antarctucim, 15% mollusca, 2% salps, 0.5% urochordata, 0.5% bryozoa, 0.1% cnidaria, 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 epi-pelagic 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 1.35 year-1 and 3.73 year-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; Sheeve *et al.* 2009).

Table 4: Calculated mortality and consumption values for fish groups. Biomass (B) is presented from surveys in t·km^{-2}. Mortality (M), production to biomass ratio (P/B) and consumption to biomass (Q/B) are presented as a yearly rate (year^{-1})

	Group	B	Species	K		M^1	M^2	Model P/B	Q/B^3	Model Q/B
20	Other Icefish	0.337	Family value	0.273	(Froese and Pauly 2008)	0.409	0.320	0.380	1.570	1.570
			P. georgianus	0.320	(Froese and Pauly 2008)	0.480				
21	Toothfish	0.047	*D elegiodes*	0.102	(Horn 2002)	0.152	0.140	0.165	0.700	0.770
			D. mawsoni	0.099	(Horn 2002)	0.148				
22	Lg. Nototheniidae	0.590	Family value	0.133	(Froese and Pauly 2008)	0.190	0.190	0.370	2.760	1.950
			N. coriiceps	0.098	(Coggan 1997)	0.147				
23	Sm. Nototheniidae	0.341	Family value	0.364	(Froese and Pauly 2008)	0.546	0.430	0.650	2.530	2.200
24	Shallow Demersals	0.031	*H. antarcticus*	0.140	(Daniels 1983)	0.210	0.370	0.750	4.650	4.125
			H. antarcticus	0.250	(Daniels 1983)	0.375				
25	Deep Demersals Lg.	0.042	*P. brachycephalum*	0.310	(Froese and Pauly 2008)	0.465	0.180	0.290	2.000	2.180
			O. amberensi	0.310	(Froese and Pauly 2008)	0.465				
26	Deep Demersals Sm.	0.08	p. brevipes		(Froese and Pauly 2008)		0.400	0.650	2.700	2.700
27	Myctophids	0.185	Family value	0.430	(Froese and Pauly 2008)	0.640	0.530	1.350	3.400	3.730
28	Other Pelagics	0.490	*A. pharao*	0.500	(Froese and Pauly 2008)	0.750	0.220	0.550	1.830	2.020
			B. antarcticus	0.140	(Froese and Pauly 2008)	0.210				
29	C. gunnari	0.290	*C. gunnari*	0.141	(Froese and Pauly 2008)	0.212	0.220	0.480	2.400	1.800
30	P. antarcticum	1.250	*P. antarcticum*	0.093	(Froese and Pauly 2008)	0.140	0.190	1.100	1.100	3.550
31	N. gibberifrons	0.810	*N. gibberifrons*	0.104	(Froese and Pauly 2008)	0.156	0.110	0.410	1.400	1.550

[1] Natural mortality calculated using eq 9 (Jensen 1997).

[2] Natural mortality calculated using eq 8 (Pauly 1980).

[3] Consumption calculated using eq 10 (Palomares and Pauly 1998).

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 notothenids, 0.1% deep demersals large, 0.1% deep demersals small, 3% myctophids, 2% other pelagics, 10% P. antarcticum, 4% molluscs, 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).

Champsocephalus gunnari

For *C. gunnari*, the P/B ratio was increased to 0.48 $year^{-1}$, and the Q/B ratio was lowered to 1.8 $year^{-1}$ 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 1.1 $year^{-1}$ and 3.55 $year^{-1}$ respectively to balance the model. The diet for this group was set to: 0.1% other icefish, 0.1% small notothenoids, 0.1% deep demersals small, 1% other pelagic, 0.5% P. antarcticum, 1% N. gibberifrons, 13.3% molluscs, 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. gibbifrons was increased to 0.41 year-1 to balance the model while the diet was set to: 2% molluscs, 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; Casaux *et al.* 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.

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 5), as provided by the GIS basemap function in Ecopath version 5 (Christensen *et al.* 2005).

Table 5: Percentage of habitat by depth range for the Antarctic Peninsula

Depth	Percentage of total Habitat
<10	1.66
11-50m	3.94
51-100m	3.89
101-200m	6.59
201-1000m	33.99
>1000m	49.94

Invertebrate groups where published production values could not be found, were calculated using equation 11 (Saiz-Salinas *et al.* 1998) where B is the biomass ($g\ DM{\cdot}m^{-2}$), M is maximum individual body mass (g DM), T is the surface temperature of the water (◦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 (1995).

$$log(P) = 0.240 + 0.960 \cdot log(B) - 0.210 \cdot log(M) + 0.030 \cdot T - 0.160 \cdot log(D+1) \tag{11}$$

Consumption rates were based on published literature as shown (table 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). Animals such as brachiopods which take advantage of the abundant summer food supply, rely on re-suspended benthic material in the winter (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 winter food source.

Molluscs

Surveys revealed the biomass and abundance of this group was dominated by bivalves. Other taxonomic groups included Gastropods, namely Opistobranchs (sea slugs) and Prosobranchs (snails), and in smaller numbers Scaphopods (tusk shells). Solenogastres (Aplacophors or shell-less molluscs) 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.

Cnidaria

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% cnidaria, 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% molluscs, 1% salps, 5% urochordata, 1% porifera, 1% bryozoa, 1% cnidaria, 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% molluscs, 0.6% urochordata, 2.5% porifera, 0.1% bryozoa, 0.2% cnidaria, 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; FAO 1985b; Brueggman 1998; Pakhomov *et al.* 2002).

Echinoderms

Echinoderms were split into family groupings, as they are one of the largest phylums 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 (Jacob *et al.* 2003).

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 ploychaetes, tunicates, diatoms, and algal matter (McClintock 1994). The diet was set to 1% molluscs, 0.5% urochordata, 5% porifera, 0.05% hemichordata, 0.2% brachiopoda, 0.8% bryozoa, 1% cnidaria, 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% molluscs, 3% porifera, 0.3% bryozoa, 0.5% cnidaria, 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% molluscs, 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 6 : Published, caluclated, and model parameters for mortality (P/B) and consumption (Q/B) for invertrbrate groups.

Group	Model P/B	Calculated P/B^1	Group	Source	Model Q/B	Published Q/B	Source
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)			
Salps	10.000				33.000		Estimated by model
Urochordata	0.234	0.230	Tunicata	(Brey and Gerdes 1998)	1.000	1	(Jarre-Teichmann *et al.* 1997)
		0.100	Tunicata	(Jarre-Teichmann *et al.* 1997)			
		0.234	combined^2	(Brey 2001)			
Porifera	0.159	0.159	Porifera	(Brey and Gerdes 1998)	0.795	0.6	(Efran and Pitcher 2005)
		0.030	Porifera	(Jarre-Teichmann *et al.* 1997)			
		0.116	combined^2	(Brey 2001)			
Hemichordata	0.375	0.155	Hemichordata	(Brey and Gerdes 1998)	2.000	2	(Jarre-Teichmann *et al.* 1997)
		0.300	Hemichordata	(Jarre-Teichmann *et al.* 1997)			
Brachiopoda	0.898	0.100	Lophophora and Cnidaria	(Jarre-Teichmann *et al.* 1997)	4.500	1	(Jarre-Teichmann *et al.* 1997)
		0.815	combined^2	(Brey 2001)			
Bryozoa	0.475	0.100	Lophophora and Cnidaria	(Jarre-Teichmann *et al.* 1997)	1.750	1	(Jarre-Teichmann *et al.* 1997)
		0.227	combined^2	(Brey 2001)			
Cnidaria	0.250	0.186	Cnidaria	(Brey and Gerdes 1998)			
		0.100	Lophophora and Cnidaria	(Jarre-Teichmann *et al.* 1997)	1.000	1	(Jarre-Teichmann *et al.* 1997)
Crusteceans	1.050	0.616	Arthropoda	(Brey and Gerdes 1998)	4.200		Estimated by model
		0.794	Isopoda	(Brey and Clarke 1993)			
		0.397	Decapoda	(Brey and Clarke 1993)			
		0.7	benthic Crustacea	(Jarre-Teichmann *et al.* 1997)		3.5	(Jarre-Teichmann *et al.* 1997)
Arthropod Other	0.616	0.616	Arthropoda	(Brey and Gerdes 1998)	3.326		
			benthic Crustacea and Chelicerata			3.5	(Efran and Pitcher 2005)
Worms	0.700	0.319	Annelida	(Brey and Gerdes 1998)	3.200		
		0.168	Scolecida	(Brey and Gerdes 1998)			
		0.6	Polychaeta and other worms	(Jarre-Teichmann *et al.* 1997)		4	(Efran and Pitcher 2005)
			all worms			4	(Jarre-Teichmann *et al.* 1997)
Echinoidea	0.116	0.164	all echinoderms	(Brey and Gerdes 1998)	0.464		Estimated by model
		0.116	Echinoidea	(Brey and Clarke 1993)			

Table 6 continued on next page

Group	Model P/B	Calculated P/B[1]	Group	Source	Model Q/B	Published Q/B	Source
Crinoidea	0.125	0.164	all echinoderms	(Brey and Gerdes 1998)			
		0.100	Crinoidea	(Jarre-Teichmann *et al*. 1997)	0.800	1	(Jarre-Teichmann *et al*. 1997)
Ophiuroidea	0.450	0.164	all echinoderms	(Brey and Gerdes 1998)	1.800		Estimated by model
		0.566	Ophiuroidea	(Brey and Clarke 1993)			
		0.173	Ophiuroidea	(Jarre-Teichmann *et al*. 1997)			
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)			
Holothuroidea	0.315	0.164	all echinoderms	(Brey and Gerdes 1998)			
		0.100	Holothuroidea	(Jarre-Teichmann *et al*. 1997)	1.100	1.100	(Jarre-Teichmann *et al*. 1997)
		0.315	combined[2]	(Brey 2001)			

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 (2005) estimated macro-zooplankton biomass ranging from 17-542 $mgC\cdot m^{-2}$ while the meson-zooplankton ranged from55-1741 $mgC\cdot m^{-2}$ for samples from the Gerlache Strait, Bransfield Strait, and Bellinghausen Sea in 2002. The meson-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 $mgC\cdot m^{-2}$ (roughly 51 $g\cdot m^{-2}$)[12] from a sample from South Georgia in 1994 sampling primarily meson-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 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 $salps\cdot m^{-2}$ in 1978, with an average abundance of 49.4 $salps\cdot m^{-2}$ from 1978-2003. Siegel *et al.* (2005) showed an average biomass of $12.17 g\cdot m^{-2}$ from 1981-2002 (range 0.76-75.23 $g\cdot m^{-2}$). $12.17 t\cdot km^{-2}$ (or $g\cdot m^{-2}$) was used as a starting biomass, but this was too high, so it was lowered to $8 t\cdot m^{-2}$ 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 $10 year^{-1}$.

Salps are generally filter feeders, whose biomass has been shown to increases 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, and 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.

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[12] Using the conversion 1gC=8.3 wet weight for general zooplankton conversion taken from (Cushing *et al.* 1958) as cited in Cauffope and Heymans (2005).

Multistanza groups were used to provide more detailed information about the life history of a species or species group within the model. For example, predation is higher on adult krill, as some species target larger size classes (Lowry *et al.* 1998). Using different life stages within the model allows us to capture these differences. 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 meson- 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 while they reach depths of 425-1090m, depending on temperature and geographic location, before re-ascending to the surface (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 greatly 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; Meyer *et al.* 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 furculia 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.* 2004), 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 migrations allow krill to feed on the meson-zooplankton community and helps them to avoid predation during daylight hours (Hernández-León *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 also 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 $g\cdot m^{-2}$) summer (95 $g\cdot m^{-2}$) fall (12 $g\cdot m^{-2}$) and winter(8 $g\cdot m^{-2}$) (Lascara *et al.* 1999). Elephant Island showed a low biomass of 0.98 $g\cdot m^{-2}$ for the 90/91 austral summer to a high of 31.16 $g\cdot m^{-2}$ 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 8-138 $g\cdot m^{-2}$ 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 $g\cdot m^{-2}$ in 1978. While this estimate likely only represents the adult and juvenile stages, the leading or adult krill biomass was set to 9.080 $g\cdot m^{-2}$, so that the total krill biomass was 35.22 $g\cdot m^{-2}$.

Krill can live up to and in some cases more than 6 years (Pakhomov 1995). Mortality ranged from 0.52 year-1 for mature stages of krill, to 1.1 for the first year, 2.41 for the last years of life. Survival at the Antarctic Peninsula averaged 0.36-0.41 year^{-1} (for age classes 2+), but can range from0.4-0.78 year^{-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).

Table 7: Natural mortality rates (year^{-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 (1995).

Age	S of AD Cooperation Sea	N of AD Cooperation Sea	Cosmonaut Sea N&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	

Based on the values in table 7 (Pakhomov 1995), the P/B values used for krill groups were set to; 1.5 year^{-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 0.9 year^{-1}, and accounts for a small amount of fishing mortality. The Larvae group was set to 2.5 year-^{1} and the embryo class was set to 8 year-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.

Consumption rates were calculated to be of 5% of body carbon per day based on fecal pellet production or 0.4-1.7% of body carbon measured from gut florescence, from February-March at South Georgia (Pakhomov *et al.* 1997). Over a 100 day growing season this could range from 40-500 year^{-1}. These values were taken 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 33 year-1. Parameters for all krill groups are shown in table 8.

Table 8: Multistanza parameters for krill functional groups. Biomass (B) is presented in t·km^{-2}, Mortality (Z) and Consumption (Q/B) are presented as annual values (year^{-1}).

	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	25.260	0.9	49.481
54	Krill Adult	36	9.080	1.5	33.000

In addition to the curvature parameter (Von Bertalanffy growth K parameter), a recruitment power parameter was set to 1. Lower values of 0.1-0.5 indicate juveniles spend time outside the model area where density dependence may affect mortality (Christensen *et al.* 2005). As krill spawn and hatch 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_∞) parameter was also included. This is described as the weight of fish at the asymptotic length (L_∞), where $W_\infty = (L_\infty)^3$. L_∞ was set to 65mm (Reid 2001), with length at maturity set at 37.5mm based on female krill reaching L_{50} at 34.65-35.9mm[13] at 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 0.141-6.99 g·m^{-2}(Calbert *et al.* 2005). Zooplankton groups (meso and macro) from Croker Passage in 1983 were estimated to be 19.07 g·m^{-2} (Hopkins 1985). While these estimates represent values in the summer when biomass is higher, the annual value was set to 8.170 t·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 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 0.3-0.6 gC·m^{-2} (or 2.49-4.98 g·m^{-2}) (Garrison *et al.* 1991). The biomass for the model was set to a conservative value of 2.9 t·km^{-2} (or g·m^{-2}). The Q/B was set to 110 year^{-1}, slightly higher than the copepod value, with an assumed P/B value of 65 year^{-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 15.14g·m^{-2}, in South Georgia and from 4.53- 23.12 g·m^{-2} in the Bellingshausen Sea (Calbert *et al.* 2005). Estimates at South Georgia range from <1 to 13 g·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 g·m^{-2} for all copepod species, based on samples from South Georgia.

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[13] L_{50} is defined where 50% of the population reaches sexual maturity.

The P/B ratio from South Georgia was estimated at about 10 $year^{-1}$ 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 $year^{-1}$, 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 50 $year^{-1}$. 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; Moline *et al.* 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. The other phytoplankton and cryptophytes were considered to be associated with open water with the exception of the sea ice. Biomass for phytoplankton was generally recorded for summer months and adjusted to an annual value. 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 and growth during summer months. Annual average values needed for model input were assumed to be 1/3 of the summer biomass.

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 in the future. Biomass ranges for this group were as high as 21.6 $t \cdot km^{-2}$ for summer values in highly concentrated areas (Varela *et al.* 2002), but reduced to 5.4 $t \cdot km^{-2}$ when accounting for the whole study region. Others (Garibotti *et al.* 2003) estimated the summer biomass to be roughly 6 $t \cdot km^{-2}$ for the summer season. The average yearly biomass was set to 2.2 $t \cdot km^{-2}$. The production for this group was set to 75 $year^{-1}$ based on a 120 day summer season for growth with published production rates ranging from 0.5-1.5 $gC \cdot m^{-2} \cdot day^{-1}$ (Varela *et al.* 2002), however it was increased to 80 $year^{-1}$ to balance the model.

Diatoms

This group contains all diatoms. The biomass was sampled to range from 130 $ugC \cdot l^{-1}$ (Garibotti *et al.* 2003) and was converted to a summer biomass range of 40.9 $g \cdot m^{-2}$ (wet weight). The annual biomass was reduced to 1/3 of the summer biomass to give 13.65 $t \cdot km^{-2}$, which was slightly lower than the regional average of roughly 21 $t \cdot km^{-2}$ for the western Antarctic Peninsula region calculated by (Varela *et al.* 2002). The final value used for the model was set to 17.41 $t \cdot km^{-2}$ to balance the model. The production of diatoms was converted from 0.87-4.54 $gC \cdot m^{-2} \cdot day^{-1}$ (Varela *et al.* 2002) to give a P/B range of 22.5-117.4 year-1. The P/B value of 90.51 year-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 Cauffopé and Heymans (2005). A late winter biomass of 3.2 $t{\cdot}km^{-2}$ provided by Kottmeier and Sullivan (1987) was slightly lower than the 5.67 $t{\cdot}km^{-2}$ 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 $t{\cdot}km^{-2}$ is still lower than the highest reports that *chl a* concentrations can be as high as 0.4 $g{\cdot}m^{-2}$ or about 140 $t{\cdot}km^{-2}$ (Arrigo *et al.* 1997). The average yearly biomass was set to 25 $t{\cdot}km^{-2}$. Winter production values for ice algae ranged from 0.017 $gC{\cdot}m^{-2}{\cdot}day^{-1}$ (Lizotte 2001) to 0.035 $gC{\cdot}m^{-2}{\cdot}day^{-1}$ (Kottmeier and Sullivan 1987) to 1 $gC{\cdot}m^{-2}{\cdot}day^{-1}$ (Arrigo *et al.* 1997). Summer production values were much higher at 1.6 $gC{\cdot}m^{-2}{\cdot}day^{-1}$ (Smith *et al.* 1998). At the maximum summer production values of 1.6 $gC{\cdot}m^{-2}{\cdot}day^{-1}$ (for 120 days of summer) would yield an annual rate of 69.12$year^{-1}$, while winter rates of 0.017 $gC{\cdot}m^{-2}{\cdot}day^{-1}$ (for 245 days) would yield an annual rate of 1.49$year^{-1}$. A value of 45.00$year^{-1}$ 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 $t{\cdot}km^{-2}$ based from a summer value of 27.9 $ugC{\cdot}l^{-1}$ (Garibotti *et al.* 2003). P/B increased from the calculated value of 77.4 $year^{-1}$ (from 0.21 $gC{\cdot}m^{-2}{\cdot}day^{-1}$) (Varela *et al.* 2002) to 105 $year^{-1}$ to balance the model.

Detritus

Detritus biomass was calculated using the following equation from (Pauly *et al.* 1993):

$$\log_{10}D=-2.41+0.954\log_{10}PP+0.863\log_{10}E \tag{12}$$

where D is the standing stock of detritus ($gC{\cdot}m^{-2}$), PP is primary productivity ($gC{\cdot}m^{-2}{\cdot}yr^{-1}$), and E is the euphotic depth in meters. Estimates of primary production for the area ranged from 0.36 $gC{\cdot}m^{-2}{\cdot}yr^{-1}$ (Vernat *et al.* 2008) for offshore areas to 55-425 $gC{\cdot}m^{-2}{\cdot}yr^{-1}$ (Smith *et al.* 2001) for areas near Palmer Station. A primary production value of 0.4 $gC{\cdot}m^{-2}{\cdot}yr^{-1}$ 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$t{\cdot}km^{-2}$ of detritus.

Ecosim Input

Krill Fishery

For this model the "krill fishery" is classified as mid-water otter trawls as cited in the CCAMLR statistical Bulletin (CCAMLR 2008). Catches 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 3). However in the fitting process, catch timeseries (figure 4) was used to force 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 1E-05 t·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, *Champsocephalus gunnari*, *Pleuragramma antarcticum*, and *Notothenia 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 timeseries. This fishery mostly includes test fisheries on finfish species with some bycatch. 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 3), however, this did not reproduce the pattern of catches (figure 4) 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 2008).

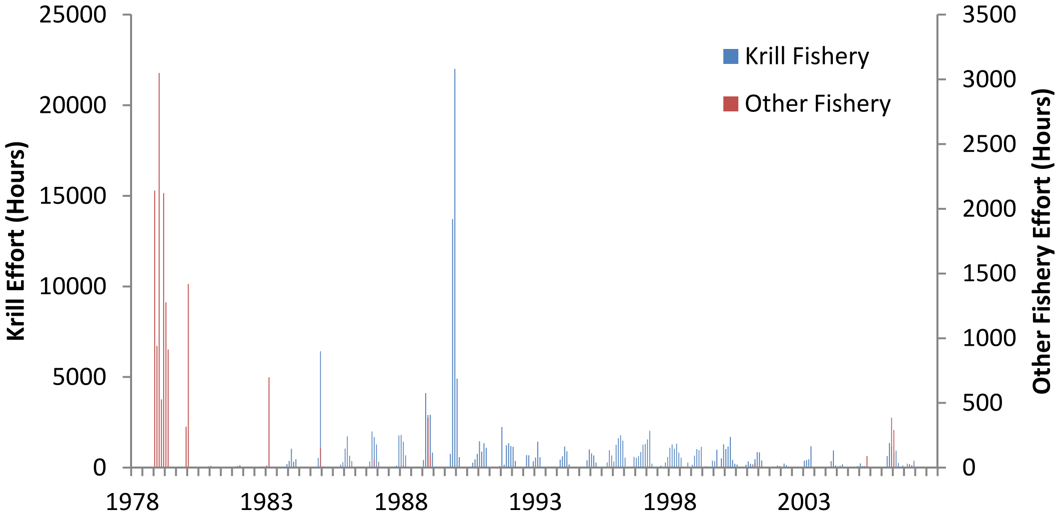

Figure 3: Fishing effort used in model fitting for the krill fishery and the other fishery representing fish catches. Data provided by CCAMLR (2008).

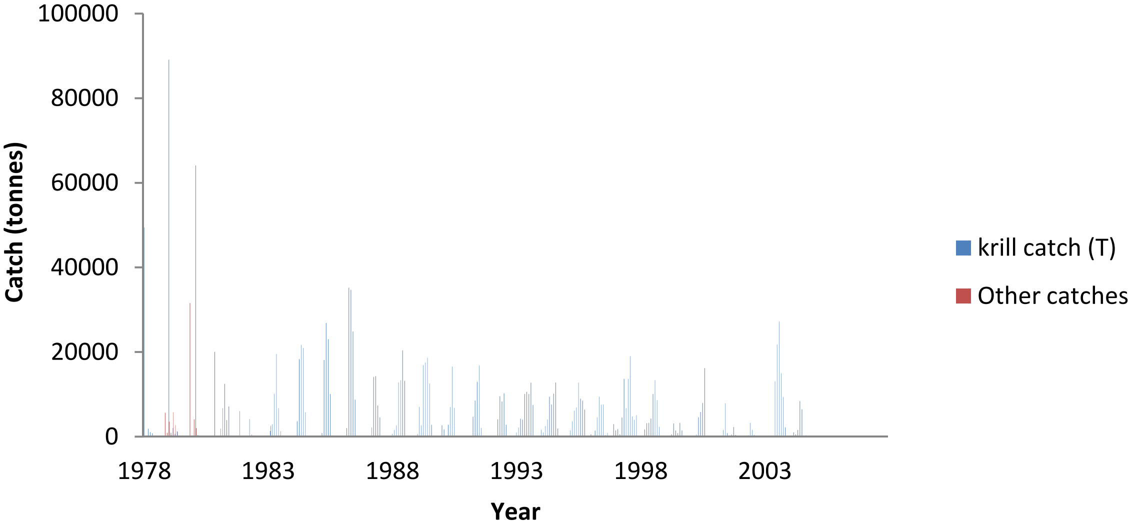

Figure 4: Fishing catches used in model fitting for the krill fishery and the other fishery representing fish catches. Data provided by CCAMLR (2008).

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 of krill (Atkinson *et al.* 2004; Quetin and Ross-Quetin 2006), or biomass (Siegel *et al.* 1998; Siegel *et al.* 2002). However ultimately the KRILLBASE (Atkinson *et al.* 2002) data was used, as it provided the most complete geographic and temporal timeseries trend for krill (figure 5).

For salps, two potential datasets 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 for model fitting as it was more complete (figure 6).

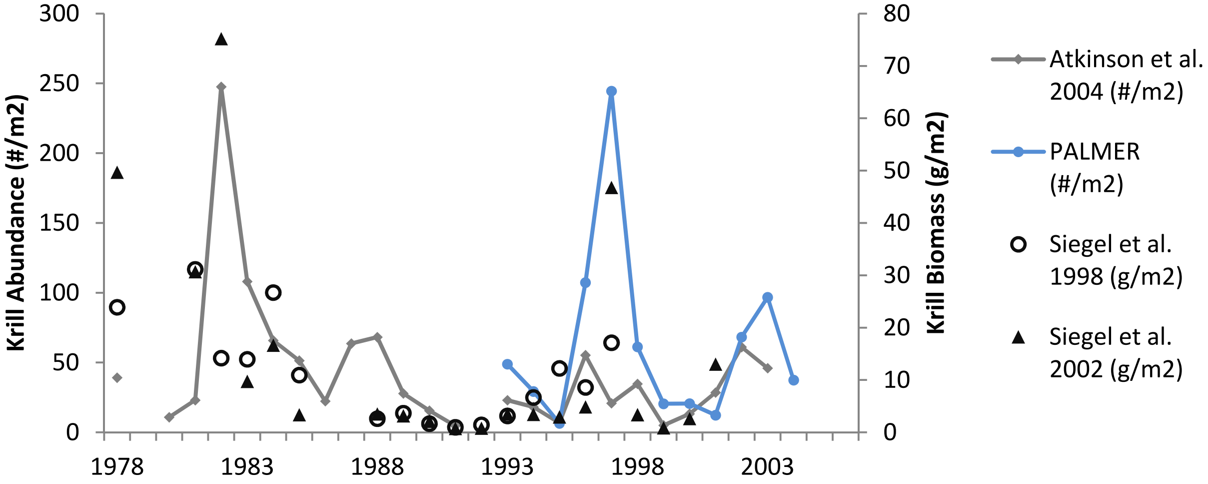

Figure 5: Krill abundance and biomass trends from the Antarctic Peninsula.

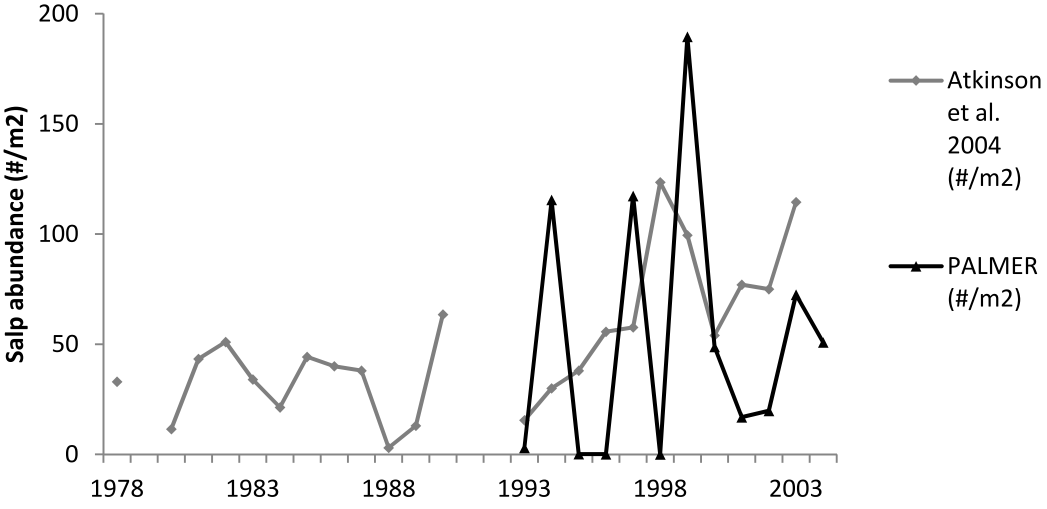

Figure 6: Salp abundance trends from the Antarctic Peninsula.

Adélie, 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 adélie 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 areas, and they most likely evolved in conditions with open water a majority of the year (McClintock *et al.* 2008). Adélie 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 adélie 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 Adélie; 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. A summary of all timeseries data used in model fitting is provided in table 9.

Table 9: Summary of timeseries data used to fit the model.

Timeseries data	Type of data used	Reference
Krill Abundance	Relative Abundance	(Atkinson *et al.* 2004)
Krill Catch	Forced Catches	(CCAMLR 2008)
Krill Effort	Effort	(CCAMLR 2008)
Salp Abundance	Relative Abundance	(Atkinson *et al.* 2004)
Other Fishery Catch	Forced Catches	(CCAMLR 2008)
Other Fishery Effort	Effort	(CCAMLR 2008)
Adélie 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 temperate (SST), sea ice cover (% cover), and the southern oscillation index (SOI). The SST and ice cover timeseries were extracted from the HadISST (Hadley Centre Sea Ice and Sea Surface Temperature data set) model by month (British Atmospheric Data Centre 2010) for cells within area 48.1. The model data is presented as the monthly average for 1°x 1°cells for the world, with the values for the Antarctic Peninsula used as the mean of all cells within the area (figure 7).

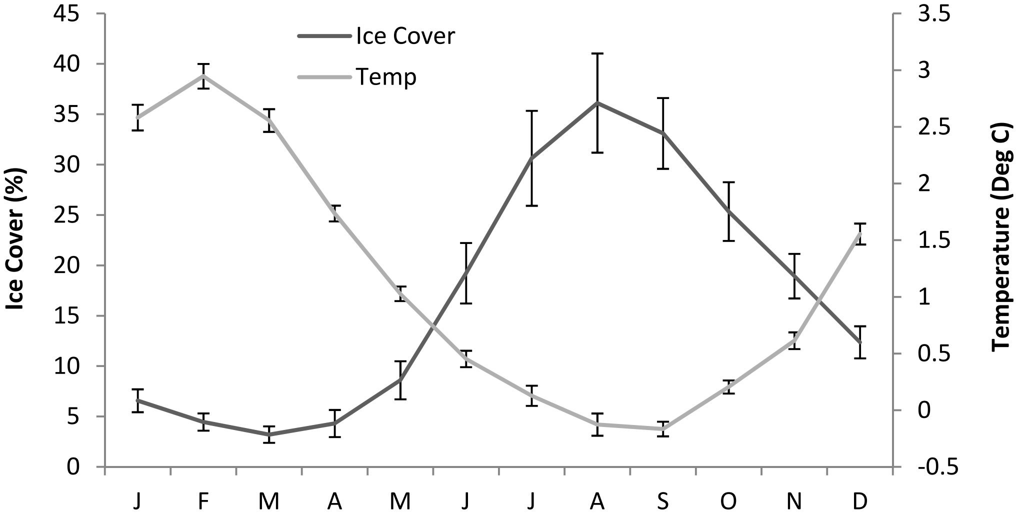

Figure 7: Ice cover and SST for data extracted from the HadISST global model for the Antarctic Peninsula model area (48.1). Values are presented as the mean monthly value from 1978-2009 with 95% confidence intervals indicated.

The 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 Niña years, while negative values are associated with El Niño years. SST is also affected by the changes in pressure, however, the SOI may give better insight as to factors determining salp abundance such as wind conditions and was therefore tested as a driver. Values for the SOI (figure 8) were taken from the PALMER station dataset (Stammerjohn 2007). All forcing functions were rescaled so that the average of the first year of the model (1978) was scaled to 1.

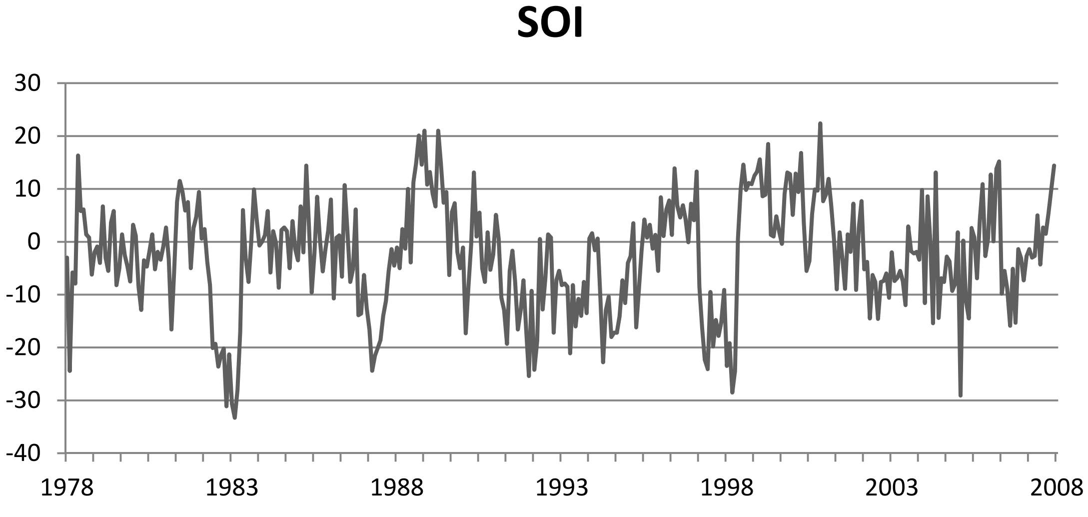

Figure 8: Southern Oscillation Index (SOI) from 1978-2008.

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 (reducing the 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). These forcing functions (FF) were used 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 timeseries of salps to model.

Other environmental timeseries 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 rescaled 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 Function

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 9). 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 (as a proxy for sea ice), 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).

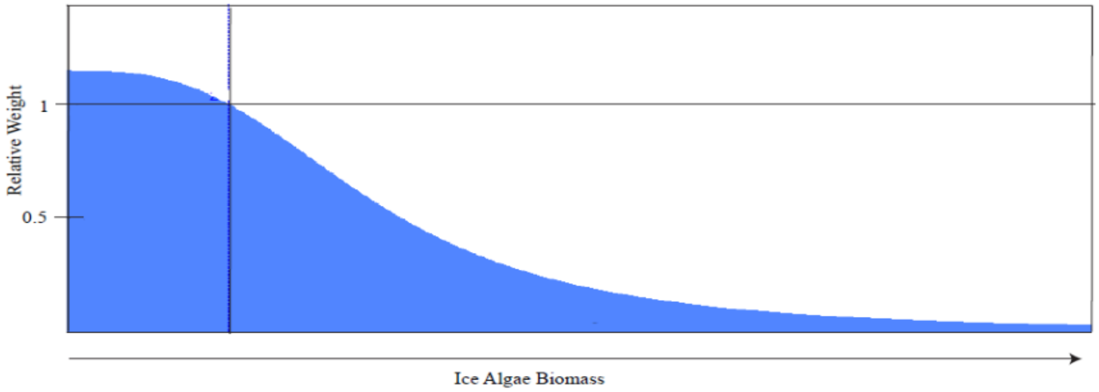

Figure 9: Mediation function for larval and juvenile krill. As ice algae biomass increases krill groups become less vulnerable to predators.

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 10). This mediation function was applied to all prey groups of salps under both fitting scenarios (SOI and SST).

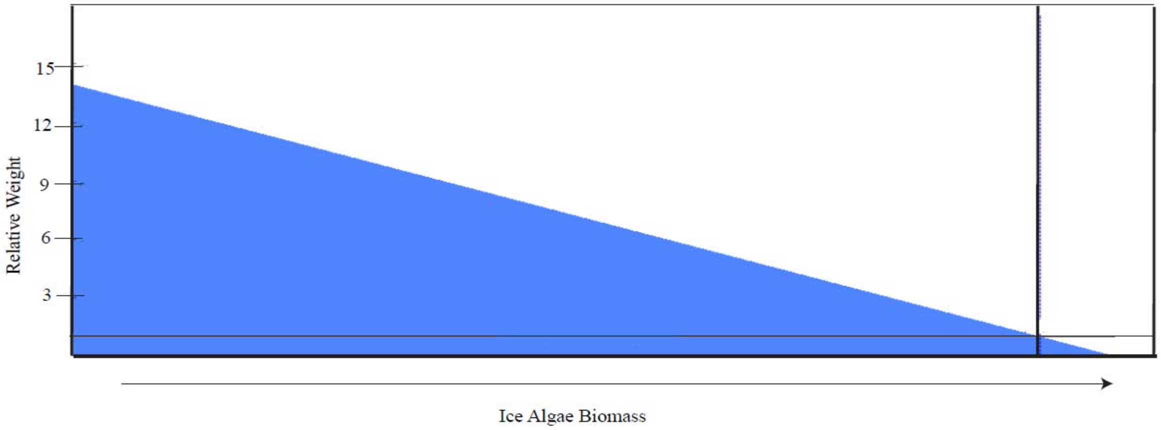

Figure 10: Mediation function used for the salp functional group. As ice increases (as determined by the biomass of ice algae) the foraging area for salps decreases. This was applied to all prey groups of salps.

A third mediation function to replicate salps dying at high food concentrations was tested to see if it would improve the fit. This 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 has caused death in lab experiments for the salp species, *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 phytoplankton 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 the other phytoplankton group increases, the search rate will also increase to a certain point and then drop off (knife-edge). 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 overall 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 terms were 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 feeding time beyond twice the Ecopath baseline value (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; Christensen *et al.* 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 also regulate the amount of time spent in the water foraging, but generally spend more time on land.

Vulnerabilities

Vulnerabilities were estimated by Ecosim using the fit to time series routine (Buszowski *et al.* 2007). 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 1.

RESULTS

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. The balanced vales are presented in table 10, showing parameters estimated by the model, with mixed trophic impacts in appendix 2. 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 (generally doubled) to balance these model groups.
3. The literature indicates a very strong dietary link between predators and krill. However, even 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 10 year^{-1} (Efran and Pitcher 2005), but was lowered as the predation mortality on prey items was too great. It was lowered to 2 year^{-1} in line with the cephalopod value for the Kerguelen Islands, a sub-Antarctic area (Provost *et al.* 2005).
5. Small changes were made to the P/B and Q/B values for invertebrates as these were mostly based on published values from other areas. Most alterations to calculated values were increases in order to balance the model.

Table 10: Balanced model with bolded values estimated by the model.

Group name	Trophic level	Biomass ($t \cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	P/Q
Killer Whales	4.543	0.001	0.050	11.000	**0.000**	**0.005**
Leopard Seal	4.139	0.006	0.120	8.100	**0.637**	**0.015**
Ross seal	4.123	0.004	0.130	15.300	**0.830**	**0.008**
Weddell seal	3.972	0.021	0.170	13.880	**0.689**	**0.012**
Crabeater Seal	3.423	0.164	0.090	15.860	**0.363**	**0.006**
Antarctic Fur Seals	3.694	0.028	0.175	25.000	**0.862**	**0.007**
S Elephant Seals	4.250	0.006	0.165	10.370	**0.437**	**0.016**
Sperm whales	4.203	0.005	0.034	7.330	**0.000**	**0.005**
Blue Whales	3.410	0.001	0.032	3.530	**0.683**	**0.009**
Fin Whales	3.441	0.003	0.035	4.120	**0.524**	**0.008**
Minke whales	3.270	0.065	0.064	6.340	**0.910**	**0.010**
Humpback whales	3.343	0.020	0.040	4.120	**0.963**	**0.010**
Emperor penguins	3.871	0.005	0.150	28.690	**0.933**	**0.005**
Gentoo Penguins	3.930	0.007	0.220	29.000	**0.642**	**0.008**
Chinstrap Penguins	3.917	0.005	0.330	34.000	**0.696**	**0.010**
Macaroni Penguin	3.670	0.014	0.300	25.000	**0.373**	**0.012**
Adélie Penguins	3.518	0.034	0.290	30.000	**0.793**	**0.010**
Flying birds	3.697	0.190	**0.340**	14.880	0.950	**0.023**
Cephalopods	3.404	2.490	0.950	2.000	**0.653**	**0.475**
Other Icefish	3.689	0.337	0.380	1.570	**0.726**	**0.242**
Toothfish	4.228	0.046	0.165	0.770	**0.627**	**0.214**
Lg Nototheniidae	3.335	0.590	0.370	1.950	**0.452**	**0.190**
Sm Nototheniidae	3.332	0.341	0.650	2.200	**0.873**	**0.295**
Shallow Demersals	3.375	0.031	0.750	4.125	**0.362**	**0.182**
Deep demersals Lg	3.684	0.042	0.290	2.180	**0.803**	**0.133**
Deep demersals Sm	3.687	0.080	0.650	2.700	**0.820**	**0.241**
Myctophids	3.263	0.185	1.350	3.730	**0.882**	**0.362**
Other Pelagics	3.776	0.490	0.550	2.020	**0.838**	**0.272**
C gunnari	3.391	0.290	0.480	1.800	**0.475**	**0.267**
P antarcticum	3.269	1.250	1.100	3.550	**0.603**	**0.310**
N gibberifrons	3.199	0.810	0.410	1.550	**0.645**	**0.265**
Mollusca	2.129	9.500	0.639	**2.556**	**0.608**	0.250
Salps	2.227	8.000	10.000	**33.333**	**0.010**	0.300
Urochordata	2.135	5.050	0.234	1.000	**0.554**	**0.234**
Porifera	2.000	12.719	0.159	0.795	**0.815**	**0.200**
Hemichordata	2.000	0.045	0.375	2.000	**0.534**	**0.188**
Brachiopoda	2.158	0.028	0.898	4.500	**0.590**	**0.200**
Bryozoa	2.108	0.491	0.475	1.750	**0.980**	**0.271**
Cnidaria	2.438	1.531	0.250	1.000	**0.982**	**0.250**
Crusteceans	2.374	3.613	1.050	**4.200**	**0.888**	0.250
Other Arthropods	2.929	1.010	0.616	3.326	**0.981**	**0.185**
Worms	2.438	12.000	0.700	3.200	**0.840**	**0.219**
Echinoidea	2.732	4.330	0.116	**0.464**	**0.774**	0.250
Crinoidea	2.428	0.164	0.125	0.800	**0.523**	**0.156**
Ophiuroidea	2.479	6.760	0.450	**1.800**	**0.551**	0.250
Asteroidea	2.345	1.778	0.231	**0.924**	**0.774**	0.250
Holothuroidea	2.000	5.450	0.316	1.100	**0.938**	**0.287**
Krill						
Krill Adult	2.529	9.08	1.500	33.000	**0.672**	**0.045**
Krill Juvenile	2.250	25.260	0.900	49.481	**0.788**	**0.018**
Krill Larvae	2.000	0.879	2.500	149.443	**0.011**	**0.017**
Krill Embryo	2.000	0.006	8.000	698.506	**0.237**	**0.011**
Macro-Zoopl	2.154	8.170	**7.577**	**25.257**	0.950	0.300
Micro-Zoopl	2.000	2.900	65.000	110.000	**0.982**	**0.591**
Cryptophytes	1.000	2.200	80.000	0.000	**0.983**	
Copepods	2.150	15.200	**26.066**	50.000	0.950	**0.521**
Diatoms	1.000	17.410	90.510	0.000	**0.396**	
Ice algae	1.000	25.000	45.000	0.000	**0.874**	
Other Phytopl	1.000	5.500	105.000	0.000	**0.806**	
Detritus	1.000	3.430			**0.176**	

Fitting the Model

The model was fit under 2 conditions: The first fitting (A) used SOI to drive cryptophytes and the other phytoplankton group, and the second fitting (B) used temperature to drive cryptophytes and other phytoplankton. For both attempts at fitting the model sea ice was used as a forcing to ice algae and diatoms as well as previously stated mediation functions for krill and salps. There was no difference to the fit of penguin groups. Declines in adélie penguins were captured through the decline of the main prey item krill, which was linked to sea ice. For the chinstrap and gentoo penguins it was not possible to obtain increases in the population while food sources (krill, cephalopods, and fish) declined. 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 9), 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). Comparison of the krill time series data with model output shows that 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 23 $t{\cdot}km^{-2}$ while the highest biomass for juveniles was in 1988 at just over 58 $t{\cdot}km^{-2}$ 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 (A and B) arose 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 11). 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 6 for graphs of all functional groups).

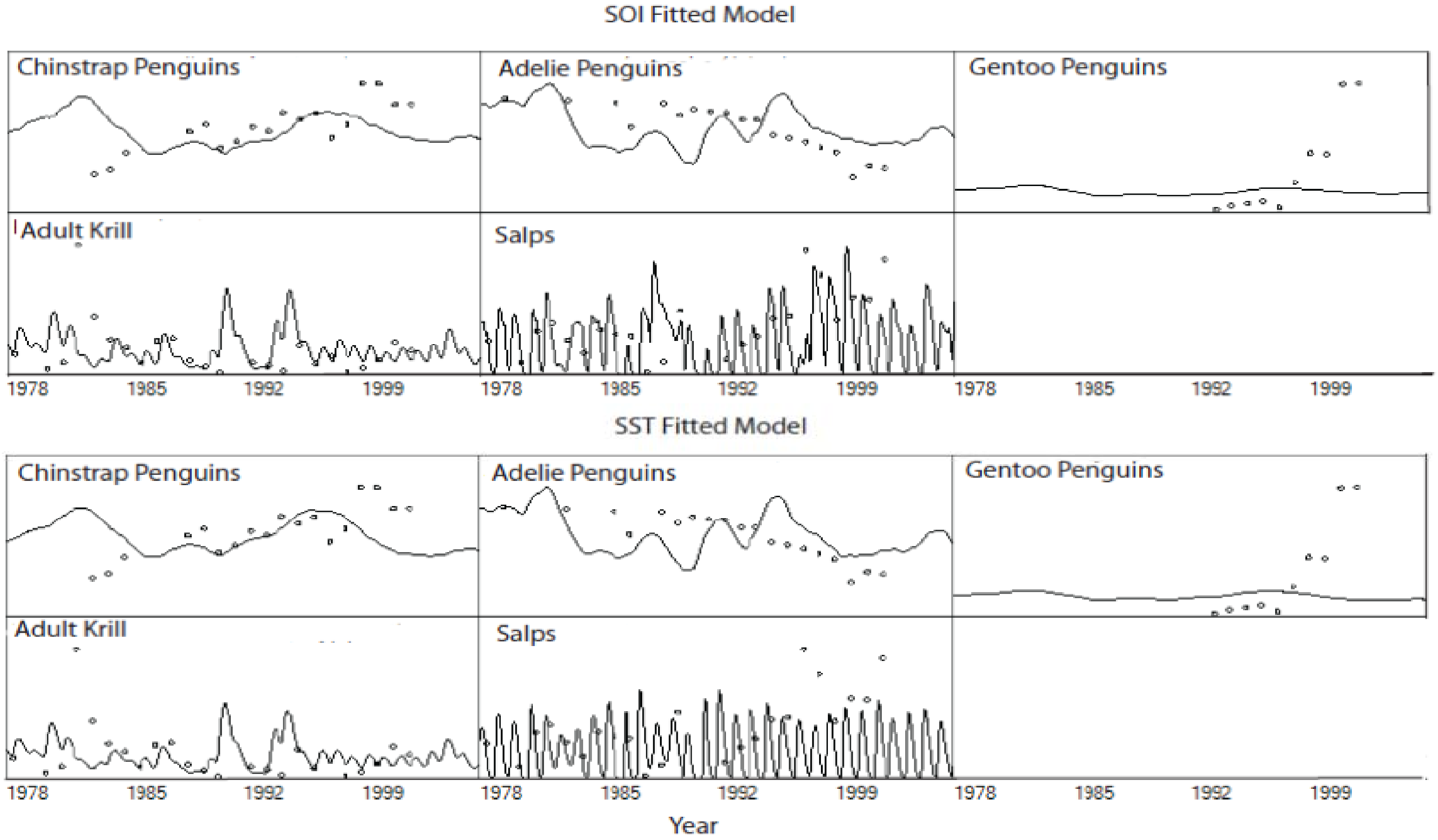

Figure 11: Fitted model using SOI (top) and temperature (bottom) to drive cryptophytes and the other phytoplankton model groups. Note the simulation forced with temperature also includes a mediation function. Starting values on the y-axis are set to the biomass starting value.

Table 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·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	0.020	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	0.000	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	0.020	0.026
13	Emperor penguins	0	0.001	0.005	0.009
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	Adélie Penguins	0.7	0.024	0.034	0.044
18	Flying birds	0.4	0.095	0.190	0.285
19	Cephalopods	0.4	1.245	2.490	3.735
20	Other Icefish	0.7	0.236	0.337	0.438
21	Toothfish	0.7	0.032	0.046	0.060
22	Large Nototheniidae	0.7	0.413	0.590	0.767
23	Small Nototheniidae	0.7	0.239	0.341	0.443
24	Shallow Demersals	0.7	0.022	0.031	0.040
25	Deep demersals Lg	0.7	0.029	0.042	0.055
26	Deep demersals Sm	0.7	0.056	0.080	0.104
27	Myctophids	0.7	0.130	0.185	0.241
28	Other Pelagics	0.7	0.343	0.490	0.637
29	C. gunnari	0.7	0.203	0.290	0.377
30	P. antarcticum	0.7	0.875	1.250	1.625
31	N. gibberifrons	0.7	0.567	0.810	1.053
32	Mollusca	1	8.550	9.500	10.450
33	Salps	1	7.200	8.000	8.800
34	Urochordata	1	4.545	5.050	5.555
35	Porifera	1	11.447	12.719	13.991
36	Hemichordata	1	0.041	0.045	0.050
37	Brachiopoda	1	0.025	0.028	0.030
38	Bryozoa	1	0.442	0.491	0.540
39	Cnidaria	1	1.378	1.531	1.684
40	Crusteceans	1	3.252	3.613	3.974
41	Arthropod Other	1	0.909	1.010	1.111
42	Worms	1	10.800	12.000	13.200
43	Echinoidea	1	3.897	4.330	4.763
44	Crinoidea	1	0.147	0.164	0.180
45	Ophiuroidea	1	6.084	6.760	7.436
46	Asteroidea	1	1.600	1.778	1.956
47	Holothuroidea	1	4.905	5.450	5.995
48	Krill Adult	1	8.172	9.080	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	8.170	10.621
53	Micro-Zooplankton	0.7	2.030	2.900	3.770
54	Cryptophytes	0.7	1.540	2.200	2.860
55	Copepods	0.4	7.600	15.200	22.800
56	Diatoms	0.7	12.187	17.410	22.633
57	Ice algae	0.7	17.500	25.000	32.500
58	Other Phytoplankton	0.4	2.750	5.500	8.250

Monte Carlo Estimates

Coefficient of Variation (CV) values were assigned based on pedigree ranking of input data (Christensen *et al.* 2005), and are provided in appendix 3. 1000 iterations were unable to improve SS value; however they did provide ranges of acceptable input parameter values. Estimates of all parameters in the Monte Carlo routine are provided in appendix 4. A summary of the biomass values obtained are provided in table 11 along with mean and 95% CI. Graphs for biomass are provided in appendix 5.

While the CV values for marine mammals were 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 staring 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 predator's 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 per the pedigree ranking in Ewe version 5. 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 *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).

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 for environmental forcing.

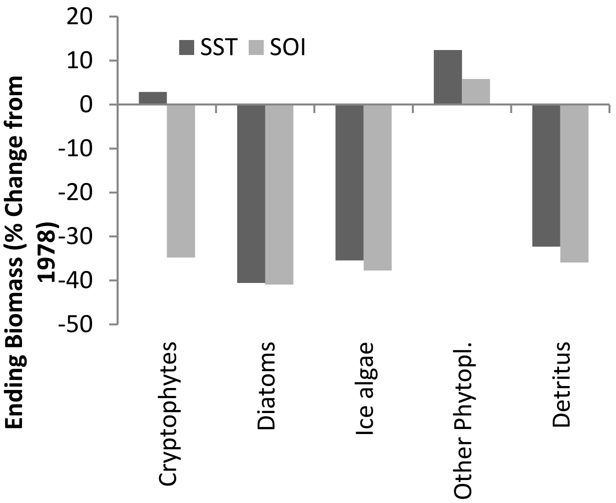

Figure 12 : Model end biomass presented as percent change from the starting Ecopath biomass for producers and detrital groups.

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 12). As these groups are large contributors to detritus, the declines in these groups drive a decline in detritus. The other phytoplankton group increases under both scenarios, however cryptophytes only 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. 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 respectively), 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.

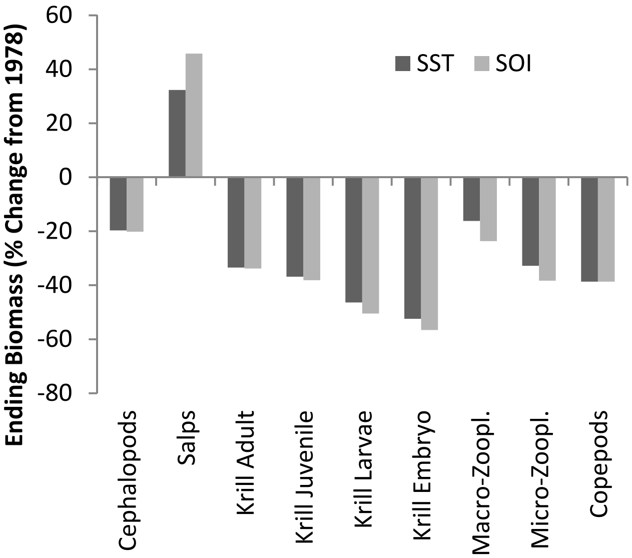

Figure 13: Model end biomass presented as percent change from the starting biomass for zooplankton functional groups.

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 13). 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 a have larger foraging area when sea ice decreases. Both factors contribute to 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 (i.e. changes from starting biomass are lower for the SST fitted model), 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 t·km^{-2} with ending values of total krill biomass at 24.1 and 24.4 t·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 6), but the SOI fitted model shows higher biomass peaks from 1990 onward due to more extreme values in the forcing function being propagates up the food web.

The decline occurring in most benthic groups (figure 14) is primarily caused by decreases in detritus as a food source. This then causes declines in many benthic species which serve as prey items for benthic scavengers. For example the diet of worms was set to ~60% detritus in the Ecopath model, therefore a reduction in this food source (detritus) contributed to the decline of worms, which in turn contributes to the decline of other benthic groups. The Echinoidea group fares the best under both scenarios as predators such as

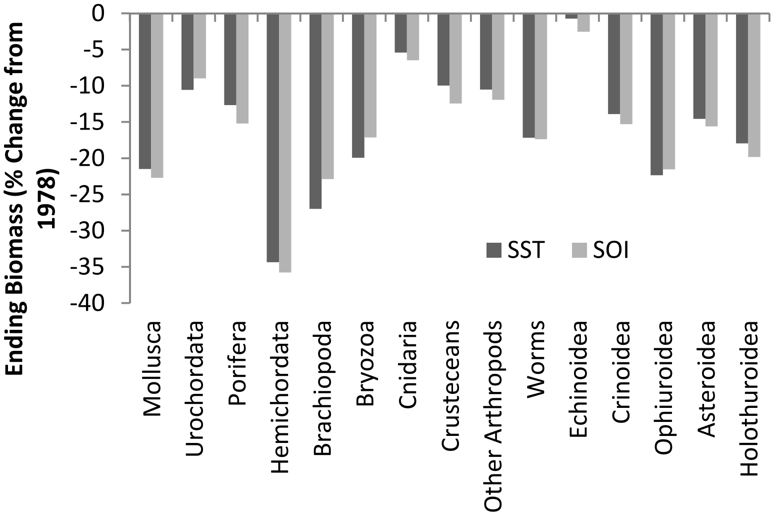

Figure 14: Model end biomass presented as percent change from the starting biomass for benthic functional groups.

worms and other arthropods decrease. The hemichordata group 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.

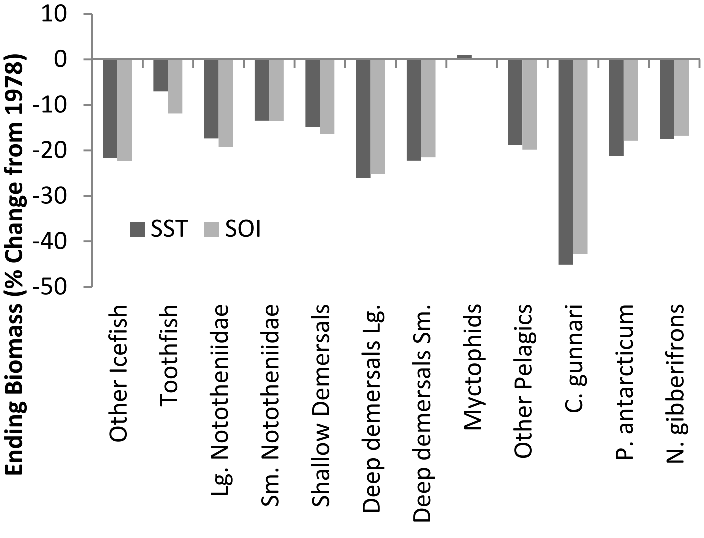

Figure 15: Model end biomass presented as percent change from the starting biomass for fish functional groups.

All fish groups in the model show declines under both fitted models, with the exception of myctophids (figure 15). 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, as total mortality remains close to the starting value throughout the model fitting. While declines appear high, biomass trends show fluctuations throughout the simulations with the ending biomass at low values (appendix 6). 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.

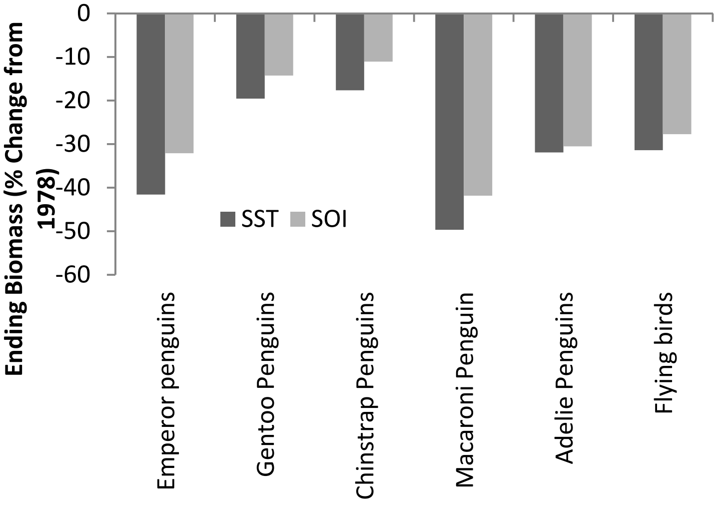

Figure 16: Model end biomass presented as percent change from the starting biomass for bird functional groups.

Penguin and marine mammal groups show varying levels of declines for both fitted models (figures 16 and 17). 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 marine mammal and penguin 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, 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. Adélie 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 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.

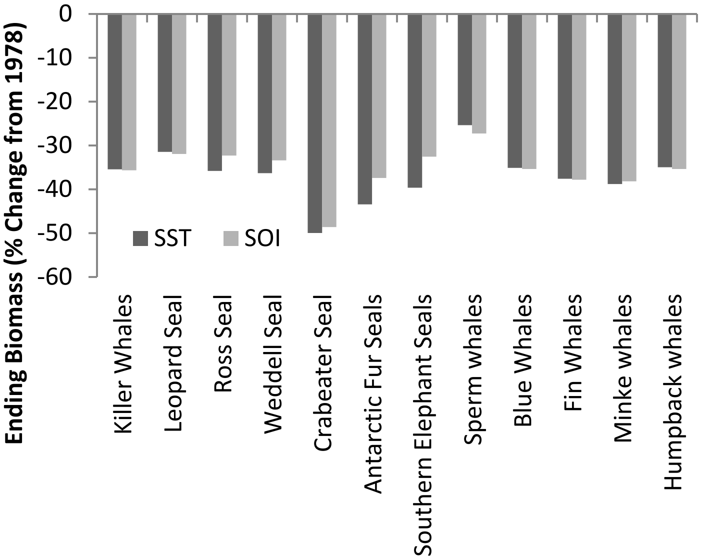

Figure 17: Model end biomass presented as percent change from the starting biomass for marine mammal functional groups

Crabeater and Antarctic fur seals show the largest declines in biomass of roughly 50% and 40% for each group (figure 17). 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 region, 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 the same year, 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 6). 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, suggesting these species may not recover as quickly. 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.

DISCUSSION

The fitted model using SST was selected, as it provided a lower SS (68.47 compared to the SOI model of 78.95). Although the salp trend is not captured as well in more recent years (1998 onwards), recent evidence suggests there may have been a levelling out of salp abundance resulting in smaller fluctuations than the data suggests[14] . The model fitted using SOI provides a better fit to salps as it captures the dynamics in later years (after 1998), through more extreme forcing function values acting on primary producers. However, the inclusion of the salp mediating function for both models lowers the SS value for the SST driven model below that of the SOI driven model.

The fitting process for krill fails to capture the high biomass in 1982. This 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 6), juvenile krill have a larger biomass and a slightly different trend over time. Combination of these groups could provide a better fit to data; however peak biomasses for both groups occur in

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[14] Pakhomov (pers. comm.) indicated the KRILLBASE dataset was to be reviewed in order to assess the possibility of more constant salp biomass since 1998.

different years (1992 and 1996 for adult krill and 1981 and 1988 for juvenile krill). Sampling of zooplankton is inherently highly variable, and could add to variability in data used to fit the model. Finally reported values in the timeseries are based on abundance, not biomass and thus could be prone to extreme recruitment events (see Siegel *et al.* 1998). While the timeseries is applied as a relative biomass, it is possible that abundance of krill and biomass of krill would have different patterns as krill can grow and shrink throughout their life (McGaffin *et al.* 2002).

Differences between the two model fits show changes to the ending composition of producers. However, total production biomass remains fairly constant. Cumulative starting biomass for all producer groups was 53.63 t·km^{-2}, with the ending value for SST fitted model at 38.15 t·km^{-2} and as ending value of 37.45 t·km^{-2} for the model fitted with SOI. The greatest differences between the two fitted models are between biomass trends for the other phytoplankton group and cryptophytes, as these were the groups forced with either SST or the SOI. Cryptophytes show the same biomass trends (appendix 6) with more extreme values under the SOI fitted model, while the trend for the other phytoplankton group differs between the two fitted models for some years. Overall the decrease in primary production of nearly 40% (for all producer group biomass combined) is much higher than the 10% estimate from Gregg *et al.* (2003) for the Antarctic. Although it should be noted that the decline of 10% is from satellite data and most excludes the contribution of ice algae to total production. *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 94-96, showed low values from 97-98 and increased again in 99-00 and 2002 (Loeb *et al.* 2010). In the Antarctic ice algae from multiyear ice can contribute at least 20% to total production, with fast ice showing *chl a* concentrations up to 120 mg chl a·m^{-2} (McMinn *et al.* 2000) or roughly 30 g·m^{-2} wet weight[15]. 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. With these considerations, declines of 40% as shown by the ecosystem model may be high, but still within realistic values when considering the contribution of sea ice algae.

Both fitted models indicate that changes in primary production and detritus are responsible for a majority of 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 levels are highly influenced by lower trophic levels indicating this is a bottom up system. In addition, predation mortality for many groups remains constant to the starting value, indicating top-down pressure is not increasing. While declines are large for some species, there is the possibility they are underestimated due to the high energetic value of krill. Replacement of krill by other species in the diet of predators may cause dramatic impacts on higher trophic levels (Dubischar *et al.* 2006), depending on the energetic value of the replacement prey item. Further simulations and energetic analysis are needed in order to address suitable prey replacements for krill.

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. The recorded increase at PALMER station for chinstrap and gentoo penguins (Fraser 2006) cannot be captured by the model suggesting there is additional information needed to capture these dynamics, or the increase at this particular location is not representative of the entire model region. Most likely, it is a combination of these two reasons the model cannot fit these data. Further use of this model should re-assess the penguin trends with the most recent data. This would include removing the biomass accumulation terms (which accounts for immigration), as the newer data suggest this is not the case. Further, the inability to capture such increases to gentoo and chinstrap penguins lends credibility to the model results, that in fact declines in krill are substantial enough to prevent increases in these groups, even with the inclusion of biomass accumulation terms. Within the framework of the model, declines in krill are the primary factor in penguin declines.

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[15] Using the following conversions: 0.36 mg Chl a=1 mg C (Cloern *et al.* 1995) and 1gC=9gww (Pauly and Christensen 1995)

While krill and salps show large inter-annual variations, or "boom and bust" cycles (Brierley and Reid 1999), it has been suggested population fluctuations have levels out since the mid 1990s (Loeb *et al.* 2009; Lee *et al.* 2010). This would indicate that populations have stabilized. Stabilizing of air and sea temperature in the Indian sector of the Southern Ocean is believed to be responsible for suggested regime shifts in this region (Weimerskirch *et al.* 2003). If this is the case for the Antarctic Peninsula also, the ecosystem may demonstrate less annual fluctuations at lower trophic levels in the future. However, based on the model results, this stabilization may be short lived.

The construction and simulations of the ecosystem model identify strong bottom-up interactions in the food web. Monte Carlo analysis reveals the ecosystem is able to support a higher biomass than the current model values. Both point to stong ecosystem connections to the krill group in that the transfer of energy from producers to predators through krill is an important link. Further simulations testing the model sensitivity will be useful in determining how the ecosystem will respond to different stressors and their potential effects to the ecosystem. This model is presented as a first step towards this goal.

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APPENDIX 1 : VULNERABILITIES USED FOR THE FITTED MODEL

Prey \ predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
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																	
Adélie Penguins	2	1																2	
Flying birds	2	2																2	
Cephalopods		2	2	2	2	2	2	2			2	2	2	10	10	2	2	2	2
Other Icefish		2	2	2		2	2						2	2	2	2		2	2
Toothfish							2	2											2
Large Nototh		2	2	2		2	2						2	2	2	2		2	2
Small Nototh		2	2	2		2							2	2	2	2		2	2
Shallow Demersals		2	2			2											2		
Deep demersals Lg.		2	2	2		2		2						2	2				
Deep demersals Sm.		2	2	2		2		2						2	2	2			
Myctophids		2	2	2	2	2	2		2	2	2	2				2	2	2	2
Other Pelagics		2	2	2	2	2	2		2	2	2	2				2	2	2	2
C. gunnari		2	2	2		2								2	2	2			
P. antarcticum		2	2	2	2		2		2	2	2	2	2	2	2	2	2	2	2
N. gibberifrons		2	2	2		2								2	2	2		2	
Mollusca			2	2	2		2	2									2	2	2
Salps			2		2			2						1	1			2	2
Urochordata														1	2				2
Porifera														2	2				
Hemichordata								2						2	2				
Brachiopoda								2						2	2				
Bryozoa								2						2	2				
Cnidaria			2					2						2	2			2	2
Arth Crustecea			2	2			2	2					2	2	2	2	2	2	2
Arth Other			2	2															2
Worms			2	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	2	1	2	2
Krill Juvenile		2	2	2	2	2	2	2	2	2	2	2	2	10	2	2	1	2	1
Krill Larvae																			
Krill Embryo																			
Macro-Zoopl.					2				2	2	2	2		2	2		2		2
Micro-Zoopl.					2				2	2	2								2
Cryptophytes									2	2	2								
Copepods									2	2	2	2						2	
Diatoms									2	2	2								
Ice algae									2	2									
Other Phytopl.									2	2	2								
Detritus																			

APPENDIX 1 (CONTINUED): VULNERABILITIES

Prey \ predator	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
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																				
Adélie Penguins																				
Flying birds																				
Cephalopods	2	2				2	2		2											
Other Icefish	2	2				2	2		2		2									
Toothfish	2		2			2														
Large Nototh	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											
Deep demersals Sm.	2	2	2			2	2		2		2									
Myctophids		2	2				2		2	2										
Other Pelagics		2	2				2		2		2									
C. gunnari	2	2	2			2														
P. antarcticum	2	2	2			2	2		2		2									
N. gibberifrons	2	2	2			2					2									
Mollusca	2		2	2	2	2	2	2	2		2	2								
Salps	2	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								
Arth Other	2	2	2	2	2	2	2				2	2								
Worms	2	2	2	2	2	2	2	2	2	2	2	2	2					2		2
Echinoidea				2														2		
Crinoidea				2														2		
Ophiuroidea				2														2		
Asteroidea				2														2		
Holothuroidea				2								2						2		
Krill Adult	2	2	2	2	2	2	2	2	2	2	2	2						2		
Krill Juvenile	2	2	2	2	2	2	2	2	2	2	2	2						2		
Krill Larvae			2	2		2	2					2						2		
Krill Embryo			2			2	2											2		
Macro-Zoopl.	2		2	2		2	2	2	2	2	2	2	2	2				2		2
Micro-Zoopl.	2			2		2	2		2	2	2	2	2	10	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
Ice algae			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

APPENDIX 1 (CONTINUED): VULNERABILITIES CONTINUED

Prey \ predator	40	41	42	43	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															
Adélie 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	2		2	2								
Salps		2	100				2								
Urochordata		2	2	2			2								
Porifera	2	2	2	2		2	2								
Hemichordata				2											
Brachiopoda				2											
Bryozoa	2	2	2	2	2	2									
Cnidaria	2	2	2	2		2									
Arth Crustecea	2	2	2	2	2	2	2								
Arth Other	2	2	2	2											
Worms	2	2	2	2	2	2	2								
Echinoidea		2	2												
Crinoidea		2	2	2											
Ophiuroidea		2	2	2		2	2								
Asteroidea		2	2	2											
Holothuroidea	2	2	2	2											
Krill Adult													1		
Krill Juvenile									2				1		
Krill Larvae		2							1						
Krill Embryo		10		2					1.3						
Macro-Zoopl.	2	2	2	2	2	2	2		2	2					
Micro-Zoopl.		2	2	2	2	2	2		2	2			3		
Cryptophytes						2			10	4.6	2		1	3	
Copepods	2	2		2	2	2	2		2	2			2		
Diatoms			2	2		2	2	2	2	2	2		2	2	3
Ice algae	2			2		2	2		2	2	2		1	2	2
Other Phytopl.	2			2		2	2	2	2	100	2		1	3	3
Detritus	2	2	2	2	2	2	2	2	2	2		2	2	2	2

APPENDIX 2: MIXED TROPHIC IMPACTS

		Killer Whale	Leopard seal	Ross seal	Weddell seal	Crabeater Seal	Antarctic fur seal	Southern Elephant seal	Sperm whale	Blue whale	fin whale	Minke whale	Humpback whale	Emperor penguin	Gentoo Penguin
	Impacting \ Impacted	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Killer Whale	-0.31	-0.62	-0.05	-0.34	0.095	0.288	0.575	-0.05	-0.71	-0.7	-0.7	-0.71	0.6	0.329
2	Leopard seal	-0.12	-0.01	-0.34	-0.12	-0.5	-0.64	-0.85	0.154	0.167	0.162	0.139	0.175	-0.9	-0.66
3	Ross seal	0.013	-0.01	-0.01	-0.01	0.002	0.001	-0	-0.01	-0.01	-0.01	-0.01	-0.01	0.006	-0
4	Weddell seal	0.107	-0.09	-0.04	-0.08	0.015	0.033	0.049	-0.04	-0.11	-0.11	-0.1	-0.1	0.068	0.029
5	Crabeater Seal	0.103	-0.08	-0.04	-0.08	-0.06	-0.02	0.042	-0.04	-0.16	-0.16	-0.13	-0.17	0.022	0.009
6	Antarctic fur seal	0.05	-0	-0.06	-0.05	-0.02	-0.03	-0.04	-0.04	-0.05	-0.05	-0.05	-0.05	-0.01	-0.04
7	S Elephant seal	-0	0.007	-0.01	-0.01	-0	-0.01	-0.03	-0.02	0.002	0.002	0.002	0.003	-0.01	-0.01
8	Sperm whale	0	-0	-0	-0	0.001	-0	-0.01	-0.01	0.001	0.001	0	0.001	0	-0
9	Blue whale	0.001	-0	0	0	0	0	0.001	0	-0	-0	-0	-0	0.001	0
10	fin whale	0.003	-0	0	-0	0	0.001	0.003	0	-0	-0	-0	-0	0.003	0.002
11	Minke whale	0.236	-0.22	-0.02	-0.12	0.029	0.096	0.199	-0.02	-0.25	-0.25	-0.24	-0.25	0.204	0.114
12	Humpback whale	0.048	-0.05	-0	-0.02	0.005	0.019	0.041	-0	-0.05	-0.05	-0.05	-0.05	0.041	0.023
13	Emperor penguin	-0	0.012	-0.02	-0.01	-0.01	-0.01	-0.02	-0.01	0.003	0.003	0.003	0.003	-0.02	-0.02
14	Gentoo Penguin	0.005	-0	-0.02	-0.01	0	-0.01	-0.02	-0.03	-0	-0	-0	-0	-0	-0.03
15	Chinstrap penguin	0.012	-0.01	-0.02	-0.01	0.001	-0	-0.01	-0.03	-0.01	-0.01	-0.01	-0.01	0.004	-0.02
16	Macaroni Penguin	0.001	0.017	-0.02	-0.01	-0.01	-0.02	-0.03	-0.01	-0	-0	-0	-0	-0.02	-0.03
17	Adélie Penguin	0	0.065	-0.04	-0.03	-0.06	-0.07	-0.06	0.005	-0.02	-0.02	-0.01	-0.03	-0.09	-0.06
18	Flying birds	-0.01	-0.02	-0.05	-0.03	0.006	-0.02	-0.1	-0.12	-0	-0	0.003	-0	-0.01	-0.03
19	Cephalopods	0.012	0.097	0.267	0.129	-0.08	0.048	0.481	0.617	-0.06	-0.05	-0.02	-0.04	-0.01	0.163
20	Other Icefish	-0	0.012	-0.01	-0.02	-0	-0.02	0.005	-0	0.009	0.008	0.005	0.008	-0.01	-0.04
21	Toothfish	0	-0	-0	0	0.001	0	0.013	0.013	0	0	0	0	0	0
22	Lg Nototheniidae	0	0.001	0.029	0.012	-0.01	0.01	-0.01	0.001	-0.01	-0.01	-0	-0.01	0.017	0.023
23	Sm Nototheniidae	-0	0.007	-0	0.001	-0.01	-0	-0.01	-0	-0	-0	0	-0	0.017	0.028
24	Shallow demersals	-0	0.01	-0	-0	-0.01	-0.01	-0.01	0.001	0.001	0.001	0.002	0.002	-0.01	-0.01
25	Deep demersals lg	0	0.001	-0	-0	0	-0	-0	0.003	0.001	0.001	0	0.001	-0	0.002
26	Deep demersals sm	0	0.005	-0	-0	-0	-0	-0.01	0.018	-0	-0	0	0	-0.01	0.024
27	Myctophids	0	0.006	0.011	0.004	-0.01	0.001	0.066	-0	0.044	0.045	0	0.005	-0.01	-0.01
28	Other pelagics	-0	-0.01	-0.05	-0.03	0.004	-0	-0.08	-0.1	0.014	0.014	0.008	0.004	-0.03	-0.03
29	C. gunni	-0	0.003	0.015	0.018	-0.02	0.01	-0.01	-0	-0.01	-0.01	-0.01	-0.01	-0.01	0
30	P. antarcticum	0.014	-0.01	0.124	0.177	-0.01	-0.02	0.044	0.026	-0.02	-0.01	-0.03	-0.04	0.185	0.009
31	N. gibberifron	0	0.003	0.013	0.012	-0.01	0.014	-0.01	-0.01	-0.01	-0.01	-0	-0.01	-0.01	0.056
32	Mollusca	0.021	-0.01	0.04	0.175	0.019	-0.01	0.094	0.018	-0.02	-0.02	-0.03	-0.03	0.021	0.001
33	Salps	-0	0.006	0.017	0.001	0.008	0.002	0	0.027	0.003	-0	-0.01	0.004	-0	0.018
34	Urochordata	0	0.004	0.01	0.004	-0	0.002	0.017	0.023	-0	-0	-0	-0	-0	0.025
35	Porifera	-0	0	-0	-0	-0	-0	-0	-0	0	0	-0	0	-0	0.008
36	Hemichordata	0	0	-0	-0	0	0	-0	0.004	0	0	0	0	0	0.019
37	Brachiopoda	0	0	-0	-0	0	0	-0	0.004	0	0	0	0	0	0.014
38	Bryozoa	0	0	-0	0	0	0	-0	0.004	0	0	0	0	0	0.014
39	Cnidaria	0.001	0.001	0.002	-0	0.001	0.001	-0	0.011	0.002	0.001	0.001	0.002	0	0.025
40	Crustaceans	0.007	0.015	0.047	0.074	-0.02	0.002	0.017	0.011	-0	-0	-0.01	-0.01	0.009	0.029
41	Arthropod other	-0	0.001	0.006	-0.01	-0	0.001	0.004	0.008	-0	-0	0.002	0.001	0	-0.01
42	Worms	0.004	0.011	0.006	-0	0	0.013	-0.01	0.011	0.011	0.008	0.003	0.011	0.009	0.003
43	Echinoidea	0	-0	-0	-0	0.001	0	-0	-0	0	0	0	0.001	0	-0.01
44	Crinoidea	0	0	0	0	0	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	0.003	0.005	0.007	-0.01	-0.01
46	Asteroidea	0	0	0	0	0	0	0	-0	0	0	0	0	0	-0
47	Holothuroidea	0	0.001	0.001	0	-0	0	0	0.004	0	0	0	0	0	0
48	Krill Adult	0.105	0.159	-0.09	-0.1	0.262	0.18	-0.15	0.033	0.263	0.24	0.02	0.339	0.102	0.056
49	Krill Sub-adult	0.102	0.052	0.003	-0.1	0.189	0.206	-0.01	0.101	0.158	0.054	0.158	0.149	0.112	-0.1
50	Krill juvenile	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	Krill Larvae	0	0	0	-0	0	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	-0.13	-0.01	-0.2	-0.06	0.106
53	Micro-zoopl.	0.017	-0.01	0.015	-0	0	0.009	0.042	0.035	-0.02	-0.01	0.054	-0.03	0.018	0.01
54	Cryptophytes	0.005	-0.01	0.015	0.007	-0	-0.01	0.023	0.022	-0.01	0.009	0.014	-0.02	0.003	0.028
55	Copepods	0.022	0.03	-0.02	-0.01	0.05	0.041	-0.04	-0.02	0.069	0.057	0.004	0.082	0.039	-0.03
56	Diatoms	0.037	0.016	0.005	-0	0.052	0.042	0.01	0.024	0.051	0.073	0.044	0.054	0.047	0.021
57	Ice Algae	0.067	0.042	0.002	-0.03	0.116	0.097	0.002	0.061	0.096	0.08	0.075	0.111	0.072	0.036
58	Other phytopl.	0.01	-0.01	0.028	0.018	-0.01	-0.01	0.044	0.039	-0.02	0.004	0.027	-0.03	0.008	0.051
59	Detritus	0.044	0.016	0.06	0.123	0.042	0.048	0.069	0.063	0.021	0.001	0.018	0.009	0.049	0.036
	Krill Fishery	-0	-0	0.001	0.001	-0	-0	0.001	0	-0	-0	0	-0	-0	0
	Other Fishery	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2 (CONTINUED): MIXED TROPHIC IMPACTS

		Chinstrap penguin	Macaroni Penguin	Adélie Penguin	Flying birds	Cephalo-pods	Other Icefish	Tooth-fish	Large Noto.	Small Noto	Shallow demersals	Deep demersals large	Deep demersals small	Mycto-phids	Other pelagics
	Impacting \ Impacted	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	Killer Whale	0.158	0.5	0.32	-0	-0.06	-0.06	-0.11	-0.14	-0.01	-0.06	-0.08	-0.05	-0	-0.01
2	Leopard seal	-0.51	-0.82	-0.52	0.017	0.183	0.134	0.136	0.327	0	0.044	0.223	0.129	0.009	0.049
3	Ross seal	-0	0.006	0.006	-0	-0.02	-0.01	0.005	-0.02	0.003	-0	-0	-0	0.001	0
4	Weddell seal	0.001	0.067	0.049	-0	-0.06	-0.02	0.002	-0.09	-0	0.014	-0.03	-0.02	-0.01	0
5	Crabeater Seal	-0.02	0.008	-0.03	-0.02	-0.04	-0.01	0.003	-0	0.018	0.031	-0	0.004	-0.03	-0.04
6	Antarctic fur seal	-0.04	-0.02	-0	-0.01	-0.06	-0.08	0.006	-0.12	0.004	-0.04	-0.03	-0	0.013	-0.02
7	S Elephant seal	-0.01	-0.01	-0	-0	-0.02	0.008	-0.19	0.008	0.008	-0	0.006	0.001	-0.02	-0
8	Sperm whale	-0.01	0.001	0.002	-0	-0.01	0.011	-0.1	0.004	0.005	0.008	-0.04	-0.01	0.004	0
9	Blue whale	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	fin whale	0.001	0.002	0.001	0	0	0	-0	-0	0	0	0	0	-0	-0
11	Minke whale	0.055	0.169	0.107	-0	-0.02	-0.02	-0.04	-0.05	0	-0.02	-0.03	-0.02	0.002	-0.01
12	Humpback whale	0.011	0.034	0.021	-0	-0.01	-0	-0.01	-0.01	0	-0	-0.01	-0	-0	-0
13	Emperor penguin	-0.01	-0.01	-0.01	-0	-0.02	-0.01	0.007	-0.03	-0.01	0.007	0.009	0.008	0.009	0.006
14	Gentoo Penguin	-0.03	-0	0.003	-0	-0.03	-0.02	0.022	-0.05	-0.01	0.066	-0.18	-0.09	0.018	0.006
15	Chinstrap penguin	-0.03	0.002	0.006	-0	-0.04	-0.01	0.031	-0.04	0.011	0.056	-0.18	-0.09	0.016	0.004
16	Macaroni Penguin	-0.02	-0.03	-0.01	-0	-0.01	-0.05	-0.01	-0.14	-0.01	0.028	0.03	-0.02	-0	0
17	Adélie Penguin	-0.05	-0.08	-0.08	-0.01	0.009	0.011	0.009	0.023	0.004	-0.35	0.009	0.008	-0.02	-0.04
18	Flying birds	-0.04	-0.01	-0.17	-0.51	-0.16	-0.13	0.054	0.014	-0.11	0.045	0.044	-0	-0.08	-0.1
19	Cephalopods	0.225	-0.03	-0.1	0.078	-0.16	-0.05	-0.5	-0.09	-0.1	0.066	-0.07	-0	-0.19	0.036
20	Other Icefish	-0.02	-0.01	-0	0.007	-0	-0.1	0.092	-0.11	-0.05	0.102	-0.16	-0.07	0.03	0.026
21	Toothfish	0	0	0.002	-0	-0	-0.07	-0.02	-0.01	-0.02	0	0	0	-0	-0
22	Lg Nototheniidae	0.019	0.031	-0.01	-0.01	0.005	0.022	0.033	-0.09	-0.09	-0.13	-0.1	-0.08	-0.09	-0.09
23	Sm Nototheniidae	0.001	0.006	-0.02	0.005	-0.01	0.005	0.138	-0.01	-0.04	-0.05	0.022	0.04	-0.02	0.008
24	Shallow demersals	-0.01	-0.01	-0	-0	0.001	0	-0	-0	-0.01	-0.02	0.02	-0	-0.01	0
25	Deep demersals lg	0.002	-0	-0	0	-0	-0.01	-0.09	-0.03	0	-0.19	-0.01	-0.14	0.01	0.009
26	Deep demersals sm	0.025	-0	-0	-0	-0	-0.09	-0.02	0.008	-0.07	-0.14	0.069	-0.05	-0.03	-0.04
27	Myctophids	-0.01	0.009	-0.01	0.006	-0	-0.01	-0	0.007	-0.02	-0.03	-0.01	0.026	-0.03	0.02
28	Other pelagics	-0.04	0.004	0.009	-0.01	-0.12	-0.08	0.07	0.043	-0.05	0	-0.07	0.033	-0.1	-0.07
29	C. gunni	0.001	0.005	-0.02	-0	-0	0.027	0.051	-0.01	-0	0.009	0.011	-0.01	-0.02	-0
30	P. antarcticum	0.018	-0.01	0.019	0	0.045	-0.04	-0.04	-0.03	-0.04	-0.05	0.04	-0.06	-0.03	-0.1
31	N. gibberifron	0.023	0.001	-0.01	-0.01	-0.01	0.144	0.079	-0.06	-0.04	-0.05	-0.04	-0.05	-0.01	0.001
32	Mollusca	-0	0.001	0.068	0.014	-0.01	-0.02	-0.03	0.001	0.038	-0.04	0.139	0.099	0.212	0.015
33	Salps	0.019	0	-0.01	0.026	0.009	0.012	0.009	0.021	-0	0.016	-0.01	0.009	-0	0.036
34	Urochordata	0.027	-0	-0.01	0.003	0.032	-0	-0.02	-0.01	0.003	-0	0.009	-0	-0.01	0.001
35	Porifera	0.018	-0	-0	-0	-0	0	0.001	-0	0	0	-0.01	-0	-0	-0
36	Hemichordata	0.019	0	0	0	-0	-0	0	-0	0	0.001	-0	-0	0.001	0
37	Brachiopoda	0.014	0	0	0	-0	-0	0.001	-0	0	0.002	-0.01	-0	0	0.005
38	Bryozoa	0.014	0	0	0	-0	-0	0.001	0	0	0.003	-0.01	0.003	0	0.004
39	Cnidaria	0.025	0.001	0.001	0.001	-0	0.019	0.006	-0.01	0.004	-0	0.004	-0.01	-0	0.011
40	Crustaceans	0.011	0.032	0.025	0.035	0.015	0.033	0.129	0.199	0.216	0.558	0.051	0.141	0.145	0.003
41	Arthropod other	-0	-0	-0.01	-0	0.017	0	-0.01	0.001	-0.04	-0.01	-0.02	-0.02	-0.02	-0
42	Worms	0.002	0.011	0.003	-0.01	0.014	0.016	0.027	0.036	0.128	-0	0.021	0.042	-0.03	-0.01
43	Echinoidea	-0.01	-0	0	-0	-0	-0	-0	-0.01	-0.01	-0.02	0.001	-0	-0	-0
44	Crinoidea	-0	0	0	0	0	0	0	0	0.001	-0	0	0	0	0
45	Ophiuroidea	-0.01	-0	-0.02	-0.01	0	-0	-0.01	-0.02	-0.04	-0.04	-0.03	-0.03	-0.05	-0.01
46	Asteroidea	-0	0	0	0	-0	0	0	-0	0	-0	0	-0	0	0
47	Holothuroidea	-0	0	-0	0	0.002	0.002	0.004	0.004	0.012	0.011	-0	0.001	-0	-0
48	Krill Adult	0.06	0.173	0.491	0.1	-0.03	0.091	0.098	0.053	-0	-0.18	0.031	0.009	0.006	0.073
49	Krill Sub-adult	-0.09	0.181	-0.11	0.068	0.109	0.023	-0.08	-0.09	-0.19	-0.24	-0.03	-0.12	-0.31	0.048
50	Krill juvenile	0	0	0	0	0	-0	-0	0	0	-0	0.01	0.003	0	0
51	Krill Larvae	0	0	0	0	0	0	0	-0	-0	-0	0	0	-0	0
52	Macro-zoopl.	0.097	-0.13	-0.12	-0.07	0.036	0.004	-0.02	0.04	0.139	0.245	0.005	0.09	0.155	-0.03
53	Micro-zoopl.	0.011	0.008	-0.01	0.002	0.05	0.012	-0.03	-0.03	0.001	-0.01	-0	-0.01	-0.03	0.012
54	Cryptophytes	0.027	-0	-0	0.007	0.021	0.011	-0.01	0.003	0.011	0.018	-0	0.01	0.007	0.016
55	Copepods	-0.03	0.043	0.073	0.034	-0.03	0.003	0.031	-0.01	-0.01	-0.04	0	-0.01	0.13	-0.01
56	Diatoms	0.02	0.045	0.067	0.034	0.019	0.023	0.006	-0.01	0.008	-0.02	0.006	0.004	0.091	0.013
57	Ice Algae	0.035	0.094	0.107	0.049	0.055	0.055	-0	0.037	-0.02	-0.08	0.007	-0.01	-0.03	0.036
58	Other phytopl.	0.048	-0	-0.01	0.009	0.039	0.022	-0.01	0.043	0.015	0.017	0.023	0.007	0.015	0.019
59	Detritus	0.03	0.064	0.031	0.041	0.045	0.027	0.049	0.109	0.178	0.248	0.101	0.127	0.116	0.022
	Krill Fishery	0	-0	-0	-0	0	-0	0	0	0	0.001	0	0	0	0
	Other Fishery	0	0	0	0	0	0	-0	0	0	0	0	0	0	0

APPENDIX 2 (CONTINUED): MIXED TROPHIC IMPACTS

		C. gunnari	P. antarcticum	N. gibberifron	Mollusca	Salps	Uro-chordata	Porifera	Hemi-chordata	Brachio-poda	Bryozoa	Cnidaria	Crust-aceans	Arthropod other	Worms
	Impacting \ Impacted	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	Killer Whale	-0.09	0.023	-0.03	-0.01	0.007	0.01	-0.01	-0.2	-0.09	-0.02	0.003	0.017	0.018	0.003
2	Leopard seal	0.269	-0	0.076	0.017	-0.02	-0.03	0.007	0.453	0.197	0.041	-0.01	-0.06	-0.06	-0.01
3	Ross seal	-0.01	-0	-0	-0	0.002	0.004	-0	0.001	0.001	-0	0	0.002	0.004	0
4	Weddell seal	-0.08	-0.05	-0.02	-0.01	0.011	0.013	-0.01	-0.02	-0.01	-0.01	0.001	0.01	0.014	-0
5	Crabeater Seal	-0.05	-0.03	0.012	-0	-0.02	0	0.008	0.027	0.022	-0.01	0.021	0.03	0.018	0.014
6	Antarctic fur seal	-0.21	0.041	-0.05	-0	0.011	0.014	-0	0.037	0.022	-0.01	0.008	0.02	0.016	0.002
7	S Elephant seal	0.007	0.01	-0	-0	0.003	0.006	0	0.009	0.006	0	0.001	-0	0.005	0
8	Sperm whale	0.001	0.007	-0	-0	0.001	0.004	0	-0.02	-0.01	-0	-0	0	0.003	0
9	Blue whale	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	fin whale	-0	0	0	0	0	0	0	-0	0	0	0	0	0	0
11	Minke whale	-0.04	0.007	-0.01	0.001	0.002	0.003	0.001	-0.06	-0.03	-0.01	0.003	0.01	0.008	0.003
12	Humpback whale	-0.01	0.002	-0	0	0	0	0	-0.01	-0.01	-0	0.001	0.002	0.002	0.001
13	Emperor penguin	0.013	-0.02	0.015	0.003	0.004	0.004	-0	0.01	0.003	-0	0.001	0.004	0.006	-0
14	Gentoo Penguin	-0.01	0.017	-0.06	-0	0.004	0.003	-0	-0.39	-0.18	-0.02	-0.01	0.01	0.007	0
15	Chinstrap penguin	-0.01	0.018	-0.03	-0	0.004	0.004	-0	-0.37	-0.18	-0.01	-0.01	0.004	0.008	0
16	Macaroni Penguin	-0.06	0.012	0.003	0.001	0.005	0.002	-0	0.019	0.009	-0	0.003	0.01	0.007	0.001
17	Adélie Penguin	0	-0.04	0.011	-0.01	-0	-0.01	-0	0.042	0.034	0.001	0.011	-0	-0	0.004
18	Flying birds	0.038	0.063	0.037	-0.01	-0.02	0.037	0.001	0.034	0.053	0.002	0.003	-0.01	0.036	0.008
19	Cephalopods	-0.03	-0.37	0.072	0.091	-0.09	-0.21	0.018	-0.15	-0.09	0.012	-0.04	0.02	-0.17	-0.01
20	Other Icefish	-0.26	-0.02	-0.37	0.003	0.002	0.009	-0.01	0.03	0.002	-0.02	-0.03	0.055	0.002	-0
21	Toothfish	-0	0.002	0.018	0	0.001	0.001	0	0	0	0	0.002	-0	0	0
22	Lg Nototheniidae	-0.1	-0.02	-0.06	0.005	-0.02	0.005	0.006	-0.01	0.024	0.022	0.014	-0.05	-0.02	0.004
23	Sm Nototheniidae	-0.01	-0.01	-0.03	-0.02	-0.01	-0.01	0.011	-0.01	-0.01	0.03	-0	-0.06	0.007	-0
24	Shallow demersals	0.003	-0	-0.01	-0	-0	-0	0.001	0.005	0.003	0.008	0.005	-0.02	-0	0.003
25	Deep demersals lg	-0.02	-0	0.001	-0	0.002	-0	-0	-0.05	-0	-0	-0.01	0.007	0.001	0
26	Deep demersals sm	0.025	-0.01	0.036	-0	0	-0	0	-0.02	0.002	-0	0.004	-0.01	-0	0
27	Myctophids	0.006	-0.01	-0.01	-0.05	-0.02	-0	0	0.01	0	0.012	0.008	-0.04	0.001	0.013
28	Other pelagics	0.026	-0.04	0.048	0	-0.01	0.03	-0	0.034	-0.3	-0.02	-0.03	-0	0.031	-0
29	C. gunni	-0.03	0.002	-0.02	0.005	-0.01	0	0.003	0.005	0.002	-0	0.003	0.008	0.003	0.002
30	P. antarcticum	-0.03	-0.09	-0.2	-0.13	-0.05	-0.01	0.023	0.037	0.049	0.031	0.023	-0.04	-0.06	0.049
31	N. gibberifron	-0.06	0.001	-0.11	0.001	-0	-0.01	0.014	-0.02	-0.01	0.035	-0.01	-0.1	-0	0
32	Mollusca	-0.03	0.093	-0.04	-0.05	0.068	0.034	0.055	-0.04	-0.05	0.001	0.022	-0.04	0.081	-0.18
33	Salps	0.023	-0.01	0	-0	-0.06	-0.03	-0	-0.02	-0.03	-0.01	0.064	-0.01	-0	0.01
34	Urochordata	-0	-0.02	0.009	-0	-0.01	-0.02	-0	-0.02	-0.01	-0.01	-0.01	-0	0.037	0.001
35	Porifera	0	-0	-0	-0.02	-0.01	-0.01	-0.03	-0.03	-0.02	-0.01	-0.01	-0	-0	0.012
36	Hemichordata	0	0.001	-0	0	0	0	0	-0.02	-0.01	-0	0	0	0	0
37	Brachiopoda	0	0	-0	0	0	0	0	-0.01	-0.01	-0	-0	0	0	0
38	Bryozoa	0	0	0	-0	0	-0	-0	-0.01	-0.01	-0.01	-0	0.003	0.008	-0
39	Cnidaria	-0.01	0	-0	-0	-0.09	0.004	0	-0.03	-0.02	-0	-0.02	0.001	0.008	-0.01
40	Crustaceans	-0.04	0.051	0.263	-0.02	0.048	0.044	-0.04	-0.04	-0.04	-0.27	-0.18	-0.16	-0.1	-0.1
41	Arthropod other	0	-0.01	-0.02	-0.06	0.022	-0.2	0.027	0.008	-0.01	-0.1	-0.06	-0.03	-0.11	-0.07
42	Worms	0.006	0.002	0.081	-0.08	-0.39	-0.26	-0.42	0.048	0.214	-0.03	-0.14	-0.02	-0.12	-0.11
43	Echinoidea	0.002	-0	-0.01	0.005	0.017	0.01	-0.04	-0.1	-0.27	-0.04	-0.04	-0.02	-0.06	-0.03
44	Crinoidea	0	0	-0	0	0.001	0	0.001	0.001	0	-0.07	0.001	-0	0.001	-0
45	Ophiuroidea	0.009	-0.02	-0.02	-0.18	0.04	0.02	-0.13	0.005	-0.01	-0.08	-0.1	-0.05	0.001	-0.06
46	Asteroidea	0	0	-0	0.002	-0.01	-0.03	-0.01	-0	-0	0.003	0.004	-0	0.026	-0.01
47	Holothuroidea	-0	-0	0.014	-0.02	-0	-0.03	-0.01	-0.01	-0.01	-0.02	-0.01	0.014	0.097	0
48	Krill Adult	0.334	-0.08	0.03	0.019	0.031	0.044	0.043	-0.01	-0.05	0.04	-0.14	-0.05	0.014	-0.01
49	Krill Sub-adult	0.252	0.035	-0.12	-0.31	0.088	0.045	-0.31	-0.49	-0.13	0.068	-0.1	-0.36	-0.21	-0.22
50	Krill juvenile	0	0	0.001	0	-0	-0	0	0	-0	-0	-0	0	0.004	0
51	Krill Larvae	0	0	-0	-0	0.001	0	-0	-0	-0	0	0.001	-0	0.001	-0
52	Macro-zoopl.	-0.29	0.033	0.069	0.103	-0.25	-0.16	0.05	0.149	0.084	-0.15	0.476	0.29	0.075	0.2
53	Micro-zoopl.	-0	-0	-0.02	-0.02	-0.05	-0.07	-0.04	-0.03	-0.03	-0.06	0.055	-0.02	0.007	0.019
54	Cryptophytes	-0.01	-0	0.011	0.015	0.296	0.11	0.01	-0.01	0.031	0.116	0.081	0.014	0.016	0.019
55	Copepods	0.077	0.091	-0.03	-0.06	-0.09	-0.11	-0.01	-0	-0.08	-0.09	-0.12	-0.01	-0.02	-0.04
56	Diatoms	0.055	0.067	-0.01	-0.02	0.023	0.071	-0.02	-0.05	-0.01	0.095	0.037	0	-0.01	0.003
57	Ice Algae	0.116	0.022	0.027	-0.05	0.007	0.108	-0.07	-0.16	-0.02	0.123	0.113	-0.05	-0.04	-0.03
58	Other phytopl.	-0.03	0.004	0.045	0.042	0.346	0.26	0.004	-0.04	0.312	0.123	0.152	0.021	0.024	0.023
59	Detritus	0.013	0.091	0.147	0.421	-0.11	-0.06	0.484	0.756	0.144	-0.02	-0.17	0.363	0.206	0.256
	Krill Fishery	-0	0	0	0	0	0	0	0.001	0	0	0.001	0.001	0	0
	Other Fishery	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2 (CONTINUED): MIXED TROPHIC IMPACTS

		Echino-idea	Crinoidea	Ophiuroidea	Asteroidea	Holo-thuroidea	Krill Adult	Krill Sub-adult	Krill juvenile	Krill Larvae	Macro-zoopl	Micro-zoopl	Crypto-phytes	Copepods
	Impacting \ Impacted	43	44	45	46	47	48	49	50	51	52	53	54	55
1	Killer Whale	-0	-0.01	-0	-0.01	-0.01	-0.04	0.002	0.004	-0	0.011	-0	-0	0.006
2	Leopard seal	0.001	0.016	0	0.016	0.026	0.107	0.012	-0.01	-0.01	-0.04	0.003	0.005	-0.03
3	Ross seal	0	-0	0	-0	-0	0.001	0.002	-0	-0	-0	-0	0	-0
4	Weddell seal	-0	-0.01	-0	-0.01	-0.01	0.001	0.008	-0	-0.01	-0	-0	0	-0.01
5	Crabeater Seal	0.005	0.005	0.006	0.005	0.004	-0.11	-0.03	0.004	0.04	0.048	0.009	-0.01	0.04
6	Antarctic fur seal	0	-0.01	0	-0	-0.01	-0.01	-0	0	-0.01	0.003	-0	-0	0.003
7	S Elephant seal	-0	-0	0	-0	-0	0.002	0.001	-0	-0	-0	-0	0	-0
8	Sperm whale	0	-0	0	-0	-0	0	0	0	-0	0	0	0	0
9	Blue whale	0	0	0	0	0	0	0	0	0	0	0	0	0
10	fin whale	0	0	0	0	0	-0	0	0	0	0	0	0	0
11	Minke whale	0.001	0	0.001	0	-0	-0.02	-0.01	0.002	0.005	0.008	0.001	-0	0.007
12	Humpback whale	0	0	0	0	-0	-0.01	-0	0.001	0.001	0.002	0	0	0.002
13	Emperor penguin	0.001	-0	0	-0	-0	-0	0.002	-0	-0.01	0	-0	0	-0
14	Gentoo Penguin	-0	-0	-0	-0	-0.01	0	0.002	0.011	-0	-0	-0	0	-0
15	Chinstrap penguin	-0	-0.01	-0	-0	-0	-0	0.002	0.007	-0	0	-0	0	-0
16	Macaroni Penguin	0.001	-0	0.001	-0	-0	-0	-0	0.002	-0	0.001	0	-0	0.001
17	Adélie Penguin	-0	-0	-0	-0	-0	-0.06	0.004	0.004	0.013	0.017	-0	0	0.009
18	Flying birds	-0	0.006	-0	-0.01	-0	-0.01	-0.01	-0.02	-0.01	0.008	0.005	0	0.005
19	Cephalopods	0.022	0.082	0.016	0.075	0.059	-0.03	-0.03	0.129	0.12	0.022	0.022	0.002	0.025
20	Other Icefish	0	0.004	-0	-0	-0.02	0.007	0.005	0.031	-0.01	-0.01	-0	0.001	-0
21	Toothfish	0	0.002	0	0	0	0.001	0	0	-0	0	0	0	0
22	Lg Nototheniidae	-0	0.022	0	0.008	0.023	-0.01	-0	-0.01	0.019	0.007	0.002	0	0.004
23	Sm Nototheniidae	0	-0.13	0.001	-0	0.016	-0.01	-0	-0.03	0	0.006	0.001	0	0.003
24	Shallow demersals	-0	0.001	-0	-0	0.006	0	0	0.001	0.001	0	0	0	0
25	Deep demersals lg	0	0	0	0	-0	0.001	0.001	-0.03	0.001	-0	0	0	0
26	Deep demersals sm	0	0.009	0	0	0.001	0	0.001	-0.04	-0.02	0	0	0	-0
27	Myctophids	-0.01	0.003	-0.01	-0.01	0.008	-0.01	0	0	0.006	0.004	0.002	0.001	0.002
28	Other pelagics	-0	-0.01	0	-0.01	-0.01	-0.01	0.005	-0.02	-0.02	0.002	-0	0	-0
29	C. gunni	0.003	0.003	0.002	0.003	0.002	-0.02	-0.01	0.003	0.01	0.011	0.003	-0	0.009
30	P. antarcticum	-0.02	0.051	-0	0.026	0.056	-0.01	-0.06	0.062	0.086	0.025	0.029	-0	0.034
31	N. gibberifron	0	0.011	0.001	0.004	0.028	-0.01	-0.01	-0.04	0.01	0.01	0.001	-0	0.006
32	Mollusca	0.154	-0.03	0.103	0.066	0.038	-0.02	-0.02	-0.06	-0.09	0.02	-0.02	-0.01	0.011
33	Salps	-0.02	-0	-0.01	-0	-0	0.003	0.006	0	0.001	-0.02	-0.13	-0.05	-0
34	Urochordata	0.004	-0.01	-0	-0	-0.01	-0	-0	-0.03	-0.02	0	-0.01	-0	0
35	Porifera	0.032	-0.02	0.009	0	-0.02	0.001	-0	0.002	-0.02	-0	0.001	-0	0.001
36	Hemichordata	0	0	0	0	0	0	0	0	0	0	0	0	0
37	Brachiopoda	0.002	-0	0	0	0	0	0	0	-0	0	0	0	0
38	Bryozoa	0.008	0.119	0.002	-0	-0	0	0	-0.01	-0.01	0	-0	-0	0
39	Cnidaria	0.014	-0.01	0.005	-0	-0	0.003	0.004	-0.01	-0.01	-0.01	0.011	0.008	-0
40	Crustaceans	0.104	0.001	0.041	0.086	-0.19	-0.01	-0	0.036	0.034	-0.02	0.002	-0	0.002
41	Arthropod other	0.056	-0.28	0.032	-0.25	-0.18	-0	0	-0.6	-0.5	0.007	0	0.001	0.001
42	Worms	-0.79	-0.07	-0.33	-0.47	-0.33	0.023	0.019	0.067	0.156	-0.08	0.051	0.044	-0.01
43	Echinoidea	0.015	-0.17	0.001	-0.03	-0.02	0	0	0.041	-0.14	0.001	-0	-0	0
44	Crinoidea	0.002	-0.01	0	0.001	0.001	0	0	0	-0	0	0	0	0
45	Ophiuroidea	0.05	-0	-0.23	0.067	0.04	0.002	0.001	0.005	-0.01	0.003	-0.01	-0	-0
46	Asteroidea	0.012	-0.01	-0.04	-0.01	-0.01	0	0	-0.02	-0.02	-0	0.001	0.001	0
47	Holothuroidea	0.035	-0.05	-0	-0.04	-0.04	0	-0	-0.07	-0.07	0	0.001	-0	0.001
48	Krill Adult	-0.01	0.02	0.016	0.017	0.05	-0.03	-0.05	-0.12	-0.22	-0.29	0.07	0.012	-0.17
49	Krill Sub-adult	-0.13	-0.24	-0.19	-0.24	-0.31	-0.12	-0.15	0.057	-0.4	-0.32	-0.33	0.093	-0.42
50	Krill juvenile	0	-0	0	-0	-0	-0	0	-0.01	-0	-0	-0	-0	0
51	Krill Larvae	0.001	-0	-0	-0	-0	0	-0	0	-0.01	0	0	0	0
52	Macro-zoopl.	0.045	0.076	0.052	0.076	0.045	-0.34	-0.38	-0.02	0.272	0.203	-0.1	-0.18	0.241
53	Micro-zoopl.	-0.02	-0.01	0.007	0.009	-0.02	-0.01	0.005	-0.08	-0.02	-0.04	-0.15	-0.39	-0.02
54	Cryptophytes	0.002	0.017	0.028	0.009	-0	-0.01	-0.03	0.012	0.007	0.092	0.11	-0.11	0.01
55	Copepods	0.028	-0.02	-0.02	-0.01	-0	0.162	0.046	-0.18	-0.06	-0.25	-0.15	-0.14	-0.43
56	Diatoms	0.026	-0.01	0.002	-0	-0.03	0.127	0.037	-0.11	-0.06	0.036	0.053	0.155	0.381
57	Ice Algae	0.003	-0.04	-0.02	-0.03	-0.09	0.207	0.166	0.601	-0.16	0.154	0.022	0.082	0.01
58	Other phytopl.	0.058	0.008	0.028	0.03	-0	-0.03	-0.04	0.166	-0	0.151	0.244	0.037	0.042
59	Detritus	0.12	0.368	0.254	0.336	0.522	-0.03	0.178	-0.19	0.673	-0.05	-0.02	0.095	-0.09
	Krill Fishery	0	0	0	0	0	-0.01	-0	0.001	0.002	0.002	0	0	0.001
	Other Fishery	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2 (CONTINUED): MIXED TROPHIC IMPACTS

		Diatoms	Ice Algae	Other phytoplankton	Detritus	Krill Fishery	Other Fishery
	Impacting \ Impacted	56	57	58	59		
1	Killer Whale	-0	0	-0	-0	-0.03	-0.05
2	Leopard seal	0.018	-0.01	0.007	-0.01	0.083	0.111
3	Ross seal	0.001	0	0	-0	0.001	-0
4	Weddell seal	0.003	-0	0.001	-0.01	0.003	-0.03
5	Crabeater Seal	-0.03	0.011	-0.01	0.024	-0.09	-0.01
6	Antarctic fur seal	-0	0.001	-0	0.002	-0.01	-0.05
7	S Elephant seal	0.001	0	0	-0	0.002	-0.02
8	Sperm whale	0	0	0	0	0	-0.01
9	Blue whale	0	0	0	0	0	0
10	fin whale	0	0	0	0	0	-0
11	Minke whale	-0.01	0.002	-0	0.005	-0.02	-0.02
12	Humpback whale	-0	0	0	0.001	-0.01	-0
13	Emperor penguin	0	-0	0	-0	0	-0
14	Gentoo Penguin	0.001	-0	0	-0	0	-0.01
15	Chinstrap penguin	0.001	-0	0	-0	0	0
16	Macaroni Penguin	-0	0.001	0	0.001	-0	-0.03
17	Adélie Penguin	-0.01	0	-0	-0	-0.04	-0
18	Flying birds	-0	0.002	-0	0.005	-0.01	-0.02
19	Cephalopods	-0.02	0.009	-0.01	0.02	-0.03	-0.14
20	Other Icefish	0.002	-0	0.001	-0	0.007	0.027
21	Toothfish	0	0	0	0	0.001	0.1
22	Lg Nototheniidae	-0	0.001	-0	0.003	-0.01	0.058
23	Sm Nototheniidae	-0	0.001	-0	0.003	-0.01	0.115
24	Shallow demersals	0	0	0	0	0	-0
25	Deep demersals lg	0	0	0	0	0.001	-0.02
26	Deep demersals sm	0	0	0	-0	0	-0.02
27	Myctophids	-0	0	0	0.002	-0.01	0.106
28	Other pelagics	0	-0	0	-0	-0.01	0.093
29	C. gunni	-0.01	0.003	-0	0.006	-0.02	0.112
30	P. antarcticum	-0.02	0.018	-0.01	0.049	-0.02	0.046
31	N. gibberifron	-0	0.002	-0	0.006	-0.01	0.105
32	Mollusca	-0.01	0.005	-0.01	-0.02	-0.02	0.028
33	Salps	0.005	0.004	-0	-0	0.004	0.01
34	Urochordata	0	0	-0	0	-0	-0
35	Porifera	-0	0.001	0	-0.02	0	-0
36	Hemichordata	0	0	0	0	0	0
37	Brachiopoda	0	0	0	0	0	0
38	Bryozoa	0	0	0	0	0	0.001
39	Cnidaria	0.002	-0	0.002	-0	0.004	0.003
40	Crustaceans	0	0.003	-0	-0.01	-0.01	0.111
41	Arthropod other	0	0.002	0.002	0.01	-0	-0.01
42	Worms	0.008	-0	0.017	-0.04	0.022	0.029
43	Echinoidea	0	0	-0	0.002	0	-0
44	Crinoidea	0	0	0	0	0	0
45	Ophiuroidea	0.001	0	0.002	0.002	0.002	-0.02
46	Asteroidea	0	0	0	-0	0	0
47	Holothuroidea	-0	0.001	0	-0.01	0	0.004
48	Krill Adult	0.118	-0	0.039	0.034	0.714	0.067
49	Krill Sub-adult	0.229	-0.23	0.112	-0.58	0.121	-0.05
50	Krill juvenile	0	-0	-0	0	0	0
51	Krill Larvae	0	0	0	-0	0	0
52	Macro-zoopl.	-0.16	0.06	-0.12	0.237	-0.35	0.012
53	Micro-zoopl.	-0.01	-0.02	-0.23	-0.02	-0.01	-0.01
54	Cryptophytes	-0.01	0.001	-0.06	0.014	-0.01	0.004
55	Copepods	-0.43	-0.19	-0.09	-0.02	0.133	0.031
56	Diatoms	-0.3	-0.15	-0.14	-0.03	0.104	0.027
57	Ice Algae	-0.04	-0.12	-0.07	-0.13	0.197	0.027
58	Other phytopl.	-0.04	-0.01	-0.12	0.014	-0.03	0.013
59	Detritus	0.047	-0.05	0.01	0	0.02	0.084
	Krill Fishery	-0	0	0	0	-0	0
	Other Fishery	0	0	0	0	0	0

APPENDIX 3: CV VALUES USED FOR THE MONTE CARLO ANALYSIS

	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	Adélie 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	Champsocephalus gunnari	0.7	0.5	0.5	0.5
30	Pleuragramma antarcticum	0.7	0.5	0.5	0.5
31	Notothenia 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	Arthropod Crustecea	1	0.2	0.2	0.5
41	Arthropod Other	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-Zooplankton	0.7	0	0	0.2
53	Micro-Zooplankton	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			

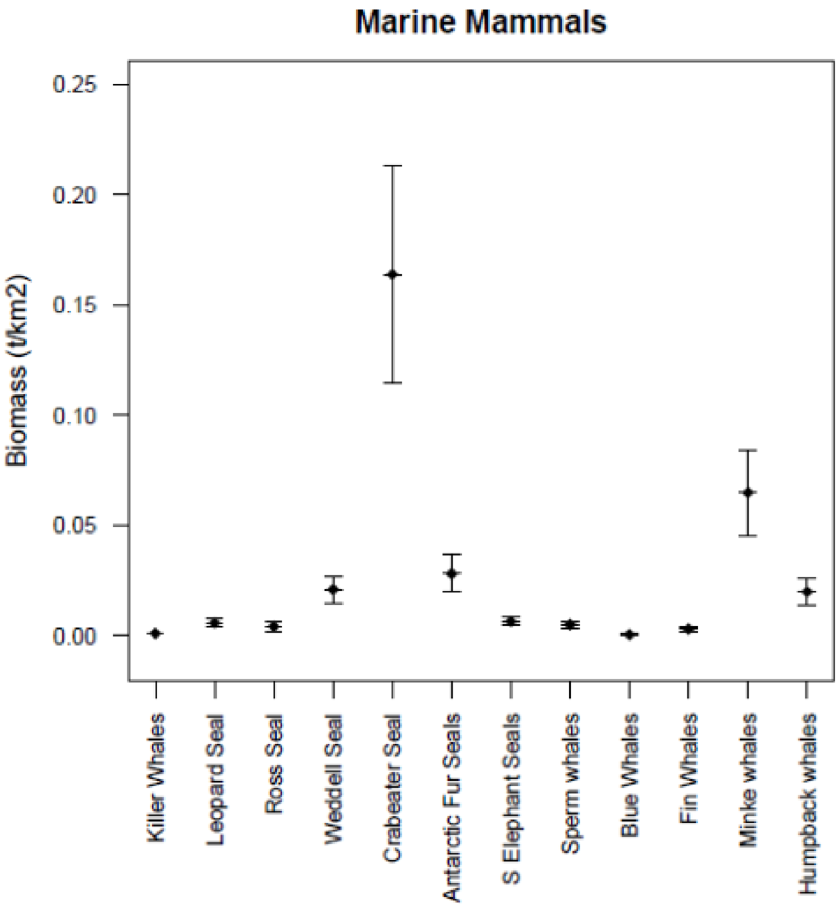
Appendix 4: Monte Carlo results for biomass, P/B, EE, and BA

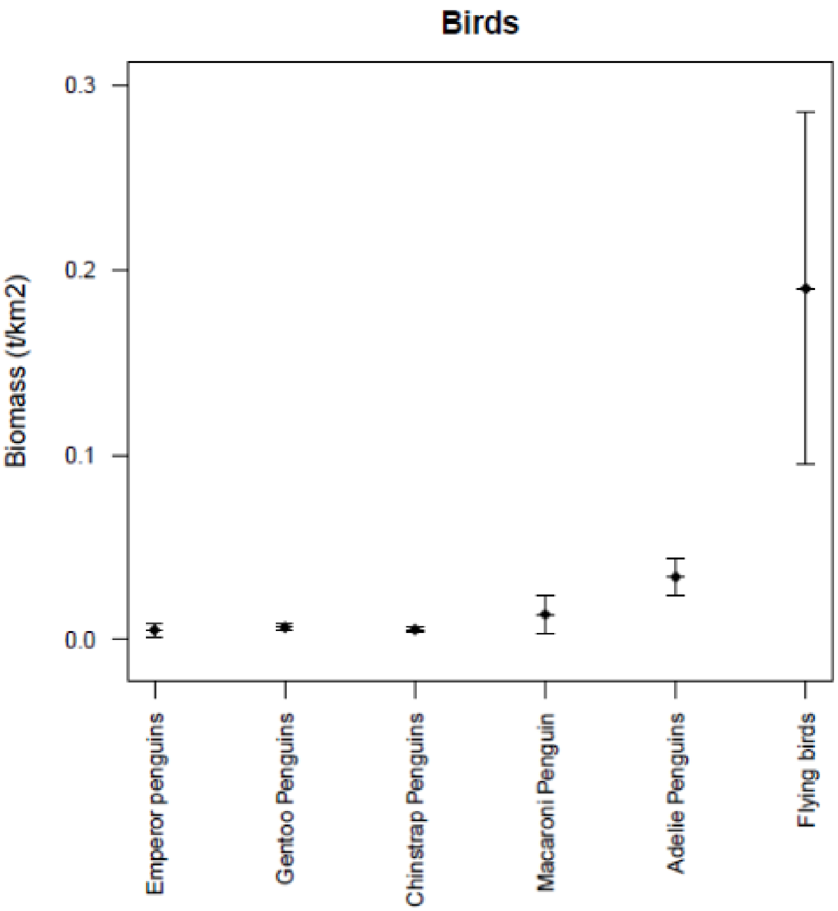
	Biomass			**P/B**			**EE**			**BA**		
Group name	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper
Killer Whales	0.001	0.001	0.001	0.025	0.050	0.075	0.000	0.000	0.000	0.000	0.000	0.000
Leopard Seal	0.004	0.006	0.007	0.060	0.120	0.180	0.509	0.637	0.764	-0.001	0.000	0.001
Ross seal	0.002	0.004	0.006	0.065	0.130	0.195	0.664	0.830	0.996	0.000	0.000	0.000
Weddell seal	0.015	0.021	0.027	0.085	0.170	0.255	0.551	0.689	0.827	-0.002	0.000	0.002
Crabeater Seal	0.115	0.164	0.213	0.045	0.090	0.135	0.290	0.363	0.435	-0.016	0.000	0.016
Antarctic Fur Seals	0.020	0.028	0.037	0.088	0.175	0.263	0.690	0.862	1.000	-0.003	0.000	0.003
S Elephant Seals	0.005	0.006	0.008	0.083	0.165	0.248	0.349	0.437	0.524	-0.001	0.000	0.001
Sperm whales	0.004	0.005	0.007	0.017	0.034	0.051	0.000	0.000	0.000	-0.001	0.000	0.001
Blue Whales	0.000	0.001	0.001	0.016	0.032	0.048	0.546	0.683	0.820	0.000	0.000	0.000
Fin Whales	0.002	0.003	0.004	0.018	0.035	0.053	0.419	0.524	0.629	0.000	0.000	0.000
Minke whales	0.046	0.065	0.085	0.032	0.064	0.096	0.728	0.910	1.000	-0.007	0.000	0.007
Humpback whales	0.014	0.020	0.026	0.020	0.040	0.060	0.770	0.963	1.000	-0.002	0.000	0.002
Emperor penguins	0.001	0.005	0.009	0.105	0.150	0.195	0.746	0.933	1.000	-0.001	0.000	0.001
Gentoo Penguins	0.005	0.007	0.008	0.110	0.220	0.330	0.514	0.642	0.771	0.000	0.000	0.001
Chinstrap Penguins	0.004	0.005	0.007	0.165	0.330	0.495	0.556	0.696	0.835	0.000	0.001	0.001
Macaroni Penguin	0.003	0.014	0.024	0.150	0.300	0.450	0.298	0.373	0.447	-0.001	0.000	0.001
Adélie Penguins	0.024	0.034	0.044	0.261	0.290	0.319	0.635	0.793	0.952	-0.003	0.000	0.003
Flying birds	0.095	0.190	0.285	0.272	0.340	0.408	0.760	0.950	1.000	-0.019	0.000	0.019
Cephalopods	1.245	2.490	3.735	0.380	0.950	1.520	0.522	0.653	0.784	-0.249	0.000	0.249
Other Icefish	0.236	0.337	0.438	0.190	0.380	0.570	0.581	0.726	0.871	-0.034	0.000	0.034
Toothfish	0.032	0.046	0.060	0.083	0.165	0.248	0.502	0.627	0.752	-0.005	0.000	0.005
Large Nototheniidae	0.413	0.590	0.767	0.185	0.370	0.555	0.362	0.452	0.543	-0.059	0.000	0.059
Small Nototheniidae	0.239	0.341	0.443	0.325	0.650	0.975	0.699	0.873	1.000	-0.034	0.000	0.034
Shallow Demersals	0.022	0.031	0.040	0.375	0.750	1.125	0.290	0.362	0.434	-0.003	0.000	0.003
Deep demersals Lg	0.029	0.042	0.055	0.145	0.290	0.435	0.642	0.803	0.964	-0.004	0.000	0.004
Deep demersals Sm	0.056	0.080	0.104	0.325	0.650	0.975	0.656	0.820	0.984	-0.008	0.000	0.008
Myctophids	0.130	0.185	0.241	0.675	1.350	2.025	0.706	0.882	1.000	-0.019	0.000	0.019
Other Pelagics	0.343	0.490	0.637	0.275	0.550	0.825	0.670	0.838	1.000	-0.049	0.000	0.049
C. gunnari	0.203	0.290	0.377	0.240	0.480	0.720	0.380	0.475	0.571	-0.029	0.000	0.029

Table continued on next page

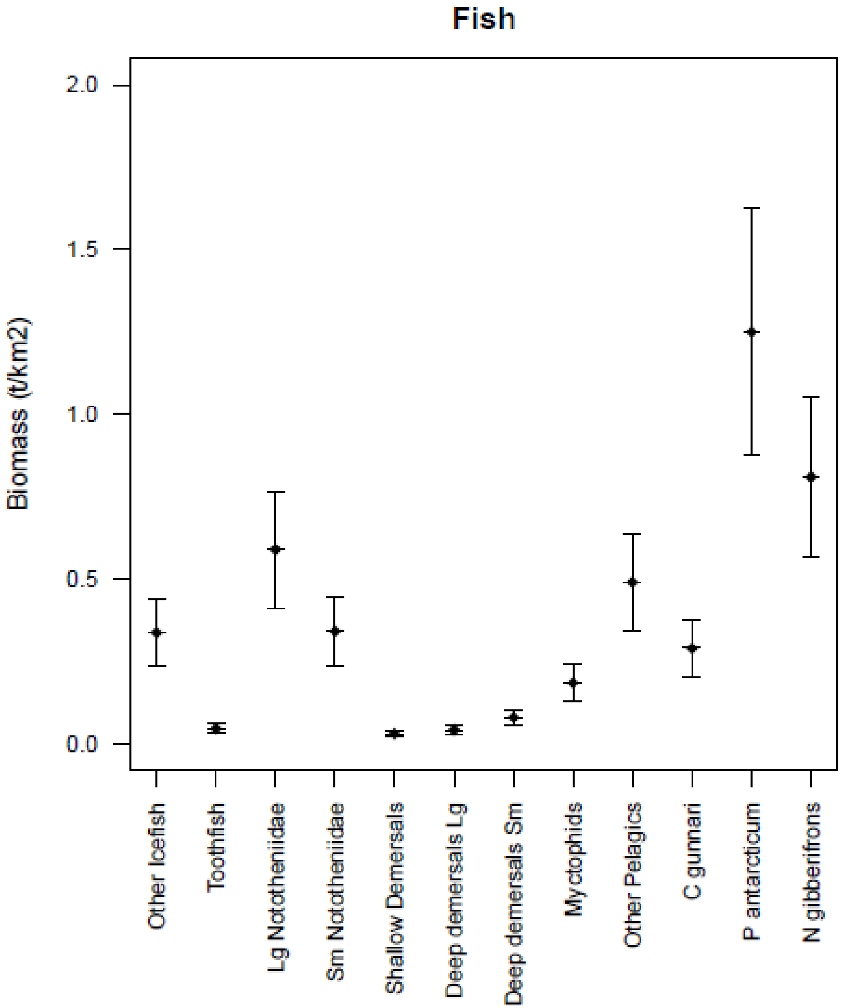
	Biomass			**P/B**			**EE**			**BA**		
Group name	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper
P. antarcticum	0.875	1.250	1.625	0.550	1.100	1.650	0.483	0.603	0.724	-0.125	0.000	0.125
N. gibberifrons	0.567	0.810	1.053	0.205	0.410	0.615	0.516	0.645	0.774	-0.081	0.000	0.081
Mollusca	8.550	9.500	10.450	0.256	0.639	1.022	0.487	0.608	0.730	-0.950	0.000	0.950
Salps	7.200	8.000	8.800	8.000	10.000	12.000	0.008	0.010	0.012	-0.800	0.000	0.800
Urochordata	4.545	5.050	5.555	0.094	0.234	0.374	0.443	0.554	0.665	-0.505	0.000	0.505
Porifera	11.447	12.719	13.991	0.064	0.159	0.254	0.652	0.815	0.979	-1.272	0.000	1.272
Hemichordata	0.041	0.045	0.050	0.150	0.375	0.600	0.428	0.534	0.641	-0.005	0.000	0.005
Brachiopoda	0.025	0.028	0.030	0.359	0.898	1.437	0.472	0.590	0.708	-0.003	0.000	0.003
Bryozoa	0.442	0.491	0.540	0.190	0.475	0.760	0.784	0.980	1.000	-0.049	0.000	0.049
Cnidaria	1.378	1.531	1.684	0.100	0.250	0.400	0.786	0.982	1.000	-0.153	0.000	0.153
Crusteceans	3.252	3.613	3.974	0.420	1.050	1.680	0.711	0.888	1.000	-0.361	0.000	0.361
Arthropod Other	0.909	1.010	1.111	0.246	0.616	0.985	0.784	0.981	1.000	-0.101	0.000	0.101
Worms	10.800	12.000	13.200	0.280	0.700	1.120	0.672	0.840	1.000	-1.200	0.000	1.200
Echinoidea	3.897	4.330	4.763	0.046	0.116	0.186	0.619	0.774	0.929	-0.433	0.000	0.433
Crinoidea	0.147	0.164	0.180	0.050	0.125	0.200	0.419	0.523	0.628	-0.016	0.000	0.016
Ophiuroidea	6.084	6.760	7.436	0.180	0.450	0.720	0.441	0.551	0.661	-0.676	0.000	0.676
Asteroidea	1.600	1.778	1.956	0.092	0.231	0.370	0.619	0.774	0.928	-0.178	0.000	0.178
Holothuroidea	4.905	5.450	5.995	0.126	0.316	0.505	0.750	0.938	1.000	-0.545	0.000	0.545
Krill Adult	8.172	9.080	9.988	1.200	1.500	1.800	0.545	0.681	0.817	-0.908	0.000	0.908
Krill Juvenile	23.303	25.893	28.482	0.720	0.900	1.080	0.623	0.779	0.935	-2.589	0.000	2.589
Krill Larvae	0.011	0.013	0.014	2.000	2.500	3.000	0.636	0.795	0.954	-0.001	0.000	0.001
Krill Embryo	0.003	0.003	0.004	6.400	8.000	9.600	0.369	0.461	0.554	0.000	0.000	0.000
Macro-Zooplankton	5.719	8.170	10.621	1.560	7.802	14.044	0.760	0.950	1.000	-0.817	0.000	0.817
Micro-Zooplankton	2.030	2.900	3.770	13.000	65.000	117.000	0.789	0.986	1.000	-0.290	0.000	0.290
Cryptophytes	1.540	2.200	2.860	64.000	80.000	96.000	0.790	0.987	1.000	-0.220	0.000	0.220
Copepods	7.600	15.200	22.800	16.024	26.707	37.390	0.760	0.950	1.000	-1.520	0.000	1.520
Diatoms	12.187	17.410	22.633	72.408	90.510	108.612	0.319	0.398	0.478	-1.741	0.000	1.741
Ice algae	17.500	25.000	32.500	36.000	45.000	54.000	0.665	0.831	0.998	-2.500	0.000	2.500
Other Phytoplankton	2.750	5.500	8.250	84.000	105.000	126.000	0.611	0.763	0.916	-0.550	0.000	0.550

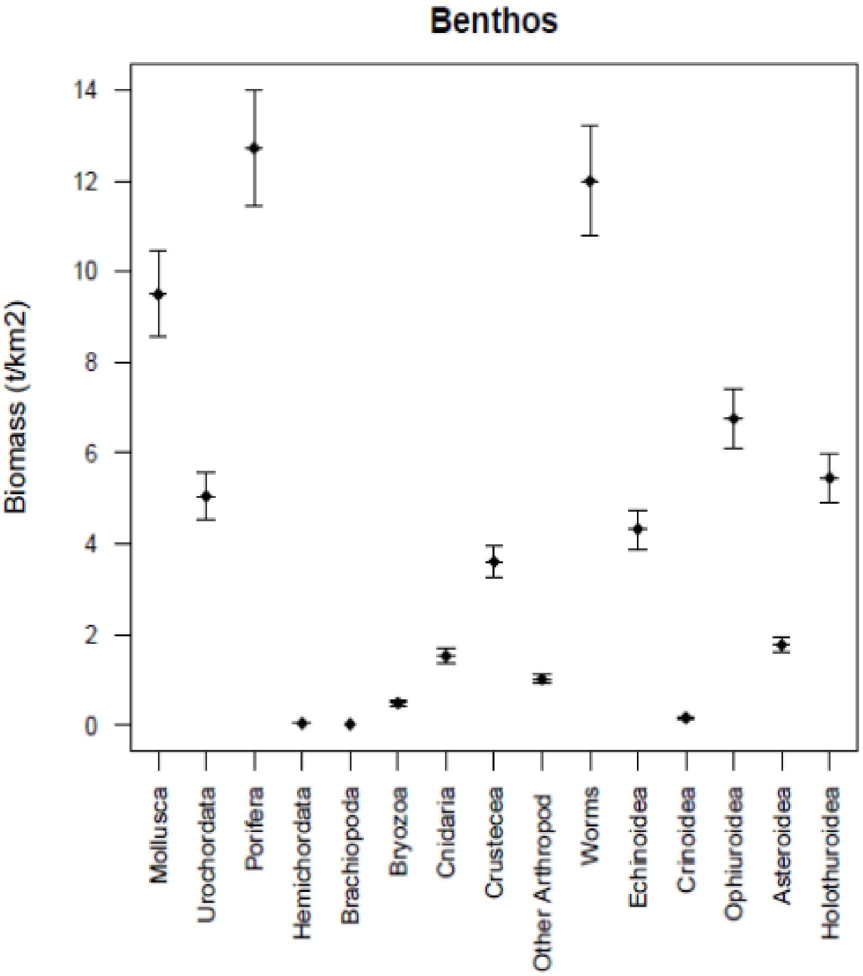
APPENDIX 5: MONTE CARLO RESULTS FOR BIOMASS



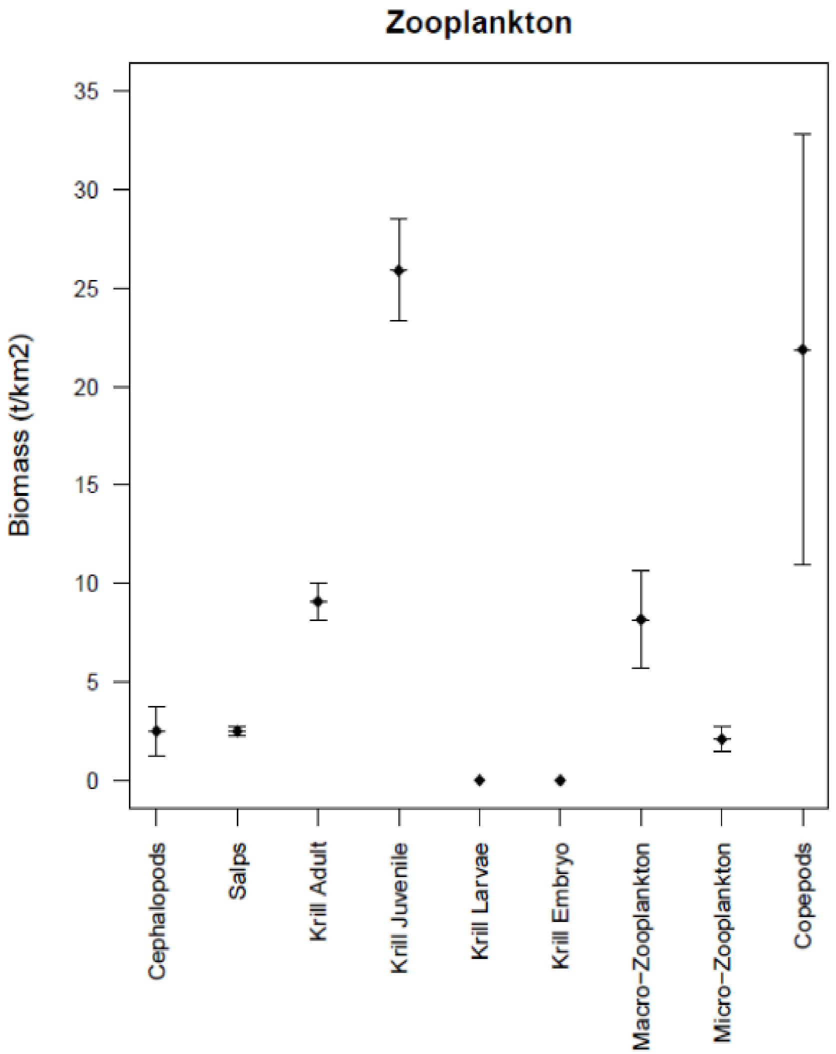


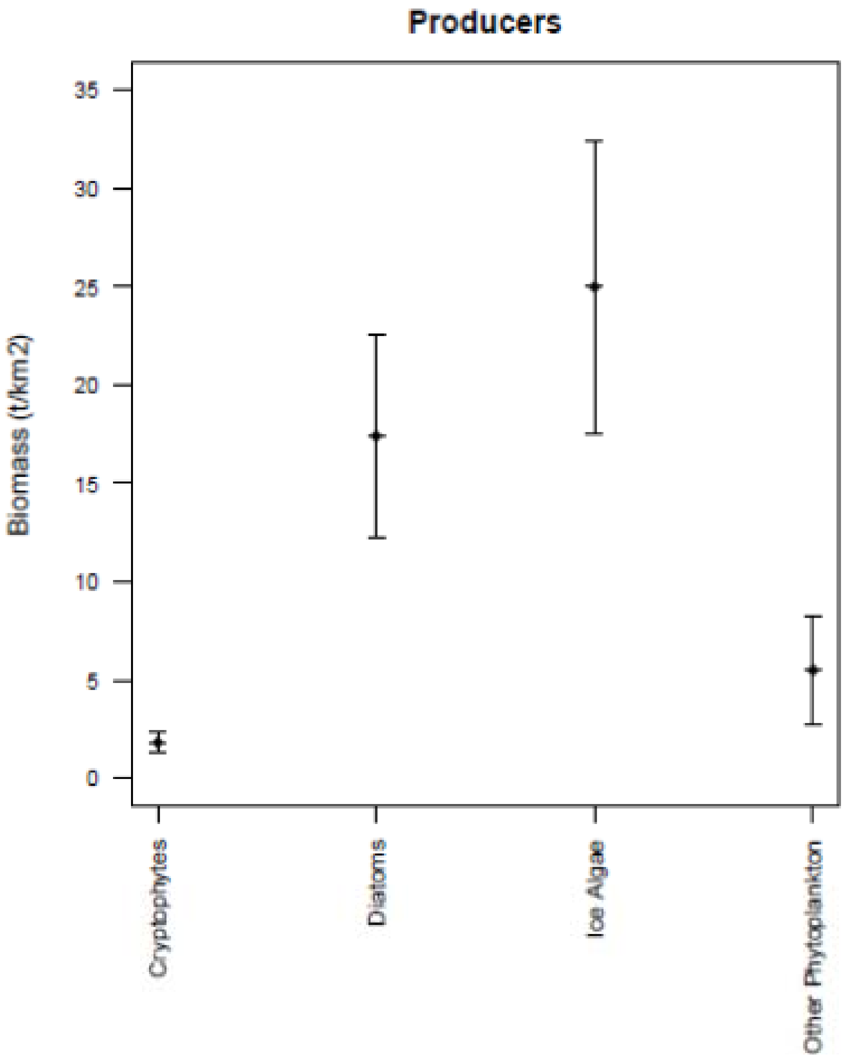
APPENDIX 5 (CONTNUED): MONTE CARLO RESULTS FOR BIOMASS



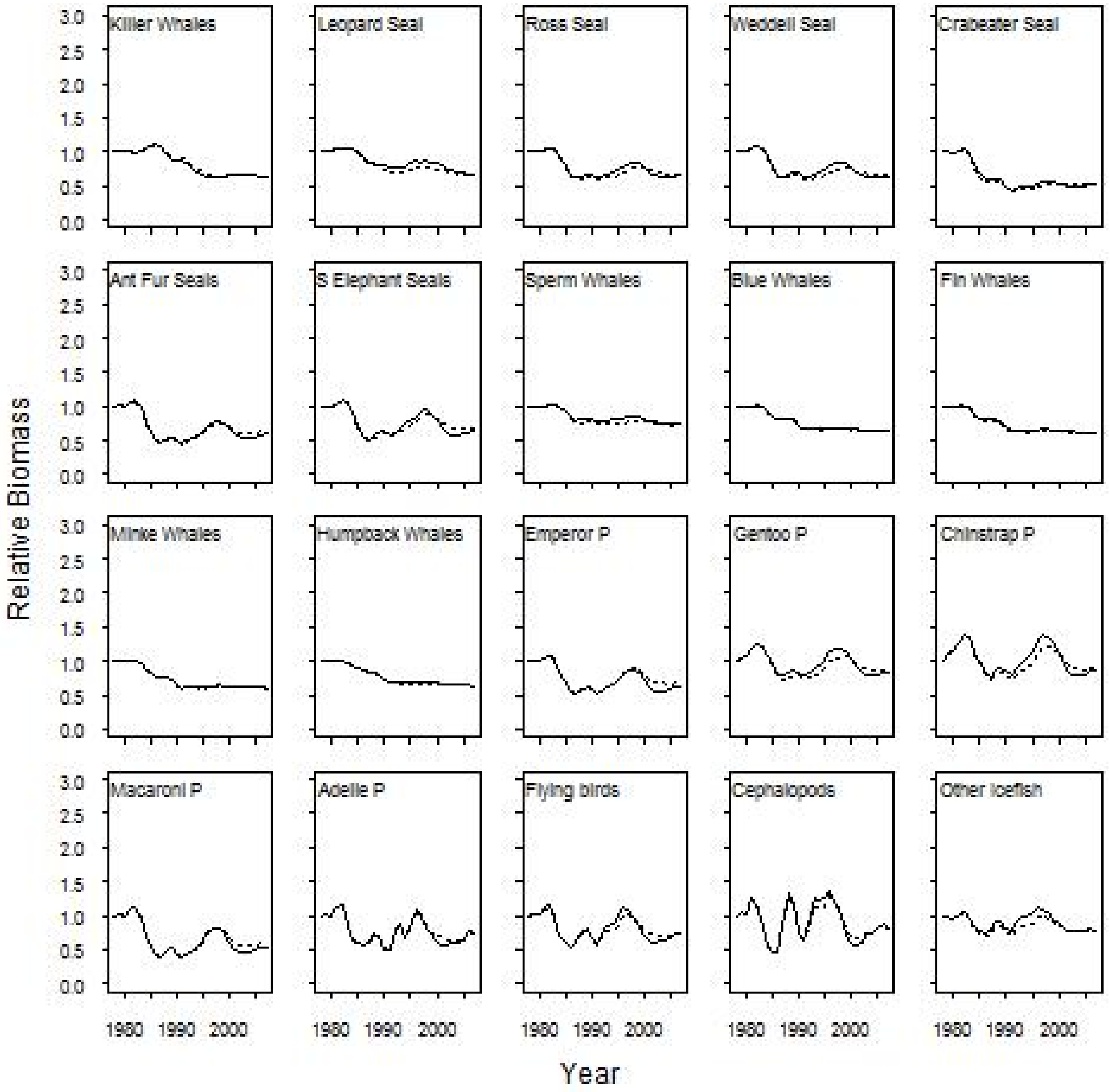


APPENDIX 5 (CONTINUED): MONTE CARLO RESULTS FOR BIOMASS

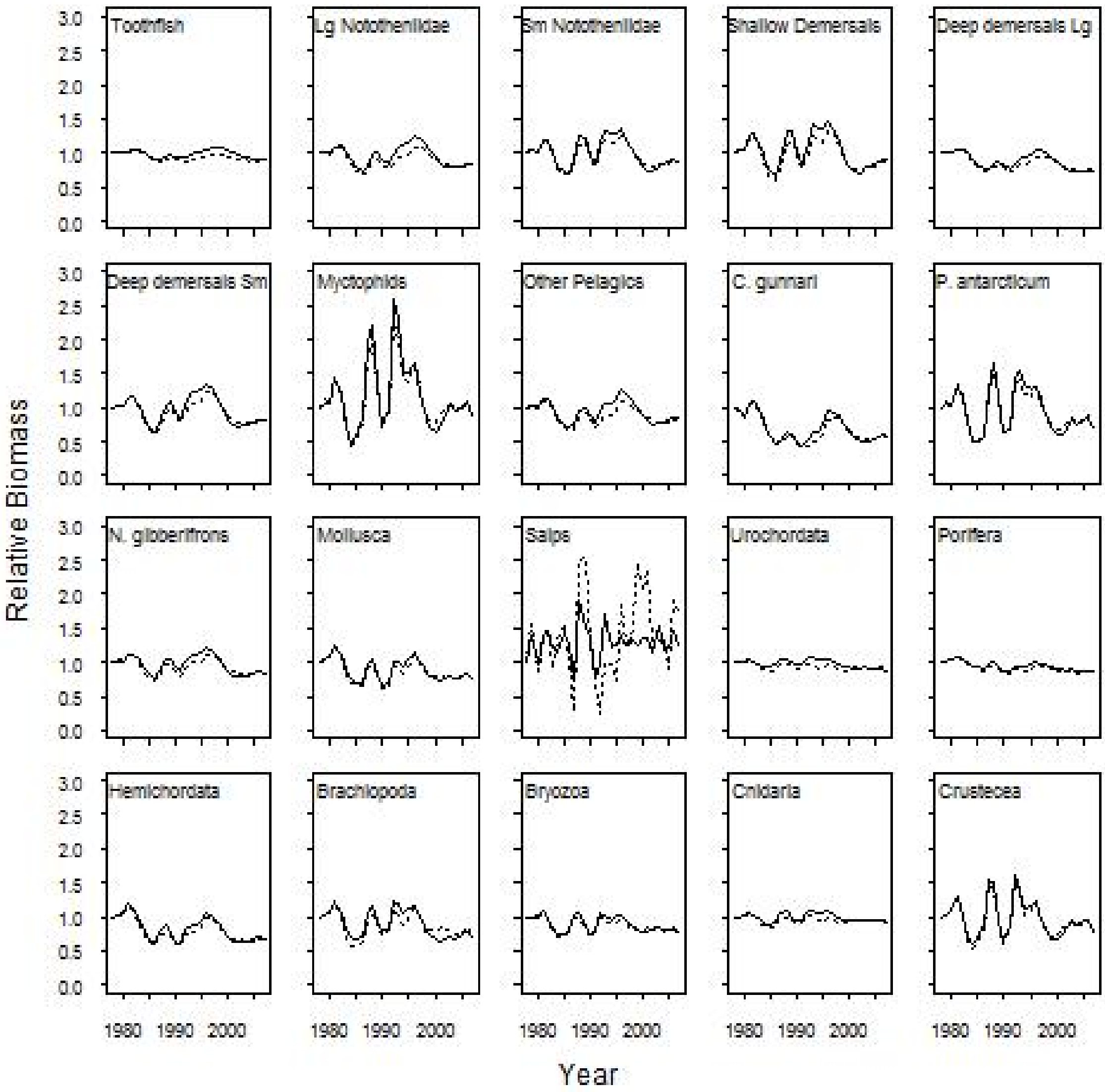




Appendix 6: Fitted Model Comparisons: SST (solid line) and SOI (dotted line)



APPENDIX 6 (CONTINUED): FITTED MODEL COMPARISONS: SST (SOLID LINE) AND SOI (DOTTED LINE)



APPENDIX 6 (CONTINUED): FITTED MODEL COMPARISONS: SST (SOLID LINE) AND SOI (DOTTED LINE)