Canadian Beaufort Sea Shelf Food Web Structure and Changes from 1970-2012

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CANADIAN BEAUFORT SEA SHELF FOOD WEB STRUCTURE AND CHANGES FROM 1970-2012

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The Beaufort Sea marine ecosystem is under increasing pressure from climate change associated impacts as well as anthropogenic stressors including resource development and shipping. It is also the location of the first Arctic marine protected area (MPA), the Tarium Niryutait MPA. In order to better understand the structure of the Canadian Beaufort Sea Shelf marine ecosystem and potential impacts of multiple stressors, an Ecopath with Ecosim food web model was created. Construction of the food web model was achieved by linking predators and prey through trophic interactions to identify the structure of the ecosystem and changes over time. The Ecopath (static) portion of the model contains 33 functional groups ranging from primary producers and detritus to whales and was set to the year 1970 to represent a past, stable ecosystem structure. The Ecopath model synthesizes existing data for the ecosystem, in addition to estimating unknown parameters such as conservative estimates of fish biomass in the system based on predator's dietary needs and ecosystem productivity. In addition, harvest mortality for all harvested fish and mammals within the model are identified and summarized. Changes to the ecosystem driven by reductions in sea ice and increases in sea surface temperature are considered large compared to harvest mortality impacts. While changes to individual species or species groups range (from -20% to +135% of starting biomass) over the 1970-2012 temporal simulation, total ecosystem biomass increases (~30%) over the historical simulation, with ecosystem trophic level remaining stable (<1% change).

Key Words: Beaufort Sea, Ecosystem Model, Ecopath with Ecosim, Inuvialuit Settlement Region,

RÉSUMÉ

C. Hoover, W. Walkusz, S. MacPhee, A. Niemi, A. Majewski, and L. Loseto. 2021. Canadian Beaufort Sea Shelf Food Web Structure and Changes from 1970-2012. Can. Data Rep. Fish. Aquat. Sci. 1313: viii + 97 p.

L’écosystème marin de la mer de Beaufort est soumis à des pressions croissantes causées par les effets liés au changement climatique et les agents de stress anthropiques, notamment l’exploitation des ressources et le transport maritime. C’est aussi dans cette région que se trouve la première zone de protection marine (ZPM) de l’Arctique, à savoir la ZPM de Tarium Niryutait. Afin de mieux comprendre la structure de l’écosystème marin du plateau continental canadien de la mer de Beaufort et les effets potentiels des différents agents de stress, un modèle de réseau trophique a été créé avec le logiciel Ecopath with Ecosim. Pour ce faire, les prédateurs et les proies ont été reliés par des interactions trophiques afin de définir la structure de l’écosystème et les changements au fil du temps. La partie Ecopath (statique) du modèle contient 33 groupes fonctionnels, y compris les producteurs primaires, les détritus et les baleines, et a été fixée à l’année 1970 pour représenter une structure d’écosystème historique et stable. Le modèle Ecopath synthétise les données existantes pour l’écosystème, en plus d’estimer des paramètres inconnus comme les estimations prudentes de la biomasse des poissons dans le réseau hydrographique selon les besoins alimentaires des prédateurs et la productivité de l’écosystème. En outre, la mortalité par récolte de tous les poissons et mammifères exploités est déterminée et résumée dans le modèle. Les modifications de l’écosystème dues à la réduction de la glace de mer et à la hausse de la température de la surface de la mer sont considérées comme importantes par rapport aux effets de la mortalité par récolte. Alors que les changements au niveau de l’espèce ou des groupes d’espèces vont de - 20 % à + 135 % de la biomasse de départ dans la simulation temporelle de 1970 à 2012, la biomasse totale de l’écosystème augmente (~ 30 %) dans la simulation historique et le niveau trophique de l’écosystème reste stable (changement < 1 %).

Mots clés : mer de Beaufort, modèle d’écosystème, Ecopath with Ecosim, région désignée des Inuvialuit

INTRODUCTION

With the Arctic experiencing warming at the rate twice the global average (IPCC, 2013) and rates of sea ice loss exceeding the modeled projections (Stroeve et al. 2007; Stroeve et al. 2011; Stroeve et al. 2012), there is cause for concern and consideration of management and conservation strategies. Impacts at the ecosystem level have been observed in numerous studies documenting recent changes (e.g. primary production (Brown and Arrigo, 2012); river hydrology (Prowse et al., 2011), carbon fluxes (McGuire et al., 2009), condition of higher trophic level species (Harwood et al. 2015). Additionally, loss of sea ice will enable increased access to the north via shipping (including tourism) as well as human activity such as resource extraction (e.g. oil and gas, mining (Arctic Council, 2009; Stephenson et al., 2011).

The Canadian Beaufort Sea Shelf (hereafter referred to as BSS) is an area north of the Mackenzie River and South of the Beaufort Sea that can be described as a rectangular platform with Amundsen Gulf to the east and the Mackenzie Canyon to the west (Carmack and Macdonald, 2002). Arctic shelves comprise greater than 30% of the Arctic Ocean surface area and play a critical role in carbon cycling and productivity as has been demonstrated on the BSS (Macdonald et al. 1998; Carmack et al. 2004; Forest et al. 2013). The BSS is the largest North American shelf in the Arctic, receiving significant riverine input from the Mackenzie River, with estimates over 300 km^3 of fresh water per year spread over an area of 60,000 km^2 (Macdonald et al., 1998). The majority of the BSS is less than 100 m deep with the shelf break along the 200 m isobath. North of the BSS lies the Canada Basin which extends roughly 1130 km (700 miles) north and reaches depths of 3600 m. The BSS provides a dynamic habitat for many species including resident (e.g. fish, seals, polar bears (Amstrup et al. 2000)) and migratory (e.g. marine birds, cetaceans, char (Krueger et al. 1999; Dickson and Gilchrist 2002; Harwood and Smith 2002)) marine species. While the BSS was heavily occupied by oil and gas industry activity in the 1980's, activity then slowed in the 1990's and has recently resumed, largely focused in the offshore (Canessa et al., 2002; Voutier et al., 2008).

The BSS is located in the Inuvialuit Settlement Region (ISR), where the Inuvialuit Final Agreement (IFA), a land claim area, was designated in 1984 for the Inuvialuit People (Western Canadian Inuit) (Indian and Northern Affairs Canada, 1984). Of the six communities in the ISR, three access marine resources directly in the BSS (i.e. Aklavik, Inuvik, Tuktoyaktuk) and the remaining three (Paulatuk, Ulukhaktok, Sachs Harbour) utilize marine resources associated with the BSS in bays off of the Amundsen Gulf. Inuvialuit continue to lead subsistence lifestyles that rely on marine resources such as beluga whales, ringed seals, and numerous fish species (Hoover et al., 2016; Loseto et al., 2018; Usher, 2002). In addition to providing a source of food, subsistence harvest contributes to psychological well-being and community integration (Condon et al., 1995). Under the (IFA) land claim the Inuvialuit are co-managers of wildlife and other renewable resources in the Beaufort Sea together with federal agencies (Indian and Northern Affairs Canada, 1984). One of the main objectives of the IFA is to “protect and preserve the arctic wildlife, environment, and biological productivity“ (Indian and Northern Affairs Canada, 1984). Similarly, the federal management of the Canadian Arctic Ocean under Canada’s Oceans Act (Fisheries and Oceans Canada (DFO)) call for “conservation, based on an ecosystem approach, is of fundamental importance to maintaining biological diversity and productivity in the marine environment” (Canada’s Oceans Act 1997).

Under the Oceans Act several management initiatives and actions have occurred in the BSS in recent years. The BSS is within DFO’s Beaufort Sea Large Ocean Marine Area (LOMA) (Cobb et al. 2008) for which an integrated oceans management plan (IOMP) was created. This IOMP was developed with multiple stakeholders and rights holders from the region including Inuvialuit, local, territorial and federal governments, and industry, with the ultimate vision that the Beaufort Sea is “healthy and supports sustainable communities and economies for the benefit of current and future generations” (Beaufort Sea Partnership, 2009). As part of the management actions plans, Ecologically and Biologically Significant Areas (EBSAs) were defined within the Beaufort Sea LOMA (Cobb et al., 2014; DFO, 2014). Among the eighteen EBSA’s, nearly half (8) are within the BSS (DFO, 2014). Lastly, the co-management board Fisheries Joint Management Committee (FJMC) and DFO together designated the first Arctic Marine Protected Area, the Tarium Niryutait Marine Protected Area, in the BSS area to conserve the long-term health of the beluga population and its supporting ecosystem (Fisheries and Oceans Canada, 2013).

Despite the many management actions and the local reliance on the marine ecosystem, much remains to be understood about the structure, function, and changes occurring in the BSS ecosystem as a whole. Concerns about ecosystem health and for harvested species regarding the effects of climate change and other cumulative stressors (disease, contaminants, food web changes) raised by co-management boards and communities led to research initiatives that examined ecosystem level changes. Under DFO’s Ecosystem Research Initiative (ERI) the BSS was selected as a priority area for research to better define ecosystem processes and to support the development of tools for ecosystem based management (Wieckowski et al., 2009). Specifically, an ecosystem modelling approach was employed to summarize the existing data and identify ecosystem structure using the Ecopath with Ecosim approach (Christensen et al. 2005). All species represented in the food web were included in the Ecopath (static) portion of the model. Historical time-series were included from 1970-2012 to capture known ecosystem dynamics and identify important drivers.

METHODS

MODEL AREA

The BSS model area covers approximately 103,000 km^{-2} of the continental shelf for depths shallower than 200 m (Figure 1). This area is strongly influenced by the Mackenzie River, the largest and longest river system in Canada, whereby freshwater and nutrients are distributed during spring ice melt and throughout the summer months. The 200 m depth was chosen as the outer limit since the continental shelf drops off beyond that depth (with the mid-shelf at 100 m) and changes in oceanography occur at the 200 m isobath (Carmack and Macdonald 2002, Weingartner 2003). In addition, including data beyond 200m increased uncertainty in the model, as data are limited for the deeper offshore areas. Past and current reports and scientific studies have been focused on the shelf area, where there is a greater understanding of the ecosystem. Recent research (2012-2014) under the Beaufort Regional Ecosystem Assessment (BREA) program has been designed to improve offshore knowledge. Specifically the Marine Fish Program (Principal Investigator: Dr. J. Reist, DFO Winnipeg) has conducted the first large scale fish sampling (in addition to zooplankton and producer samples) on the BSS, in order to fill gaps in existing fish biology and ecology. While data from this program is still be being completed, preliminary reports of shelf assessments have allowed a greater understanding of the food web, with more information expected in the near future. The Ecopath model was created to represent the early 1970s food web, as there are limited data and reports prior to this time. Simulations depicting changes in the ecosystem (Ecosim) are run from 1970-2012 to re-create past changes and garner a greater understanding of ecosystem dynamics.

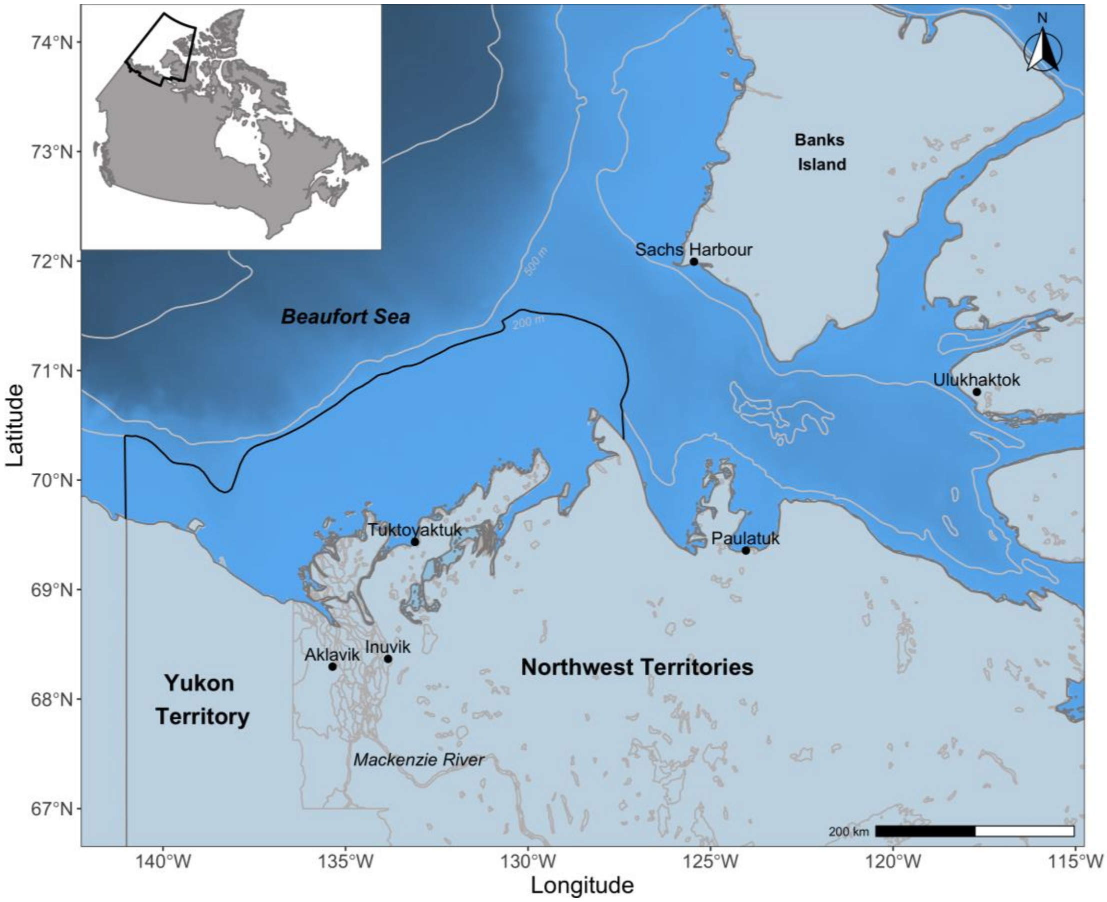

Figure 1. Beaufort Sea and surrounding communities. The BSS Model area includes the coastal shelf up to a depth of roughly 200 m and is outlined in black.

MODEL EQUATIONS

The model was created using a mass-balance approach and the ecosystem modelling software Ecopath with Ecosim (Buszowski et al., 2009; Christensen et al., 2007). This allows for all components of the food web to be linked through diets, where the production (P) of each group i is represented as:

(1)

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

and is dependent upon the biomass B_j of each predator group j, with predation mortality on prey group i from predator group j as $M2_{ij}$ (Christensen and Walters, 2004). Here Y_i represents the fishery catch (for group i), the net migration rate E_i is the emigration-immigration, biomass accumulation is BA_i, and the ecotrophic efficiency EE_i represents the proportion of production accounted for within the system (consumed by predators, exported from the system, fishing or migration). There must be energy produced by each group to balance energy removed through predation, fishing, migration, etc. under the mass-balance assumption. Equation 1 can also be expressed as equation 2 (Christensen et al., 2007):

(2)

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

Where P_i again represents the production of prey group i, and is dependent on the biomass of predator group j (B_j), the consumption per unit of biomass for predator j $(Q/B)_j$, the proportion of prey i in the diet of predator j (DC_{ji}), and other non-predator dependent parameters such as fishery catch (Y_i), net migration (E_i), biomass accumulation (BA_i), the production to biomass ratio $(P/B)_i$, and Ecotrophic Efficiency (EE_i). It should be noted that the production to biomass ratio $(P/B)_i$ is also equal to the total mortality (Z) (Allen 1971) for the first year or Ecopath portion of the model. In order to balance the model, one of the four basic parameters (B, P/B, Q/B, EE) for each species group is allowed to be missing. Using a set of linear equations, an algorithm estimates the missing parameter, based on the parameter values of other predator and prey groups in order to "balance" the model.

For each functional group within the Ecopath model, basic parameters are calculated from available data and published information. Details on how basic parameters such as B, P/B, Q/B, EE, and diet were calculated based on available data are presented for all species groups. Calculations for parameters differ by species, but are all presented in the respective sections. In cases where data were lacking, expert knowledge was used to estimate parameters. Units are consistent across species groups; biomass is presented in $t \cdot km^{-2}$ and refers to wet weight values unless otherwise indicated, Production/Biomass (P/B) and Consumption/Biomass (Q/B) are presented as annual values (y^{-1}), Ecotrophic Efficiency (EE) is a dimensionless parameter, and diets are incorporated as the percent contribution in wet weight to the annual diet.

Temporal simulations were generated in Ecosim using equation 3 (Christensen et al., 2007):

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

Where the change in biomass for group i over time t (dB_i/dt) can generally be thought of in three components: (1) the prey consumed (increases in biomass) presented as the net growth efficiency (g_i) or production/consumption ratio, times the total consumption of prey group i ($\sum_j Q_{ji}$) for each prey group consumed; (2) Predation (decreases in biomass) from all predators on group i ($\sum_j Q_{ij}$); and (3) other changes such as mortality associated with old age (MO_i), the fishing mortality rate (F_i), immigration rate (I_i) and emigration rate (e_i) where net migration equals B_i*(e_i-I_i) (Christensen and Walters, 2004). In order to make simulations reflective of past changes, Ecosim simulations are fit to past known data trends. This process of fitting the model to data includes altering predator prey relationships to capture more detailed interactions. The foraging area theory dictates the biomass of a group is split between vulnerable and invulnerable states, whereby the prey are only vulnerable to predators during the vulnerable state (Walters et al. 1997). Vulnerabilities are set during the model fitting process in Ecosim, where low vulnerabilities (<2) indicate a bottom up interaction where biomass of the group is close to carrying capacity and prey production determines the predation mortality. High vulnerabilities (>2, ranging upwards of 100) indicate a top down interaction whereby biomass is more unstable and far from carrying capacity and predator biomass determines how much prey is consumed (Christensen and Walters, 2004).

MARINE MAMMAL PARAMETERS

There are five marine mammal groups representing five species, each group contains one species. For all marine mammal functional groups, the biomass (B) of each group was calculated as the number of animals multiplied by the average weight for each species (in tonnes), divided by the total model area (km^2). This calculation assumes marine mammals are year round inhabitants, however this is not true for species such as beluga and bowhead who only reside in this area during late spring and summer (Fraker and Fraker 1979; Harwood and Smith 2002). It is uncertain how much of the annual food budget comes from within the model area for these species, so the biomass was originally set to the total population, and then reduced during model balancing, in order to explore the ecological consequences of feeding outside the model area. Starting and final biomass values are described in methods (individual group descriptions) and results (model balancing section), respectively.

The P/B calculated for marine mammals combines both natural and harvest mortality. Natural mortality rates were calculated for each species using the life table from Barlow and Boveng (1991), where natural mortality is calculated for each species over all life stages up to a maximum age using survivorship as an inverse for natural mortality (full equations and parameters for P/B calculations are available in Appendix A). The harvest mortality is calculated as catch/biomass for the first year of the Ecopath model with values presented in Table 1. This used the number (or estimated number) of individuals harvested for the first year of the model, as the proportion of the total population. The consumption/biomass ratios (Q/B) was calculated using equation 5 (Cauffopé and Heymans 2005; Hunt, et al. 2000) which calculates the energy required per day E in $Kcal \cdot day^{-1}$:

(4) $E = aM^{0.75}$

where a is a coefficient with different values for each group of marine mammals (a=320 for otariids, 200 for phocids, 192 for mysticetes, and 317 for odontocetes), and M is the mean body weight of the species in kg. The daily energy requirement is compared to the energetic value of foods in the diet (Cauffopé and Heymans, 2005) to give the Q/B ratio. See Table 1 for calculated natural mortality, harvest mortality, and total mortality values for marine mammals.

Table 1: Data and calculated values for marine mammal Ecopath parameters. Natural mortality (y^{-1}) was calculated using longevity and survivorship equations in appendix A. Harvest mortality is presented as catch/biomass (t·km^{-2}). P/B and Q/B values are presented as annual values (y^{-1}). All values represent the 1970 starting values for biomass and harvest.

Species	Population Size	Source	Mean Weight (kg)	Source	Longevity (Years)	Source	Mortality (calculated)	Harvest Mortality	Model P/B	Calculated Q/B	Model Q/B	Catch
1: Polar Bear*	1778	(Amstrup et al., 1986)	300	(Stirling and Parkinson, 2006)	25	(Stirling, 2002a)	0.096	0.088	0.150^{1}	3.029	3.029	2.56E-04
2: Beluga*	39258	(Allen and Angliss, 2010)	725	(Fisheries and Canada, 2002; NAMMCO, 2005)	50	(Harwood and Smith, 2002; Stewart et al., 2006)	0.044	0.006	0.065^{2}	21.448	17.000^{1}	8.10E-04
3: Bowhead*	4500	(Gerber et al., 2007; Moore and Clarke, 1991)	31100	(Trites and Pauly, 1998)	200	(George et al., 1999)	0.018	4.44E-04	0.072^{2}	5.475	5.475	3.02E-04
4: Ringed Seal	21630	Estimated from (Kingsley, 1984)	42.5	(Trites and Pauly, 1998)	43	(Miyazaki, 2002)	0.150	0.401	1.100^{2}	16.050	16.05	8.96E-04
5: Bearded Seal	7500	(Stewart, 2006)	275	(Kovacs, 2002)	25	(Kovacs, 2002)	0.131	0.003	0.124^{1}	13.848	13.848	1.26E-04

* indicates a percentage of the population or catch was used in the model to account for non-full time resident species

[1] Value was decreased from calculated value during model balancing

[2] Value was increased from calculated value during model balancing

1: Polar Bears

The polar bear group represents bears (*Ursus maritimus*) located in the model area from the Southern Beaufort Sea stock. This stock of polar bears ranges from Barrow, US to just south of Banks Island and east of the Baillie Islands, Canada (Allen and Angliss 2010; Paetkau et al. 1999; Regehr et al. 2006). In the US, this stock is currently classified as depleted under the Marine Mammal Protection Act and is considered threatened under the U.S. Endangered Species Act (Allen and Angliss 2010). Population estimates of southern Beaufort Sea polar bears identified 1778 bears from 1972-1983, between 1800-2185 bears in 1986, 2272 bears in 2001, and 2185 bears in 2006 (Allen and Angliss 2010; Amstrup et al. 1986). This stock had no growth, or very little, during the 1990s (Amstrup et al. 2001), followed by low growth rates in 2004 and 2005, and then a decline of 3% a year in 2001-2005 (Allen and Angliss 2010; Hunter et al. 2007). In Alaska, polar bear distribution has been observed to change from bears primarily located on ice along the shelf break in the early 1980s to bears being observed on islands or along the coast in the early 2000s. This change was linked to changes in ice type and cover, and coincides with the decline of 3% a year (Allen and Angliss 2010; Gleason and Rode 2009). Polar bears are harvested in both Canada and the US with the potential biological removal (PBR: maximum number that can be sustainably removed) set to 22 bears per year (Allen and Angliss 2010). Starting biomass was calculated to be 0.005 $t\cdot km^{-2}$ based on a population of 1778 bears. However, this number was lowered to 0.002 $t\cdot km^{-2}$ during model balancing, accounting for roughly 40% of the southern Beaufort Sea stock within the area. This is not unexpected as the range of this population extends into the US and the model area is a subset of the total range. A biomass value of 0.005 $t\cdot km^{-2}$ would indicate all feeding of the entire population occurs within the model area and is not realistic based on polar bear ecology. The harvest was set to 81 bears for the first year based on statistics for the US and Canada (Allen and Angliss 2010). Survivorship estimates are close to 0.9 taking into account both sexes and different age classes of bears (IUCN, 2010), indicating a natural mortality rate of 0.1 y^{-1}. The P/B ratio was calculated to be 0.184 y^{-1} accounting for harvest and natural mortality however it was lowered to 0.150 y^{-1} during model balancing. The calculated Q/B value of 3.029 y^{-1} was used.

Ringed seals are the primary prey for polar bears with bearded seals also contributing. It has been noted that when seal production is high, pups comprise over half the seals killed, and when seal production is low, polar bears have been observed to display cannibalism (Stirling and Archibald 1977; Stirling 2002a; Peacock et al. 2010). The diet of Polar Bears was set at: 3% Beluga Whales, 2% Bowhead Whales, 85% Ringed Seals, 9.9% Bearded Seals, and 0.1% Polar Bears (to account for cannibalism).

2: Beluga Whales

Of the five stocks of beluga whales (*Delphinapterus leucas*) that over-winter in the Bering Sea, only the eastern Beaufort Sea beluga stock summers in the Canadian Beaufort Sea (Allen and Angliss 2010). They are found in offshore waters associated with pack ice and once in the model area (BSS), they gather along the edge of the land-fast ice until a passage into the warmer Mackenzie Estuary becomes available (Braham et al. 1980; DFO 2000; Hornby et al. 2016). The estuary is thought to provide important moulting and calving habitat (Sergeant and Brodie 1969; Braham et al. 1980). This population has been estimated at 19,629 in 1992 (not including submerged whales), although calculations that include submerged animals (using a correction factor of 2) increase the estimate to nearly 40,000 whales (Allen and Angliss 2010; Fisheries and Oceans Canada 2002; Harwood et al. 1996). Belugas only summer in the model area, and the amount of feeding in this area during their residence is unknown. An initial biomass of 0.070 $t \cdot km^{-2}$ was lowered to 0.030 $t \cdot km^{-2}$, representing 25% of the total population biomass.

This population is harvested in the US (along migration routes) and Canada (summering locations), with potential, although unrecorded, catches possibly occurring in Russia along migration routes (Harwood et al. 2002). Harvest rates range between 100 to 200+ whales a year for the communities in the ISR, in addition to roughly 64 whales harvested per year in Alaskan communities (Harwood et al. 2002; The Joint Secretariat 2003). Although harvest rates are likely underestimated, they are still low in relation to population size, with the combined US and Canada harvest comprising 1% of the population. This would increase to 1.1% if the Russian harvest of approximately 25 whales annually were included (DFO 2000; Harwood et al. 2002). The P/B was increased from the calculated value of 0.05 y^{-1} to a value of 0.065 y^{-1} to balance the model. Q/B was lowered from the calculated value of 21.45 y^{-1} to 17.00 y^{-1} to balance the model (Table 1).

The diet of belugas is diverse. 62 whale stomachs sampled from 1983-2003 in Alaska showed Arctic Cod (*Boreogadus saida*) as a dominant fish species with lesser amounts of Shorthorn Sculpin, Arctic Sculpin (*Myoxocephalus scorpioides)*, Pacific Sandlance (Quakenbush et al., 2015). Invertebrate species in the Alaskan harvested whales were dominated by shrimp with contributions by cephalopods, echiurids, amphipods (Quakenbush et al., 2015). Diets of belugas harvested in the Mackenzie Estuary were noted to include cephalopods (specifically squid), Arctic Cisco (*Coregonus autumnalis*), whitefish, Pacific Herring (Clupea pallasii), Least Cisco (*Coregonus sardinella*), Rainbow Smelt (*Osmerus mordax*), and Inconnu (*Stenodus leucichthys*) (Harwood and Smith, 2002). Fatty acid analysis for Canadian Beaufort Sea belugas showed Arctic Cod as a primary prey species, with Pacific Herring, Least Cisco, shrimp, and mysids showing varying levels of dietary contributions along with other fish and invertebrate species (Loseto et al., 2009). The diet for belugas was set to: 1% Anadromous Chars, 16% Ciscos & Whitefish, 7% Herring & Smelt, 45% Arctic & Polar Cods, 5% Capelin, 2% Flounders & Benthic Cods, 10% Small Benthic Marine Fish, 2% Other Fish, 5% Macro-zooplankton, 2% Med Copepods, 3% Lg Copepods, 2% Other Meso-zooplankton.

3: Bowhead Whales

The Western Arctic bowhead whale (*Balaena mysticetus*) stock summers in the Beaufort Sea, arriving through flaw leads in the ice in May, and remaining in this feeding ground until September (Braham, 1984; Fraker and Bockstoce, 1980). This population migrates along the coast of Alaska to its winter location in the Bering Sea, and is harvested along this migration by hunters from indigenous communities in both US and Canada (Braham et al. 1980). While commercial whaling reduced this population in the late 1800s and early 1900s, the population is believed to be increasing. Rates of increase from 1978-2001 are believed to be as high as 3.4% (increasing from 5000 to 8000 whales during this time), with the population reaching over 10,000 whales in 2000 (George et al. 2004; Gerber et al. 2007; Moore and Clarke 1991; Zeh and Punt 2005). In Alaska an average of 41 whales per year were landed during 1997-2006, with a total of 1149 landed between 1974-2011 (Suydam and George 2012; Suydam et al. 2007). In the Northwest Territories the bowhead hunt is sporadic, with only 2 bowheads landed, one in 1991 and one in 1996 (Harwood and Smith 2002). The starting biomass was initially set to 0.75 $t \cdot km^{-2}$ (equivalent to 2500 whales), but was decreased to 0.34 $t \cdot km^{-2}$ (equivalent to approximately 100 whales) during model balancing. The P/B ratio was calculated to be 0.018 y^{-1}, but was increased to 0.072 y^{-1} during model balancing and fitting, to account for biomass accumulation. A biomass accumulation of 0.0105 $t \cdot km^{-2} \cdot y^{-1}$ was included in the model to allow bowhead to rebound from historical whaling. The calculated Q/B ratio of 5.47 y^{-1} was used in the model.

Although summer feeding is thought to be an important driver in migrations, whales sampled in Alaska were identified to be feeding along spring and fall migration routes (Lowry, et al. 2004; Schell et al. 1989). Bowhead whales feed predominantly on copepods (*Limnocalanus macrurus, Calanus hyperboreus, Calanus glacialis*), with some samples of harvested whales containing large amounts of euphausiids (Pomerleau et al., 2011; Schell et al., 1989). Diets also include gammarid and hyperiid amphipods, isopods, and mysids in varying amounts (COSEWIC 2009; Harwood and Smith 2002; Lowry et al. 2004; Schell et al. 1989). The diet for this group was set to: 12% Macro-Zooplankton, 20% Med Copepods, 50% Lg Copepods, 13% Other-Meso-Zooplankton, 5% Micro-Zooplankton.

4: Ringed Seals

Ringed seals (*Pusa hispida*) are one of the most abundant seals in the Arctic with a circumpolar distribution, including the Beaufort Sea (Kingsley, 1984; Miyazaki, 2002). They are an important prey item for polar bears, and are harvested by local communities. Although the model area is covered in solid ice throughout the winter, it was assumed that the population of seals within the area are year-round residents. During spring, seals build birthing lairs in the snow drifts on the sea ice to haul out and give birth while hiding from polar bears, and often take advantage of ridges in the sea ice to conceal themselves (Stirling et al., 2008). Observations of seals from a 1983 survey observed 5400 seals in the model area, however this was not a population estimate, and did not account for submerged animals (Kingsley, 1984). More detailed population estimates from surveys within the model area in 1974 and 1975 yielded estimates of 26,660 and 7657 seals, respectively, attributing the large inter-annual difference to changes in ice conditions and potential changes in seal distributions (Stirling et al. 1977). However, the total population for the larger Beaufort Sea including offshore areas and the Amundsen Gulf was estimated at 41,983 seals during the 1970s, indicating the population may be moving within a larger area (Stirling et al.1977). Stirling (2002b) calculated a population size of 360,000 seals would be required to satisfy the needs of the local polar bear population, while remaining stable. Initially the biomass was set to 0.009 $t \cdot km^{-2}$ (equivalent to 21,630 seals), based on estimated seal densities of 0.21 $seals \cdot km^{-2}$ by Kingsley (1984), and estimates by Stirling et al. (1977). This value was increased to 0.02 $t \cdot km^{-2}$ (roughly 48,000 seals) in order to balance the model, primarily to satisfy the diet needs of polar bears. Ringed seals are harvested within the model area, however, harvest levels are not well recorded. Seal harvest for the 1970s were estimated based on more current harvest records (1988-1997), and were set to 0.001 $t \cdot km^{-2}$ (2600 seals) from the Inuvialuit Harvest Study where harvest ranged from 1244-3162 seals (The Joint Secretariat, 2003). The P/B was increased from the calculated value of 0.55 y^{-1} to 1.10 y^{-1} to balance the model. The calculated Q/B value of 16.05 y^{-1} was used (Table 1).

The diets of ringed seals include many prey items such as euphausiids, amphipods, isopods, shrimp, mysids, some squid, and fish (such as Polar Cod (*Arctogadus glacialis*), Capelin (*Mallotus villosus*), and Saffron Cod (*Eleginus gracilis*)) (Lowry et al. 1987). Near Barrow, AK, euphaisiids were the primary prey item (Lowry et al. 1987), while in the Baffin Bay area fish such as Arctic Cod and Polar Cod were the primary prey for adults, and amphipods for juveniles (Holst et al. 2001). Large scale changes in carbon-13 (C^{13}) stable isotope values from the Amundsen Gulf indicate seals are currently feeding more on pelagic offshore fish than they did in the 1960s (Outridge et al. 2009). The diet for ringed seals was set to: 10% Anadromous Chars, 8% Ciscos & Whitefish, 3% Herring & Smelt, 12% Arctic & Polar Cods, 3% Capelin, 5% Flounder & Benthic Cods, 9% Small Benthic Marine Fish, 1% Other Fish, 9% Arthropods, 5% Echinoderms, 5% Molluscs, 5% Worms, 5% Other Benthos, 10% Macro-Zooplankton, 3% Med Copepods, 5% Lg Copepods, and 2% Other Meso-Zooplankton.

5: Bearded Seals

Bearded seals (*Erignathus barbatus*) are circumpolar in distribution, reside in the Arctic year round, and prefer shallow areas (<200 m) that are seasonally ice covered (Allen and Angliss 2010). Surveys on seal abundance and location are conducted in the spring and summer, confirming their presence in these seasons, but vocalizations indicate they are present near the model area (Penny Strait, Northwest Territories) in winter and early spring (Cleator and Stirling, 1989; Stewart, 2006). For the model, they are assumed to be full-time residents. The bearded seal population was estimated in 1974 and 1975 at 1513 and 679 individuals, respectively (considering survey results overlapped with model area), with the discrepancy most likely due to weather conditions and changes in animal location during surveys (Stirling et al. 1977). Population estimates for the greater Beaufort Sea, including areas surveyed outside the model area were 2757 and 1197 seals for 1974 and 1975, respectively (Stirling et al. 1977). The biomass for the model area was set at $0.02t \cdot km^{-2}$ to reflect a population size of 7500, which was increased from survey estimates. The higher value was needed to balance the model. Harvest levels for the Ecopath model were based on the Inuvialuit Harvest Study (1988-1997) with values ranging from 32-66 seals per year (The Joint Secretariat, 2003). The catch was set to 1.71E-04 $t \cdot km^{-2}$ (64 seals) for 1970. The model P/B was lowered from the calculated value of 0.134 y^{-1} to 0.124 y^{-1} to balance the model. The Calculated Q/B value of 13.84 y^{-1} was used to balance the model (Table 1).

Bearded seals are primarily benthic feeders consuming both benthic fish and invertebrates, although they consume a wide variety of prey items that can include pelagic fish (Stewart, 2006). For example, all prey items for seals sampled from the Belcher Islands, were benthic or epibenthic fish (Smith, 1981). However, in other areas benthic invertebrates and fish dominate the diet with large quantities of decapods, pelecypods and fish (Arctic Cod and sculpins) and lesser amounts of holothuroideans, gastropods, and polychaetes (Smith, 1981). Summer diet in the high Arctic has been noted to consist of sculpins and Arctic Cod, with smaller quantities of eelpouts, Polar Cod, gastropods, clams, cephalopods, holothuroideans, and polychaetes (Stewart 2006). The diet was set to: 5% Anadromous Chars, 4% Ciscos & Whitefish, 4% Salmonids, 1% Herring & Smelt, 11% Arctic & Polar Cods, 2% Capelin, 10% Flounder & Benthic Cods, 10% Small Benthic Marine Fish, 3% Other Fish, 25% Arthropods, 9% Echinoderms, 6% Molluscs, 5% Worms, and 5% Other Benthos.

6: Birds

The diversity of marine mammals and seabirds in the eastern Beaufort Sea is significantly lower than in other parts of the maritime Arctic, such as Baffin Bay to the east or the Chukchi Sea to the west (Stirling and Parkinson, 2006). Near-shore ocean waters in the summer attract thousands of waterfowl including oldsquaw ducks, surf scoters, sea ducks, tundra swans, geese, and loons, which all use the shallow waters as a staging and moulting area (Wildlife Management Advisory Council, 2006). Herschel Island (just offshore of the Yukon, within the model area) is an important habitat for birds with over 121 species recorded, and 46 confirmed as breeding on the island. (Wildlife Management Advisory Council, 2006). This is also the only know nesting location of the black guillemot in the Yukon, and one of a few known areas in the Arctic (Eckert et al., 2005). In addition to Herschel Island, the Tuktoyaktuk Peninsula, Mackenzie Estuary, and Cape Bathurst are considered key staging (resting or feeding) areas for common species such as common eiders, king eiders, and long-tailed ducks, surf scoters, and white-winged scoters (Dickson and Gilchrist, 2002). A full list of the 121 species know to occur within the model area is presented in Appendix B, along with its relative presence in the region ranging from common to rare. Changes to individual species are difficult to determine at a regional scale as there is a general lack of trend data (Environment Canada, 2013). No assumptions were made about changes in abundance or biomass to the group as a whole.

The biomass of this group was set to 0.001 $t \cdot km^{-2}$ to reflect a bird population of roughly 500,000 birds in the summer (or 125,000 birds year round), using an average bird weight of 825 grams. Bird weights for common species such as eiders, king eiders, black guillemots, and longtail ducks ranged from 320 – 3040g (Cornell Lab of Ornithology, 2015). A P/B estimate of 0.9 $year^{-1}$ was used to balance the model, and account for the roughly 30,000 birds harvested annually by Inuvialuit (The Joint Secretariat, 2003), which accounted for a harvest mortality of 0.3 $year^{-1}$. A Q/B value of 10 $year^{-1}$ was used. Diets of all species are not well known within the region, but black guillemots are known to consume Arctic Cod and sculpins, with availability of Arctic Cod linked to fledging success (Eckert et al., 2005). Studies in the nearby Alaskan Beaufort Sea highlight the importance of Arctic Cod to black guillemots, while nearshore demersal fish and sculpins contribute significantly to the diet when Arctic Cod is less available (Divoky et al., 2015). Due to the diversity of birds within this group, diets were set to include a variety of fish and invertebrates. The diet of birds was set to 5% Anadromous Chars, 6% Ciscos & Whitefish, 5% Salmonids, 10% Herring & Smelt, 11% Arctic & Polar Cods, 2% Capelin, 3% Flounder & Benthic Cods, 9% Small Benthic Marine Fish, 1% Other Fish, 7% Arthropods, 2% Bivalves, 2% Echinoderms, 2% Molluscs, 3% Worms, 2% Other Benthos, 2% Jellyfishes, 5% Macro-Zooplankton, 8% Med Copepods, 10% Lg Copepods, 5% Other Meso-Zooplankton.

FISH

Fish species present on the Beaufort Sea Shelf include both diadromous (moving between freshwater and marine environments) and marine fishes. Although migratory fish are not present in the model area year round, it was assumed that feeding occurred within the model area (e.g., Craig 1984; Bond and Erickson 1989; Jarvela and Thorsteinson 1999), therefore they were considered residents for modelling purposes, and biomass was not adjusted to compensate for time spent outside the area. Species included in the model were based on fish identified to be present in the Beaufort Sea – Amundsen Gulf ecozone (Majewski et al. 2009; Majewski et al. 2011; Coad and Reist 2004), with common species or those important to the food web having their own/smaller groups. This resulted in 10 model groups. Species listed as common are marked (*) in the functional groups below. It has been noted that species such as Dolly Varden (*Salvelinus malma*), Arctic Char (*Salvelinus alpinus*), coregonids (whitefishes and ciscoes), and Arctic Cod are some of the more important species in the Beaufort Sea food web (Alaska Department of Natural Resources 2009). Surveys of fish within the area have been small-scale and sporadic during the model temporal scale, primarily based on hunter catches (The Joint Secretariat, 2003) or very focused scientific studies (e.g., Galbraith and Hunter 1975; Percy 1975; Bond and Erickson 1987). Furthermore, the majority of information on marine fish diets is limited to anadromous and coastal marine fishes. All fish species were divided into 10 functional groups based on life history, diets, and familial characteristics. Biomass estimates for all fish groups were estimated by the model, as there have been no comprehensive surveys completed within the model area. Using P/B, Q/B, EE, and diets, biomass was estimated using Ecopath Equation 2, based on ecosystem constraints.

P/B is set to total annual mortality to balance the Ecopath model, and is comprised of natural and fishing mortality. Catches for each group (Table 2) were based on harvest surveys (Appendix B: The Joint Secretariat, 2003), although estimates may be low due to under-reporting. Fishing mortality was negligible and P/B was generally set to natural mortality (M). The widely accepted calculation of M using equation 5 from Pauly (1980) underestimates polar fish production values, therefore a second method developed by Lorenzen (1996) was also used. Applying equation 5 (Pauly, 1980), L_∞ is the maximum length of the fish, with species specific values taken from Froese and Pauley (2012), and T is the temperature (^{0}C) of the water in the model area. T was set to 1^0C (British Atmospheric Data Centre, 2010) as the annual average for the first year of the model. The second approach by Lorenzen (1996) using equation 6, calculates mortality at weight (M_W) using parameters b = -0.292 (constant) and natural mortality rate at unit weight M_u=1.69, based on Polar natural ecosystem values. Weight of fish (W) was taken from the BREA Marine Fish Program samples for available species using the average weight of each species caught, if available (DFO unpublished data), otherwise they were taken from species averages for other regions in Fishbase (Froese and Pauley, 2008). The BREA samples were taken from 2012-2014 within the model area. The second approach (eq. 6) resulted in a higher P/B value that was used in model parameterization.

(5)

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

(6)

$$M_W = M_\mu * W^B$$

Q/B ratios were calculated using equation 7 from Palomares and Pauly (1998), where W_∞ is the weight a fish would reach if it grew to L_∞ or the ultimate length of an individual, T′ is the mean temperature in Kelvin (1000/(C + 273.15)) with C being the temperature in degrees Celsius, A is the aspect ratio of the caudal fin, h and d represent variables for feeding types whereby if a fish is herbivorous h=1 (h=0 if it consumes other food types), d=1 if a fish is a detritivore (d=0 if it consumes other food types). As with the P/B calculations, parameters for the Q/B ratio using equation 7 (L_∞, A, h, and d) were taken from species information available on Fishbase (Froese and Pauley, 2008), using an annual temperature value of 1°C (British Atmospheric Data Centre, 2010).

(7)

$$Log(Q/B) = 7.964 - 0.204Log(W_\infty) - 1.965T' + 0.083A + 0.532h + 0.390d$$

In order to balance the model and allow the program to estimate the biomass parameter, the Ecotrophic Efficiency (EE) was set to 0.95 for all fish groups. An EE value of 0.95 indicates 95% of the population will die from predation and fishing mortality, meaning most of the population will be consumed or fished and only a small proportion of the population, in this case 5% will die from old age (Christensen et al. 2005). Because the biomass for the fish groups was unknown during model creation, an assumed EE value of 0.95 indicated nearly all of the fish is consumed or fished within the system, and would lead to a conservative biomass estimate by Ecopath. While it is unknown if this is true, the authors proceed under this conservative assumption, realizing it will lead to a minimum biomass estimate for the ecosystem.

Table 2: Model Production (P/B) and consumption (Q/B) values for fish functional groups in comparison to calculated values using equations 5-7. Ranges of values are provided when parameters have been calculated for multiple species within the functional group and are presented as an annual value (year^{-1}). Catches are also presented as an annual value (t·k^{-2}·y^{-1}) and were assumed to be a minimal 0.001 t·km^{-2}·y^{-1} for model initialization based on estimates provided by the Inuvialuit Harvest Study (The Joint Secretariat, 2003).

Model	Group	M[1]	M[2]	Model P/B	Q/B[3]	Model Q/B	Catch
7	Anadromous Chars	0.09-0.10	-	0.68	1.1-1.7	2.3	0.0001
8	Ciscos & Whitefish	0.15-0.36	-	0.95	1.1-2.7	3.8	0.0001
9	Salmonids	0.12-0.52	-	0.85	0.8-1.7	6.0	0.0001
10	Herring & Smelt	0.38-0.57	-	1.50	2.5-3.9	4.9	0.0001
11	Arctic & Polar Cods	0.31	0.90-1.50	0.80	2.5	3.9	0.0001
12	Capelin	0.79	-	0.95	4.0	4.0	0.0001
13	Flounder & Benthic Cods	0.11-0.29	-	0.75	1.1-2.4	2.4	0.0001
14	Small Benthic Marine Fish	0.28-0.78	0.45-1.40	1.06	1.6-6.7	3.5	0.0001
15	Other Fish	0.15-1.03	1.01-1.48	0.51	0.9-5.2	2.4	0.0001

[1] Mortality (M) calculated using equation 5 (Pauly 1980)

[2] Mortality (M) calculated using equation 6 (Lorenzen, 1996)

[3] Q/B calculated using equation 7 (Palomares and Pauly, 1998)

7: Anadromous Chars

This group includes Arctic Char* and Dolly Varden, two anadromous species that feed in the ocean during the ice-free season, and overwinter in freshwater. Dolly Varden are associated with montane rivers west of the Mackenzie River, while Arctic Char are associated with inland lakes east of Tuktoyaktuk Peninsula (Reist and Sawatzky, 2010). However, Arctic Char and Dolly Varden exhibit similar feeding ecologies in the coastal Beaufort Sea and are both important to subsistence harvests throughout the model simulation time frame (The Joint Secretariat, 2003). These species are common along the Beaufort Sea coast in summertime, usually within depths of 20 m (Coad and Reist, unpublished data) although they have been shown to venture great distances offshore (Decicco, 1992). In the marine environment Dolly Varden are known to feed primarily on small fishes, invertebrates and mysids and to a lesser extent on insects, insect larvae, and small crustaceans (Alaska Department of Natural Resources 2009). Arctic Char are carnivorous fish that feed primarily on benthic organisms and other small fishes, including large quantities of Capelin (DFO 1999; Dempson et al. 2002; Moore and Moore 1974). The diet for this group was set to: 1% Ciscos & Whitefishes, 10% Herring & Smelt, 1% Arctic & Polar Cods, 12% Capelin, 8% Flounders & Benthic Cods, 5% Small Benthic Marine Fish, 1% Other Fish, 15% Arthropods, 5% Bivalves, 2% Echinoderms, 2% Molluscs, 5% Worms, 2% Other Benthos, 3% Macro-Zooplankton, 5% Med Copepods, 20% Lg Copepods, 3% Other Meso-Zooplankton.

8: Ciscos and Whitefishes

The whitefish and cisco functional group is comprised of various species of coregonids with populations that are either anadromous or primarily freshwater-oriented, including Arctic Cisco*, Lake Whitefish (*Coregonus clupeaformis*)*, Broad Whitefish (*Coregonus nasus*)*, Least Cisco*, Cisco (*Coregonus artedi*) and Round Whitefish (*Prosopium cylindraceum*) (Coad and Reist, 2004). Whitefishes are important forage fish for other species found in both marine and freshwater environments (Alaska Department of Natural Resources 2009). Mysids and copepods are important prey items for Lake Whitefish, Broad Whitefish, and Least Cisco (Lacho, 1981). Arctic Cisco has a more diverse diet including polychaetes, copepods, and a variety of other small invertebrates (Lacho, 1981). The diet for this group was set to: 6% Herring & Smelt, 2% Small Benthic Marine Fish, 2% Other Fish, 10% Arthropods, 3% Echinoderms, 2% Molluscs, 5% Worms, 5% Macro-Zooplankton, 10% Med Copepods, 30% Lg Copepods, 10% Other Meso-Zooplankton, 5% Micro-Zooplankton, 7% Large Pelagic Producers (>5um), and 3% Ice Algae.

9: Salmonids

The most abundant species in the salmonids group are Arctic Grayling (*Thymallus arcticus*)* and Inconnu*. Pink Salmon (*Oncorhynchus gorbuscha*), Chum Salmon (*Oncorhynchus keta*), Coho Salmon (*Oncorhynchus kisutch*), Sockeye Salmon (*Oncorhynchus nerka*) and Chinook Salmon (*Oncorhynchus tshawytscha*) occur in low numbers. Salmon species (Chum, Coho, Chinook, Pink, Sockeye) are anadromous, with limited resident time on the Beaufort Sea Shelf. While Inconnu are considered a freshwater fish, they have been shown to move from the Mackenzie River system into the Beaufort Sea, with some fish tagged in northern British Columbia being recaptured near

Tuktoyaktuk, NWT (Stephenson et al., 2005). In lake ecosystems, Inconnu feed on planktonic crustaceans (Copepods) and insects, while larger fish feed primarily on aquatic insects and Ciscos (Fuller 1955). Preliminary stable isotope analysis from the model area indicates broad whitefish, lakefish, and ciscos are an important prey to Inconnu (Heidi Swanson, pers. comm.). Arthropods are a key prey item of Arctic Grayling while fish such as Humpback Whitefish (*Coregonus pidschian*), Slimy Sculpin (*Cottus cognatus*), and Ninespine Stickleback (*Pungitius pungitius*) contribute moderately to the diet, and worms, crustaceans, and plant materials provide minor contributions (Stewart et al. 2007). Pink Salmon stomachs sampled in the Chukchi Sea contained mostly fish with some amphipods and mysids, with the most important fish prey being Arctic Cod (Craig and Haldorson 1986). Another study sampled Pink Salmon from the Alaskan Beaufort and Chukchi seas and identified amphipods as important prey items (Hoekstra et al., 2003). The salmonid group diet was set to: 10% Ciscos & Whitefish, 12% Arctic & Polar Cods, 3% Capelin, 5% Small Benthic Marine Fish, 5% Other Fish, 31% Arthropods, 5% Worms, 2% Other Benthos, 3% Macro-Zooplankton, 2% Med Copepods, 15% Lg Copepods, 2% Other Meso-zooplankton, and 5% Large Pelagic Producers >5um.

10: Small Nearshore Forage Fish

This group contains three marine species: Pacific Herring*, Northern Sand Lance (*Ammodytes dubius*) and Pacific Sand Lance (*Ammodytes hexapterus*), as well as the diadromous Rainbow Smelt *. These are schooling species that inhabit coastal to inner shelf areas and are important prey in the diet of other larger fishes (Hunter, 1981) and beluga whales (Loseto et al., 2009). Young Rainbow Smelt feed on diatoms and small zooplankton (Cyclops spp., Diaptomus spp., copepod nauplii, rotifers) and move onto larger zooplankton species (daphnia, calanoid copepods, ostracods, amphipods, mysids, placyopods, isopods), fish (Rainbow Smelt, cisco, sculpins, trout, Burbot (*Lota lota*)) and algae as they grow (Evans and Loftus, 1987). Adult Rainbow Smelt have a wide size range for prey items such as fish and zooplankton (Hrabik et al. 1998). Fish, mysids, and amphipods are important prey items for Rainbow Smelt in the Alaskan Beaufort Sea (Haldorson and Craig, 1984). This diet of Pacific Herring in more temperate regions is variable, containing up to 90 different food items such as high frequencies of copepods, amphipods, euphausiids, and diatoms, with a moderate frequency of molluscs (Wailes, 1936). There is no region specific diet information available at the time of model creation, therefore the diet for this group was set to: 3% Ciscos & Whitefish, 2% Flounders 2% Benthic Cods, 2% Small Benthic Marine Fish, 5% Arthropods, 2% Echinoderms, 2% Molluscs, 5% Worms, 1% Other Benthos, 20% Macro-Zooplankton, 5% Med Copepods, 20% Lg Copepods, 5% Other Meso-Zooplankton, 5% Micro-Zooplankton, 10% Large Pelagic Producers, 10%Small Pelagic Producers, and 3% Ice Algae.

11: Arctic and Polar Cods

This group includes two species, Arctic Cod* and Polar Cod, which inhabit the pelagic zone from coastal areas as well as deeper depths beyond the continental shelf break. Arctic Cod were found consistently across stations sampled within the model area including waters around Herschel Island (<50m) and across the Beaufort Sea Shelf (>50m) (Majewski et al., 2013). Arctic Cod are the most abundant fish in the Beaufort Sea and are critical in transferring energy from secondary producers to higher trophic levels in arctic marine systems (Bradstreet and Cross, 1982; Geoffroy, 2016; Hobson and Welch, 1992). In the high arctic, Arctic Cods have been shown to be reliant upon sea ice to avoid predators and find food (Gradinger and Blumm, 2004). In general Arctic Cod diet varies, containing copepods, amphipods, mysids (Dodson et al., 2007) and other zooplankton species (Craig et al. 1982; Lacho 1986; Hoekstra et al. 2003). Polar Cod in the Barents Sea consume Calanoid Copepods and Euphausiids (Hop and Gjøsæter, 2013). Bottom dwelling Arctic Cod in the model area were found to mainly consume copepods (*Pseudocalanus* spp., *Calanus glacialis*, *Calanus hyperboreus*, *Limnocalanus macrurus* and *Jaschnovia tolli*), with dietary contributions of amphipods (*Apherusa glacialis* and *Themisto libellula*) and mysids (Mysis oculata) (Walkusz et al., 2013a). Further research has shown that Calanus sp. were the primary contributor to diets in Arctic Cod on the Beaufort Shelf (<200m depth), while Themisto sp. were the primary contributor to diets on the slope (>200m) (Majewski et al., 2016). The diet for cods was set to: 2% Salmonids, 20% Herring & Smelt, 5% Arthropods, 2% Echinoderms, 2% Molluscs, 4% Worms, 1% Other Benthos, 7% Macro-Zooplankton, 10% Med Copepods, 40% Lg Copepods, 5% Other Meso-Zooplankton, and 2%Large Pelagic Producers.

12: Capelin

Capelin* have only been observed to occur sporadically along the Beaufort Sea coast, but in large numbers when present, (Hunter 1981, Dodson et al. 2007) and so can be an important forage fish for other fishes such as Arctic Char (Dempson et al. 2002) and beluga whales (Loseto et al. 2009). Capelin have a more southern distribution than Arctic Cod, and therefore, have different life history characteristics (e.g., faster growth, aversion to ice and cold temperatures) (Hop and Gjøsæter, 2013). However, given their similar feeding ecologies and preference for warmer, ice-free waters, Capelin may increasingly compete with Arctic Cod with future climate change (Abookire and Piatt, 2005; Orlova et al., 2005; Rose, 2005). In the Barents Sea Capelin feed on planktonic crustaceans, copepods, euphausiids, amphipods, marine worms, and small fishes (GJØSÆTER, 1998). In west Greenland, dietary contributions by wet weight were euphausiids, amphipods, copepods, other zooplankton, mysids, and decapods (Hedeholm et al., 2012). In colder years in the Barents Sea, copepods dominate the diet contributing >50% of the diet, with euphausiids also contributing greatly and hyperiids and chaetognaths in lesser quantities (Orlova et al., 2010). In warmer years, euphausiids increased in dietary contribution, surpassing copepods in some locations (Orlova et al., 2010). Capelin diet was set to: 5% Arthropods, 2% Echinoderms, 2% Molluscs, 4% Worms, 1% Other Benthos, 30% Macro-Zooplankton, 15% Med Copepods, 35% Lg Copepods, 5% Other Meso-Zooplankton, and 2% Large Pelagic Producers.

13: Flounders and Benthic Cods

This group includes Starry Flounder (*Platichthys stellatus*)*, Arctic Flounder (*Pleuronectes glacialis*)*, Bering Flounder (*Hippoglossoides robustus*), Saffron Cod*, Burbot*, and Greenland Cod (*Gadus ogac*). Although the flounders and large benthic cods have distinct morphologies and feeding strategies (ambush and active foraging, respectively), they are all benthopelagic species that share a relatively diverse diet that is dominated by smaller benthic fishes and larger invertebrate prey items such as crabs, decapods, isopods, larger bivalves, mysids, amphipods, and some chironomids (Percy 1975; Hunter 1981, Morin and Dodson 1986; Mikhail and Welch 1989). Greenland Cod consume Capelin and/or benthic crustaceans (crabs, amphipods) depending on the availability of prey items (Mikhail and Welch, 1989). Saffron Cod in Prince William Sound Alaska, prey mostly on crustaceans, polychaetes, and gammarids as well as some fish and molluscs (Johnson et al. 2009). Juvenile Saffron Cod consume a variety of zooplankton and benthic prey such as polychaetes, larvaceans, caprelids, copepods, other epibenthic species, hyperid amphipods, other pelagic gamariids, crustaceans, and molluscs (Johnson et al. 2009). Juvenile Burbot primarily consume zooplankton species such as rotifers, nauplii, cyclopoid copepods, cladocerans, calanoid copepods (Ghan and Sprules, 1993). Arctic Flounder are known to consume polychaetes, crustaceans, and molluscs, with polychaetes considered the most important prey item (Lacho 1981; Atkinson and Percy 1992). For Starry Flounder, isopods and mysiids are important prey items (Lacho, 1981). The diet of Bering Flounder in the Chukchi Sea is composed of fish (Lumpenus sp. (other fish group in model), zoarcids, cods and benthic and epibenthic crustaceans (amphipods, copepods, euphausiid, and mysids) (Coyle et al. 1994; Alaska Department of Natural Resources 2009). The diet for this group was set to: 2% Small Nearshore Forage Fish, 2% Arctic and Polar Cods, 1% Capelin, 1% Flounder & Benthic Cod, 9% Small Benthic Marine Fish, 2% Other Fish, 20% Arthropods, 15% Bivalves, 5% Echinoderms, 10% Molluscs, 17% Worms, 5% Other Benthos, 2% Macro-Zooplankton, 2% Med Copepods, 5% Lg Copepods, 2% Other Meso-Zooplankton.

14: Small Benthic Marine Fish

While the small benthic marine fishes are the most diverse group in the study, relatively little is known about their diet or life history. The group is mostly comprised of sculpins and zoarcids, with the Fourhorn Sculpin (*Myoxocephalus quadricornis*)* being the most common in coastal areas. Other species that inhabit the coastal Beaufort Sea include Hamecon (*Artediellus scaber*), Shulupaoluk (*Lycodes jugoricus*), and Fish Doctor (*Gymnelus viridis*). A diverse assemblage of small benthic fishes are found across the Beaufort Shelf, including Arctic Hookear Sculpin (*Artediellus uncinatus*), Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*), Twohorn Sculpin (*Icelus bicornis*), Spatulate Sculpin (*Icelus spatula*), Arctic Sculpin , Shorthorn Sculpin (*Myoxocephalus scorpius*), Bigeye Sculpin (*Triglops nybelini*), Ribbed Sculpin (*Triglops pingelii*), Halfbarred Pout (*Gymnelus hemifasciatus*), White Sea Eelpout (*Lycodes marisalbi*), Saddled Eelpout (*Lycodes mucosus*), Canadian Eelpout (*Lycodes polaris*), Threespot Eelpout (*Lycodes rossi*), Longear Eelpout (*Lycodes seminudus*), Arctic Alligatorfish (*Ulcina olrikii*), Leatherfin Lumpsucker (*Eumicrotremus derjugini*), Atlantic Spiny Lumpsucker (*Eumicrotremus spinosus*), Sea Tadpole (*Careproctus reinhardti*), Kelp Snailfish (*Liparis tunicatus*), Gelatinous Seasnail (*Liparis fabricii*), Variegated Snailfish (*Liparis gibbus*), Blackline Prickleback (*Acantholumpenus mackayi*)*, Fourline Snakeblenny (*Eumesogrammus praecisus*), Slender Eelblenny (*Lumpenus fabricii*), Daubed Shanny (*Lumpenus maculatus*), Stout Eelblenny (*Lumpenus medius*) and Arctic Shanny (*Stichaeus punctatus*). Prey items for this group vary by species and site, and therefore contain a diverse diet. Fourhorn Sculpin consume various fishes and benthic invertebrates, with isopods being an important prey item in other high latitude ecosystems (Hoekstra et al., 2003; Leonardsson et al., 1988). Arctic Staghorn Sculpin in the Beaufort Sea also have a diverse diet containing benthic polychaetes, molluscs, amphipods, cumaceans, larvaceans, copepods, euphausiid/mysids, shrimps, and fish (Atkinson and Percy 1992; Alaska Department of Natural Resources 2009). Diets for Twohorn, Spatulate, Shorthorn, Mustache, and Ribbed Sculpins from southern Baffin Island, contain items such as amphipods, mysids, and other fish along with lesser quantities of isopods, copepods, cumaceans, polychaetes, decapods, gastropods, benthic molluscs, pteropods, ascidians, chaetognaths, euphausiids, and various other crustaceans (Atkinson and Percy 1992). In general, polychaetes are an important food for eelpouts and zoarcids (Lacho 1981; Atkinson and Percy 1992). However, species such as Polar Eelpouts prey primarily on molluscs, but also commonly consume a variety of other taxa such as amphipods, isopods, copepods, and other crustaceans, pelecypods, polychaetes, euphausiids, and fish (Atkinson and Percy 1992; Coyle et al. 1997; Alaska Department of Natural Resources 2009). Bivalves are the most important contributor to the diet of Arctic Alligatorfish in the shallow Beaufort Sea, however in Russia the diet has been known to include amphipods, isopods, ostracods, and nemerteans (Atkinson and Percy 1992). Variegated Snailfish from southern Baffin Island have been shown to be active bottom feeders with large contributions of amphipods and polychaetes in their diet (Atkinson and Percy 1992). Slender Eelblenny in the Beaufort Sea feed primarily on polychaetes, although the diet also includes amphipods, pelecypods, marine worms, and small crustaceans (Lacho 1981; Atkinson and Percy 1992). The diet for this diverse group was set to: 1% Flounder & Benthic Cods, 3% Small Benthic Marine Fish, 3% Other Fish, 21% Arthropods, 10% Bivalves, 10% Echinoderms, 10% Molluscs, 15% Worms, 8% Other Benthos, 0.5% Jellyfishes, 3% Macro-Zooplankton, 2% Med Copepods, 3% Lg Copepods, 5% Other Meso-Zooplankton, 3% Micro-Zooplankton, 2.5% Large Pelagic Producers.

15: Other Fish

This group contains fishes with life histories not captured in the groups above, but that may represent a food source to higher trophic levels on the Beaufort Shelf, as based on expert knowledge or previous studies. These include the parasitic Arctic Lamprey (*Lampetra camtschatica*)*, the diadromous Threespine Stickleback (*Gasterosteus aculeatus*), and freshwater species that can tolerate brackish conditions and inhabit coastal areas in summertime, such as), Ninespine Stickleback), Longnose Sucker (*C. catostomus*)* and Northern Pike (*Esox lucius*). Sticklebacks prey mainly on copepods and are consumed by larger fishes such as Arctic Char (Gallagher and Dick, 2011). As this is a diverse group, the diet was also assumed to be diverse, with a variety of benthic and pelagic invertebrates in addition to producers. The diet for this group was set to: 13% Arthropods, 7% Bivalves, 4% Echinoderms, 4% Molluscs, 5% Worms, 4% Other Benthos, 1% Jellyfishes, 5% Macro-Zooplankton, 4% Med Copepods, 30% Lg Copepods, 5% Other Meso-Zooplankton, 5% Micro-Zooplankton, 10% Large Pelagic Producers, 1% Small Pelagic Producers, 2% Ice Algae.

BENTHOS

The most comprehensive study available to provide starting parameters for the model area was completed during 1971-1975 by Wacasey et al., (1977) and provides much of the data for model initialization. Numerous other studies have been completed in or near the model area during the model time frame including: Banks Island in 1981,1983 (Heath and Thomas, 1984), areas in and around Tuktoyaktuk in 1980, 1984-1988, (Heath et al., 1981; Hopky et al., 1994a, 1994d, 1994b, 1994c), the Beaufort Sea Shelf from 2002-2004 (Conlan et al., 2008), and 2005 by Ramal et al. (unpublished data). It is generally noted that benthic biomass for this region is lower than for other regions of the Canadian or Alaskan Arctic (Carey Jr, 1991). Benthos occur in the greatest quantities in the north-eastern Bering Sea through the shallow Chukchi Sea, while the lower primary productivity of the Beaufort Sea is reflected in the lower quantity of benthic invertebrates (Carey Jr, 1991). The majority of these benthic macro-infauna in the Beaufort Sea are deposit/detritus-feeding forms (Carey and Ruff, 1977). Groups for the ecosystem model were based primarily on species composition and biomass estimated from historical reports, with consideration of life history traits and importance to predators. The following 6 groups were created as functional groups for benthic invertebrates: arthropods, bivalves, echinoderms, molluscs, worms, and other benthos.

Depth is believed to be an important factor in determining benthic biomass, along with sediment type and amount of primary production available. As the Mackenzie Shelf area is characterized by high outputs of freshwater, it has been shown to produce very low levels of benthic biomass (<1 $g \cdot m^{-2}$) at the mouth of the Mackenzie River (Dunton et al., 2005), with the lower salinity resulting in lower species diversity and biomass (Carey Jr, 1991; Wacasey et al., 1977). Species richness has been shown to increase with depth, to a peak in richness at about 100 m depth (Cobb et al., 2008). Wacasey et al. (1977) sampled different depth zones and classified them by general characteristics (biomass, salinity, and species composition). Samples were digitized and averaged over each year (1971-1975) based on the functional groups created for the model, and used for starting model biomass (Wacasey et al., 1977). A more recent comprehensive study by Conlan et al. (2008) sampled areas both inside the model area and surrounding areas; they found there was no significant difference in community composition between the areas for similar depths. It was noted that many benthic species are sufficiently long lived and able to adapt to environmental variability (Conlan et al., 2008), with benthic fauna distribution determined primarily by the type of substrate.

Benthic Biomass

Benthos biomass ($g \cdot m^{-2}$) across the Mackenzie Shelf generally increases with depth, with the highest amount at about 100 m (range 0-220 $g \cdot m^{-2}$) (Cobb et al., 2008). Initial model values were taken from 1971-1975 benthic estimates (Wacasey et al., 1977; Wacasey, 1975), broken down by species group and reorganized into model groups. The reported values were then averaged for the four years sampled to account for inter-annual variability, as the shelf was surveyed at various depths over 4 years (Table 3). Based on the depth profile of the region and biomass data per depth range, the mean biomass for the Mackenzie Shelf area was estimated at 7.82 $g \cdot m-2$ (Table 3). As expected, worms, bivalves, and arthropods dominate the communities. However, for the 1975 samples, echinoderms (which in previous years only contributed <1 g·m^{-2} of biomass) accounted for the majority of the species composition (Table 3) (Wacasey et al. 1977). It should be noted that the biomass summaries only account for macrobenthos. In comparison, macrobenthos biomass estimates from models in other Arctic regions, indicate higher biomass levels, although these are for later years, and are highly variable across studies (Table 4). Only one study within the model area sampled the meiofauna (nematodes, copepods, nauplii, turbellarians, kinorhynchs, and polychaetes) in sediments, with nematodes contributing the most to samples (Bessière et al., 2007). Meiofauna biomass was noted to decrease with depth, ranging from 27-145 mg C·m^{-2} in 2003 and 24-913 mg C·m^{-2} in 2004 (Bessière et al., 2007).It was also noted the highest meiofauna densities were found in Franklin Bay and on the Mackenzie Shelf (Bessière et al., 2007). Converting these values to wet weight yields a maximum biomass of approximately 0.13 g·m^{-2} for all benthic groups, which is relatively low compared to total macrobenthos biomass. Therefore meiofauna biomass was not added to the individual benthic group biomasses.

Table 3: Summary of benthic samples from Wacasey et al. (1977). Mean values of each group are presented for each year of the survey (1971-1975). Average biomass values (g·m^{-2} or t·km^{-2}) were taken as the average of all samples from 1971-1975, and served as the starting estimates for the Ecopath values. They are provided with the final balanced Ecopath biomass values.

Average Biomass	1971	1973	1974	1975	Average	Balanced Ecopath Model Value
16: Arthropods	0.79	5.72	1.20	2.42	2.12	2.50
17: Bivalves	3.77	3.12	1.98	2.79	2.75	1.20
18: Echinoderms	0.05	0.64	0.25	36.13	9.26	2.40
19: Mollusks	0.17	0.54	0.09	1.79	0.81	1.70
20: Worms	1.43	1.57	3.56	2.83	1.97	1.10
21: Other	0.47	0.00	1.13	1.97	0.59	1.40
Biomass total	6.11	10.20	7.31	25.19	12.20	10.30

Table 4: Summary of benthic sample biomass (g·m^{-2} wet weight (WW)) for areas in the Canadian and Alaskan Arctic .

Biomass (g·m^{-2}) WW	**Area**	**References**
77	Beaufort Sea (general)	Carey and Ruff (1977); Carey Jr (1991)
45.51-94.54	Tuktoyaktuk Harbour and Mason Bay	Hopky et al. (1994a)
41.5	Banks Island	Heath and Thomas (1984)
50-100	Barter Island (Alaskan Beaufort)	Dunton et al. (2005)
33	Eastern Beaufort Sea (Alaska)	Dunton et al. (2005)
370	Bering Sea	Dunton et al. (2005)
225	East Siberian Sea	Dunton et al. (2005)
167	Chukchi Sea	Dunton et al. (2005)

16: Arthropods

This groups includes: Amphipoda, Isopoda, Tanaidacea, Cumacea (hooded shrimp), Decapoda, Pycnogonida (sea spiders), and Maxillopoda, listed in order of importance from samples across the Arctic (Piepenburg et al., 2010). Local studies also note the importance of Ostracoda (seed shrimp), Acari (mites/ticks), Insects, Cladocera (water fleas) and Mysida (opossum shrimp) (Wacasey 1975; Wacasey et al. 1977; Atkinson and Wacasey 1989). Although little is known about the ecology of this group in this region, estimates from Wacasey et al. (1977) indicate a moderate abundance compared to other benthic species. The trophic importance of this group is demonstrated through diet linkages. For example, ringed seals diet near Tuktoyaktuk in spring shows high prevalence of invertebrates, with large contributions from Isopods, Cumaceans, Ostracods, and Mysids (Harwood et al. 2007), indicating their prevalence and importance to predators.

The P/B was set to 0.75 y^{-1} and the Q/B to 3.5 y^{-1} based on the Benthic Crustacea and Chelicerata group from the Weddell Sea ecosystem model (Jarre-Teichmann et al., 1997). Diets for this group varied and included herbivores, carnivores, and detritivores (Arndt and Swadling, 2006; Scott et al., 2001), with many species in this region identified as deposit or detritivore feeders (Carey and Ruff, 1977). A generalized diet of 2% Bivalves, 5% Echinoderms, 5% Molluscs, 5% Worms, 3% Other Benthos, 3% Benthic Plants, 10% Pelagic Detritus, 67% Benthic Detritus was assumed to capture diverse feeding dynamics.

17: Bivalves

Bivalves (Phylum Mollusca, Class Bivalvia) are prevalent across the Arctic (Piepenburg et al., 2010) and contribute a large portion to the benthic biomass on the shelf (Wacasey et al. 1977). The P/B was set to 0.6 y^{-1}, based on bivalve group P/B values from the Newfoundland and Hudson Bay models (Table 5: Heymans 2003; Hoover et al. 2013). The Q/B was set to 2.4 y^{-1} assuming a Production/Consumption (P/Q) ratio of 2.5 (Christensen et al. 2005). As bivalves are suspension feeders, they primarily consume seston (free-floating living and non-living matter) (Hawkins et al., 1996; Loo and Rosenberg, 1989), and have been shown to consume kelp detritus as well (Dunton and Schell 1987; Sauriau and Kang 2000). The diet was set to: 2% Small Pelagic Producers, 3% Large Pelagic Producers, 5% Benthic Plants, 10% Ice Algae, 10% Pelagic Detritus, 70% Benthic Detritus.

18: Echinoderms

The Echinoderm group contains Ophiuroidea (brittle stars), Asteroidea (sea stars), Holothuroidea (sea cucumbers), Echinoidea (urchins), and Crinoidea (sea lilies and feather stars) (Piepenburg et al., 2010). Based on samples from 1971-1975, this group Asteroidea and Ophiuroidea are most common (Wacasey et al. 1977). The P/B was set to 0.55 y^{-1}, slightly lower than the echinoderm group for the Newfoundland model (Heymans, 2003). A Q/B value of 1.8 y^{-1} was used after increasing from a starting value of 1.1 y^{-1} based on Holothuroidea in the Weddell Sea model (Jarre-Teichmann et al., 1997). This group contains a variety of suspension feeders, predators, scavengers, and mud ingesters (Howell et al., 2003). For example, brittle stars are opportunistic generalists who scavenge a variety of other benthos, detritus, phytoplankton and algae (Fratt and

Dearborn 1984; McClintock 1994; Dearborn et al. 1996). Due to the diverse feeding strategies, the diet was set to: 4% Arthropods, 2% Bivalves, 5% Echinoderms, 5% Molluscs, 5% Worms, 2% Benthic Plants, 10% Pelagic Detritus, 67% Benthic Detritus.

19: Molluscs

This includes all molluscs except bivalves (see above): Gastropods (snails and slugs), Polyplacophora (chitons), Scaphopoda (tusk shells), Cephalopoda (cephalopods), and shell-less molluscs Caudofovaeta (also known as Chaetodermomorpha under the class Aplacophora) (Piepenburg et al., 2010). Gastropods were second to bivalves in terms of diversity, within the mollusc group, with only a few species of Scaphopoda and Aplacophora sampled from the Beaufort Shelf during 1970-1975 (Wacasey et al. 1977). The P/B was set to 0.85 y^{-1} after increasing from a starting value of 0.40 y^{-1} based on P/B values of 0.309 y^{-1} (molluscs) and 0.497 y^{-1} (average for Gastropods: Antarctic) (Brey and Clarke 1993; Brey and Gerdes 1998; Hoover et al. 2012). The Q/B was set to 3.4 y^{-1} in order to ensure a P/Q of 0.25 (Christensen et al. 2005). Marine molluscs are primarily detritivores and suspension feeders (Aitken and Gilbert, 1996; Vanderklift and Ponsard, 2003), therefore the diet was set to: 10% Benthic Plants, 15% Pelagic Detritus, 75% Benthic Detritus.

20: Worms

This includes all worms from various phyla: primarily Annelids (segmented worms: Polychaetes and Ciltellata), but also from Entoprocta, Nematoda (round worms), Nemertea (ribbon worms), and Priapulida (penis worms) (Wacasey et al. 1977; Piepenburg et al. 2010). In Steffanson Sound just west of the Canadian border in Alaska, nematodes comprised 90% of the community population from March to May (Carey Jr, 1991). However, in other areas such as the nearshore Beaufort, some samples indicate a small contribution of nematodes to the community (Carey Jr, 1991), and high contributions from polychaetes (Conlan et al., 2008). The P/B was set to 0.95 y^{-1}, a value in between P/B values for the Weddell Sea and Newfoundland models, 0.6 and 2.0 y^{-1}, respectively (Heymans, 2003; Jarre-Teichmann et al., 1997), to yield a P/Q value of 0.23. The Q/B was set to 4.0 y^{-1}, based on the Polycheata and other worm group from the Weddell Sea model (Jarre-Teichmann et al., 1997). The most abundant polychaetes from 1970s surveys on the Alaskan Beaufort Shelf were identified as surface deposit and filter feeders (Carey Jr, 1978). The diet for all worms was set to: 1% Arthropods, 2% Echinoderms, 2% Molluscs, 1% Other Benthos, 1% Benthic Plants, 13% Pelagic Detritus, 80% Benthic Detritus.

21: Other Benthos

All remaining benthic groups have been combined : Cnidarians (Anthozoa: sea anemones and Hydrozoa: sea serpent), Ascidiacea (sea squirts), brachiopods, and bryozoa (moss animals) (Wacasey et al. 1977; Piepenburg et al. 2010). The P/B was set to 0.75 y^{-1} based on calculated values for bryozoans, brachiopods, and cnidarians in the Antarctic Peninsula model (see Hoover et al. 2012 and refs therein). The Q/B was set to 3.0 y^{-1}, based on a P/Q value of 0.25 (Christensen et al. 2005). In the Antarctic, these species have diverse feeding strategies such as suspension (bryozoans), pelagic and benthic feeding (brachiopods), and omnivory (hydroids, anthozoans) (Barnes and Clarke 1995;

Orejas et al. 2001; Peck et al. 2005). The diet for other benthos was set to: 2% Arthropods, 1% Echinoderms, 1% Molluscs, 3% Worms, 2% Benthic Plants, 16% Pelagic Detritus, 75% Benthic Detritus.

Table 5: Parameters for benthic functional groups from high latitude Ecopath models. Production/Biomass (P/B) and Consumption/Biomass (Q/B) ratios are presented in y^{-1} based on published models.

Functional Group	Model Area	Model Year	P/B	Q/B	Reference
Epibenthic Carnivores	Gulf of Alaska	1963	2	17	(Heymans, 2005)
Benthic Invertebrates	Gulf of Alaska	1963	0.98	6.553	(Heymans, 2005)
Deep benthic omnivores	Kerguelen Is.	1987	3	10	(Pruvost et al. 2005)
Shallow benthic omnivores	Kerguelen Is.	1987	2.1	10	(Pruvost et al. 2005)
Shallow benthic carnivores	Kerguelen Is.	1987	2	10	(Pruvost et al. 2005)
benthic mollusca	Weddell Sea	1980's	0.3	1	(Jarre-Teichmann et al., 1997)
Tunicata	Weddell Sea	1980's	0.3	1	(Jarre-Teichmann et al., 1997)
Porifera	Weddell Sea	1980's	0.18	0.6	(Jarre-Teichmann et al., 1997)
Hemichordata	Weddell Sea	1980's	0.3	2	(Jarre-Teichmann et al., 1997)
Lophophora and Cnidaria	Weddell Sea	1980's	0.1	1	(Jarre-Teichmann et al., 1997)
Benthic Crustacea and Chelicerata	Weddell Sea	1980's	0.7	3.5	(Jarre-Teichmann et al., 1997)
Polychaeta and other worms	Weddell Sea	1980's	0.6	4	(Jarre-Teichmann et al., 1997)
Echinoidea	Weddell Sea	1980's	0.07	0.233	(Jarre-Teichmann et al., 1997)
Crinoidea	Weddell Sea	1980's	0.3	1	(Jarre-Teichmann et al., 1997)
Ophiuroidea	Weddell Sea	1980's	0.173	0.577	(Jarre-Teichmann et al., 1997)
Asteroidea	Weddell Sea	1980's	0.08	0.267	(Jarre-Teichmann et al., 1997)
Holothuroidea	Weddell Sea	1980's	0.2	1.1	(Jarre-Teichmann et al., 1997)
Large Crabs	Newfoundland	1995-1997	0.3	1.2	(Heymans, 2003)
Small Crabs	Newfoundland	1995-1997	0.3	1.5	(Heymans, 2003)
Lobster	Newfoundland	1995-1997	0.38	4.42	(Heymans, 2003)
Shrimp	Newfoundland	1995-1997	1.45	9.667	(Heymans, 2003)
Echinoderms	Newfoundland	1995-1997	0.6	6.667	(Heymans, 2003)
Polychaetes	Newfoundland	1995-1997	2	22.222	(Heymans, 2003)
Bivalves	Newfoundland	1995-1997	0.57	6.333	(Heymans, 2003)
Other Benthic Invertebrates	Newfoundland	1995-1997	2.5	12.5	(Heymans, 2003)
Worms	Hudson Bay	1970's	0.6	4	(Hoover et al. 2013)
Echinoderms	Hudson Bay	1970's	0.3	1	(Hoover et al. 2013)
Bivalves	Hudson Bay	1970's	0.5	6.3	(Hoover et al. 2013)
Other Benthos	Hudson Bay	1970's	2.5	12.5	(Hoover et al. 2013)
Mollusca	Antarctic Peninsula	1978	0.639	2.556	(Hoover et al. 2012)
Urochordata	Antarctic Peninsula	1978	0.234	1	(Hoover et al. 2012)
Porifera	Antarctic Peninsula	1978	0.159	0.795	(Hoover et al. 2012)
Hemichordata	Antarctic Peninsula	1978	0.375	2	(Hoover et al. 2012)
Brachiopoda	Antarctic Peninsula	1978	0.898	4.5	(Hoover et al. 2012)
Bryozoa	Antarctic Peninsula	1978	0.475	1.75	(Hoover et al. 2012)
Cnidaria	Antarctic Peninsula	1978	0.25	1	(Hoover et al. 2012)
Curstaceans	Antarctic Peninsula	1978	1.05	4.2	(Hoover et al. 2012)
Other Arthropods	Antarctic Peninsula	1978	0.616	3.326	(Hoover et al. 2012)
Worms	Antarctic Peninsula	1978	0.7	3.2	(Hoover et al. 2012)
Echinoidea	Antarctic Peninsula	1978	0.116	0.464	(Hoover et al. 2012)
Crinoidea	Antarctic Peninsula	1978	0.125	0.8	(Hoover et al. 2012)
Ophiuroidea	Antarctic Peninsula	1978	0.45	1.8	(Hoover et al. 2012)
Asteroidea	Antarctic Peninsula	1978	0.231	0.924	(Hoover et al. 2012)
Holothuroidea	Antarctic Peninsula	1978	0.315	1.1	(Hoover et al. 2012)

ZOOPLANKTON

Zooplankton are the primary link between producers and higher trophic levels. Both ice algae and the spring phytoplankton bloom are important food sources for zooplankton, with ice algae providing an early pulse of food to zooplankton groups before the spring bloom (Campbell et al., 2009). Changes to environmental variables are predicted to alter the ecosystem. For example, increased primary production and changes to phytoplankton size classes are predicted to cause the replacement of large copepods by small copepods, potentially making the ecosystem unfavourable for planktivorous fish and birds (Uye, 1994). Other factors which have been considered important to determining the size and structure of the zooplankton community include: circulation patterns, wind stress, position of the frontal zone, wind, and ice cover (Carmack et al. 2004; Walkusz et al. 2010). Future increases to Mackenzie River discharge will likely enhance phytoplankton production which may be beneficial to zooplankton (Carmack et al. 2004).

Zooplankton groups were separated based primarily on size: Macro-Zooplankton (>2 cm), Meso-Zooplankton (0.2 -2 cm), and Micro-Zooplankton (< 0.2 cm). The dominant Meso-Zooplankton taxa in this region are copepods; *Calanus glacialis, Calanus hyperboreus, Metridia longa*, and *Pseudocalanus spp*. Since Macro and Micro-Zooplankton have not been target in sampling protocols so less is known about the species present in these groups. The copepods in the Meso-Zooplankton group were further subdivided into three groups based on relative size, how different groups are influenced by different environmental variables, and how each group contributes to predators' diets. The 'large copepod' group, referred to as Lg Copepod throughout the paper, contains the larger species (*Calanus glacialis, Calanus hyperboreus, Metridia longa),* which in general favor colder waters. The 'medium sized copepod' group, referred to as Med Copepods, includes the smaller medium size copepods such as *Pseudocalanus spp*., which are less influential in the food web and have broader thermal optimal ranges than the large copepods. Gelatinous zooplankters were also placed in a separate group, Jellyfishes, due to their intermittently high biomass, unique trophic roles, and lack of representation within the food web. The remaining meso-zooplankton taxa identified through surveys were grouped together to form the group Other Meso-zooplankton.

Zooplankton Biomass

Zooplankton samples collected during ecosystem surveys were used to determine the species composition and biomass of each group within the model. These surveys covered various areas of the Mackenzie Shelf region (years: 1986-1987, 2000, 2003, 2005-2006), however, they did not sufficiently sample the Micro- and Macro-Zooplankton groups. Mean total biomass and standard deviation are presented for all meso-zooplankton groups from multiple samples collected within these surveys (Table 6), with grouping biomass values broken down further into Lg Copepods, Med Copepods, Other Meso-Zooplankton, and Jellyfishes provided in Table 7.

The model initialization used biomass values from oblique tows conducted during the 1986 and 1987 Northern Oil and Gas Assessment Program (NOGAP) surveys (Hopky et al. 1994b,1994d). The oblique tows were deeper, up to 153 m (1986) and 344 m (1987), than the horizontal, undulating or vertical tows and produced a higher biomass. Biomass estimates for meso-zooplankton sampled from areas outside of the model area (western Canadian Archipelago, deep water off the Mackenzie Shelf , Amundsen Gulf, and Coronation Gulf) ranged from 0.12-15.18 $g \cdot m^{-2}$ (mean value 3.18 $g \cdot m^{-2}$) and were also considered when determining starting biomasses (Mclaughlin et al., 2009). The 1986 and 1987 NOGAP survey results did not calculate biomass separately for the Lg and Med Copepod groups (Hopky et al., 1994d, 1994b), therefore, species composition was implied based on later surveys (Mclaughlin et al. 2009; Walkusz et al. 2010), where Med Copepods contributed <1 to 10% of the total mezo-zooplankton biomass and Lg Copepods contributed 9 to 38% (Table 7). The Med Copepod to Lg Copepod ratio was estimated to be 1:4. The oblique tow biomass from the 1986 survey for all Meso-zooplankton groups (11.35 $g \cdot m^{-2}$) and the composition from Table 7 were used to determine the following contributions to the model: Lg Copepods 7.4 $g \cdot m^{-2}$ (65.2% of biomass), Med Copepods 1.8 $g \cdot m^{-2}$, (15.8% of biomass), Other Meso-Zooplankton 1.2 $g \cdot m^{-2}$ (10.5% of biomass), and Jellyfishes 0.965 $g \cdot m^{-2}$ (8.5% of biomass). Biomass for Lg Copepods was lowered to 5.8 $g \cdot m^{-2}$ in order to reduce predation on primary producers and allow the model to balance.

Table 6: Summary of surveys in the Beaufort Sea and nearby areas providing zooplankton biomass estimates. Given the mesh size used, it was assumed only zooplankton were caught and the biomass would only count towards Jellyfishes, Med Copepods, Lg Copepods, and Other Meso-Zooplankton.Net Type: Bongo (B), Neuston (N), and Conical (C) with mesh size (micrometers), and average Biomass (g·m^{-2} wet weight).

Survey name	**Area**	**Year**	**Net Type/ Mesh size**	**Biomass (Mean)**	**Biomass (Range)**	**Reference**	**Notes**
NOGAP	Mackenzie Shelf	1986	B500, N500	0.86	7.00E-05-9.17	(Hopky et al., 1994d)	Horizontal tows
		1986	B85, B500	4.37	2.00E-03-24.18	(Hopky et al., 1994d)	Undulating tows
		1986	B85, B500	11.35	2.47-38.38	(Hopky et al., 1994d)	Oblique tows
NOGAP	Mackenzie Shelf	1987	N500, B500	0.22	2.00E-05-1.69	(Hopky et al. 1994b)	Horizontal tows
		1987	B500	1.88	0.16-8.57	(Hopky et al. 1994b)	Undulating tows
		1987	B85, B500	17.14	3.19-43.61	(Hopky et al. 1994b)	Oblique tows
Institute of Ocean Sciences (IOS)	Beaufort Sea, Amundsen Gulf, Coronation Gulf	2000	B235 um	3.12	0.12-15.18	(Mclaughlin et al., 2009)	Only catching Meso-zooplankton species
Mirai Cruise	Beaufort Sea including Mackenzie Shelf	2002	B330	1.20	3.00E-03-3.68	(Walkusz et al. 2008)	
Nahidik	Mackenzie Shelf	2005	C135	7.07	0.13-26.06	(Walkusz et al., 2010)	Vertical tows
		2006	C135	11.61	1.37-52.98	(Walkusz et al., 2010)	Vertical tows

Table 7: Contribution of different species groups to total Meso-Zooplankton biomass by surveys listed in Table 6. NOGAP surveys did not distinguish among different copepod species, therefore, these values are considered for large and medium copepods combined (denoted with *). All values are presented as percent (%) contribution to total biomass.

Survey	Tow Type	Jelly-fishes	Med copepods	Lg Copepods	Other
NOGAP 1986	HOR	2.382	89.084*		8.534
	OBL	7.442	82.912*		9.646
	UOL	12.688	78.344*		8.968
NOGAP 1987	HOR	12.881	42.396*		44.723
	OBL	5.710	86.352*		7.938
	UOL	15.733	62.271*		21.996
Nahidik 2005	Vertical	13.203	7.370	8.641	70.785
Nahidik 2006	Vertical	11.954	9.789	24.874	53.383

22: Jellyfishes

The Jellyfish group contains ctenophores, cnidarians (Scyphozoa, Hydrozoa), and larvaceans, which have been identified from meso-zooplankton surveys (Hopky et al., 1994c,a). It is likely that biomass is underestimated for this group due to net avoidance, damage by nets, and net selectivity (Darnis et al. 2008). Ctenophores and Hydrozoans (notably: *Halitholus cirratus, Euphysa flammea, Sarsia princeps, Aglantha digitale, Aeginopsis laurentii, Obelia sp*.,) have been noted as dominant groups in the 1980s and/or 2000s (Richardson, 1982; Walkusz et al., 2010).

Region specific parameter estimates are not available for this group so values from other locations were considered for model inputs. P/B and Q/B values for various jellyfish species from different latitudes ranged from 5-40 y^{-1} and 2-80 y^{-1}, respectively (Pauly et al. 2008). An Ecopath model for the East China Sea (China) used a P/B of 5.01 y^{-1} and a Q/B of 25.05 y^{-1} for a large jellyfish functional group (Hong et al., 2008). A Lancaster Sound model used a P/B value of 8.2 y^{-1} and a Q/B value of 29.41 y^{-1} for the ctenophore functional group comprised of *Mertensia ovum* (Mohammed, 2001). However, lab experiments identify higher consumption rates, with daily rations (% of body carbon) exceeding 10% (range 10-1000%) of body carbon (Reeve, 1980). In the Black Sea, Ctenophore *Beroe ovata* required a minimum of 20% of its body weight per day (Finenko et al., 2000). These daily consumption rates would yield annual rates in the hundreds, even assuming food is abundant only during the peak growing season (~150 days). The Initial P/B and Q/B were set to 10 y^{-1} and 25 y^{-1}, and while these were increased during model fitting to 20 y^{-1} and 45 y^{-1} respectively, the values still fall within reported parameters for other high latitude ecosystem models. Feeding experiments on ctenophores indicate they feed on ciliates, Pseudocalanus and other Med Copepods species (Sullivan and Reeve, 1982). In this model, the diet of jellyfish was assumed to be 5% Med Copepods, 5% Lg Copepods, 5% Other Meso-

Zooplankton, 5% Micro-Zooplankton, 15% Large Pelagic Producers, 55% Small Pelagic Producers, and 10% pelagic detritus.

23: Macrozooplankton

Macro-zooplankton (organisms larger than 20 mm), have never been sampled in this system, but krill, shrimps, mysiids, amphipods, and chaetognaths (arrow worms), have been reported in predators' diets (see marine mammal section). One species of Amphipoda (*Themisto Libellula*) is a main prey item of fish, seals, and seabirds and is an important link between lower and higher trophic levels in the Arctic (Auel and Werner, 2003). Biomass was estimated by the model, and should be considered as the minimum biomass needed to support higher trophic levels. Assuming and EE of 0.95, yielded an initial minimum biomass of 0.15 $t{\cdot}km^{-2}$, which was used when creating the model to ensure the model would balance. This value was increased during the model balancing to 0.2 $t{\cdot}km^{-2}$, and this value was retained in the balanced model.

Daily mortality rates of a temperate mysid (*Metamysidopsis elongate*) showed values of 0.013 d^{-1} (roughly 4.745 y^{-1}) for larvae, and 0.06 d^{-1} (roughly 21.9 y^{-1}) for juveniles with adults having slightly lower rates (Clutter and Theilacker, 1971; Facer and Clutter, 1968). Mortality rates for Antarctic krill (*Eupahusia superba),* which span the meso- and macro-zooplankton size classes depending on life stage, range from 0.52-2.41 y^{-1} (Pakhomov, 1995). However, *E. superba* can live up to 6 years with higher survivorship each year than shorter lived species, indicating shorter lived species would have higher mortality (and therefore higher P/B) rates than Antarctic krill. The P/B ratio for Macro-zooplankton in this model was set to 8.5 y^{-1}, higher than for Antarctic krill, but within the range for temperate species. In lab experiments daily consumption of chaetognaths ranges from 0.1-10% of body carbon, even at low food concentrations (Reeve, 1980). A conservative value of 0.5% of body carbon per day combined with an estimated 150 day growth season (in northern latitudes), would yield an annual consumption rate of 75 y^{-1}. For the hyperiid amphipod *T. libellula*, ingestion rates range from 5% of body carbon per day for small amphipods (>5 mg dry body mass) to 1.5% for large amphipods (107 mg dry body mass) (Auel and Werner, 2003), yielding Q/B values ranging from 5.4-14.6 y^{-1}. Using a P/B value of 8.5 y^{-1} and a P/Q ratio of 0.3 would yield a Q/B ratio of 28.3 y^{-1} which would correspond to a daily consumption rate of 0.186 d^{-1} for an estimated 150 day feeding season (Reeve, 1980). The Q/B was set to 28.0 y^{-1}. *T. libellula* is a predator and primarily feeds on Calanus copepods (Auel and Werner, 2003). The diet for this group was assumed to be 3% Macro-zooplankton, 10% Med Copepods, 20% Lg Copepods, 15% Other Meso-Zooplankton, 2% Micro-Zooplankton, 15% Large Pelagic Producers, 5% Small Pelagic Producers, 15% ice algae, and 15% pelagic detritus.

24: Medium Copepods (Med Copepods)

This groups contains medium sized copepod species: Pseudocalanus spp., *Oithona simils*, and *Limnocalanus macrurus* (known previously as *L. grimaldii*), which are believed to favor warmer water. Pseudocalanus species are abundant when overall production is high, such as the 2004 season (Campbell et al., 2009), and have the potential to increase in the future with warmer climates and reduced sea ice (Darnis et al. 2008). The nauplli and copepodite stages of Pseudocalanus are prey for larval and juvenile Arctic cod (Darnis et al. 2008). *Limnocalanus macrurus* is an important component of the zooplankton in river influenced areas of the Arctic (Lischka et al., 2001). It has a high lipid content and is considered an important contributor to the summer bowhead whale diet, as a whale taken from here in 1999 had 99% of its stomach filled with this species (Hirche et al., 2003; Lischka et al., 2001; Pomerleau et al., 2011; Walkusz et al., 2010).

Mortality rates under lab conditions for *Pseudocalanus elongatus* ranged from 0.016-0.089 d^{-1} (leading to annual values 5.84-32.49 y^{-1}) for high and low food conditions respectively (Breteler et al. 1995). *Pseudocalanus newmani* mortality rates of all life stages from a temperate fjord ranged from 0.021 d^{-1} (for adult females) to 0.128 d^{-1} (for the C5 stage in their first year) (Ohman and Wood, 1996), yielding annual values ranging from 7.66-46.72 y^{-1}. Monthly natural mortality rates for *Acartia clausii* (near the United Kingdom) were extrapolated to give an annual estimate of 68.17 y−1 (range 3.65-124.1 y−1) (Myers and Runge, 1983). The P/B was set to 18.0 y^{-1}, a midrange value based on annual mortality rates from previous studies. The Q/B was set to 45.0 y^{-1}, to allow for a P/Q ratio of 0.4.

Pseudocalanus readily consume ice algae and has high consumption rates of micro-zooplankton in the spring and summer (Campbell et al., 2009). Compared to larger Calanus species, Pseudocalanus are better able to handle lower food concentrations (Breteler et al. 1995). In shelf habitat medium-size copepods, including Pseudocalanus, are primarily herbivorous, while some species such as *Oithona similis* feed on fecal matter when other prey items decline (Darnis et al. 2008). The diet for this group was set to: 5% Other Meso-Zooplankton, 5% Micro-Zooplankton, 30% Large Pelagic Producers, 40% Small Pelagic Producers, 10% Ice Algae, and 10% Pelagic Detritus.

25: Large Copepods (Lg Copepods)

The Lg Copepods group includes 3 species: *C. hyperboreus, C. glacialis* and *Metridia longa*. Based on samples from the Beaufort Sea these calanoid copepods represented over 70% of the biomass in 2002 (Darnis et al. 2008), and are an important prey source for polar cod which in turn is important for top predators (Loseto et al., 2008). *Calanus glacialis* has shown to be a dominant species in high arctic fjords accounting for 60-80% of the total Calanus abundance (Arnkværn et al., 2005), with nutrient rich waters thought to contribute to the reproductive success in the Chukchi and Beaufort Seas (Plourde et al., 2005). For *C. hyperboreus* the highest abundances in the

Beaufort Sea occurred at 200 m in the eastern Amundsen Gulf (Ota et al., 2008). A study based on 2008 abundance, showed a significant decrease of these species from winter to summer in the central Amundsen Gulf (Forest et al., 2010) indicating their association with cooler waters.

Younger stages (copepodids), for a range of copepod species, had daily mortality rates at roughly 0.1 d^{-1} (36.5 y^{-1}), with adults at roughly 0.2 d^{-1} (73 y^{-1}) (Hirst and Kiorboe, 2002). Ohman and Wood (1995) identify mortality values ranging from 0.02-0.12 d^{-1} (7.3-43.8 y^{-1}) for various copepod life stages. Estimates from other Arctic regions (Norway) indicate mortality rates up to a maximum of 0.149 d^{-1} (5.4 y^{-1}) for *C. hyperboreus* females in late spring (Arnkværn et al. 2005). Based on these estimates, the P/B for copepods was set to 5.5 y^{-1} and EE was set to 0.95.

Feeding strategies for these species show their effectiveness as grazers and ability to utilize energy resources quickly when needed. *C. glacialis* are able to take advantage of the ice algae on the underside of sea ice preceding the spring bloom in order to build energy reserves for spawning (Plourde et al., 2005). During spring bloom, they have the ability to respond and can cope with timing changes in blooms (Forest et al., 2010). Younger copepodids of *C. glacialis* and *C. hyperboreus* do not feed during the winter (Forest et al., 2011), which makes them more reliant on ice algae and spring bloom conditions for feeding. Older *C. glacialis* feed on micro-zooplankton when they are abundant in the summer (Forest et al., 2010). During spring and summer, micro-zooplankton were the preferred prey of copepods (large and medium groups), however, this prey source is not always readily available (Campbell et al., 2009). *Metridia longa* is an opportunistic omnivore that feeds year round and has the ability to switch to carnivory and possibly cannibalism (Forest et al., 2011). These copepod species are an important prey source for polar cod which in turn is important for top predators (Loseto et al., 2008). Based on these different feeding strategies (herbivory, omnivorory, and carnivory), the diet for this group was set to: 5% Med Copepods, 25% Micro-Zooplankton, 15% Large Pelagic Producers, 5% Small Pelagic Producers, 40% Ice Algae, 3% Pelagic Detritus, and 7% Ice Detritus.

26: Other Meso-Zooplankton

This includes all sampled taxa within surveys in the 0.2-20 mm size class that did not fall into the other functional groups. A summary of species sampled within the region is presented in Appendix C. Few parameter estimates are available for the taxa within this group, therefore, biomass was set based on individual samples (Hopky et al., 1994d, 1994b), The P/B and Q/B were set to 15 y^{-1} and 60 y^{-1}, higher than larger zooplankton groups, but lower than Micro-zooplankton. However, during model fitting P/B was adjusted to 22.0 y^{-1} and Q/B to 80.0 y^{-1}, yielding a P/Q value of 0.275. The diet of the Other Meso-Zooplankton group was set to: 5% Med Copepods, 3% Other Meso-Zooplankton, 24% Micro-Zooplankton, 25% Large Pelagic Producers, 18% Small Pelagic Producers, 15% Ice Algae, and 10% Pelagic Detritus.

27: Micro-Zooplankton

Most of the zooplankton surveys do not capture Micro-zooplankton (<0.2mm) due to net mesh size. However, they consume smaller phytoplankton and bacteria, up to 120% (average 21.5%) of phytoplankton daily growth, and are important in the food web, (Sherr et al., 2009). Growth rates for North Atlantic Micro-zooplankton average 0.288 d^{-1} (105 y^{-1}) (Verity et al., 1993). The P/B was set to 55 y^{-1} and Q/B to 150 y^{-1} based on P/B (65 y^{-1}) and Q/B (110 y^{-1}) values for a micro-zooplankton group in the Antarctic Peninsula model (Hoover et al. 2012). . A moderate starting biomass of 2.4 $t{\cdot}km^{-2}$ was used, and was enough to balance the model.

Based on this groups' effectiveness as grazers (Sherr et al. 2009), the diet was assumed to be dominated by the small phytoplankton group. The diet was set to: 85% Small Pelagic Producers, 5% Ice Algae, 5% Ice Detritus, and 5% Pelagic Detritus.

PRIMARY PRODUCERS

In the Canada Basin (deeper waters offshore from the Beaufort Shelf) deep water layer, primary production is thought to be nitrogen limited rather than light limited (Li et al., 2009), while the Beaufort Sea is considered oligotrophic in nature (Carmack et al. 2004). No change in overall chl a concentrations have been observed, however, there has been a reduction in the average size of producers indicating a decrease in large phytoplankton and an increase in small phytoplankton (Li et al., 2009).

Within the model primary production is broken up into two main groups: (1) pelagic phytoplankton, representing the summer bloom, and (2) ice algae, representing under-ice spring production . Pelagic phytoplankton is further divided into size classes; the Large Pelagic Producers represent large pelagic phytoplankton (>5um), and are an important link between zooplankton and higher trophic levels. Small Pelagic Producers represent small pelagic phytoplankton (<5um) and are important contributors to the microbial food web (not explicit in the model) and detrital pools. In addition, large and small pelagic phytoplankton are thought to respond differently to changes in climate (Li et al., 2009). Brugel et al., (2009) determined that large phytoplankton sampled at 50 m contributed 25% to chl a biomass during early fall 2002, and 26-34% during fall 2003. Biomass and production rates from different studies are presented in Table 8. An annual average biomass for all primary producer groups (Ice Algae, Large Pelagic Producers, and Small Pelagic Producers) was set at 15.5 $t{\bullet}km^{-2}$ (1.72 $gC{\bullet}m^{-2}$ using a conversion of 1gC=9g wet weight: Pauly and Christensen 1995).

28: Large Pelagic Producers (>5um)

Large Pelagic Producers include the following commonly sampled groups; Diatoms, Dinofagellates, Cryptophytes, Crysophytes, Haptophytes, Eulenophytes, Chlorophytes, and Cyanophytes (Cobb et al., 2008). The spring bloom (large and small pelagic phytoplankton in this model) represents roughly 40% of the total annual primary production, with nutrients from the previous fall and winter, and wind mixing being important factors in determining the production (Lavoie et al. 2009). The duration of the vegetative season has been estimated at 150 days (Sergeeva et al., 2010). While most production occurs in summer and spring recent assessments indicate considerable production during autumn (Brugel et al., 2009), suggesting a longer vegetative season. Estimates of production could increase by 14-19% if the fall bloom is included, bringing the combined spring, summer, and fall bloom contributions to nearly 60%.

The biomass for Large Pelagic Producers was set to 2.5 $t \cdot km^{-2}$, or roughly 16% of the total phytoplankton biomass (Large Pelagic Producers, Small Pelagic Producers, and Ice Algae combined) and nearly 30% of the total primary producer biomass (Large and Small Producers combined). This is within the range of observed values where large phytoplankton contribute 25-62% of the chl a biomass or all phytoplankton sampled (Brugel et al., 2009; Riedel et al., 2007). (Table 8), P/B values for large and Small Pelagic Producers combined ranged from 15-178 y^{-1}(Table 8). The P/B was set to 30.0 y^{-1} to balance the model. This resulted in an EE=97.7, meaning nearly all Large Pelagic Phytoplankton are consumed by predators. Algae retained in the upper water column during summer have high photosynthetic activity (Sukhanova et al., 2009), indicating low sinking rates, therefore, this values makes ecological sense.

Table 8. Summary of producer biomass (standing stock) and production values for the model area and surrounding areas. Values have been converted from original recorded values to t·km^{-2} for model compatibility. Model groups include IA (Ice Algae) LP (Large Pelagic Producers) and SP (Small Pelagic Producers).

Model Group(s)	**Year**	**Converted Biomass (t•km^{-2})**	**Original Biomass***	**Converted Production**	**Original Production***	**Notes**	**Location**	**Reference(s)**
LPP, SPP	2003	0.99-2.89	0.11-2.89 gC•m^{-2}	-	-	(July-Aug)	Chikchi Sea	(Sergeeva et al., 2010)
LPP, SPP	2002	5.25	11 mg chl a •m^{-2}	-	-	Autumn	Model Area	(Brugel et al., 2009)
LPP, SPP	2003	6.68	14 mg chl a •m^{-2}	-	-	Autumn	Model Area	(Brugel et al., 2009)
IA	2003-2004	1.37	153 mgC•m^{-2}	-	-	CASES study	Model Area	(Riedel et al., 2007)
IA	2004	0.0063-0.171	0.7-19 mgC•m^{-2}	-	-	Pre-bloom high\ low ice cover	Franklin Bay	(Riedel et al., 2008)
IA	2004	1.098-3.753	122-417 mgC•m^{-2}	-	-	Bloom high \ low ice cover	Franklin Bay	(Riedel et al., 2008)
LPP, SPP, IA (80% ice cover)	2002	3.25 (range 0.0-77.21)	21.99 mgC•m^{-3}			May-June	Beaufort/ Chukchi Seas	(Sukhanova et al., 2009)
IA	2004	3.114-4.581	346-509 mgC•m^{-2}	-	-	post-bloom high\ low ice cover	Franklin Bay	(Riedel et al., 2008)
IA	1974	-	-	207 g•m^{-2}•y^{-1}	23 gC•m^{-2}•y^{-1}	high ice year	Model Area	(Carmack et al. 2004; Macdonald et al. 1987)
IA	1975	-	-	144 g•m^{-2}•y^{-1}	16 gC•m^{-2}•y^{-1}	low ice year	Model Area	(Carmack et al. 2004; Macdonald et al. 1987)
LPP, SPP	1974	-	-	135-1471 g•m^{-2}•y^{-1}	0.10-1.09 gC•m^{-2}•y^{-1}		Model Area	(Hsiao et al. 1977)
LPP, SPP	1975	-	-	229-1606 g•m^{-2}•y^{-1}	0.17-1.19 gC•m^{-2}•y^{-1}		Model Area	(Hsiao et al. 1977)

* Notes units are different based on units presented in each paper

Conversions used for conversions to g•m^{-2} or t•km^{-2}

Phytoplankton: 10fg C per cell (Terrado et al., 2008)

Phytoplankton: 1 g Carbon =9g wet weight (Pauly and Christensen, 1995)

Phytoplankton: carbon: chl a=53 (Kang et al., 2001)

Ice Algae: carbon: chl a=20-35 (Riedel et al., 2008)

29: Small Pelagic Producers (<5um)

Zooplankton species tend to favor Large Pelagic Producers, therefore, Small Pelagic Producers are thought to be an important direct contributor to pelagic detritus. . Estimates of Small Pelagic Producers have generally occurred in late spring to early fall, when open water allows access to the water column. One study by Li et al. (2009) suggests the biomass of small phytoplankton species is increasing in the Arctic.

Small Producer biomass was set to 6.5 $t{\cdot}km^{-2}$, roughly 42% of total primary producer biomass, and 60% of total pelagic production biomass. Initially, this value was set lower, but based on information from predator diets, it was increased to balance the model. The P/B was set to 60 y^{-1}, double the rate of Large Pelagic Producers, and based on the range of 15-178 y^{-1}.

30: Ice Algae

Ice algae is a term used to describe living organisms which get frozen into sea ice during the fall and are released during spring melt, contributing to the early spring bloom community (Riedel et al. 2007; Zhang et al. 1998). Ice algae are an important source of food for organisms throughout the winter months and particularly in the spring when the cells are released into the pelagic environment and transferred to the benthos as particulate organic carbon (POC). While growth is limited by light and nutrient availability, ice algae are a major component of biomass associated with first year Arctic sea ice (Riedel et al. 2006). Productivity was shown to be reduced by 30% in a low ice year (1975) compared to high ice year (1974) (Carmack et al. 2004; Macdonald et al. 1987), highlighting the large contribution of ice algae to total production. Other studies found that ice algae contributed 15% of total production (Carmack et al. 2004; Horner and Schrader 1982). Sampling during summer in the eastern Beaufort Sea found evidence that large amounts of dead ice algae cells (ice algae Detritus POC) were being transported to the benthos during the ice free period (Juul-Pedersen et al. 2010) supporting the theory that most of the organic matter produced from ice algae sinks to the bottom (Carmack et al., 2004).

The biomass for Ice Algae was set to 6.5 $t{\cdot}km^{-2}$, roughly 42% of total production biomass estimated in 1970. The P/B value was calculated to be between 22.1 and 31.8 y^{-1}, based on sea ice production values of 144 and 207 $t{\cdot}km^{-2}{\cdot}y^{-1}$ (see Table 8) for a high ice year, and model biomass (6.5 $t{\cdot}km^{-2}$). The P/B value was lowered to 20.0 y^{-1} during model balancing to account for 46% of total carbon flux from winter to spring was lost in the upper 25 m, with POC being the main component (Juul-Pedersen et al., 2008), indicating the EE value should be near 0.5 (to account for 50% of the biomass being exported to detrital groups). Lowering the P/B to 20.0 y^{-} resulted in a final EE value of 0.678, after final balancing of all groups, indicating an annual value which would account for export during all seasons.

31: Benthic Plants

Benthic plants are relatively understudied in the model area. An area known as the boulder patch off the Alaskan coast, just west of the model area, is home to a high arctic kelp community with 78 identified benthic algal species (see Wilce and Dunton 2014 for a summary of species). Kelp beds have been identified in other areas of the Alaskan shelf (Dunton et al. 1982), although there is no evidence of high density kelp beds in the Canadian Beaufort Sea.

In the nearshore Beaufort Sea, Horner and Schrader (1982) found that benthic contribution to total primary production was negligible during spring, although biomass in certain areas was as large or larger than other producers. Benthic samples from Mason Bay and Tuktoyaktuk Harbor during 1986-1988 identify the average contribution of "plant/vegetative matter" to range from 41.15 to 52.47 $t \cdot km^{-2}$ (Hopky et al. 1994a). Benthic microalgae in the model area are primarily pennate diatoms (Horner and Schrader, 1982). Benthic Plant biomass was set to a conservative estimate of 3.50 $t \cdot km^{-2}$, to account for their patchiness. A P/B value of 10.0 y^{-1} was used to balance the model, as this is considered a low productivity producer group.

DETRITAL GROUPS

Detritus is broken up into two components: (1) pelagic detritus and (2) benthic detritus. The distinction captures the processes determining the fate of each group, rather than the absolute location in the water column. The pelagic detritus group represents detritus that is retained within the water column, primarily derived from the spring bloom (large and Small Pelagic Producers) and is a food source for zooplankton. The benthic detritus group represents detritus that sinks quickly from the water column, originating primarily from ice algae and feeding by benthic invertebrates. For a summary of detritus fates see Table 9.

Total detritus from sediment traps in 1987 estimated annual carbon flux of 4.6 $gC \cdot m^{-2} \cdot y^{-1}$ (Converted to 41.4$g \cdot m^{-2} \cdot y^{-1}$: using 1gC=9g wet weight (WW) for phytoplankton) (O'Brien et al. 1991; Pauly and Christensen 1995; Carmack et al. 2004; Cauffopé and Heymans 2005). POC samples from ice holes in 1986, produced an ice detritus average of 1.67 $gC \cdot m^{-2}$ (Range: 0.00669- 13.80) or 15.03 $g \cdot m^{-2}$ (range: 0.06-124.2) (Juul-Pedersen et al., 2008). The flux to detritus is greater during the spring melt, as this likely contains both spring bloom and ice algae (detritus for pelagic and benthic fates). Flux rates during spring melt are at least double the values during early spring or winter: 42.3mg POC $m^{-2} \cdot y^{-1}$ vs 19.2 and 19.7, respectively, at 25 m (Juul-Pedersen et al., 2008). During melt, the values of POC reach levels of 123.5 mg POC $m^{-2} \cdot y^{-1}$ at 1 m (compared to the 42.3mg POC $m^{-2} \cdot y^{-1}$ at 25 m), indicating large amounts of organic matter are being utilized primarily by zooplankton, before reaching deeper water. In winter and early spring, the sinking fluxes are constant at all sampled depths (1 m, 15 m, 25 m), identifying the lack of retention in the water column, and the potential increased contribution to the benthos (see Table 2 in Juul-Pedersen et al. 2008).

Table 9: Detritus fate of model functional groups, as proportion of total. For each model group the fate of unassimilated food and dead organisms is divided among the model detritus groups (Pelagic Detritus and Benthic Detritus) and Export.

Source Group		**Pelagic Detritus**	**Benthic Detritus**	**Export**
1	Polar Bear	1	0	0
2	Beluga	1	0	0
3	Bowhead	1	0	0
4	Ringed Seal	1	0	0
5	Bearded Seal	1	0	0
6	Birds	1	0	0
7	Anadromous Chars	1	0	0
8	Ciscos & Whitefish	1	0	0
9	Salmonids	1	0	0
10	Herring & Smelt	1	0	0
11	Arctic & Polar Cods	1	0	0
12	Capelin	1	0	0
13	Flounder & Benthic Cods	1	0	0
14	Small Benthic Marine Fish	1	0	0
15	Other Fish	1	0	0
16	Arthropods	0	0.5	0.5
17	Bivalves	0	0.5	0.5
18	Echinoderms	0	0.5	0.5
19	Molluscs	0	0.5	0.5
20	Worms	0	0.5	0.5
21	Other Benthos	0	0.5	0.5
22	Jellyfishes	0.5	0	0.5
23	Macro-Zooplankton	0.5	0	0.5
24	Med Copepods	0.5	0	0.5
25	Lg Copepods (Calanus)	0.5	0	0.5
26	Other Meso-Zooplankton	0.5	0	0.5
27	Micro-Zooplankton	0.5	0	0.5
28	Large Pelagic Producers	0.5	0	0.5
29	Small Pelagic Producers	0.5	0	0.5
30	Ice Algae	0	0.9	0.1
31	Benthic Plants	0	0.5	0.5
32	Pelagic Detritus	0	0	1
33	Benthic Detritus	0	0	1

32: Pelagic Detritus

Pelagic Detritus represents the contribution to the detrital pool derived primarily from large and small pelagic phytoplankton in the model. Summer bloom production has different characteristics from ice algae in terms of retention time in the water column and sinking rates out of the euphotic zone. Flux of POC during the summer months, when there is little to no ice cover, is used as an indication of the pelagic detritus contribution. June to September sinking rates of POC (average 80.3mg POC·m^{-2}) is lower than the spring melt values, but higher than winter/early spring when ice algae dominates (Sergeeva et al., 2010), identifying the importance of spring bloom derived detritus to the water column and food web. Flux rates from Juul-Pedersen et al. (2008) show large amounts of POC being retained in the upper water column during spring melt. Carmack et al. (2004) estimate 40% of annual carbon flux occurs during early April to early September, due to summer and fall phytoplankton blooms. In order to balance the model a low biomass of 0.5 t·km^{-2} was used for Pelagic Detritus.

33: Benthic Detritus

Detritus derived from sea ice algae is believed to be an important driver in determining the benthic community. Ice algae are key contributors of POC in the bottom of first year sea ice (Riedel et al. 2006). POC is released from brine channels during ice growth in the fall and winter (Melnikov, 1998). Sinking fluxes are higher in summer than fall, with some retention within the water column (Juul-Pedersen et al., 2008). However, export of POC from ice algae does occur during the winter (Juul-Pedersen et al. 2010).

In Northern Baffin Bay, up to 75% of ice carbon (POC) was observed to sink through the water column as intact algal cells (Juul-Pedersen et al., 2008; Michel et al., 2002). In early spring, low zooplankton biomass contributes to a higher export to the benthos, as there is not enough zooplankton to efficiently graze the released ice algae and ice algae detritus (Lavoie, et al. 2009). This serves as a potential food source for benthic and pelagic communities during the winter and spring before the larger pelagic blooms begin to sink within the water column. Benthic species have the ability to quickly process the ice algae, although the algae have the ability to remain in sediments for longer time periods (months to years) (McMahon et al., 2006; Morata et al., 2008). The model was balanced using a value of 0.05 t·km^{-}2 for Benthic Detritus, much lower than reported values from sinking fluxes.

ECOSIM INPUT: TIME-SERIES FOR MODEL FITTING

Harvest Trends

In order to fit the model to time-series data using Equation 3, data trends were compiled to ensure the temporal simulations re-created the past trends for any species with available data. These datasets include abundance trends, catch trends, forcing functions (direct forcing in the model), and mediation functions (indirect forcing in the model). Each trend is described below.

Polar Bear Harvest Time-Series

Southern Beaufort Sea (SBS) polar bear population harvest is difficult to estimate as population boundaries have changed recently (IUCN, 2010), and records from the US and Canada are sporadic throughout history and often differ. Harvest from the US and Canada were combined to provide one time-series. Harvest from Barrow, Alaska includes both the SBS population and the Chukchi polar bear population, therefore catches for each population are difficult to separate. Average annual harvest of both populations located in the US (SBS and Beaufort/Chukchi) decreased considerably from 81 bears during 1960-1972 to 39 bears during the 1980s, then the rate of decline slowed with to 33 bears in the 1990s) and 32 bears by the 2000s (Allen and Angliss 2010). Harvest time-series for the model assumed 60 bears per year (average of 81 and 39) for the 1972-1980 gap in data. Because these values include both bear populations, US harvest of the SBS population was assumed to be half of the total US harvest for both areas combined during the years 1970-2003.

The Inuvialuit Harvest Study (The Joint Secretariat, 2003) reported harvest from the ISR ranged from 40 to 126 bears per year from 1988-1997. Prior to 1988 the Canadian harvest was assumed to be 113 bears per year, the average reported in the Harvest Study for 1988-1992. Post 1997, the Canadian harvest was assumed to be 62 bears (average for the last 5 years of the Harvest Study). Combined harvest records show an average of 53.6 bears per year taken from this population (US and Canada) with an average of 21 from the Canadian portion of the stock during 2003-2007 (Allen and Angliss 2010). However, other sources (IUCN, 2010) indicate the 2010 harvest limit of 80 bears per year is potentially exceeded, meaning the 2003-2007 estimate of 53.6 bears per year may be an underestimate. Because the combined estimated harvest from 1998-2003 was 79 bears per year (based on the US data and Canadian Harvest Study data), and the 2010 combined US/Canada harvest limit was 80 bears, the post 2003 harvest was set to 80 bears per year. Final values used in the model fitting are presented in Figure 2.

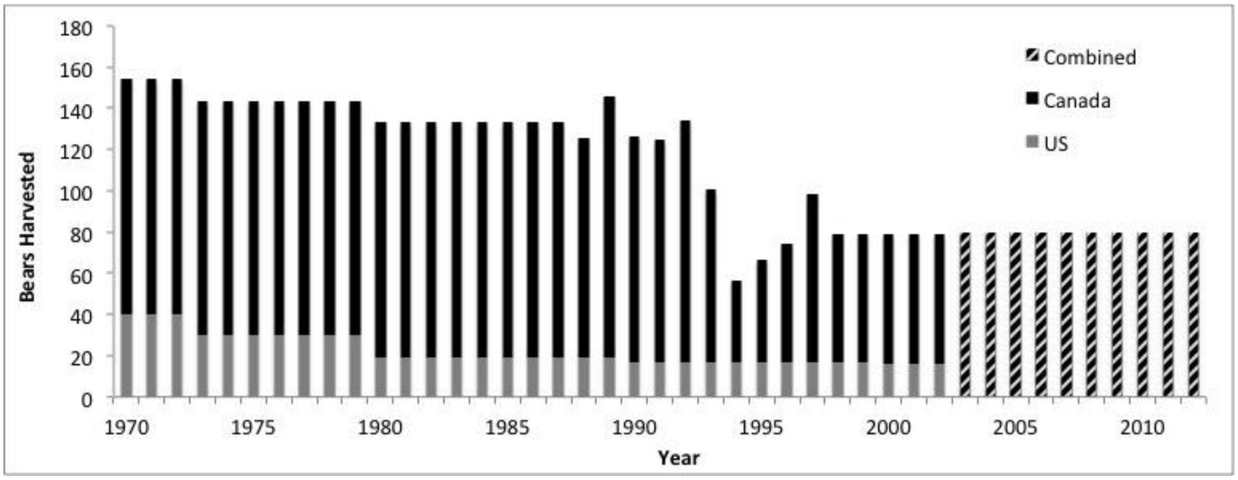

Figure 2: Summary of polar bear harvest estimated from the US, Canada, and combined values. See supporting text for information on time-series calculations and source data.

Beluga Harvest Time-Series

The Eastern Beaufort Sea (EBS) population is harvested in the US (along migration routes) and in Canada (summering locations), with potential (unrecorded) catches possibly occurring in Russia during migration (Harwood et al. 2002). Harvest rates range between 100-200+ whales a year for the communities in the ISR, plus roughly 64 whales per year from the US (Harwood et al. 2002; Suydam et al. 2007; Harwood et al. 2015). US contributions to harvest of this stock were available from 1987-2006 for the communities of Barrow, Diomede, Kaktovik, Nuiqsut, Point Hope and Wales. Combined US harvest, number of whales landed, is shown in Figure 3, although some communities were missing data in certain years (see Table 1 in Frost and Suydam 2010). Struck and loss rates are not included in the harvest calculation, however, they are believed to be low in relation to population size. Struck and loss rates have been estimated at 1% for the US and Canadian combined harvest, which would increase to 1.1% if the roughly 25 whales from the Russian harvest were included (DFO 2000; Harwood et al. 2002). Landings from the US and Canada (Figure 3) were combined with the estimated 25 whales a year harvested from Russia to produce a combined time-series from 1970-2009. As the harvest time-series is for the entire beluga population, and only a subset of the population utilizes the model area, the total harvest was divided in half, to allow half of the harvest mortality, while retaining the same trend.

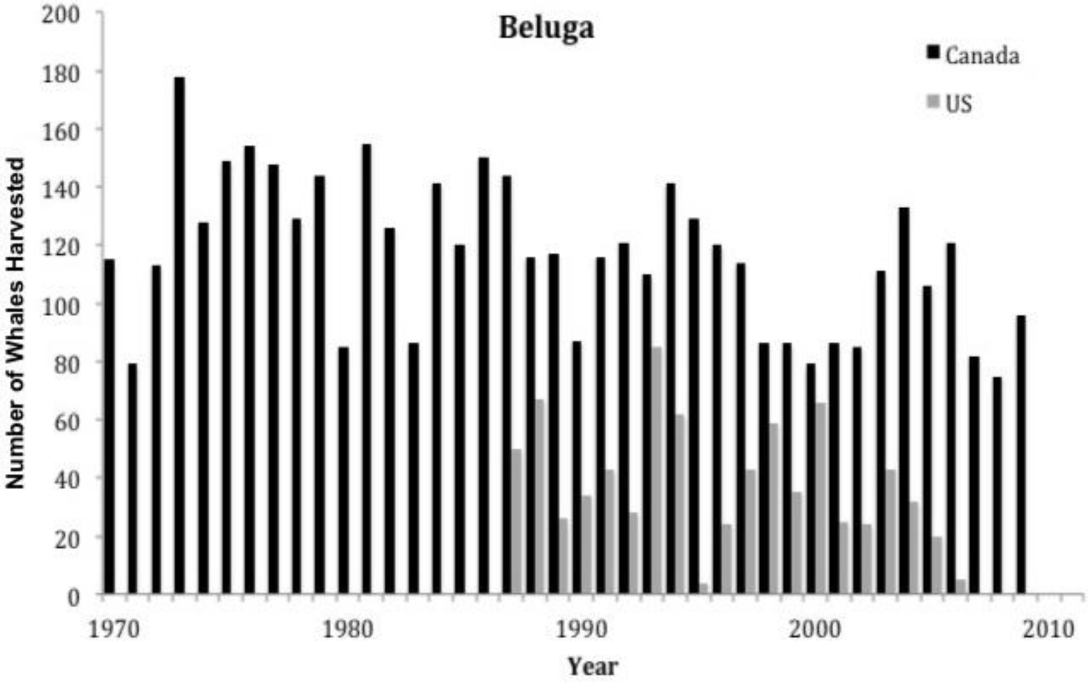

Figure 3: Summary of Beluga harvest for the US and Canada with records from (Harwood et al. 2002; Frost and Suydam 2010; L. A. Harwood et al. 2015). Struck and lost (S&L) animals, are not included.

Bowhead Harvest Time-Series

Canada's contribution to the harvest of bowhead whales from the Bering-Chukchi-Beaufort Sea population is small compared to harvest in the United States (Figure 4), with only 2 whales taken (1 each in 1991 and 1996) in the Northwest Territories (Harwood et al. 2002; The Joint Secretariat 2003). In Alaska a total of 1149 whales were harvested from 1974-2011, with an average of 41 whales per year from 1997-2006 (Suydam et al. 2007; Suydam and George 2012). The US catches do not include struck and lost rates, however success rate (No. Landed/ No. Struck) was estimated at 76% for 2001-2010 (IWC, 2013, 2010). Russian catches for this population have been documented at 8 whales from 1999-2005 (Allen and Angliss 2010), 2 whales in 2008, and 2 whales in 2010 (IWC, 2014, 2010). Initially, all landings (US and Canada) were included, but after reducing the biomass during model balancing to reflect the proportion of the population in the model area, the catch time-series was adjusted to include only Canadian catches. Harvest for 1970 was set to 1 whale, to initiate the model harvest, with additional whales taken in 1991 and 1996.

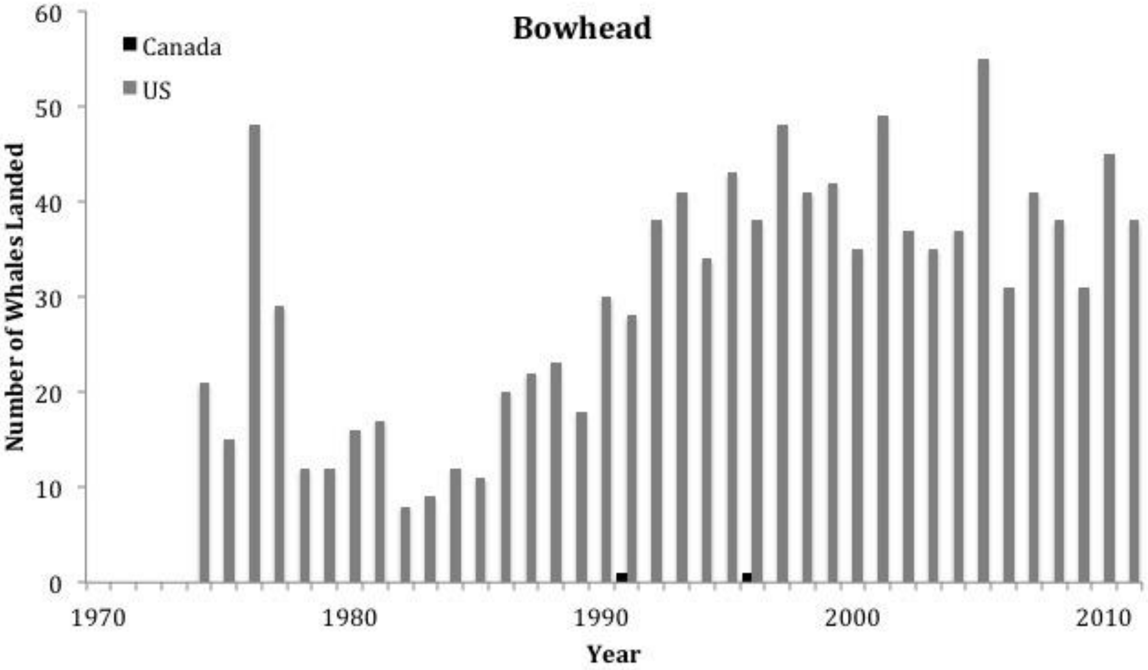

Figure 4: Summary of bowhead harvest from the US and Canada (Harwood et al. 2002; The Joint Secretariat 2003; Suydam et al. 2007). This figure does not contain missing values or Russian catches (Allen and Angliss 2010; IWC 2010; IWC 2014).

Ringed and Bearded Seal Harvest Time-Series

Ringed seals and bearded seals are residents of the model area year round. Harvest records for pinniped species are not as comprehensive as those for whales, with the best data coming from the Inuvialuit Harvest Survey (The Joint Secretariat, 2003). Ringed seals are more abundant than bearded seals and are harvested in higher quantities. As data is only available for 1988-1996, 1970-1987 values were set to the average of the first 5 years of the harvest study data (1202 ringed seals and 32 bearded seals), and post 1996 values were set to the average of the last 5 years (968 ringed seals and 33 bearded seals). Smith (1981) reported 66 bearded seal harvested by hunters from the communities of Sachs Harbour and Holman (Uluhaktok) over 7 years (sporadic sampling from 1971-1977), although the years are not specified (see Table 2 in Smith 1981). The Inuvialuit Harvest Study reported fewer bearded seal (average 24 seals, range 17-33) harvested from all ISR communities from 1988-1997. However, the model was fitted using the harvest of 66 bearded seals during 1970-1976 (7 years), as this record was higher than the Inuvialuit Harvest Study data. Even though it only included 2 communities, it is likely more reflective of actual harvest levels as seal harvest may often be underestimated. See Figure 5 for seal harvest time-series trend.

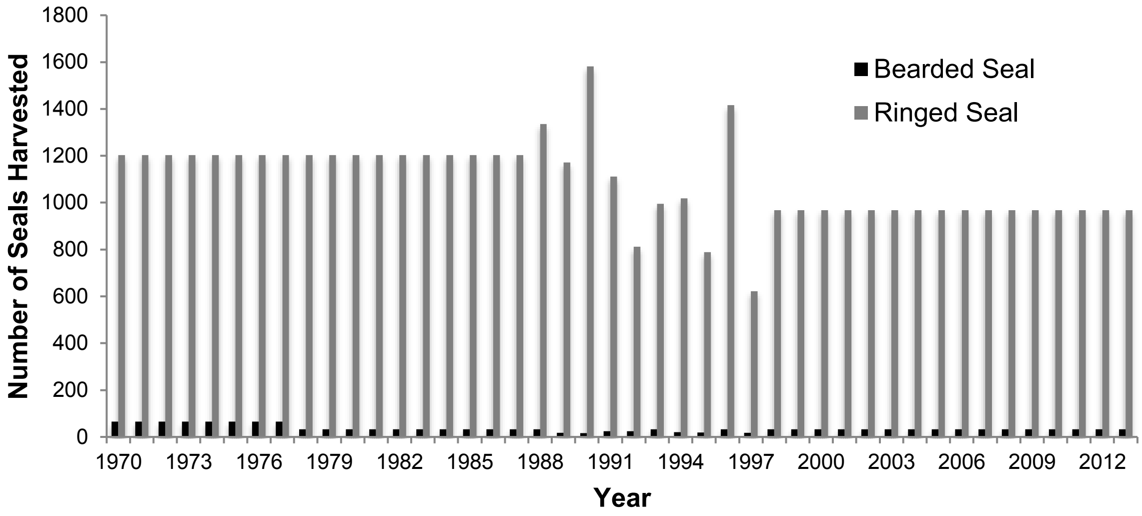

Figure 5: Generated time-series of bearded and ringed seal harvests used in the model fitting.

Fish Harvest Time-Series

The Inuvialuit Harvest Study (The Joint Secretariat, 2003) summarized catches of each fish species for all communities within the ISR from 1988-1997. These are presented as number of each species caught per year (Appendix D, Table D.1), and is the most comprehensive synthesis of fish catch in the ISR to date. Harvest was included for the years of the Inuvialuit Harvest Study, and read in as relative catches. The large number of species harvested and overall catch made it difficult to fit the model, so numbers of fish were rescaled according to average fish weight provided by BREA cruise data (DFO unpublished data). For fish groups not represented in the BREA samples (Anadromous Chars, Ciscos & Whitefish, Salmonids, Herring & Smelt, and Flounder & Benthic Cods), an average weight of all fish was used to rescale these groups, to weight ($t \cdot km^{-2}$) rather than total numbers.

Bird Harvest Time-Series

Bird harvest was included in the Inuvialuit Harvest Study (The Joint Secretariat, 2003) and a summary of birds caught by species is shown in Appendix D, Table D.2 for 1988-1997. Harvest was included as relative catches using the total number of birds for the years available.

SPECIES ABUNDANCE TIME-SERIES

Polar Bear Abundance Time-Series

The southern Beaufort Sea population of polar bears has shown fluctuations throughout the model simulation. A time-series was generated based on population estimates of 1778 for 1972-1983; 1800 bears in 1986; 1480 bears in 1992, 2272 bears in 2001, and 1526 bears in 2006 (Amstrup et al. 1986; Regehr et al. 2006; Allen and Angliss 2010). This time-series was used as a relative abundance trend in model fitting.

Bowhead Abundance Time-Series

Bowhead whales have increased from roughly 5000 to 8000 in the early 2000s, and over 10,000 in the late 2000s (George et al. 2004; Zeh and Punt 2005; Gerber et al. 2007). The annual rate of increase has been estimated at 3.1-3.5% depending on the years included in the assessment (George et al. 2004; Brandon and Wade 2006; Allen and Angliss 2010). Bowhead relative abundance was included in the model with starting biomass of 5000 whales and an annual increase of 3.2%.

Ringed Seal Abundance Time-Series

Surveys in the 1980s provided estimates of seal abundance for 1982, 1984, 1985, and 1986, with values of 42.20, 14.73, 7.92, and 19.35 seals per 100 km^2, respectively (Harwood and Stirling 1992). These abundances were converted to t·km^{-2} and rescaled against the Ecopath starting value to generate a relative abundance trend.

Zooplankton Abundance Time-Series

Zooplankton abundance estimates were sporadic and, given inconsistent methodology (e.g. location and net (mesh) size), difficult to compare over the historical simulation. The Nahidik cruises (2005, 2006, 2007, 2009, and 2012) provided a comparable time series for summer biomass (mg·m^{-2} dry weight) of the most abundant taxa (Walkusz et al., 2013b, 2010). Each species was organized into ecosystem model groups, converted to g·m^{-2} WW using species-specific conversion factors (Cauffopé and Heymans, 2005; Hunt et al., 1981) and then the group biomass was used as a time-series in the model (Figure 6). Time-series for each of the zooplankton groups (Jellyfish, Macro-Zooplankton, Med Copepods, Lg Copepods, and Other Meso-Zooplankton) was read in as absolute biomass reference, and was considered to be a minimum biomass estimate when fitting the model.

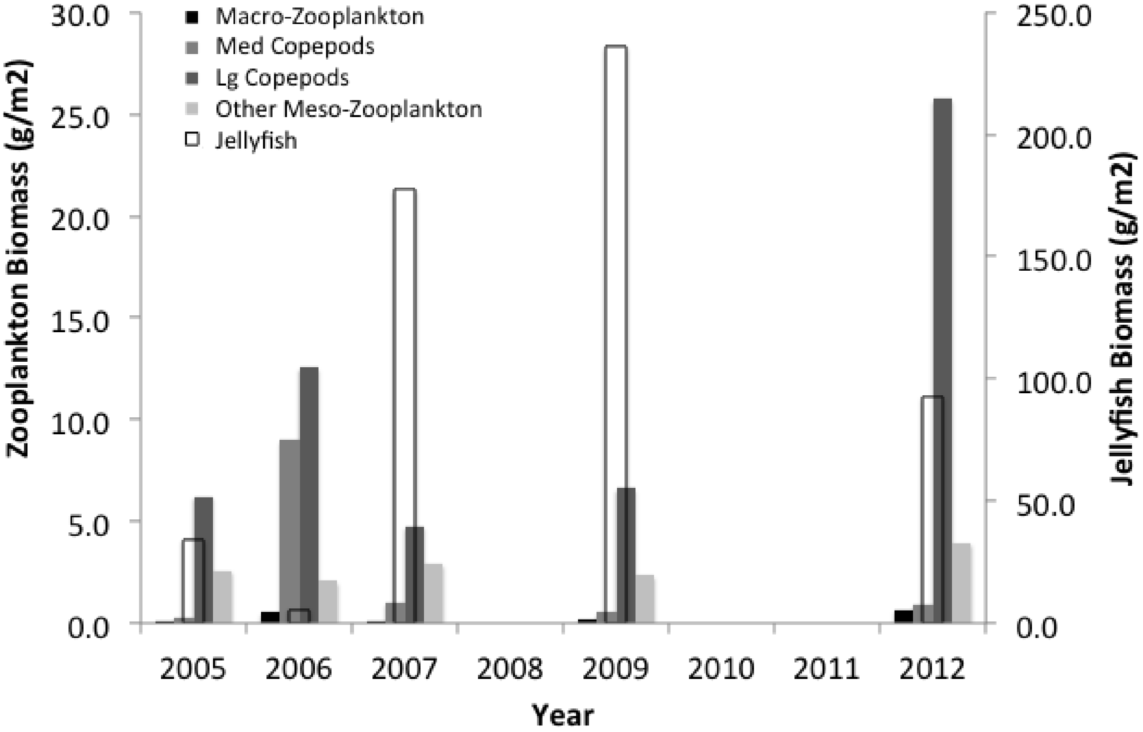

Figure 6: Biomass of zooplankton groups (excluding Micro-Zooplankton) for years sampled from 2005-2012.

Harvest Effort Time-Series

Effort was driven within the model fitting using human population numbers from the six ISR communities (Inuvik, Aklavik, Holman (aka Ulukhaktok), Paulatuk, Sachs Harbour, and Tuktoyaktuk: Table 10). Census data was used where available (Government of Northwest Territories Bureau of Statistics 2013, Statistics Canada, 2017). Population size was used as a proxy for hunting effort and a regression fit (R^2 value=0.6507 and p-value=0.028) to the census data was used to create a relative time series for the model.

Table 10: Inuvialuit Settlement Region community population size (Government of Northwest Territories Bureau of Statistics 2013, Canada, 2017).

Year	Population size
1981	5275
1986	5735
1991	5666
1996	5801
2006	5764
2011	5777
2016	5940

Forcing Functions

Forcing functions (FF) were included in the model to drive primary producers and other dynamics such as mediation functions. In order to test their impact on the model and ability to reduce errors between observed data (as incorporated from historical studies above) and modeled data from the Ecosim simulation, multiple environmental drivers were considered. Monthly environmental data tested included: sea ice cover (% of the model area), sea ice extent (total km^{-2} in the model area), minimum, maximum, and average sea surface temperature (SST) (°C), river flow (monthly mean discharge m $m^{-3} \cdot s^{-1}$), water level (monthly mean height m), and the Arctic Oscillation Index (AOI) (British Atmospheric Data Centre, 2010; Environment Canada, 2014; National Oceanic and Atmospheric Administration, 2014) were incorporated in different capacities to improve model fit. However, ultimately only SST and sea ice data (% cover) were retained. All datasets were standardized to 1 for the first year of the Ecopath model (1970).

Sea surface temperature and ice cover were extracted from the global model data (HadISST: Hadley Centre Data Sea Ice and Sea Surface Temperature data set), with the time-series generated as the average values over the 1° x 1° cells contained in the model area (British Atmospheric Data Centre, 2010). SST was tested as a FF to drive large and Small Pelagic Producers. Increases in SST are linked to lower sea ice and larger phytoplankton biomass over the open water season, with blooms occurring into autumn (Brugel et al., 2009). The seasonal decline of phytoplankton biomass is thought to be linked to reductions in light availability (Brugel et al., 2009), indicating the same peak and decline pattern as SST. Maximum, minimum, and average SST were all tested as FF applied to Large and Small Pelagic Producers. Sea ice cover was tested as a FF for ice algae, as ice algae refers to producers found within the sea ice, and ice is necessary for at least some of their life cycle (Horner et al. 1992). Ice algae remain in the sea ice during the winter and are a major contributor to the first year sea ice biomass (Riedel et al. 2006). Average SST and ice cover lowered the model sum of squares (SS) value and were therefore retained in the fitted model (Figure 7).

Other variables incorporated, but not retained in the fitted model include river flow and the AOI. Mackenzie river flow brings organic matter (dissolved organic carbon) into the Mackenzie Shelf area (Retamal et al., 2007) and was incorporated as an input source for both pelagic and benthic detritus. The AOI (also known as the Northern Hemisphere annular mode) is used to describe large-scale climate patterns in the Arctic. A positive value indicates strong winds are concentrated around the North Pole, retaining cold air to higher latitudes. A negative value indicates weaker winds moving further south and bringing the colder Arctic air into lower latitudes (National Oceanic and Atmospheric Administration, 2014). Ultimately the AOI did not improve the SS value and was not retained in the model.

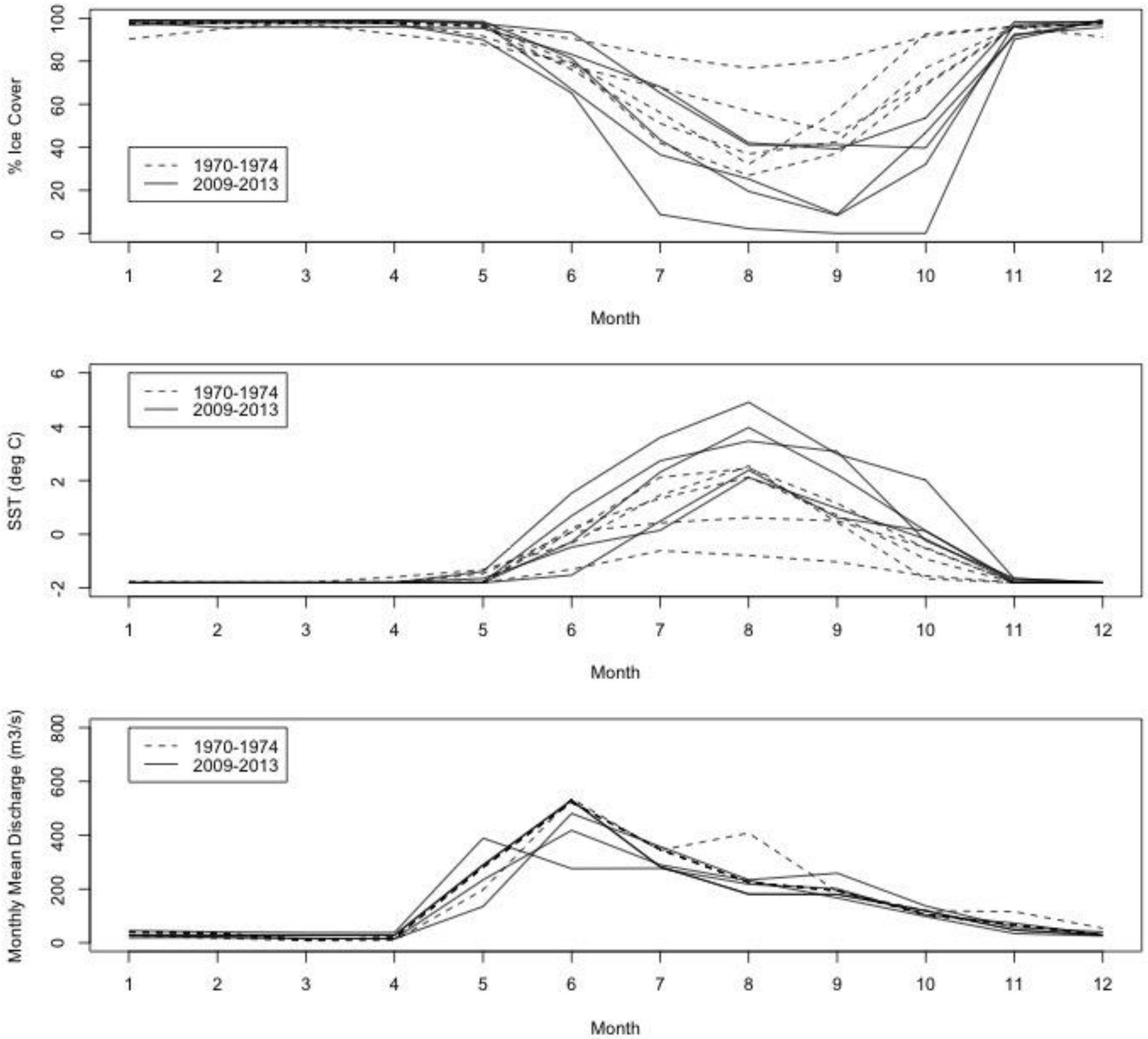

Figure 7: Ice cover (% of area), SST and Mackenzie River flow time-series used in model fitting.

Mediation Functions

Two mediation functions were included in the model fitting to incorporate the indirect relationship between sea ice and two species groups: polar bears and arctic and polar cods. Both species groups have predator-prey interactions that are dependent on sea ice. Sea ice decline in other areas has had a negative effect on polar bear populations. In western Hudson Bay, decline in polar bears from 1981-1988 was linked to reproductive stress in females, potentially caused by reduced sea ice conditions that forced bears to spend more time on land where food was less available (i.e. seals) (Stirling et al. 1999). For the southern Beaufort Sea (SBS) population, Hunter et al., (2007) modeled population growth against sea ice and identified positive growth in years with more sea ice. Specifically, within shelf areas occupied by the SBS polar bear population, low ice years are associated with increased unsuccessful hunting attempts (polar bears digging through empty sea dens), increased cannibalism, and more time spent on land (Schliebe et al. 2008; Stirling et al. 2008). During low ice years these observations occur in the model area, but not in surrounding areas (Amundsen Gulf, Chukchi Sea, deeper Beaufort Sea), and may be influenced by seal availability rather than ice conditions directly (Stirling et al. 2008). As polar bears require the sea ice as a platform to hunt and access seals, a mediation function was created to represent increased vulnerability for prey, and increased foraging area, as sea ice increases. As sea ice was used as a proxy for ice algae within this model to drive the ice algae pattern, this group was used as the mediating group, with a sigmoid pattern (Figure 8). The sigmoid shape was chosen, with the starting year (Ecopath model, where y=1) close to the maximum y-value, as the 1970s had higher ice coverage, and bears had more access to seals (Stirling 2002b). The placement of the Ecopath starting point was tested during model fitting.

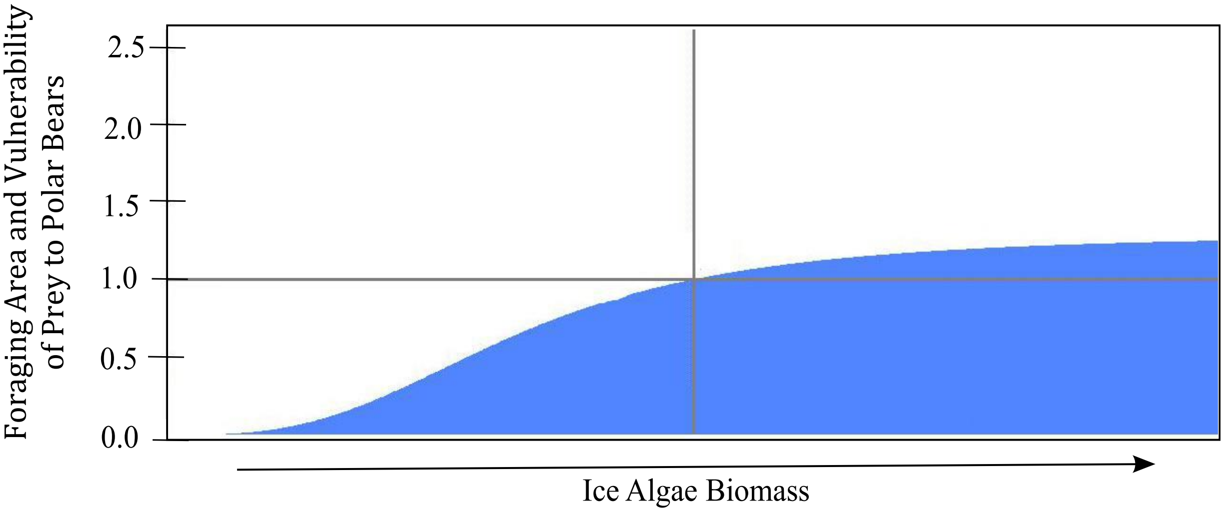

Figure 8: Mediation function applied to polar bears. Use of Ice Algae as a proxy for sea ice to alter the vulnerability of prey to polar bears and the foraging area of polar bears as sea ice changes.

The second mediation function captures the dynamics between Arctic Cod and sea ice. Arctic Cod overwintering under the sea ice preform daily vertical migrations consistent with predator avoidance (Benoit et al., 2010). Divers under ice stations have noted Arctic Cod residing in ice crevasses, suggesting they are using the ice habitat to hide from predators (Gradinger and Blumm, 2004; Wieckowski et al., 2009). In Resolute Bay, when more sea ice habitat was available schools of Arctic Cod were lower in density and occupied more space compared to open water or low ice cover conditions when fish schools were denser (Crawford and Jorgenson, 1993). The sigmoid mediation function included for the Arctic and Polar Cod group represented increased protection from predators when more sea ice is available, while at higher sea ice coverage little extra protection is offered past a threshold. As sea ice decreases past the mid-point, vulnerability increases as sea ice diminishes (Figure 9). As the biomass of ice algae (as a proxy for sea ice) increases, the Arctic and Polar Cod group is less vulnerable to predators (more protection).

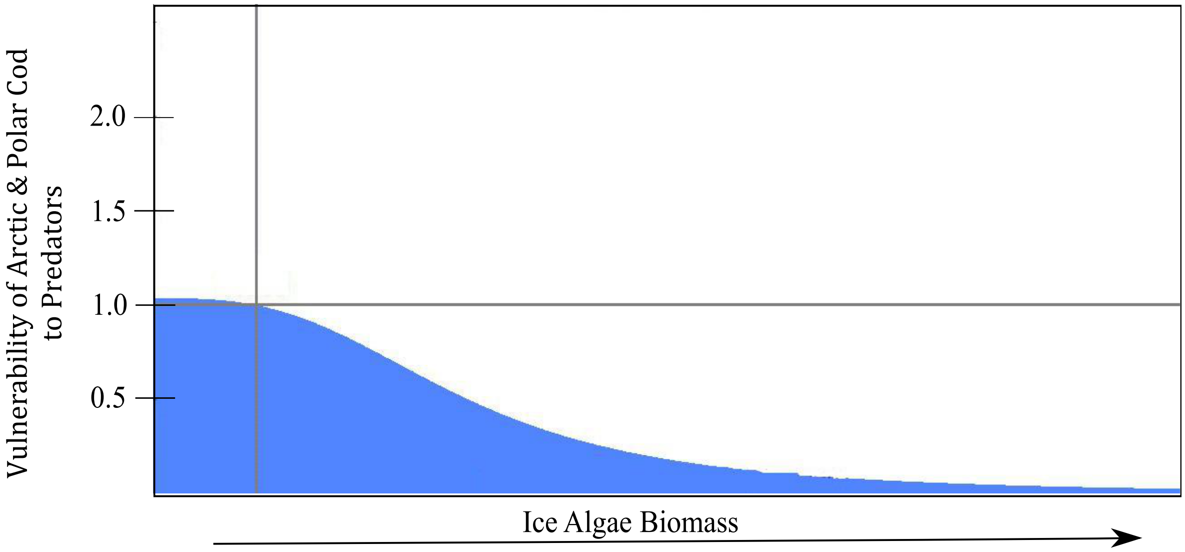

Figure 9: Mediation function applied to Arctic and Polar Cod group. Use of ice algae as a proxy for sea ice to alter the vulnerability of cods to their predators as sea ice changes.

Group Information

Parameters referring to group information include: the maximum relative P/B (allows the P/B value to increase to a set limit if prey are abundant), Maximum relative feeding time (ability to increase feeding time if prey is scarce), Feeding time adjustment rate (allows groups to respond differently to changes in feeding time), and fraction (or proportion) of other mortality sensitive to changes in feeding time (Buszowski et al., 2009). The maximum relative P/B was set to 2 for all producer groups: Large Pelagic Producers, Small Pelagic Producers, ice algae, and benthic plants, indicating the ability to double growth rate if food is plentiful. The maximum relative feeding time parameter default value is 2 to indicate the potential to double feeding time if prey becomes scare, with lower values indicating that although food is available some species will not risk predation to increase consumption (Christensen et al. 2005; Christensen et al. 2007). The maximum value of 2 was set for marine mammals and zooplankton, with fish and benthic groups set at 1.5.

Feeding time adjustment rates range from 0 to 1, with 0 causing feeding time to remain constant (changes in consumption result in growth change), and 1 causing fast response times (leading to lower vulnerability to predation when food increases) (Buszowski et al., 2009). The default value is 0 for all groups except for marine mammals, where a value of 0.5 is used. The fraction of other mortality (1-EE) sensitive to feeding time ranges from 0-1, with a value of 0 causing mortality to remain constant. A nonzero value allows the proportion of mortality to change along with time spent feeding (Buszowski et al., 2009). See table 11 for a summary of group parameters used in model fitting.

Ecosim Vulnerabilities

Vulnerabilities were estimated through multiple iterations of the fit to time series routine (Buszowski et al., 2009), using various combinations of FF and vulnerability combinations. Once harvest trends, abundance trends, FF, and mediation functions were incorporated into Ecosim, vulnerabilities were manipulated to improve the fit of the model, by reducing the SS. Once the automated fit to time-series was complete, individual predator prey manipulations were made in an attempt to improve the SS value. Changed values were retained only if they improved (lowered) the SS value of the fitted model.

Table 11: Group information parameters for Ecosim model fitting.

Group name		Max rel. P/B	Max relative feeding time	Feeding time adjust rate [0,1]	Fraction of other mortality sensitive to changes in feeding time
1	Polar Bear	2	2	0	0.5
2	Beluga	2	2	0.2	0.5
3	Bowhead	2	2	0.2	0.5
4	Ringed Seal	2	2	0.2	0.5
5	Bearded Seal	2	2	0.2	0.5
6	Birds	2	1.5	0	0.5
7	Char & Dolly Varden	2	1.5	0	0.5
8	Ciscos & Whitefish	2	1.5	0	0.5
9	Salmonids	2	1.5	0	0.5
10	Herring & Smelt	2	1.5	0	0.5
11	Arctic & Polar Cods	2	1.5	0	0.5
12	Capelin	2	1.5	0	0.5
13	Flounder & Benthic Cods	2	1.5	0	0.5
14	Small Benthic Marine Fish	2	1.5	0	0.5
15	Other Fish	2	1.5	0	0.5
16	Arthropods	2	1.5	0	0.5
17	Bivalves	2	1.5	0	0.5
18	Echinoderms	2	1.5	0	0.5
19	Molluscs	2	1.5	0	0.5
20	Worms	2	1.5	0	0.5
21	Other Benthos	2	1.5	0	0.5
22	Jellyfishes	2	2	0	0.5
23	Macro-Zooplankton	2	2	0	0
24	Med Copepods	2	2	0	0
25	Lg Copepods	2	2	0	0
26	Other Meso-Zooplankton	2	2	0	0
27	Micro-Zooplankton	2	2	0	0
28	Large Pelagic Producers	2	-	-	-
29	Small Pelagic Producers	2	-	-	-
30	Ice Algae	2	-	-	-
31	Benthic Plants	2	-	-	-

RESULTS

ECOPATH: MODEL BALANCING

In order to balance the model, the EE of each group needed to fall between 0 and 1. Initial parameterization identified model groups needing parameter adjustments to balance the model. While many parameters were edited, the main changes to the model fall into the following categories: high marine mammal predation on their prey items, high fish biomass estimated by Ecopath, and predator over-predation on benthic groups. While these model adjustments are noted by trophic groupings here, they were not completed in this order. Rather, changes were made iteratively among one or more groups to correct multiple parameters at the same time.

First, predation mortality caused by marine mammals was too high for many groups. The biomass for the marine mammal groups had been based on population estimates for areas larger than the area modeled. The Ecopath (mass-balanced) model could not support entire populations of all marine mammal groups. The most notable case was polar bears with their high predation on other marine mammal groups resulting in the need to lower biomass for this group. The biomasses for all marine mammal groups had to be reduced to bring predation mortalities of lower trophic levels to reasonable levels (i.e. EE between 0 and 1). Beluga biomass had to be reduced the most, indicating the model could not support the full-time feeding of the entire EBS beluga population. Other adjustments to marine mammal parameters included high bowhead whale mortality caused by polar bears (even though it is only 2% of the diet), so the P/B of bowhead was increased. This was supported by documented increases in annual population levels of 3.2% each year, and was included as biomass accumulation in the model. In addition, the Q/B value for beluga whales was too high, and was lowered to 17 y^{-1} to balance the model.

Because the biomass of marine mammals was too high, it caused the biomass of fish groups to be overestimated (73 $t{\cdot}km^{-2}$), as they were calculated based on the needs of predators. Once the biomasses of marine mammals were lowered, the minimum biomass of fish needed to support these predators was also reduced. The relatively low initial P/B values from the literature (see Table 2) still required biomass estimates to remain high (12 $t{\cdot}km^{-2}$) for all fish groups combined. The P/B of all fish groups was increased to the upper limits of P/B ranges, as the initial model balancing resulted in a high biomass for the area. Although there were no comprehensive fish surveys for the model area during the model simulation (1970-2012), preliminary results from DFO's BREA Marine Fish project has sampled benthic fish during 2012-2013, with preliminary biomass results of less than $1g{\cdot}m^{-2}$ (or 1 $t{\cdot}km^{-2}$) for all benthic fish groups in the model area (BREA unpublished data), available at the time of model completion. Taking this conservative approach, increasing the P/B values resulted in a lower biomass estimation by Ecopath, resulting in a total fish biomass of 1.95 $t{\cdot}km^{-2}$.

The biomass of benthic groups had to be adjusted to compensate for the diets of predators. Lower biomass groups such as molluscs and worms had too much predation pressure from predators (primarily fish and arthropods). In addition, due to predation of benthic groups by other benthic groups, multiple iterations of dietary changes were made to balance the EE values for each of these groups. Through these dietary changes the biomass of all groups was lowered, more in line with reported data. Initial biomass for all benthic groups started at 19.11 t·km^{-2}, but was lowered to a total biomass of 10.3 t·km^{-2} in the balanced model. For example, the EE for Molluscs was too high (>20), so some of the diets of predators were shifted to Echinoderms to remove predation mortality on Molluscs.

The EE for some zooplankton groups was much lower than the expected value of 0.95. For the Med Copepod group, the EE was too low so the biomass was lowered to 1.8 t·km^{-2}. This resulted in an EE value of 0.438, still low, but this is expected as there are enough Lg Copepods, the preferred food for predators, to satiate predators. The PB values of Macro-Zooplankton, Lg Copepods, and Med Copepods were lowered to alleviate the predation on primary producers, and the biomass of Lg Copepods was increased. Changes to the zooplankton diets alleviated over-predation on producers to balance these groups to EE values under 1. The detritus in the model was quite high compared to other groups, therefore in the model balancing, some of the detritus from the lower Trophic Level (TL) groups was exported from the model. This was supported based on the Mackenzie River's influence and timing of river melt, on the flushing out of some existing detritus, regardless of its origin. Benthic groups (benthic invertebrates and benthic plants) were assumed to contribute to benthic detritus with some being exported from the system, while Zooplankton and Pelagic Producers (Large and Small) were assumed to contribute to pelagic detritus and with some being exported from the system. Ice Algae was assumed to contribute primarily to benthic detritus due to fast particle sinking rates (see Ice Algae section). Table 9 shows the detrital fate of each model group contributing to either pelagic detritus (retained in the water column), benthic detritus, or exported out of the ecosystem via the Mackenzie River, that resulted in a balanced model

Final values for the balanced Ecopath model are presented in Table 12, with the diet matrix in Appendix E. Once the model was considered balanced, Ecosim model fittings were started.

Table 12: Basic Ecopath parameters used in the balanced model. Parameters include Trophic Level (TL), Biomass (B) in t·km^{-2}, Production/Biomass (P/B) in y^{-1}, Consumption/Biomass (Q/B) in y^{-1}, Ecotrophic Efficiency (EE), Production/ Consumption (P/Q), and Landings in t·km^{-2} for the first year of the model.

	Group name	TL	B	P/B	Q/B	EE	P/Q	Landings
1	Polar Bear	4.81	0.002	0.15	3.03	**0.79**	0.05	2.36E-04
2	Beluga	4.22	0.030	0.07	17.00	**0.46**	0.00	7.18E-04
3	Bowhead	3.30	0.339	0.07	5.48	**0.45**	0.01	3.02E-04
4	Ringed Seal	3.82	0.020	0.80	16.05	**0.35**	0.05	4.69E-04
5	Bearded Seal	3.75	0.020	0.12	13.85	**0.25**	0.01	1.80E-05
6	Birds	3.80	0.001	0.90	10.00	**0.33**	0.09	3.00E-04
7	Anadromous Chars	3.59	**0.080**	0.68	2.30	0.95	0.30	1.00E-04
8	Ciscos & Whitefish	3.21	**0.243**	0.95	3.80	0.95	0.25	1.00E-04
9	Salmonids	3.55	**0.066**	0.85	6.00	0.95	0.14	1.00E-04
10	Herring & Smelt	3.09	**0.399**	1.50	4.90	0.95	0.31	1.00E-04
11	Arctic & Polar Cods	3.44	**0.471**	0.80	3.90	0.95	0.21	1.00E-04
12	Capelin	3.44	**0.065**	0.95	4.00	0.95	0.24	1.00E-04
13	Flounder & Benthic Cods	3.31	**0.173**	0.75	2.40	0.95	0.31	1.00E-04
14	Small Benthic Marine Fish	3.19	**0.258**	1.06	3.50	0.95	0.30	1.00E-04
15	Other Fish	3.06	**0.201**	0.51	2.40	0.95	0.21	1.00E-04
16	Arthropods	2.22	2.500	0.75	3.50	**0.63**	0.21	-
17	Bivalves	2.00	1.200	0.60	2.40	**0.63**	0.25	-
18	Echinoderms	2.23	2.400	0.55	1.80	**0.66**	0.31	-
19	Molluscs	2.00	1.700	0.85	3.40	**0.75**	0.25	-
20	Worms	2.07	1.400	0.95	4.00	**0.95**	0.24	-
21	Other Benthos	2.08	1.100	0.75	3.00	**0.88**	0.25	-
22	Jellyfishes	2.24	0.965	20.00	45.00	**4.95E-04**	0.44	-
23	Macro-Zooplankton	2.64	0.200	7.50	28.00	**0.74**	0.27	-
24	Med Copepods	2.12	1.800	18.00	45.00	**0.44**	0.40	-
25	Lg Copepods	2.31	5.800	5.50	20.00	**0.19**	0.28	-
26	Other Meso-Zooplankton	2.34	1.200	22.00	80.00	**0.40**	0.28	-
27	Micro-Zooplankton	2.00	2.400	55.00	150.00	**0.44**	0.37	-
28	Large Pelagic Producers	1.00	2.500	30.00	-	**0.98**	-	-
29	Small Pelagic Producers	1.00	6.500	60.00	-	**0.99**	-	-
30	Ice Algae	1.00	6.500	20.00	-	**0.68**	-	-
31	Benthic Plants	1.00	3.500	10.00	-	**0.03**	-	-
32	Pelagic Detritus	1.00	0.500	-	-	**0.22**	-	-
33	Benthic Detritus	1.00	0.050	-	-	**0.80**	-	-

ECOSIM FITTING

Once all of the abundance and time-series data trends were applied to the model, effort (in the form of human population: Table 10) was applied to all harvest activities. Next, the group information was adjusted based on the TL of the model group (Table 11). Then vulnerabilities were adjusted using the fit to time-series tool in an attempt to lower the overall SS for the historical simulation. Once the fit to time-series routine did not result in a lower SS value, individual species interactions were manipulated in an attempt to improve the SS. If the value was not reduced, then the change was not retained. A summary of all Ecosim components retained in the model fitting is presented in Table 13.

Prior to adjusting vulnerabilities (V) the initial SS was 6497, using default vulnerabilities of 2 indicating mixed trophic interactions. Setting all V's =1 resulted in SS=6334, indicating a slightly better fit under bottom-up ecosystem conditions. The fit to time series tool reduced the SS to 2067, but produced unrealistic simulations due to low fish and bird harvest levels relative to effort (human population), and limited data over the Ecosim simulation period. Once the fish and bird harvest time-series were removed, the SS dropped to 323.3. Searching for sensitivity of SS to vulnerabilities by predator groups yielded a SS=235.7, and another attempt using predator-prey interactions yielded a SS=194.1. Attempts to further reduce the SS were unsuccessful, and this was considered to be the best fitting model. The harvest for fish and birds was then re-applied, to understand the magnitude of error associated with these groups. These harvest time-series added an additional SS=6192.54 (Total SS=6387), thereby contributing enormous amounts of error to the model. The final vulnerabilities in the fitted model are presented in Table 14. The best fitting model had more than half of all predator-prey interactions as bottom-up (V<2) or mixed trophic interactions (V=2). The model fits for each individual group are shown in Figure 10.

Table 13: Summary of temporal data used in Ecosim model fitting

Time-series Data	**Years (Raw Data)**	**Years (Total Time-series)**	**Time-series Type**	**Contribution to SS**
Polar Bear Harvest	1970-2012	1970-2012	Forced Catches	0.00279
Beluga Harvest	1970-2012	1970-2012	Forced Catches	0.000102
Bowhead Harvest	1970-2012	1970-2012	Forced Catches	0.000088
Ringed Seal Harvest	1988-1997	1970-2012	Forced Catches	0.00777
Bearded Seal Harvest	1988-1997	1970-2012	Forced Catches	0.000137
Fish Harvest[1,2]	1988-1997	1988-1997	Relative Catches	**(2886.5)**
Bird Harvest[2]	1988-1997	1988-1997	Relative Catches	**(3306)**
Polar Bear Abundance	1970-2012	1970-2012	Relative Abundance	0.519
Bowhead Abundance	1970-2012	1970-2012	Relative Abundance	0.385
Ringed Seal Abundance			Relative Abundance	6.163
Jellyfishes Abundance	2005-2012	2005-2012	Relative Abundance	160.4
Macro-Zoopl. Abundance	2005-2012	2005-2012	Relative Abundance	4.428
Large Copepod Abundance	2005-2012	2005-2012	Relative Abundance	0.738
Medium Copepod Abundance	2005-2012	2005-2012	Relative Abundance	9.468
Other Meso-Zoopl. Abundance	2005-2012	2005-2012	Relative Abundance	11.94
Human Population	1970-2012*	1970-2012	Effort	NA
Sea Surface Temperature	1970-2012	1970-2012	Forcing Function	NA
Sea Ice (% cover)	1970-2012	1970-2012	Forcing Function, Mediation Function	NA

* Incomplete time-series: estimated values were included

[1] Fish harvest is divided into 8 subgroups based on model functional groups (see Appendix D) for breakdown of fish catch)

[2] Fish and Bird harvest (**bolded**) was used in the original model fitting, but removed for the fit-to-time-series exercises to estimate vulnerabilities, as they produced poor results. SS value is the error to the fitted model if these time-series are reapplied after the model fitting.

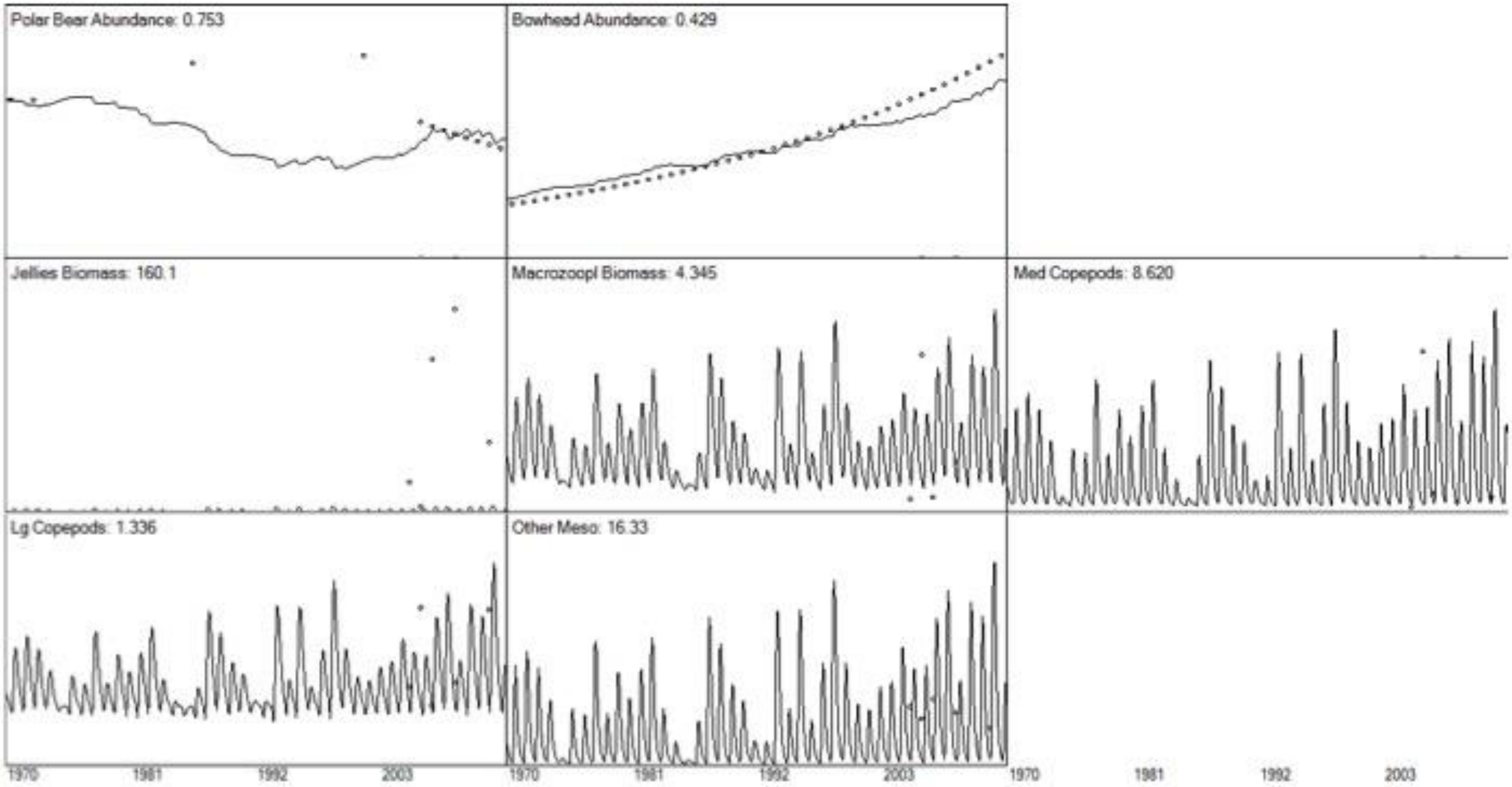

Figure 10: Model simulations of fitted group biomasses with imported data values, as described in Table 14. Each figure depicts how close the model simulation captures the data references, noting in some cases relative data values are shown, not absolute values. The SS (error) contribution is shown for each time-series.

Table 14: Final vulnerabilities for all predator-prey interactions for the fitted historical simulation

	Prey \ predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
1	Polar Bear	2													
2	Beluga	2													
3	Bowhead	2													
4	Ringed Seal	2													
5	Bearded Seal	2													
6	Birds														
7	Char & Dolly Varden		2		2	2	2								
8	Ciscos & Whitefish		2		2	2	2	2		2	2				
9	Salmonids					2	2					2	2		
10	Herring & Smelt		2		2	2	2	2	2			2	2	2	
11	Arctic & Polar Cods		2		2	2	2	2		2				2	
12	Capelin		2		2	2	2	2		2				2	
13	Flounder & Benthic Cods		2		2	2	2	2			2			2	2
14	Small Benthic Marine Fish		2		2	2	2	2	2	2	2			2	2
15	Other Fish		2		2	2	2	2	2	2				2	2
16	Arthropods				2	2	2	2	2	2	2	2	2	2	2
17	Bivalves						2	2						2	2
18	Echinoderms				2	2	2	2	2		2	2	2	2	2
19	Molluscs				2	2	2	2	2		2	2	2	2	2
20	Worms				2	2	2	2	2	2	2	2	2	2	2
21	Other Benthos				2	2	2	2		2	2	2	2	2	2
22	Jellyfishes						2								2
23	Macro-Zooplankton		2	1.0	2		2	2	2	2	2	2	2	2	2
24	Med Copepods		2	2	2		2	2	2	2	2	2	2	2	2
25	Lg Copepods		2	3.2	2		2	2	2	2	2	2	2	2	2
26	Other Meso-Zooplankton		2	2	2		2	2	2	2	2	2	2	2	2
27	Micro-Zooplankton			2					2		2				2
28	Large Pelagic Producers								2	2	2	2	2		2
29	Large Pelagic Producers										2				
30	Ice Algae								2		2				
31	Benthic Plants														
32	Pelagic Detritus														
33	Benthic Detritus														

Table 14: Final vulnerabilities for all predator-prey interactions for the fitted historical simulation (Continued)

	Prey \ predator	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
1	Polar Bear													
2	Beluga													
3	Bowhead													
4	Ringed Seal													
5	Bearded Seal													
6	Birds													
7	Anadromous Chars													
8	Ciscos & Whitefish													
9	Salmonids													
10	Herring & Smelt													
11	Arctic & Polar Cods													
12	Capelin													
13	Flounder & Benthic Cods													
14	Small Benthic Marine Fish													
15	Other Fish													
16	Arthropods	2			2		2	2						
17	Bivalves	2	2		2									
18	Echinoderms	2	2				2	2						
19	Molluscs	2	2		2		2	2						
20	Worms	2	2		2			2						
21	Other Benthos	2	2		2		2							
22	Jellyfishes	2												
23	Macro-Zooplankton	2								2				
24	Med Copepods	2							2	2		1.00E+10	1.00E+10	
25	Lg Copepods	2							1	2				
26	Other Meso-Zooplankton	2							1	2	1.00E+10		1.00E+10	
27	Micro-Zooplankton	2							1	2	1	1.00E+10	1	
28	Large Pelagic Producers	2		2					1	2	1	1.00E+10	1	
29	Large Pelagic Producers	2		2					1	2	1	2.01E+09	1	1
30	Ice Algae	2		2						2	1	1	1	1.00E+10
31	Benthic Plants		2	2	2	2	2	2						
32	Pelagic Detritus		2	2	2	2	2	2	1	2	1	2	1	1.00E+10
33	Benthic Detritus		2	2	2	2	2	2				2		1.08883

ECOSIM RESULTS

Over the simulated historical reconstruction, there is an increase in total ecosystem biomass (Figure 11), when comparing the last 5 years of the simulation (average biomass= 62.52 t·km^{-2}) to the first five years of the simulation (average biomass= 47.99 t·km^{-2}). However, there are large biomass fluctuations throughout the simulation, with a minimum value of 34.01 t·km^{-2} in 1985 and a maximum value of 78.22 t·km^{-2} in 2012. Despite these changes in biomass, the overall ecosystem TL remains fairly constant. During the first 5 years of the simulation the ecosystem TL was 1.71 (average), and increased to a value of 1.73 (average) for the last 5 years (range 1.65-1.79). This change is less than 1%, implying fluctuations in ecosystem biomass did not significantly alter ecosystem structure.

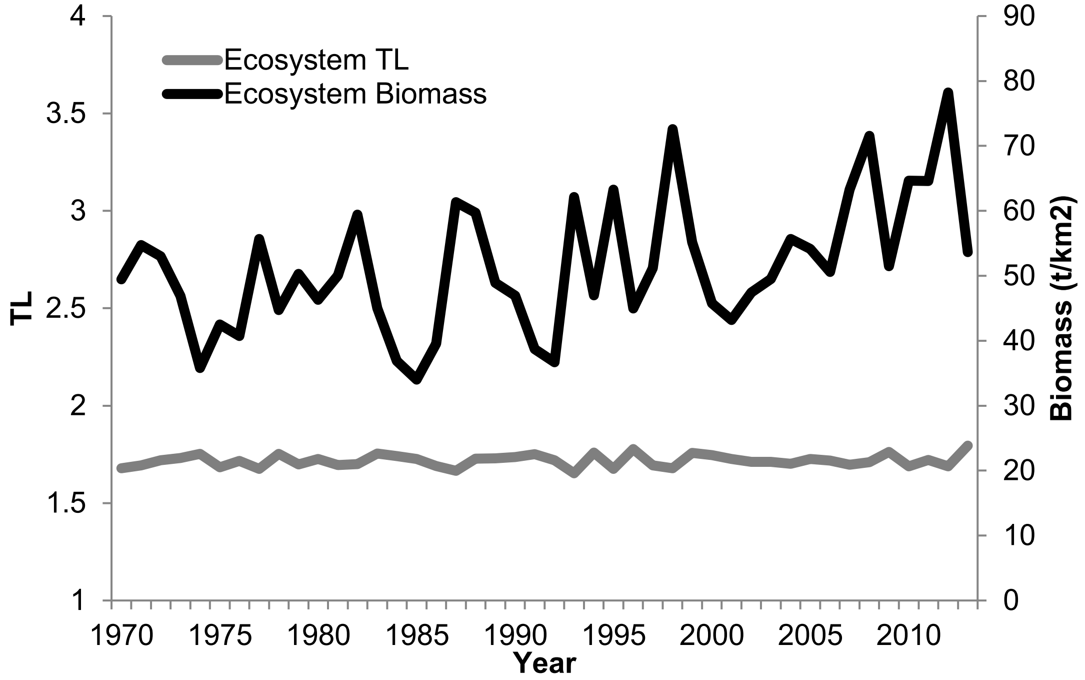

Figure 11: Total ecosystem Biomass (t·km^{-2}) and average ecosystem TL for each year of the historical simulation.

The largest change in biomass occurs for marine mammals (131%). However, the final combined biomass of 1.05 t·km^{-2} is a small overall contribution, 1.7%, to total ecosystem biomass. Bowhead whales show the largest increase in biomass (153%), while Polar Bears are the only marine mammal group declining (-20%). All fish groups combined increase in biomass by 26%, with the largest increase in Herring & Smelt (39%) and the smallest in Flounder and Benthic Cods (10%). The ending biomass for all fish groups combined was 2.68 t·km^{-2} or 4.3% of total ecosystem biomass. Benthic groups are the only species grouping to show a decline in biomass (4%), with the largest decrease shown for Arthropods (-6%) and the lowest for Other Benthos (-1%). However, total benthic ending biomass was 10.35 t·km^{-2} or roughly 17% of the total ecosystem biomass. Zooplankton groups increased nearly 51% (all groups combined), with a total combined biomass of 20.25 t·km^{-2}. Of the zooplankton groups the Other Meso-Zooplankton group increased the most (83%), while Lg Copepods increased the least (24%). Total biomass for producers and detritus increased 33%, with an ending combined biomass of 28.27 t·km^{-2}, contributing roughly 45% of total ecosystem biomass. The largest increase for this group came from the Small Pelagic Producers (87%), while the Ice Algae group had the largest decrease (-27%).

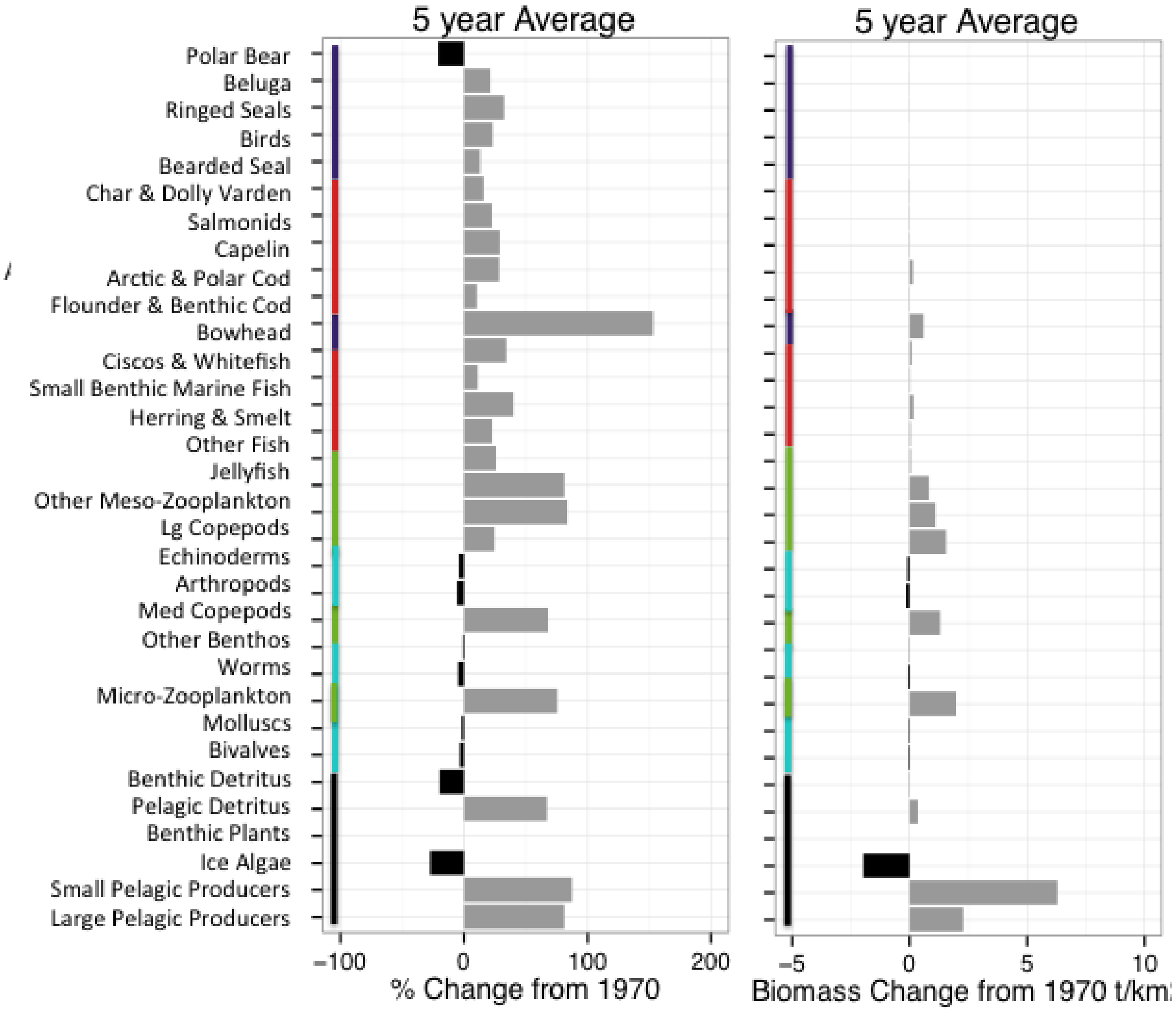

Figure 12: Biomass change for each species group identifying the percent biomass change (A) and total biomass change (B). Both calculations use values for the first five years of the simulation and the last five years of the simulation to account for large fluctuations in lower TL values. Species groupings are indicated to the left of each figure to identify marine mammals and birds (purple), fish (red), zooplankton (green), benthos (blue), and producers/ detritus (black), and are organized by TL, with the highest TL species at the top of the figure, and the lowest TL species at the bottom.

DISCUSSION

As the first ecosystem model for the Beaufort Sea, there are both basic and integrated findings that contribute to the structure and function of this system. By assessing the system in its entirety, we are able to identify research strengths and weaknesses, and move forward to address those gaps. Simulated historical reconstruction of the Beaufort Sea Shelf food web identifies a strong influence from climate drivers. While harvesting pressures were accounted for based on reported harvest levels, the impact of harvest on the food web is minimal in comparison to climate change. The increase in SST and longer open water season favor pelagic species such as zooplankton, while the decreases in sea ice leads to reductions in benthic invertebrates via the benthic detritus pathway. As increases in SST and open water continue with changes to the global climate, these ecosystem impacts are expected to be more significant in the future. Better estimates of mid to low trophic level species will increase the understanding of the food web in addition to the precision of the ecosystem model.

ECOSYSTEM STRUCTURE

Construction of the model and the historical simulations allowed for a comparative evaluation of various ecosystem components and the identification of the strengths and weaknesses of this approach, in terms of species knowledge and available data. Marine mammals are by far the most well-known species group in the ecosystem. All marine mammal species had some level of abundance estimates and catch records for the historical simulation period, in particular there were well-documented abundance trends for beluga and bowhead whales. As a result marine mammals had the greatest certainty in terms of Ecopath input parameters and Ecosim simulations. Information collected for lower trophic level species as a by-product of marine mammal programs, such as relative abundance or importance of lower trophic level estimated from the diets of marine mammals, helps to fill information gaps for lesser-known trophic levels.

Biomass estimates for benthic groups were available for the Ecopath calculations, but no recent comprehensive estimates were available to provide trend information for the simulation. In contrast, zooplankton biomass estimates were taken from more recent estimates. Fish groups were the least well known in this ecosystem, with no comprehensive estimates for any time period in the model simulation. These circumstances lead to the potential for the largest errors to come from the fish groups in terms of their contribution to ecosystem abundance. Because their abundance is estimated based on the need of higher predators, and what can be sustained by lower trophic levels, these estimates are considered minimum biomasses. Yet fish have the potential to contribute much more to the ecosystem structure and dynamics than captured within this model. Since the completion of the model and simulations, a large-scale fish assessment has taken place (BREA- Marine Fishes Program), and while individual fish weights were included to assist in fish P/B calculations, fish biomass estimates and trends were not available for this modelling exercise. This is recognized as a much-needed contribution to the Beaufort ecosystem knowledge. In addition to fish, benthic invertebrates and zooplankton sampling programs would benefit from repeated sampling efforts for multiple years in order to gain an understanding of sampling variance in addition to mean biomass estimates. Estimates provided by the model should be considered conservative and serve as a comparison with observed methods.

ECOSYSTEM CHANGES

In attempting to re-create past changes in the ecosystem, the largest errors in the model fitting stem from fish and zooplankton groups (Figure 10), not unexpected given the lack of knowledge for these groups and results from the Ecopath model. The ecosystem changes in biomass are primarily driven by bottom-up forcing in the model. Because the lower TLs in the ecosystem retain the largest biomass, 92% of ecosystem model biomass for producers, detritus, benthos, and zooplankton, for the last year of the model simulation, the fluctuations observed in ecosystem biomass over time are due to environmental forcing and the response from these lower TLs. Predator groups such as fish and marine mammals, are slower to respond to these changes, with less intense responses as these changes are propagated through the food web. While higher TL groups do indicate responses, the amplitudes are dampened, and have less overall impact on ecosystem biomass, as they contribute less overall to the total biomass.

Because the lower TLs contribute greatly to the biomass of the ecosystem, the responses to SST and sea ice model drivers are significant to the ecosystem as a whole. Mortality from harvesting activities contributed minimally to total mortality for each species groups, with 26 out of 31 functional groups (excluding detritus) incurring less than 5% change in total mortality over the historical simulation. The largest changes in mortality are shown for Macro-Zooplankton (+20%) and Beluga (-17%). Mechanisms for increased mortality on Macro-Zooplankton stem from increases in Bowhead Whale biomass and increased predation, while decreases in Beluga mortality stem from reductions in Polar Bear biomass and predation combined with decreased catches. The relatively stable mortality values for most groups over the simulation support the primary mechanism for ecosystem change being driven by bottom-up environmental forcing. Furthermore, the process of model fitting indicates the best fitting vulnerability values are primarily lower values (≤2), support a bottom-up driven ecosystem.

Changes in environmental drives favor specific pathways in the food web. As the sea ice trend is the driver of ice algae in the model, and sea ice declines from an average annual ice cover of 82% (range 32-98%) in 1970 to an average of 62% (range 0-99%) in 2012, it reduces the pathway for ice algae sinking to benthic detritus. Since benthic detritus is a major contributor to the diets of benthic groups (67-80%), this 27% decline in Ice Algae biomass and 19% decrease in Benthic Detritus biomass is an important change to benthic invertebrates and subsequent predators of benthic groups. The relative stability of benthic invertebrates results from groups being able to utilize other food sources such as Large and Small Pelagic Producers and the potential for Ice Algae to still be abundant enough, even considering declines, to sustain the levels of benthic groups in the model. Future declines may identify a tipping point for this group.

Sea Surface Temperature increases from an annual average value of -0.8°C (range -1.8 -2.5) in 1970 to 0.3°C (-1.8-4.9) in 2012. Not only has the average become positive, but the maximum value has also increased to nearly double the previous maximum value. The increase in SST favours the Pelagic Producers (Large and Small) and the availability of Pelagic Detritus, all of which benefit zooplankton primarily and then subsequent pelagic predators. Of the pelagic producers, Large Pelagic Producers increase by 81% while Small Pelagic Producers increase by 87%. These increases result in an increase in pelagic detritus of 67% and increases in zooplankton groups ranging from 24% for Lg Copepods to 83% for Other Meso-Zooplankton.

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APPENDICES

APPENDIX A: Marine Mammal Parameter Equations

Mortality for marine mammal functional groups was calculated based on life history information and longevity from (Barlow and Boveng, 1991). Estimates of longevity L(x) were made using equation A.1 to estimate the probability of survivorship from birth to age x, with information from equations A.2, where $L_j(x)$ is the mortality due to juvenile factors, A.3 representing $L_c(x)$ or the constant mortality experienced by all age classes, and A.4 where $L_s(x)$ is the mortality due to senescent factors. Longevity (**Ω**) is used as the maximum recorded age of each species.

Flexibility in the survivorship curve is determined by constant parameters: a_1, a_2, a_3, b_1, and b_3 (Table A.1), which are based on species specific life history traits. However, when species specific information is not available, a surrogate representing similar life mortality throughout their life span is used as a replacement. For pinniped groups northern fur seals was used as a surrogate, where there is high mortality for young age classes and less mortality as seals age. Human survivorship was used for polar bears, as there are few to zero predators, lowering juvenile mortality (compared to other surrogates). Beluga and bowhead survivorship was calculated using monkey and human survivorship parameters with the monkey life history parameters having a slightly higher juvenile mortality. The natural mortality used in the model was taken as mortality averaged over all ages up to a max age (longevity) and was calculated as 1-the survivorship.

$$L(x) = L_j(x) * L_c(x) * L_s(x) \tag{A.1}$$

$$L_j(x) = exp[(-a_1/b_1) * 1 - exp(-b * x/\Omega)] \tag{A.2}$$

$$\mathrm{L_c(x)} = \exp[-\mathrm{a}_2 * \mathrm{x}/\Omega] \tag{A.3}$$

$$\mathrm{L_s(x)} = \exp(\mathrm{a}_3/\mathrm{b}_3) * 1 - \exp(\mathrm{b}_3 * \mathrm{x}/\Omega) \tag{A.4}$$

Table A.1: Survivorship curve parameters based on life histories of fur seals, monkeys, and humans as provided in Barlow and Boveng (1991:Table 2).

Species group	a_1	a_2	a_3	b_1	b_3
Northern Fur Seal	14.343	0.171	0.0121	10.259	6.6878
Old World Monkeys	30.430	0.000	0.7276	206.72	2.3188
Human (female)	40.409	0.4772	0.0047	310.36	8.0290

APPENDIX B: Bird Species Identified in the Model Area

Table B.1: Overview of bird species identified within the Beaufort Sea Shelf model area. Each species is designated as C (common), U (uncommon), R (rare) CA (casual), AC (accidental) by the Yukon Bird Club (2015) or as C (common) or R (rare) by Eckert et al. (2005) at Herschel Island. Species observed in Dickson and Gilchrist (2002) are also included in the table.
* denotes the species has been observed breeding on Herschel Island.

Common Name	**Scientific Name**	**Yukon Bird Club (2015)**	**Eckert (2005)**
American Golden-plover	*Pluvialis dominica*	U*	
American Kestrel	*Falco sparverius*	AC	
American Pipit	*Anthus rubescens*	C*	C
American Robin	*Turdus migratorius*	R*	
American Tree Sparrow	*Spizelloides arborea*	U	
American Wigeon	*Anas americana*	U	
Arctic Tern	*Sterna paradisaea*	R*	
Baird's Sandpiper	*Calidris bairdii*	C*	C
Bald Eagle	*Haliaeetus leucocephalus*	CA	
Bank Swallow	*Riparia riparia*	CA	
Barn Swallow	*Hirundo rustica*	CA	
Black Guillemot	*Cepphus grylle*	U*	C
Black Scoter	*Melanitta americana*	CA	
Black-bellied Plover	*Pluvialis squatarola*	R	
Black-legged Kittiwake	*Rissa tridactyla*	CA	
Bonaparte’s Gull	*Chroicocephalus philadelphia*	CA	
Brant	*Branta bernicla*	U*	
Buff-breasted Sandpiper	*Tryngites subruficollis*	R*	
Canada Goose	*Branta canadensis*	C*	C
Cliff Swallow	*Petrochelidon pyrrhonota*	CA	
Common Eider	*Somateria mollissima*	C*	C
Common Goldeneye	*Bucephala clangula*	CA	
Common Loon	*Gavia immer*	R	
Common Merganser	*Mergus merganser*	CA	
Common Raven	*Corvus corax*	U*	C
Common Redpoll	*Acanthis flammea*	U*	C
Common Ringed Plover	*Charadrius hiaticula*	CA	
Dark-eyed Junco	*Junco hyemalis*	CA	
Dunlin	*Calidris alpina*	CA	
Eastern Yellow Wagtail	*Motacilla tschutschensis*	CA	
Gadwall	*Anas strepera*	AC	
Glaucous Gull	*Larus hyperboreus*	CA*	C
Glaucous-winged Gull	*Larus glaucescens*	CA	R

Common Name	**Scientific Name**	**Yukon Bird Club (2015)**	**Eckert (2005)**
Golden Eagle	*Aquila chrysaetos*	CA	
Golden-crowned Sparrow	*Zonotrichia atricapilla*	AC	
Greater Scaup	*Aythya marila*	U	
Greater White-fronted Goose	*Anser albifrons*	C*	C
Green-winged Teal	*Anas carolinensis*	U*	
Gyrfalcon	*Falco rusticolus*	R	
Harlequin Duck	*Histrionicus histrionicus*	CA	
Harris's Sparrow	*Zonotrichia querula*	CA	
Herring Gull	*Larus argentatus*	R	C
Hoary Redpoll	*Acanthis hornemanni*	U*	C
Horned Grebe	*Podiceps auritus*	CA	
Horned Lark	*Eremophila alpestris*	U*	
Horned Puffin	*Fratercula corniculata*	CA	
Hudsonian Godwit	*Limosa haemastica*	AC	
King Eider	*Somateria spectabilis*	U	C
Lapland Longspur	*Calcarius lapponicus*	C*	C
Least Sandpiper	*Calidris minutilla*	R*	
Lesser Scaup	*Aythya affinis*	U	
Lesser Yellowlegs	*Tringa flavipes*	CA	
Long-billed Dowitcher	*Limnodromus scolopaceus*	U	
Long-tailed Duck	*Clangula hyemalis*	C*	C
Long-tailed Jaeger	*Stercorarius longicaudus*	C*	C
Mallard	*Anas platyrhynchos*	U*	
McKay's Bunting	*Plectrophenax hyperboreus*	AC	R
Merlin	*Falco columbarius*	R	
Mew Gull	*Larus canus*	CA	
Northern Flicker	*Colaptes auratus*	AC	
Northern Harrier	*Circus cyaneus*	U*	
Northern Hawk Owl	*Surnia ulula*	CA	
Northern Pintail	*Anas acuta*	C*	
Northern Shoveler	*Anas clypeata*	U*	
Northern Waterthrush	*Parkesia noveboracensis*	AC	
Northern Wheatear	*Oenanthe oenanthe*	CA*	
Pacific Loon	*Gavia pacifica*	U	C
Pacific Brant	*Branta bernicla*		
Parasitic Jaeger	*Stercorarius parasiticus*	U*	C
Pectoral Sandpiper	*Calidris melanotos*	C	C
Peregrine Falcon	*Falco peregrinus*	C*	C
Pomarine Jaeger	*Stercorarius pomarinus*	U*	
Red Phalarope	*Phalaropus fulicarius*	R	
Red-breasted Merganser	*Mergus serrator*	U	C
Red-necked Grebe	*Podiceps grisegena*	CA	

Common Name	**Scientific Name**	**Yukon Bird Club (2015)**	**Eckert (2005)**
Red-necked Phalarope	*Phalaropus lobatus*	U*	C
Red-necked Stint	*Calidris ruficollis*	AC	
Red-throated Loon	*Gavia stellata*	C*	C
Red-winged Blackbird	*Agelaius phoeniceus*	CA	
Rock Ptarmigan	*Lagopus muta*	U*	
Ross’s Gull	*Rhodostethia rosea*	AC	
Rough-legged Hawk	*Buteo lagopus*	C*	C
Ruddy Turnstone	*Arenaria interpres*	CA*	
Rusty Blackbird	*Euphagus carolinus*	CA	
Sabine’s Gull	*Xema sabini*	CA	
Sanderling	*Calidris alba*	R	
Sandhill Crane	*Grus canadensis*	C*	
Savannah Sparrow	*Passerculus sandwichensis*	C*	C
Say's Phoebe	*Sayornis saya*	CA	
Semipalmated Plover	*Charadrius semipalmatus*	C*	C
Semipalmated Sandpiper	*Calidris pusilla*	C*	C
Sharp-shinned Hawk	*Accipiter striatus*	AC	
Short-eared Owl	*Asio flammeus*	U*	C
Smith’s Longspur	*Calcarius pictus*	R*	
Snow Bunting	*Plectrophenax nivalis*	U*	C
Snow Goose	*Chen caerulescens*	U*	
Snowy Owl	*Bubo scandiacus*	U*	
Spotted Sandpiper	*Actitis macularius*	CA	
Stilt Sandpiper	*Calidris himantopus*	R	
Surf Scoter	*Melanitta perspicillata*	C	C
Thayer’s Gull	*Larus thayeri*	CA	
Thick-billed Murre	*Uria lomvia*	CA	
Tree Swallow	*Tachycineta bicolor*	CA	
Trumpeter Swan	*Cygnus buccinator*	AC	
Tundra Swan	*Cygnus columbianus*	C*	C
Varied Thrush	*Lxoreus naevius*	CA	
Western Meadowlark	*Sturnella neglecta*	AC	
Western Sandpiper	*Calidris mauri*	CA	
Whimbrel	*Numenius phaeopus*	R*	
White-crowned Sparrow	*Zonotrichia leucophrys*	U	
White-rumped Sandpiper	*Calidris fuscicollis*	R	
White-throated Sparrow	*Zonotrichia albicollis*	CA	
White-winged Scoter	*Melanitta deglandi*	C	C
Whooper Swan	*Cygnus cygnus*	AC	
Willow Ptarmigan	*Lagopus lagopus*	CA	
Wilson's Snipe	*Gallinago delicata*	R*	

Common Name	**Scientific Name**	**Yukon Bird Club (2015)**	**Eckert (2005)**
Wood Sandpiper	*Tringa glareola*	AC	
Yellow Warbler	*Setophaga petechia*	CA	
Yellow-billed Loon	*Gavia adamsii*	R	
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	AC	
Yellow-rumped Warbler	*Setophaga coronata*	CA	

APPENDIX C: Meso-zooplankton species as reported by sampling surveys

Table C.1: Summary of Meso-zooplankton species identified in the Beaufort Sea.

Taxa	Species	Source
Copepoda	*A. hudsonica*	Walkusz et al. (2010)
Copepoda	*A. longiremis*	Walkusz et al. (2010)
Copepoda	*Aetipeodis armata*	Walkusz et al. (2010)
Copepoda	*Aetideus armatus*	Walkusz et al. (2010)
Copepoda	*Bradyidius similis*	Walkusz et al. (2010)
Copepoda	*Chiridius obtusifrons*	Walkusz et al. (2010)
Copepoda	*Diaptomus sicilis*	Walkusz et al. (2010)
Copepoda	*Ephischura lacustris*	Walkusz et al. (2010)
Copepoda	*Ephischura nevadensis*	Walkusz et al. (2010)
Copepoda	*Eucalanus bungii*	Walkusz et al. (2010)
Copepoda	*Eurytemora americana*	Walkusz et al. (2010)
Copepoda	*Eurytemora herdmanii*	Walkusz et al. (2010)
Copepoda	*Eurytemora hirundoides*	Walkusz et al. (2010)
Copepoda	*Eurytemora pacifica*	Walkusz et al. (2010)
Copepoda	*Eurytemora rabotti*	Walkusz et al. (2010)
Copepoda	*Eurytemora thompsonii*	Walkusz et al. (2010)
Copepoda	*Gaetanus brevispinus*	Walkusz et al. (2010)
Copepoda	*Paraheterrorhabdus compactus*	Walkusz et al. (2010)
Copepoda	*Paraheterrorhabdus norvegicus*	Walkusz et al. (2010)
Copepoda	*Jaschnovia brevis*	Walkusz et al. (2010)
Copepoda	*Jaschnovia tolli*	Walkusz et al. (2010)
Copepoda	*Limnocalanus johanseni*	Walkusz et al. (2010)
Copepoda	*Microcalanus sp.*	Walkusz et al. (2010)
Copepoda	*Paraeuchaeta glacialis*	Walkusz et al. (2010)
Copepoda	*Paraeuchaeta norvegica*	Walkusz et al. (2010)
Copepoda	*Paraeuchaeta sp.*	(Stasko et al., 2016)
Copepoda	*Scaphocalanus acrocephalus*	Walkusz et al. (2010)
Copepoda	*Scolecithricella minor*	Walkusz et al. (2010)
Copepoda	*Spinocalanus spp.*	Walkusz et al. (2010)
Copepoda	*Temora spp.*	Walkusz et al. (2010)
Copepoda	*Triconia (Oncea) borealis*	Walkusz et al. (2010)
Copepoda	*Podon leuckarti*	Walkusz et al. (2010)
Pteropoda	*Clione limacina*	Stasko et al. (2017)
Pteropoda	*Limacina helicina*	Stasko et al. (2017)
Appendicularia	*Fritillaria borealis*	Walkusz et al. (2010)
Appendicularia	*Okiopleura vanhoeffeni*	Walkusz et al. (2010)

APPENDIX D: Seal, Fish and Bird Harvest

Table D.1: Number of fish caught, by species as summarized from the Inuvialuit Harvest Survey. Communities include Aklavik, Ulukhaktok (Holman), Inuvik, Paulatuk, Sachs Harbour, and Tuktoyaktuk. Numbers presented are based on hunter survey responses (The Joint Secretariat, 2003)

Group	**Species**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**
7	Char (Arctic)	7397	9726	10291	7385	12215	10735	12698	14616	10702	7848
7	Char (Arctic/Dolly Varden)	8058	10837	10952	7734	12965	11976	15440	15132	12756	8865
7	Char (Dolly Varden)	661	1111	661	349	750	1241	2742	516	2054	1017
7	Char (unspec.)	12484	0	0	0	0	2	0	0	0	0
7	Totals	28600	21674	21904	15468	25930	23954	30880	30264	25512	17730
8	Cisco (unspec.)	92866	14496	17456	74266	31576	31030	21906	17894	17512	31966
8	Whitefish (Broad)	90770	33894	40130	56804	50520	39362	46076	42216	30264	33638
8	Whitefish (Lake)	49316	24178	18238	20040	16272	6200	5088	10246	8218	4782
8	Whitefish (unspec.)	4378	13950	14324	0	0	4	0	0	4	816
8	Totals	237330	86518	90148	151110	98368	76596	73070	70356	55998	71202
9	Grayling (Arctic)	22	44	10	42	82	208	106	120	76	12
9	Inconnu	12262	13026	16132	16736	10720	7208	6898	8632	7378	7678
9	Totals	12284	13070	16142	16778	10802	7416	7004	8752	7454	7690
10	Herring (Lake)	0	80	0	0	0	0	0	0	80	510
10	Herring (Pacific)	15274	14410	11298	14232	11040	3414	10530	16474	11176	10242
10	Herring/Cisco (unspec.)	5008	17680	38666	2074	402	0	0	0	0	118
10	Totals	20282	32170	49964	16306	11442	3414	10530	16474	11256	10870
11	Cod (Arctic)	0	0	0	12	4	0	308	174	346	6
11	Cod (unspec.)	2	0	0	40	2	20	0	0	0	18
11	Totals	2	0	0	52	6	20	308	174	346	24
13	Burbot	24546	13116	13396	5812	5216	3746	1668	1582	2808	2034
13	Cod (Saffron)	80	290	44	1170	0	146	22	52	202	192
13	Flounder	18	2	152	526	104	152	600	2628	6	364
13	Totals	24626	13406	13440	6982	5216	3892	1690	1634	3010	2226
14	Sculpin (fourhorn)	2	30	100	224	40	40	250	24	0	2
15	Fish (unspec.)	700	0	0	4	0	0	0	0	700	0
15	Pike (Northern)	14104	11544	6866	5204	3926	4164	2250	1558	1332	524
15	Sucker (unspec.)	0	98	18	0	0	60	120	4	0	0
15	Totals	14804	11642	6884	5208	3926	4224	2370	1562	2032	524
-	Char (Arctic Land-locked)	376	218	797	468	366	20	206	294	52	142
-	Char (Land-locked Arctic)	0	0	43	0	0	0	0	0	0	0
-	Trout (Lake)	6808	6066	9756	11722	12532	13052	11572	11258	9726	9252
-	Trout (unspec.)	0	72	122	0	0	0	0	0	0	0

Table D.2 Number of birds caught by species as summarized from the Inuvialuit Harvest Survey. Communities include Aklavik, Ulukhaktok (Holman), Inuvik, Paulatuk, Sachs Harbour, and Tuktoyaktuk. Numbers presented are based on hunter survey responses (The Joint Secretariat, 2003).

Species	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**
Brant	2032	442	396	1828	828	450	934	1094	732	1046
Canvasback	66	68	78	64	10	8	2	0	14	36
Crane (Sandhill)	24	24	28	20	26	30	42	44	18	40
Duck (unspec.)	190	40	0	0	0	0	14	0	0	0
Eider (Common)	0	0	0	0	0	2	0	0	0	0
Eider (unspec.)	10026	7522	4788	7818	9032	3642	5454	6590	5862	4890
Goldeneye (unspec.)	28	0	0	14	0	2	6	6	44	32
Goose (Canada)	1656	664	1128	1170	1198	1280	1758	1162	1436	1700
Goose (Greater White-fronted)	5662	2172	3592	2818	3898	2788	2964	2518	3558	5244
Goose (Ross)	0	4	4	2	0	36	0	12	6	16
Goose (Snow)	14156	7842	11278	11684	17570	9158	10792	11384	9686	13860
Goose (unspec.)	46	0	0	20	10	0	0	0	0	0
Loon (Arctic)	22	30	40	32	0	0	68	64	162	40
Loon (Common)	12	18	8	0	0	0	2	0	0	6
Loon (unspec.)	14	10	4	0	0	0	0	0	2	6
Loon (Yellow-billed)	4	6	8	12	46	36	8	4	36	36
Mallard	1142	530	382	366	256	164	184	308	400	766
Merganser (unspec.)	36	6	0	4	40	48	0	20	0	0
Oldsquaw	760	236	106	102	22	78	70	52	4	74
Owl (Snowy)	0	0	0	0	26	66	0	0	4	2
Pintail (Northern)	536	194	98	20	50	62	26	52	24	138
Ptarmigan (unspec.)	5268	2492	1336	1172	1876	2188	1080	1056	2520	1512
Scaup (unspec.)	196	128	18	12	88	26	44	12	0	22
Scoter (unspec.)	814	422	684	278	162	212	232	136	200	202
Shoveler	32	24	14	2	0	14	10	8	20	0
Swan (unspec.)	144	130	176	156	274	308	298	290	398	356
Teal (Green-winged)	12	6	14	0	6	0	0	0	0	2
Wigeon (American)	1612	654	600	206	132	360	132	440	534	716
Totals	44490	23664	24780	27800	35550	20958	24120	25252	25660	30742

APPENDIX E: Diets of all species groups in the Ecopath model

Table E.1 Summary of all diet inputs used in the balanced Ecopath model

	Prey \ predator	Polar Bear	Beluga	Bowhead	Ringed Seal	Bearded Seal	Birds	Char & Dolly Varden
1	Polar Bear							
2	Beluga	0.03						
3	Bowhead	0.02						
4	Ringed Seal	0.85						
5	Bearded Seal	0.1						
6	Birds							
7	Char & Dolly Varden		0.01		0.1	0.05	0.05	
8	Ciscos & Whitefish		0.16		0.08	0.04	0.06	0.01
9	Salmonids					0.04	0.05	
10	Herring & Smelt		0.07		0.03	0.01	0.1	0.2
11	Arctic & Polar Cods		0.45		0.12	0.11	0.11	0.01
12	Capelin		0.05		0.03	0.02	0.02	0.01
13	Flounder & Benthic Cods		0.02		0.05	0.1	0.03	0.09
14	Small Benthic marine Fish		0.1		0.09	0.1	0.09	0.05
15	Other Fish		0.02		0.01	0.03	0.01	0.01
16	Arthropods				0.09	0.25	0.07	0.15
17	Bivalves						0.02	0.05
18	Echinoderms				0.05	0.09	0.02	0.02
19	Molluscs				0.05	0.06	0.02	0.02
20	Worms				0.05	0.05	0.03	0.05
21	Other Benthos				0.05	0.05	0.02	0.02
22	Jellies						0.02	
23	Macro-Zooplankton		0.05	0.12	0.1		0.05	0.03
24	Other Calanus sp. (Pseudo)		0.02	0.2	0.03		0.08	0.05
25	Lg Copepods (Calanus)		0.03	0.5	0.05		0.1	0.2
26	Other Meso-Zooplankton		0.02	0.13	0.02		0.05	0.03
27	Micro-Zooplankton			0.05				
28	Producers >5um							
29	Producers <5um							
30	Ice Algae							
31	Benthic Plants							
32	Pelagic Detritus							
33	Benthic Detritus							
34	Import							

Table E.1 Continued on the next page

Table E.1 (Continued): Summary of all diet inputs used in the balanced Ecopath model

	Prey \ predator	**Ciscos & Whitefish**	**Salmonids**	**Herring & Smelt**	**Arctic & Polar Cods**	**Capelin**	**Flounder & Benthic Cods**	**Small Benthic marine Fish**
1	Polar Bear							
2	Beluga							
3	Bowhead							
4	Ringed Seal							
5	Bearded Seal							
6	Birds							
7	Char & Dolly Varden							
8	Ciscos & Whitefish		0.1	0.03				
9	Salmonids				0.02	0.02		
10	Herring & Smelt	0.06			0.2	0.2	0.02	
11	Arctic & Polar Cods		0.12				0.02	
12	Capelin		0.03				0.01	
13	Flounder & Benthic Cods			0.02			0.01	0.01
14	Small Benthic marine Fish	0.02	0.05	0.02			0.09	0.03
15	Other Fish	0.02	0.05				0.02	0.03
16	Arthropods	0.1	0.31	0.05	0.05	0.05	0.2	0.21
17	Bivalves						0.15	0.1
18	Echinoderms	0.03		0.02	0.02	0.02	0.05	0.1
19	Molluscs	0.02		0.02	0.02	0.02	0.1	0.1
20	Worms	0.05	0.05	0.05	0.04	0.04	0.17	0.15
21	Other Benthos		0.02	0.01	0.01	0.01	0.05	0.08
22	Jellies							0.005
23	Macro-Zooplankton	0.05	0.03	0.2	0.07	0.07	0.02	0.03
24	Other Calanus sp. (Pseudo)	0.1	0.02	0.05	0.1	0.1	0.02	0.02
25	Lg Copepods (Calanus)	0.3	0.15	0.2	0.4	0.4	0.05	0.03
26	Other Meso-Zooplankton	0.1	0.02	0.05	0.05	0.05	0.02	0.05
27	Micro-Zooplankton	0.05		0.05				0.03
28	Producers >5um	0.07	0.05	0.1	0.02	0.02		0.025
29	Producers <5um			0.1				
30	Ice Algae	0.03		0.03				
31	Benthic Plants							
32	Pelagic Detritus							
33	Benthic Detritus							
34	Import							

Table E.1 Continued on the next page

Table E.1 (Continued): Summary of all diet inputs used in the balanced Ecopath model

	Prey \ predator	Other Fish	Arthropods	Bivalves	Echinoderms	Molluscs	Worms	Other Benthos
1	Polar Bear							
2	Beluga							
3	Bowhead							
4	Ringed Seal							
5	Bearded Seal							
6	Birds							
7	Char & Dolly Varden							
8	Ciscos & Whitefish							
9	Salmonids							
10	Herring & Smelt							
11	Arctic & Polar Cods							
12	Capelin							
13	Flounder & Benthic Cods							
14	Small Benthic marine Fish							
15	Other Fish							
16	Arthropods	0.13			0.04		0.01	0.02
17	Bivalves	0.07	0.02		0.02			
18	Echinoderms	0.04	0.05				0.02	0.01
19	Molluscs	0.04	0.05		0.05		0.02	0.01
20	Worms	0.05	0.05		0.05			0.03
21	Other Benthos	0.04	0.03		0.05		0.01	
22	Jellies	0.01						
23	Macro-Zooplankton	0.05						
24	Other Calanus sp. (Pseudo)	0.04						
25	Lg Copepods (Calanus)	0.3						
26	Other Meso-Zooplankton	0.05						
27	Micro-Zooplankton	0.05						
28	Producers >5um	0.1		0.02				
29	Producers <5um	0.01		0.03				
30	Ice Algae	0.02		0.1				
31	Benthic Plants		0.03		0.02	0.1	0.01	0.02
32	Pelagic Detritus		0.1	0.1	0.1	0.15	0.13	0.16
33	Benthic Detritus		0.67	0.75	0.67	0.75	0.8	0.75
34	Import							

Table E.1 Continued on the next page

Table E.1 (Continued): Summary of all diet inputs used in the balanced Ecopath model

	Prey \ predator	Jellies	Macro Zoo-plankton	Other Calanus sp. (Pseudo)	Lg Copepods (Calanus)	Other Meso Zoo-plankton	Micro-Zooplankton
1	Polar Bear						
2	Beluga						
3	Bowhead						
4	Ringed Seal						
5	Bearded Seal						
6	Birds						
7	Char & Dolly Varden						
8	Ciscos & Whitefish						
9	Salmonids						
10	Herring & Smelt						
11	Arctic & Polar Cods						
12	Capelin						
13	Flounder & Benthic Cods						
14	Small Benthic marine Fish						
15	Other Fish						
16	Arthropods						
17	Bivalves						
18	Echinoderms						
19	Molluscs						
20	Worms						
21	Other Benthos						
22	Jellies						
23	Macro-Zooplankton		0.03				
24	Other Calanus sp. (Pseudo)	0.05	0.1		0.05	0.05	
25	Lg Copepods (Calanus)	0.05	0.2				
26	Other Meso-Zooplankton	0.05	0.15	0.05		0.03	
27	Micro-Zooplankton	0.05	0.02	0.05	0.25	0.24	
28	Producers >5um	0.15	0.15	0.3	0.15	0.25	
29	Producers <5um	0.55	0.05	0.4	0.05	0.18	0.85
30	Ice Algae		0.15	0.1	0.4	0.15	0.05
31	Benthic Plants						
32	Pelagic Detritus	0.1	0.15	0.1	0.03	0.1	0.05
33	Benthic Detritus				0.07		0.05
34	Import						