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Preliminary Mass-balance Food Web Model of the Eastern Chukchi Sea

by
G. A. Whitehouse

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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ABSTRACT

A preliminary mass-balance food web model was developed for the eastern Chukchi Sea continental shelf, describing the trophic structure and function of this ecosystem. The model was developed with the Ecopath framework and provides an annual snapshot of the food web structure in the eastern Chukchi Sea. Species were represented individually where data permitted or were aggregated into functional groups with species of similar diet, life history, and habitat requirements where data were sparse. The model consists of 52 living functional groups, two detrital compartments, and nine subsistence harvest groups. The purpose of this report is to document the construction of this trophic model and the development of model input parameters for all functional groups; including literature and data sources, data quality, model assumptions and limitations, any parameter adjustments, and parameter estimation methods.

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Figure 1.-- The Chukchi Sea, with the model area filled in with hatched lines. The model area is bounded by the United States-Russia Convention Line in the west, Pt. Barrow to the east, Bering Strait to the south, and a combination of the 70 m isobath and U.S. Exclusive Economic Zone (EEZ, 200-mile limit) in the north. Nearshore, the model is bounded by the 20 m isobath. 3

INTRODUCTION

Evidence of climate impacts on Arctic marine ecosystems is accumulating (Wassmann et al. 2011) and Arctic marine ecosystems face additional pressures that may accompany increased human activities due to improved access following reductions in sea ice cover, such as petroleum extraction, increased shipping, and commercial fisheries. In recognition of the changing climatic conditions in the Arctic and the potential for development of new commercial fisheries, the Arctic Fishery Management Plan (FMP) (NPFMC 2009) was implemented by the National Marine Fisheries Service on 3 December 2009 (U.S. Fed. Reg. V. 74 No. 211). The Arctic FMP prohibits the development of new commercial fisheries until sufficient information to support the implementation of a sustainable fishery becomes available (NPFMC 2009). The continental shelves of the Alaskan Arctic also contain large petroleum reserves (Gautier et al. 2009) and industrial activities related to petroleum extraction are expected to increase in the near future (U.S. Dep. Int. 2010, Shell Gulf of Mexico Inc 2011, U.S. Dep. Int. 2011). Commensurate with growing anthropogenic activity in the Arctic, is a growing need to provide stakeholders, resource managers, and decision makers with sufficient amounts of information to support an ecosystem based approach to managing Arctic resources (Clement et al. 2013).

Ecosystem models, such as Ecopath with Ecosim (Christensen and Pauly 1992, Walters et al. 1997), can be an effective tool in support of ecosystem-based fisheries management (Hollowed et al. 2000, Plagányi and Butterworth 2004, Gaichas et al. 2010, Link et al. 2012). Ecopath with Ecosim (EwE) is a mass balance food web model that describes the web of trophic interactions between species in an ecosystem. Scientists in the Resource Ecology and Ecosystem Modeling (REEM) Program at the Alaska Fisheries Science Center (AFSC) have previously developed Ecopath mass-balance food web models for the eastern Bering Sea, Gulf of Alaska, and Aleutian Islands (Aydin et al. 2007). These food web models of large marine ecosystems (LME) in Alaska are updated frequently and regularly contribute to fishery management advice through contributions to annual Stock Assessment and Fishery Evaluation (SAFE) reports (Zador 2011).

In support of an ecosystem-based approach to managing living marine resources in the Alaska Arctic, a preliminary mass-balance food web model has now been developed for the eastern Chukchi Sea (Whitehouse 2011). This model describes the food web of the continental shelf waters of the eastern Chukchi Sea between 20 and 70 m depth (Fig. 1). The model area, estimated at 192,054 km², is bounded by the U.S.-Russian Convention Line to the west, Bering Strait in the south, Pt. Barrow to the east, and a combination of the U.S. Exclusive Economic Zone (EEZ, 200-mile limit) and 70 m isobath in the north.

The development of a mass-balance food web model and the necessary parameters contained within for each functional group requires the synthesis of a large body of literature, crossing disciplines, and taxa from all trophic levels. Many model parameters can be taken directly from the literature while others require adjustment in order to accommodate the spatial and temporal restrictions of a model. Still other parameters may need to be calculated following empirical relationships. This report details the construction of the eastern Chukchi Sea mass-balance food web model, the development of all necessary parameters, and the model balancing process. In an effort to provide an ecosystem-scale view of the Chukchi Sea food web, this report attempts to summarize presently available data and rates for organisms on all trophic levels in this ecosystem. As a result this report may also aid in identification of important data gaps.

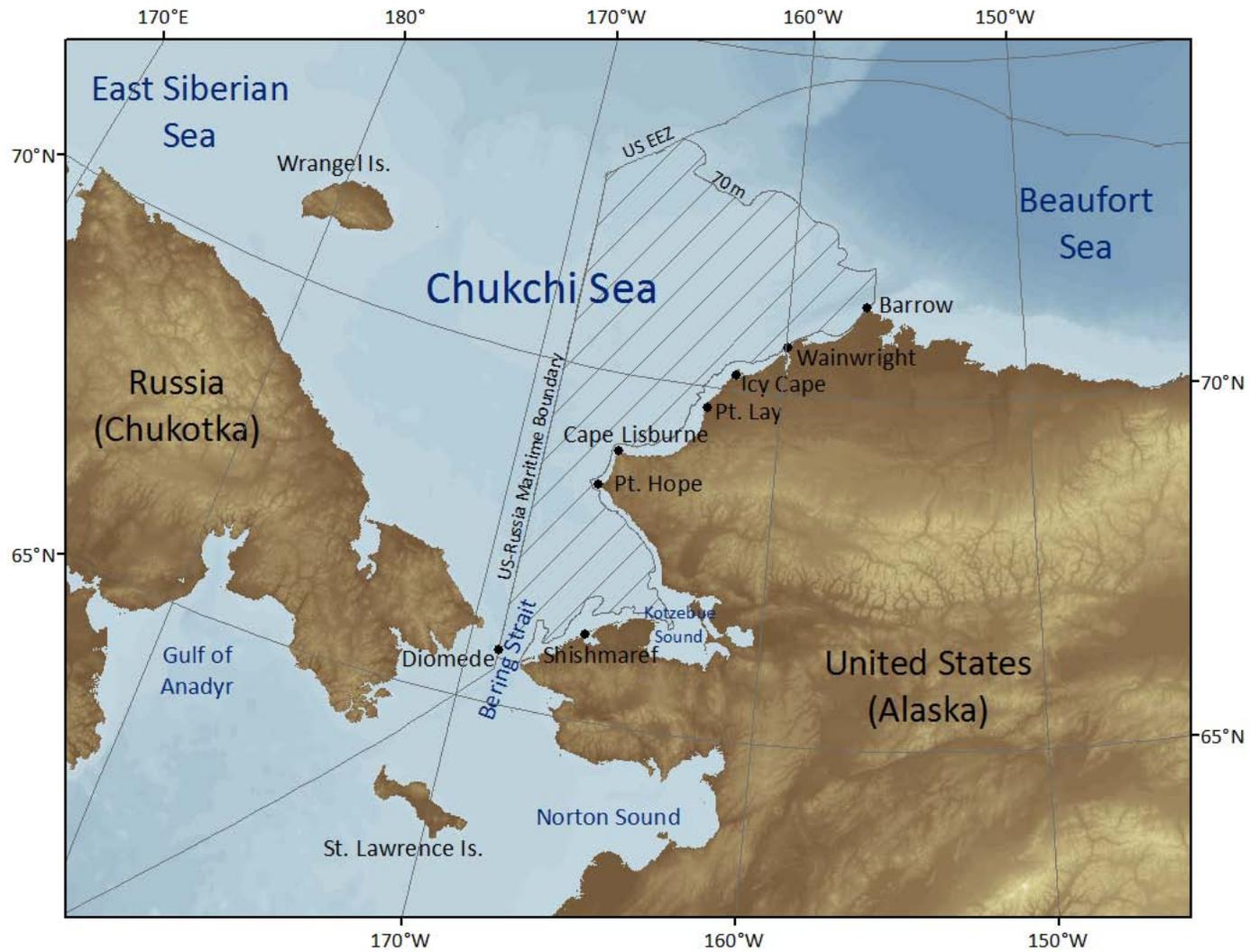


Figure 1.-- The Chukchi Sea, with the model area filled in with hatched lines. The model area is bounded by the United States-Russia Convention Line in the west, Pt. Barrow to the east, Bering Strait to the south, and a combination of the 70 m isobath and U.S. Exclusive Economic Zone (EEZ, 200-mile limit) in the north. Nearshore, the model is bounded by the 20 m isobath.

METHODS

The food web model was developed for the eastern Chukchi Sea continental shelf using the Ecopath modeling framework (Ecopath with Ecosim (EwE) version 6.2; Christensen et al. 2008). Ecopath is a biomass compartment model describing the trophic flows between groups in a food web. Each compartment or model group represents a species or functional group of multiple species with similar diet, life history, and habitat requirements. Under equilibrium conditions this relationship is expressed as:

$$B_i \left(\frac{P}{B}\right)_i * EE_i = \sum_j B_j * \left(\frac{Q}{B}\right)_j * DC_{ij} - C_i , \quad (1)$$

where B is the biomass density (t km^{-2}) in wet weight, P/B (yr^{-1}) is the production to biomass ratio, Q/B (yr^{-1}) is the consumption to biomass ratio, DC_{ij} is the average proportion of prey i in the diet of predator j , and C_i (t km^{-2}) is the fishery removal of group i . Ecotrophic efficiency (EE) is the proportion of total production that is consumed by predators or removed by fisheries included in the model and must be ≤ 1 . Mass-balance is ensured by solving this linear equation for one missing parameter for each functional group. Typically B , P/B , Q/B , DC , and C are entered and the equation is solved for EE. When a reliable estimate for a model parameter is unavailable, EE can be set to an arbitrary value and the equation solved for the missing parameter (usually B). Setting EE to an arbitrary value and solving for B is commonly referred to as a “top-down balance” because it is estimating prey biomass based on estimated predator demand and fishery removals. All top-down balancing was done with an assumed EE of 0.8, which implies that the model explains 80% of the total mortality experienced by these groups, via consumption by predators or fishery removals. Other sources of mortality not explicitly represented in the model ($1-EE_i$) include disease, starvation, senescence, and possible outmigration. This non-predation mortality is not generally measurable; a uniform percentage of 20% for this other “unexplained” mortality allows a standardized analysis and is generally consistent with dynamic fits of unexplained mortality across a

range of species (Aydin et al. 2007). If EE is set closer to one, the biomass estimate would decrease, and if set closer to zero the estimate would increase. EE is difficult to accurately measure in nature, but it is generally thought to be close to one for groups subject to predation and exploitation and closer to zero for top predators who experience little predation or exploitation (Christensen et al. 2005).

This model of the eastern Chukchi Sea includes 52 living functional groups, two detrital compartments (pelagic and benthic), and nine marine mammal subsistence harvest groups that were parameterized separately. The model is neither temporally nor spatially dynamic, but rather presents an annual average snapshot of the food web that is spatially homogeneous. Many marine mammals and seabirds occupy the model area seasonally or make limited use of the model area as a migratory corridor to other wintering or summering grounds. For these groups, biomass estimates were reduced accordingly to represent time spent in the model area. The base time period for the model is the late 1980s and early 1990s as much of the data needed to parameterize the model are available from this time period.

The parameter estimates and/or data used to calculate parameter estimates are graded for quality and uncertainty based upon the data source, collection methodology, time coverage, spatial coverage, and taxonomy following the methods of Aydin et al. (2007). These data grades are based on the data “pedigree” originally described by Christensen et al. (2005), where each data pedigree (or grade) corresponds to a prescribed confidence interval based on the data origin. The confidence intervals used here are taken from Aydin et al. (2003). The pre-defined list of data grades and corresponding confidence intervals for each of the basic model inputs, B, P/B, Q/B, DC, and C, are included in Appendix C.

Ecosim is the temporal dynamic counterpart of Ecopath included in the EwE software package. Ecosim allows the user to observe changes in functional group biomasses and trophic interactions in time by simulating the effects of external forcing events, changes in mortality, or changes in fishing pressure. The balanced Ecopath model outputs may be used as the initial model inputs in Ecosim analyses. Though the Ecopath model presented here lacks the necessary time series data needed to calibrate Ecosim for quantitative predictions, the Ecopath model outputs can still be used with Ecosim to perform simple perturbation analyses and to make qualitative evaluations of directional relationships (biomass increases

or decreases) within the food web. The data pedigree and associated confidence intervals included here can be used as prior probability distributions for future Ecosim experiments and sensitivity analyses.

RESULTS and DISCUSSION

Detailed model results and estimated parameters are presented in the appendices and appendix tables. Appendix A provides detailed descriptions of parameter (B, P/B, Q/B, DC, C) development for all functional groups, including the data sources, any parameter adjustments, data pedigree, and the diet matrix. All of the basic model parameters (B, P/B, Q/B, EE, C, and GE [growth efficiency]) and trophic level estimates are presented in Table A1 of Appendix A. The complete diet matrix can be viewed in Table A2 of Appendix A. Appendix B provides further details on specific parameter estimation techniques when values could not be taken directly from the literature. Appendix C lists the criteria for data quality grading and the associated confidence intervals. The data pedigree for all model parameters can be viewed in Table C3 of Appendix C.

The eastern Chukchi Sea is data poor when compared with other large marine ecosystems in Alaska, such as the eastern Bering Sea which is subject to annual NMFS trawl surveys. However, sufficient data or literature estimates were available to inform most model parameters. We attempted to specify biomass density for every functional group. Of the 52 living functional groups, we had to top-down balance biomass density for 16 of them. This was primarily the result of inadequate survey information to determine biomass or groups that are poorly sampled by trawl surveys. Estimates of P/B were input to the model for all groups. P/B was frequently available in the literature or was calculated following published empirical relationships. Q/B estimates were entered into the model for most model groups or were calculated by the model with an assumed production/consumption ratio (P/Q, also known as growth efficiency, GE). The diet compositions of all mammal, seabird, and invertebrate groups were acquired from published and unpublished sources including other food web models. A limited number of fish diet studies were available for the eastern Chukchi Sea; however, most lack the quantitative detail

required for a mass balance food web model. Alternatively, fish diets were obtained from quantitative diet studies conducted in the neighboring eastern Bering Sea by scientists at the Alaska Fisheries Science Center (<http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm>).

The primary diagnostic tool used to achieve mass balance was to identify groups with EE values greater than one, which implies that the loss rates of these groups exceeded production rates. Input data for those groups are then necessarily adjusted to balance the model. Groups with the highest initial EE values are balanced first before proceeding to groups with lower EE values in excess of one. For each group with an EE value in excess of one, data with low quality grades are considered for adjustment first before proceeding to data with higher quality grades.

During initial attempts to balance the model most of the fish functional groups, with the exception of large-mouth flatfish, walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and salmonids, had EE values greater than one with initial parameter inputs. The initial estimates of biomass density for fish groups were calculated from the catch data of a single bottom trawl survey conducted in the northeastern Chukchi Sea during the summer of 1990. After reviewing the input parameters for all unbalanced fish groups, the most likely cause of this misbalance was determined to be widespread underestimation of fish biomass in the trawl survey. An underestimation of biomass density by the survey derived estimates may reflect low catchability of some groups to bottom-trawl gear, spatial limitations of survey coverage, patchy fish distribution, and high interannual variation in fish abundance (Barber et al. 1997). To correct this imbalance, a top-down balance was performed resulting in biomass density estimates that were considerably larger than those derived from the trawl survey data.

A top-down balance was also used for several invertebrate groups for which adequate estimates of biomass density were unavailable. They include miscellaneous crabs, shrimps, cephalopods, miscellaneous crustaceans, copepods, other zooplankton, and pelagic and benthic microbes. Region-specific biomass density estimates for these functional groups were unavailable in the literature and these groups are thought to be poorly sampled or not sampled at all by trawl surveys.

Ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) were both out-of-balance ($EE > 1$) with initial model inputs. A review of the predation mortality inflicted on these two species revealed they were experiencing heavy predation pressure from Pacific walrus (*Odobenus rosmarus*). Consumption of seals by Pacific walrus has been noted through direct observation and from stomach contents in the northern Bering Sea and western Chukchi Sea (Fay 1982, Lowry and Fay 1984). It is unclear if the seals were taken by predation and most are thought to have been preyed upon as carrion (Fay 1982). To bring the two seal species back into balance ($EE \leq 1$), the seal portion of the Pacific walrus diet was reduced from 3% to 0.1%. The portion of the Pacific walrus diet removed from seals was reallocated to their primary prey item, bivalves.

Benthic detritus was also out of balance with an EE of 2.29. This misbalance resulted from high predation on benthic detritus by abundant benthic invertebrates coupled with insufficient flow of material into the benthic detrital pool. Phytoplankton is the greatest source of detritus in this model and phytoplankton was initially top-down balanced ($EE = 0.8$). Phytoplankton in the water column of the eastern Chukchi Sea experience low predation pressure from micro- (Sherr et al. 2009) and mesozooplankton (Cooney and Coyle 1982, Coyle and Cooney 1988, Campbell et al. 2009), permitting much of this organic content to be advected downstream or to settle to the sea floor where it becomes available to support the benthic food web (Walsh et al. 1989, Shuert and Walsh 1993, Grebmeier et al. 1995, Sakshaug 2004, Cooper et al. 2009). Top-down balancing of phytoplankton resulted in a conservative estimate of phytoplankton biomass, the minimum amount required to satisfy the trophic demands of its predators. Benthic detritus was brought back into balance with two model adjustments, first the detrital fate of phytoplankton was tilted in favor of benthic detritus (70%) over pelagic detritus (30%). This adjustment is consistent with previous studies and modeling exercises that have correlated primary productivity in the water column with high benthic biomass (Grebmeier et al. 1988, Grebmeier and McRoy 1989, Grebmeier 1993, Shuert and Walsh 1993, Walsh et al. 2005). Second, we incrementally increased the biomass of phytoplankton to the lowest level that would bring benthic detritus back into balance. This increased the phytoplankton biomass density estimate from the initial top-down

balanced value of 2.91 to 34. In combination with the phytoplankton P/B of 75, this was equivalent to an annual primary production of $170 \text{ g C m}^{-2} \text{ yr}^{-1}$, which, though high, falls within a range of values reported in the literature (e.g., Sakshaug 2004).

This food web model is the first attempt to describe the trophic structure and material flows of the eastern Chukchi Sea food web with an Ecopath trophic mass balance model. It represents just one of many possible mass-balanced states and could be improved in the future with updated parameters and data specific to the study area. Several assumptions and parameter adjustments were required to achieve mass balance, but despite these limitations this model provides an instructive broad scale view of this ecosystem and is a step forward in developing a baseline understanding of the eastern Chukchi Sea food web. The constraint of mass balance requires the reconciliation of parameter estimates for biomass, production, consumption, and diet composition for functional groups on all trophic levels. The balancing process highlighted instances where these parameters were not compatible, and in combination with the data pedigree can aid in the identification of data gaps and provide direction for future research.

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APPENDICES

Appendix A Functional Group Descriptions and Data Sources

Cetaceans

Beluga (*Delphinapterus leucas*) – Both the Chukchi Sea and Beaufort Sea stocks of belugas are thought to overwinter in the Bering Sea along the ice edge and among the pack ice in leads and polynyas. During spring when the ice begins to fracture and leads form, belugas from both stocks begin a northward migration through the Bering Strait and into the Chukchi Sea. Belugas from both stocks follow regularly occurring nearshore leads between Cape Krusenstern to Pt. Hope (Frost et al. 1983) and from Pt. Hope and Pt. Barrow (Moore et al. 1993). At Pt. Barrow, whales from the Beaufort stock turn east following another set of leads the rest of the way into the Beaufort Sea towards the MacKenzie Delta area (Moore et al. 1993). The Beaufort Sea stock is assumed to migrate through the Chukchi Sea quickly during spring migration as long as the ice permits. The Chukchi Sea stock migrates to bays and lagoons along the Alaskan coast where they molt, calve, and breed (Frost et al. 1983). Belugas from Kasegaluk Lagoon fitted with satellite transmitters indicate that following their brief stay in shallow water the belugas migrate north into dense pack ice (ice coverage > 90%) over deep continental slope waters and beyond, over the Arctic Basin as far as 80°N (Suydam 2009). Migrations into dense ice coverage (> 90%) over the deep Arctic Ocean basin has also been observed in the Beaufort Sea stock (Richard et al. 2001). In the fall several whales from the Beaufort Sea stock have been observed migrating far offshore north of 72°N (Clarke et al. 1993) and tracked migrating to the western Chukchi Sea (Richard et al. 2001).

Based on aerial surveys conducted between 1989 and 1991, Frost et al. (1993) estimated the minimum size of the eastern Chukchi Sea stock to be 1,200. Allen and Angliss (2010) corrected this count for animals that were diving and not visible at the time of survey, and for animals missed because of small size and dark coloration, resulting in a corrected estimate of 3,710. This estimate is still

considered to be the most reliable for this population (Allen and Angliss 2010). The minimum population estimate for the Beaufort Sea stock is 32,453 (Allen and Angliss 2010). Because both populations use the Chukchi Sea, the population estimates are combined yielding a total estimate of 36,163. The Beaufort Sea stock passes through rather quickly (estimated < 2 weeks) and the Chukchi Sea stock only appears to stop in shallow water long enough to molt, calve, and move on to deeper water off the continental shelf. To scale this total estimate to an annual average occupancy the total estimate was multiplied by their approximate annual residence time in the Chukchi Sea, estimated as 2 weeks, to migrate north and 2 weeks to migrate south. The resulting equation and model estimate is $36,163 \times (4/52) = \sim 2,782$. Multiplying by the mean body mass of an adult beluga from these two stocks (800 kg; Hunt et al. 2000) yields a biomass estimate of 2,225 t, or $1.16 \times 10^{-2} \text{ t km}^{-2}$.

A reliable estimate of maximum net productivity is currently unavailable for both the eastern Chukchi Sea and Beaufort Sea stocks of belugas (Allen and Angliss 2010). An estimated P/B for belugas in the eastern Bering Sea was previously developed by Aydin et al. (2007) using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991) (for details see Marine Mammal Production Rates in Appendix B this document). Belugas are susceptible to predation by polar bears (*Ursus maritimus*) and killer whales (*Orcinus orca*) throughout their lives. A monkey life-history surrogate was used for eastern Bering Sea belugas, which assumes a relatively constant mortality rate across juvenile, adult, and senescent periods. Belugas taken in the subsistence harvest at Pt. Lay, Alaska, were primarily between the ages of 6 and 30 for males, and 11 and 30 for females, with older individuals also present (Suydam 2009). The monkey life history surrogate was combined with an assumed longevity of 30 years to produce an estimated P/B of 0.112 (Aydin et al. 2007). The estimate of P/B for eastern Bering Sea belugas is used here for belugas in the Chukchi Sea.

The Q/B of belugas was calculated from daily caloric requirements, estimated following the methods of Perez et al. (1990), and scaling up to an annual rate. This resulted in a Q/B of 14.504 or a daily intake of about 31.8 kg.

The food habits of belugas in the eastern Chukchi Sea are not well known. The limited available diet data indicate they primarily prey on fish (~90%) while in the eastern Chukchi Sea and secondarily prey on cephalopods and shrimp (~10%) (Seaman et al. 1982). The fish portion of their diet was allocated to pelagic forage fish (55%), Arctic cod (*Boreogadus saida*) (28%), saffron cod (*Eleginus gracilus*) (4%), and other fish (3%).

Belugas are an important subsistence resource in the eastern Chukchi Sea. The mean annual number of belugas belonging to the eastern Chukchi Sea stock landed by Alaska Native subsistence hunters from 2002 to 2006 was 59 (Allen and Angliss 2010). The mean subsistence harvest of belugas from the Beaufort Sea stock taken in both Canadian and U.S. waters is 139 (Allen and Angliss 2010). The total annual harvest for the model is calculated in the same fashion as the biomass estimate. The mean harvests from the two populations are added together then multiplied by their approximate residence time in the model area resulting in $(59 + 139) \times (4/52) \approx 15.2$ animals. When multiplied by the average individual weight and divided by the model area this results in a model harvest density estimate of $6.34 \times 10^{-5} \text{ t km}^{-2}$.

The data pedigree for beluga biomass and harvest are both considered a 5 due to limited confidence in direct estimates with limited coverage and extrapolation based on uncertain migration patterns. The estimates of P/B and Q/B are both given a pedigree of 6 because they are based on general life history proxies. The diet composition has a pedigree of 5; based on single study of the same species within the same region but during a previous time period.

Gray Whale (*Eschrichtius robustus*) – Gray whales are baleen whales that seasonally migrate from their wintering grounds in Baja California, north to the Bering and Chukchi seas in the summer (Braham 1984). Gray whales occupy the Chukchi Sea for about 6 months from June to November and may first begin to arrive near St. Lawrence Island in the northern Bering Sea in about April. As the ice-edge retreats, about 70% of the grays proceed through Bering Strait and into the Chukchi Sea (Highsmith and Coyle 1992). Detailed data on the distribution of gray whales within the Chukchi Sea are not available

but it is assumed here that only about a third occupy the eastern half. Gray whales focus their foraging in areas of high production that support abundant benthic communities (Highsmith and Coyle 1990, 1992, Highsmith et al. 2006). Within the Chukchi Sea many of these foraging sites are found west of, or straddling the U.S.-Russia Convention Line (Bogoslovskaya et al. 1982b, Highsmith et al. 2006). Concentrations of gray whales presumed to be feeding have been observed in the south-central Chukchi Sea and along the northern coast of Chukotka (Berzin 1984, Nerini 1984, Miller et al. 1985). Fall southbound migration usually begins by October.

A recent re-analysis of gray whale survey data resulted in increased abundance estimates for the years 1967-87 while estimates from the years 1992-2006 were adjusted downward (Laake et al. 2009). Population abundance estimates peaked just prior to 1990 (Laake et al. 2009, Punt and Wade 2010). The abundance estimate of 26,916 used here corresponds to 1987-88 (Laake et al. 2009). This number was reduced to account for seasonal occupation (0.5), the estimated fraction of the population migrating into the Chukchi Sea (0.7), and for the proportion occupying the eastern half of the Chukchi Sea (0.33). This resulted in an estimate of approximately 3,140 whales in the model area. Assuming an average weight of 16,177 kg (Hunt et al. 2000) this equals a density estimate of 0.265 t km⁻².

An estimated P/B for gray whales was previously developed by Aydin et al. (2007) using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991) (for details see Marine Mammal Production Rates in Appendix B this document). Other than humans, the only known predators of gray whales are killer whales (*Orcinus orca*). A monkey life-history surrogate was used for gray whales, which assumes a relatively constant mortality rate across juvenile, adult, and senescent periods. The monkey life history surrogate was combined with an assumed longevity of 60 years and produced an estimated P/B of 0.063 (Aydin et al. 2007). The estimate of gray whale P/B developed by Aydin et al. (2007) applies to the same stock of gray whales that seasonally occupy the eastern Chukchi Sea and therefore, is used here as a best estimate of gray whale P/B. The Q/B of 8.873 was calculated by scaling the daily caloric requirements listed in Hunt et al. (2000) up to an annual rate.

Different from other baleen whales, the diet of gray whales is primarily composed of benthic invertebrates; specifically they are thought to primarily consume benthic amphipods (Nerini 1984, Highsmith and Coyle 1990, 1992). Here 90% of their diet is attributed to benthic amphipods with the remaining 10% divided up amongst other benthic invertebrates in proportion to their biomass.

The data pedigree for gray whale biomass is considered a 5 due to limited confidence in direct estimates with limited coverage and extrapolation based on uncertain migration patterns. The estimates of P/B and Q/B are both given a pedigree of 6 because they are based on general life history proxies. The diet composition has a pedigree of 5; based on diet studies of gray whales within the same region but with limited coverage.

Bowhead Whale (*Balaena mysticetus*) – Bowhead whales are large baleen whales that annually migrate between wintering grounds in the northern Bering Sea and summering grounds in the Beaufort Sea. The timing of the spring migration is in part determined by the timing of ice break-up but generally begins in about mid-April and takes bowheads through the eastern Chukchi Sea following persistent, recurring leads that follow the Alaska coast between Pt. Hope and Pt. Barrow (Ljungblad et al. 1986, Moore and Reeves 1993, Quakenbush et al. 2010). During their spring migration it takes about 2 weeks to traverse the Chukchi Sea on their way to the Beaufort Sea (Moore and Reeves 1993, Quakenbush et al. 2010). The timing of the fall migration from the Beaufort Sea back to the Bering Sea is not as well defined as the spring migration but generally begins by September and concludes by December (Ljungblad et al. 1986, Quakenbush et al. 2010). Bowheads do not follow as precise a route during their fall migration as they do during their spring migration and may disperse over a wider area in the Chukchi Sea (Ljungblad et al. 1986, Quakenbush et al. 2010). The exact route and timing of the fall migration may be influenced by ice dynamics and prey availability (Ljungblad et al. 1986, Moore and Reeves 1993). The general route is west from Pt. Barrow across the northern Chukchi Sea over Hanna and Herald Shoals or near the continental slope (Ljungblad et al. 1986, Quakenbush et al. 2010) on their way to Wrangel Island and the Chukotka Coast in the western Chukchi Sea (Bogoslovskaya et al. 1982a,

Miller et al. 1986). The remainder of the eastern Chukchi Sea receives little use during the fall migration (Quakenbush et al. 2010). Areas near Pt. Barrow and other areas in the northeast Chukchi Sea receive considerable use as foraging grounds during fall migration (Moore et al. 2010, Quakenbush et al. 2010). Because the fall migration is spread out over 3 to 4 months and whales may spend differing amounts of time in the model area, I assume that in general the bowheads spend about half of this migration time (~8 weeks) occupying and feeding in the Chukchi Sea. Combined with the estimated 2-week duration of the spring migration, bowheads are assumed to occupy the model area for a total of 10 weeks of the year.

The bowhead population abundance estimate of 6,928 (CV = 0.12) (George et al. 2004) for 1988 is used here as it closely corresponds best to the base time period of the model. The abundance estimate is reduced to reflect the seasonal use of the model area by bowheads, about 10 weeks yr⁻¹. This results in a model abundance estimate of 1,332. Multiplying this abundance by a mean body mass of 31,506 kg (Hunt et al. 2000) produces a density estimate of 0.219 t km⁻².

Bowhead whales are an important subsistence resource and the number landed varies considerably from year to year (Suydam and George 2004). From 1978 to 2004 the average subsistence harvest was ~28 (Suydam and George 2004). The number of whales harvested in the present model is 30 and corresponds to 1990 (Suydam and George 2004). Similar to the population abundance estimate this number is reduced for seasonal occupation of the model area resulting in a model harvest of 5.77 whales or 9.46 x 10⁻⁴ t km⁻².

The estimated bowhead whale P/B of 0.010 was derived by Aydin et al. (2007) from survival estimates reported in (Zeh et al. 2002). The Q/B of 5.260 was calculated by scaling the daily caloric requirements of bowheads listed in Hunt et al. (2000) up to an annual rate.

The amount of feeding that takes place during the spring migration is not entirely clear. Some studies have shown bowheads to exhibit feeding behavior during their spring migration (Carroll et al. 1987, Quakenbush et al. 2010) and stomach contents have shown them to feed primarily on pelagic zooplankton, including copepods and euphausiids, near Pt. Barrow (Carroll et al. 1987). Other stomachs

collected from whales harvested during the spring migration are mostly empty (Würsig and Clark 1993). Here all whales are assumed to feed while in the model area.

The diet of bowheads is primarily composed of copepods, euphausiids, and other zooplankton along with a small proportion of benthic invertebrates (Lowry and Burns 1980, Hazard and Lowry 1984, Lowry 1993, Moore et al. 2010). The diet used here is 71% copepods, 24% other zooplankton, and 5% benthic invertebrates including miscellaneous crabs, benthic amphipods, and other epifauna and infauna.

The data pedigree for bowhead whale biomass is considered a 5 due to limited confidence in direct estimates with limited coverage and extrapolation based on uncertain migration patterns. The pedigree for the subsistence harvest is 2 based on a single region-specific estimate. The estimates of P/B and Q/B are both given a pedigree of 6 because they are based on general life history proxies. The diet composition has a pedigree of 5; based on multiple diet studies of bowhead whales within the same region but with limited spatial and temporal coverage.

Caniformia

Polar Bear (*Ursus maritimus*) –Polar bears have a circumpolar distribution and are comprised of 19 subpopulations that range throughout the Arctic and portions of the subarctic (Obbard et al. 2010). The total global population is estimated to be between 20,000 and 25,000 (Obbard et al. 2010). In Alaska polar bears are found in the Bering, Chukchi, and Beaufort seas and belong to two subpopulations, the Chukchi/Bering (CS) and Southern Beaufort Sea (SBS) stocks (USFWS 2010b, c). Both of these stocks are classified as depleted under the Marine Mammal Protection Act and listed as threatened under the Endangered Species Act (1973). Radiotelemetry data has revealed the two stocks have overlapping distributions with CS bears found well east of Barrow into the Beaufort Sea (153° W) and SBS bears found as far west as Icy Cape (162° W) along the Chukchi Sea coast (Amstrup et al. 2005). The management boundary between these two stocks as adopted by the International Union for the Conservation of Nature (IUCN) Polar Bear Specialist Group (PBSG) is a northwesterly projected line

from about Icy Cape into the Chukchi Sea (Obbard et al. 2010). Amstrup et al. (2005) conducted an analysis of tagging and radiotelemetry data where they calculated probabilities that a bear sighted or caught in a particular location belonged to one of the Alaska stocks. The resulting probability contours revealed that the 50% contour for the CS and SBS populations intersected the mainland near Pt. Barrow (~157° W). The 33% probability contour for SBS bears intersected the mainland at Icy Cape in the Chukchi Sea, while the 33% contour for CS bears met the land in the Beaufort Sea (153° W). Due to this overlap within the bounds of the model area (east of 156° 30' W) both stocks are included in this model. Another telemetry study has indicated that bears originating in the SBS may spend 25% of their time in the northeastern Chukchi Sea, while those of CS origin may only spend 6% of their time east of Pt. Barrow (Amstrup 1995).

The annual advance and retreat of ice over the Chukchi and Bering seas allows for CS polar bears to cover a considerable range in latitude seasonally as many migrate south following the advancing ice in the fall and winter and return north ahead of the receding ice edge during spring and summer (Garner et al. 1990, Garner et al. 1994). In winter they have occurred as far south as the Pribilof Islands in the Bering Sea (Ray 1971) but more routinely are observed near St. Lawrence Island in the northern Bering Sea (Garner et al. 1990, Garner et al. 1994, Garner et al. 1995). The southern extent of their range is in part dictated by annual variation in the maximum extent of ice coverage, and their distribution in summer is related to location of the ice edge at its minimum (Garner et al. 1990, Garner et al. 1994). When the ice retreats in summer, CS polar bears are infrequently stranded on land and most manage to stay with the sea-ice throughout the year (Garner et al. 1990, Garner et al. 1994). Of 21 tracked females which denned on Wrangel Island, only 2 were stranded when the ice rapidly retreated in August 1990 (Garner et al. 1994). The distance between the ice-edge at maximum extent to its minimum may reach 1,400 km and individual polar bears of the CS stock may cover an extensive range annually (Garner et al. 1990). From April 1986 to May 1988 the average area occupied by females tracked in the Chukchi and Bering seas was 244,463 km² (± 80,038 km²) (Garner et al. 1990), while females from the SBS in the years 1985 to 1995 had an average range of 166,694 km² (range 14,440 to 616,800 km²) (Amstrup et al. 2000). The CS

stock also crosses an international boundary shared between the U.S. and Russia. Telemetry data indicates females den on Wrangel and Herald Islands in the western Chukchi Sea and occasionally foray into the East Siberian Sea (Garner et al. 1990, Garner et al. 1994). Satellite telemetry data have indicated that female polar bears utilized roughly equivalent areas on either side of the convention line, but spent more than two-thirds of their time in the Russian territory versus the U.S. territory (Garner et al. 1990). A study of dispersal patterns of maternal polar bears from Wrangel Island indicated that the bears spread themselves throughout the southern Chukchi Sea after emerging from dens in spring, then moved north as the ice receded (Garner et al. 1994).

Polar bears are among the largest ursids, rivaled in size only by the largest brown bears (*Ursus arctos*) (Reeves et al. 1992). Regional variation in size and weight has been observed throughout the polar bear's range, but other factors may have affected the bear's size at the time they were measured, including genetics, season, prey availability, and measurement error (Stirling and Guravich 1988, Derocher and Stirling 1998, Derocher and Wiig 2002). Polar bears demonstrate strong sexual dimorphism with adult males weighing approximately 2.1 times as much as adult females, and males are also about 1.18 times longer than their female counterparts (Derocher and Wiig 2002, Derocher et al. 2005). Males range in weight from 300 to 800 kg and females from 150 to 300 kg (DeMaster and Stirling 1981). At birth, cubs weigh less than 1 kg and a few months later, at the time of emergence from the den in about April, weigh between 10 and 15 kg (DeMaster and Stirling 1981, Reeves et al. 1992, Schliebe et al. 2006). Females grow to 90% of their asymptotic weight in about 4 years, while it takes males just over 9 years to accomplish the same percentage of asymptotic weight (Derocher 1991). Kingsley (1979) fit a von Bertalanffy growth curve to age-weight data and calculated asymptotic weights of polar bears in the Beaufort Sea during the years 1974-75 as 198 kg (SE = 7.1) for females and 470 kg (SE = 31.4) for males. More recently, and also using a von Bertalanffy growth curve, Derocher (1991) calculated asymptotic weights for Beaufort Sea polar bears as 199 kg (SE = 2.3) for females and 421 kg (SE = 7.6) for males. Similar analyses of growth patterns are not available for polar bears of the CS stock. Satellite tracking data indicates a considerable amount of overlap between these two populations (Amstrup et al.

2005), and analyses of microsatellite loci have indicated they are genetically similar as well (Paetkau et al. 1999). Therefore, in the absence of average body size estimates specific to the CS stock, the sex-specific estimates of asymptotic body mass for the SBS stock were used for both populations.

Lentfer et al. (1980) estimated the combined Alaskan polar bear population composition between the years 1967 to 1976 as 32% young (≤ 2 years old), 43% females (≥ 3 years old), and 25% males (≥ 3 years old). These numbers are potentially inaccurate because they may have undersampled families with cubs that had not yet emerged from maternity dens, subadult males (3-years-old) may have dispersed from the area following family break-up, and mature males may have been underrepresented because they had a tendency to range farther offshore out of the sample area (Lentfer et al. 1980). In general, the sex and age composition for both Alaskan stocks of polar bears is not known with great precision so a sex ratio of 1:1 was assumed and the average individual body mass was calculated without respect for age composition. The asymptotic weights for Beaufort Sea polar bears provided by Derocher (1991) were averaged (310 kg) and this weight was used as the average individual body mass. This may be an overestimate of individual average size because the size and abundance of younger year classes is not considered. However, in the U.S. portion of the Chukchi Sea, preliminary observations from work conducted by the USFWS and USGS reported by DeBruyn et al. (2010) indicated a very low instance of cubs and a higher than expected occurrence of males. Both of these observations would have the effect of increasing the average weight.

Different from hibernating brown and black bears, only pregnant polar bears are known to den (Stirling and Guravich 1988, Reeves et al. 1992). Maternity dens are dug by expecting females in the snow on either land or sea-ice in late October to early November and cubs are born the following December and January (Lentfer and Hensel 1980, Reeves et al. 1992, Amstrup and Gardner 1994, Fischbach et al. 2007). Some of the primary requirements for denning sites are weather and topography that facilitate the formation of snowdrifts that will be stable throughout the denning season (Lentfer and Hensel 1980). Another key requirement is a location that is or will be near an area of high prey availability during the post-denning period (Lentfer and Hensel 1980). Wrangel Island in the western

Chukchi Sea is a known denning location for the CS stock (Garner et al. 1990, Garner et al. 1994), while dens are less frequently observed along the Alaskan coast in the eastern Chukchi Sea (Lentfer and Hensel 1980). Lentfer and Hensel (1980) suggested a possible explanation for this by comparing the two sites. On Wrangel Island the topography and weather combine to provide ample opportunities for up to 200 female bears to den (Lentfer and Hensel 1980). In contrast, the relatively flat and unsculptured landscape of the northwest Alaskan coast provides fewer opportunities for adequate snowdrifts to develop and persist (Lentfer and Hensel 1980). Conversely, a study of radio-collared females from the Beaufort Sea revealed that numerous den sites were located in areas of apparently flat landscapes that were somehow sufficient to catch enough snow to maintain a den (Amstrup and Gardner 1994). On Wrangel Island numerous CS females den annually (Garner et al. 1994). While in the eastern Chukchi Sea, Lentfer and Hensel (1980) only located a single den on the northwest coast of Alaska near Point Hope and Garner et al. (1990) did not document a single denning in American territory of bears tagged in the Bering and Chukchi seas. Of 90 confirmed dens belonging to females tagged in the Beaufort Sea, 13 denned west of Pt. Barrow including 3 on land along the Chukchi Sea coast in Alaska (Amstrup and Gardner 1994). Though instances of denning on the northwest coast of Alaska have been recorded, concentrations of denning sites like those observed on Wrangel Island do not appear to be present along the Chukchi Sea coast in Alaska. Preliminary observations from work performed by the USFWS and USGS in the U.S. portion of the Chukchi Sea in 2008 and 2009 have indicated a lack of first year cubs which supports the results of previous studies (e.g., Lentfer and Hensel 1980, Garner et al. 1990) that indicated most CS subpopulation denning occurs in the Russian portion of the Chukchi Sea (DeBruyn et al. 2010).

An accurate estimate of abundance for the CS stock does not currently exist (Obbard et al. 2010, USFWS 2010b). The best estimate available of about 2,000 bears in 1993 is a revised estimate based on an extrapolation of denning data from Wrangel Island (Lunn et al. 2002, Aars et al. 2006, USFWS 2010b). There are no measures of precision associated with this estimate and it is largely based on expert opinion (Obbard et al. 2010). But due to a lack of better information, it is considered the best estimate of population size (USFWS 2010b). The model area was assumed to comprise about 25% of the range of

the CS stock based on a visual examination of the 95% probability contours derived by Amstrup et al. (2005). Due to seasonal loss of ice the bears were assumed to occupy the eastern Chukchi Sea model area for only 50% of the year. The resulting equation to determine CS stock model abundance was $2,000 \times 0.25 \times 0.5 = 250$ bears. This number was multiplied by the average individual size (310 kg) then divided by the total model area ($192,054 \text{ km}^2$) yielding an estimated density of $4.04 \times 10^{-4} \text{ t km}^{-2}$.

The most accurate estimate of abundance for the SBS stock is 1,526 (95% CI: 1,211-1,841) in the years 2004-2006 (Regehr et al. 2006). The previous best estimate for this population was 1,776 (SD \pm 803; Amstrup et al. 1986) for the period 1972-83. During the model base time period of 1990, the estimate of 1,800 was still considered the best estimate (Wiig et al. 1995, Derocher et al. 1998, Lunn et al. 2002) and remained so until 2006 (Aars et al. 2006). Neither the estimate from Amstrup et al. (1986) nor from Regehr et al. (2006) apply directly to the base model time period and it is unclear whether the population has changed over this time period (Regehr et al. 2006). The more recent estimate of Regehr et al. (2006) has a smaller coefficient of variation (CV = 0.206) than the Amstrup et al. (1986) estimate (CV = 0.45) and was used to estimate the model abundance. The model area was visually estimated to comprise 20% of the range of the SBS stock as defined by the 95% probability contour produced by Amstrup et al. (2005). Telemetry studies have indicated that bears of the SBS stock may spend 25% of their time in the northeastern Chukchi Sea (Amstrup 1995). The model abundance was calculated as $1,526 \times 0.2 \times 0.25 \approx 76$ bears. Multiplying by the individual body mass and dividing by total model area resulted in a model density estimate of $1.23 \times 10^{-4} \text{ t km}^{-2}$. This brings the combined stock model density estimate to $0.00052 \text{ t km}^{-2}$.

Both males and females may be mature as early as 3.5 years of age but the estimated age of first reproduction for females is 5.4 years (Lentfer et al. 1980). Males may not be large enough to successfully compete for mates until they are 8 years of age (Stirling and Guravich 1988). The breeding season occurs from about late March through May (Reeves et al. 1992, Schliebe et al. 2006) and the cubs are born the following winter in December or January (Reeves et al. 1992). Females do not breed again until cubs are fully weaned which occurs at just over 2 years of age (Amstrup and DeMaster 1988, Stirling and

Guravich 1988, Schliebe et al. 2006) and as a result the average breeding interval is about 3.6 years (Lentfer et al. 1980). Estimated mean natural survival rates for the SBS subpopulation are 0.335 for cubs, 0.900 for ages 1 to 4, and 0.961 for ages greater than 4 (Table 2 in Obbard et al. 2010). The estimated annual intrinsic growth rate (excluding human-caused mortality) for the SBS stock is 6.03% (Amstrup 1995) and this value was used as an estimate of P/B in this model (0.0603). There are no such estimates of population growth available for the CS stock and it is recommended in the most recent stock assessment report (USFWS 2010b) that the SBS intrinsic growth estimate be used as the default value for productivity of the CS stock.

Polar bears from both stocks have been hunted for subsistence purposes and for recreation (Reeves et al. 1992, USFWS 2010b, c). The average Alaskan harvest has declined from 132 yr⁻¹ between 1980 and 1990 to 79 yr⁻¹ between 1990 and 2008 (DeBruyn et al. 2010). For the CS stock the average harvest in the 1980s was 92 yr⁻¹ and then dropped to 49 yr⁻¹ in the 1990s (DeBruyn et al. 2010). The total Alaskan harvest averaged 98 yr⁻¹ (SD = 51.2) over the years 1988 to 1992 (Schliebe and Evans 1995). Over this same time period the SBS accounted for 28.4% of the harvest with the remaining 71.6% allocated to the CS stock (Schliebe and Evans 1995). These percentages were calculated from reported kills and as such are treated as a minimum estimate; however they are believed to very closely match the true harvest (Schliebe and Evans 1995). The CS and SBS harvests were calculated for the model by multiplying the respective percent allocation reported by Schliebe and Evans (1995) times the total Alaskan annual average harvest of 98. For the CS stock this amounted to an estimated annual U.S. harvest of $98 \times 0.716 \approx 70$ bears and for the SBS stock $98 \times 0.284 \approx 28$ bears. Hunting for polar bears has not been allowed in Russia since 1956 and limited data are available during the model base time period for the Russian harvest of the CS stock. In the early 1990s it is estimated that approximately 10 (± 5) problem bears were killed per year in the entire Russian Arctic (Belikov 1995) but it is not known how many to attribute to the CS stock. In the absence of more specific information the Russian harvest of the CS stock is approximated at 10 bears. The harvest biomasses in the model are calculated using the same general formula as those for the model abundance. The U.S. portion of the CS stock harvest is estimated

as $70 \times 0.5 \times 0.25 = 8.75$ bears and the Russian portion as $10 \times 0.5 \times 0.25 = 1.25$ bears. After multiplying by individual body mass (310 kg) and dividing by model area the U.S. and Russian CS harvests are $1.41 \times 10^{-5} \text{ t km}^{-2}$ and $2.02 \times 10^{-6} \text{ t km}^{-2}$, respectively ($1.61 \times 10^{-5} \text{ t km}^{-2}$ combined). The SBS harvest is $28 \times .25 \times .2 \approx 1.4$ bears, which yields a model biomass density estimate of $2.26 \times 10^{-6} \text{ t km}^{-2}$.

Throughout their range, ringed seals (*Phoca hispida*) are the primary prey of polar bears and of secondary importance are bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980, Derocher et al. 2002, Iverson et al. 2006, Bentzen et al. 2007). Polar bears have been reported to hunt walrus (*Odobenus rosmarus*) calves but are not thought to successfully hunt adult walrus often (Kiliaan and Stirling 1978, Fay 1982, Amstrup and DeMaster 1988, Stirling and Guravich 1988, Calvert and Stirling 1990). However, in the Foxe Basin area of the Canadian Arctic, walrus have been estimated to compose 7% of the polar bear's diet (Thiemann et al. 2008). During summer when the sea-ice is near its minimum, polar bears have been observed scavenging walrus carcasses at haulouts on Wrangel Island and along the Chukotka coast (Kochnev 2006, Ovsyanikov 2010). The polar bears fed on the remains of walruses that had died in previous years and on individuals that were trampled to death when the walrus were panicked (Kochnev 2006). In 1990, 148 polar bears were observed near walrus haulouts on Wrangel Island and fed on 58 walrus carcasses which amounted to about 115 kg of food per bear (Kochnev 2006). Polar bears have also occasionally been sited killing and consuming belugas (Freeman 1973, Smith 1985, Lowry et al. 1987, Smith and Sjare 1990, Rugh and Shelden 1993). Belugas may be killed by polar bears when whales become entrapped by freezing or shifting ice or when traveling through narrow leads (Lowry et al. 1987). In one instance near Bering Strait a minimum of 40 belugas were killed and 15 bears were present at the time of the observation (Lowry et al. 1987). Two weeks later, the ice and carcasses had moved several kilometers and there were approximately 30 polar bears still scavenging the carcasses (Lowry et al. 1987). This example highlights that even though belugas may be an uncommon prey, because of their size they may be of high local significance to bears (Lowry et al. 1987, Rugh and Shelden 1993). Assuming a caloric density equivalent to a ringed seal as estimated by Best (1977), Lowry et al. (1987) estimated that a 600 kg beluga could provide a polar bear up to 140 days of

nourishment. For the population as a whole the number of belugas killed by polar bears is thought to be low and they are not believed to form a significant portion of the polar bears overall diet (Stirling and Archibald 1977, Smith 1985, Amstrup and DeMaster 1988). In a study of polar bear diets in portions of the Canadian High Arctic, including Lancaster Sound, Baffin Bay and the Gulf of Boothia, belugas comprised between 25 and 33% of their total prey biomass (Thiemann et al. 2008). Whale carcasses (beluga, bowhead, and gray) either from subsistence hunts or beached whales are also opportunistically fed on by polar bears (Kochnev 2006, Miller et al. 2006, Ovsyanikov 2010). The extremely large size of bowhead whale carcasses means they may provide substantial amounts of food for an extended period of time for numerous bears (Bentzen et al. 2007). Throughout their circumpolar range, polar bears have also been reported to hunt and utilize other prey sources including caribou (Brook and Richardson 2002), musk ox (Ovsyanikov 2010), other polar bears (Taylor et al. 1985, Amstrup et al. 2006, Stone and Derocher 2007), fish (Ovsyanikov 2006, Dyck and Romberg 2007), birds (Donaldson et al. 1995, Ovsyanikov 2010), landfills (Lunn and Stirling 1985), and various species of berries (Dyck and Kebreab 2009). Observations of polar bears utilizing these other prey resources are scarce and their relative importance to their annual dietary budget is thought to be minimal (Lunn and Stirling 1985, Ramsay and Hobson 1991, Dyck and Kebreab 2009).

The exact composition of polar bear diets is not well known in part due to the inaccessibility and remoteness of their habitat but also due to variation related to age, sex, location, season, and interannual variation in prey abundance (Iverson et al. 2006, Bentzen et al. 2007, Thiemann et al. 2008). For example, preliminary results from a fatty acid analysis of polar bear diets in the Chukchi Sea have indicated that polar bears in the Chukchi Sea may consume more bearded seals and walrus than those in the adjacent southern Beaufort Sea (DeBruyn et al. 2010). This is not surprising as the Chukchi Sea is home to a large walrus population (Gilbert et al. 1992) and the combined Chukchi/Bering continental shelf is the largest continuous expanse of bearded seal habitat in the world (Burns and Frost 1983). Stirling and Archibald (1977) also observed spatial variation in the relative contribution of ringed and bearded seals to the diet of polar bears. The proportion of bearded seals in the diet of polar bears in the

eastern high Arctic was significantly lower than in the western Arctic (Stirling and Archibald 1977). A study of polar bear diet composition in Svalbard and the western Barents Sea showed that ringed seals were the numerically dominant prey (63%), however by biomass bearded seals accounted for 50% of the diet and ringed seals 30% (Derocher et al. 2002). Bearded seals are more than twice the size of ringed seals and though they are preyed upon less frequently, as individual prey items they are of greater importance to the polar bear diet (Stirling and Archibald 1977).

In a study of 10 subpopulations across the Canadian Arctic, Thiemann et al. (2008) found the greatest similarities in diet between adjacent populations, which they in part attributed to range overlap and shared prey resources. In lieu of diet data specific to the Chukchi Sea region, a Southern Beaufort Sea diet is assumed here. The SBS diet derived through fatty acid analysis by Thiemann et al. (2008) is used and is composed of approximately 65% ringed seal, 25% bearded seal, and 10% beluga. The absence of walrus in the diet reported by Thiemann et al. (2008) may be due to location as the samples were collected from the Canadian portion of the southern Beaufort Sea where walrus is uncommon. An analysis of winter diet of SBS polar bears in the Alaskan portion of the Beaufort Sea attributed a mean of 64% of the diet to ringed seals and 17% to bearded seals (Bentzen et al. 2007). The lower contribution of bearded seals in the diet reported by Bentzen et al. (2007) may be due to seasonal and spatial differences.

Captive bears have been observed consuming up to 10% of their body weight in less than 30 minutes and their total stomach capacity has been estimated to be between 15% and 20% of the bear's weight (Best 1977). Additionally, the rate of food passage is inversely related to caloric density (Hunt and Stubbs 1975), so a polar bear feeding on blubber will not likely feed again as soon as a bear feeding on prey of lower caloric density (Best 1977). Best (1985) found the gastrointestinal transit time of bears fed on a diet of skin and blubber to be significantly slower than bears fed on other diets including seal muscle, viscera, and bone.

The Q/B for polar bears was determined by first calculating the basal metabolic rate (BMR) then converting that to a daily metabolic rate (DMR). The BMR for polar bears was previously calculated by Best (1977) using the formula of Kleiber (1961) and that same approach is used here. The polar bear

DMR has been estimated to range from 2.0 to 2.6 times the BMR for high Arctic polar bears in midsummer (Best 1985). The DMR used here fell in the middle of this range at 2.3 times the BMR. This resulted in an estimated daily caloric requirement for a 310 kg polar bear of 11,895 kcal day⁻¹. In this model, ringed seals account for nearly two-thirds of the polar bear diet and their caloric value is assumed to be representative of all polar bear prey. Ringed seal caloric density has been estimated to range between 2.3 and 5.3 kcal g⁻¹ wet weight (Stirling and McEwan 1975) and an average density of 3.5 kcal g⁻¹ is used here. This produced a polar bear consumption rate of 1.1% of their body weight per day (3.4 kg day⁻¹) and, when scaled up to an annual rate yielded a Q/B of 4.001. This estimate of polar bear consumption is consistent with a previous estimate used in a trophic dynamics model of the Lancaster Sound Region of Canada where daily consumption was set at 1% of body weight per day (Welch et al. 1992). A similarly low consumptive value was calculated for polar bears who were exclusively fed energy rich seal blubber (not the rest of the seal), where a 280 kg polar bear would need only consume 0.6 kg per day (0.2% of body weight) to balance daily metabolic loss (Dyck and Kebreab 2009).

The data pedigree for the biomass of the eastern Chukchi Sea stock of polar bears is considered a 7 because the biomass estimate is largely based on expert opinion and extrapolation of uncertain migration patterns. The U.S. harvest of eastern Chukchi Sea polar bears has a pedigree of 2 based on a direct harvest estimate but with limited subregional resolution. The data pedigree for the Russian harvest of eastern Chukchi Sea polar bears is 7 based on a single estimate with little documentation. The estimated P/B is given a pedigree of 5 because it is based on the P/B of the same species in an adjacent population. The pedigree for Q/B is 6 because it based on a general life history proxy. The diet composition has a pedigree of 6; based on a diet study of the same species in an adjacent region.

The biomass estimate of the southern Beaufort Sea stock of polar bears has a data pedigree of 5 because the biomass estimate is region-specific but requires extrapolation based on uncertain migration patterns. The pedigree for the subsistence harvest is 2 based on a single region-specific estimate but with limited subregional resolution. The estimate of P/B has a pedigree of 4 based on a direct estimate with incomplete coverage. The pedigree for Q/B is 6 because it based on a general life history proxy. The diet

composition has a pedigree of 4; based on a direct study of polar bear food habits within this population but with limited spatial and temporal coverage.

Pacific Walrus (*Odobenus rosmarus divergens*) – The prominent large tusks of the walrus make it one of the most recognizable of all the ice-associated pinnipeds. The tusks are used in displays and fighting among males to establish dominance and to help with climbing onto and anchoring themselves to ice floes (Reeves et al. 1992). Walrus are found in the western and eastern Arctic and two subspecies are generally recognized. The Pacific walrus (*O. r. divergens*) comprises the bulk of the global walrus population (Sease and Chapman 1988) and is found in the Bering and Chukchi seas. The Atlantic walrus (*Odobenus rosmarus rosmarus*) is found in Hudson Bay, eastern Greenland, the Barents Sea, and the Laptev Sea (Fay 1982, Sease and Chapman 1988, Reeves et al. 1992). The taxonomic status of the Laptev population has been debated and listed previously as *O. r. laptevi* by some Soviet scientists (Fay 1982). Only the Pacific walrus occurs in Alaskan waters and therefore is the only walrus species included in this model.

The vast majority of the Pacific walrus population migrates north following the receding ice-edge into the Chukchi Sea in spring (Fay 1982). Following the southward expansion of ice in late fall, Pacific walrus return to the northern Bering Sea to overwinter spending a total of about 6 months in the Chukchi Sea (Fay 1982). The timing of migration varies from year to year with annual variation in the ice conditions, but the northward migration is generally underway by mid-April with practically all migrating individuals in the Chukchi Sea by July (Fay et al. 1986). The southward migration begins in October and most Pacific walrus have passed through Bering Strait by the end of November (Fay et al. 1986). Pacific walrus are benthic foragers which utilize the shallow depths and high benthic productivity throughout the Bering and Chukchi seas (Fay 1982). Pacific walrus use the ice for transportation during seasonal migration, to rest between foraging trips, for breeding, giving birth, and nursing (Fay 1982). During the summer when the sea-ice is at its minimum they are also known to use coastal haulouts on Wrangel

Island, northern Chukotka coast, and less frequently northwestern Alaska, especially during years of low ice coverage (Fay et al. 1986, Reeves et al. 1992).

The abundance of Pacific walrus is not known with precision but was estimated to have been reduced to a low in the 1950s primarily due to intensive commercial harvests in the previous decades (Fay 1982), and to have recovered to a peak of approximately 255,000 around 1980 (Fay et al. 1997). A series of cooperative surveys between the United States and Russia that occurred at 5-year intervals between 1975 and 1990 produced population estimates that ranged from a high of 246,360 in 1980 to a low of 201,039 in 1990 (all surveys summarized with references in Table 1 of USFWS 2010a). In 2006 the U.S. and Russia partnered again to survey the Pacific walrus population and produced a population estimate of 129,000 with 95% confidence limits of 55,000 to 507,000 (USFWS 2009, Speckman et al. 2011). This estimate is negatively biased however, as it did not cover the entire range that Pacific walrus are known to occur and is therefore considered a minimum population estimate (USFWS 2009, 2010a, Speckman et al. 2011).

The vast majority of Pacific walrus migrate north through the Bering Strait in spring with the receding ice edge, however several thousand stay behind and summer in the Bering Sea at haulouts along northern Bristol Bay, the Gulf of Anadyr and in Bering Strait on Big Diomedede Island (Lowry and Frost 1981b, Fay 1982, Gilbert et al. 1992, Reeves et al. 1992). estimated about 12,000 spend the summer in Bristol Bay and 6,000 to 8,000 in the Gulf of Anadyr and Bering Strait, totaling approximately 20,000 animals. Similarly, a survey in September and October of 1990 found a total of approximately 28,000 Pacific walrus at haulouts south of the Bering Strait on the coasts of Chukotka and Kamchatka and at haulouts in Bristol Bay (Gilbert et al. 1992). A survey conducted in the summer of 1985 counted at least 15,238 in Bristol Bay (Gilbert 1989). The estimated number of Pacific walrus not migrating into the Chukchi Sea by Reeves et al. (1992) and the counts of Gilbert (1989) and Gilbert et al. (1992) are all near 20,000 animals. This is approximately 10% of the total estimated abundance of 201,039 in 1990 (Gilbert et al. 1992). The model abundance was reduced by 10% to reflect this reduction.

In an aerial census conducted in September and October of 1985, 62,177 (SD = 19,480) Pacific walrus were estimated to be in the pack ice of the eastern Chukchi Sea (Gilbert 1989). At the same time, survey partners in the Soviet Union estimated 115,531 Pacific walrus along the pack ice in the western Chukchi Sea (Gilbert 1989). During the summer of 1990, more than two-thirds of the population was estimated to reside in the western Chukchi Sea associated with haulouts on Wrangel Island and the northern coast of Chukotka (Gilbert et al. 1992). This was in part attributed to the low ice coverage at the time of survey, with the ice edge far north of typical feeding grounds forcing many Pacific walrus to haul out on Wrangel Island instead of on the pack ice (Gilbert et al. 1992). Pacific walrus occupying pack ice in the eastern Chukchi Sea were relatively abundant but were not of the same magnitude as previous surveys (Gilbert et al. 1992). The abundance estimated for the survey strata in the eastern Chukchi Sea by Gilbert et al. (1992) is likely an underestimate as they did not survey the open water south of the pack ice and therefore that estimate is not used here. The 1990 total abundance estimate provided by Gilbert et al. (1992) is an estimate of the visible population and is not corrected for individuals under the surface of the water and as such they recommend it be considered a minimum population estimate. The model abundance was calculated using the total abundance estimate for 1990 provided by Gilbert et al. (1992) because it corresponds with the base time period for the model. The total population estimate was reduced by 10% to account for those not migrating north through the Bering Strait. This number was reduced further to account for the estimated two-thirds of the migrating population that occupy the western Chukchi Sea. The number was then cut in half to account for Pacific walrus only occupying the Chukchi Sea for approximately 6 months out of the year. The resulting equation is: $201,039 \times 0.9 \times 0.333 \times 0.5 \approx 30,156$.

Pacific walrus are second in size only to elephant seals (*Mirounga* sp.) among pinnipeds (Reeves et al. 1992). They are the largest pinnipeds in the Chukchi Sea with adult males and females growing to average sizes of 1,210 and 832 kg, respectively (Fay 1982). Females will typically reach their maximum size between 12 and 14 years of age while males attain their maximum size at about age 16 (Fay 1982). During their first month, most calves weigh between 45 and 75 kg (Fay 1982). At birth the sex ratio is

1:1, however the sex ratio of adult Pacific walrus is not well known (Fay 1982). This is in part due to size and sex bias in harvest statistics, but it is thought not to be 1:1 (Fay 1982). The sex ratio has been estimated to be anywhere from 1 males:1.74 females in 1960 to 1:3 in 1985 (DeMaster 1984, Fay et al. 1997). Similarly, the age composition of the population is not well known but several studies were summarized by Fay (1982) yielding an estimated composition of 30-40% immature and 60-70% mature. The average individual size used to calculate total biomass within the model area will be affected by the relative abundance of each sex and age class.

Trites and Pauly (1998) calculated average weights for both sexes over all age classes from digitized growth curves derived by Fay (1982) and by using a fur seal surrogate survivorship curve resulting in estimates of 530 kg for females and 643 kg for males. Fay (1982) inferred from data collected in the early 1970s that the Pacific walrus population in 1972 was 62% female and 38% male, more specifically 46% females older than 5 years and 10% males older than 14 years. Using these inferred values of sex and age composition, Fay (1982) calculated the average body weight as 720 kg. In a previous ecosystem model of the eastern Bering Sea (Aydin et al. 2007) with approximately the same base time period used here, a 1:1 sex ratio was assumed and the average weights used were those of mature adults as reported by Reeves et al. (1992), 1,215 kg for males and 812 kg for females. This was in part due to the summertime occupation of large groups of Pacific walrus in Bristol Bay, predominately composed of large adult males (Fay 1982, Fay et al. 1986, Gilbert et al. 1992) and due to much of the rest of the Pacific walrus population not ever migrating far enough to the south to be within the modeled area (K. Aydin, AFSC, pers. comm.). The specific sex and age composition of the Pacific walrus population during the base time period (~1990) within the Chukchi Sea is not known. The sex of Pacific walrus that were counted at haulouts in the Bering Sea in 1990 was determined to be predominately males with relatively few immature individuals (Gilbert et al. 1992). During the same survey in the Chukchi Sea it was not possible to determine the sex or age composition but based on visual estimations the authors believed the age and sex composition of Pacific walrus along the ice edge to be mixed (Gilbert et al. 1992). In 1982 a joint Soviet-American summer survey of the ice edge in both the western and eastern Chukchi Sea, male

Pacific walrus were more common near Barrow, but females and dependent young dominated throughout the rest of the ice edge in the eastern Chukchi Sea (Fay et al. 1986). Pacific walrus herds in the eastern Chukchi Sea were composed of approximately 73% females 6 years and older, 1% males 6 years and older, and 25% individuals of both sexes 5 years and younger (Fay et al. 1986). Female Pacific walrus give birth shortly after the ice begins to recede in late April and May (Burns 1970, Sease and Chapman 1988). Within days of giving birth, females and newborn calves form large “nursery herds” which will remain together throughout summer (Burns 1970, Fay et al. 1986). There is a lack of accurate observations on the sex and age composition of Pacific walrus within the eastern Chukchi Sea but the preponderance of evidence indicates that adult females and immature individuals of both sexes dominate while adult males are in the minority.

Considering all the evidence, I have adopted the conservative estimates of average size derived by Trites and Pauly (1998). I have assumed a 1:1 sex ratio due to the presence of both sexes especially at younger age classes and averaged their mean sizes for males and females, resulting in an estimated average individual body size of 587 kg (0.587 tons). The average body mass is multiplied by the estimated total number of Pacific walrus in the model ($n = 30,156$) then divided by the estimated model area ($192,054 \text{ km}^2$) resulting in a biomass density estimate of $0.09209 \text{ t km}^{-2}$.

Estimates of Pacific walrus net productivity have a considerable range (USFWS 2010a). Fay et al. (1997) estimated the overall net increase over the years 1960 to 1975 to be about 7% and Chivers (1999) approximated the maximum population growth rate as 8%. Sease and Chapman (1988) fit an exponential curve to Pacific walrus abundance estimates over the years 1958 to 1975 within the Soviet portion of their range and found an instantaneous growth rate of 6.7%. Detailed information on survivorship is not available but natural mortality is assumed to be low (Fay 1982, DeMaster 1984). For juvenile age classes this likely in part attributed to the prolonged period of parental care of about 2 years (Fay 1982). Fay et al. (1997) estimated natural mortality to be approximately 1.5% per year. DeMaster (1984) considered both natural mortality and mortality due to harvests and estimated adult survivorship to be above 95% and similarly, Fay et al. (1986) estimated adult survivorship as about 95%. The age-specific survival rates

used by Chivers (1999) in an individual age-based model with the population approaching carrying capacity, resulted in a weighted average survival of 95.6% for adults and 87.4% for all age classes. In a food web model of the eastern Bering Sea, Aydin et al. (2007) assumed a constant mortality rate of 5% per year. Similar to the methods employed by Aydin et al. (2007) for other pinniped species, Trites and Pauly (1998) used a fur seal surrogate to calculate age-specific survival rates for Pacific walrus. The fur seal surrogate is likely appropriate as calves are expected to experience higher natural mortality compared to adolescents or adults because they are more vulnerable to predators (e.g., polar bears, killer whales), many die from trampling, and they may be more vulnerable to hypothermia (Fay 1982, Sease and Chapman 1988). Compared to other pinnipeds the reproductive potential of walrus is relatively low in part due to long pregnancy duration lasting about 15 to 16 months, with female reproductive intervals of 2 to 5 years (Fay 1982, Fay et al. 1986). Because the reproductive rate is so low, it is assumed that natural mortality must also be low (Fay 1982, Sease and Chapman 1988). Trites and Pauly (1998) calculated sex-specific estimates of longevity as 29 for females and 36 for males. Using a fur seal surrogate and an average longevity of 33 years, the P/B calculated for use in this model is 0.0688, which is consistent with the net productivity estimates of Chivers (1999) and Fay et al. (1997) and the constant mortality rate assumed by Aydin et al. (2007).

Pacific walrus is an important subsistence resource and is used for food, fuel, the skins for lines and boat coverings, and ivory and bones for other implements (Fay 1982, Reeves et al. 1992). Over the years 1960 to 2007, the average harvest of Pacific walrus by both the United States and Russia was 6,713 (USFWS 2010a). There was no record of the Alaska harvest of Pacific walrus in 1990 or 1991 (Fay et al. 1997) and it is possible it may have been higher than the mean harvest (Fig. 2 in USFWS 2010a). For this study the reported mean (6,713) is the harvest used in the model. To calculate the harvested biomass within the model area, the estimated harvest was treated the same as the biomass density estimate by multiplying the total number harvested from the total population by the portion of the population migrating into the Chukchi Sea (0.9), the approximate percentage that occupy the eastern Chukchi Sea (0.333), and the fraction of the year spent in the model area (0.5). This produces the equation and model

harvest estimate: $6,713 \times 0.9 \times 0.333 \times 0.5 \approx 1,007$. Multiplying the estimated number of Pacific walrus harvested by the average weight and dividing by model area produces a harvest biomass density estimate of $0.00308 \text{ t km}^{-2}$.

The Q/B ratio was calculated using the prey caloric density and daily caloric requirements reported by Hunt et al. (2000). The daily rate was scaled up to an annual rate resulting in a Q/B ratio of 21.662. This is equivalent to a consumption of about 35 kg day^{-1} or about 6% of total body mass. This is in agreement with the consumptive values reported by Fay (1982) and Fay et al. (1977) who estimated that walrus consume at least 5 to 7% of their total body weight per day. Fay (1982) went on to note that this is net consumption and because walrus only consume the soft portions of their prey (e.g., feet and siphons of bivalves) the gross predation rate is likely 3 to 4 times this rate.

The primary prey of walrus are bivalves (Fay et al. 1977, Lowry et al. 1980a, Lowry and Frost 1981b, Fay 1982, Lowry et al. 1982, Fay et al. 1986, Perez 1990, Sheffield and Grebmeier 2009) though the exact composition of their diet may vary with season and location (Fay 1982, Fay et al. 1986, Sheffield and Grebmeier 2009). Most of the published information on Pacific walrus diet comes from stomachs that were collected in the eastern Bering Sea and Bering Strait area in spring (Fay et al. 1977), with a few additional stomachs collected during winter in the eastern Bering Sea and during summer in the western and central Chukchi Sea (Fay et al. 1986). During winter and spring on the eastern Bering Sea shelf and in the Bering Strait area, bivalves were the primary prey by weight (Fay et al. 1986). The food habits data from specimens collected in the western and central Chukchi Sea suggest a more balanced diet that included polychaetes, snails, priapulans, sipunculans, and tunicates in proportions equal to or greater than the amount of bivalves (Fay et al. 1986). Very few stomachs from the eastern Chukchi Sea have been examined and of those, bivalves were the dominant prey (Fay 1982). Regional variation in the diet is in part due to differences in prey abundance and flexibility in walrus diet (Sheffield and Grebmeier 2009). The exact composition of secondary prey items may vary with season and location but bivalves appear to be the most important prey throughout their range and in all seasons (Fay 1982, Dehn et al. 2007).

Consumption of seals by Pacific walrus has been noted through direct observation and from stomach contents in the northern Bering Sea and in the western Chukchi Sea (Fay 1982, Lowry and Fay 1984). Pieces of ringed, spotted, and bearded seals have all been found in Pacific walrus stomachs (Lowry and Fay 1984). It is speculated that some of the seals may have been taken by predation but most are probably fed on as carrion (Fay 1982). The frequency of occurrence of seal consumption has been estimated to be as high as 3% in the 1970s and as low as 0.05% in the 1960s from Pacific walrus food habits data collected during subsistence harvests (Lowry and Fay 1984). Food habits data collected during subsistence harvests could be biased as walrus hunting often occurs coincident to seal hunting and those walrus may have increased access to struck and lost seals (Lowry and Fay 1984). Data on the sex and age of carnivorous Pacific walrus suggest this may primarily be limited to adult and subadult males 7 years and older (Fay 1982, Lowry and Fay 1984). It has also been hypothesized that seal consumption may be related to limited availability of other benthic prey (Lowry and Fay 1984, Fay et al. 1986).

The estimated diet composition for Pacific walrus used in this model is the diet reported by Perez (1990), who compiled diet compositions from throughout their range. The only change made to this diet was the proportion allocated to other pinnipeds which was reduced from 3% to 0.1%. This is in part due to potential bias of stomach contents from subsistence harvests and because it is unknown how much is due to predation as opposed to feeding on carrion (Fay 1982, Lowry and Fay 1984). Additionally, the balancing process revealed that any consumption of pinnipeds by Pacific walrus higher than 0.1% would drive all other pinnipeds out of balance ($EE > 1.0$). As modeled here, the other pinniped groups lacked the productivity to withstand any greater consumption by Pacific walrus. The proportion of Pacific walrus diet removed from pinnipeds was reallocated to the most dominant prey item bivalves (69.9%). The second most dominant prey item in the diet described by Perez (1990) was “other invertebrates” (18%). This category was apportioned by weight to invertebrate functional groups and taxa reported in Pacific walrus diets including sea cucumbers, anemones, tunicates, marine worms, and benthic amphipods. Similarly, Perez (1990) allocated 3% of the Pacific walrus diet to crabs which were divided

up by biomass between *C. opilio* and miscellaneous crabs. Other prey items are snails (6%), shrimp (2%), and octopus (1%).

The Pacific walrus biomass estimate has a data pedigree of 5 because the biomass estimate is region-specific but requires extrapolation based on uncertain migration patterns. The pedigree for the subsistence harvest of Pacific walrus is 4 based on direct estimates single but with incomplete coverage. The estimates of P/B and Q/B both have data pedigrees of 6 because the estimates are based on general life history proxies. The diet composition of Pacific walrus is based on a general diet of Pacific walrus from throughout their range and the data pedigree is a 5.

Bearded Seal (*Erignathus barbatus*) – The Bering-Chukchi stock of bearded seals ranges over continental shelf waters (< 200 m depth) of the Bering, Chukchi, Beaufort, and East Siberian seas (Cameron et al. 2010). Bearded seals are benthic foragers and the combined shallow shelf of the Bering and Chukchi seas is the largest continuous expanse of bearded seal habitat in the world (Burns and Frost 1983). Bearded seals use sea ice for whelping, nursing, molting, and as a platform to haulout and rest between foraging excursions. The seasonal ice coverage over the shallow depths of the Bering-Chukchi continental shelf provide bearded seals with the necessary habitat to reproduce, molt, and feed without hauling out on shore (Burns 1981). Bearded seals generally migrate north starting in the spring as the ice-edge recedes northward. In the fall when the sea ice begins to reform they migrate south with the advancing ice edge. This pattern of migration is in part due to a selection for preferred ice habitat (Burns and Frost 1983, Simpkins et al. 2003). Simpkins et al. (2003) studied pinniped habitat selection in the Bering Sea and found bearded seals to demonstrate a preference for medium ice coverage (70-90% cover) with a mixture of different sized ice floes. By migrating north with the receding ice in spring and south in the fall with the advancing ice edge they can maintain association with their preferred ice habitat (Johnson et al. 1966, Burns 1981, Burns and Frost 1983, Simpkins et al. 2003). Some bearded seals do occupy the Chukchi Sea year-round. They have been reported to occasionally maintain breathing holes in thin ice (Burns 1981); however, they primarily occupy areas of shifting ice which form openings and leads (Burns

1981, Lowry et al. 1983). One such lead occurs regularly north of the Bering Strait and it approximately mirrors the northwest Alaskan coast from Pt. Hope to Pt. Barrow (Burns et al. 1981, Burns and Frost 1983). Openings and leads formed by the shifting ice only allow for limited bearded seal occupation of the Chukchi Sea during winter and the majority of their population is thought to overwinter south of the Bering Strait (Burns 1981, Burns and Frost 1983).

The weight of adult bearded seals varies throughout the year but roughly averages between 250 and 300 kg (Kovacs and Lydersen 2008). The range of bearded seal average weights has also been reported as 200 to 250 kg (Reeves et al. 1992) and Trites and Pauly (1998) reported an average weight of 200 kg over all age classes. Additionally, Burns and Frost (1983) report a mean weight of 242 kg for mature bearded seals in the Bering and Chukchi seas. They are heaviest from late fall through early spring and are at their lightest in summer following molt (Burns and Frost 1983, Cameron et al. 2010). Burns and Frost (1983) reported adult females and males having average weights of 250 and 290 kg, respectively, in late winter/early spring and 229 and 244 kg in summer. Females in particular can lose a considerable amount of weight during lactation in late spring (Burns and Frost 1983). Adults have an average length of 2.0-2.4 m (Johnson et al. 1966, Burns and Frost 1983). At birth pups weigh approximately 34 kg and average 132 cm long (Burns 1970, Burns 1981). At weaning, 2 to 3 weeks later they will have increased their weight to 85 kg (Burns 1970, Burns 1981, Cameron et al. 2010). For this study, the average body mass of 200 kg calculated by Trites and Pauly (1998) is assumed.

It is thought that bearded seals may live up to 31 years (Reeves et al. 1992). Previously reported maximum ages for bearded seals in the Bering-Chukchi population are 26 years for males and 23 years for females (Burns and Frost 1983). Bearded seals near Svalbard had observed maximum ages of 27 and 18 years for males and females, respectively (Andersen et al. 1999). Trites and Pauly (1998) reported a maximum age of 31 and a longevity of 30 years, which is used here for the calculation of P/B.

There are no reliable abundance estimates for the Bering-Chukchi population (Allen and Angliss 2013); however, early estimates range as high as 300,000 (Burns 1981). In 1999 and 2000 aerial surveys flown during May and June in the eastern Chukchi Sea yielded density estimates of 0.07 seals km⁻² and

0.14 seals km⁻², respectively (Bengtson et al. 2005). Due to a lack of information on haulout behavior and because no correction factor for unobserved seals in the water is available, both Bengtson et al. (2005) and Allen and Angliss (2010) advise against using these densities to develop abundance estimates as they would likely be an underestimate. Cameron et al. (2010) went ahead and calculated a crude abundance estimate of 13,600 from the density estimates of Bengtson et al. (2005) and assuming there is similar occupation in the western Chukchi Sea, estimated a total Chukchi Sea population of ~27,000. Ver Hoef et al. (2013) calculated an estimate of 61,800 (95% credible interval 34,900-171,600) for bearded seals in the Bering Sea over a portion of their range. For the entire Bering Sea population, the Bearded Seal Biological Review Team (BRT) suggested an estimate double that of Ver Hoef et al. (2013), approximately 125,000 individuals (Cameron et al. 2010). Considering the high historical estimate of 300,000 (Burns 1981) and the more recent estimates of 125,000 for the Bering Sea and ~27,000 for the Chukchi Sea (Cameron et al. 2010), I estimated the total number of bearded seals for the combined Bering-Chukchi population to be 150,000. This number is assumed to be valid for the model base time period of 1990. Of the estimated 150,000, I assume that all migrate north through the Bering Strait into the Chukchi Sea in spring to maintain association with the pack ice, then return to the Bering Sea in fall spending a total of approximately 6 months in the Chukchi Sea. As there is not yet data available on the distribution of bearded seals throughout the Chukchi Sea, I am assuming half occupy the eastern Chukchi Sea and half the western Chukchi Sea. Therefore, 150,000 seals x half the year x half of the Chukchi Sea area = ~37,500 bearded seals in the model (150,000 x 0.5 x 0.5 = 37,500). A density estimate was calculated by multiplying the estimated model abundance times the individual weight (in metric tons) and dividing by the estimated model area ([37,500 x 0.200 tons]/192,054 km²). This produced a density estimate of 0.03905 t km⁻² within the model.

Currently, there is no reliable estimate of maximum net productivity so it is therefore recommended by Allen and Angliss (2010) to use the pinniped maximum theoretical net productivity rate (R_{MAX}) of 0.12 (Wade and Angliss 1997). Assuming harvest data during the 1960s and 70s are representative of the age and sex composition of the population, the gross productivity of the Bering-Chukchi population has

previously been estimated as 0.24 (Kelly 1988a). Life tables constructed from harvest data over the years 1975-1978 in the Bering, Chukchi, and Beaufort seas revealed pup mortality to be nearly 60% (Burns and Frost 1983). Estimated mortality dropped to 19% by age 1, to 10% by age 4, and averaged approximately 8% between the ages of 5 and 20 (Burns and Frost 1983). Beyond age 20, mortality rates increase until reaching 100% at age 26, which is the oldest age in the dataset of Burns and Frost (1983). This pattern of survivorship is consistent with the surrogate survivorship curve of fur seals. Production was calculated using a generalized model for marine mammal survivorship (Barlow and Boveng 1991, see Marine Mammal Production Rates in Appendix B). The P/B estimate of 0.0751 was calculated assuming a fur seal surrogate survivorship curve and a longevity of 30 years.

The Q/B was calculated assuming a prey caloric density of 1.5 kcal g^{-1} (Hunt et al. 2000) and a daily caloric requirement of $10,637 \text{ kcal d}^{-1}$, following the methods of Perez et al. (1990). This was scaled up to an annual rate producing a Q/B of 12.941.

Bearded seals are benthic foragers with relatively flexible diets, feeding primarily on brachyuran crabs, shrimp, mollusks, and to a lesser extent fish (Kenyon 1962, Johnson et al. 1966, Lowry et al. 1980a, Burns and Frost 1983, Lowry et al. 1983, Perez 1990, Dehn et al. 2007). The flexibility of the bearded seal diet also means they are not restricted to areas where a preferred prey item is abundant and allows for them to forage over the entire Bering-Chukchi shelf, while maintaining association with preferred ice conditions (Burns 1970). There is some evidence for an ontogenetic shift in diet with pups consuming a higher proportion of shrimp and isopods, then after their first year incorporating more crabs and clams in their diet (Lowry et al. 1980a, Burns and Frost 1983, Lowry et al. 1983). Diet has also been shown to vary with location and season (Lowry et al. 1980a, Burns 1981, Burns and Frost 1983, Lowry et al. 1983) making it difficult to quantify the proportions of particular prey in the bearded seal diet (Kelly 1988a, Dehn et al. 2007, Cameron et al. 2010). In the Bering Sea, bivalves only compose 4% of the bearded seal diet (Perez 1990); while in the Chukchi Sea they exceed 20% of the diet (Lowry et al. 1980a). Fish are estimated to comprise 23% of bearded seal diet in the eastern Bering Sea (Perez 1990) whereas they are estimated to only represent 6% or less at 3 of 4 sites within the Chukchi Sea (Lowry

et al. 1980a). Shrimp and crabs are amongst the most important prey in both the Chukchi and Bering seas (Kenyon 1962, Lowry et al. 1980a, Perez 1990).

The diet used here was derived from the values reported in Lowry et al. (1980a) for bearded seals collected at the Chukchi Sea coastal communities of Diomedea (N = 18) in Bering Strait, Shishmaref (N = 91) in the southeastern Chukchi Sea, Pt. Hope (N = 87, from Johnson et al. 1966) in the central eastern Chukchi Sea, and Wainwright (N = 26) from the northeastern Chukchi Sea. Lowry et al. (1980a) reported diets from seven total communities in the northern Bering and Chukchi seas but for the purposes of this Chukchi Sea model the data were limited to only those communities bordering the Chukchi Sea. The diets from the four communities were treated as having equal weight and averaged. When summed, the average diet only added up to 86% due to unidentified prey items and prey items of higher taxonomic classification. The remaining 14% of the diet was distributed amongst existing prey groups based on their relative portion in the existing diet. The prey group “crabs” was divided amongst the functional groups *C. opilio* and miscellaneous crabs and weighted by biomass. The top three prey items in the bearded seal diet are bivalves (33%), shrimp (25%), and *C. opilio* (19.5%).

Bearded seals have been an important subsistence resource as long as man has occupied Alaska (Burns and Frost 1983). They are taken for their meat and hides and many byproducts are derived from bearded seals including boot soles, boat skins, lines, clothing, window coverings, dyes from their blood, and implements made from their bones (Kenyon 1962, Burns 1981, Burns and Frost 1983, Reeves et al. 1992, Cameron et al. 2010). Over the years 1966 to 1977 the Alaska harvest of bearded seals averaged about 1,800 seals, ranging from a low of 1,050 in 1968 to a high of 4,750 in 1977 (Burns and Frost 1983). Records of the Alaska Eskimo Walrus Commission showed that 791 bearded seals were taken by five communities in the Bering Strait region between August of 1985 and July of 1986, 44% of which was taken by the Chukchi Sea coastal community of Shishmaref (Kelly 1988a). More recently, the total annual average harvest of bearded seals over the years 1994 to 2003 by North Slope Borough communities is estimated to be 1,314 (Bacon et al. 2009). The vast majority of the North Slope harvest reported by Bacon et al. (2009) is from the coastal Chukchi Sea communities of Barrow, Wainwright, Pt.

Lay, and Pt. Hope. Allen and Angliss (2011) examined data from an ADF&G subsistence harvest database covering the 1980s and 90s, and estimated the annual average harvest of bearded seals in Alaska as 6,788. Applying this annual harvest estimate to the aforementioned population estimate of 150,000 reduced the population estimate to 143,212. Calculating the abundance and density again using the same formula ($143,212 \times 0.5 \times 0.5 = 35,803$) and subtracting it from the previous density estimate (0.03534-0.03374) yielded an estimated annual harvest rate of $0.00177 \text{ t km}^{-2}$.

The bearded seal biomass estimate has a data pedigree of 7 because the estimate required selection from multiple incomplete sources with a wide range of estimates and extrapolation based on uncertain migration patterns. The pedigree for the subsistence harvest of bearded seals is 4, based on direct estimates but with incomplete coverage. The estimates of P/B and Q/B both have data pedigrees of 6 because they are based on general life history proxies. The diet composition has a pedigree of 4 because it is based on direct studies of bearded seal diet composition but with incomplete coverage of the model area.

Ringed Seal (*Phoca hispida*) – Ringed seals are found in ice-covered seas throughout the northern hemisphere including the Bering, Chukchi, and Beaufort seas in Alaska (Kelly 1988b, Kelly et al. 2010). They are year-round residents in ice-covered Arctic waters and are able to maintain breathing holes in ice up to 2 m thick by scratching the ice with claws on their foreflippers (Johnson et al. 1966, Lowry et al. 1983, Kelly 1988b). Ringed seals also tunnel into snow that accumulates above their breathing holes and create resting lairs and birth lairs which provide protection from the elements and from predators (Burns 1970, Smith et al. 1991, Kelly et al. 2010). Birth lairs are where females give birth to and nurse pups in late winter and early spring (Smith et al. 1991, Kelly et al. 2010). During spring and summer, those individuals that occupied the Bering and southern Chukchi Sea in winter follow the receding ice edge northward (Burns 1970, Kelly 1988b). Ringed seals rarely haul out on land and by migrating north in summer they can maintain association with their preferred ice habitat (Lowry et al. 1983, Kelly 1988b).

In the northern Bering Sea they have demonstrated a preference for dense ice coverage, with > 90% ice coverage and for large floes > 48 m in diameter (Simpkins et al. 2003).

Males mature at 5 to 7 years of age and females at 4 to 8 years (Johnson et al. 1966, Kelly 1988b) and the breeding season is from late March to mid-May (Johnson et al. 1966, Kelly 1988b). After fertilization, implantation is delayed about 3 to 3.5 months before active gestation begins which delays whelping until early the following spring from about mid-March to mid-April (Kelly 1988b, Kelly et al. 2010). Reported weights for pups at birth range from 4 to 5.4 kg (Burns 1970, Hammill et al. 1991, Smith et al. 1991) and at weaning they are estimated to weigh ~22 kg (Hammill et al. 1991, Smith et al. 1991). A typical adult ringed seal weighs 70 kg (Kelly et al. 2010) and the average size over all age classes for males is 44.3 kg and 40.7 kg for females (Trites and Pauly 1998). Ringed seals have an annual cycle in weight and are at their heaviest in mid-winter then drop weight from March through June (Johnson et al. 1966, Kelly 1988b, Kelly et al. 2010). Females lose weight in early spring when they reduce feeding during whelping and lactation and will continue to lose weight while molting in late spring (Kelly et al. 2010). Males also lose weight during the breeding season as they spend increasing amounts of time defending territories and finding prospective mates (Kelly et al. 2010). Following mating season they will continue losing weight while molting (Kelly et al. 2010). During molt ringed seals spend considerable amounts of time on the ice basking to facilitate the shedding and regeneration of skin and spend less time in the water feeding (Johnson et al. 1966, Lowry et al. 1980b, Kelly et al. 2010). Feeding increases following molting and weight is recouped through the summer, fall, and winter (Johnson et al. 1966, Lowry et al. 1980b, Kelly et al. 2010). The average individual body mass used in this study was calculated assuming a sex ratio of 1:1 and by averaging the sex-specific weights of Trites and Pauly (1998) which produced an average individual weight of 42.5 kg.

An accurate abundance estimate of the entire Alaska stock of ringed seals is not currently available (Allen and Angliss 2013). Estimates for the combined Bering, Chukchi, and Beaufort seas population have ranged as high as 1.5 million (Frost 1984) and Kelly et al. (2010) gave a “reasonable” estimate of one million. Aerial surveys were conducted in the eastern Chukchi Sea to estimate the density of ringed

seals during May and June of 1999 and 2000 between Bering Strait and Pt. Barrow and produced population estimates of 252,488 (SE = 47,204) in 1999 and 208,857 (SE = 25,502) in 2000 (Bengtson et al. 2005). The average of these two estimates is approximately 231,000 and was initially used here as the best available abundance estimate for ringed seals in the eastern Chukchi Sea. The area surveyed in 1999 (132,169 km²) and 2000 (128,703 km²) was less than the total area being modeled in this study (192,054 km²) and may therefore underestimate the actual number of ringed seals in the model area. Because ringed seals are year-round residents in the eastern Chukchi Sea this estimate was not reduced for seasonal changes in abundance. When multiplied by average individual body mass and divided by model area, the estimated biomass density was 0.05112 t km⁻². Using this biomass estimate produced an EE of 1.09. To bring this functional group into balance the higher population estimate of 252,488 from 1999 was used instead. This increased the biomass density estimate to 0.05587 t km⁻² and subsequently reduced the EE to 0.99.

Ringed seals are an important subsistence resource (Kenyon 1962) and are harvested by over 100 villages in Alaska (Allen and Angliss 2011). They are used for food and oil, handicrafts, and their skins are used for articles of clothing and other equipment (Georgette et al. 1998). The harvest from all villages is not reported in all years and the best estimate of annual Alaska harvest is 9,567 (Allen and Angliss 2011). This estimate was multiplied by the individual average body mass (42.5 kg) then divided by total model area giving a model harvest biomass density estimate of 0.00212 t km⁻².

Production was calculated using the generalized model of Barlow and Boveng (1991) for marine mammal survivorship. A fur seal surrogate life history was assumed and the longevity of 28 was the average (rounded to whole year) of sex-specific longevities calculated by Trites and Pauly (1998). Mortality rates summarized by Kelly (1988b) indicated that pup mortality was between 30 and 41%, which declined to 10% for adults, then gradually increased beyond the age of 15. The trend in mortality rates described by Kelly (1988b) is consistent with that of the fur seal surrogate. The P/B estimate for ringed seals is 0.0877.

The Q/B was calculated assuming a prey caloric density of 1.5 kcal g^{-1} (Hunt et al. 2000) and a daily caloric requirement of $3,358 \text{ kcal day}^{-1}$, following the methods of Perez et al. (1990). This was scaled up to an annual rate producing a Q/B of 19.228.

Ringed seals have a diverse diet and may utilize multiple species of fish and crustaceans (Kenyon 1962, Johnson et al. 1966, Lowry et al. 1978, 1980b, Lowry et al. 1983). Arctic cod and saffron cod are the primary fish prey but also consumed in smaller quantities are sculpins, forage fish, eelpouts, and flatfish (Lowry et al. 1980b, Lowry et al. 1983, Perez 1990). Shrimp are the dominant crustacean prey but other well represented crustaceans include euphausiids, mysids, and hyperiid and gammarid amphipods (Lowry et al. 1980b, Lowry et al. 1983, Perez 1990). The flexibility in their diet is made apparent in spatial and temporal differences in diet (Lowry et al. 1980b, Lowry et al. 1983). In the Chukchi Sea the overall pattern is for a diet dominated by fish, in particular Arctic cod from late fall to early spring and crustaceans dominating from late spring to fall (Johnson et al. 1966, Lowry et al. 1980b, Lowry et al. 1983). Nektonic crustaceans like shrimp, hyperiid amphipods, and euphausiids can occur in dense concentrations and at those different times and locations they may constitute the bulk of ringed seal stomach contents (Lowry et al. 1980b, Lowry et al. 1983). In spring at Little Diomedede, the primary prey of harvested ringed seals was shrimp followed by small amounts of mysids, gammarid amphipods, and fish (Kenyon 1962). The diet used here was compiled from multiple studies in the eastern Chukchi, Beaufort, and northern Bering seas by Perez (1990). The three most dominant prey items by volume are Arctic cod (45%), saffron cod (33%), and shrimp (10%).

The ringed seal biomass estimate has a data pedigree of 6 because the estimate comes from a single study with limited spatial coverage and does not overlap in time with the base model time period. The ringed seal subsistence harvest data pedigree is 4, based on direct estimates but with incomplete coverage. The estimates of P/B and Q/B both have data pedigrees of 6 because they are based on general life history proxies. The diet composition has a pedigree of 4 because it is based on direct studies of ringed seal diet composition but does not overlap with the base model time period.

Spotted Seal (*Phoca largha*) – In Alaska, spotted seals are found in the Chukchi, Bering and Beaufort seas. During winter in the Bering Sea their distribution is focused near the southern edge of the ice pack which is characterized by smaller ice floes (Burns 1970, Frost et al. 1983, Braham et al. 1984, Lowry et al. 2000, Simpkins et al. 2003). The ice is used by spotted seals to rest, pup, and molt (Burns 1970, Fay 1974, Braham et al. 1984). Occupation of the ice edge in winter puts them beyond the southern extent of the polar bear's range and significantly reduces their risk of predation (Burns 1970). When the ice-edge recedes during spring and summer, spotted seals migrate north and coastward into the northern Bering, Chukchi, and Beaufort seas (Burns 1970, Frost et al. 1983, Braham et al. 1984, Lowry et al. 1998, Lowry et al. 2000). In summer months when the ice has retreated to its minimum, spotted seals will regularly use coastal areas to haulout and rest (Frost et al. 1983, Quakenbush 1988, Frost et al. 1993, Lowry et al. 1998). A tagging study conducted in the eastern Chukchi Sea in the early 1990s showed spotted seals to haul-out for an average duration of just less than 2 days between foraging trips that averaged ~9 days in length (Lowry et al. 1998). Additionally, the at-sea locations indicated that foraging trips were focused on the eastern Chukchi Sea, specifically within 120 km of the Alaskan coast (Lowry et al. 1998). The location of haul out sites may be related to the proximity of prey as some of the regular haul-out sites in the eastern Bering and eastern Chukchi seas are near herring and capelin spawning areas (Quakenbush 1988).

Spotted seals are described as being slightly larger than ringed seals, though leaner and not as plump (Lowry 1984, Boveng et al. 2009). In the Bering Sea and Sea of Okhotsk, mature females on average weigh 68.3 kg and males 78.4 kg (Tikhomirov 1968, cited in Boveng et al. 2009). Trites and Pauly (1998) estimated mean body masses over all age classes for spotted seals using a sex-specific regression as 38.9 kg for females and 50.0 kg for males. A sex ratio of 1:1 is assumed and the mean body mass estimates of Trites and Pauly (1998) were averaged resulting in an estimated individual body mass of 44.5 kg.

The Bering-Chukchi population has previously been estimated at 280,000-300,000 with approximately 80,000 of those attributed to the Karaginski Bay concentration in the western Bering Sea

(Burns 1986). Reeves et al. (1992) has also described the Bering-Chukchi population as numbering at least 200,000. A provisional population estimate for the area surveyed (119,454 km²) in the central and eastern Bering Sea in the spring of 2007 and 2008 is 101,568 (SE = 17,869) (Boveng et al. 2009). More recently, Ver Hoef et al. (2013) calculated an overall population abundance estimate of 233,700 spotted seals (95% credible interval 137,300-793,100) for the area they surveyed in the central and eastern Bering Sea during the spring of 2007. Currently there is no reliable minimum estimate of spotted seal abundance in the Bering and Chukchi seas (Allen and Angliss 2013), therefore the total population estimate of ~200,000 (Burns 1986, Reeves et al. 1992) is used. It is clear that many spotted seals migrate north through the Bering Strait during the ice-free season and make extensive use of the eastern Chukchi Sea (Frost et al. 1993). In light of more detailed information I am making the crude assumption that half of the estimated population migrates into the Chukchi Sea, half of which occupy the eastern Chukchi Sea for half of the year. This produces an estimated model abundance of $200,000 \times 0.5 \times 0.5 \times 0.5 = 25,000$. Multiplying this estimated abundance by the average size (44.5 kg) gives a model biomass density estimate of 0.00579 t km⁻².

Spotted seals are an important subsistence resource in Alaska and may be harvested by over 100 villages (Allen and Angliss 2011). They are used for food, oil, and the skins are used to make clothing, floats, and other equipment (Georgette et al. 1998). Between the years 1966 to 1976 an average of about 2,400 spotted seals were harvested per year along the Bering-Chukchi coast of Alaska (Lowry 1984). A more recent assessment of subsistence harvest data compiled by the Alaska Department of Fish and Game (ADFG) through August 2000 resulted in an estimated annual harvest of 5,265 (Allen and Angliss 2011). At present this is the most reliable harvest estimate and is used here. This harvest estimate is for all of Alaska including areas outside the model area. And as such it is treated in the same manner as the total population estimate which is reduced to account for the proportion of the population seasonally migrating north into the Chukchi Sea (0.5), the estimated proportion in the eastern Chukchi Sea (0.5), and the portion of the year spent occupying the eastern Chukchi Sea (0.5). The resulting equation is $5,265 \times 0.5 \times$

0.5 x 0.5 \approx 658 harvested seals. Multiplying by average size (0.0445 t) and dividing by model area yields an estimated harvest biomass density of 1.52×10^{-4} t km⁻².

The P/B of spotted seals was estimated using a fur seal surrogate survivorship curve (Barlow and Boveng 1991) and assuming a longevity of 35 years (Burns 1986). This produced an estimated P/B of 0.068.

The Q/B was calculated with an average prey caloric density of 1.5 kcal g⁻¹ (Hunt et al. 2000) and the daily caloric requirement of 3,417 kcal was calculated following the methods of Perez (1990). The consumption estimate of 5% body weight per day was scaled up to an annual average resulting in a Q/B of 18.705.

The diet of spotted seals in the eastern Chukchi Sea and Bering Sea is dominated by fish (Lowry et al. 1983, Bukhtiyarov et al. 1984, Perez 1990, Dehn et al. 2007). This is supported by stable isotope analysis which has indicated a higher trophic level for spotted seals than for other benthic foraging pagophilic pinnipeds in the U.S. and Canadian Arctic (Dehn et al. 2007). In the Chukchi Sea the most important fish prey are pelagic forage fish, Arctic cod, saffron cod, and sculpins (Lowry et al. 1983). More recent stomach collections from the southeastern Chukchi Sea in 2000-2003 have also shown pelagic forage fish to be the dominant prey followed by the gadids, Arctic cod and saffron cod (Dehn et al. 2007). Other fish prey includes flatfish, pricklebacks and snailfish; and reported invertebrate prey items are shrimp, mysids, and amphipods (Lowry et al. 1983, Dehn et al. 2007). More than 95% of the stomach contents of spotted seals collected in the northern Bering Sea were fish, and of those prey Arctic cod, capelin, and saffron cod were the most prevalent (Bukhtiyarov et al. 1984). There are anecdotal reports of spotted seals feeding on salmon (*Oncorhynchus* sp.) (Frost et al. 1983), however salmon as prey are not quantitatively represented in any spotted seal diet studies that I am presently aware of.

Perez (1990) estimated the diet composition of spotted seals from multiple diet studies and a modified version of that diet is used in this model. Prey items that comprised less than 1% of the diet reported by Perez (1990) are not included. The compiled diet of Perez (1990) was derived from studies conducted throughout the species range in the eastern, western, and northern Bering Sea in addition to the

eastern Chukchi Sea. This resulted in a diet that included species that have not been reported as spotted seal prey in the eastern Chukchi Sea including walleye pollock (19%), Pacific cod (1%), and eelpouts (12%), which together account for 32% of the diet. In the Bering Sea these species represent significant portions of the overall fish biomass (Aydin et al. 2002, Aydin et al. 2007) and may be more available to spotted seals as prey, whereas in the eastern Chukchi Sea they are considerably less common and contribute less to the total fish biomass (Wolotira et al. 1977, Barber et al. 1997). The proportions of these prey items were reallocated by biomass to fish species (functional groups) that have been recorded in the diet of spotted seals in the eastern Chukchi Sea. This eliminated walleye pollock, eelpouts, and Pacific cod from the diet and increased the proportions of pelagic fish (+18%), Arctic cod (+10%), large-mouth sculpins (+2%), saffron cod (+1%), small-mouth flatfish (+1%), other sculpins (+<1%), and miscellaneous shallow fish (+<1%). The vast majority of the final diet is composed of fish (96%) and primarily pelagic forage fish (46%) which is consistent with the observations of previous diet studies (Lowry et al. 1983, Bukhtiyarov et al. 1984, Dehn et al. 2007).

The spotted seal biomass estimate has a data pedigree of 7 because the estimate required selection from multiple incomplete sources with a wide range of estimates and extrapolation of uncertain migration patterns. The subsistence harvest data pedigree for spotted seals is 5 because it is based on a direct estimate with limited confidence and requires the inclusion of uncertain scaling factors. The estimates of P/B and Q/B both have data pedigrees of 6 based on general life history proxies. The diet composition has a pedigree of 5 because it is based on direct studies of spotted seal diet composition but does not overlap with the base model time period.

Seabirds

Murres (*Uria spp.*) – The murre functional group is composed of two species, the common murre (*Uria aalge*) and the thick-billed murre (*Uria lomvia*). The biomass density estimate for this group is based on colony counts from the Beringian Seabird Colony Catalog (USFWS 2003). The total biomass

was estimated by multiplying the colony counts for each species from within the model area by their respective average body mass and summing to arrive at a total group biomass. For the common murre and thick-billed murre there are an estimated 82,470 and 152,330 birds, respectively. The average individual body mass of common murres is 0.993 kg and for thick-billed murres it is 0.964 kg (Hunt et al. 2000). In the case of unidentified murres (*Uria* spp.), the average body mass of both species was used to calculate an average body mass weighted by the observed proportion of species. This weighted average (0.974 kg) was multiplied by the estimated abundance of unidentified murres (435,305). Due to seasonal ice coverage, seabirds were assumed to only occupy the eastern Chukchi Sea for about one-third of the year (~4 months). The total biomass estimate was multiplied by 0.333 then divided by the total model area to result in a biomass density estimate of 0.00114 t km⁻².

Estimates of P/B (see Seabird Production Rates in Appendix B) and Q/B were taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The P/B of 0.169 was derived from a range of survival rates reported in Schreiber and Burger (2001). The Q/B of 72 was calculated from generalized diet information and prey energy densities reported in (Hunt et al. 2000). The diet used here was based on the diet data reported in multiple studies (Springer et al. 1984, Fadely et al. 1989, Hunt et al. 2000). The murre functional group diet is comprised of copepods (45%), Arctic cod (19.5%), other zooplankton (15%), pelagic forage fish (13%), and a mixture of fish functional groups make up the remainder of the diet.

The data pedigree for murre biomass is 4 based on direct estimates with incomplete coverage and extrapolation of uncertain migration patterns. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are taken from the eastern Bering Sea Ecopath model. The diet composition has a pedigree of 6 based on diet studies of the same species in adjacent regions.

Kittiwakes – The kittiwake group is represented by a single species, the black-legged kittiwake (*Rissa tridactyla*). The biomass density estimate is based on colony counts from the Beringian Seabird Colony Catalog (USFWS 2003). The total biomass was estimated by summing the colony counts from

within the model area then multiplying by the average body mass (0.407 kg). Kittiwakes were assumed to only occupy the model area for about one-third of the year (~4 months) due to seasonal ice coverage. Reducing the total biomass estimate to account for seasonal occupation and dividing by the model total area resulted in a density estimate of $8.43 \times 10^{-5} \text{ t km}^{-2}$.

Estimates of P/B (see Seabird Production Rates in Appendix B) and Q/B were taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The P/B of 0.076 was derived from multiple survival rates reported in Schreiber and Burger (2001). The Q/B of 110 was calculated from generalized diet information and prey energy densities reported in (Hunt et al. 2000). The diet used here is based on diet descriptions from multiple studies (Hunt et al. 1981, Fadely et al. 1989, Hunt et al. 2000). Arctic cod are the dominant prey item accounting for 71% of the diet by volume. The remainder of the diet is attributed to saffron cod (9%), pelagic forage fish (9%), worms etc. (5%), copepods (4%), other zooplankton (1%), and other gadids (< 1%).

The data pedigree for kittiwake biomass is 4 based on direct estimates with incomplete coverage and extrapolation of uncertain migration patterns. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are taken from the eastern Bering Sea Ecopath model. The diet composition has a pedigree of 6 based on diet studies of the same species in adjacent regions.

Puffins (*Fratercula spp.*) – Puffins are represented in the eastern Chukchi Sea by two species, the tufted puffin (*Fratercula cirrhata*) and the horned puffin (*F. corniculata*). The biomass density estimate for this group is based on colony counts from the Beringian Seabird Colony Catalog (USFWS 2003). The total biomass was estimated by summing the colony counts from within the model area then multiplying by the average body mass. Puffins were assumed to only occupy the model area for about one-third of the year (~4 months) due to seasonal ice coverage. The total biomass estimate was reduced to account for seasonal occupation, and then divided by the model total area, producing a density estimate of $2.18 \times 10^{-5} \text{ t km}^{-2}$.

Estimates of P/B (see Seabird Production Rates in Appendix B) and Q/B were taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). P/B was approximated with an estimated annual mortality rate of 0.040 for Atlantic puffins (Furness and Monaghan 1987). The Q/B of 73 was calculated from generalized diet information and prey energy densities reported in (Hunt et al. 2000). The diet of puffins was estimated based on the diet information reported by Hunt et al. (1981) and Hunt et al. (2000). The primary prey items of puffins are pelagic forage fish (43%) and Arctic cod (37%). Secondarily, puffins prey upon copepods (5%), saffron cod (5%), benthic amphipods (4%), worms etc. (4%), and other zooplankton (2%).

The data pedigree for puffin biomass is 4 based on direct estimates with incomplete coverage and extrapolation of uncertain migration patterns. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are taken from the eastern Bering Sea Ecopath model. The diet composition has a pedigree of 6 based on diet studies of the same species in adjacent regions.

Cormorants – Cormorants are represented by a single species, the pelagic cormorant (*Phalacrocorax pelagicus*). The biomass density estimate is based on colony counts from the Beringian Seabird Colony Catalog (USFWS 2003). The total biomass was estimated by summing the colony counts from within the model area then multiplying by the average body mass. Pelagic cormorants were assumed to only occupy the model area for about one-third of the year (~4 months) due to seasonal ice coverage. Reducing the total biomass estimate to account for seasonal occupation and dividing by the model total area resulted in a density estimate of $1.46 \times 10^{-6} \text{ t km}^{-2}$.

Estimates of P/B (see Seabird Production Rates in Appendix B) and Q/B were taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The P/B of 0.159 was derived from a range of survival rates reported in Schreiber and Burger (2001). The Q/B of 73 was calculated from generalized diet information and prey energy densities reported in (Hunt et al. 2000). The diet of pelagic cormorants (Furness and Monaghan 1987) is based on diet descriptions reported by Hunt et al. (1981) and Hunt et al. (2000). The majority of the diet is comprised of fish (90%), with zooplankton making up the rest (10%).

Arctic cod are the primary prey (75%) followed by saffron cod (10%), copepods (7.5%), pelagic forage fish (5%), and other zooplankton (2.5%).

The data pedigree for cormorant biomass is 4 based on direct estimates with incomplete coverage and extrapolation of uncertain migration patterns. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are taken from the eastern Bering Sea Ecopath model. The diet composition has a pedigree of 6 based on diet studies of the same species in adjacent regions.

Gulls – The gull group is made up of three species: the glaucous gull (*Larus hyperboreus*), Sabine's gull (*Xema sabini*), and mew gull (*Larus canus*). The biomass density estimate for this group is based on colony counts from the Beringian Seabird Colony Catalog (USFWS 2003). The total biomass was estimated by summing the colony counts from within the model area then multiplying by the average body mass. Gulls were assumed to only occupy the model area for about one-third of the year (~4 months) due to seasonal ice coverage. The total biomass estimate was reduced to account for seasonal occupation, and then divided by the model total area, producing a density estimate of $8.42 \times 10^{-6} \text{ t km}^{-2}$.

Estimates of P/B (see Seabird Production Rates in Appendix B) and Q/B were taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The P/B of 0.166 was derived from a range of survival rates reported in Schreiber and Burger (2001). The Q/B of 73 was calculated from generalized diet information and prey energy densities reported in (Hunt et al. 2000). The diet of gulls was derived from the general diet reported in Hunt et al. (2000). Their diet composition is estimated as 45% pelagic forage fish, 39% Arctic cod, 5% saffron cod, 5% benthic amphipods, 4% copepods, and 1% other zooplankton.

The data pedigree for gull biomass is 4 based on direct estimates with incomplete coverage and extrapolation of uncertain migration patterns. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are taken from the eastern Bering Sea Ecopath model. The diet composition has a pedigree of 6 based on diet studies of the same species in adjacent regions.

Planktivorous Seabirds – The planktivorous seabird group is comprised of three species of auklets, the parakeet auklet (*Aethia psittacula*), least auklet (*A. pusilla*), and crested auklet (*A. cristatella*). The biomass density estimate for this group is based on colony counts from the Beringian Seabird Colony Catalog (USFWS 2003). The total biomass was estimated by summing the colony counts from within the model area then multiplying by the average body mass. Auklets were assumed to only occupy the model area for about one-third of the year (~4 months) due to seasonal ice coverage. The total biomass estimate was reduced to account for seasonal occupation, and then divided by the model total area, producing a density estimate of $1.39 \times 10^{-4} \text{ t km}^{-2}$.

Estimates of P/B (see Seabird Production Rates in Appendix B) and Q/B were taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The P/B of 0.169 was derived from a range of survival rates reported in Schreiber and Burger (2001). The Q/B of 110 was calculated from generalized diet information and prey energy densities reported in (Hunt et al. 2000). The diet of auklets was derived from the general diet reported in Hunt et al. (2000). The estimated diet composition of this group is 71% copepods, 24% other zooplankton, and 4% Arctic cod.

The data pedigree for planktivorous seabird biomass is 4 based on direct estimates with incomplete coverage and extrapolation of uncertain migration patterns. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 based on diet studies of the same species in adjacent regions.

Fish

Large-mouth Flatfish –The large-mouth flatfish group includes two species of large predatory flatfish, the Pacific halibut (*Hippoglossus stenolepis*) and the Greenland turbot (*Reinhardtius hippoglossoides*, also known as Greenland halibut).

The biomass density estimate of this group comes from the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994). This group is scarcely represented with the low density

estimate of $3.50 \times 10^{-4} \text{ t km}^{-2}$. Small numbers of Pacific halibut and Greenland turbot have also been found in the southeastern Chukchi Sea during a bottom-trawl survey conducted in 1976 (Wolotira et al. 1977).

Region-specific estimates of P/B or Q/B, or the data required to calculate these parameters were not available for this group. An average P/B and Q/B was calculated from species-specific values for the eastern Bering Sea (Aydin et al. 2007) weighted by the biomass estimates derived from the 1990 survey of the northeastern Chukchi Sea. This resulted in a P/B of 0.188 and a Q/B of 1.114.

The diet data was attained by querying the REEM food habits database of stomach collections made in the eastern Bering Sea (see Fish Diets in Appendix B). Queries were limited to data collection in the eastern Bering Sea from northern survey strata only and to stations less than 100 m depth. The final diet is an average diet, weighted by the estimated total consumption of each species. The major prey items are Arctic cod (48%), miscellaneous crabs (13%), snow crab (8%), small-mouth flatfish (6%), other zooplankton (4%), pelagic forage fish (4%), shrimps (3%), eelpouts (2%), miscellaneous shallow fish (2%), Pacific cod (2%), large-mouth sculpin (1%), other sculpin (1%), cephalopods (1%), benthic amphipods (1%), saffron cod (1%), and worms etc. (1%). The remaining 3% is comprised of an assortment of benthic invertebrates and fishes.

The data pedigree for large-mouth flatfish biomass is 2 because it is based on a direct estimate but with limited coverage. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are based on species-specific parameter values taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 based on diet studies of the same species in adjacent regions.

Small-mouth Flatfish –Small-mouth flatfish is comprised of a number of benthic foraging flatfish and includes Bering flounder (*Hippoglossoides robustus*), yellowfin sole (*Limanda aspera*), longhead dab (*L. proboscidea*), Sakhalin sole (*L. sakhalinensis*), Arctic flounder (*Liopsetta glacialis*), starry flounder (*Platichthys stellatus*), and Alaska plaice (*Pleuronectes quadrituberculatus*).

The biomass density of this group was initially calculated from the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) using the area-swept method (Wakabayashi et al. 1985). The survey-derived density estimate of 0.022 t km^{-2} proved to be too low as initial balancing efforts produced EE values greater than 1. A top-down balance was used instead to solve for B, assuming an EE of 0.8, and produced a density estimate of 0.3128 t km^{-2} .

P/B was calculated for Bering flounder, yellowfin sole, starry flounder, and Alaska plaice using a regression estimator of mortality from Hewitt and Hoenig (2005). This method requires only a single input, an estimate of maximum age. The P/B of Bering flounder was calculated with a maximum age derived from the 1990 bottom trawl survey, while the P/Bs of yellowfin sole, starry flounder, and Alaska plaice were calculated with maximum ages derived from the 1976 bottom trawl survey of the southeastern Chukchi Sea (Wolotira et al. 1977). The P/Bs for longhead dab and Sakhalin sole were taken from the miscellaneous flatfish functional group of the eastern Bering Seafood web model (Aydin et al. 2007). An estimate of P/B or the data required to calculate it were not available for Arctic flounder, so the other members of this functional group are taken as representative of this species. The final P/B estimate of 0.386 for this group was calculated as an average, weighted by survey-derived biomass estimates.

The Q/B for this group was calculated following the methods of Aydin (2004) which requires a minimum of data; an estimate of mortality (Z) and an estimate of K from the von Bertalanffy growth function (vBGF). Estimates of mortality were taken from the previous calculations of P/B following the methods of Hewitt and Hoenig (2005). The vBGF parameter K was taken from Smith et al. (1997a) for Bering flounder and from Wolotira et al. (1977) for yellowfin sole, starry flounder, and Alaska plaice. Estimates of Q/B for longhead dab and Sakhalin sole are taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The required parameters were not available for Arctic flounder, so the other members of this group are taken as representative for this species. The final Q/B estimate of 1.699 for this group was calculated as an average, weighted by the survey-derived biomass estimates.

A limited number of diet studies describing the diets of small-mouth flatfish within the Chukchi Sea and adjacent waters have been conducted. The autumn diet of starry flounder collected in the

northeastern Bering Sea and southeastern Chukchi Sea was generally dominated by brittle stars and bivalves, though the importance of different food items varied between the two regions (Jewett and Feder 1980). In the southeastern Chukchi Sea, the most important prey of starry flounder were echiuran worms, prickleback fish (Stichaeidae), and shrimps (Hippolytidae), while in the northeastern Bering Sea the dominant prey were bivalves, brittle stars, and sand dollars (Jewett and Feder 1980). In the northeastern Chukchi Sea, the dominant prey items of Bering flounder were fish, benthic amphipods, and shrimps (Coyle et al. 1997). Atkinson and Percy (1992) reported on the diet of Arctic flounder collected in the southeastern Beaufort Sea, where they found the diet to be dominated by benthic invertebrates including polychaetes, tunicates, and bivalves. In the absence of more detailed region-specific data, the composite diet for the small-mouth flatfish group was taken from the REEM food habits database of stomach collections made in the eastern Bering Sea (see Fish Diets in Appendix B). The diets of Bering flounder, yellowfin sole, Sakhalin sole, and Alaska plaice were calculated from stomachs collected in the northern Bering Sea during the summer of 2010 (see Fish Diets in Appendix B). The food habits of longhead dab and starry flounder were derived from collections made on the eastern Bering Sea shelf. No food habits data were available for Arctic flounder, so the other species in this functional group are taken as representative. The final diet is an average diet, weighted by the estimated total consumption of each species. The primary prey items are benthic amphipods (37%), other zooplankton (27%), polychaetes (12%), pelagic fish (9%), shrimps (9%), and bivalves (5%). The remaining ~1% of the diet is comprised of trace amounts from several benthic invertebrate groups.

The data pedigree is 8 for the biomass estimate of small-mouth flatfish because it is estimated by Ecopath. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are based on a combination of region-specific data and parameter values taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 because it is based on diet studies of the same species in an adjacent region.

Large-mouth sculpin –The large-mouth sculpin group includes at least four species from the genera *Myoxocephalus* and *Hemilepidotus*. Sculpins identified as *M. scorpius groenlandicus* during a trawl survey of the southeastern Chukchi Sea in 1976 (Wolotira et al. 1977) and sculpins identified as *M. verrucosus* during the 1990 trawl survey of the northeastern Chukchi Sea (Barber et al. 1997) are thought to be *M. scorpius*, however further work is required to resolve the taxonomy and zoogeography of these species (Mecklenburg et al. 2011).

The biomass estimate of this group was initially calculated from the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) as 0.064 t km^{-2} . However, initial model balancing produced EE values greater than 1 so a top-down balance assuming $EE = 0.8$ was used. This produced a biomass estimate of 0.267 t km^{-2} .

The data required to estimate P/B and Q/B were not available for any species of this functional group, so the P/B of 0.4 and Q/B of 2 were taken directly from the eastern Bering Sea Ecopath model (Aydin et al. 2007). In the absence of large-mouth sculpin life history data, these default values, which closely approximate other groundfish (e.g., walleye pollock, Pacific cod, saffron cod, other sculpins), are used in their place (Aydin et al. 2007).

A limited amount of information is available describing the food habits of species from this functional group within the Arctic. The diet of *Myoxocephalus scorpius* collected from South Baffin Island in the eastern Canada Arctic included fish, decapods, amphipods, snails, and polychaetes (Atkinson and Percy 1992). In nearshore waters (< 3 m) of Cumberland Sound, Baffin Island, *M. scorpius* preyed upon the ice-associated amphipod *Onisimus glacialis*, Hyperiid amphipods, snails, and bivalves (Moore and Moore 1974). During spring in the northern Bering Sea, Cui et al. (2012) examined stomachs from *M. scorpius* and found crabs, benthic amphipods, and polychaetes to be the dominant prey items. Within the crab group, *C. opilio* was the dominant prey species (Cui et al. 2012). In the absence of region-specific data, the diet composition of this group was derived from queries of the REEM food habits database (see Fish Diets in Appendix B). Food habits data were only available for three species from this group; the butterfly sculpin (*Hemilepidotus papilio*), great sculpin (*Myoxocephalus*

polyacanthocephalus), and the warty sculpin (*M. verrucosus*). Queries for the butterfly sculpin and warty sculpin were limited to northern strata and stations less than 100 m depth. The great sculpin query was not spatially limited. The final diet is an average diet, weighted by the estimated total consumption of each species. The primary prey items are snow crab (*Chionoecetes opilio*) (57%) and miscellaneous crabs (24%). Other prey groups include worms etc. (4.5%), shrimps (4%), polychaetes (3%), benthic amphipods (2.5%), Arctic cod (1%), other sculpins (1%), eelpouts (1%), and other zooplankton (1%). The remaining ~2% of the diet is divided among several fish and invertebrate groups.

The data pedigree is 8 for the biomass estimate of large-mouth sculpins because it is estimated by Ecopath. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameter values are taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 because it is based on diet studies of the same species in an adjacent region.

Other Sculpins –The other sculpins group includes species from at least 10 genera including *Artediellus*, *Blepsias*, *Enophrys*, *Gymnocanthus*, *Icelus*, *Megalocottus*, *Microcottus*, *Nautichthys*, and *Triglops*.

A biomass estimate of 0.013 t km⁻² was calculated from the 1990 bottom-trawl survey and used in initial model balancing. Many of the species in this group are small and not consistently caught by bottom-trawl gear and initial EE values greater than 1 were interpreted as indicating the biomass estimate was too low. A top-down balance was used instead, assuming an EE of 0.8 and increased the biomass estimate to 0.04942 t km⁻².

The only species from this group for which the requisite data to calculate P/B and Q/B was available was the Arctic staghorn sculpin (*Gymnocanthus tricuspis*). P/B was calculated following the methods of Hewitt and Hoenig (2005) and Q/B according to Aydin (2004). The calculation of P/B requires an estimate of maximum age and Q/B requires an estimate of the von Bertalanffy growth function (vBGF) parameter K, both of which are reported by Smith et al. (1997b). An estimate of P/B and Q/B for the rest of the species in this functional group is taken from the taxonomically similar “small sculpin” group of

the eastern Bering Sea Ecopath model (Aydin et al. 2007). The final P/B of 0.461 was calculated as a weighted average of the 1990 survey-derived biomass estimate of the Arctic staghorn sculpin and the estimated biomass of the remaining sculpins of this group combined. The final Q/B of 2.428 was calculated in a similar fashion but was instead weighted by total consumption.

A limited amount of information is available describing the food habits of species from this functional group within Arctic waters. Atkinson and Percy (1992) reported on the food habits of five species of “other” sculpins (*Gymnocanthus tricuspis*, *Icelus bicornis*, *I. spatula*, *Triglops murrayi*, *T. pingeli*) collected in the Canada Arctic. They found the dominant prey items to include amphipods, polychaetes, cumaceans, isopods, copepods, and other zooplankton. Cui et al. (2012) examined the food habits of *G. tricuspis* during spring in the northern Bering Sea and identified benthic amphipods as the most important prey, followed by polychaetes and bivalve siphons. In the northeastern Chukchi Sea, Coyle et al. (1997) found the diet of *G. tricuspis* to include polychaetes, snails, benthic amphipods, miscellaneous crustaceans, shrimp, and euphausiids. In lieu of detailed region-specific data, the diet composition for this group was obtained from food habits collections made on the eastern Bering Sea shelf during National Marine Fisheries Service (NMFS) bottom trawl surveys (see Fish Diets in Appendix B). Diet data were only available for three species (*Icelus spiniger*, *Triglops forficata*, *T. pingeli*), which in-turn represents the diet of the entire functional group. The final diet is an average diet, weighted by the estimated total consumption of the three species. The most prominent prey items are benthic amphipods (73%), polychaetes (10%), other zooplankton (8.5%), misc. shallow fish (5.5%), and bivalves (2%). The remaining diet is comprised of copepods and benthic invertebrates.

The data pedigree is 8 for the biomass estimate of other sculpins because it is estimated by Ecopath. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are based on a combination of region-specific data and parameter values taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 based on diet studies of the same species in an adjacent region.

Eelpouts –The eelpout (family Zoarcidae) group is made of at least seven species from two genera, *Gymnelus* and *Lycodes*.

Initially, the biomass estimate of this group was calculated as 0.022 t km^{-2} from the catch data of a 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994). This estimate proved to be too low as initial model balancing produced EE values greater than 1. A top down balance assuming an EE of 0.8 was used instead and produced a biomass estimate of $0.03564 \text{ t km}^{-2}$.

The data required to estimate P/B and Q/B were not available for any species of this functional group, so the P/B of 0.4 and Q/B of 2 were taken directly from the eastern Bering Sea Ecopath model (Aydin et al. 2007). In the absence of eelpout life history data, these default values which closely approximate other groundfish (e.g., walleye pollock, Pacific cod, saffron cod, other sculpins) are used in their place (Aydin et al. 2007).

Atkinson and Percy (1992) examined the diet of *Gymnelus viridus* and *Lycodes polaris*, collected from the south end of Baffin Island in the eastern Canada Arctic, and found polychaetes to be the most important prey for *G. viridus*, while bivalve siphons dominated the diet of *L. polaris*. In lieu of region-specific data, the composite eelpout diet was taken from the Resource Ecology and Ecosystem Modeling program's food habits database of stomach collections made in the eastern Bering Sea (see Fish Diets in Appendix B). Diet data were only available for two species (*Lycodes palearis* and *L. raridens*) from this group and they are taken as representative of the rest of the group. The diet query for *L. palearis* was limited to northern survey strata and stations less than 100 m depth. The final diet is an average diet, weighted by the estimated total consumption of the two species. The major prey items are benthic amphipods (49%), polychaetes (13%), bivalves (11%), miscellaneous shallow fish (7%), snow crab (*Chionoecetes opilio*) (5%), Arctic cod (5%), worms etc. (4%), shrimps (2%), pelagic forage fish (1%), brittle stars (1%), small-mouth flatfish (1%), and miscellaneous crustaceans (1%). Walleye pollock and miscellaneous crabs each comprised less than 1% of the diet composition.

The data pedigree is 8 for the biomass estimate of eelpouts because it is estimated by Ecopath. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameter values reflect general life

history proxies and are taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 because it is based on diet studies of the same species in an adjacent region.

Pelagic Forage Fish –Pelagic forage fish is a composite group comprised of species from three families. This group includes Pacific sand lance (*Ammodytes hexapterus*) from the family Ammodytidae, Pacific herring (*Clupea pallasii*) from Clupeidae, and capelin (*Mallotus villosus*) and rainbow smelt (*Osmerus mordax*) from Osmeridae.

A biomass estimate for this group was originally calculated as 0.020 t km⁻² from the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994). Initial model balancing using this estimate produced EE values greater than 1. This group of pelagic fish was assumed to be undersampled by the bottom-trawl gear used in the 1990 survey resulting in a low estimate of B. A top-down balance assuming EE = 0.8 was used instead and produced a biomass estimate of 0.54552 t km⁻².

The P/B of Pacific herring and rainbow smelt was calculated following the methods of Hewitt and Hoenig (2005). This method requires an estimate of maximum age which was obtained from Wolotira et al. (1977). An estimate of capelin P/B was taken directly from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). No estimate of Pacific sand lance P/B was available. The final P/B of 0.551 is an average P/B weighted by the 1990 survey-derived biomass estimate.

An estimate of Q/B could only be calculated for Pacific herring and rainbow smelt. It was calculated according to the methods of Aydin (2004), which requires an estimate of mortality (Z) and an estimate of the parameter K from the von Bertalanffy growth function. Estimates of mortality for Pacific herring and rainbow smelt are available from the previous calculation of P/B and estimates of K for both these species are available from Wolotira et al. (1977). The Q/B of capelin was taken from the eastern Bering Sea Ecopath model (Aydin et al. 2007) and no estimate of Q/B was available for Pacific sand lance. The final Q/B of 2.978 was calculated as an average, weighted by the survey-derived biomass estimates.

The diet composition for this group was obtained from food habits collections made on the eastern Bering Sea shelf during NMFS bottom trawl surveys (see Fish Diets in Appendix B). Diet data was only

available for Pacific herring, rainbow smelt, and capelin, who in-turn represent the diet of the entire functional group. Diet queries for capelin and Pacific herring were spatially limited to northern survey strata and to stations less than 100 m depth. The final diet is an average diet, weighted by the estimated total consumption of the three species. The primary prey items for this group are other zooplankton (87%), copepods (10%), misc. crustaceans (2%), and benthic amphipods (1%). Polychaetes and shrimps each account for less than 1% of the diet composition.

The data pedigree is 8 for the biomass estimate of pelagic forage fish because it is estimated by Ecopath. The data pedigree is 6 for the estimates of P/B and Q/B because the parameters are based on a combination of region-specific data and parameter values taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 based on diet studies of the same species in an adjacent region.

Miscellaneous Shallow Fish –Miscellaneous shallow fish is a composite group of at least 18 species of demersal fish including poachers (Agonidae), wolffish (Anarhichadidae), lumpsuckers (Cyclopteridae), greenlings (Hexagrammidae), snailfish (Liparidae), and pricklebacks (Stichaeidae).

An initial biomass estimate of 0.008 t km^{-2} was calculated from the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994). Initial model balancing produced EE values greater than 1 and was interpreted to reflect the low catchability to bottom-trawling of many species in this group. Instead the biomass was estimated by the model as $0.19294 \text{ t km}^{-2}$ assuming $EE = 0.8$.

The data required to estimate P/B and Q/B were not available for any species of this functional group, so the P/B of 0.4 and Q/B of 2 were taken directly from the eastern Bering Sea Ecopath model (Aydin et al. 2007). In the absence of species-specific life history data these default values, which closely approximate other groundfish (e.g., walleye pollock, Pacific cod, saffron cod, other sculpins) are used in their place (Aydin et al. 2007).

Limited information is available describing the food habits within the Arctic for species included in this functional group. In the Canada Arctic, Atkinson and Percy (1992) reported on the diets of three

species of fish from this group, *Ulcina olrikii* (Agonidae), *Liparis gibbus* (Liparidae), *Lumpenus fabricii* (Stichaeidae). From fish collections made in the southeastern Beaufort Sea, the most important prey items in the diets of *U. olrikii* were bivalve siphons and amphipods. From the same region, the diet of *Lumpenus fabricii* was dominated by polychaetes with amphipods of secondary importance. The diet of *Liparis gibbus*, collected at the south end of Baffin Island in the eastern Canada Arctic, was dominated by amphipods (Atkinson and Percy 1992). Byers and Prach (1988) examined the food habits of the kelp snailfish (*Liparis tunicatus*) in Jones Sound, Canadian High Arctic, and found benthic amphipods to be the dominant prey, but the diet also included cumaceans, mysids, and cyclopoid copepods. During spring in the northern Bering Sea, Cui et al. (2012) identified benthic amphipods as the most important prey in the diets of snailfish (Liparidae) and *U. olrikii*. Due to a lack of region-specific data the diet composition for this group was obtained from food habits collections made on the eastern Bering Sea shelf during NMFS bottom trawl surveys (see Fish Diets in Appendix B). Diet data were only available for six species (*Hexagrammos stelleri*, *Aspidophoroides bartoni*, *Ocella dodecaedron*, *Podothecus acipenserinus*, *Liparis gibbus*, and *Eumicrotremus orbis*) who in-turn represent the diet of the entire functional group. The final diet is an average diet, weighted by the estimated total consumption of the three species. The major prey items of the final diet are benthic amphipods (28%), shrimps (19%), snow crab (*Chionoecetes opilio*) (18%), polychaetes (11%), zooplankton (10%), and misc. shallow fish (5%). The remainder of the diet includes demersal fish, benthic invertebrates, and copepods.

The data pedigree is 8 for the biomass estimate of miscellaneous shallow fish because it is estimated by Ecopath. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameter values reflect general life history proxies and are taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 because it is based on diet studies of the same species in an adjacent region.

Walleye Pollock (*Theragra chalcogramma*) –Walleye pollock are a demersal roundfish belonging to the family Gadidae. They are a dominant component of the ecosystem in the nearby eastern Bering

Sea, supporting one of the world's largest single-species fisheries (Zador and Gaichas 2010). Due to their commercial importance and ecological significance elsewhere walleye pollock are modeled as a single-species separate from other gadids.

Where walleye pollock have a highly significant presence in the eastern Bering Sea they account for a much smaller proportion of the fish biomass in the eastern Chukchi Sea. A biomass estimate of $0.00189 \text{ t km}^{-2}$ was calculated from the catch data of the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) and is used here without adjustment.

The data required to make region-specific estimates of P/B and Q/B were not available for walleye pollock in the eastern Chukchi Sea. In their place, estimates of P/B (0.548) and Q/B (2.713) from another gadid, Arctic cod, are used. The two species had similar maximum sizes recorded during the 1990 bottom trawl survey (21 cm for walleye pollock and 23 cm for Arctic cod) and are assumed to have similar habitat requirements, diet, and life history within the eastern Chukchi Sea. Walleye pollock are likely less productive within the eastern Chukchi Sea and using eastern Bering Sea values may provide overestimates of production and consumption.

The diet composition for this group was obtained from food habits collections made on the eastern Bering Sea shelf during NMFS bottom trawl surveys (see Fish Diets in Appendix B). Queries were spatially restricted to northern survey strata in water less than 100 m depth and temporally restricted to collections made during 1990. Because a predator's diet may change with increasing size (Buckley et al. 1999, Yang et al. 2006), queries were also restricted to predators who were ≤ 21 cm, which is equal to the maximum length reported from the 1990 bottom trawl survey of the northeastern Chukchi Sea. The final diet is comprised of other zooplankton (46%), copepods (25%), benthic amphipods (20%), misc. crustaceans (4%), shrimps (3%), Arctic cod (2%), polychaetes (0.5%), and walleye pollock ($< 0.1\%$).

The data pedigree for the biomass of walleye pollock is 2 because it is based on a direct estimate but with limited coverage. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are based on general life history proxies. The diet composition also has a data pedigree of 6 because it is based on diet studies of the same species in an adjacent region.

Pacific cod (*Gadus macrocephalus*) –Pacific cod are a predatory groundfish from the family Gadidae. They are a species of commercial importance in other parts of Alaska and as such are treated as an individual functional group here.

A biomass estimate of $0.00188 \text{ t km}^{-2}$ was calculated from the catch data of the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) and is used here without adjustment.

Region-specific estimates of P/B and Q/B are not available for this species. In their place the P/B (0.488) and Q/B (2.288) calculated for saffron cod (*Eleginus gracilis*) are used, based on the presumption that they have similar life histories, diet, and habitat requirements. Pacific cod are likely less productive within the eastern Chukchi Sea and using eastern Bering Sea values may provide overestimates of production and consumption.

The diet composition for this group was obtained from food habits collections made on the eastern Bering Sea shelf during NMFS bottom trawl surveys (see Fish Diets in Appendix B). Queries were spatially restricted to northern survey strata in water less than 100 m depth and temporally restricted to collections made during 1990. Additionally, because a predator's diet may change with increasing size (Buckley et al. 1999, Yang et al. 2006), queries were restricted to predator's ≤ 32 cm, which is the maximum length reported from the 1990 bottom trawl survey of the northeastern Chukchi Sea. The primary prey items in the Pacific cod diet are shrimps (28%), Arctic cod (16%), snow crab (*Chionoecetes opilio*) (14%), benthic amphipods (14%), polychaetes (7%), other zooplankton (5%), miscellaneous crabs (5%), miscellaneous shallow fish (5%), small-mouth flatfish (2%), other sculpins (1%), and eelpouts (1%). Walleye pollock, bivalves, snails, and miscellaneous crustaceans each comprise less than 1% of the diet composition.

The data pedigree for Pacific cod biomass is 2 because it is based on a direct estimate but with limited coverage. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are based on general life history proxies. The diet composition also has a data pedigree of 6 because it is based on diet studies of the same species in an adjacent region.

Saffron cod (*Eleginus gracilis*) –Saffron cod are a demersal groundfish from the family Gadidae. The biomass estimate for saffron cod was initially calculated as 0.039 t km^{-2} from the catch data of a 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994). Initial model balancing produced EE values greater than 1 that were believed to be the result of an underestimation of biomass. A top-down balance was then used assuming an EE of 0.8 and produced a biomass estimate of $0.98065 \text{ t km}^{-2}$.

The P/B of 0.488 for saffron cod was calculated following the methods of Hewitt and Hoenig (2005). This method requires an estimation of maximum age which was obtained from Wolotira et al. (1977). Q/B was calculated using the methods of Aydin (2004) which require an estimation of mortality (Z) and the parameter K from the von Bertalanffy growth function. The previous P/B calculation was used as an estimate of mortality and K was taken from Wolotira et al. (1977) resulting in a Q/B of 2.288.

Few food habits studies have examined the diet of saffron cod, and of those available amphipods, shrimp, and other epibenthic invertebrates are reported among the most important prey (Wolotira 1985, Coyle et al. 1997). In the absence of detailed region-specific data, the diet composition for saffron cod was obtained from food habits collections made on the eastern Bering Sea shelf during NMFS bottom trawl surveys (see Fish Diets in Appendix B) where they ate both benthic and pelagic invertebrates. The diet composition is 46% zooplankton, 29% shrimps, 22% benthic amphipods, 3% polychaetes, and < 1% misc. crustaceans.

The data pedigree is 8 for the biomass estimate of saffron cod because it is estimated by Ecopath. The data pedigree is 5 for estimates of P/B and Q/B because both parameter values are species-specific but from a previous time period. The data pedigree for diet composition is 6 because it is based on diet studies of the same species in an adjacent region.

Arctic cod (*Boreogadus saida*) –Arctic cod are a demersal groundfish from the family Gadidae. In Alaska they are found in the northern Bering, Chukchi, and Beaufort seas. Sampling throughout the

Chukchi Sea has consistently found Arctic cod to be the most abundant fish species (Alverson and Wilimovsky 1966, Wolotira et al. 1977, Frost and Lowry 1983, Barber et al. 1997). They occur in both benthic and pelagic habitats and are also found in association with sea-ice during ice covered periods (Bradstreet et al. 1986, Gradinger and Bluhm 2004, Benoit et al. 2008, Geoffroy et al. 2011, Parker-Stetter et al. 2011, Crawford et al. 2012, Renaud et al. 2012).

There are few biomass estimates for Arctic cod in the eastern Chukchi Sea. Quast (1974) calculated an average density of 0.7 t km^{-2} for juvenile Arctic cod, sampled in the northeastern Chukchi Sea during the fall of 1970 with a mid-water trawl. The initial biomass density input of 0.302 t km^{-2} for Arctic cod was calculated from the catch data of a 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994). Initial model balancing produced EE values greater than 1 and were thought to reflect an underestimation of biomass for this group. A top-down balance assuming an EE of 0.8 was used instead to solve for biomass and resulted in a density estimate of 1.412 t km^{-2} . This is approximately double the density estimate of Quast (1974).

The P/B of Arctic cod was calculated from a regression estimator of mortality following the methods of Hewitt and Hoenig (2005), which requires an estimate of maximum age as input. The maximum age of 8 was taken from Gillispie et al. (1997) and resulted in a P/B of 0.548. Q/B was calculated according to the methods of Aydin (2004) and requires an estimate of mortality and an estimate of the parameter K from the von Bertalanffy growth function. An estimate of mortality was taken from the previous P/B calculation and K was taken from Gillispie et al. (1997) resulting in a Q/B of 2.713.

A wide range of prey items have been reported in the diet of Arctic cod including sympagic amphipods, benthic amphipods, copepods, epibenthic invertebrates, shrimp, and occasionally fish (Lowry and Frost 1981a, Bradstreet and Cross 1982, Craig et al. 1982, Lønne and Gulliksen 1989, Coyle et al. 1997, Hop et al. 1997, Benoit et al. 2010, Christiansen et al. 2012, Cui et al. 2012, Renaud et al. 2012, Walkusz et al. 2012). Variation in diet composition between feeding studies and sample locations is thought to reflect local prey availability and flexibility of the Arctic cod diet (Lowry and Frost 1981a, Craig et al. 1982, Lønne and Gulliksen 1989, Renaud et al. 2012). Food habits studies previously

conducted in the northeastern Chukchi Sea have found copepods, gammarid and hyperiid amphipods, and shrimp to be among the most important prey items of Arctic cod (Lowry and Frost 1981a, Coyle et al. 1997). During spring in the northern Bering Sea, Cui et al. (2012) found benthic amphipods and copepods to be the most common prey of Arctic cod, with proportions varying by predator size and sample location. Few studies have examined the diet of Arctic cod within the eastern Chukchi Sea and most lack the quantitative detail required of a mass-balance food web model. In lieu of region-specific data, the food habits of Arctic cod were taken from collections made on the eastern Bering Sea shelf during NMFS bottom trawl surveys (see Fish Diets in Appendix B). The Arctic cod diet consisted of other zooplankton (48%), benthic amphipods (23%), copepods (17%), misc. crustaceans (6%), and shrimps (2%). The remaining 2% of the diet is comprised of fish, bivalves, miscellaneous crabs, and polychaetes.

The data pedigree is 8 for Arctic cod biomass because it is estimated by Ecopath. The data pedigree is 4 for estimates of P/B and Q/B because both parameter values are developed from data-specific to the base model time period and model region but limited in spatial coverage. The data pedigree for diet composition is 6 because it is based on diet studies of the same species in adjacent regions.

Pacific Salmon (*Oncorhynchus* spp.) – The Pacific salmon functional group is represented by at least six anadromous species: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*) sockeye salmon (*O. nerka*), and Chinook salmon (*O. tshawytscha*), in the eastern Chukchi Sea (Alverson and Wilimovsky 1966, Smith et al. 1966, Wolotira et al. 1977). Pacific salmon are unique by being present in two distinct pulses, the outgoing smolts leaving streams for the ocean, and adults returning to spawn in streams. As such they are divided into two functional groups: **Salmon outgoing** and **Salmon returning**.

The biomass and abundance of Pacific salmon are not known with precision in the Chukchi Sea. A limited number of historical abundance estimates are available for a few streams in the Kotzebue Sound area (Smith et al. 1966), otherwise catch records are the best indication of abundance. North of Bering

Strait, chum salmon are the dominant species reported in nearshore gillnet fisheries catches (Smith et al. 1966, Booth and Zeller 2008, Eggers et al. 2010). On average chum salmon account for 93% of the total catch (Booth and Zeller 2008). In 1990 the catch of chum salmon was approximately 1,000 t (Booth and Zeller 2008). In the absence of any suitable data for abundance estimation, the 1990 estimated catch of chum salmon is used as a conservative estimate of returning salmon abundance. This results in a returning salmon density estimate of $5.21 \times 10^{-4} \text{ t km}^{-2}$. Though the abundance of outgoing salmon is expected to be much greater than returning salmon, their biomass is assumed to be much lower. Here, I assume the biomass of outgoing salmon is about 1/10 of the returning salmon biomass. This is consistent with similar assumptions made for salmon in food web models of other Alaskan LMEs (Aydin et al. 2007). The density estimate of outgoing salmon is $5.21 \times 10^{-3} \text{ t km}^{-2}$.

The data required for calculating region-specific estimates of P/B and Q/B for either salmonid group is not presently available. P/B and Q/B parameters have been estimated for taxonomically similar groups in the eastern Bering Sea (Aydin et al. 2007) and are used here in lieu of region-specific parameters. For outgoing salmon the P/B and Q/B are 1.28 and 13.56, respectively. For returning salmon the P/B is 1.65 and the Q/B is 11.6.

Diet studies of juvenile pink and chum salmon in the northern Bering and eastern Chukchi seas indicate their diet here is dominated by zooplankton, including copepods (Moss et al. 2009). A review of salmon food habits throughout the Bering Sea similarly indicated a strong preference zooplankton prey, including ichthyoplankton in the eastern Bering Sea (Davis et al. 2009). The diet used here is divided evenly between copepods and other zooplankton.

The biomass estimates for outgoing and returning salmon have data pedigrees of 7 due to the dearth of abundance or biomass data. The data pedigree is 6 for estimates of P/B and Q/B for both outgoing and returning salmon because the estimates reflect general life history proxies and are taken from the eastern Bering Sea Ecopath model. The diet composition for both salmon groups are given data pedigrees of 6 because the diet is based on general knowledge for these species.

Benthic Invertebrates

Cephalopods –This group is assumed to be composed of only octopods, as I am presently unaware of any documented occurrences of squids (Order Teuthoidea) on the eastern Chukchi Sea shelf. Octopods (Order Octopoda) have been recorded in the southeastern and northeastern Chukchi Sea. Sparks and Pereyra (1966) identified specimens from the genera *Benthoctopus* and *Octopus* in the southeastern Chukchi Sea. Feder and Jewett (1978) identified their specimens from the southeastern Chukchi Sea as Octopodidae. From the northeastern Chukchi Sea, Feder et al. (1994) identified *Benthoctopus leioderma* from the catch of a 1990 bottom-trawl survey. More recently, Blanchard et al. (2010b) identified *Benthoctopus sibiricus* from epifaunal surveys in the northeastern Chukchi Sea.

Octopods were not well represented in the catch of the 1990 bottom trawl survey of the northeastern Chukchi Sea (Barber et al. 1994). Using their survey catch data to estimate biomass produced EEs in excess of 1,000, so a top-down balance was used assuming an EE of 0.8. This produced a biomass density estimate of $0.01566 \text{ t km}^{-2}$. Producing reliable biomass estimates for octopods from bottom trawl surveys has been similarly difficult in the eastern Bering Sea where annual surveys have produced octopus biomass estimates with considerable inter-annual variability ranging over two orders of magnitude (Connors and Conrath 2010).

Very little is known of the productivity or life span of the octopod species that have been found in the eastern Chukchi Sea. A P/B of 0.8 was assumed for octopods of the eastern Bering Sea (Aydin et al. 2007) but the octopod biomass there is dominated by the North Pacific giant octopus (*Enteroctopus dofleini*). The maximum life span for octopods of the eastern Bering Sea is about 5 years (Connors and Conrath 2010). Using a generalized formula for marine macrobenthos P/B ratios (Robertson 1979) and assuming a maximum age of 5 produced a P/B of 1.42. In lieu of region-specific or species-specific estimates of P/B I am assuming the molluscan mean P/B of 1.77 reported by Cusson and Bourget (2005).

Chukchi Sea specific estimates of Q/B are not currently available. The Q/B of 8.85 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

A study of *E. dofleini* food habits in Prince William Sound, Alaska, found they largely consumed crabs with bivalves as a somewhat distant second place prey item (Vincent et al. 1998). Other prey items of lesser importance were gastropods, barnacles, and sea urchins (Vincent et al. 1998). In the eastern Bering Sea octopods have been assumed to consume crabs (20%), bivalves (40%), and snails (40%) (Aydin et al. 2007). In the absence of region or species-specific data I have divided the diet of octopus evenly between *C. opilio*, miscellaneous crabs, bivalves, and snails.

The data pedigree is 8 for cephalopod biomass because it is estimated by Ecopath. P/B has a data pedigree of 6 because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is based on qualitative descriptions of food habits for a limited number of related species.

Bivalves –This functional group includes all members of the Class Bivalvia in the eastern Chukchi Sea including clams, mussels, cockles, scallops, and scaphopods. Bivalves have two shells (or valves) that are hinged on one side, allowing them to close together, encapsulating the body. In the eastern Chukchi Sea they are represented by 13 families and are an important prey resource for pinnipeds and many benthic invertebrates.

The burrowing nature of many bivalves means they are not only underrepresented in bottom-trawl surveys but some deep burrowing species (*Mya* sp. and *Spisula* sp.) may even escape the reach of benthic grab samples (Stoker 1981). The bivalve biomass density estimate of 114.9 t km⁻² used here is taken from a survey that targeted benthic invertebrate macrofauna, utilizing benthic grabs (Stoker 1981). This biomass estimate is an average density over the entire eastern Bering/Chukchi continental shelf and may be biased due to a large concentration of sampling stations in the northern Bering Sea-Bering Strait region

and due to the patchy distribution of bivalves (Stoker 1981). Exceptionally high benthic biomass estimates ($>1,000 \text{ g m}^{-2}$) have been observed in both the northern Bering and southern Chukchi seas (Stoker 1981, Grebmeier et al. 1988, Sirenko and Gagaev 2007). Stations sampled in 2004 in the southern Chukchi Sea dominated by the bivalve *Macoma calcarea*, had total bivalve densities ranging from $167 \text{ g m}^{-2} (\pm 25)$ to $4,024 \text{ g m}^{-2} (\pm 557.7)$ (Sirenko and Gagaev 2007). Bivalves are also among the dominant benthic taxa at locations in the northeastern Chukchi Sea (Feder et al. 1994, Blanchard et al. 2010b). Local density estimates for *Astarte borealis* and *M. calcarea* were as high as 230 g m^{-2} and 178 g m^{-2} , respectively (Blanchard et al. 2010b). The region-wide density estimate of Stoker (1981) is fairly high but so are the consumptive demands for bivalves from predators. Using a top-down balance with $EE = 0.8$ produced a biomass density estimate of 62.3 t km^{-2} . Bivalves are important prey for other benthic invertebrates including sea stars, snails, brittle stars, and crabs. They are also important prey for benthic feeding marine mammals, in particular Pacific walrus and bearded seal. Though the predation pressure exerted by walrus and to a lesser degree by bearded seals is seasonal in nature.

Estimates of the P/B ratio for bivalves in the eastern Chukchi Sea are not currently available. A P/B ratio of 1.3 for bivalves in the eastern Bering Sea was obtained from Evans (1984) by Trites et al. (1999). In the western Bering Sea the P/B of bivalves was estimated from multiple sources as 1.47 (Aydin et al. 2002). Burke and Mann (1974) calculated P/B ratios of 2.53 and 1.54 for two intertidal species of bivalve from Canada's east coast. Banse and Mosher (1980) reported P/B ratios for three species of bivalves with a mean of about 2.6. McLusky and McIntyre (1988) gave P/B values for 17 mostly subtidal and intertidal bivalves which averaged about 2.7. Asmus (1987) gave P/B ratios for three intertidal bivalves of the North Sea which averaged approximately 0.8. P/B ratios ranging from 0.2 to 0.9 were given for four intertidal bivalve species from England (Warwick and Price 1975). Low P/B ratios of 0.76 and 0.41 were calculated for the long-lived bivalve *Yoldia notabilis* in nearshore waters of northern Japan (Nakaoka 1992). Estimates of the P/B ratio for the long-lived (> 40 years) species, *Arctica islandica* from the northeast Atlantic ranged from 0.20 to 0.29 (Begum et al. 2010). In a meta-analysis of marine benthic macroinvertebrate production, Cusson and Bourget (2005) calculated a mean molluscan P/B ratio of 1.77.

Lacking region-specific information on bivalve production and life span, and considering the range of aforementioned P/B estimates for bivalves, I use the estimated P/B ratio of 1.3 from the neighboring eastern Bering Sea (Trites et al. 1999).

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B of 6.5 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

Bivalves are assumed to be benthic detritivores and to also filter feed on suspended detritus and small phytoplankton (Ruppert and Barnes 1994). Their diet is split between benthic bacteria (25%) and benthic detritus (75%).

The data pedigree for bivalve biomass is 7 because it was selected from multiple estimates with a wide range. P/B has a data pedigree of 6 because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is based on qualitative descriptions of food habits for a limited number of related species.

Snails –The snail functional group includes all members of the Class Gastropoda (except pteropods) found in the eastern Chukchi Sea. A bottom-trawl survey of the southeastern Chukchi Sea and Kotzebue Sound in 1976 (Wolotira et al. 1977) produced records for 10 snail families, including 20 genera and 33 species (Feder and Jewett 1978). The dominant snail in the 1976 survey was *Neptunea heros* which accounted for approximately 77% of the total snail biomass within the southeastern Chukchi Sea and Kotzebue Sound. A study of northeastern Chukchi Sea mollusks in 1990 also found *N. heros* to be the dominant molluscan epifauna in terms of biomass and abundance (Feder et al. 1994). The ubiquity of *Neptunea* was also noted in a survey of the southeastern Chukchi Sea during the summer of 1959 (Sparks and Pereyra 1966).

The biomass estimate originally calculated from the 1990 bottom trawl survey proved to be too low as initial model balancing produced EE values greater than 1. Many smaller snails may not be retained in

a bottom trawl and others may escape capture by burrowing in sand (MacIntosh and Somerton 1981). Instead the estimated biomass density of 11.5 t km⁻² for gastropods of the combined eastern Bering/Chukchi shelf from Stoker (1981) was used (see Other Benthic Invertebrate Biomass in Appendix B).

P/B estimates for Chukchi Sea snails are not presently available. The average P/B for 20 species of gastropod reported in Robertson (1979) is 2.22. A molluscan mean P/B was calculated as 1.77 (Cusson and Bourget 2005). The P/B of 1.81 used here has previously been derived for Bering Sea snails (Aydin et al. 2007) from values reported on intertidal snails in the North Sea (Asmus 1987).

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B of 9.05 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

Information on the diet of snails is not region-specific and is taken from benthic feeding studies conducted in the eastern Bering Sea. Feder and Jewett (1981) provide a qualitative description of eastern Bering Sea gastropod prey which includes bivalves, polychaetes, small benthic inverts, benthic diatoms, and benthic detritus. A region-specific quantitative breakdown of snail diets was not available so the diet was assumed to be evenly distributed (20% each) amongst these five groups with the portion allocated to small benthic invertebrates shared evenly by worms etc. and misc. crustaceans.

The data pedigree for snail biomass is 7 because it was selected from multiple estimates with a wide range. P/B has a data pedigree of 6 because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is primarily based on qualitative descriptions of food habits for a limited number of related species in neighboring systems.

Snow crab (*Chionoecetes opilio*) – Snow crabs belong to the genus *Chionoecetes* within the brachyuran crab family Majidae. Tanner crabs (*C. bairdi*) found in the Bering Sea are also commonly referred to as snow crabs but are not included here as their range does not extend north into the Chukchi

Sea (Jewett and Feder 1981, Otto 1981). Snow crabs are an important commercial species in the eastern Bering Sea and within the Arctic management area have been identified as a target species of potential commercial importance (NPFMC 2009). Survey data from 1990 to 1991 indicate that snow crabs within the eastern Chukchi Sea are on average smaller than those of the eastern Bering Sea and may rarely, if ever grow to a commercially viable size (> 100 mm carapace width) (Paul et al. 1997, Fair and Nelson 1999, NPFMC 2009). Further studies of their reproductive biology indicate some flexibility in the size at maturation (Orensanz et al. 2007), allowing snow crabs of the Chukchi Sea to mature at a smaller size (Paul et al. 1997).

Data on the snow crab stock size comes from a single survey conducted in the northeastern Chukchi Sea during the summer of 1990 (Barber et al. 1994). A biomass density estimate of 0.680 t km^{-2} was derived from the 1990 survey data using the area-swept method (Wakabayashi et al. 1985).

The model parameters P/B and Q/B have previously been derived by Trites et al. (1999), Aydin et al. (2002) and Aydin et al. (2007) from stock assessment data-specific to the eastern Bering Sea. The previously derived adult snow crab values of 1 and 2.75 (Aydin et al. 2007) are used here as best estimates of P/B and Q/B, respectively.

The food habits of snow crabs are thought to be similar throughout their range (Feder and Jewett 1978). Studies in the eastern Bering Sea indicate that polychaetes and brittle stars are the most commonly consumed prey by adults, while younger crabs may also incorporate various crustaceans and mollusks in their diet (Feder and Jewett 1981). In Norton Sound and the southeastern Chukchi Sea the dominant prey item was the bivalve *Nucula tenuis* (Feder and Jewett 1978). Other frequently encountered prey included polychaetes, amphipods, sediment and detritus (Feder and Jewett 1978). Detailed diet data for *C. opilio* is primarily known from a Russian survey conducted in the eastern Bering Sea in 1972 (Tarverdieva 1981). The diet data presented by Tarverdieva (1981) was specific to juvenile and adults and has been used previously in an ecosystem model of the eastern Bering Sea (Aydin et al. 2007). For lack of data-specific to the Chukchi Sea, the eastern Bering Sea model diets for juveniles and adults were averaged to make a single diet which is used here. In the resulting diet the three most dominant prey items are polychaetes

(27%), benthic detritus (27%), and bivalves (21%). Other prey items include brittle stars (6%), benthic amphipods (6%), miscellaneous crabs (4%), snails (3%), worms etc. (3%), and misc. crustaceans (1%).

The data pedigree for snow crab biomass is 2 because it is based on a direct estimate but with limited coverage. The estimates of P/B and Q/B both have data pedigrees of 6 because the parameters are based on general life history information and are taken from the eastern Bering Sea Ecopath model. The diet composition also has a data pedigree of 6 because it is based on a general diet of the same species in an adjacent region.

Miscellaneous crabs –This group includes all anomuran and brachyuran crabs of the eastern Chukchi Sea with the exception of *C. opilio*. A survey of the northeastern Chukchi Sea in 1990 provided catch records for two other spider crabs (*Hyas coarctatus*, *Oregonia gracilis*), helmet crab (*Telmessus cheiragonus*), three species of hermit crab (*Labidochirus splendescens*, *Pagurus capillatus*, and *P. rathbuni*), and two species of king crab (*Paralithodes camtschaticus* and *P. platypus*).

The biomass density estimate of 0.21 t km⁻² for miscellaneous crabs was initially calculated from a single survey conducted in the northeastern Chukchi Sea in 1990 (Barber et al. 1994) using the area-swept method (Wakabayashi et al. 1985). Hermit crabs accounted for approximately 70% of the estimated biomass, while king crabs accounted for only 1%. During model balancing this initial biomass density estimate proved to be too low as the initial EE value was 1.48. Biomass density was instead determined using a top-down balance with EE set to 0.8 producing a biomass density estimate of 0.45034 t km⁻².

A P/B value for hermit crabs has previously been estimated for both the eastern and western Bering Sea as 0.82 (Aydin et al. 2002, Aydin et al. 2007). Previously, P/B values for king crabs and miscellaneous crabs (including *Hyas* sp.) have also been estimated as 0.6 and 1.0, respectively (Aydin et al. 2002, Aydin et al. 2007). Since hermit crabs account for the vast majority of the biomass in this functional group their previously estimated P/B of 0.82 for Bering Sea populations is used.

Chukchi Sea-specific estimates of Q/B are not currently available. Q/B is calculated from P/B by assuming a growth efficiency of 0.2 (an average growth efficiency for benthic groups from Trites et al. (1999). Assuming P/B = 0.82 produced a Q/B of 4.1.

Within the Chukchi Sea, little is known about the food habits of the crab species comprising this functional group. For a lack of region-specific information, the estimated diet composition of taxonomically similar functional groups from an ecosystem model of the eastern Bering Sea is used here. Miscellaneous crabs are assumed to consume equal parts bivalves, polychaetes, worms etc., and benthic detritus (Aydin et al. 2007).

The data pedigree is 8 for the biomass estimate of miscellaneous crabs because it is estimated by Ecopath. The data pedigree is 6 for P/B because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on assumed growth efficiency averaged over a range of species. The data pedigree is 7 for diet composition because it is based on a general knowledge of food habits for related species.

Shrimp –The shrimp functional group is comprised of all decapod shrimp in the eastern Chukchi Sea. They are represented in trawl survey data by the families Crangonidae, Hippolytidae, and Pandalidae. These families all had at least one species represented in the catch data from a survey of the northeastern Chukchi Sea in 1990 and from the southeastern Chukchi Sea in 1976. From the 1990 bottom trawl survey the Crangonid genus *Argis* was the most abundant accounting for nearly 47% of the total estimated shrimp biomass. Pandalids were predominately represented by the humpy shrimp (*Pandalus goniurus*) and Hippolytids by the spiny lebbeid (*Lebbeus groenlandicus*).

The biomass estimate initially calculated from the 1990 survey of the northeastern Chukchi Sea was assumed to underestimate the actual biomass of shrimp due to the low catchability of shrimp in a bottom trawl. Instead a top-down balance was used assuming an EE of 0.8. This produced a biomass density estimate of 2.56373 t km⁻².

Lacking region-specific data, the P/B ratio of 0.576 and Q/B of 2.409 used here have previously been derived for shrimp in other regions of Alaska (eastern Bering Sea, Gulf of Alaska, and Aleutian Islands) by Aydin et al. (2007) from spot shrimp (*P. platyceros*) studies conducted in Prince William Sound, Alaska (Kimker et al. 1996).

Due to a lack of region-specific information, the diet of shrimp is estimated from descriptions found in multiple studies (Rice et al. 1980, Feder and Jewett 1981, Feder et al. 1981, Rice 1981). Frequently observed prey items in the stomachs of *Crangon dalli* collected in the northeastern Gulf of Alaska included polychaetes, planktonic and benthic diatoms, bivalves, miscellaneous crustaceans (including cumaceans, ostracods, barnacles, and other decapods), and amphipods (Feder et al. 1981, Rice 1981). The stomachs of pink shrimp (*Pandalus borealis*) collected near Kodiak Island, Alaska, were found to frequently contain diatoms, miscellaneous crustaceans, polychaetes, and bivalves (Feder and Jewett 1981). Similarly, stomach contents collected from three species of *Pandalus* in Lower Cook Inlet were all found to most frequently contain crustaceans, polychaetes, and bivalves (Rice et al. 1980). The diatom component of the *Crangon dalli* diet has been attributed to the deposition of phytodetritus to the benthos (Rice 1981). Additionally, the stomachs of *C. dalli*, *P. borealis*, *P. goniurus*, and *P. hypsinotus* were found to typically contain noteworthy amounts of sediment (Feder and Jewett 1981, Feder et al. 1981, Rice 1981). Based on dry weight, the stomach contents of *C. dalli* were up to 50% sediment and all three *Pandalus* species contained approximately 60% sediment (Rice et al. 1980, Feder and Jewett 1981, Feder et al. 1981, Rice 1981). Given the observed sediment content and frequent occurrence of diatoms in stomach contents, 40% of the diet is attributed to detritus with the remaining 60% evenly divided among polychaetes, bivalves, miscellaneous crustaceans, and amphipods.

The data pedigree is 8 for the biomass estimate of shrimp because it is estimated by Ecopath. The data pedigree is 6 for P/B because it is based on general knowledge of related species in nearby regions. For Q/B and diet composition, the data pedigree is 7 because both are based on general knowledge of similar and related species in neighboring regions.

Sea stars –In the eastern Chukchi Sea, sea stars are represented in survey data by the families Asteroiidae, Echinasteridae, Gonioplectinidae, Pterasteridae, and Solasteridae, all of which belong to the class Asteroidea. In particular, their biomass is dominated by the genera *Asterias* and *Leptasterias* of the family Asteroiidae (Feder et al. 2005). The two species *A. amurensis* and *L. polaris* together accounted for 65.5% of the total estimated echinoderm biomass in the southeastern Chukchi Sea in 1976 (Feder et al. 2005) and similarly account for 66% of the estimated sea star biomass from the 1990 survey of the northeastern Chukchi Sea as calculated in this study. Collectively, echinoderms comprised almost 56% of the total demersal biomass in the southeastern Chukchi and northern Bering seas with most of that biomass attributed to the family Asteroiidae (Wolotira et al. 1977).

The biomass of sea stars was originally calculated from survey data that was collected in the northeastern Chukchi Sea during the summer of 1990 (Barber et al. 1994). The resulting biomass density estimate of 0.61 t km^{-2} was calculated using the area-swept method (Wakabayashi et al. 1985). This estimate proved to be considerably lower than the combined Bering/Chukchi shelf density estimate for asteroids of 10.6 t km^{-2} provided by Stoker (1981). The earlier density estimate of Stoker (1981) was an average density calculated from a survey specifically designed to sample and evaluate the quantitative distribution of benthic invertebrate macrofauna over the combined Bering and Chukchi shelf. Because the survey was designed specifically to sample benthic invertebrates, it is used here as a best estimate of density.

Previous modeling efforts in the eastern Bering Sea gave sea stars P/B values of 1.50 (Trites et al. 1999) and 1.21 (Aydin et al. 2007). In the western Bering Sea, Aydin et al. (2002) assigned sea stars a P/B of 1.23 taken from Asmus (1987). The most recent P/B estimate of 1.21 from Aydin et al. (2007) is used here in lieu of region-specific estimates.

Chukchi Sea-specific estimates of Q/B are not currently available. Q/B is calculated from P/B by assuming a growth efficiency of 0.2 (an average growth efficiency for benthic groups from Trites et al. (1999)). The P/B of 1.21 divided by the assumed growth efficiency of 0.2 yields a Q/B of 6.05.

Descriptions of sea star diets throughout Alaska are summarized by Feder and Jewett (1981). In the southeastern Bering Sea they noted *A. amurensis* to feed primarily on shrimp and sand dollars, while in the northeastern Bering Sea they similarly preyed on sand dollars but also sea urchins. *Leptasterias polaris* predominately fed on bivalves in the southeastern Bering Sea and additionally fed on sand dollars and barnacles in the northeastern Bering Sea (Feder and Jewett 1981). Within the southeastern Chukchi Sea and Kotzebue Sound the chief prey items of *L. polaris* were ascidians, gastropods, polychaetes, and bivalves (Feder and Jewett 1978). Two other species of Asterids (*Evasterias echinosoma* and *Lethasterias nanimensis*) are also described as feeding predominately on bivalves in the southeastern Chukchi Sea (Feder and Jewett 1978). Though sea stars are mobile predators their diet is likely heavily influenced by the relative abundance of prey species (Feder and Jewett 1978). Within the northeastern Bering and southeastern Chukchi seas the predominate prey items are bivalves, snails, sand dollars, ascidians, and polychaetes (Feder and Jewett 1978). Lacking more specific information, the diet of sea stars was divided up amongst these prey groups weighted by biomass. The resulting diet composition is bivalves (52%), sand dollars (27%), polychaetes (13%), snails (5%), and ascidians (3%).

The data pedigree for sea star biomass is 7 because it was selected from multiple estimates with a wide range. P/B has a data pedigree of 6 because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is based on qualitative descriptions of food habits for a limited number of species, within and outside the model region.

Brittle stars –The brittle star functional group is comprised of species from at least 3 families belonging to the order Ophiurida. Families recorded in the eastern Chukchi Sea are Ophiuridae, Ophiactidae, and Amphiuroidae. The species include *Diamphiodia craterodmeta*, *Ophiopholis aculeata*, *Ophiura sarsi*, *O. maculata*, and *Stegophiura nodosa* (Sparks and Pereyra 1966, Wolotira et al. 1977, Stoker 1981, Ambrose et al. 2001, Feder et al. 2007). Brittle stars are important prey items for several species of groundfish throughout Alaska (Yang 1996, Lang et al. 2005, Yang et al. 2006) and along the

west coast of North America (Buckley et al. 1999). They are also known to be preyed on by snow crabs (Feder and Jewett 1981).

A recent study of a limited area in the northeastern Chukchi Sea indicated brittle stars were the most dominant species (in particular *O. sarsi*) of epifauna by biomass with density estimates ranging from 13.3 to 69.3 t km⁻² (Blanchard et al. 2010b). Within the study area brittle stars accounted for approximately 70% of the total benthic biomass (Blanchard et al. 2010b). The biomass density estimate used here of 9.8 t km⁻² comes from Stoker (1981) and is an average density estimate for the combined eastern Bering-Chukchi platform (see Other Benthic Invertebrate Biomass in Appendix B).

Lacking region-specific data, Trites et al. (1999) approximated the P/B of brittle stars in the eastern Bering Sea as 1.50. Aydin et al. (2002) refined this estimate further applying a P/B of 1.21 to brittle stars of the eastern and western Bering Sea. McLusky and McIntyre (1988) report a single P/B of 0.8 for *Ophiura* sp. of temperate or northern boreal origin. In lieu of a Chukchi Sea-specific estimate, the P/B of 1.21 from the Bering Sea models (Aydin et al. 2002) is used here.

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B is calculated from P/B assuming a growth efficiency of 0.2 (an average growth efficiency for benthic groups from Trites et al. (1999)). The resulting estimate of Q/B is 6.05.

Brittle stars may employ multiple feeding methods including deposit feeding, suspension feeding, scavenging, and predation (Warner 1982). *Ophiura* spp. are primarily described as predators of benthic prey but may also scavenge and deposit feed (Warner 1982). *Ophiura sarsi* off the coast of Nova Scotia fed on at least 31 taxa, but benthic amphipods were the primary prey item accounting for 47% of all stomach contents (Harris et al. 2009). The diets of *Ophiura* spp. from numerous studies have been summarized by Warner (1982) as consisting mainly of detritus and small invertebrates including polychaetes, bivalves, and small crustaceans. Ice algae (in particular *Melosira arctica*) that has been deposited on the sea floor following ice melt may also be an important prey source in ice-covered waters, particularly early in the year (Ambrose et al. 2001). The diet assumed here is 50% benthic detritus with

the remaining 50% divided evenly among bivalves, benthic amphipods, polychaetes, and miscellaneous crustaceans.

The data pedigree for brittle star biomass is 7 because it was selected from multiple estimates with a wide range. P/B has a data pedigree of 6 because it is based on related species in adjacent ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is primarily based on qualitative descriptions of food habits for a limited number of related species.

Basket stars –Basket stars belong to the class Ophiuroidea along with brittle stars but are members of a different order, Phrynophiurida. In Alaska they are represented by a single species, *Gorgonocephalus eucnemis* of the family Gorgonocephalidae. Contrary to brittle stars, basket stars are not a known prey item of groundfish or benthic invertebrates. As such, basket stars are treated as a separate functional group from brittle stars.

The biomass density estimate of $0.38714 \text{ t km}^{-2}$ was derived from a bottom trawl survey of the northeastern Chukchi Sea in the summer of 1990 (Barber et al. 1994) and was calculated using the area-swept method (Wakabayashi et al. 1985). This may underestimate their biomass as basket stars may be fragmented in the trawl losing some of their biomass.

The P/B of basket stars in the eastern Bering Sea has previously been estimated by Aydin et al. (2007) as 1.21 and is used here in lieu of a Chukchi Sea-specific estimate.

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B is calculated from P/B assuming a growth efficiency of 0.2 (an average for benthic groups from Trites et al. (1999) yielding a Q/B of 6.05.

Basket stars have five arms which are highly branched and armed with numerous spines and hooks which they use to catch their planktonic prey from the water column (Warner 1982). During feeding a basket star will fully extend its arms into the water column forming a parabolic net (Warner 1982). Once a prey item comes into contact with an arm, the arm quickly rolls up trapping the prey with its assorted

armaments (Patent 1970, Emson et al. 1991, Rosenberg et al. 2005). The remaining arms continue “fishing” in this manner for some period of time until most of the arms are knotted up with prey (Patent 1970). The knotted arms then curl all the way back toward the central disk delivering the prey to the mouth (Patent 1970, Emson et al. 1991, Rosenberg et al. 2005). In Puget Sound in Washington State, *G. eucnemis* stomach contents primarily consisted of crustacean zooplankton, chaetognaths, and bottom-dwelling crustaceans (Patent 1970). Additionally, a larval fish and a jellyfish were also found among the stomach contents (Patent 1970). The largest single prey item found by Patent (1970) was a 2.5 cm long crustacean (mysid or euphausiid). In the Bay of Fundy specimens of *G. arcticus* were collected and of the stomachs that contained prey they were almost entirely composed of euphausiids about 1 cm in length (Emson et al. 1991). A single larval fish and a single polychaete were also found, each just over 2 cm in length (Emson et al. 1991). Warner (1982) reviewed several basket star feeding studies and summarized their diet as virtually all planktonic organisms. Noting the relatively large size of prey items in the stomachs of *G. arcticus*, Emson et al. (1991) suggested that this species may specialize in capturing large prey items. Emson et al. (1991) compared the similarly robust nature and branching pattern of the arms between *G. arcticus* and *G. eucnemis* and suggested that neither would be very efficient at capturing small prey. Considering the above and lacking region-specific data, the diet of basket stars is divided evenly among zooplankton, copepods, miscellaneous crustaceans, and benthic amphipods.

The data pedigree for basket star biomass is 2 because it is based on a direct estimate but with limited coverage. P/B has a data pedigree of 6 because it is based on related species in adjacent ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is primarily based on qualitative descriptions of food habits for a limited number of related species.

Urchins, dollars, and cucumbers –Urchins, dollars, and cucumbers is a composite group containing echinoderms from the orders Clypeasteroidea (sand dollars), Dendrochirotida (sea cucumbers), and Echinoida (sea urchins). Sand dollars are represented by the single species *Echinarachnius parma*

(common sand dollar), sea urchins by *Strongylocentrotus droebachiensis* and sea cucumbers by the genera *Psolus* and *Cucumaria* (Feder and Jewett 1978).

The biomass of this functional group was not estimated from the 1990 trawl survey as the taxa in this group may be greatly damaged during the course of trawling, reducing their mass upon catch processing and they may have a low catchability in the trawl. The biomass density estimate used here of 60.7 t km^{-2} is taken from Stoker (1981) and is an average density estimate from the combined eastern Bering/Chukchi continental shelf (see Other Benthic Invertebrate Biomass in Appendix B).

The P/B of *Strongylocentrotus droebachiensis* has been reported as 0.8 by Banse and Mosher (1980). Robertson (1979) gave P/B ratios for two sea urchins as 0.3 and 1.0. In the western Bering Sea an average P/B has been estimated for a similar functional group as 0.61 (Aydin et al. 2002) and is used here.

Chukchi Sea-specific estimates of Q/B are not currently available. The estimated Q/B of 3.05 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999)).

Echinarachnius parma is primarily a deposit feeder, sifting through sediment feeding on detritus, infauna, and phytoplankton (DeRiddler and Lawrence 1982, Ables 2000). Qualitative descriptions of the diet of *S. droebachiensis* summarized by DeRiddler and Lawrence (1982) indicate they primarily consume plant material. Sea cucumbers of the order Dendrochirotida are primarily suspension feeders consuming plankton and at times may also deposit feed by brushing the bottom with their tentacles (Massin 1982). Lacking any specific diet information, this functional group is assumed to feed on benthic detritus (75%) and phytoplankton (25%).

The data pedigree for the biomass estimate of the urchins, dollars, cucumber group is 7 because it was selected from multiple estimates with a wide range. P/B has a data pedigree of 6 because it is based on related species in adjacent ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is

also 7 because it is primarily based on qualitative descriptions of food habits for a limited number of related species.

Sponge – The sponge functional group contains all taxa from the Phylum Porifera. This group is poorly identified in the eastern Chukchi Sea and is frequently only referred to as Porifera in catch data (Wolotira et al. 1977, Barber et al. 1994).

The biomass of this group in the eastern Chukchi Sea is not well known. Sponge had a mean density of 0.025 t km^{-2} in the southeastern Chukchi Sea in 1976 (Jewett and Feder 1981). Epifaunal surveys of oil lease sites in the northeastern Chukchi Sea in 2009 produced a single density estimate for sponge of 0.8 t km^{-2} at one of the survey sites (Blanchard et al. 2010b). A density of 0.661 t km^{-2} was calculated from bottom-trawl survey data of the northeastern Chukchi Sea in 1990 and is used here.

There are no estimates of P/B available for this group in the eastern Chukchi Sea, so instead the P/B of 1.0 for sponge of the eastern Bering Sea (Aydin et al. 2007) is used. The Q/B of 5.0 was estimated by the model assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

The diet of this group was assumed to largely consist of detritus and microbes, so the diet was divided-up between benthic bacteria (25%) and benthic detritus (75%).

The data pedigree for sponge biomass is 2 because it is based on a direct estimate but with limited coverage. The estimate of P/B has a data pedigree of 6 because it is based on related species in a nearby ecosystem. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is based on qualitative descriptions of food habits.

Benthic Urochordate –The benthic urochordate functional group is composed of tunicates (sea squirts) from the Class Ascidiacea. They are widely thought of as invertebrates; however they belong to the Phylum Chordata because of the notochord they possess during the larval stage, which is the

developmental precursor of the vertebrate backbone (Ruppert and Barnes 1994). In the eastern Chukchi Sea tunicates are represented by the two orders Enterogona and Pleurogona, containing at least 7 families (Abbott 1966).

During a survey of the southeastern Chukchi Sea in 1959 ascidians were one of the dominant invertebrate groups and were found at nearly 2/3 of all sample stations (Abbott 1966). Similarly, a survey of the southeastern Chukchi Sea in 1976 found tunicates at 83% of the stations sampled and they comprised approximately 10% of the biomass (Jewett and Feder 1981, Feder et al. 2005). Stoker (1981) calculated a mean density of 7.0 t km^{-2} across the whole Bering/Chukchi continental shelf. Epifaunal surveys of oil lease sites in the northeastern Chukchi Sea in 2009 produced tunicate density estimates as high as 4.5 t km^{-2} (Blanchard et al. 2010b). A density estimate of 1.08 t km^{-2} was calculated from the catch data of the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) and is used here.

The P/B ratio of ascidians is only known from a single source in the North Sea, where Asmus (1987) estimated the P/B for an unknown species of ascidian as 3.58. Lacking any other estimates, this is the P/B ratio used here.

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B of 17.9 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

The species comprising this group are filter feeders who consume small plankton and detritus (Abbott 1966, Ruppert and Barnes 1994). Their diet is assumed to be 25% benthic bacteria and 75% benthic detritus.

The data pedigree is 2 for benthic urochordate biomass because it is based on a direct estimate but with limited coverage. P/B has a data pedigree of 6 because it is based on related species in another ecosystem. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is primarily based on qualitative descriptions of food habits for related species.

Anemones –This functional group is composed of species from the Order Actinaria of the Class Anthozoa. They are primarily represented by the genus *Stomphia* from the family Actinostolidae (Sparks and Pereyra 1966). *Stomphia* species are also known as swimming anemones for their ability to detach from the substratum and swim to another location. Also present in the southeastern Chukchi Sea is *Urticina crassicornis* from the family Actiniidae (Sparks and Pereyra 1966, Feder and Jewett 1978). In the northeastern Chukchi Sea, Blanchard et al. (2010b) only identified *Stomphia* sp. but noted the possibility of three additional species.

There are few estimates of anemone biomass in the eastern Chukchi Sea. Stoker (1981) calculated a mean density for the Class Anthozoa (including soft corals) across the entire Bering/Chukchi shelf as 7.0 t km^{-2} . Epifaunal surveys of oil lease sites in the northeastern Chukchi Sea in 2009 had Anthozoa densities ranging from 0.4 to 2.9 t km^{-2} (Blanchard et al. 2010b). Catch data from the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) yielded an anemone density of 0.044 t km^{-2} . Anemones were present at 44% of the stations sampled in the southeastern Chukchi Sea in 1976, accounting for 4% of the epifaunal biomass (Feder et al. 2005). Lacking a region-wide density estimate specific to anemones, the density estimate of 0.044 t km^{-2} derived from the 1990 bottom-trawl survey is used here.

There are few estimates of P/B for anemones. Asmus (1987) produced estimates of P/B for two species in the North Sea which together averaged 5.10. Previous modeling efforts in the Bering Sea have lumped anemones in a functional group with other epifaunal species and collective P/Bs of 1.16 (Trites et al. 1999) and 1.58 (Aydin et al. 2002). As a single functional group in a more recent eastern Bering Sea ecosystem model they have been assigned a P/B of 1.0 (Aydin et al. 2007). Lacking any region-specific information I have also assigned a P/B of 1.0.

Chukchi Sea specific estimates of Q/B are not currently available. The Q/B of 5.0 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

The food habits of anemones in the Arctic and Alaska are not well known. Anemones are generally described as consuming small crustaceans and some fish (Ruppert and Barnes 1994). A study of *S. didemon* food habits along the coast of British Columbia, Canada, indicated their diet was primarily composed of small crustaceans and bivalves (Dalby 1992). Other potential prey could not be ruled out as their lack of hard parts may have prevented them from being identified or present in gut contents at the time of analysis (Dalby 1992). The diet of *Nematostella vectensis* in Nova Scotia, Canada, primarily consisted of snails, small crustaceans, and worms (Frank and Bleakney 1978). Anemones of the southwestern Cape region of South Africa were found to primarily consume isopods, bivalves, gastropods, barnacles, amphipods, and polychaetes (Kruger and Griffiths 1998). The barnacles and bivalves that were consumed were believed to have been dislodged individuals caught by the anemones (Kruger and Griffiths 1998). A previous ecosystem model of the eastern Bering Sea has most of the anemone diet devoted to detritus (75%) and the rest to small benthic crustaceans (Aydin et al. 2007). Considering the paucity anemone diet data I am dividing the diet up evenly (20% each) between benthic amphipods, misc. crustaceans, bivalves, benthic bacteria, and benthic detritus.

The data pedigree for anemone biomass is 2 because it is based on a direct estimate but with limited coverage. P/B has a data pedigree of 6 because it is based on related species in adjacent ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is primarily based on qualitative descriptions of food habits for a limited number of related species.

Corals – The coral group is composed of Anthozoan Cnidarians and is not well described in the eastern Chukchi Sea. Multiple fishery investigations and studies have produced catch records of corals, in particular *Gersemia* spp. (Sparks and Pereyra 1966, Wolotira et al. 1977, Barber et al. 1994, Blanchard et al. 2010a), but not much else is known.

There are few density estimates in the eastern Chukchi Sea for taxa in this group. Stoker (1981) calculated a mean density for the Class Anthozoa (including soft corals and anemones) across the entire

Bering/Chukchi shelf as 7.0 t km^{-2} . Epifaunal surveys of oil lease sites in the northeastern Chukchi Sea in 2009 had Anthozoa densities ranging from 0.4 to 2.9 t km^{-2} (Blanchard et al. 2010b). A mean density estimate of 1.81 t km^{-2} for the soft coral *Gersemia rubiformis* was calculated from density estimates produced from an epifaunal survey of the same areas in 2008 (Blanchard et al. 2010a). A density estimate of $0.00673 \text{ t km}^{-2}$ was calculated from the catch data of the 1990 bottom-trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) and is used here.

There are no estimates of P/B available for this group in the eastern Chukchi Sea. Instead I use the P/B of 0.046 for corals of the eastern Bering Sea (Aydin et al. 2007). The Q/B of 0.23 was estimated by the model assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

The diet of this group was assumed to largely consist of detritus and microbes, so the diet was divided-up between benthic bacteria (25%) and benthic detritus (75%).

The data pedigree is 2 for coral biomass because it is based on a direct estimate but with limited coverage. P/B has a data pedigree of 6 because it is based on related species in a nearby ecosystem. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is based on qualitative descriptions of food habits.

Benthic amphipods – The benthic amphipod functional group is comprised of several crustacean families from the Amphipod suborders of Gammaridea and Caprellidea. Benthic amphipods have temperature-dependent life histories, where at high latitudes and in cold waters they may require up to 4 years to mature, live for up to 6 years, and are larger than their more southerly counterparts (Highsmith and Coyle 1991). They are also the primary prey for gray whales that migrate to the Chukchi Sea to feed during summer (Highsmith and Coyle 1992).

Presently there is no region-wide density estimate of benthic amphipods in the Chukchi Sea. In lieu of a Chukchi Sea-specific estimate, I use a density estimate of 33.9 t km^{-2} from Stoker (1981). This

estimate is a mean density from across the combined Bering-Chukchi continental shelf (see Other Benthic Invertebrate Biomass in Appendix B).

A P/B of 3.48 was reported for a single benthic amphipod species by Robertson (1979). Closer to the Chukchi Sea, Highsmith and Coyle (1992) estimated P/B ratios for benthic amphipods in the northern Bering Sea to range from 0.7 to 1.3. Similarly, Thomson (1986) calculated an annual P/B of 1.8 for benthic amphipods of the same region. In the North Sea, Asmus (1987) calculated a P/B of 2.03 for *Gammarus locusta*. In ecosystem models of neighboring ecosystems, Trites et al. (1999) used a P/B of 3.50 for amphipods in the eastern Bering Sea and Aydin et al. (2002) used 2.5 for benthic amphipods of the western Bering Sea. Lacking Chukchi Sea-specific estimates I use a P/B of 1.0 taken from Highsmith and Coyle (1992) for benthic amphipods in the adjacent northern Bering Sea.

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B of 5.0 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999)).

The stomach contents of benthic amphipods in the north Bering Sea were found to most frequently contain sediment (Thomson 1986). They are assumed to primarily be detritivores and their diet is divided evenly between benthic detritus and benthic bacteria.

The data pedigree for benthic amphipod biomass density is 7 because the estimate comes from a single historical study that encompassed a larger region than the model area. P/B has a data pedigree of 6 because it is based on related species in an adjacent ecosystem. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The diet composition also has a data pedigree of 7 because it is based on qualitative descriptions of food habits for related species.

Polychaetes –Polychaetes are a prominent part of the benthos in Alaska and are equally prevalent in the diet of fishes. At least 37 polychaete families have been identified in the stomach contents of fishes from Alaska (Aydin et al. 2007). Across the combined eastern Bering and Chukchi seas, Stoker (1981) identified 143 species and 93 genera of polychaetes.

Polychaetes are an abundant part of the benthos and can have very high local densities. Density estimates for *Maldane glebifex* from surveyed areas in the northeastern Chukchi Sea are as high as 109.3 g m⁻² (Blanchard et al. 2010b). A density estimate for the entire eastern Chukchi Sea is not presently available. Here I use a density estimate of 28.8 t km⁻² that encompasses the combined eastern Bering and Chukchi continental shelf (Stoker 1981, see Other Benthic Invertebrate Biomass in Appendix B).

Presently, there are no precise estimates of P/B or Q/B for polychaetes in the Chukchi Sea. Two intertidal species from England are reported to have P/B ratios of 5.5 and 1.9 (Warwick and Price 1975). The higher value of 5.5 was attributed to an annual species (*Ampharete acutifrons*) and 1.9 to a species (*Nephtys hombergi*) with at least 3 year classes present at the time of the study (Warwick and Price 1975). The mean of 17 P/B ratios reported for 16 species by Robertson (1979) is 2.20. While a higher mean of 3.61 was calculated from P/B values recorded by Asmus (1987) for 18 different species in the North Sea. A mean P/B of 1.645 was calculated from a list of 15 P/B ratios presented for temperate and northern boreal species of polychaetes by McLusky and McIntyre (1988). The mean P/B of 1.645 is used here and is consistent with an estimated P/B of 1.50 for an ecosystem model of the eastern Bering Sea (Trites et al. 1999). A Q/B of 8.227 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999).

The diet of this group was assumed to largely consist of detritus and the diet was evenly divided between benthic bacteria and benthic detritus.

The data pedigree for polychaete biomass is 7 because it was selected from multiple estimates with a wide range. P/B has a data pedigree of 6 because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is based on qualitative descriptions of food habits.

Worms, etc. – Worms, etc. is a composite group containing the phyla Sipuncula, Echiura, Priapula, Nemertea, Brachiopoda, and Bryozoa, as well as leeches (subclass Hirudinea) and hydroids (class Hydrozoa).

Sipunculans are the only members of this functional group for which an estimate of biomass exists. The estimate of 5.9 t km^{-2} is not specific to the eastern Chukchi Sea but is an average density from stations sampled across the both the eastern Chukchi and eastern Bering continental shelves (Stoker 1981, see Other Benthic Invertebrate Biomass in Appendix B). In lieu of any other density estimates, this is the biomass density used for the entire functional group.

Few estimates of P/B exist for the taxa in this group. Asmus (1987) estimated the P/B of two species of Nemerteans (1.88 and 2.36), two oligochaetes (4.13, 4.28), and a single Bryozoan (4.40). The mean of the P/Bs provided by Asmus (1987) is 3.41. Banse and Mosher (1980) provided P/Bs for two Hirudineans that averaged 2.33. Taxonomically similar functional groups from ecosystem models of the neighboring western and eastern Bering Sea both had a P/B ratio of 2.23 (Aydin et al. 2002). In the absence of region or species-specific data, I used the P/B ratio of 2.23 from the Bering Sea models.

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B of 11.15 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999)).

The diet of this group was assumed to largely consist of detritus and the diet was evenly divided between benthic bacteria and benthic detritus.

The data pedigree for the worms, etc. biomass density is 7 because the estimate comes from a single historical study that encompassed a larger region than the model area. P/B has a data pedigree of 6 because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The diet composition also has a data pedigree of 7 because it is based on qualitative descriptions of food habits.

Miscellaneous Crustaceans – Miscellaneous crustaceans is a composite group consolidating many benthic crustaceans including isopods, cumaceans, barnacles, pycnogonids (sea spiders), and ostracods. Biomass density estimates do not presently exist for taxa of this group in the Chukchi Sea. A top-down balance with and assumed EE of 0.8 is used producing a density estimate of 6.42544 t km⁻².

The P/B ratios of taxa from this functional group are not well known. Asmus (1987) estimated the P/B ratios of three species of barnacles (mean = 2.20) and one species of isopod (7.01) in the North Sea. Cartes et al. (2001) estimated the P/B ratio of two isopod species from the Bay of Biscay in the northeastern Atlantic which averaged 6.1. McLusky and McIntyre (1988) recorded the P/B of a single cumacean species as 1.00. In the absence of region-specific P/B estimates, I use a mean value of 3.829 calculated from the aforementioned sources.

Chukchi Sea-specific estimates of Q/B are not currently available. The Q/B of 19.143 was calculated assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. (1999)).

The diet of this group was assumed to largely consist of detritus and the diet was evenly divided between benthic bacteria and benthic detritus.

The data pedigree is 8 for the biomass of miscellaneous crustaceans because it is estimated by Ecopath. P/B has a data pedigree of 6 because it is based on related species in other ecosystems. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is also 7 because it is based on qualitative descriptions of food habits.

Pelagic Invertebrates and Microbes

Jellyfish – The jellyfish functional group is comprised of large gelatinous planktonic predators from the Class Scyphozoa (Phylum Cnidaria). In the eastern Chukchi Sea this group is not well documented

but several studies have recorded their presence (Wolotira et al. 1977, Barber et al. 1994, Hopcroft et al. 2010, Purcell et al. 2010).

Region-wide estimates of biomass are not presently available. A density estimate of 0.658 t km^{-2} was calculated from the catch data of the 1990 bottom trawl survey of the northeastern Chukchi Sea (Barber et al. 1994) and is used here as a best estimate.

The P/B and Q/B of jellyfish in the eastern Chukchi Sea is not known. A P/B of 0.88 and Q/B of 3 are taken from an Ecopath model of the eastern Bering Sea (Aydin et al. 2007) and are used here as best estimates. The P/B estimate for jellyfish in the eastern Bering Sea was calculated by Aydin et al. (2007) from sources cited in Trites et al. (1999). The jellyfish Q/B was estimated by Aydin et al. (2007) from the summer ration reported in Brodeur et al. (2002).

The food habits of jellyfish within the eastern Chukchi Sea are unknown but they are assumed to feed on pelagic prey. Their assumed diet is composed of copepods (67%), other zooplankton (23%), pelagic microbes (5%), and phytoplankton (5%).

The data pedigree for jellyfish biomass is 2 because it is based on a direct estimate but with limited coverage. The estimates of P/B and Q/B have data pedigrees of 6 because they are based on related species and are taken from an Ecopath model in a nearby ecosystem. The data pedigree for diet composition is 7 because it is based on qualitative descriptions of food habits.

Copepods – Copepods are a dominant component of the zooplankton community in the Chukchi Sea, both numerically and in terms of biomass (Springer et al. 1989, Ashjian et al. 2003, Lane et al. 2008, Hopcroft et al. 2010, Matsuno et al. 2011). This functional group is primarily composed of calanoids and some of the common genera are *Acartia*, *Calanus*, *Eucalanus*, *Metridia*, *Microcalanus*, *Neocalanus*, *Oithona*, *Triconia*, and *Pseudocalanus* (Hopcroft et al. 2010). Many of the copepods found in the Chukchi Sea are of Pacific origin and have been advected into the Chukchi Sea through Bering Strait (Springer et al. 1989, Hopcroft et al. 2010). Copepods are important consumers of phytoplankton and herbivorous microzooplankton (Frost 1987, Kleppel 1993, Levinsen et al. 2000, Olson et al. 2006), and

their grazing rates effect the amount of primary production retained in the pelagic food web versus what is available to settle to the benthos or be advected downstream (Cooney and Coyle 1982, Coyle and Cooney 1988, Campbell et al. 2009). Additionally, copepods are important prey items for larger zooplankton (Båmstedt and Karlson 1998, Brodeur and Terazaki 1999, Dalpadado et al. 2008), fish (Coyle et al. 1997, Moss et al. 2009), seabirds (Springer and Roseneau 1985), and marine mammals (Moore et al. 2010). Copepods are treated separately from other zooplankton for three primary reasons; 1) they are a distinctly dominant part of the zooplankton, 2) they are frequently preyed upon by other zooplankton, and 3) copepods are generally smaller than their larger macrozooplankton counterparts (e.g., Euphausiids, Hyperiid, Chaetognaths) and as a result are expected to have a higher turnover rate and P/B ratio (Banse and Mosher 1980).

Copepods have been estimated to account for about half of the zooplankton biomass south of Bering Strait (Springer et al. 1989) and have similarly been observed to account for a large portion of the zooplankton biomass within the Chukchi Sea (Ashjian et al. 2003, Hopcroft et al. 2010, Matsuno et al. 2011). A biomass estimate specific to copepods within the eastern Chukchi Sea is not available at present. Instead a top-down balance is used assuming an EE of 0.8, producing a biomass estimate of $1.84879 \text{ t km}^{-2}$.

The P/B and Q/B of copepods within the eastern Chukchi Sea is not known. A P/B of 6.0 and Q/B of 27.74 has previously been used for a taxonomically similar groups in an Ecopath models of the eastern Bering Sea (Trites et al. 1999, Aydin et al. 2007). Copepods are smaller than other zooplankton (e.g., euphausiids, amphipods) and the smaller size leads to a higher turnover rate and higher P/B ratio (Banse and Mosher 1980). The P/B of 6.0 used in previous eastern Bering Sea models was selected from the upper range of values reported in the literature (Banse and Mosher 1980, Cooney 1981) for these reasons (Trites et al. 1999). Since, much of the copepod community in the eastern Chukchi Sea is believed to be of Pacific origin (Springer et al. 1989, Hopcroft et al. 2010) and in the absence of region-specific estimates, the P/B and Q/B parameters from the eastern Bering Sea model are considered best estimates and are used here.

In general, Arctic copepods are omnivorous, feeding on both phytoplankton (Conover et al. 1986, Runge and Ingram 1988, 1991) and microzooplankton (Levinsen et al. 2000, Campbell et al. 2009). During grazing experiments, some of the dominant copepod species of the Chukchi and Beaufort seas have demonstrated a strong preference for microzooplankton over phytoplankton under most conditions, with the strength of the preference related to prey availability (Campbell et al. 2009). The specific diet of copepods within the eastern Chukchi Sea is not well described but is assumed to be reasonably similar to that of copepods found in the eastern Bering Sea. In the absence of diet data specific to the eastern Chukchi Sea, the diet used here is based on the estimated diet of a taxonomically similar functional group from an eastern Bering Sea Ecopath model (Aydin et al. 2007). The diet is split evenly between pelagic microbes (microzooplankton) and phytoplankton.

The data pedigree is 8 for copepod biomass because it is estimated by Ecopath. The estimates of P/B and Q/B have data pedigrees of 6 because they are based on related species and are taken from an Ecopath model in a nearby ecosystem. The data pedigree for diet composition is 7 because it is based on qualitative descriptions of food habits.

Other Zooplankton – The other zooplankton functional group is composed of all meso- and macrozooplankton, excluding copepods, and includes Euphausiids, Mysids, Hyperiid amphipods, Larvaceans, Pteropods, Chaetognaths, meroplankton, and Ctenophores. Similar to copepods, much of the zooplankton community in the Chukchi Sea is of Pacific origin and has been advected into the Chukchi Sea through Bering Strait (Springer et al. 1989, Hopcroft et al. 2010).

A biomass estimate for other zooplankton in the eastern Chukchi Sea is not available at present. Instead a top-down balance is used assuming an EE of 0.8, resulting in a biomass estimate of 1.33528 t km⁻².

The P/B and Q/B of zooplankton, or any of the component groups included here, is not known within the eastern Chukchi Sea. Because much of the zooplankton community is of Pacific origin, I use a P/B of 5.475 taken from the Euphausiid group of an Ecopath model of the eastern Bering Sea (Aydin

et al. 2007). This P/B was originally calculated for euphausiids of the southeastern Bering Sea (Smith 1991) and is used here as best approximation of P/B. The Q/B of 15.643 is solved for by Ecopath assuming a growth efficiency of 0.35 (Aydin et al. 2007).

The diet of zooplankton within the eastern Chukchi Sea is not known but is assumed to be reasonably similar to that in the eastern Bering Sea. Diet studies of related taxa in other marine ecosystems indicate that species of this functional group may feed on phytoplankton, copepods, pelagic microbes, and other zooplankton (Båmstedt and Karlson 1998, Brodeur and Terazaki 1999, Acuña et al. 2002, Dalpadado et al. 2008). In the absence of region-specific diet data, the diet used here is based on the estimated diet of taxonomically similar functional groups in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The diet is composed of phytoplankton (60%), copepods (25%), and pelagic microbes (15%).

The data pedigree is 8 for other zooplankton biomass because it is estimated by Ecopath. P/B has a data pedigree of 6 because it is based on related species in a nearby ecosystem. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. The data pedigree for diet composition is 7 because it is based on qualitative descriptions of food habits for related species in other ecosystems.

Pelagic microbes (microzooplankton) – Pelagic microbes are a composite group primarily composed of bacteria and protozoans and is intended to represent processes within the pelagic microbial loop.

No data are available to estimate the biomass of microzooplankton on the eastern Chukchi Sea shelf so a top-down balance is used assuming an EE of 0.80. This resulted in a density estimate of 1.37498 t km⁻².

The production of this group is not well known. Kirchman et al. (2007) estimated the growth rate of bacteria as about 0.18 per day and approximately 0.175 per day for the total prokaryotic community in shelf areas (< 100 m) of the western Arctic. To model the production of microzooplankton in the eastern

Bering Sea, a daily growth rate of 0.2 was derived from Russian literature (Sorokin et al. 1995) by Aydin et al. (2002). Here the daily growth estimate of 0.175 is used and when scaled up for a growing season of 150 days, the P/B is 26.25. A Q/B of 75 is estimated by the model by assuming a growth efficiency of 0.35 (Aydin et al. 2007).

Pelagic microbes are assumed to primarily consume phytoplankton (Sherr et al. 2009) and to also consume pelagic detritus. The diet of pelagic microbes consists of 70% phytoplankton and 30% pelagic detritus.

The data pedigree for pelagic microbe biomass is 8 because it is estimated by Ecopath. P/B has a data pedigree of 7 because it is based on a general review of a range of species. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. For diet composition, the data pedigree is 6 because it is based on qualitative descriptions of food habits for related species in the same region.

Benthic microbes – Benthic microbes is a composite group primarily composed of bacteria and protozoans and is intended to represent processes within the benthic microbial loop.

No data are available to estimate the biomass of benthic microbes on the eastern Chukchi Sea shelf, so a top-down balance is used assuming an EE of 0.80. This resulted in a density estimate of 23.33516 t km⁻².

Little is known of the production of this group so the P/B for pelagic microbes is assumed here. A P/B of 0.2 per day was derived from Russian sources (Sorokin et al. 1995) by Aydin et al. (2002) for microzooplankton and the benthic bacteria of the Bering Sea. Similarly, daily growth rates for bacteria and the total prokaryotic community of shelf areas (< 100 m) in the western Arctic are approximately 0.175 (Kirchman et al. 2007). The daily growth estimate of 0.175 is used here, and when scaled for a growing season of 150 days the P/B becomes 26.25. A Q/B of 75 is estimated by the model by assuming a growth efficiency of 0.35 (Aydin et al. 2007).

The diet of benthic microbes is assumed to consist of 100% benthic detritus.

The data pedigree for benthic microbe biomass is 8 because it is estimated by Ecopath. P/B has a data pedigree of 7 because it is based on a general review of a range of species. The data pedigree is 7 for Q/B because it is based on an assumed growth efficiency averaged over a range of species. For diet composition, the data pedigree is 7 because it is based on qualitative descriptions of food habits for related species.

Primary Production

Phytoplankton – This is a composite group bringing together all the primary producers of the eastern Chukchi Sea. The dominant component of autotrophic phytoplankton biomass in the Chukchi Sea is diatoms and they also rank second in terms of abundance (Sukhanova et al. 2009). Primary production in the Chukchi Sea is seasonal in nature and is generally restricted to the spring and summer when light is plentiful. High levels of interannual variability in primary production have been observed and are largely attributed to interannual variation in ice coverage (Wang et al. 2005). In heavy ice years with late ice break-up and retreat, phytoplankton biomass may peak up to 2 months later than warmer years with less ice coverage (Wang et al. 2005). The annual cycle of primary production begins with the return of daylight in late winter and an ice algae bloom which continues until it is terminated with the onset of ice melt in late spring (Cota and Smith 1991). The melting and breaking up of ice strengthens stratification of the water column and exposes the nutrient rich water below to increasing amounts of light providing conditions for an explosive ice-edge bloom, which follows the retreating ice-edge northward (McRoy and Goering 1974, Niebauer et al. 1981, Sakshaug 2004). Satellite data has indicated that chlorophyll concentration has a single peak occurring in late spring or early summer (Wang et al. 2005). As summer progresses production is generally limited to the northward retreating ice edge and to the southern Chukchi Sea which is fueled by nutrient enriched water flowing in from the Bering Sea (Springer and McRoy 1993, Wang et al. 2005).

Light for photosynthesis is limited during fall and winter by seasonal darkness and ice coverage. The amount of irradiance under sea-ice at the ice-seawater interface is affected by ice thickness and snow cover, forcing ice algae to grow in light levels rarely exceeding 1-2% of that measured at the ice surface (Maykut and Grenfell 1975, Cota 1985, Smith and Sakshaug 1990). Ice algae have adapted to these conditions and many species have high photosynthetic efficiencies allowing them to photosynthesize at light intensities as low as 0.01% of the surface irradiance (Cota 1985, Suzuki et al. 1997). The ice algae bloom which precedes open water production can last for 2 months or more (Cota et al. 1991) and extends the grazing season for about the same amount of time (Bradstreet and Cross 1982). Ice algae are fed upon by a sympagic community of infaunal and epifaunal organisms that are in turn fed upon by fish including Arctic cod (Legendre et al. 1992). Under multi-year ice coverage, ice algae may contribute as much as 57% of total (ice and water column) primary production (Gosselin et al. 1997). In Arctic shelf seas like the Chukchi Sea where seasonal ice dominates, ice algae only contribute about 3% to total primary production (Subba Rao and Platt 1984, Gosselin et al. 1997). As such the most significant contribution of ice algae is not their total production but may be the timing of the bloom providing early season forage for sympagic invertebrates at a time when food is limited (Bradstreet and Cross 1982).

The average maximum daily growth rate at -0.5°C for 10 species of Arctic diatoms from the Barents Sea is 0.5 d^{-1} (Gilstad and Sakshaug 1990). Other Arctic algae growth rate studies conducted at temperatures less than 5°C produced growth rates ranging from 0.35 d^{-1} to 0.9 d^{-1} (Sakshaug 2004 and sources therein). In the Canadian Arctic, Suzuki et al. (1997) measured in situ specific growth rates ranging from 0.17 to 0.23 d^{-1} for the total ice algal community. Sherr et al. (2009) calculated an average intrinsic growth rate of $0.16\text{ d}^{-1} \pm 0.15$ in the western Arctic Ocean, though this estimate may be low due to sampling of light limited phytoplankton under heavy sea-ice, post bloom ice-algae, and senescing pelagic diatoms. Olson and Strom (2002) calculated the nutrient enhanced specific growth rate of phytoplankton on the eastern Bering Sea shelf which ranged from 0.28 to 1.10 d^{-1} . Lacking more comprehensive estimates specific to the Chukchi Sea, I assume a daily specific growth rate of 0.5 . The

total growing season in the Chukchi Sea can roughly be approximated as 150 days (Shuert and Walsh 1993, Hill and Cota 2005, Ji et al. 2012). Scaling the daily growth rate up to 150 days yields a P/B of 75.

Primary productivity is known to vary across the Chukchi Sea shelf (Parrish 1987). Parrish (1987) estimated annual phytoplankton production in the eastern Chukchi Sea to range from 50 g C m⁻² in the northeastern Chukchi Sea to 150 g C m⁻² in the southern Chukchi Sea. Hill and Cota (2005) estimated annual primary production over the northeastern Chukchi Sea continental shelf to be slightly higher at 70.5 g C m⁻². Springer and McRoy (1993) described a very rich plume of productivity in the southern Chukchi Sea as having an annual average production of 470 g C m⁻² and may range as high as 720 g C m⁻². In a more recent review of Arctic primary production, Sakshaug (2004) estimated annual primary productivity in the Chukchi Sea to range from 20 to >400 g C m⁻². Kirchman et al. (2009) calculated average daily primary productivity estimates of 1.581 and 0.458 g C m⁻² over the Chukchi Sea continental shelf during the spring and summers of 2004 and 2002, respectively. Assuming a 150-day growing season these produce annual productivity estimates of 237 and 69 g C m⁻² in 2004 and 2002, respectively. The estimates of primary production during the summer of 2004 were exceptionally high, nearly reaching a daily average productivity of 4.5 g C m⁻² (Kirchman et al. 2009), or again assuming a 150-day growing season an annual rate of 675 g C m⁻². Gosselin et al. (1997) calculated a daily rate of 1.14 g C m⁻² on the northern Chukchi Sea continental shelf in the summer of 1994 which is equal to an annual rate of 171 g C m⁻² when assuming a 150-day growing season.

The biomass of phytoplankton was determined in a top-down fashion. An EE of 0.8 was assumed and this produced a biomass estimate of 2.91 but also caused benthic detritus to be out of balance with an EE of 2.29. It is assumed that phytoplankton is the largest flow into benthic detritus and that phytoplankton production is necessary to balance the trophic demands of the largely detritivorous population of benthic invertebrates (See Appendix B Benthic-Pelagic Flows to Detritus). Phytoplankton biomass was then increased in whole number increments until a biomass of 34 where benthic detritus was balanced (EE < 1). Combined with a P/B of 75, this is equivalent to a total annual primary production of 170 g C m⁻². A great deal of research in the Chukchi Sea has correlated primary productivity in the water

column above with the productive benthos below (Grebmeier et al. 1988, Grebmeier and McRoy 1989, Walsh et al. 1989, Grebmeier 1993, Shuert and Walsh 1993, Walsh et al. 2005). Despite the well-supported benthic-pelagic coupling of the Chukchi Sea and the similarity between this estimate of primary productivity with those reported in the literature, this biomass estimate should be viewed with these assumptions in mind.

The data pedigree for phytoplankton biomass is 8 because it is estimated in a “top-down” fashion with Ecopath. The phytoplankton estimate of P/B has a data pedigree of 7 because it is based on a general review of related species from other ecosystems.

Model Parameters

Table A1.-- Ecopath model inputs (bolded) and balanced outputs for the eastern Chukchi Sea. TL = trophic level, B = biomass, P/B = production/biomass, Q/B = consumption/biomass, EE = ecotrophic efficiency, P/Q = production/consumption (or growth efficiency), catch = fishery or harvest take. Biomass and catch is in t km⁻²; P/B, Q/B, and P/Q are in yr⁻¹; and EE is dimensionless.

Functional Group	TL	B	P/B	Q/B	EE	P/Q	Catch
Beluga	4.48	0.01159	0.112	14.504	0.21110	0.008	6.34*10⁻⁵
Gray whale	3.48	0.26450	0.063	8.873	0.0	0.007	
Bowhead whale	3.50	0.21856	0.010	5.260	0.43087	0.002	9.46*10⁻⁴
Polar bear Chukchi stock	5.31	4.04*10⁻⁴	0.060	4.001	0.66336	0.015	1.61*10⁻⁵
Polar bear S. Beaufort stock	5.31	1.23*10⁻⁴	0.060	4.001	0.30430	0.015	2.26*10⁻⁶
Pacific walrus	3.34	0.09209	0.069	21.662	0.48560	0.003	0.00308
Bearded seal	3.83	0.03905	0.075	12.941	0.98435	0.006	0.00177
Ringed seal	4.47	0.05587	0.088	19.228	0.99819	0.005	0.00212
Spotted seal	4.60	0.00579	0.068	18.705	0.38547	0.004	1.52*10⁻⁴
Murres	3.94	0.00114	0.169	72.000	0.0	0.002	
Kittiwakes	4.46	8.43*10⁻⁵	0.076	110.000	0.0	0.001	
Puffins	4.39	2.18*10⁻⁵	0.040	73.000	0.0	0.001	
Cormorants	4.46	1.46*10⁻⁶	0.159	73.000	0.0	0.002	
Gulls	4.44	8.42*10⁻⁶	0.166	73.000	0.0	0.002	
Seabirds planktivorous	3.56	1.39*10⁻⁴	0.169	110.000	0.0	0.002	
Large-mouth flatfish	4.40	3.50*10⁻⁴	0.188	1.114	0.08573	0.168	
Small-mouth flatfish	3.62	0.31280	0.386	1.699	0.80000	0.227	
Large-mouth sculpin	4.03	0.26695	0.400	2.000	0.80000	0.200	
Other sculpin	3.57	0.04942	0.461	2.428	0.80000	0.190	
Eelpout	3.67	0.03564	0.400	2.000	0.80000	0.200	
Pelagic forage fish	3.52	0.54552	0.551	2.978	0.80000	0.185	
Miscellaneous shallow fish	3.79	0.19294	0.400	2.000	0.80000	0.200	
Walleye pollock	3.54	0.00189	0.548	2.713	0.20884	0.202	
Pacific cod	4.00	0.00188	0.488	2.288	0.31831	0.213	
Saffron cod	3.62	0.98065	0.488	2.288	0.80000	0.213	
Arctic cod	3.56	1.41225	0.548	2.713	0.80000	0.202	
Salmon outgoing	3.51	5.21*10⁻⁴	1.280	13.560	0.00012	0.094	
Salmon returning	3.51	0.00521	1.650	11.600	0.00009	0.142	
Cephalopods	3.81	0.01566	1.770	8.850	0.80000	0.200	
Bivalves	2.25	114.90000	1.300	6.500	0.43423	0.200	
Snails	2.85	11.50000	1.810	9.050	0.17045	0.200	
Snow crab	3.09	0.68008	1.000	2.750	0.81971	0.364	
Miscellaneous crabs	3.06	0.45034	0.820	4.100	0.80000	0.200	
Shrimps	2.86	2.56373	0.576	2.409	0.80000	0.239	
Sea stars	3.25	10.60000	1.210	6.050	0.00111	0.200	
Brittle stars	2.72	9.80000	1.210	6.050	0.01029	0.200	
Basket stars	3.51	0.38714	1.210	6.050	0.00089	0.200	
Urchins, dollars, cucumbers	2.00	60.70000	0.610	3.050	0.47820	0.200	
Sponge	2.25	0.66053	1.000	5.000	0.00886	0.200	
Benthic urochordate	2.25	1.08345	3.580	17.900	0.52633	0.200	
Anemones	3.05	0.04434	1.000	5.000	0.22175	0.200	
Corals	2.25	0.00673	0.046	0.230	0.02343	0.200	
Benthic amphipods	2.50	33.90000	1.000	5.000	0.38779	0.200	
Polychaetes	2.50	28.80000	1.645	8.227	0.81774	0.200	
Worms etc.	2.50	5.90000	2.230	11.150	0.83471	0.200	
Miscellaneous crustaceans	2.50	6.42544	3.829	19.143	0.80000	0.200	
Jellyfish	3.41	0.65834	0.880	3.000	0.00228	0.293	
Copepods	2.50	1.84879	6.000	27.740	0.80000	0.216	
Other zooplankton	2.53	1.33528	5.475	15.643	0.80000	0.350	
Pelagic microbes	2.00	1.37498	26.250	75.000	0.80000	0.350	
Benthic microbes	2.00	23.33516	26.250	75.000	0.80000	0.350	
Phytoplankton	1.00	34.00000	75.000		0.06963		

Diet Matrix

Table A2.-- Eastern Chukchi Sea diet matrix, where rows represent prey groups and the columns are predators. The predator column numbers correspond to the prey group numbers and names. Each column represents a single predator's diet and the values sum to 1 (some columns may not sum to 1 due to rounding). Values of 0.0000 are prey items in trace amounts.

Functional Group	1	2	3	4	5	6	7	8	9
1 Beluga				0.1000	0.1000				
2 Gray whale									
3 Bowhead whale									
4 Polar bear Chukchi stock									
5 Polar bear S. Beaufort stock									
6 Pacific walrus									
7 Bearded seal				0.2500	0.2500	0.0003			
8 Ringed seal				0.6500	0.6500	0.0007			
9 Spotted seal									
10 Murres									
11 Kittiwakes									
12 Puffins									
13 Cormorants									
14 Gulls									
15 Seabirds planktivorous									
16 Large-mouth flatfish									
17 Small-mouth flatfish							0.0430		0.0171
18 Large-mouth sculpin	0.0100						0.0586	0.0331	0.1197
19 Other sculpin	0.0100							0.0069	0.0247
20 Eelpout	0.0100								
21 Pelagic forage fish	0.5544						0.0023	0.0300	0.4574
22 Miscellaneous shallow fish									0.0325
23 Walleye pollock									
24 Pacific cod									
25 Saffron cod	0.0359						0.0180	0.3300	0.0924
26 Arctic cod	0.2797						0.0085	0.4500	0.2163
27 Salmon outgoing									
28 Salmon returning									
29 Cephalopods	0.0001					0.0100			0.0200
30 Bivalves		0.0434	0.0192			0.6990	0.3286		
31 Snails		0.0043	0.0019			0.0600	0.0170		
32 Snow crab		0.0003	0.0001			0.0230	0.1948		
33 Miscellaneous crabs		0.0001	0.0000			0.0070	0.0601		
34 Shrimps	0.0999	0.0000	0.0000			0.0200	0.2464	0.1000	0.0100
35 Sea stars		0.0040	0.0018						
36 Brittle stars		0.0037	0.0016						
37 Basket stars		0.0001	0.0001						
38 Urchins, dollars, cucumbers		0.0229	0.0102			0.0802			
39 Sponge		0.0002	0.0001						
40 Benthic urochordate		0.0026	0.0012			0.0092			
41 Anemones		0.0026	0.0012						
42 Corals		0.0000	0.0000						
43 Benthic amphipods		0.9000	0.0057			0.0448	0.0113	0.0400	0.0100
44 Polychaetes		0.0109	0.0048			0.0380	0.0113		
45 Worms etc.		0.0022	0.0010			0.0078			
46 Miscellaneous crustaceans		0.0026	0.0011						
47 Jellyfish									
48 Copepods			0.7125						
49 Other zooplankton			0.2375					0.0100	
50 Pelagic microbes									
51 Benthic microbes									
52 Phytoplankton									
53 Pelagic detritus									
54 Benthic detritus									

Table A2--Continued.

Functional Group	10	11	12	13	14	15	16	17	18
1 Beluga									
2 Gray whale									
3 Bowhead whale									
4 Polar bear Chukchi stock									
5 Polar bear S. Beaufort stock									
6 Pacific walrus									
7 Bearded seal									
8 Ringed seal									
9 Spotted seal									
10 Murres									
11 Kittiwakes									
12 Puffins									
13 Cormorants									
14 Gulls									
15 Seabirds planktivorous									
16 Large-mouth flatfish									0.0000
17 Small-mouth flatfish							0.0567		0.0019
18 Large-mouth sculpin	0.0409						0.0145		
19 Other sculpin	0.0085						0.0128		0.0092
20 Eelpout							0.0247		0.0082
21 Pelagic forage fish	0.1287	0.0900	0.4250	0.0497	0.4500	0.0028	0.0426	0.0939	0.0022
22 Miscellaneous shallow fish							0.0198		0.0022
23 Walleye pollock	0.0012	0.0044	0.0023	0.0046	0.0025	0.0003	0.0030		0.0001
24 Pacific cod	0.0012	0.0044	0.0023	0.0046	0.0025	0.0003	0.0187		0.0003
25 Saffron cod	0.0250	0.0912	0.0478	0.0957	0.0506	0.0053	0.0065		
26 Arctic cod	0.1946	0.7100	0.3725	0.7453	0.3944	0.0414	0.4871		0.0116
27 Salmon outgoing							0.0002		
28 Salmon returning							0.0021		
29 Cephalopods							0.0108		0.0001
30 Bivalves							0.0021	0.0478	0.0000
31 Snails							0.0021	0.0001	0.0020
32 Snow crab							0.0772		0.5694
33 Miscellaneous crabs							0.1282	0.0002	0.2405
34 Shrimps							0.0277	0.0935	0.0395
35 Sea stars									0.0000
36 Brittle stars							0.0006	0.0002	0.0001
37 Basket stars									
38 Urchins, dollars, cucumbers								0.0014	0.0022
39 Sponge									
40 Benthic urochordate								0.0029	
41 Anemones							0.0016	0.0003	
42 Corals									
43 Benthic amphipods			0.0371		0.0500		0.0076	0.3670	0.0251
44 Polychaetes							0.0032	0.1180	0.0286
45 Worms etc.		0.0500	0.0379				0.0056	0.0068	0.0462
46 Miscellaneous crustaceans							0.0003	0.0010	0.0003
47 Jellyfish									0.0025
48 Copepods	0.4500	0.0375	0.0563	0.0750	0.0375	0.7125			
49 Other zooplankton	0.1500	0.0125	0.0188	0.0250	0.0125	0.2375	0.0442	0.2669	0.0076
50 Pelagic microbes									
51 Benthic microbes									
52 Phytoplankton									
53 Pelagic detritus									
54 Benthic detritus									

Table A2--Continued.

Functional Group	19	20	21	22	23	24	25	26	27
1 Beluga									
2 Gray whale									
3 Bowhead whale									
4 Polar bear Chukchi stock									
5 Polar bear S. Beaufort stock									
6 Pacific walrus									
7 Bearded seal									
8 Ringed seal									
9 Spotted seal									
10 Murres									
11 Kittiwakes									
12 Puffins									
13 Cormorants									
14 Gulls									
15 Seabirds planktivorous									
16 Large-mouth flatfish									
17 Small-mouth flatfish		0.0086		0.0041		0.0171		0.0182	
18 Large-mouth sculpin				0.0057					
19 Other sculpin				0.0021		0.0132			
20 Eelpout				0.0137		0.0111			
21 Pelagic forage fish		0.0148							
22 Miscellaneous shallow fish	0.0555	0.0665		0.0544		0.0509		0.0064	
23 Walleye pollock		0.0003		0.0000	0.0001	0.0010			
24 Pacific cod									
25 Saffron cod									
26 Arctic cod		0.0466		0.0015	0.0180	0.1576		0.0067	
27 Salmon outgoing									
28 Salmon returning									
29 Cephalopods									
30 Bivalves	0.0198	0.1120		0.0046		0.0014		0.0001	
31 Snails				0.0047		0.0015			
32 Snow crab	0.0004	0.0495		0.1804		0.1453			
33 Miscellaneous crabs		0.0003		0.0101		0.0526		0.0017	
34 Shrimps	0.0048	0.0207	0.0000	0.1892	0.0264	0.2859	0.2911	0.0238	
35 Sea stars									
36 Brittle stars	0.0000	0.0148							
37 Basket stars									
38 Urchins, dollars, cucumbers									
39 Sponge									
40 Benthic urochordate									
41 Anemones									
42 Corals									
43 Benthic amphipods	0.7329	0.4936	0.0099	0.2832	0.1989	0.1378	0.2179	0.2271	
44 Polychaetes	0.0984	0.1278	0.0007	0.1071	0.0044	0.0692	0.0286	0.0056	
45 Worms etc.	0.0000	0.0362		0.0037					
46 Miscellaneous crustaceans		0.0082	0.0166	0.0377	0.0430	0.0015	0.0010	0.0590	
47 Jellyfish									
48 Copepods	0.0021		0.1011	0.0001	0.2480			0.1740	0.5000
49 Other zooplankton	0.0861		0.8717	0.0978	0.4611	0.0539	0.4615	0.4775	0.5000
50 Pelagic microbes									
51 Benthic microbes									
52 Phytoplankton									
53 Pelagic detritus									
54 Benthic detritus									

Table A2--Continued.

Functional Group	28	29	30	31	32	33	34	35	36
1 Beluga									
2 Gray whale									
3 Bowhead whale									
4 Polar bear Chukchi stock									
5 Polar bear S. Beaufort stock									
6 Pacific walrus									
7 Bearded seal									
8 Ringed seal									
9 Spotted seal									
10 Murres									
11 Kittiwakes									
12 Puffins									
13 Cormorants									
14 Gulls									
15 Seabirds planktivorous									
16 Large-mouth flatfish									
17 Small-mouth flatfish									
18 Large-mouth sculpin									
19 Other sculpin									
20 Eelpout									
21 Pelagic forage fish									
22 Miscellaneous shallow fish									
23 Walleye pollock									
24 Pacific cod									
25 Saffron cod									
26 Arctic cod									
27 Salmon outgoing									
28 Salmon returning									
29 Cephalopods									
30 Bivalves		0.2500		0.2000	0.2075	0.2500	0.1500	0.5155	0.1250
31 Snails		0.2500			0.0326			0.0516	
32 Snow crab		0.2500							
33 Miscellaneous crabs		0.2500			0.0411				
34 Shrimps									
35 Sea stars					0.0015				
36 Brittle stars					0.0590				
37 Basket stars									
38 Urchins, dollars, cucumbers					0.0081			0.2723	
39 Sponge					0.0028				
40 Benthic urochordate								0.0314	
41 Anemones					0.0012				
42 Corals									
43 Benthic amphipods					0.0553		0.1500		0.1250
44 Polychaetes				0.2000	0.2720	0.2500	0.1500	0.1292	0.1250
45 Worms etc.				0.1000	0.0313	0.2500			
46 Miscellaneous crustaceans				0.1000	0.0143		0.1500		0.1250
47 Jellyfish									
48 Copepods	0.5000								
49 Other zooplankton	0.5000				0.0041				
50 Pelagic microbes									
51 Benthic microbes			0.2500						
52 Phytoplankton				0.2000	0.0039				
53 Pelagic detritus									
54 Benthic detritus			0.7500	0.2000	0.2657	0.2500	0.4000		0.5000

Table A2--Continued.

Functional Group	37	38	39	40	41	42	43	44	45
1 Beluga									
2 Gray whale									
3 Bowhead whale									
4 Polar bear Chukchi stock									
5 Polar bear S. Beaufort stock									
6 Pacific walrus									
7 Bearded seal									
8 Ringed seal									
9 Spotted seal									
10 Murres									
11 Kittiwakes									
12 Puffins									
13 Cormorants									
14 Gulls									
15 Seabirds planktivorous									
16 Large-mouth flatfish									
17 Small-mouth flatfish									
18 Large-mouth sculpin									
19 Other sculpin									
20 Eelpout									
21 Pelagic forage fish									
22 Miscellaneous shallow fish									
23 Walleye pollock									
24 Pacific cod									
25 Saffron cod									
26 Arctic cod									
27 Salmon outgoing									
28 Salmon returning									
29 Cephalopods									
30 Bivalves					0.2000				
31 Snails									
32 Snow crab									
33 Miscellaneous crabs									
34 Shrimps									
35 Sea stars									
36 Brittle stars									
37 Basket stars									
38 Urchins, dollars, cucumbers									
39 Sponge									
40 Benthic urochordate									
41 Anemones									
42 Corals									
43 Benthic amphipods	0.2500				0.2000				
44 Polychaetes									
45 Worms etc.									
46 Miscellaneous crustaceans	0.2500				0.2000				
47 Jellyfish									
48 Copepods	0.2500								
49 Other zooplankton	0.2500								
50 Pelagic microbes									
51 Benthic microbes			0.2500	0.2500	0.2000	0.2500	0.5000	0.5000	0.5000
52 Phytoplankton		0.2500							
53 Pelagic detritus									
54 Benthic detritus		0.7500	0.7500	0.7500	0.2000	0.7500	0.5000	0.5000	0.5000

Table A2--Continued.

Functional Group	46	47	48	49	50	51
1 Beluga						
2 Gray whale						
3 Bowhead whale						
4 Polar bear Chukchi stock						
5 Polar bear S. Beaufort stock						
6 Pacific walrus						
7 Bearded seal						
8 Ringed seal						
9 Spotted seal						
10 Murres						
11 Kittiwakes						
12 Puffins						
13 Cormorants						
14 Gulls						
15 Seabirds planktivorous						
16 Large-mouth flatfish						
17 Small-mouth flatfish						
18 Large-mouth sculpin						
19 Other sculpin						
20 Eelpout						
21 Pelagic forage fish						
22 Miscellaneous shallow fish						
23 Walleye pollock						
24 Pacific cod						
25 Saffron cod						
26 Arctic cod						
27 Salmon outgoing						
28 Salmon returning						
29 Cephalopods						
30 Bivalves						
31 Snails						
32 Snow crab						
33 Miscellaneous crabs						
34 Shrimps						
35 Sea stars						
36 Brittle stars						
37 Basket stars						
38 Urchins, dollars, cucumbers						
39 Sponge						
40 Benthic urochordate						
41 Anemones						
42 Corals						
43 Benthic amphipods						
44 Polychaetes						
45 Worms etc.						
46 Miscellaneous crustaceans						
47 Jellyfish						
48 Copepods		0.6750		0.2500		
49 Other zooplankton		0.2250				
50 Pelagic microbes		0.0500	0.5000	0.1500		
51 Benthic microbes	0.5000					
52 Phytoplankton		0.0500	0.5000	0.6000	0.7000	
53 Pelagic detritus					0.3000	
54 Benthic detritus	0.5000					1.0000

Appendix B Detailed Parameter Estimation Methods

Benthic-Pelagic Flows to Detritus

The benthic or pelagic flows to detritus were always tilted in favor of benthic detritus. Studies and modeling exercises in the Chukchi Sea have linked pelagic primary production and organic carbon content in the water column above with benthic biomass below (Grebmeier et al. 1988, Grebmeier and McRoy 1989, Walsh et al. 1989, Shuert and Walsh 1993, Walsh et al. 2005). It is presumed that much of the primary production and organic carbon available in the water column goes unutilized by zooplankton and microzooplankton and is advected downstream or settles to the bottom where it contributes to an abundant community of benthic invertebrates (Cooney and Coyle 1982, Coyle and Cooney 1988, Walsh et al. 1989, Shuert and Walsh 1993, Grebmeier et al. 1995, Sakshaug 2004, Cooper et al. 2009, Sherr et al. 2009). In the western Arctic, including a portion of the eastern Chukchi Sea, microzooplankton are estimated to only consume about one-fifth of daily phytoplankton production (Sherr et al. 2009). Microzooplankton and mesozooplankton combined may only graze up to 44% of total primary production leaving the rest to be delivered to the benthos or exported (Campbell et al. 2009). The detrital flow of all mammals, seabirds, fish, copepods, zooplankton, jellies, and phytoplankton is 70% benthic and 30% pelagic. For all benthic invertebrates and benthic bacteria the detrital flow is 90% benthic and 10% pelagic.

Marine Mammal Production Rates

Under the equilibrium conditions, P/B is equal to the instantaneous mortality rate Z (Allen 1971). The P/B of marine mammal groups was estimated with a variation of Siler's competing risk model (Siler 1979) as modified by Barlow and Boveng (1991) following the methods of Aydin et al. (2007). The model uses surrogate life histories scaled by longevity to produce survivorship curves. The resultant survivorship curves incorporate different mortality risks associated with juveniles, adults, and senescence. Longevity is not the maximum reported age but rather the 99th percentile of the age distribution. The equations of Barlow and Boveng are:

$$\text{Survivorship at age} \quad l(x) = l_j(x) * l_c(x) * l_s(x) \quad (\text{B1})$$

$$\text{Juvenile mortality} \quad l_j(x) = \exp[(-a1/b1) * \{1 - \exp(-b1 * x/W)\}] \quad (\text{B2})$$

$$\text{Constant mortality} \quad l_c(x) = \exp[-a2 * x/W] \quad (\text{B3})$$

$$\text{Senescent mortality} \quad l_s(x) = \exp[(a3/b3) * \{1 - \exp(b3 * x/W)\}] \quad (\text{B4})$$

Where $l(x)$ is the survivorship at age, $l_j(x)$ is the mortality risk associated with juveniles, $l_c(x)$ is a constant mortality risk experienced by all ages, $l_s(x)$ is the mortality risk associated with senescence. The parameters $a1$, $a2$, $a3$, $b1$, and $b3$ refine the shape of the function. The values of these parameters for the different surrogate life histories are listed in Table B1. The fur seal life history has a relatively high level of mortality associated with juvenile stages, low mortality through adulthood, and increasing mortality risk with senescence. The monkey surrogate experiences a relatively constant mortality throughout the three life stages. The human surrogate has low mortality throughout the juvenile and adult stages, with mortality sharply increasing with senescence.

Table B1.--Estimated model parameters for surrogate mammal life histories from Barlow and Boveng (1991).

Surrogate	a1	a2	a3	b1	b3
Fur seal	14.343	0.1710	0.0121	10.259	6.6878
Monkey	30.430	0.0000	0.7276	206.720	2.3188
Human	40.409	0.4772	0.0047	310.360	8.0290

Marine Mammal Consumption Rates

Consumption rates for marine mammals were calculated by using the average individual body mass (kg) and daily individual allometric energy requirements (1,000 kJ d⁻¹). Where available the values were taken from Hunt et al. (2000, Table 9.1) or were computed following the methods of Hunt et al. (2000) who utilized a generalized formula from Perez et al. (1990) for calculating marine mammal energy requirements using body mass (kg):

$$E = \frac{(a * M^{0.75})}{239} , \quad (B5)$$

where E = energy required in 1,000 kJ/day, M = body mass in kg, a is a taxonomic-specific coefficient, and 239 is a constant to convert from kcal to kJ. This formula is a modification of Kleiber's (1961) generalized relationship between body mass and basal metabolism for terrestrial mammals. The coefficients (a) presented by Perez et al. (1990) and used here are listed in Appendix Table B2. Perez et al. (1990) did not estimate a coefficient (a) for polar bears, so instead Kleiber's (1961) formula for basal metabolic rate (BMR) is used:

$$BMR = 70W^{0.75} , \quad (B6)$$

where BMR is in kcal/day and W is body mass in kg. The daily energy requirements were converted to calories then multiplied by the estimated prey caloric density (cal/g) to determine the mass of daily consumption. This was then divided by the average individual body mass to determine the percent of body weight consumed daily. These values were then scaled up to annual rates to arrive at the model Q/B rates (Table B2).

Table B2.-- The Q/B ratios, daily energy requirements, average body mass, and estimated prey caloric density for marine mammals. The coefficient (a) is a taxonomic specific parameter from Perez et al. (1990) used to calculate energy requirements from equation B5. There is no coefficient (a) for polar bears.

Species	Coefficient (a)	Body weight (kg)	1000 KJ day ⁻¹	Prey Cal g ⁻¹	Cal day ⁻¹	g day ⁻¹	% Body wt day ⁻¹	Q/B
Beluga	317	800	199.51	1,500	47,684,447	31,790	0.040	14.504
Gray whales	192	16,177	1,152.30	700	275,406,837	393,438	0.024	8.873
Bowhead whales	192	31,506	1,899.71	1,000	454,042,159	454,042	0.014	5.260
Polar bear		310	49.77	3,500	11,894,526	3,398	0.011	4.001
Pacific walrus	380	587	189.49	1,300	45,288,153	34,837	0.059	21.662
Bearded seal	200	200	44.50	1,500	10,636,592	7,091	0.035	12.941
Ringed seal	200	43	14.05	1,500	3,358,392	2,239	0.053	19.228
Spotted seal	200	44	14.30	1,500	3,416,800	2,278	0.051	18.705

Seabird Biomass

The biomass of seabirds was calculated from seabird colony counts in the Beringian Seabird Colony Catalog (maintained by the U.S. Fish and Wildlife Service, USFWS 2003). The total biomass (Table B3) was estimated by summing the colony counts from within the model area then multiplying by the average body mass (Hunt et al. 2000). For the composite group unidentified murre; a weighted average body mass was used, based on the observed proportion of species. The total biomass was then divided by the model area to produce a biomass density estimate ($t\ km^{-2}$).

Table B3.-- Summary of the average individual weights, abundance estimates, and estimated total biomass for all seabird groups represented in the eastern Chukchi Sea model. Average weights are from Hunt et al. (2000) and abundance estimates from the Beringian Seabird Colony Catalog (USFWS 2003).

Common name	Species name	Weight (kg)	Abundance	Biomass (t)
Common Murre	<i>Uria aalge</i>	0.99	82,470	81.85
Thick-billed Murre	<i>Uria lomvia</i>	0.96	152,330	146.85
Unidentified Murre	<i>Uria</i> spp.	0.97	435,305	423.99
Black-legged Kittiwake	<i>Rissa tridactyla</i>	0.41	119,318	48.56
Parakeet Auklet	<i>Aethia psittacula</i>	0.26	20,000	5.16
Least Auklet	<i>Aethia pusilla</i>	0.08	207,000	17.39
Crested Auklet	<i>Aethia cristatella</i>	0.26	219,000	57.82
Tufted Puffin	<i>Fratercula cirrhata</i>	0.78	506	0.39
Horned Puffin	<i>Fratercula corniculata</i>	0.62	19,670	12.18
Pelagic Cormorant	<i>Phalacrocorax pelagicus</i>	0.47	449	0.21
Glaucous Gull	<i>Larus hyperboreus</i>	1.41	4,306	6.08
Sabine's Gull	<i>Xema sabini</i>	0.19	16	< 0.01
Mew Gull	<i>Larus canus</i>	0.40	20	0.01

Seabird Production Rates

There are few published estimates of P/B for seabirds. For this model we use the P/B values of taxonomically equivalent functional groups from the Ecopath model of the eastern Bering Sea by Aydin et al. (2007). They estimated P/B with a constant mortality rate (Z). Estimates of annual mortality were taken directly from the literature (Furness and Monaghan 1987) or were calculated from survival rates (Schreiber and Burger 2001) by setting P/B equal to the negative logarithm of the survival rate:

$$\frac{P}{B} = -\ln(\text{survival rate}) \quad . \quad (B7)$$

Species-specific rates were preferred when they were available, otherwise estimates for higher taxonomic classifications were used (Table B4). When more than one rate was available, the average was used.

Table B4.-- Seabird functional group P/B values along with the literature values of annual mortality or survival they were derived from . (Table recreated from Aydin et al. (2007)).

Functional group	P/B (or Z)	Annual mortality rate* or survival rate**	Resolution (taxonomic level rate refers to)	Source
Murres	0.169488	0.75-0.95**	order level	Schreiber and Burger 2001
Kittiwakes	0.075804	0.926** Middleton Is. AK; 0.930** St. George, Bering Sea; 0.925** Shoup Bay AK	black-legged kittiwake	Schreiber and Burger 2001
Puffins	0.04	0.04*	Atlantic puffin	Furness and Monaghan 1987
Cormorants	0.158727	0.80-0.91**	order level	Schreiber and Burger 2001
Gulls	0.165782	0.74-0.97**	order level	Schreiber and Burger 2001
Seabirds planktivorous	0.169488	0.75-0.95**	order level	Schreiber and Burger 2001

Fish and Selected Invertebrate Biomass

Biomass density estimates were calculated for all fish groups (except salmonids) and many benthic invertebrates from the catch data of a bottom-trawl survey conducted in the northeastern Chukchi Sea between Cape Lisburne (approx. 68.4° N) and the ice-edge (approx. 72° N) during August and September of 1990 (Barber et al. 1994). The data is housed and maintained in the RACEBASE database at NOAA's Alaska Fisheries Science Center in Seattle. A total of 95 successful trawls were made at 48 stations along 11 transects that ran perpendicular to the shore. The sampling stations covered a depth range from 18 to 55 m. The trawl data and catch processing are briefly reviewed here and the reader is referred to Barber et al. (1994) for complete details. The net used in this survey had no roller gear on the footrope allowing for consistent contact with the bottom and thorough sampling of demersal fish and benthic macrofauna. The catch was sorted to the lowest taxonomic level practical then counted and weighed (kg). The catch per unit effort (CPUE, t km⁻²) of each functional group was calculated for the entire survey area using the area-swept method (Wakabayashi et al. 1985). These biomass estimates served as the initial model inputs for all fish groups and many benthic invertebrate groups including snow crab, basket stars, sponge, anemones, benthic urochordates, and corals.

Fish Diets

There are few reports of fish diets from the Chukchi Sea (e.g., Frost and Lowry 1983, Coyle et al. 1997) and most are qualitative in nature or lack the quantitative detail to be of use in a mass-balance model. Many species from the Chukchi Sea are also found on the eastern Bering Sea continental shelf and have been subject to stomach sampling during NOAA trawl surveys. Due to the lack of region-specific data, the fish diets used in this model were derived from stomach data collected in the eastern Bering Sea by scientists from the Resource Ecology and Ecosystem Modeling (REEM) program at NOAA's Alaska Fisheries Science Center in Seattle. The diet compositions were acquired by querying the REEM food habits database (a detailed description of the database can be found at, <http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm>) with their Diet Analysis Tool (Lang 2004). The diet compositions were the mean percent weight of each prey item in the predator's diet averaged across hauls.

For species with abundant sampling, diet queries were spatially limited to the northernmost survey strata and inshore from the continental slope (< 100 m) (NMFS survey strata 20, 41, 42, and 43, see figure 2 in Lauth 2011). These strata encompass much of the eastern Bering Sea cold pool (see figure 6 in Lauth 2011) and were thought to most closely resemble the biotic and abiotic conditions of the eastern Chukchi Sea amongst the standard eastern Bering Sea survey strata. Spatially limiting diet queries was considered impracticable, if by doing so it reduced the stomach sample size to less than 100 non-empty stomachs. Queries were spatially limited for Greenland turbot, Pacific halibut, butterfly sculpin, warty sculpin, Pacific cod, and walleye pollock. Stomach samples from Pacific cod and walleye pollock in the eastern Bering Sea are particularly abundant in the REEM food habits database (Pacific cod $n = 52,926$, walleye pollock $n = 109,624$). Queries for these two species were also temporally limited to the base model time period of 1990. For all other species all available years were used. Because the diet composition of many species of fish are known to change with size (e.g., Buckley et al. 1999, Yang et al. 2006), the diet queries for Pacific

cod and walleye pollock were further limited to the maximum lengths recorded in the northeastern Chukchi Sea during the 1990 bottom trawl survey. This reduced their stomach sample sizes to 229 Pacific cod and 157 walleye pollock.

In 2010 the standard NMFS eastern Bering Sea summer bottom trawl survey area was expanded north to the Bering Strait (~65°N), including Norton Sound in the east and extending to the U.S.-Russia Convention Line in the west (see figure 2 from Lauth 2011). Food habits data were collected from several species belonging to the small-mouth flatfish functional group within this northern extension area during the 2010 survey. Diet data queries for the small-mouth flatfish group were limited to this northern extension area because it was presumed to more closely resemble the abiotic and biotic conditions of the eastern Chukchi Sea than the standard eastern Bering Sea survey strata.

Other Benthic Invertebrate Biomass

Biomass density estimates for bivalves, snails, sea stars, brittle stars, urchins-dollars-cucumbers, anemones, benthic urochordates, benthic amphipods, polychaetes, and worms etc. are compiled from Stoker (1981). The density estimates are averages from 176 sampling stations from a survey of benthic invertebrate macrofauna covering the combined eastern Bering/Chukchi continental shelf over the years 1970 to 1974. Most of the sampling stations are concentrated in the northern Bering Sea and the density estimates are therefore biased towards the prevailing conditions in that area. Species composition, abundance, and biomass of benthic communities are known to vary between location in the Chukchi Sea and are affected by many abiotic factors including the properties of the overlying water mass (e.g., temperature, salinity), primary productivity, pelagic-benthic coupling, and sediment size (Stoker 1981, Feder et al. 2005, Grebmeier et al. 2006, Feder et al. 2007, Blanchard et al. 2010b, Iken et al. 2010). Lacking other region wide studies of the benthic invertebrate macrofauna the average densities of Stoker (1981) are considered best estimates.

The biomass density of miscellaneous crabs, shrimp, cephalopods, and miscellaneous crustaceans was determined with a top-down balance assuming an EE of 0.8. Shrimp have a low catchability in bottom trawls and it was believed that the 1990 survey catch data was an underestimate of the actual biomass. The resulting biomass density estimate of 2.6 t km^{-2} was two orders of magnitude greater than the survey derived estimate. Similarly, the top-down estimate of cephalopod biomass was three orders of magnitude greater than the estimate from survey data. Initial balancing produced an EE of 1.48 for miscellaneous crabs, so a top-down balance was used and increased the biomass density estimate by about 85%. Miscellaneous crustaceans are generally too small to be effectively caught by bottom trawl gear and estimates with enough detail and precision were not available from the literature so a top-down balance was performed for this group as well.

Appendix C Data quality grading

Table C1.--Criteria for data quality pedigree (or grade) based on the data pedigree originally described for Ecopath with Ecosim (EwE) by Christensen et al. (2005). B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest (Table recreated from Aydin et al. 2007).

Data pedigree and corresponding data characteristics	
B, P/B, Q/B, DC, and C	
1	Assessment data is established and substantial, from more than one independent method (from which the best method is selected) with resolution on multiple spatial scales.
2	Data is a direct estimate but with limited coverage/corroborations, or established regional estimate is available while subregional resolution is poor.
3	Data is proxy, proxy may have known but consistent bias.
4	Direct estimate or proxy with high variation/limited confidence or incomplete coverage.
B and C	P/B, Q/B, and DC
5	Estimate requires inclusion of highly uncertain scaling factors or extrapolation
6	Historical and/or single study only, not overlapping in area or time.
7	Requires selection between multiple incomplete sources with wide range.
8	Estimated by Ecopath
5	Estimation based on same species but in "historical" time period, or a general model specific to the area.
6	For P/B and Q/B, general life history proxies or other Ecopath model. For DC, same species in adjacent region or similar species in the same region.
7	General literature review from a wide range of species, or outside the region. For DC, from other Ecopath model.
8	Functional group represents multiple species with diverse life history traits. For P/B and Q/B, estimated by Ecopath.

Table C2.-- Confidence intervals taken from Aydin et al. (2003) with their corresponding data pedigree (or grade) for the different model parameters. B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest.

Grade	B and C	P/B	Q/B	DC
Confidence Interval (+/-)				
1	0.1	0.1	0.1	0.1
2	0.1	0.2	0.2	0.3
3	0.5	0.3	0.3	0.5
4	0.5	0.4	0.4	0.6
5	0.5	0.5	0.5	0.7
6	0.8	0.6	0.6	0.8
7	0.8	0.7	0.7	0.8
8	0.8	0.8	0.8	0.8

Table C3.-- Data pedigree (grade) and corresponding confidence intervals (C.I.) for eastern Chukchi Sea model parameters. Colors highlight the range of data quality based on the confidence interval from good (green, ~0.1), to acceptable (yellow, ~0.5), to poor (red, ~0.8). *The Chukchi Sea stock of polar bears has two separate subsistence harvests (U.S. and Russian) that were parameterized separately. The data grade for the U.S. harvest is 2 (C.I.=0.1) and 7 (C.I.=0.8) for the Russian harvest. B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest.

Model parameter	B		P/B		Q/B		DC		C	
	Grade	C.I.								
Beluga	5	0.5	6	0.6	6	0.6	5	0.7	5	0.5
Gray whale	5	0.5	6	0.6	6	0.6	5	0.7		
Bowhead whale	5	0.5	6	0.6	6	0.6	5	0.7	2	0.1
Polar bear Chukchi stock	7	0.8	5	0.5	6	0.6	6	0.8	7, 2*	0.8, 0.1*
Polar bear S. Beaufort stock	5	0.5	4	0.4	6	0.6	4	0.6	2	0.1
Pacific walrus	5	0.5	6	0.6	6	0.6	5	0.7	4	0.5
Bearded seal	7	0.8	6	0.6	6	0.6	4	0.6	4	0.5
Ringed seal	6	0.8	6	0.6	6	0.6	4	0.6	4	0.5
Spotted seal	7	0.8	6	0.6	6	0.6	4	0.6	5	0.5
Murres	4	0.5	6	0.6	6	0.6	6	0.8		
Kittiwakes	4	0.5	6	0.6	6	0.6	6	0.8		
Puffins	4	0.5	6	0.6	6	0.6	6	0.8		
Cormorants	4	0.5	6	0.6	6	0.6	6	0.8		
Gulls	4	0.5	6	0.6	6	0.6	6	0.8		
Seabirds planktivorous	4	0.5	6	0.6	6	0.6	6	0.8		
Large-mouth flatfish	2	0.1	6	0.6	6	0.6	6	0.8		
Small-mouth flatfish	8	0.8	6	0.6	6	0.6	6	0.8		
Large-mouth sculpin	8	0.8	6	0.6	6	0.6	6	0.8		
Other sculpin	8	0.8	6	0.6	6	0.6	6	0.8		
Eelpout	8	0.8	6	0.6	6	0.6	6	0.8		
Pelagic forage fish	8	0.8	6	0.6	6	0.6	6	0.8		
Miscellaneous shallow fish	8	0.8	6	0.6	6	0.6	6	0.8		
Walleye pollock	2	0.1	6	0.6	6	0.6	6	0.8		
Pacific cod	2	0.1	6	0.6	6	0.6	6	0.8		
Saffron cod	8	0.8	5	0.5	5	0.5	6	0.8		
Arctic cod	8	0.8	4	0.4	4	0.4	6	0.8		
Salmon outgoing	7	0.8	6	0.6	6	0.6	6	0.8		
Salmon returning	7	0.8	6	0.6	6	0.6	6	0.8		
Cephalopods	8	0.8	6	0.6	7	0.7	7	0.8		
Bivalves	7	0.8	6	0.6	7	0.7	7	0.8		
Snails	7	0.8	6	0.6	7	0.7	7	0.8		
Snow crab	2	0.1	6	0.6	6	0.6	6	0.8		
Miscellaneous crabs	8	0.8	6	0.6	7	0.7	7	0.8		
Shrimps	8	0.8	6	0.6	7	0.7	7	0.8		
Sea stars	7	0.8	6	0.6	7	0.7	7	0.8		
Brittle stars	7	0.8	6	0.6	7	0.7	7	0.8		
Basket stars	2	0.1	6	0.6	7	0.7	7	0.8		
Urchins, dollars, cucumbers	7	0.8	6	0.6	7	0.7	7	0.8		
Sponge	2	0.1	6	0.6	7	0.7	7	0.8		
Benthic urochordate	2	0.1	6	0.6	7	0.7	7	0.8		
Anemones	2	0.1	6	0.6	7	0.7	7	0.8		
Corals	2	0.1	6	0.6	7	0.7	7	0.8		
Benthic amphipods	7	0.8	6	0.6	7	0.7	7	0.8		
Polychaetes	7	0.8	6	0.6	7	0.7	7	0.8		
Worms etc.	7	0.8	6	0.6	7	0.7	7	0.8		
Miscellaneous crustaceans	8	0.8	6	0.6	7	0.7	7	0.8		
Jellyfish	2	0.1	6	0.6	6	0.6	7	0.8		
Copepods	8	0.8	6	0.6	6	0.6	7	0.8		
Other zooplankton	8	0.8	6	0.6	7	0.7	7	0.8		
Pelagic microbes	8	0.8	7	0.7	7	0.7	6	0.8		
Benthic microbes	8	0.8	7	0.7	7	0.7	7	0.8		
Phytoplankton	8	0.8	7	0.7						
Pelagic detritus	8	0.8								
Benthic detritus	8	0.8								

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