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A Comparison of the Eastern Bering and Western Bering Sea Shelf and Slope Ecosystems Through the Use of Mass-Balance Food Web Models

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U.S. DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

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ABSTRACT

A comparison of the food webs of the eastern and western Bering Sea continental shelf large marine ecosystems (EBS and WBS LMEs) is presented, with a literature review of Russian and English sources for the western Bering Sea food web. A model is constructed using Ecopath, a tool for performing quantitative mass-balance calculations to synthesize food web data. The model focuses on the earliest period for which detailed diet data was available in both systems, 1980-85.

The results show that the broad EBS shelf supports a benthic community of considerable diversity, while the narrower WBS shelf contains an ecosystem with a higher per-unit-area production in the pelagic layers and a more productive pelagic phytoplankton and zooplankton community. Keystone species in both systems are walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*). In the eastern Bering Sea, small flatfish and crab species have a large impact on the energy flow from the benthic web to upper trophic levels. On the other hand, in the WBS, a large proportion of detritus entering the benthic food web is consumed by epifaunal species such as urchins and brittlestars. This may be due to the larger percentage of WBS shelf area close to shore. Additional measures of ecosystem structure, maturity, and sensitivity are presented.

Future steps in pursuing ecosystem modeling efforts through the food webs in these two systems should lie in determining the importance and role of deep Bering Sea Basin processes, especially through mesopelagic forage fish, and in further subpartitioning each model into fine scale biophysical domains.

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INTRODUCTION

In order to develop meaningful measures of large marine ecosystem (LME) function and health, a comparative study of ecosystems is required. Unfortunately, the unique nature of each separate LME makes drawing comparisons between systems difficult. Furthermore, such comparisons may require a synthesis of large bodies of literature that exist in different locations and contain results in different contextual formats that are not readily adaptable for comparison.

The Bering Sea (Fig. 1) covers more than 2.3 million km², and as a whole supports high biological production and multiple fisheries (NRC 1996). In a management context, its waters lie in both Russian and U.S. Exclusive Economic Zones (EEZs), with international waters in a section of the central basin (the “donut hole”).

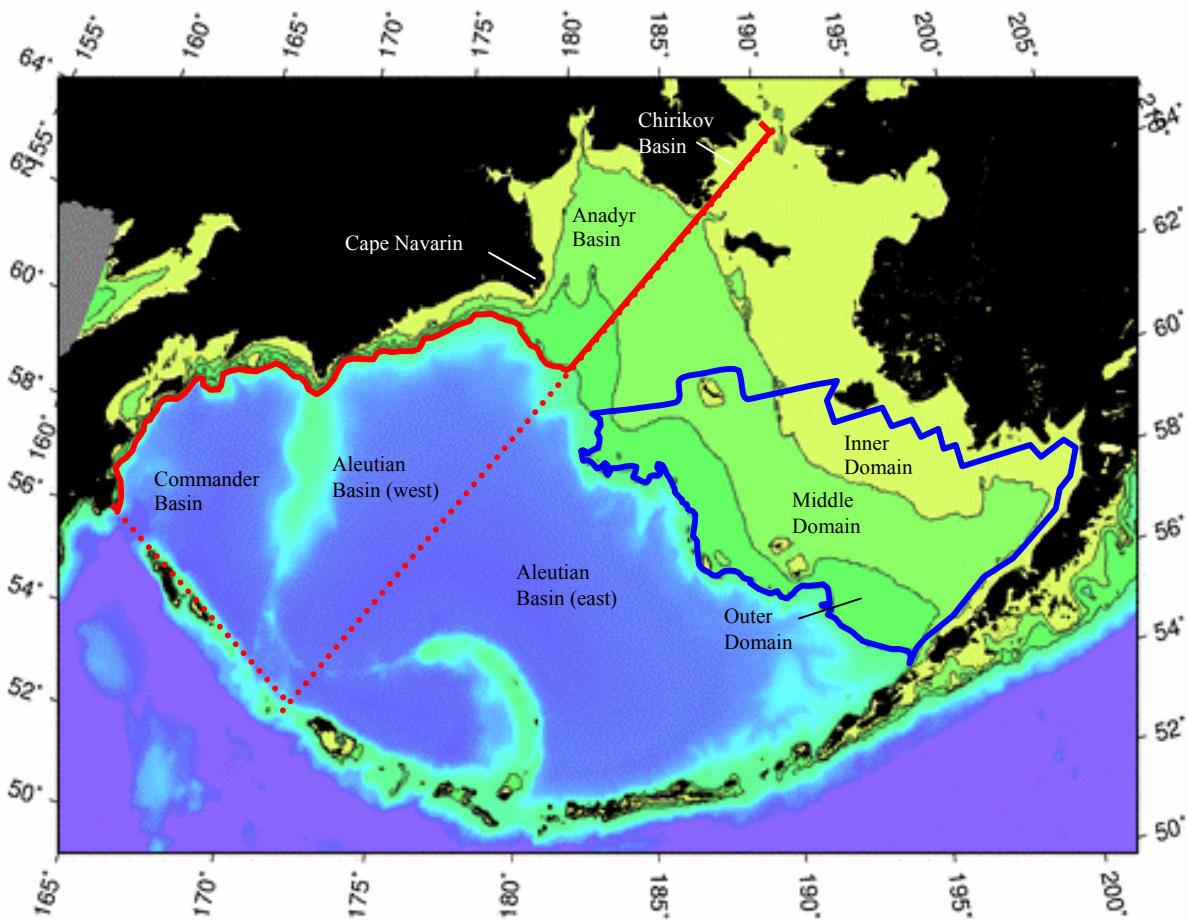


Figure 1. The Bering Sea, with boundaries of the EBS shelf model (eastern solid line), the WBS shelf model (western solid line), and the WBS shelf+basin model (dotted line). Isobaths shown are 50m (between inner and middle domains), 100m (between middle and outer domains) and 200m (between outer domain and slope/basin).

Sherman and Alexander (1986) define LMEs as ocean spaces of at least 200,000 km², characterized by distinct hydrographic regimes, submarine topography,

productivity, and trophically dependent populations. With respect to the biophysical setting of the Bering Sea, three ecosystems have been defined as relevant LMEs (Sherman 1993): the eastern Bering Sea (EBS), the western Bering Sea (WBS), and the adjacent Gulf of Alaska (GOA). A unified framework for concurrently exploring the food webs of each of these regions has not been presented in the past, and such a framework is useful for examining large scale climate and human-induced changes as they occur in these systems.

The Alaska Fisheries Science Center (AFSC) and the Russian Pacific Institute of Fisheries and Ocean Research (TINRO) have each been conducting ecosystem studies in their respective sides of the Bering Sea. It is evident from the published Russian literature and data listings provided to the National Marine Fisheries Service (NMFS) that Russian researchers have data on the abundance and trophic links of marine ecosystem components in the western Bering Sea. Similarly, scientists on the eastern side of the Pacific have been updating energy flow models of the eastern Bering Sea shelf.

Unfortunately, there have never been any joint integrative studies looking at the food webs of the Bering Sea as a whole. The difference in physical and biological conditions between the eastern and western areas may result in fundamentally different responses to ecosystem change. On the other hand, the presence of similar important fish species such as walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) targeted by fisheries may result in profound similarities.

The goal of this project is to elucidate ecosystem production and energy pathways in the eastern and western Bering Sea shelf and slope regions by developing and comparing quantitative food web models of these areas. The third LME mentioned above, the Gulf of Alaska, is a target for future modeling work. By using a common modeling framework, Ecopath, we hope that this effort shall serve two primary purposes:

1. It shall synthesize the predator and prey data from the western Bering Sea into a quantitative food web, while providing a substantial literature review similar to that provided for the eastern Bering Sea in Trites et al. (1999).
2. It will allow the examination of the resulting food web models as a preliminary exploration and comparison of the ecosystem interactions which occur in both ecosystems, and also of the independent data analysis methodologies used to derive the predator/prey quantitative interactions used in each model.

The primary results of the western Bering Sea data review and initial model building are contained in Appendix A of this report, as provided by the Russian participants in this project; this Appendix serves as a companion piece to the eastern Bering Sea data review contained in Appendix 2 of Trites et al. (1999). The results of the comparison and synthesis of the eastern Bering Sea shelf and Western Bering Sea models (hereafter referred to as the EBS and WBS models) are contained in the Results section of this report, and represent a joint effort of all of the current authors.

METHODS

The Ecopath Model

Ecopath is a food web analysis tool that has gained broad recognition as a sound methodology for assembling and exploring data on marine food webs (Polovina 1985, Christensen and Pauly 1992, Pauly et al. 2000; see the website www.ecopath.org for the latest available software, manuals, and list of published models). The methodology's strength lies in its emphasis on using data collected and analyzed in many common types of fisheries analyses, especially stock assessment and food habits studies; and its ability to combine the data into a single coherent picture. A resulting model both highlights the dominant predator/prey processes as they can be gleaned from the data, and helps focus attention on major data gaps relative to their importance in the functioning of the ecosystem as a whole.

Ecopath is a mass-balance model, built by solving a simple set of linear equations which quantify the amount of material (measured in biomass, energy, or tracer elements) moving in and out of each compartment in a modeled food web. The master Ecopath equation is, for each functional group (i) with predators (j):

$$B_i \left(\frac{P}{B} \right)_i * EE_i + IM_i = \sum_j \left[B_j * \left(\frac{Q}{B} \right)_j * DC_{ij} \right] + EM_i + C_i .$$

For each compartment, a subset of the parameters:

1. B (biomass);
2. P/B (production/biomass);
3. Q/B (consumption/biomass);
4. DC (full proportional diet matrix);
5. IM (Immigration) and EM (emmigration);
6. C (Fisheries catch + discards);

may be provided as data inputs and the model will estimate a seventh parameter, "Ecotrophic Efficiency" (EE), the fraction of input production which is utilized by other compartments. The estimation of EE is the primary tool for data calibration in Ecopath: independent estimates of consumption and production of different species often lead to initial conclusions that species are being preyed upon more than they are produced ($EE > 1.0$), which is impossible under the mass-balance assumption.

Therefore, by using an EE greater than 1.0 as a diagnostic tool for error, it is then possible to assess the relative quality of each piece of input data to adjust inputs to a self-consistent whole. This process is known as "balancing" the model: it does not imply that the true ecosystem is in equilibrium but rather quantifies the uncertainty contained in the estimates of supply and demand present in the system.

For the EBS and WBS models, data for Parameters 1-6 listed above were gathered from numerous sources. In cases where reasonable estimates of biomass were not available, the EE for the compartment was set to a constant, to estimate the minimum biomass required to supply the rest of the food web's consumption of that compartment. The compartments for which this approach was taken are discussed below.

Model Setting

Geographic setting

A simple “box-type” food-web model contains no explicit differentiation of biogeography. The ideal ecosystem box model is both closed in terms of migration and uniform in terms of spatial processes. Unfortunately, in selecting the size of the region to be modeled, the goals of closure and uniformity are mutually exclusive, especially when examining higher trophic level fish stocks. Furthermore, the offshore boundaries of marine ecosystems are flexible, and may differ for different marine plant and animal communities and may shift with time as environmental changes occur.

Pacific waters flow into the Bering Sea from the Alaskan Stream and by the Western Subarctic Gyre currents (Ohtani 1973). Intensive water exchange makes the Bering Sea a relatively open gulf of the Pacific Ocean (Shuntov and Dulepova 1991). The counterclockwise circulation of water along the shelf creates several regions of differing biological productivity; for example, the inner, middle and outer fronts described below, and the “Green Belt”, a region of intense primary productivity associated with the shelf break (Springer et al. 1996).

Each of these regions possesses distinct communities of lower trophic level species with differing process rates (McRoy et al. 1986). However, many fish and mammal species are part of single stocks which are distributed throughout these zones. The model’s capability to partition stocks by subregion is limited: therefore, all of the zones were included in a single model and lower trophic level processes were weighted by subarea to calculate averages over the system as a whole.

The eastern Bering Sea shelf consists of inner, middle, and outer shelf ecological zones separated by oceanographic fronts associated with the 50, 100, and 200 m isobaths, respectively, each of which possesses fundamentally different physical processes and species compositions (Fig. 1; Table 1). The EBS model was limited entirely to the area of the EBS south of 61°N and 20 km or more offshore as representing the extent of the NMFS trawl survey area.

The wide shelf of the EBS was considered self-contained, with no major input of diet items from the Bering Sea basin. The only exception to this was for Pacific salmon (*Oncorhynchus* spp.), for which 75% of their diet was considered to come from outside the eastern Bering Sea. Marine mammals’ migration and off-the-shelf foraging was handled by lowering the average biomass of seasonal migrants. However, since some species were resident on the shelf while taking short foraging trips over the basin, some of the diet of these animals necessarily reflected basin species.

The shelf/basin split was more difficult to model in the western Bering Sea. The total area of the Bering Sea in the Russian EEZ is dominated by the Bering Sea Basin: the western Bering Sea shelf is narrow and covers less than 10% of the total western area (Fig. 1; Table 1). Moreover, the cyclonic circulation of the main basin contributes strongly to the Kamchatka Current south of Cape Navarin (Stabeno et al. 1999).

South of Cape Navarin, the shelf (0-200 m) varies from less than 5 km to 50 km in width, but in general this whole shelf area is closer to shore than the inshore border of the EBS study area (Fig. 1). While temperature and salinity may divide this part of this

narrow shelf into coastal, transitional and oceanic waters, the divisions are not stationary and may vary interannually with the strength and east/west position of the Kamchatka Current (Khen 1999). North of Cape Navarin, the shallow (50-100 m) Anadyr Basin and the most northern Chirikov Basin are northward extensions of the EBS shelf.

The western main basin is divided into two sub-basins by the Shirshov Ridge: the Commander Basin, adjacent to the Commander Islands, Kamchatka Peninsula, and Shirshov Ridge; and the Aleutian Basin, north-eastward from the Shirshov Ridge, bordered by the Aleutian Arc on the south, and by the wide eastern Bering Sea shelf on the east. The area of the Aleutian basin included in the initial WBS model and listed in Table 1 is bounded by the EEZ boundary rather than by a natural boundary (Fig. 1).

Table1. Surface area (thousands of km²) of distinct biogeographical subareas included in the modeled regions.

Eastern Bering Sea (EBS) Model subregions	Area
Inner Domain (20 km offshore-50 m depth)	118.9
Middle Domain (50-100 m depth)	211.1
Outer Domain (100-200 m)	133.4
Slope	21.1
Total	484.5
Western Bering Sea (WBS) Model subregions	
<i>Shelf and slope model only</i>	
The north-western Chirikov Basin	23.5
The Anadyr Basin	145.0
The western Bering Sea shelf area southward from Cape Navarin	55.0
The western Bering Sea continental slope area	30.7
Total shelf and slope area	254.2
<i>Additional area in shelf, slope and basin model</i>	
The Commander Basin	226.0
The north-western Aleutian Basin	222.0
Total shelf, slope, and basin area	702.2

Because the WBS shelf is much narrower than the EBS shelf, a greater relative proportion of shelf species might have significant inputs from basin food sources. Further, Russian stock assessments consider many major fish species to be single stocks throughout their EEZ. To reflect this, the initial WBS model was a combined shelf/basin model, bounded by the shore and the Russian EEZ boundary. This model, including a WBS literature review of both shelf and basin species, is presented in Appendix A.

However, for the purposes of comparison with the EBS model, it was decided that the most meaningful initial comparison would result from restricting the WBS model to the shelf and slope, including shelf areas both north and south of Cape Navarin (Fig. 1; Table 1). The procedure used for restricting the WBS model in this manner is discussed below. The resulting WBS shelf/slope model was compared with the EBS shelf/slope model as described in the Results section. It is recognized that this large-scale averaging across shelf zones in the EBS and the shelf/basin split in the WBS may have introduced inaccuracies in the data which should be more thoroughly explored. Further, possible

stock migrations between regions, especially across the northern shelf boundaries which are nearly contiguous between the two modeled regions, are not explored. An important step in future modeling should be to create refined subregional models for each distinct biogeographic area.

Data sources, time period, and model units

The mass-balance model of the southeastern Bering Sea shelf and slope for the years 1979-85, including a substantial literature review of available data sources, is provided in Trites et al. (1999). The most detailed version of that model, with 40 functional groups (Appendix 3 in Trites et al. 1999) formed the basis of both the EBS and WBS models presented here. The literature reviewed in Appendix 2 of Trites et al. (1999) was not substantially updated and thus continues to serve as the primary reference for the EBS model.

A WBS literature review, not previously available in English, is presented in Appendix A. One of the main information sources was a regular series of reprint documents “Description of stocks’ condition of the major species and groups in the Far Eastern seas in (past year) and possible catches prediction in (next year).” This series (TINRO 1986-91, 1993, 1997-98) presents collective papers for all commercial fishery objects on the Russian Far East (analogous to NMFS documents “Stock assessment with yield consideration for year ...”). It is published by TINRO annually and has limited distribution through Russian fisheries agencies. Some western Bering Sea ecosystem information was taken from the preliminary report presented by Radchenko et al. (1991) at the PICES Workshop in December of 1991. All other literature sources are listed in Appendix A.

The time period 1979-85 was used as the “base” model in Trites et al. (1999). This time period represents the ecosystem immediately following the great increase of walleye pollock biomass in the EBS, and this time period was chosen in Trites et al. (1999) in order to compare the 1980s EBS with limited data available from the 1950s, and thus capture some of the ecosystem changes resulting from this shift in dominant fish biomass over 30 years. For building the WBS model, this time period was extended slightly up to 1990 to increase the pool of available data. For the WBS, all existing data were averaged from 1981 to 1990 inclusively, when it was possible. If data from all years were not accessible, data from available years from that decade were used. Data from before 1980 and after 1990 were used for comparisons and model parameter verification.

The unit of biomass used in the model was wet weight/ocean surface area (listed as metric tons per square kilometer, t/km^2). All results in this model are compared on a per-unit-area (km^2) basis, to emphasize the characteristics of energy flows through each system. It is important to note in the following comparisons that WBS shelf model covers 254,000 km^2 , while the EBS shelf model covers 485,000 km^2 (Table 1). Therefore, if two fish stocks have the same density (or fishing pressure) per-unit area in each system, the total biomass (or catch) in the EBS region would be nearly twice that of the WBS region. While the per-area comparison stresses the role of competitors, it is important to remember this difference in total areas, especially when considering the relative magnitudes of fishing with respect to overall stock size.

Data were averaged over an entire year to remove seasonal effects. For many parameters, especially diet, winter estimates were unavailable, and summer estimates (May-September) were weighted by assumptions of extremely low production and/or biomass during winter months.

Functional groups

The Trites et al. (1999) EBS model began with the examination of over 50 functional groups and was subsequently narrowed to 24 groups, although detailed information was preserved for many of the initial species groups (Trites et al. 1999, Appendix 2). The selection of species groups was based on taxonomic and functional identity, and emphasized diversity in the assessed fish groups while greatly aggregating lower trophic levels (phytoplankton and zooplankton), and the upper trophic level non-fish species (marine mammals and seabirds).

For consistency, the WBS model began with a list of functional groups identical to that of the EBS model. However, this list was modified and adapted during the literature review process in several ways: large zooplankton categories were subdivided into many types; a few species of lesser importance in the WBS were dropped; and a protozoan group was added as a detrital recycling stage. In both models, the detrital flow was split into benthic and pelagic components.

After the literature review and initial balancing, several of the groups were combined again based on similarity of habitat, dietary niche, or lack of data. The final models contained 38 functional groups in the EBS and 36 groups in the WBS. The only groups in the EBS model missing in the WBS model due to low biomass were sablefish (*Anoplopoma fimbria*) and rockfish (*Sebastes* spp., which were combined with sculpins, Family Cottidae). The full, final list, along with all input parameters is found in Appendix B.

The two functional groups for which aggregation remained a serious problem were forage fish (“other pelagic fish”) and cephalopods. Each of these functional definitions combines pelagic and deepwater species into a single functional group, due to lack of data. In the diet analysis of larger fish and mammals, pelagic forage fish other than walleye pollock were lumped in with deepwater forage fish, primarily the extremely important lanternfishes (Myctophidae). This resulted in predictions of some spurious competitive interactions between shallow water nearshore marine mammals and deepwater slope fish for the “other pelagic fish” group. This same problem is seen to a lesser extent in the combining of the pelagic and benthic cephalopods.

Balancing the Models and Preparations for Comparative Studies

The steps for creating and balancing the EBS model are found in Trites et al. (1999). The initial stages of building the initial 50+ functional group combined basin/shelf/slope WBS model included many iterations of examination and data refinement on the part of the Russian colleagues; the details of this process are found in Appendix A. Many of the issues surrounding the balancing of the WBS model arose out of attempts to correctly apportion both diet proportions and overall biomass between basin and shelf/slope processes.

For most functional groups, the preferred mass-balancing technique was to calculate Ecotrophic Efficiency (EE) from the other provided input parameters. However, for a few functional groups, biomass estimates were not available and thus EE was set to a constant in order to estimate the biomass of these groups required to supply calculated predator demand. This was done for the same two prey groups in both the EBS and WBS models: “other” forage fish and shrimp.

Some groups of prey species were aggregated if the majority of predator diet information did not distinguish between them, or the separate species filled almost identical ecosystem roles. The four groups created through aggregation were large zooplankton, infauna, epifauna, and small flatfish. Their component species and biomasses are listed in Table 5. This aggregation solved some of the mass-balance discrepancies ($EE > 1.0$) as it removed the models’ reliance on detailed diet composition where the information was missing. This aggregation simplified the food web structure of the lower trophic levels into a few primary flows and, as a side effect, created a degree of “cannibalism” within the epifauna and large zooplankton groups. While further specification of these groups would be helpful, it is probably not possible with the data currently available on the component species or their predators.

To restrict the WBS model to shelf-only processes, the Russian researchers provided, in addition to the total biomass estimates for shelf/slope/basin areas combined, an estimated apportionment of the residence time or relative concentration of biomass and/or production between basin and shelf/slope for each functional group (Appendix Tables C1 and C2). Diet compositions in the shelf-only WBS model were initially left unadjusted due to the limitations of the data. However, this created a few imbalances which were fixed by lowering the occurrence of some primarily basin species in predators’ diets. No adjustments in diets of greater than 5% were made to achieve this balancing. Fisheries catch was apportioned between the basin and shelf/slope areas in proportion to the relative biomass in each region. This apportionment may have underestimated the extra fishing mortality on nearshore species.

The final adjustments required to compare the EBS and WBS models involved the accounting of detritus and heat dissipation in the system overall. For estimating summary ecosystem statistics such as community respiration and biomass supported per unit production, it was important that the use of differing methodologies did not bias the results. Initially, the WBS model included protozoa as part of the microbial loop, which were not included in the EBS model.

Little Bering Sea data exists on the apportioning of animal waste between respirative heat and detritus: of biomass lost during the consumption process, the proportion that was considered unassimilated energy (entering detritus) was set to 0.2 for all functional groups with the exception of infaunal, epifaunal, and benthic amphipod groups which were set to 0.4 due to the relative indigestibility of these species. The remainder of the lost biomass was considered to be burned as respirative heat. Additionally, all “other” mortality in the model $[(1-EE) \cdot \text{Production}]$ was considered to flow into detritus.

Detritus was considered to be particulate organic matter (POM) only: the role of dissolved organic matter (DOM) nutrients such as ammonia was not considered in the

Ecopath models. Rather, phytoplankton production was considered to be wholly modeled by its measured production rate, assuming sufficient DOM for this growth. Pelagic POM may reenter the food web in several ways: it can be eaten directly as pelagic detritus; sink and be eaten as benthic detritus, or it can be “reprocessed” by microzooplankton, protozoa and bacteria. Data on the actual flow rates of each of these pathways may vary substantially from region to region. For these basic models, it was decided to remove the microbial loop from the accounting process. Part of the reason for this decision was to ensure that the calculation of trophic levels was consistent with previous studies. Including a substantial microbial loop has the effect of raising the estimations of trophic level in an ecosystem, leading to higher estimations of the trophic level of fisheries and community respiration.

Therefore, POM (detritus) was considered to flow from living species into a single detrital box, and thereafter be partitioned into benthic and pelagic detritus. While microbial processes would occur along this pathway, these processes were not considered to raise the trophic level of the detritus before it was consumed by macrofauna. The relative flow of detritus to pelagic and benthic components was set by top-down demand of each detritus type’s predators. In the future, the detrital calculations in these models could benefit from the inclusion of results of more detailed lower trophic-level (nutrient-phytoplankton-zooplankton) process models.

RESULTS AND DISCUSSION

Outline

With the exception of the minor balancing adjustments discussed above, the results shown here are based on the independently assessed biomass, production, consumption and diets of individual species groups in the eastern and western Bering Sea models. Differences between the two system models may represent actual ecosystem differences or differences in methodologies used to estimate parameters from the data.

Results are summarized either by model compartment (functional group), larger functional collections of groups, or trophic level or whole ecosystem. Summaries by model compartment may represent a taxonomic level between individual species on the upper trophic levels to large aggregations of species on the lower trophic levels. The preliminary notion of larger functional collections is both ecological and fisheries-based; for example, “groundfish” are considered as a single category in the initial analysis. This notion is refined based on predator and prey niches discussed in the Food Web Network Structure section.

Trophic level has two distinct but related definitions depending on whether one is speaking of the flows through compartments or the biomass of compartments. First, the trophic level of energy flow through a compartment is a weighted average of the path lengths (number of compartments) through which energy needed to pass to reach the compartment, using phytoplankton and detritus as the first flow level. In this report, ‘flow’ trophic level is referred to as “Pathway Level” and represented with Roman numerals (I-VII+) following Christensen and Pauly 1995.

The “traditional” trophic level of each functional group, hereafter referred to as “Trophic Level,” is 1.0 plus the average of a group’s preys’ trophic levels. It may be computed directly from an input diet matrix, or a weighted average of pathway levels. The trophic level of a compartment may be fractional and is reported with Arabic numerals (1.0-5.0+) including a decimal placeholder for clarity. Note that a compartment with a Trophic Level of (for example) 4.0 may contribute to Pathway Levels of VIII and above, if complicated interconnections increase the number of steps that energy takes through a web.

Overall Biomass and Flow Between Trophic Levels

On a per-unit-area basis, the estimate of total biomass (excluding detritus) in the WBS (568 t/km^2) was 2.3 times higher than in the EBS (240 t/km^2 ; Table 2). The total production requirements from Pathway Level I (phytoplankton and detritus) to support all consumers were similarly scaled between the two systems, with $6,031 \text{ t/km}^2/\text{year}$ required in the WBS and $2,566 \text{ t/km}^2$ required in the EBS. The amount of production as a proportion of supported biomass was similar for the two systems: 10.7 in the EBS and 10.6 in the WBS.

However, the proportion of Pathway Level I production required from each of phytoplankton, benthic detritus and pelagic detritus differed between the two systems (Table 2). In the EBS, 57% of the production requirements were satisfied by

phytoplankton production versus 43% in the WBS. Pelagic detrital requirements were similar between the two systems at 18% and 20% for the EBS and WBS respectively, while benthic detritus made up a lesser proportion of the EBS food requirements (24%) than in the WBS (37%).

Table 2. Total biomass and primary production rates (phytoplankton + recycling) per unit area in the EBS and WBS models.

	EBS	WBS	Units
Total Biomass (excluding detritus)	240	568	t/km ²
<i>Trophic Pathway Level I (Consumed) Production</i>			
Phytoplankton	1,468 (57.2%)	2,591 (43.0%)	
Pelagic Detritus	474 (18.5%)	1,225 (20.3%)	
Benthic Detritus	624 (24.3%)	2,214 (36.7%)	
Total TL 1 Production	2,566	6,031	t/km ² /year
P(TL 1)/B(total)	10.7	10.6	1/year

The throughput of each pathway level is defined as the pathway's yearly input plus output, or in a steady state, double the pathway level's production less production consumed within the pathway level. The throughput is consistently higher by a factor of two in the WBS for all levels between Pathway Levels I and VII (Table 3). The excess biomass, however, is not evenly spread: in the WBS, most of this excess occurs on Pathway Level II (Table 3; Fig. 2a). The biomass of Pathway Levels IV-V are similar or higher in the EBS (Fig. 2b). Further, the amount of throughput per unit biomass shows that, on all pathway levels except Pathway Level II, the EBS uses less throughput for each unit of supported biomass (Table 3).

Table 3. Throughput (t/km²/year), biomass (t/km²), throughput/biomass (1/Year) and transfer efficiency (percentage) by pathway (trophic) level in the EBS and WBS models.

Path Level	Throughput		Biomass		Through. /Bio.		Transfer Eff.	
	EBS	WBS	EBS	WBS	EBS	WBS	EBS	WBS
VII	0.003	0.017	0.001	0.003	3.0	5.7	0.0%	0.0%
VI	0.20	0.57	0.05	0.11	3.9	5.1	2.5%	4.2%
V	5.4	10.3	1.5	1.8	3.7	5.6	5.0%	6.4%
IV	62	111	18	17	3.5	6.7	10.0%	9.6%
III	466	1,151	66	111	7.1	10.4	13.6%	9.7%
II	2,566	6,031	144	424	17.9	14.2	18.1%	19.1%
I	4,904	10,442	12	15	416.8	696.1	84.6%	86.8%

Transfer efficiencies (percentage of energy passed through each trophic level without being lost to heat or detritus) show a similar decreasing pattern in the two systems from near 20% on Pathway Level II to 2-4% on Pathway Level VI. The transfer efficiency near 85% of Pathway Level I is due to an accounting definition: the respirative assimilation of nutrients by phytoplankton, which creates considerable heat loss, is not directly modeled in Ecopath. Excluding Pathway Level I, a weighted (geometric)

average of transfer efficiency gives a result of 13.5% flow passed up per level for the EBS and 12.1% per level in the WBS.

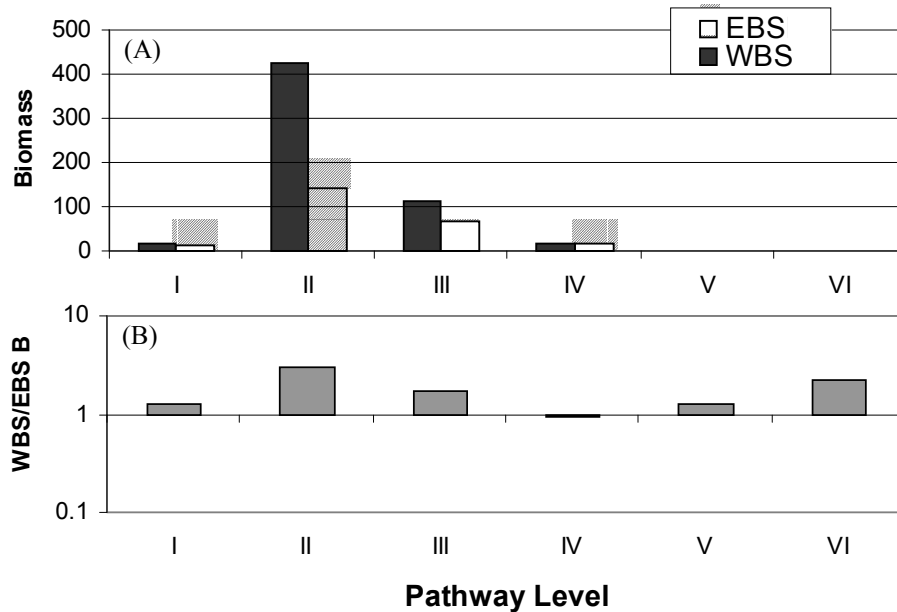


Figure 2. (A) Biomass as a function of pathway level in the EBS and WBS shelves. (B) WBS/EBS biomass by pathway level on a log scale: values above 1 indicate higher values in the WBS.

Biomass and Trophic Level of Individual Compartments

Biomass and biomass estimates for individual compartments may fluctuate greatly from year to year: however, using the long-term averages highlights some fundamental differences between the two systems during the 1980s. For the purposes of this discussion, differences of per-unit-area biomass more than 100% and differences of trophic level of more than 5% between the two systems are considered “worth noting”: these cutoffs are arbitrary.

The yearly average standing stock of phytoplankton biomass does not differ greatly between the EBS (11.8 t/km²) and the WBS (15.0 t/km²). However, estimates of pelagic zooplankton—copepods and large zooplankton—are 2-3 times higher in the WBS than in the EBS (Table 4; Fig. 3). A closer examination of the “large zooplankton” functional group shows that this abundance of large zooplankton is not due to a higher euphausiid biomass in the WBS: euphausiid biomasses are comparable between the two systems (35 t/km² in the EBS and 38 t/km² in the WBS). Rather, the high biomasses are attributable to chaetognaths, pelagic amphipods, and gelatinous zooplankton, each of which have estimated biomasses 5-10 times higher in the WBS (Table 5a).

The overall biomass of pelagic forage species is comparable between the two systems, with a total of 24 t/km² in the EBS and 30 t/km² in the WBS. The largest proportion of this biomass is attributable to miscellaneous (“other”) pelagic fish. Further, this group includes small pelagic and mesopelagic fish and thus captures at least two distinct types of forage fish. No biomass estimates were available for these species in

either system, and so the biomass levels indicated are the minimum requirement to satisfy the measured demands of predators in the system—the actual biomass of forage fish could be considerably higher in both systems.

Table 4. Biomass (t/km²) and trophic level of all boxes in the EBS and WBS models. Shaded trophic levels are higher in indicated system by more than 5%. Differences in biomass are also shown in Figure 3. Groups in bold italics are aggregated from original models.

		<i>Trophic Level</i>		<i>Biomass</i>	
		<i>EBS</i>	<i>WBS</i>	<i>EBS</i>	<i>WBS</i>
Lower trophic level pelagic species	Phytoplankton	1.0	1.0	11.77	15.00
	Copepods	2.0	2.1	55.00	122.62
	<i>Large zooplankton</i>	2.3	2.6	44.00	120.74
Pelagic forage species	Juv. pollock age 0-1	3.1	3.4	6.00	3.76
	Pacific herring	3.2	3.3	0.78	0.79
	Other Pelagic Fish	3.2	3.4	(*)13.46	(*)19.08
	Cephalopods	3.8	3.7	3.50	4.83
	Salmon	3.5	3.7	0.05	0.04
	Jellyfish	3.3	3.1	0.05	1.40
Lower trophic level benthic species	<i>Epifauna</i>	2.4	2.2	5.86	114.96
	<i>Infauna</i>	2.0	2.0	46.50	125.69
	Benthic Amph.	2.0	2.0	3.62	13.81
Benthic particulate species	Tanner crab	3.0	3.0	0.60	0.08
	Snow crab	3.0	3.0	1.60	0.25
	King crab	3.0	3.0	0.60	0.12
	Shrimp	2.5	2.4	(*)3.00	(*)2.10
Groundfish species	Adult pollock age 2+	3.3	3.4	27.45	15.00
	Pacific cod	4.0	4.0	2.42	3.19
	Pacific halibut	4.1	4.6	0.14	0.08
	Greenland turbot	4.1	4.5	0.96	0.06
	Arrowtooth flounder	3.9	4.3	0.80	0.05
	<i>Small flatfish</i>	3.1	3.2	9.18	0.99
	Skates	4.1	4.4	0.29	0.27
	Sculpins	3.9	3.8	0.56	(**)0.68
	Sablefish	4.2	-	0.11	-
	Rockfish	3.6	(**)	0.09	(**)
	Macrouridae	4.1	3.9	0.20	1.16
	Zoarcidae	3.1	4.1	0.64	0.90
	Bird and marine mammal species	Baleen whales	3.6	3.8	0.25
Toothed whales		4.3	4.6	0.02	0.04
Sperm whales		4.7	4.7	0.21	0.02
Walrus and bearded seals		3.5	3.2	0.16	0.26
Other seals		3.9	4.5	0.06	0.10
Steller sea lions		4.3	4.5	0.01	0.04
Seabirds		4.0	4.0	0.01	0.01

(*) Biomass set by "top-down" demand.

(**) rockfish are included with sculpins in the WBS.

- no biomass assessed (minimal)

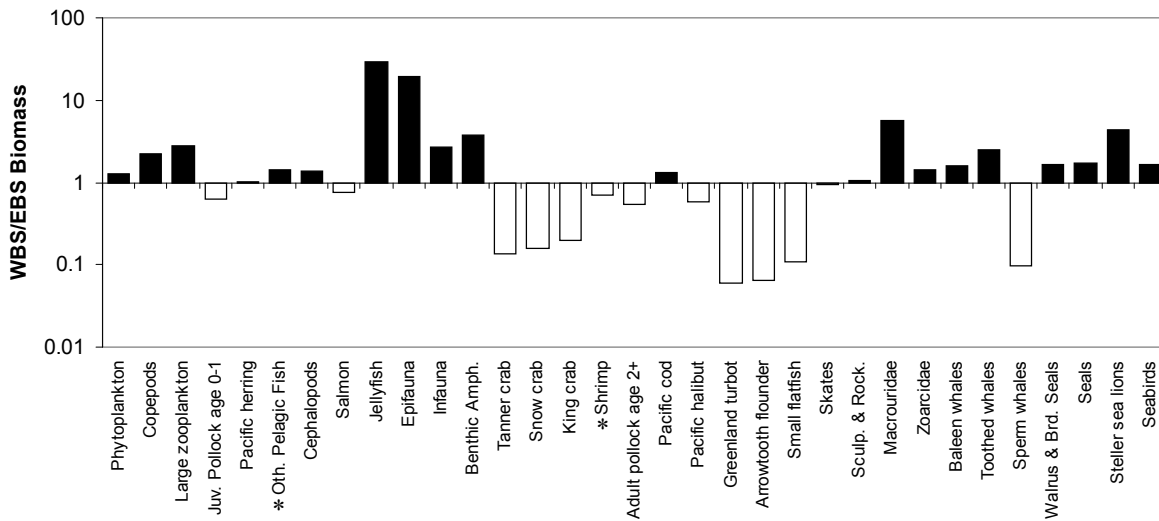


Figure 3. WBS/EBS biomass density (t/km^2), log scale. A black bar indicates a higher value in the WBS (WBS/EBS value greater than 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value less than 1.0). (*)species biomass set by top-down balance (demand).

The estimates of infaunal biomass are higher in the WBS ($126 t/km^2$ vs. $47 t/km^2$ in the EBS), while the epifaunal biomass is almost 20 times higher in the WBS ($115 t/km^2$ vs. $6 t/km^2$ in the EBS). A breakdown of these groups shown in Table 5c-d indicates that while all of these benthic species groups had a higher biomass in the WBS, the large majority of the WBS epifaunal biomass was due to a high estimated biomass ($96 t/km^2$) of sea urchin populations.

On the other hand, the biomass of higher trophic-level benthic species is greater in the EBS. Tanner crab (*Chionoecetes bairdi*), snow crab (*C. opilio*) and king crabs (*Paralithodes* spp.) have biomass levels 2-6 times higher in the EBS. There were no estimates for shrimp biomass in either system, so again these biomass levels were set by top-down demand and the estimates are similar between the ecosystems. The biomass estimates of flatfish species—Greenland turbot (*Reinhardtius hippoglossoides*), Arrowtooth flounder (*Atheresthes stomias*) and Pacific halibut (*Hippoglossus stenolepis*), and especially the small flatfish community as a whole—was considerably higher in the EBS (Tables 4 and 5b).

In both systems, the fish species with the largest biomass was walleye pollock, which due to the importance of cannibalism, was divided into juvenile and adult (age 2+) groups. Pollock have an age 2+ biomass of $27 t/km^2$ in the EBS and $15 t/km^2$ in the WBS.

Groundfish species other than flatfish showed similar per-area biomass levels between the two systems (Table 4; Fig. 3). Toothed whales and Steller sea lions (*Eumetopias jubatus*) have a higher biomass in the WBS, while estimates of sperm whale (*Physeter macrocephalus*) presence is higher in the EBS. The biomass estimates of other marine mammals and seabirds are comparable between the two systems. However, many

of the marine mammal estimates are based on Bering Sea or North Pacific-wide estimates of biomass weighted by residence time in each region: these residence time calculations are other potentially large sources of error.

Table 5. Breakdown of biomass (t/km²) of individual groups within post-balance aggregated groups in EBS and WBS models. (A) Large Zooplankton; (B) Small Flatfish; (C) Infauna; (D); Epifauna.

(A) Large Zooplankton	EBS	WBS	(B) Small Flatfish	EBS	WBS
Pelagic amphipods	2.0	19.0	Flathead sole	0.5	0.2
Gelatinous plankton	2.0	13.6	Yellowfin sole	6.1	0.2
Euphausiids	35.0	38.0	Rock sole	1.3	0.2
Mysiids	3.0	1.4	Alaska plaice	1.3	0.2
Chaetognaths	6.0	(*)48.8	Other small flatfishes(**)	-	0.1
Total	48.0	120.7	Total	9.2	1.0

(C) Infauna	EBS	WBS	(D) Epifauna	EBS	WBS
Clams	29.5	80.3	Hermits & other decapods	1.0	2.1
Polychaetes	14.0	38.3	Snail	0.5	1.2
Other worms	3.0	7.1	Brittlestar	3.0	14.5
Total	46.5	125.7	Starfish	1.3	1.0
			Other benthos(**)	-	96.2
			Total	5.9	115.0

(*)Lowered to 44 to achieve balance.

(**)See Appendix A for WBS “other species” groups not included in the EBS model.

The trophic level (TL) of each species (Table 4) is determined entirely by the input diet matrix (Appendix Tables B4-B6). Since bacterial and micro-zooplankton processes have been removed from both models, phytoplankton and detrital biomass have a trophic level of 1.0 in both models, and copepods have a trophic level near 2.0. In the WBS model, cannibalism in copepods (5% of their diet) raises their trophic level with respect to the EBS, where cannibalism is not included in these species.

The large zooplankton group consumes a mix of phytoplankton, detritus, and copepods in both models. The diet of large zooplankton in the WBS is considerably higher in copepods (48% vs. 25%) and correspondingly lower in phytoplankton and detritus. The higher proportion of copepods in large zooplankton diets and the existence of cannibalism in the WBS large zooplankton group is probably due to the considerably higher measured biomass of chaetognaths versus euphausiids in that model (Table 5). As large zooplankton are a major link in both pelagic food webs, their higher trophic level has the effect of increasing the modeled trophic level of many fish species in the WBS.

Differential zooplankton apportionment does not explain all of the differences in fish trophic levels, however. The high trophic level of Zoarcidae (eelpouts) in the WBS, the only group with a difference of more than 0.5 of a trophic level, is due to a fundamental difference in the input diet data between the models: the EBS diet matrix shows them as primarily benthic feeders on infauna, while the WBS model places them as feeders on forage fish, cephalopods, and pollock. It is not known if this is an ecological or methodological difference.

In the benthic web, trophic levels of the EBS and WBS groups are similar, with infauna and amphipods (TL 2.0) feeding on benthic detritus (TL 1.0); while epifauna and shrimp feed on a combination of infauna and detritus. Crabs feed on these groups in similar proportions in the two systems. Walrus and bearded seals show a higher trophic level in the EBS due to a weighting of their diet towards benthic particulate feeders (crabs; TL 3.0) instead of infauna and epifauna in the WBS (TL 2-2.5).

Production and Consumption of Individual Compartments

Production-per-unit-biomass (P/B) and Consumption-per-unit-biomass (Q/B) represent a combination of the population age structure and the life-history characteristics for each functional group. These life-history traits are expected to vary less over time than biomass—in this study, differences are noted between systems if these quantities differ by more than 50%. It should be noted that, due to a lack of data, many of these quantities were shared between the two systems and thus do not represent independent estimates. The full list of values used for these parameters is found in Appendix Tables B1-3.

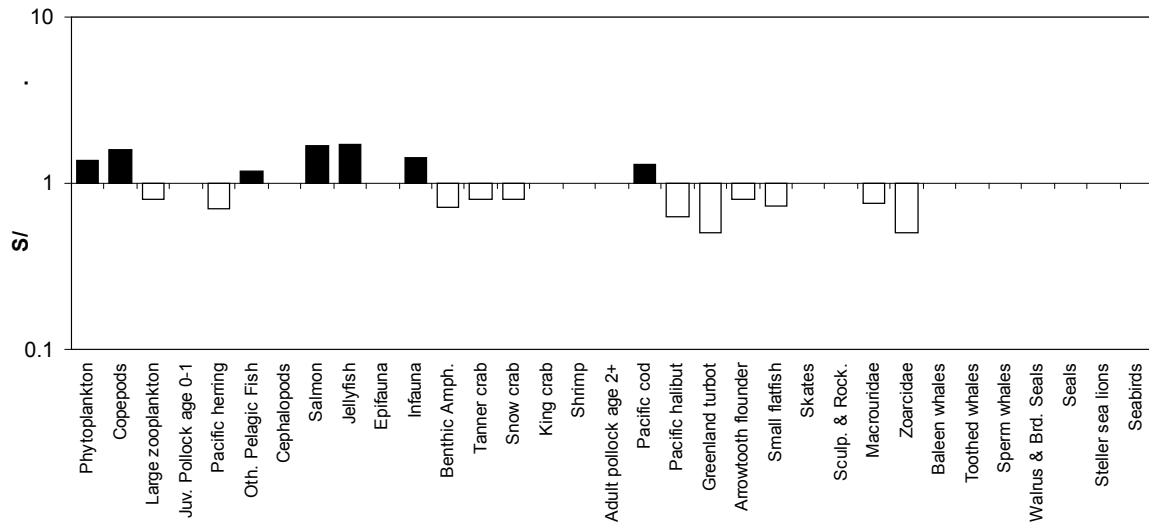


Figure 4. WBS/EBS production to biomass (P/B) ratio (1/year), log scale. A black bar indicates a higher value in the WBS (WBS/EBS value greater than 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value less than 1.0).

The difference between WBS and EBS P/B estimates for each system are shown in Figure 4. Generally, the two systems have very similar values, reflecting the derivation of P/B from similar estimates of mortality in both systems. Only a few species differ in P/B by more than 50% between the two systems.

Estimates of Q/B, on the other hand, were more variable between the two systems (Fig. 5). The estimates of consumption rates for most fish species were 1.5-5 times higher in the WBS. However, at the same time, as mentioned above, P/B estimates were similar between the two systems.

Taking P/B and Q/B estimates together, it is evident that a larger amount of respirative dissipation takes place in the WBS model, where respirative loss is defined in this case as the difference between the consumption and production of a species box (and includes material “unassimilated” during feeding). The relative apportionment of dissipative energy flow within the food webs into metabolic costs (respiration, including reproductive costs), unassimilated food, “other” mortality (disease, etc.), and bacterial recycling are difficult to compare between the two systems, as “other” mortality, calculated from the Ecotrophic Efficiency (EE) values in the models, represents aspects of the “balancing” terms in the population level mass-balance. At this juncture, it is not possible to accurately partition food web dissipation between detrital flows, recycled (bacterial) nutrients, and heat loss, therefore, further results on respirative flow are not presented here.

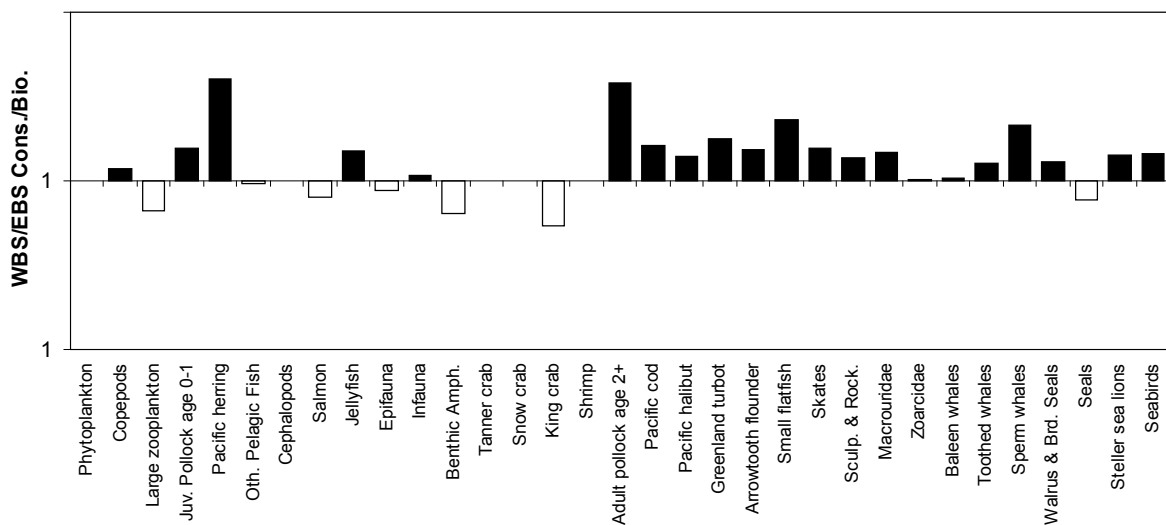


Figure 5. WBS/EBS consumption to biomass (Q/B) ratio (1/year), log scale. A black bar indicates a higher value in the WBS (WBS/EBS value greater than 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value less than 1.0).

Primary Production Required

Regardless of the causes of energy dissipation, the effects of the overall dissipation may be compared. To compare the differences in compartment transfer efficiency of the two systems, the statistic PPR, or Primary Production (+Detritus) Required, was calculated for each compartment. The PPR statistic captures the overall transfer efficiency of each food web without differentiating between energy lost through respiration versus “other” (EE-calculated) mortality.

For each compartment, the PPR value is the amount of Pathway Level I production required to support the biomass of that compartment, and in an iterative fashion to support its prey, and its prey’s prey, and so on. It thus reveals the effect that overestimating a prey’s energy consumption will have on the demand estimates of predators above it. The PPR value for all of the compartments in the system will sum to

greater than the actual Pathway Level I production, as the “required” energy is counted for a prey species itself and for all of its predators.

The per-group PPR values are shown in Figure 6, sorted in decreasing order. In both systems, the standing stocks of copepods and large zooplankton require the most primary production, followed by the species with highest biomass in the two systems: adult pollock, cephalopods, forage fish, infauna, and Pacific cod in the EBS; and epifauna, infauna, Pacific cod, and pollock in the WBS.

As might be expected from higher standing stock per-unit-area in the WBS (Fig. 2), the primary production required to support small and large plankton in the WBS is about double that in the EBS. However, the primary production required to support Pacific cod and pollock in the WBS is also about twice as high, despite the lower standing stock of these species: this is likely attributable to the higher consumption/biomass estimates used for these species in these models.

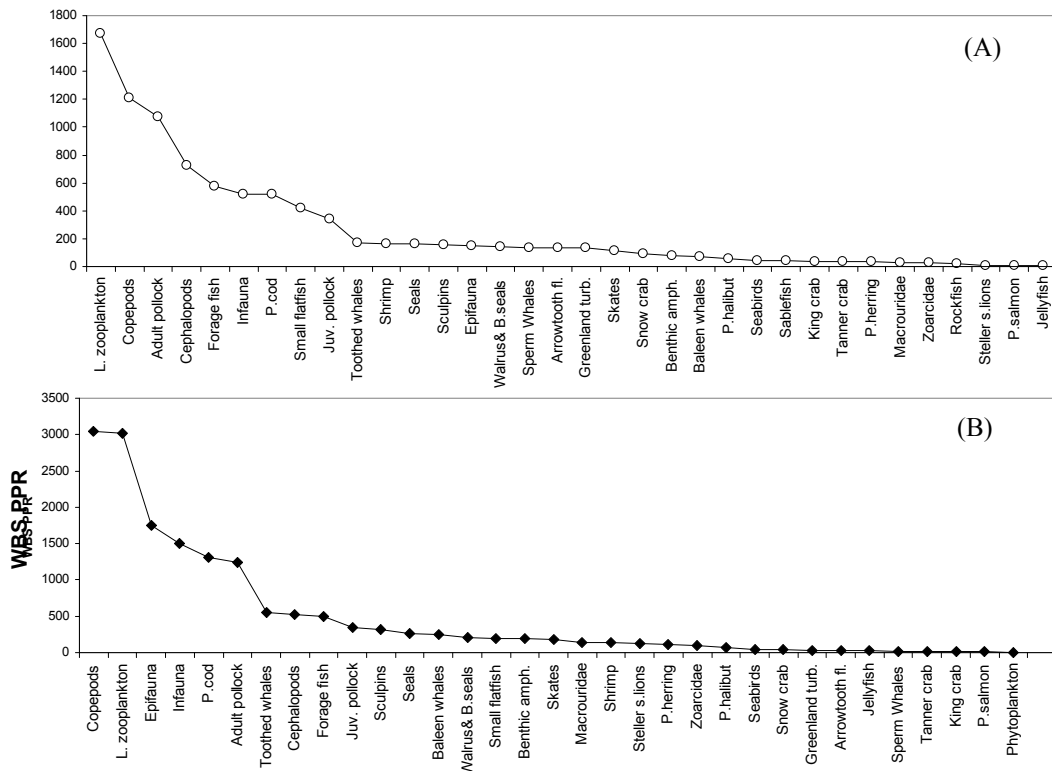


Figure 6. Primary production required (PPR) to support the standing stock of each indicated predator, taking into account the energy required to support the prey of each predator (t PPR/km²/year). Species are shown in order of decreasing PPR in the (A) EBS; (B) WBS.

This difference is more noticeable if the PPR values are normalized by the biomass in each compartment, resulting in a measurement of the primary production required to support a single unit of predator biomass (Fig. 7; units are primary production required(t)/predator(t)/km²/year). From Figure 7, it is evident that a single unit of biomass of most groundfish species requires 2-4 times more primary production in the WBS than in the EBS, indicating the modeling of a less efficient food web between primary production and groundfish in the WBS.

Finally, normalizing the PPR values per unit supported biomass by total ecosystem primary production (Fig. 8) shows that the EBS utilizes more of each unit of primary production in supporting many of its functional groups. The implication here is that the EBS is a more efficient system in terms of the primary production required to support a unit of biomass. Overall, the standing stocks in the EBS utilize a larger percentage of their primary production than those in the WBS.

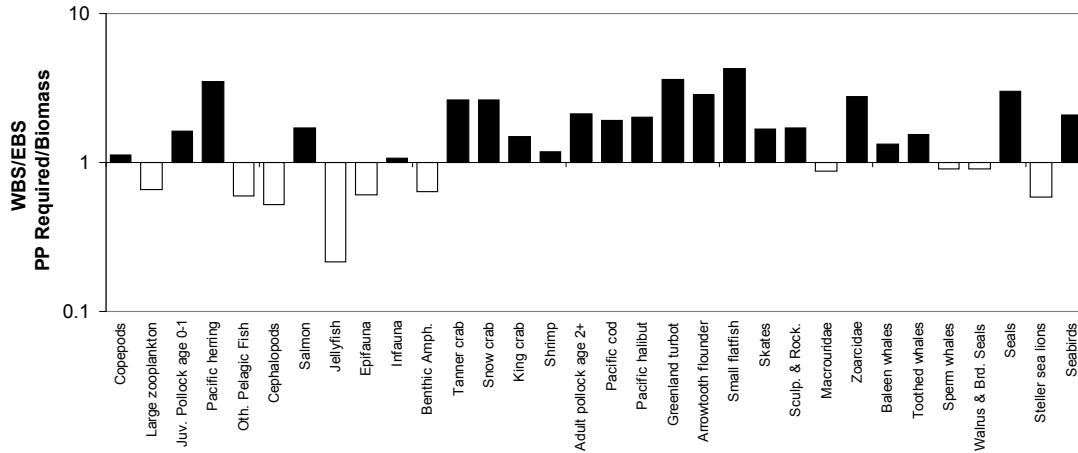


Figure 7. Primary production required to support a unit biomass each indicated predator, taking into account the energy required to support the prey of each predator (t PPR/t predator/year; WBS/EBS, log scale). A black bar indicates a higher value in the WBS (WBS/EBS value greater than 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value less than 1.0).

Since the estimates of lower trophic level production were balanced and in a few cases augmented to account for upper trophic level consumption (demand) estimates, it is worth asking if this pattern is an artifact of a few artificially high consumption rates for predators in the WBS. Energy required to support a single unit of biomass should increase logarithmically with trophic level, as each successive jump represents a 80-90% loss to dissipation (Table 3).

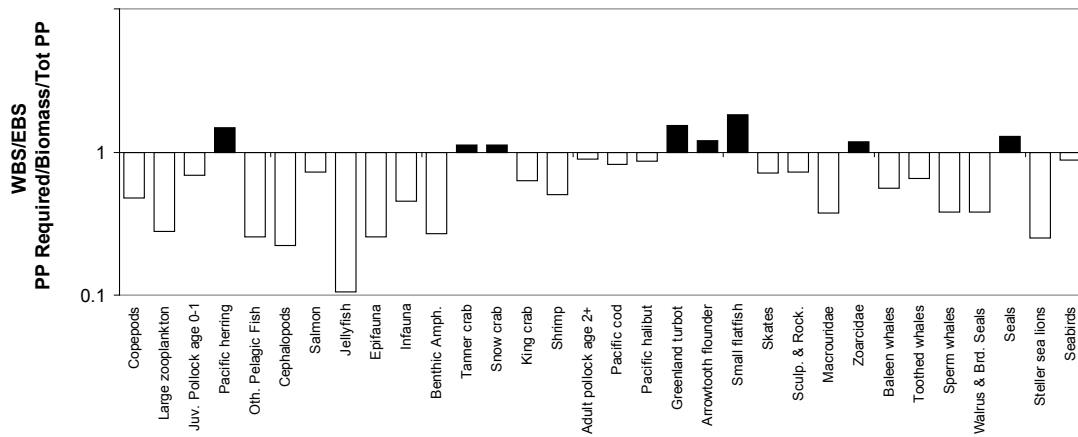


Figure 8. Primary Production Required (PPR)/Total Ecosystem Primary Production (PP) to support a unit biomass each indicated predator, taking into account the energy required to support the prey of each predator (PPR/Tot PP/t predator; WBS/EBS, log scale). A black bar indicates a higher value in the WBS (WBS/EBS value above 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value below 1.0).

Figure 9 shows an exponential regression of EBS and WBS PPR by trophic level. The regression is significant for both ecosystems ($R^2 \sim 0.60$ for both systems; $P < 0.0001$) As shown in the figure, while the slopes of the two regressions do not differ significantly, the intercepts of the WBS and EBS regressions do ($P < 0.05$), with the EBS having a higher PPR/Total Primary Production/Predator at any given trophic level.

The residuals of the outliers do not reveal any major biases as might be expected if a limited group of species were “driving” the results. The consistency of a higher proportion of utilized primary production in the EBS than in the WBS suggest an ecological rather than methodological effect, although it is possible that a systematic bias of all consumption rates throughout one ecosystem could lead to the same result.

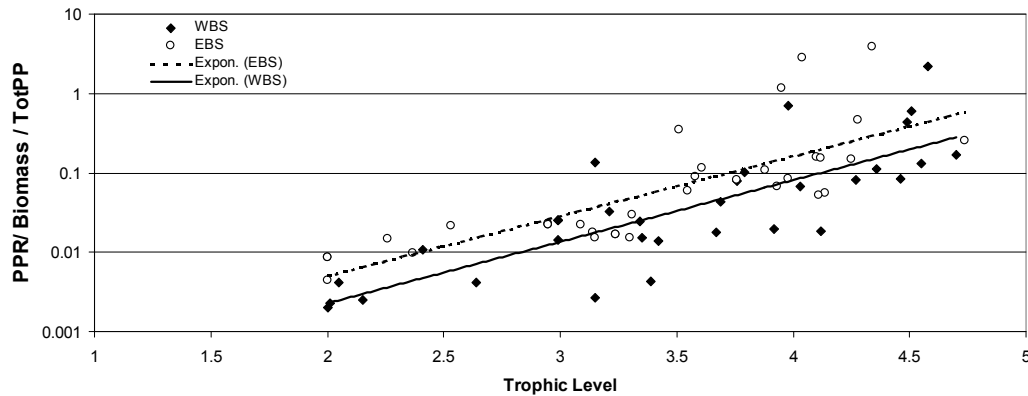


Figure 9. Primary production required (PPR)/Total ecosystem primary production (PP) to support a unit biomass each indicated predator, taking into account the energy required to support the prey of each predator (PPR/Tot PP/t predator), shown as a function of predator trophic level in the EBS (open circles) and the WBS (closed diamonds) The regressions shown are both significant ($P < 0.0001$) with R^2 values near 0.60.

Fishing, Predation, and Unexplained (“other”) Mortality

Total biomass mortality (Z) for each species grouping can be broken down into fishing mortality (F), predation mortality (M_2) and “unexplained” mortality (M_0). This latter quantity is a “balancing” term required to make the total mortality Z for each box equal to total per-unit production (P/B).

In gauging the relative impact of fishing, the value $F/(M_2+M_0)$ is a useful preliminary index to use—in the simplest single-species fisheries models, an F/M_{total} of 1.0 implies that a population is being fished at its maximum sustainable yield (MSY; Hilborn and Walters 1994). Estimates of discards are included in the catch estimations.

The values for F/M_{total} varied greatly between the two systems during the modeled time period (Table 6). In particular, many of the groundfish species in the WBS were more heavily exploited according to this measure in the WBS than in the EBS—relative fish exploitation rates in the EBS during the 1980s were comparatively low. The highest values for this index came from indigenous catch of marine mammals: even though they were exploited at a low total tonnage during the 1980s, this represented a substantial fraction of their mortality. In the EBS, Pacific salmon are the only other species showing high exploitation rates during that time period due to the inclusion of the

Bristol Bay salmon fishery. In the WBS, only Greenland turbot had an exploitation rate for which $F > M_{total}$.

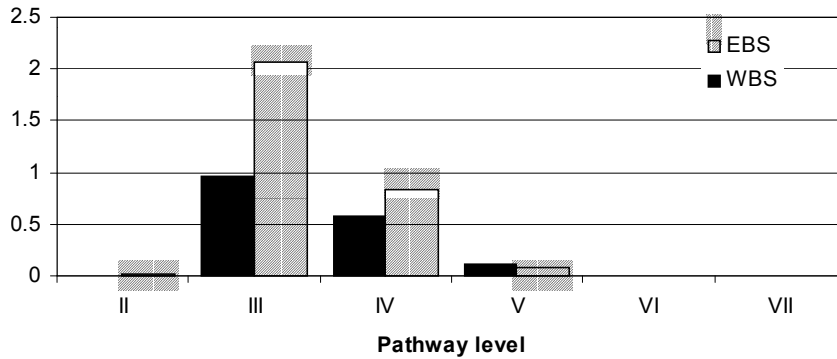


Figure 10. Biomass ($t/km^2/year$) of fisheries catch by pathway level in the EBS and WBS.

The total overall biomass taken was greater in the EBS on both an overall and a per-unit area basis (Table 6). The EBS fisheries took a proportion of total primary productivity six times larger than in the WBS, 0.12% versus 0.028%. Most of this catch came from Pathway Levels III and IV in both systems (Fig. 10), the average trophic level of the catch was 3.35 in the EBS and 3.58 in the WBS. The Primary Production Required (PPR) to support the total catch of all fisheries was 278 $t/km^2/year$ in the EBS and 520 $t/km^2/year$ in the WBS, placing the fisheries of the 1980s on a similar scale to dominant fish predators such as cod and pollock as shown in Figure 6.

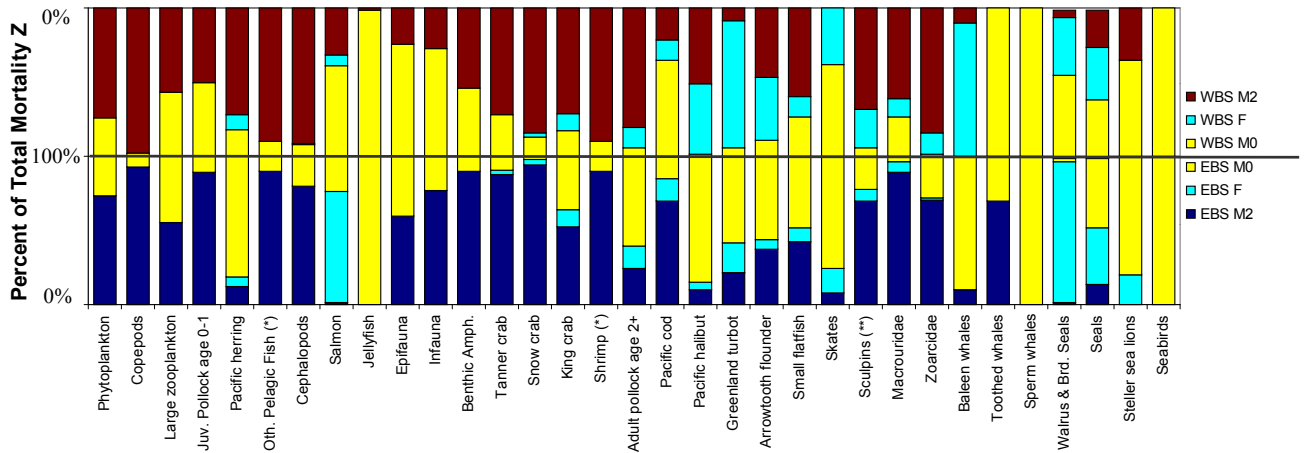


Figure 11. Apportionment of total mortality Z between predation (M_2 ; black and white solid bars), fishing (F ; black and white dotted bars) and unexplained (“other”) mortality (M_0 ; grey background with white or black dots). The line in the center is 100% mortality from the bottom for EBS, and from the top for WBS. (*) M_0 set at 10% of Z for top-down balance; (**) includes rockfish.

The apportionment of total natural mortality between predation and unexplained mortality varied greatly between the two models when compared by individual

compartments (Fig. 11), but it was not significantly different in the models when averaged over all species. The average M_2/Z was 0.50 (SD 0.35) and 0.47 (SD 0.32) for the EBS and WBS, respectively. The average M_0/Z was 0.41 (SD 0.31) and 0.40 (SD 0.32) for the EBS and WBS, respectively.

Table 6. Catch (t/year and t/km²/year), fishing mortality F, and F/Natural mortality M_{total} in the EBS and WBS, averaged for the years 1980-85.

EBS	Catch		F	F/ M_{tot}	WBS	Catch		F	F/ M_{tot}
	tons	T/km ²				tons	t/km ²		
Walrus & B. seals	4,400	0.009	0.057	20.68	Baleen whales	1,800	0.007	0.018	8.54
P. salmon	46,000	0.094	1.808	3.05	Greenland turb.	2,500	0.010	0.172	6.25
Seals	630	0.001	0.023	0.63	P. halibut	2,500	0.010	0.120	0.93
Steller sea lions	49	0.000	0.013	0.26	Arrowtooth fl.	1,800	0.007	0.135	0.73
Greenland turbot	37,000	0.077	0.080	0.25	Walrus & B. seals	1,500	0.006	0.023	0.62
Skates	9,000	0.019	0.064	0.19	Skates	10,500	0.041	0.151	0.61
P. cod	73,000	0.151	0.062	0.19	Seals	500	0.002	0.021	0.52
Adult pollock	1,010,000	2.080	0.076	0.18	Sculpins	18,000	0.070	0.103	0.35
King crab	20,000	0.042	0.070	0.13	Zoarcidae	9,900	0.039	0.043	0.17
Sablefish	2,400	0.005	0.045	0.13	Small flatfish	10,500	0.041	0.041	0.17
Small flatfish	158,000	0.326	0.036	0.10	Adult pollock	267,000	1.051	0.070	0.16
Rockfish	1,500	0.003	0.033	0.09	P. cod	57,500	0.226	0.071	0.16
Sculpins	8,200	0.017	0.031	0.08	Macrouridae	10,500	0.041	0.035	0.13
Macrouridae	2,900	0.006	0.030	0.08	King crab	2,000	0.008	0.067	0.13
P. herring	26,500	0.055	0.070	0.08	P. herring	14,000	0.055	0.070	0.11
Arrowtooth fl.	9,900	0.021	0.026	0.07	P. salmon	3,000	0.012	0.308	0.08
P. halibut	1,400	0.003	0.021	0.05	Snow crab	1,500	0.006	0.024	0.03
Tanner crab	9,300	0.019	0.032	0.03	Cephalopods	5,100	0.020	0.004	<0.01
Snow crab	23,500	0.049	0.030	0.03	Shrimp	500	0.002	0.001	<0.01
Zoarcidae	2,900	0.006	0.009	0.02	Forage fish	250	0.001	5x10 ⁻⁵	<0.01
Cephalopods	3,400	0.007	0.002	<0.01	Epifauna	1,000	0.004	4x10 ⁻⁵	<0.01
Total	1,450,000	2.990			Total	421,000	1.659		
Total Catch/Prim. Prod.			0.1165%		Total Catch/Prim. Prod.			0.0275%	
Average trophic level of fishery			3.35		Average trophic level of fishery			3.58	

Most lower trophic level pelagic species had high predation mortality rates, while predation rates on epifauna and infauna were low in both models (Fig. 11). Higher trophic level benthic particulate feeders (crabs and shrimps) saw a larger degree of predation pressure in the EBS than in the WBS. Groundfish predation varied from relatively high for sculpins, macrouridae and zoarcidae to low for most flatfish species. Naturally, very low relative predation pressure existed on the upper trophic levels of marine mammals and seabirds.

Food Web Network Structure

Overall network characteristics

The Eastern Bering Sea shelf model contains 320 described predator/prey (diet) links between distinct functional groups, compared to 235 links in the Western Bering Sea (Fig. 12). The number of energy pathways between primary production and any given upper trophic level box was considerably larger in the EBS, with over 19,000 energy pathways leading to the toothed whales in the EBS as compared to approximately 9,000 in the WBS (the maximum for a predator in both systems). These complex pathways are the result of a more detailed set of cross-connections between fish modeled in Trophic Levels 3 and 4.

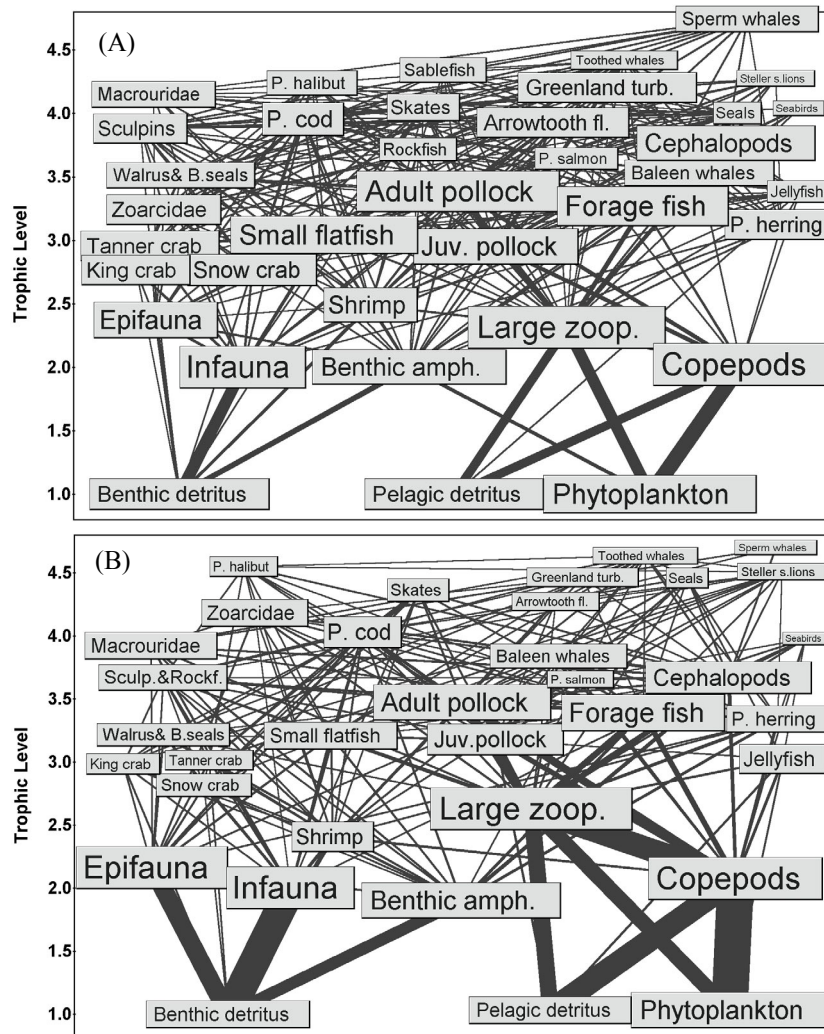


Figure 12. The trophic webs of the (A) Eastern and (B) Western Bering Sea models. Trophic level is shown on the Y-axis; box areas are proportional to log biomass (t/km^2). All predator prey flows are shown; the width of each predator/prey flow is proportional to the square root of the volume of the flow ($t/km^2/year$).

It is important to distinguish between two hypotheses for the higher number of flow connections in the EBS Ecopath model: either more sampling effort or different data treatment gives rise to the differences as a data artifact, or the more complex set of shelf habitats available in the EBS has created a more complex set of ecological relationships.

The number of pathways at any given trophic level in either model is set by the level of model aggregation. Figure 13 shows a logarithmic plot of number of pathways from primary production for each species, versus trophic level. It is expected that the number of pathways will show a natural exponential progression with trophic level, as the pathways for each trophic level are multiplied by the number of pathways in the trophic level below it. However, the sudden jump in number of pathways above Trophic Level 3, especially in the EBS, reveals the change in the level of diet detail available for each trophic level in the literature and data sources.

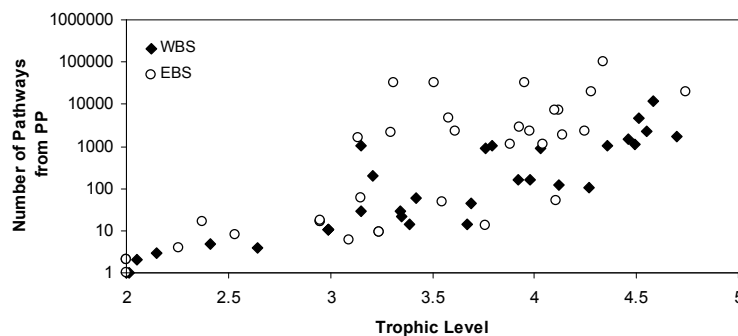


Figure 13. Number of distinct pathways from primary production to each separate compartment (log scale), plotted by compartment trophic level for both the EBS and WBS.

To investigate the relative importance of flows, each flow was ranked on an importance scale, where the “importance” of a flow was its percentage, measured in flow volume ($t/km^2/year$) in either the diet of the predator or the predation mortality of the prey, whichever was greater. Sorted by increasing importance, the number of flows for any given cumulative level of importance is shown in Figure 14: plotting by cumulative importance ensures that the most important predator and prey flows for every compartment are shown. As shown in Figure 14, 85% of the volume of predator and prey flows can be captured with a similar number of predator/prey flows in each system: 184 in the EBS and 172 in the WBS. However, in the EBS, the remaining 15% of the flow volume is spread over 136 flows, while in the WBS this 15% is spread over only 63 flows.

This result does not distinguish whether the larger number of low volume flows in the EBS model are due to increased sampling effort in the EBS or the increased complexity of the broad shelf environment. However, it indicates that the large majority of these “excess” flows are low in importance to the predator and the prey involved and may be excluded in this preliminary analysis, in order to focus on major energy pathways. Note that some of these flows may be low in importance due to a limited

spatial or temporal overlap between predator and prey: environmental shifts could change the relative importance of many prey items in a predator’s diet.

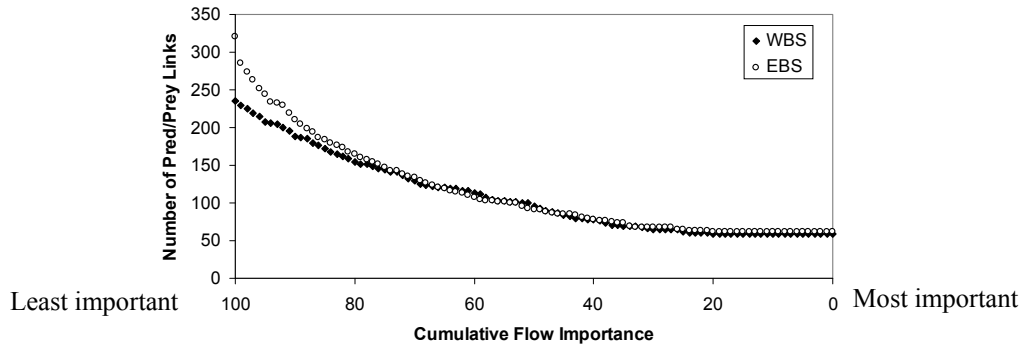


Figure 14. Cumulative number of flows of all compartments plotted as a function of the cumulative “importance” of the included flows (the importance of a single flow is measured as the maximum of the percentage of diet for a predator and the percentage of predation mortality for a prey item that a flow volume represents).

Another measure of food web complexity is degree of omnivory: the degree to which individual species feed on different trophic levels. Christensen and Pauly (1995) suggest using the variance of the measured trophic level of each compartment, calculated for each predator i by summing over all prey j : $\sum_j (TL_j - (TL_i - 1))^2 \cdot DC_{ij}$. This index is unrelated to diet diversity overall but, as opposed to diversity, is relatively independent to the level of aggregation within a single trophic level. An index of system omnivory is the average of all omnivory indices weighted by $\log(\text{consumption})$ for all compartments.

The overall omnivory index for the EBS is 0.147, and for the WBS is 0.193. This higher index is mainly due to a difference in apportioning the diet of small pelagic fish. In the WBS the diets of forage fish, juvenile pollock, and herring are an approximately equal mix of copepods and large zooplankton: in the EBS, each of these groups’ prey is generally in one trophic level or the other (Fig. 15).

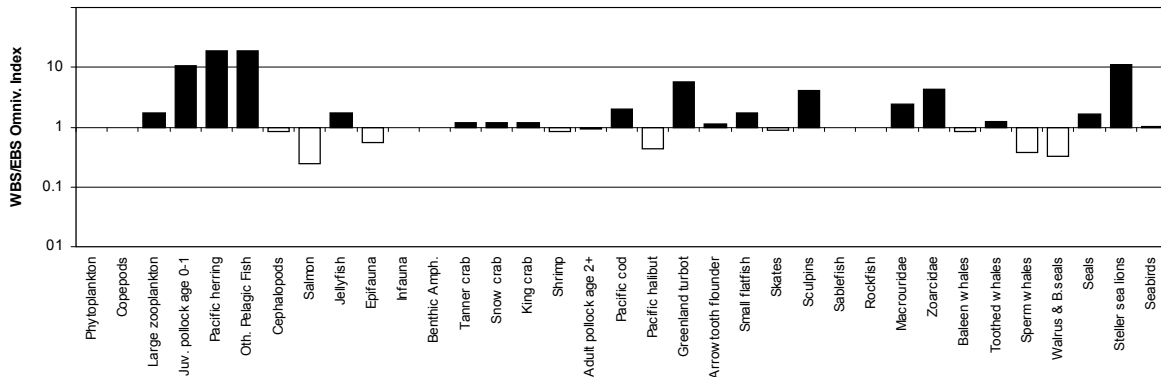


Figure 15. Omnivory indices of species in both models, shown as WBS/EBS (log scale). A black bar indicates a higher value in the WBS (WBS/EBS value greater than 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value less than 1.0).

Detailed dietary differences

While trophic level gives us a first look at the links in the food web, one more detailed approach is to define functional groups using prey and predator overlap indices. Rather than examine all of the diet composition entries on a 38 by 38 matrix, the summary of differences and similarities presented here is based on niche statistics and trophic level calculated for the two ecosystems. Diet overlap (niche) and trophic level are both wholly dependent on the input diet composition matrices. Predator overlap indices of a prey further depend on the relative consumption rates of each predator.

The diet (prey) overlap between two species boxes may be calculated from a diet matrix: for each pair of species boxes, the index takes a value between 0 (no diet overlap) and 1 (complete diet overlap). Similarly, the predator overlap between two species boxes may be calculated from a mortality matrix and also takes on a value between 0 (when two species have no predators in common) to 1 (when the percentage of predation mortality attributable to each of a set of predators is identical for the two species).

Overlap indices may be calculated for multiple functional groups within a single ecosystem, or between identical functional groups in two ecosystems. The latter comparison is shown in Figure 16. Functional groups which have almost identical predator and prey niches in both systems are clustered near the upper right hand corner of Figure 16. Rockfish and sablefish have overlap indices of 0.0 since they are not modeled in the WBS.

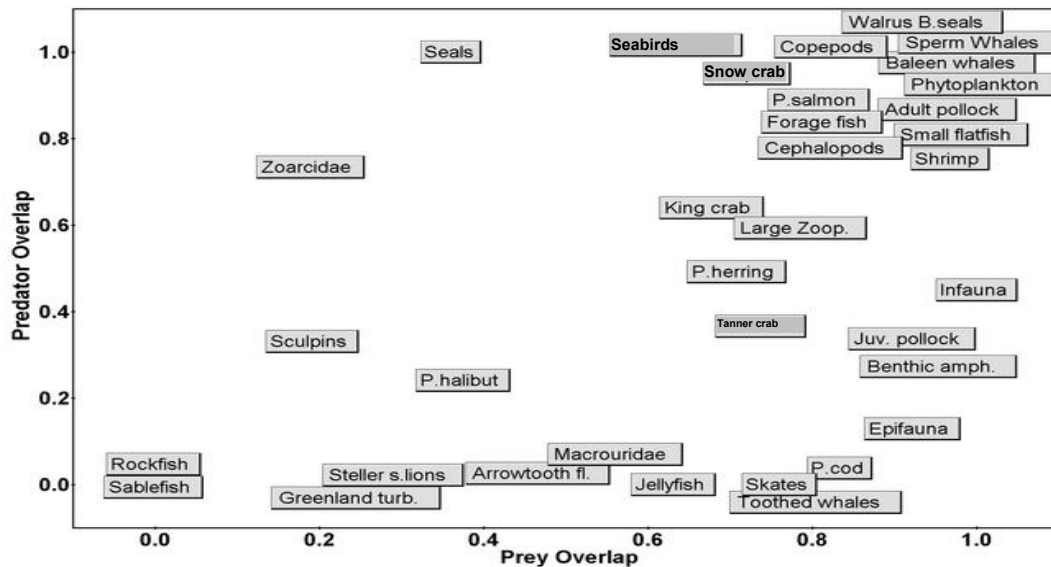


Figure 16. Prey (diet) overlap (X-axis) and predator, or mortality overlap of identical functional groups compared between the WBS and EBS systems. Groups with overlap indices near 1.0 have similar suites of predator or prey between the two systems. Functional groups near 1.0,1.0 are staggered slightly for legibility

Of the ten functional groups that show a prey overlap of 0.7 or less between the two systems, several are due to a larger proportion of cephalopods in the diets of WBS fish species (Table 7). Also, juvenile pollock are in higher proportion in some species (especially flounder and turbot) diets in the EBS while adult pollock are in higher proportion same species' diets in the WBS.

The average predator niche overlap between the two systems is less than the average prey niche overlap overall, with 18 functional groups with a predator overlap index of 0.6 or less (Fig. 16). Many of these differences are due to the inclusion of small amounts of predation on high trophic level fish by marine mammals: the marine mammal causing the most mortality varies greatly for each fish species between systems. However, the estimates in the marine mammal predation on these top fish predators may contain a greater degree of inaccuracy in both models, as often diet data for marine mammals broadly lumps fish together as a single category.

Table 7. Primary prey (items with 10% or more presence in listed predators' diets) of species with dietary niche overlaps of 0.70 or less between the EBS and WBS models.

Predator (prey similarity)	EBS diet	WBS diet
Seabirds (0.65)	60% Juv. pollock 12% L. Zoop. Remainder diverse fish species	32% L. Zoop 26% Juv. Pollock 18% Forage fish
Jellyfish (0.63)	65% L. Zoop. 15% Copepods	30% Copepods 60% L. Zoop.
Macrouridae (0.56)	42% Forage fish(*) 32% Shrimp 23% Cephalopods	30% Cephalopods 20% Infauna 16% Forage fish (*) 12% L. Zoop.
Arrowtooth flounder (0.47)	48% Juv. Pollock 20% L. Zoop. 16% Adult Pollock	50% Adult Pollock 20% Cephalopods 15% Shrimp
Pacific halibut (0.37)	50% Adult pollock 12% Epifauna Remainder diverse fish species	50% Cephalopods 18% Adult pollock 15% Juvenile pollock
Seals (0.36)	20% L. Zoop. 15% Forage Fish 14% Shrimp Remainder diverse fish species	26% Cephalopods 23% Adult Pollock 20% Juvenile Pollock
Steller sea lion (0.31)	60% Forage Fish 19% Juv. Pollock	31% Cephalopods 23% Adult Pollock 19% Juv. Pollock
Greenland turbot (0.26)	71% Juv. Pollock 24% Adult Pollock	45% Adult Pollock 30% Cephalopods 10% Forage Fish
Sculpins (0.19)	38% Sm. Flatfish 28% Shrimp 13% Snow crab	25% Adult Pollock 21% Epifauna 14% Infauna 13% Juv. Pollock
Zoarcidae (0.18)	53% Infauna 23% Benthic amphipods 14% Epifauna	35% Cephalopods 15% Forage Fish 12% L. Zoop. 10% Juv. Pollock

(*) primarily myctophids

This matrix of prey or predator pairwise overlap values within a single ecosystem may then be made into a “similarity tree” using a variety of algorithms: in this case, using the relatively simple unweighted arithmetic average clustering or UPGMA method (Rohlf 1963, Sneath and Sokal 1973, Legendre and Legendre 1998). The resulting trees show functional “families” of increasing predator or prey overlap.

Figures 17-18 show prey and predator similarity trees, respectively, for the two ecosystems. In these trees, a branch is drawn on the x-axis at the similarity (overlap) that is the average pairwise overlap between all groups on each tree branch. In these figures, an arbitrary cutoff similarity of 0.70 was used to distinguish functional groups for the purposes of this discussion. The branches are sorted so that trophic level increases from bottom to top as much as the branching structure allows.

For prey (dietary) overlap, the cutoff of 0.70 divided the EBS into 16 major dietary niche groupings, while dividing the WBS into 14 major groupings. Of these groups, phytoplankton and detritus make up four groups with no consumption, leaving 12 groups in the EBS and 14 groups in the WBS. Some of these groups are the same in both systems while some differ (Table 8).

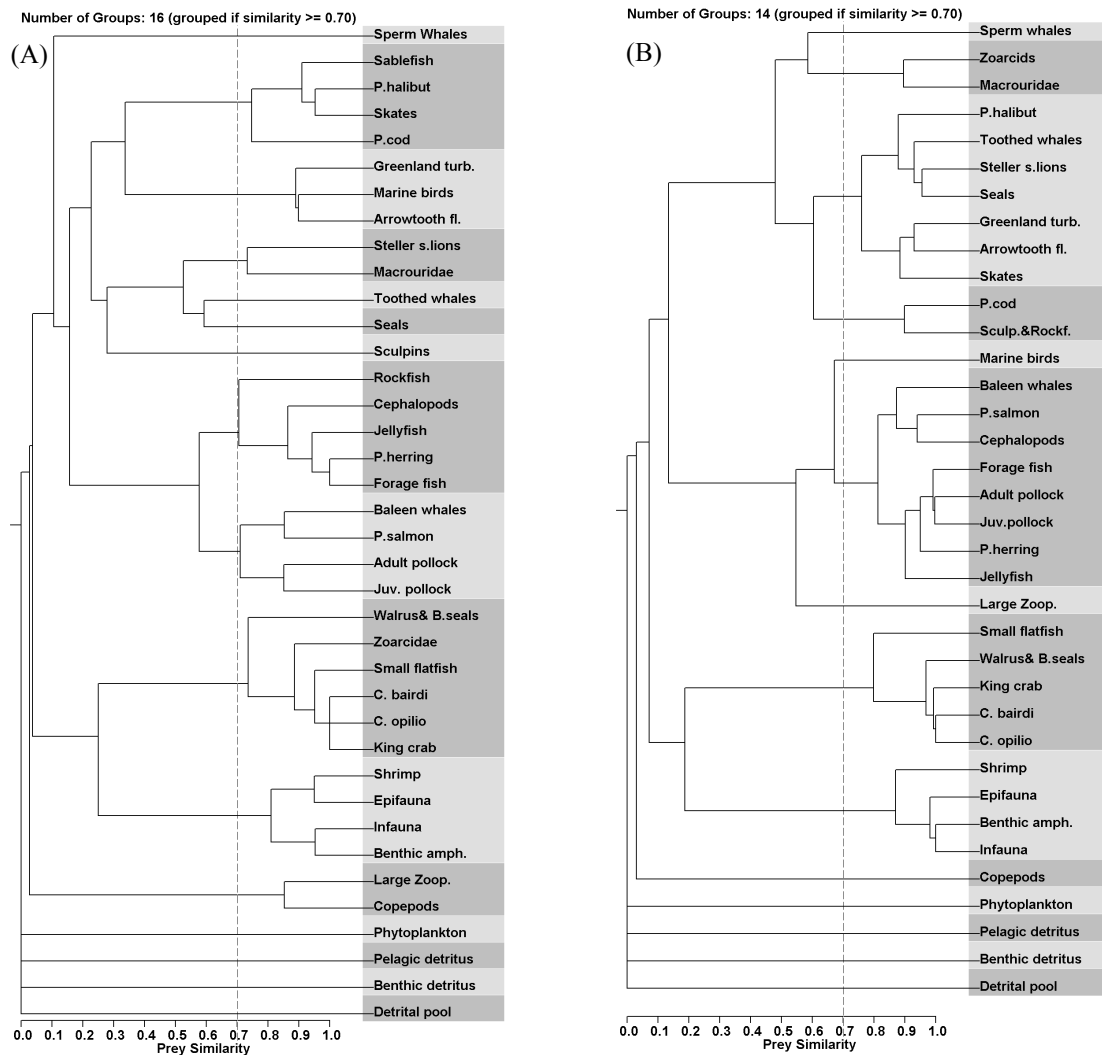


Figure 17. Cladogram of prey (diet) similarity groups based on pairwise prey similarity indices. The x-axis position of each branch indicated the average similarity between all species on the two branches. Grey shading shows functional groups with a similarity greater than or equal to 0.70 (dotted line). (A) eastern Bering Sea shelf; (B) western Bering Sea shelf.

The first few divisions at low overlap levels indicate major functional groups common to both systems, but also reveal some fundamental differences. Examining the branching tree of Figure 17 from left (least diet overlap) to right (most diet overlap) shows that after the Trophic Level 1 producers that have no diet overlap with any group (overlap 0.0), the first group to branch out is copepods at an overlap index near 0.05; however, in the EBS, large zooplankton share this branch with copepods due to their shared consumption of phytoplankton. The second major branch separates the components into benthic and pelagic categories at approximately 0.10.

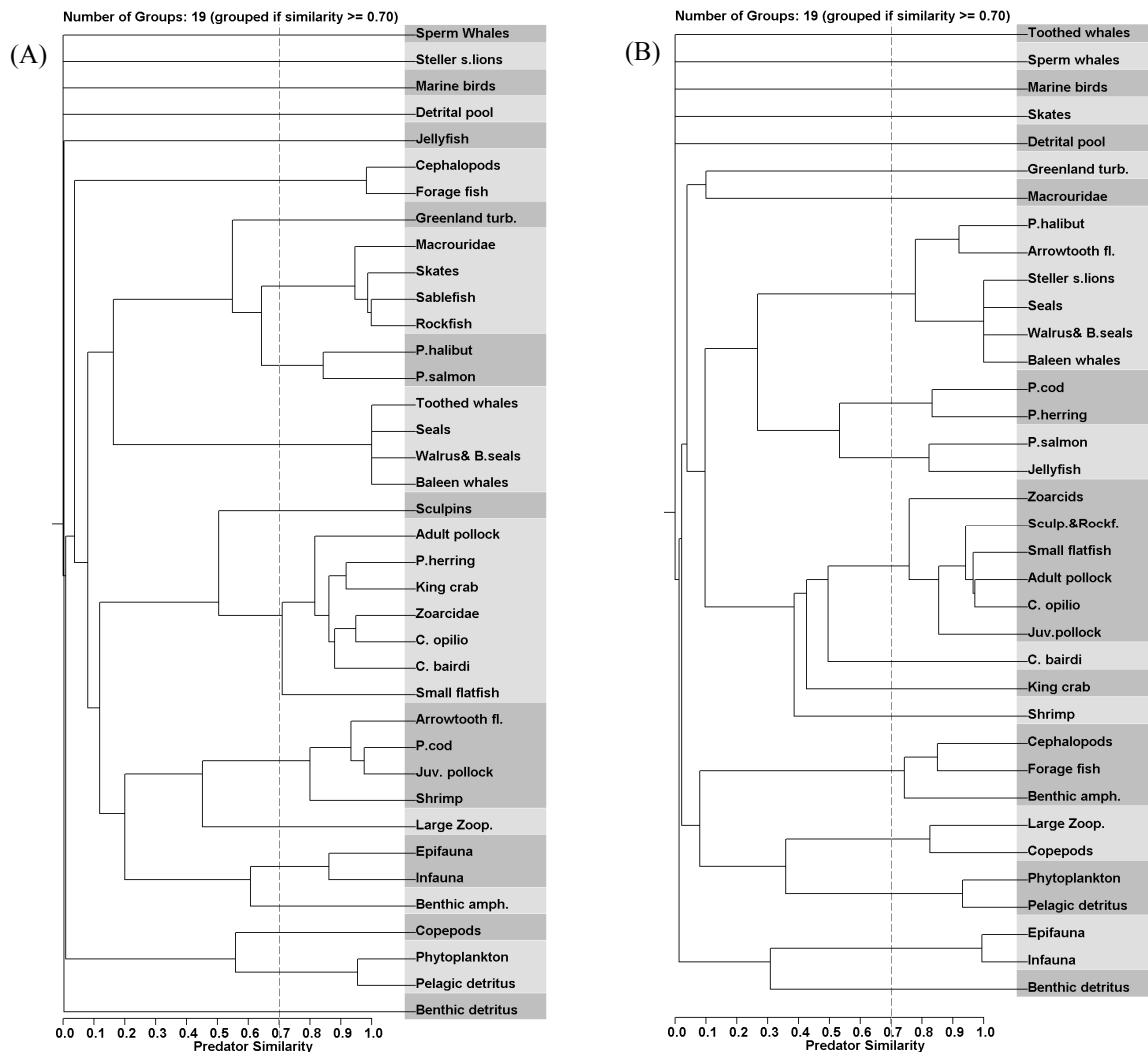


Figure 18. Cladogram of predator (mortality source) similarity groups based on pairwise predator similarity indices. The x-axis position of each branch indicated the average similarity between all species on the two branches. Grey shading shows functional groups with a similarity greater than or equal to 0.70 (dotted line). (A) eastern Bering Sea shelf; (B) western Bering Sea shelf.

The benthic and pelagic group separation is identical for all functional groups in the two systems with the exception of Zoarcidae (eelpouts), which were placed in the benthic web in the EBS, and close to Macrouridae (grenadier) and sperm whales in the WBS: however, this may be an artifact of the collapsing of the benthic and pelagic forage fish and cephalopod categories on which they feed (Table 8).

Within the benthic web, a further division occurs in both the EBS and WBS near an overlap of 0.20-0.25, effectively dividing the benthic web into two trophic levels. The lower grouping feeds on detritus directly while the top grouping feeds primarily on infauna. The high level of aggregation in infauna may obscure a considerable amount of the specialization within the benthic community in these models.

Table 8. Descriptions of major prey items of each group of predators sharing similar niches (groupings are made if diet niche similarity is greater than or equal to 0.70).

Dominant Prey Group	EBS predators	WBS predators
Phytoplankton and pelagic detritus	Copepods, large zooplankton	Copepods
Benthic detritus with some infauna (10-20%)	Benthic amphipods, infauna, epifauna, shrimp	Benthic amphipods, infauna, epifauna, shrimp
Infauna, with some epifauna (10-15%)	Crabs, small flatfish, walrus and bearded seals, Zoarcidae	Crabs, small flatfish, walrus and bearded seals
Copepods		Large zooplankton
Large zooplankton and copepods	Juvenile pollock, adult pollock, Pacific salmon, baleen whales	Jellyfish, Pacific herring, juvenile pollock, adult pollock, forage fish, cephalopods, Pacific salmon, baleen whales
Large zooplankton	Forage fish, Pacific herring, jellyfish, cephalopods, rockfish	
Small flatfish and shrimp	Sculpins	
Diverse fish (differing proportions)	Toothed whales, seals	
Juvenile pollock, forage fish, and large zooplankton		Seabirds
Forage fish and cephalopods (*)	Macrouridae, Steller sea lions	
Diverse fish and benthic predators		Pacific cod, sculpins and rockfish
Juvenile pollock	Arrowtooth flounder, seabirds, Greenland turbot	
Adult pollock, juvenile pollock, and cephalopods		Skates arrowtooth flounder, Greenland turbot, seals Steller sea lions, toothed whales, Pacific halibut
Mainly Adult pollock, some other fish	Pacific cod, skates, Pacific halibut, sablefish	
Cephalopods, forage fish, and large zooplankton		Zoarcidae, Macrouridae
Cephalopods only	Sperm whales	Sperm whales

(*) Strong niche overlap due to combining mesopelagic and pelagic forage fish, and mesopelagic and pelagic cephalopods.

Outside of the benthic web, the primary distinction of dietary niche between Trophic Levels 3-4 is the extent to which species feed on copepods versus large zooplankton. On Trophic Level 4+, the primary distinction is the extent to which species feed on pollock (adult or juvenile) versus cephalopods (Table 8).

Predator niches (based on a partitioning of predation mortality by proportion for each prey) are shown in Figure 18. In general, there are more “types” of unique predator suites for individual prey items than prey suites for individual predators, and predator similarity values tend to be lower than prey similarity values. By grouping functional groups at the level of similarity ≥ 0.70 , 19 distinct groupings are indicated.

In each model, one of these is a detrital “flow through” compartment with no predation. Four groups in the EBS (sperm whales, marine mammals, and Steller sea lions and jellyfish) and four in the WBS (sperm whales, seabirds, toothed whales, and skates) are top predators with no predation mortality or cannibalism only. Much of this decreased similarity in predator niches was the result of less aggregation in the top trophic levels. Therefore, predator groups were broadly aggregated to find groups of prey items with “similar” predators between the two systems: these results are shown as 12 distinct groups with associated important prey items in Table 9.

Table 9. Descriptions of major predators of each group of prey sharing similar niches (groupings are made if predator (mortality) niche similarity is greater than or equal to 0.70).

Dominant predator	EBS prey group	WBS prey group
Copepods (30-60%) Large zooplankton (30-60%)	Phytoplankton, pelagic detritus	Phytoplankton, pelagic detritus
Large zooplankton (60-80%), pollock (10-25%)	Copepods	Copepods, large zooplankton
Pollock (30-35%), forage fish (33%), cephalopods (17%)	Large zooplankton	
Infauna (60-80%)	Benthic detritus	Benthic detritus
Epifauna (80%)		Infauna, epifauna
Small flatfish (35-40%), crabs (20-30%), shrimp (5-10%), epifauna (5-10%)	Infauna, epifauna	
Cephalopods (40-80%)	Forage fish, cephalopods	Cephalopods, forage fish, benthic amphipods
Adult pollock (40-70%), seals (5-10%) no other common predators	Shrimp, juvenile pollock, Pacific cod, arrowtooth flounder	
Pacific cod (34-85%), marine mammals (5-40%)	Small flatfish, tanner crab, snow crab, king crab, Zoarcidae, Pacific herring adult pollock	Juvenile pollock, snow crab, adult pollock, small flatfish, Sculpins and Rockfish, Zoarcidae
Mixed fish species (no dominant)	Sculpins, Greenland turbot	Shrimp, tanner crab, Macrouridae
Toothed whales (80-100%)	Baleen whales, walrus and bearded seals, other seals, toothed whales	Baleen whales, walrus and bearded seals, other seals, Steller sea lions, arrowtooth flounder, Pacific halibut, Greenland turbot
Pinnipeds (30-80%), baleen whales (20-30%) toothed whales (10-50%), seabirds (5-25%)	Pacific salmon, Pacific halibut, rockfish, sablefish, skates, Macrouridae	Jellyfish, Pacific salmon, Pacific herring, king crab

Keystone Species, Top-down and Bottom-up Control

Bottlenecks and control

A key question in fisheries ecology is one of functional control: if a quantity of a species is removed from a system, how will it affect its predators (bottom-up control) or its prey (top-down control)? Developed functional responses between predator and prey are thought to depend on nonlinear interactions such as food saturation, schooling behavior or issues of refuge and foraging risk. The dynamic Ecosim model introduces such nonlinear control theory, while the Ecopath food web in itself is a static model. Investigating control using an Ecopath food web amounts to conducting various types of first-order (linear) perturbation tests. As such, these tests simultaneously answer two questions: (1) What is the first order effect of removing a quantity of a species from a system, assuming the removal is small enough that the effect is linear on affected predator and/or prey? (2) What effect would an error in data estimation for a species have on assumptions of predator/prey dynamics? In other words, the results presented here are simultaneously testing for biological sensitivity and model parameter sensitivity.

The primary focus in the following results is the identification of keystone functional groups: functional groups for which a change in biomass (or estimation of biomass) would substantially change the model's function. This will also help to narrow the view of 200-300+ trophic links into a smaller number of dominant pathways.

The control analyses in this section focus on investigating small perturbations around the "mean" ecosystem, or balanced state. This methodology investigates which functional groups would have a greater effect on the food web, given a small change of fixed proportion (for example, 1%) in the throughput of that component (input + output, measured in $t/km^2/year$). Since throughput is calculated from biomass, P/B, and Q/B together, no distinction is made between these parameters in the following discussion: a 1% increase in biomass is assumed to have the same effect as a 1% increase in P/B or Q/B. However, it is expected that the life-history traits P/B and Q/B are less variable than biomass, and that these results effectively focus on control implications resulting from changes in biomass. It should be noted, though, that P/B and Q/B are dependent on stock age structure and growth-at-age, and removals of biomass greater than a few percentage points may result in nonlinear compensatory changes in P/B and Q/B—calibrating such responses falls to dynamic modeling techniques such as Ecosim and is not addressed here.

In most cases, this proportional scaling will result in the species with higher overall production having greater effects on the food web. These analyses do not address fixed removals; for example, we do not investigate which species are more vulnerable to the removal of 1 metric ton of biomass through fishing. Again, asking such questions would require investigations of compensatory and depensatory responses on a stock-by-stock basis.

Trophic levels 1-2 (benthic vs. pelagic production)

Defining functional groups on the lowest trophic levels (1-2) as “keystone” functional groups is not meaningful, as the high amount of aggregation at those trophic levels results in almost all functional groups—phytoplankton, copepods, large zooplankton, infauna and epifauna,—acting as important bottom-up conduits of energy for the rest of the system. Whereas the trophic level of upper trophic level species may be defined by the proportion of their diet, for example, split between ‘copepods’ and ‘large zooplankton,’ groups in Trophic Levels 1 and 2 are already so aggregated as to make differentiating one or the other as a ‘primary control source’ unnecessary, although individual species within these aggregated groups may be keystones.

Rather, the main functional split at Trophic Levels 1-2 is simply between the benthic components (feeding on benthic detritus) and pelagic components (feeding on phytoplankton and pelagic detritus). The ultimate source of all production, benthic and pelagic, is phytoplankton, and relatively few steps are taken from primary production before the majority of living material is respired or enters the detrital food web.

In both the EBS and the WBS, the same top 7 groups produce 95% of the detritus in the system (Fig. 19): all of these except pollock are below Trophic Level 2.5. It should be noted, as discussed in the Methods section, that the overall detrital flows, phytoplankton flows, and apportionment of detritus between pelagic and benthic components are calibrated by predator demand rather than through direct knowledge of annual detrital accumulation in the Bering Sea. Phytoplankton, in particular, may have a greater contribution to detritus due to unexploited material from seasonal blooms.

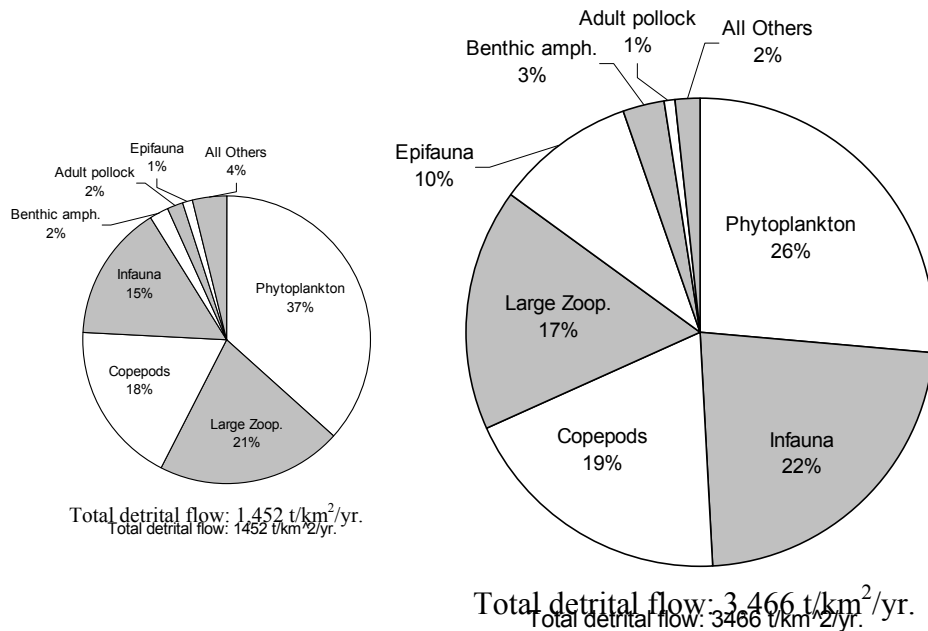


Figure 19. The amount of material flowing from “living” boxes into detritus in the EBS (left small circle) and the WBS (right large circle). The area of each circle is proportional to the total detrital flow of the system.

Despite the higher demand for benthic detritus in the WBS, it is evident that the benthic food web provides a greater proportion of food to Trophic Levels 3 and above in

the EBS than it does in the WBS (Fig. 20). This is in spite of the fact that demand for benthic detrital production is a greater proportion of the overall total production in the WBS than in the EBS (37% vs. 24%; Table 2).

This dichotomy is the result of the structure of the benthic web between Trophic Levels 2 and 3. The consumption demands of the twenty-fold higher epifaunal biomass are modeled in the WBS ecosystem (biomass 115 t/km² in the WBS vs. 6 t/km² in the EBS; Table 4). As shown in Figure 21 (A and B), epifauna consume a greater relative proportion of benthic detritus in the WBS than in the EBS.

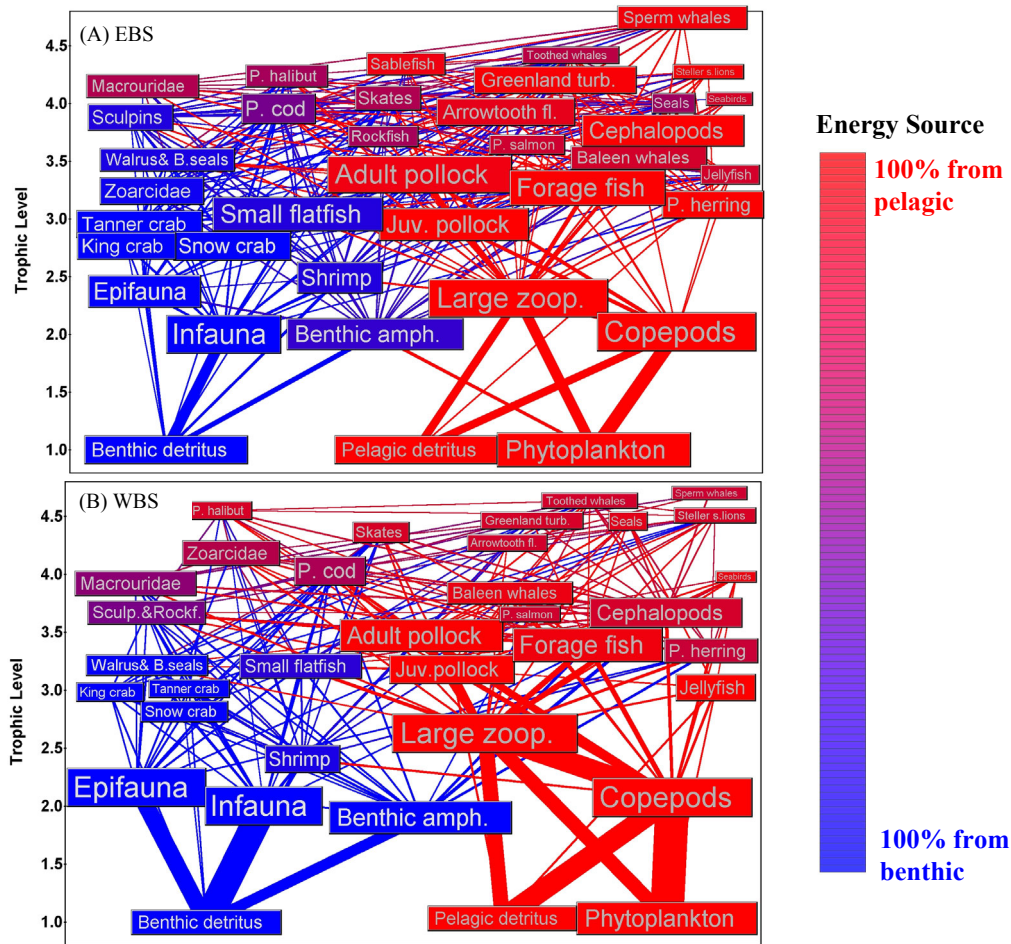


Figure 20. The proportion of energy flow into each compartment above Trophic Level 1 ultimately deriving from pelagic sources (phytoplankton and pelagic detritus; red) or benthic sources (benthic detritus; blue). (A) eastern Bering Sea shelf; (B) western Bering Sea shelf. Box and text size is proportional to log(biomass) of each compartment, while the area of each connection link is proportional to the volume of flow.

Moreover, epifauna is the dominant predator of infauna in the WBS: in the EBS, the larger proportion of infaunal biomass passes upwards into crab and fish species (Figs.

21C and 21D; Table 9). The small flatfish community has approximately a 10 times higher biomass in the EBS in comparison to the WBS (Table 4). These flatfish species, especially yellowfin sole and rock sole, are a major source of energy for Pacific cod and other predators. Conversely, in the WBS, a great majority (84%) of the energy entering the epifaunal group is lost to “cannibalism”; that is, to a detailed trophic structure that is not visible in this model, within the highly aggregated epifaunal functional group (Table 5).

Keystone species on Trophic Levels 3+

Due to the aggregation of Trophic Levels 2-3 into copepod, large zooplankton, epifauna, and infauna, the function of omnivory and fractional trophic levels is not possible to examine thoroughly. Starting on Trophic Level 3, however, the increasing diversity of the energy pathways in the models allow a finer investigation of functional groups.

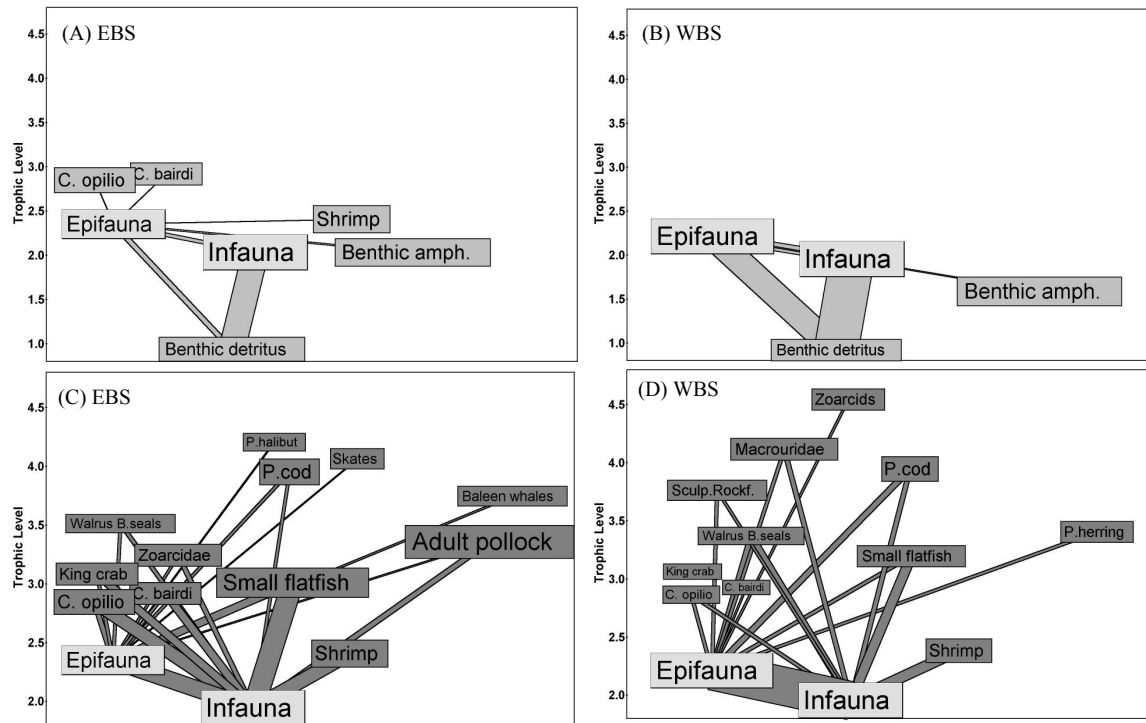


Figure 21. A subsection of the EBS and WBS benthic food webs, showing the major prey (A,B, lighter grey) and predators(C,D, darker grey) of infauna and epifauna. A few predators for which these groups are of minor importance are not shown. In (A), some predation on higher trophic level crabs by epifauna is shown. Box and text size is proportional to $\log(\text{biomass})$ of each compartment, while the width of each connection link is proportional to the square root of the volume of flow. The absolute scale of the flow differs between the prey flows (A and B) and the predator flows (C and D).

Figure 22 shows total consumption (A) and total utilized production (B) of each functional group regressed against trophic level (exponential regression) starting on Trophic Level 3.0. Consumption may partially determine the degree of top-down control each functional group may put on its prey, while utilized production, defined as all production of a group which is either consumed by predators or caught in a fishery), may partially determine the degree of bottom-up control.

As expected by the 80-90% loss of energy per trophic level (Table 3), there is a significant trend for both consumption and production in both systems: this is a way of visualizing the “trophic pyramid” on a group-by-group basis. This trend is fit for fractional trophic levels rather than for “collapsed” levels shown in Table 3 (the aggregation of predator and prey below Trophic Level 3.0 leads to overall measurement error if these levels are included in the regression).

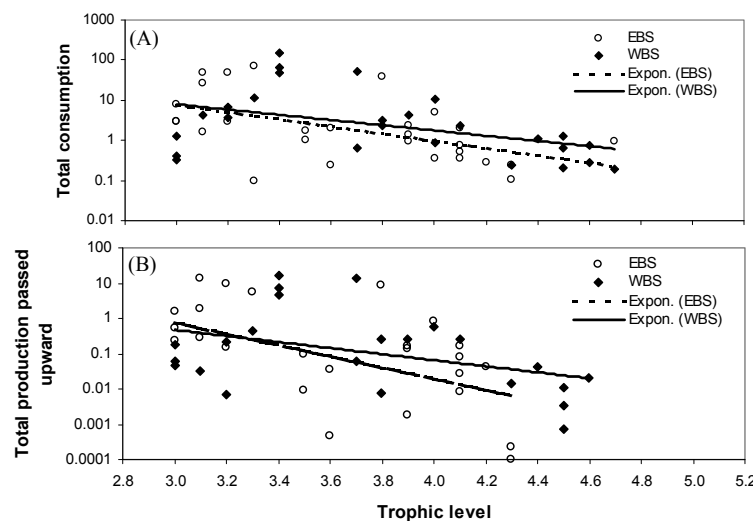


Figure 22. Total consumption (A; t/km²/year, log-scale) and total utilized production (B; t/km²/year, log scale) as a function of trophic level, for functional groups of Trophic Level 3.0 and above in the WBS and the EBS. Lines show fits of the formula $\ln(\text{Cons. Or Prod.}) = \text{TL}_0 + m \cdot \text{TL}$. All fits are significant ($P < 0.05$) with R^2 values between 0.16 and 0.29. The fits are not significantly different between the EBS and the WBS. For Figure (B), unfished species with no predation (top predators) (species with no utilized production) are not included.

Table 10 shows the functional groups which produce over 95% of utilized production in Trophic Levels 3+ in the EBS and WBS: this consists of eight species in the EBS and six species in the WBS. Given the regressions in Figure 22, it is not surprising that these species, except Pacific cod and cephalopods, are between Trophic Level 3.0-3.5.

An examination of the predators of each of the species in Table 10 suggests three separate major routes through Trophic Levels 3.0-3.5: (1) forage fish and cephalopods; (2) pollock (adult and juvenile combined); and (3) benthic components such as crabs and small flatfish (Fig. 23). Cephalopods are included with forage fish as keystones because of their high ranking on Table 10, and despite their high trophic level, much of their consumption comes directly from large zooplankton, with forage fish as the other major

component of their diet other than cannibalism resulting from condensing multiple cephalopod species.

Table 10. Trophic level, biomass (t/km^2), and utilized production above Trophic Level 3.0 (shown as percentage of all utilized production, in $t/km^2/year$, above Trophic Level 3.0), shown for groups contributing 1% or more of the utilized production above Trophic Level 3.0 in the EBS and WBS. Utilized production is that which is consumed by predators or the fishery.

EBS				WBS			
Group	T.L.	Biom.	TL 3+ Prod. %	Group	T.L.	Biom.	TL 3+ Prod. %
Juvenile pollock	3.1	6.0	30.7%	Forage fish	3.4	19.1	36.4%
Forage fish	3.2	13.5	22.2%	Cephalopods	3.7	4.8	31.7%
Cephalopods	3.8	3.5	20.5%	Adult pollock	3.4	15.0	15.9%
Adult pollock	3.3	27.5	12.4%	Juvenile pollock	3.4	3.8	10.5%
Small flatfish	3.1	9.2	4.3%	Pacific cod	4.0	3.2	1.3%
Tanner crab	3.0	1.6	3.6%	Pacific herring	3.3	0.79	1.0%
Pacific cod	4.0	2.4	1.9%				
Snow crab	3.0	0.6	1.2%				
Total Percent of T.L. 3.0+ prod.			96.7%	Total Percent of T.L. 3.0+ prod.			96.7%

To examine relative bottom-up importance of each of these three routes of energy through specific prey, the functional groups above Trophic Level 4 may then be categorized by the relative proportion of their consumption which comes from each of these groups. Figure 24 shows one such categorization scheme. Each of the functional groups in Table 10 is given a color based on its grouping (blue for benthic; green for small pelagic; red for pollock). Each functional group above Trophic Level 2.5 that is not on Table 10 is given a color that reflects the proportion of its diet that ultimately passes through functional boxes belonging to each of these three color groupings.

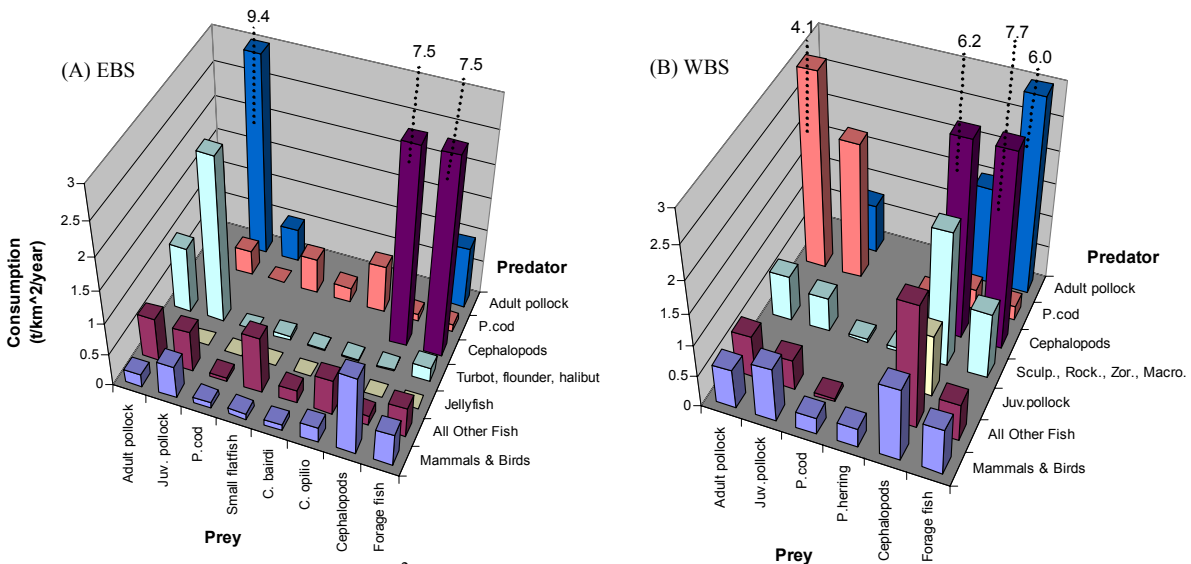


Figure 23. Consumption rates ($t/km^2/year$) of dominant functional groups between Trophic Levels 3.0-3.5 shown on Table 10. (A) EBS; (B) WBS.

As noted above, the benthic web plays a much smaller role in the WBS than in the EBS. Pollock are more dominant as prey of upper trophic level fish in the EBS, especially large flatfish (arrowtooth flounder and Greenland turbot). In the EBS, Pacific cod play a “bridging” role between pollock and small flatfish. Small pelagics, especially through cephalopods, are dominant in the WBS relative to pollock. Two groups in the EBS, baleen whales and seals, feed on an equal mix of all three groups, although seals feed on a higher trophic level. Baleen whales and seals do not have a benthic component in their diet in the WBS.

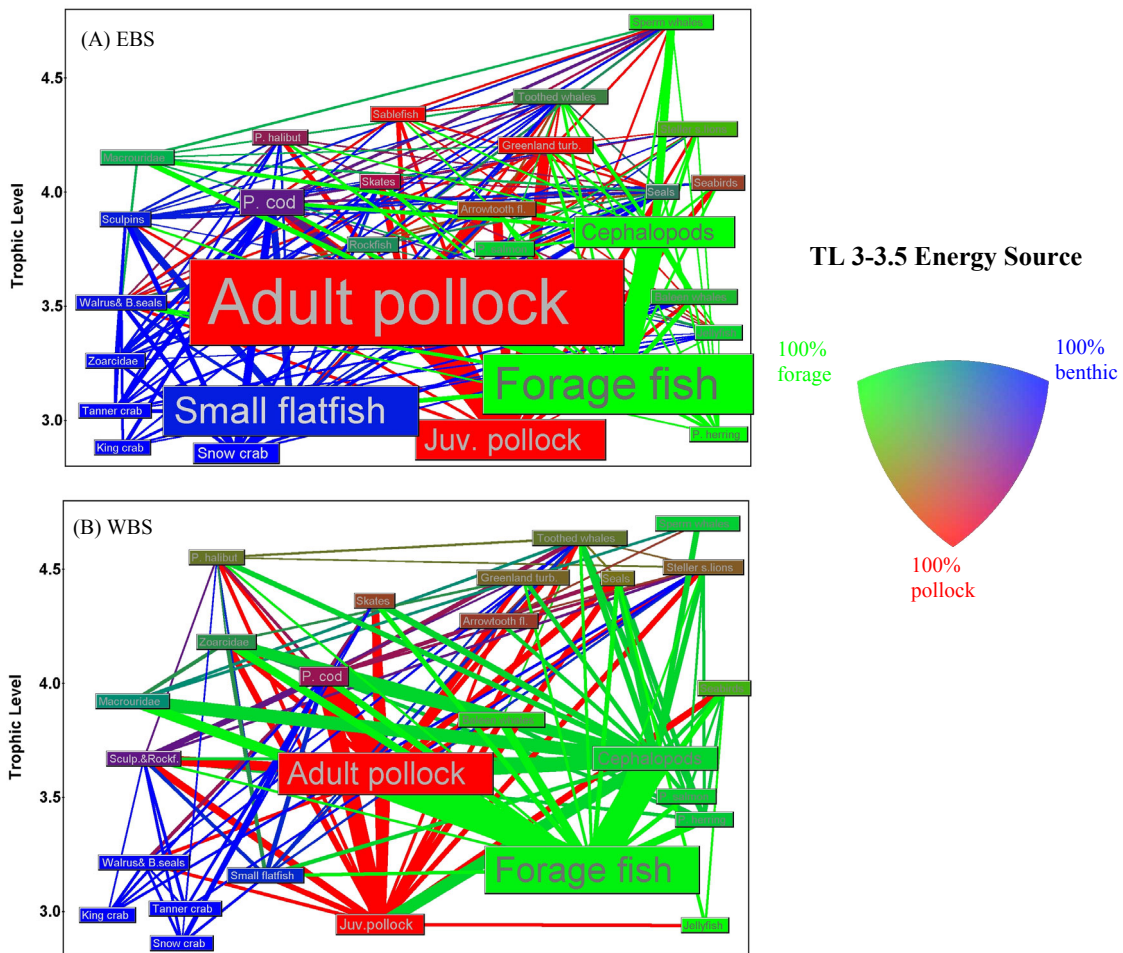


Figure 24. Proportion of energy flow into each compartment above Trophic Level 3.5 that passed through Trophic Level 3-3.5 by way of pollock compartments (adult and juvenile; red); other pelagic forage species (forage fish, large zooplankton and herring, green); and benthic compartments (crab and small flatfish, blue). Energy not passing directly through these Trophic Level 3 compartments (for example, direct flow from zooplankton to Trophic Level 4+) are not shown. Box area is directly proportional to biomass (t/km^2). (A) eastern Bering Sea shelf; (B) western Bering Sea shelf.

The other two species groups in Table 10, cephalopods and Pacific cod, are the dominant predators between Trophic Levels 3.5-4.0. The cephalopod functional group in both ecosystems is an aggregation of species on more than one trophic level, and are more important as a prey item in the WBS than in the EBS (Figs. 25 A and B). Their diet includes a high degree of cannibalism. Pacific cod, as shown by their purple coloring in Figure 24A and in Figure 25 C and D, are a “bridge” species between benthic and pelagic components in the EBS, while in the WBS they feed primarily on pollock.

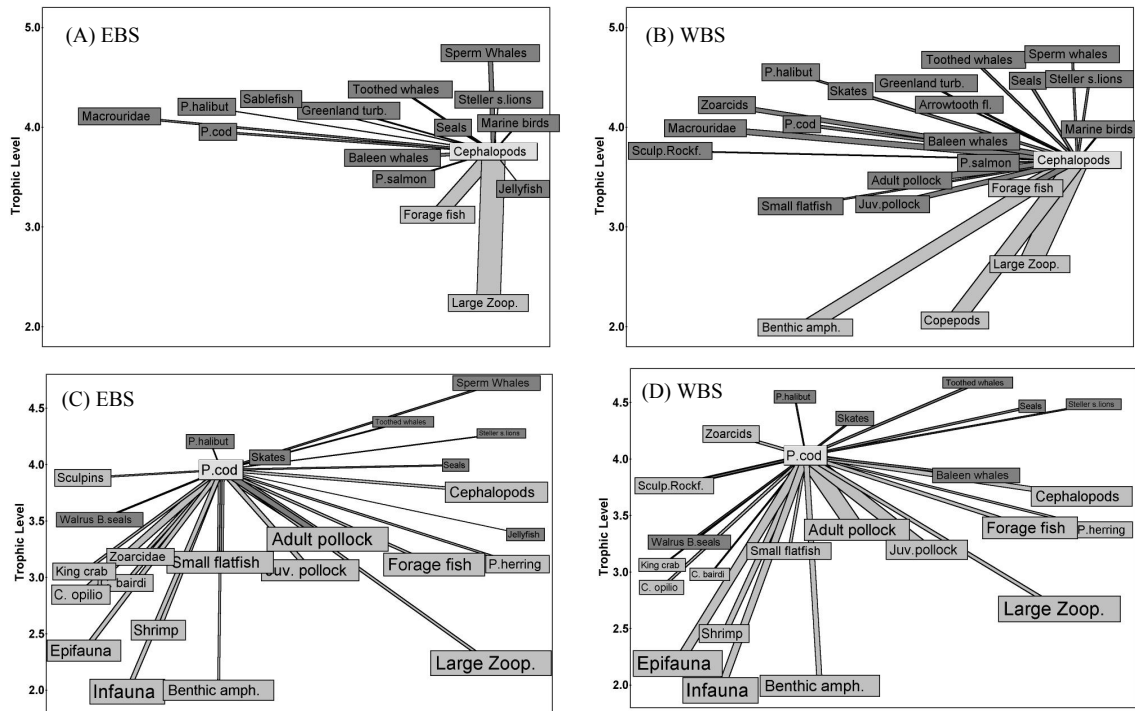


Figure 25. Predator and prey of cephalopods (A,B) and Pacific cod (C,D) in the EBS and the WBS. Light gray boxes indicate prey; dark gray indicate predators. The width of the connecting flow lines is proportional to the volume of flow ($t/km^2/year$).

For a more holistic examination of bottom-up and top-down control, there are multiple metrics that may be used. Two are presented here: residual fitting of the regressions in Figure 22, and trophic impact (Christensen and Pauly 1995).

The first method is useful for species of Trophic Level 3.0 and above—it does not work for lower trophic levels due to the lower-level aggregation mentioned above. As seen in Table 10, Pacific cod (Trophic Level 4.0) and cephalopods (Trophic Level 3.7-3.8) have production levels ranking with species on Trophic Level 3.0-3.5, suggesting that they represent a large proportion of production on the higher trophic levels. This examination can be generalized by calculating the standardized residuals from the regression in Figure 22.

If a species has a greater level of utilized production than predicted for its trophic level from the regression in Figure 22B, it would be a source of relatively strong bottom-up control. If a functional group has a positive deviation from the exponential regression

of consumption versus trophic level (Fig. 22A), then relative to other groups on near its trophic level, it would exert stronger top-down control. A species with a negative residual would exert relatively weak top-down control for its trophic level. A functional group could exhibit strong top-down and bottom-up control simultaneously (middle-out control). The measurement of the residuals takes into account control anomalies resulting from both high per-biomass production and consumption rates (P/B and Q/B) and the actual biomass of the species in the system.

Figure 26 shows the residuals to the fit of $\ln(\text{utilized production})$ to trophic level for groups of Trophic Level 3.0 and above, sorted in order of decreasing residuals. In both systems, the groups with the highest positive residuals (>1.0), and therefore most important for bottom-up forcing, are cephalopods, pollock (adult and juvenile), forage fish, and Pacific cod. Interestingly, cephalopods have a much higher residual than either adult or juvenile pollock in the EBS as well as the WBS: this is a reflection of the cephalopod's high trophic level relative to its production.

In the EBS, small flatfish, turbot and flounder also are stronger bottom-up providers. Crabs and "minor" fish tend to show little deviation from the production slope in either system. Species with negative deviations higher than 0.5 include jellyfish, all marine mammals, and seabirds: this is expected, as these species, regardless of their trophic level, represent uneaten "end points" for energy in their ecosystems.

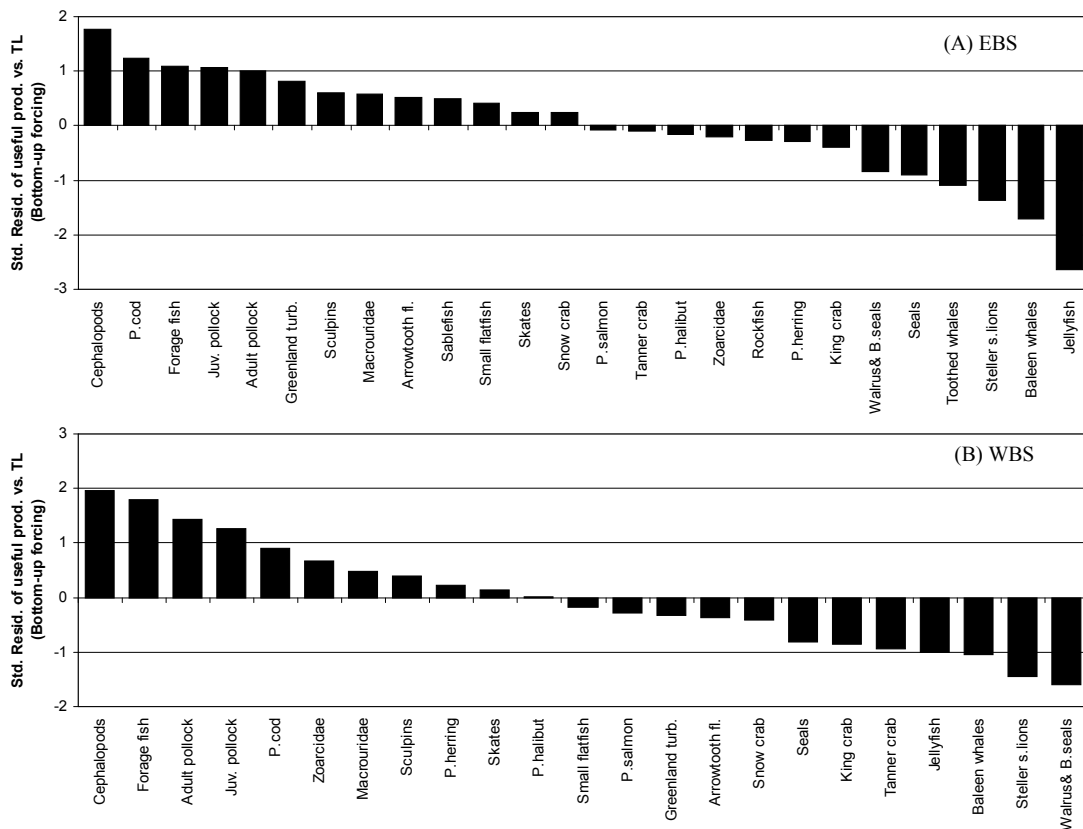


Figure 26. Standardized residuals from the fit $\ln(\text{utilized production}) = TL_0 + m \cdot TL$ for (A) EBS and (B) WBS. Functional groups are sorted in order of decreasing residuals. Positive values indicate relatively strong bottom-up control for a group's trophic level; negative values indicate relatively weak bottom-up control.

The residuals of the fit of $\ln(\text{consumption})$ to trophic level, sorted in order of decreasing residuals, are shown in Figure 27. Again, the “top 5” groups listed above for bottom-up forcing—cephalopods, adult and juvenile pollock, Pacific cod, and forage fish—have the highest positive residuals for top-down forcing, indicating that these groups are sources of both top-down and bottom-up forcing within the web. On the negative side, jellyfish, rockfish, and Steller sea lions have little top-down effect in the EBS, while crabs have little top-down effect in the WBS.

Plotting predator and prey residuals on a single XY graph results in Figure 28. The five species responsible for high levels of both bottom-up and top-down control are visible in the upper right for both the EBS and the WBS. In the EBS, a secondary tier of species with both top-down and bottom-up residuals are small flatfish and large flatfish (Greenland turbot and arrowtooth flounder).

Jellyfish show the lowest level of bottom-up and top-down importance of any species in the EBS given their trophic level. While weak bottom-up forcing is not unexpected (few species consume large jellyfish), the weak top-down forcing may result from an underestimate of jellyfish consumption rates in the EBS—the estimate of 2.0/year in the EBS is 33% lower than the estimate of 3.0/year in the WBS, and both values should be considered relatively uncertain.

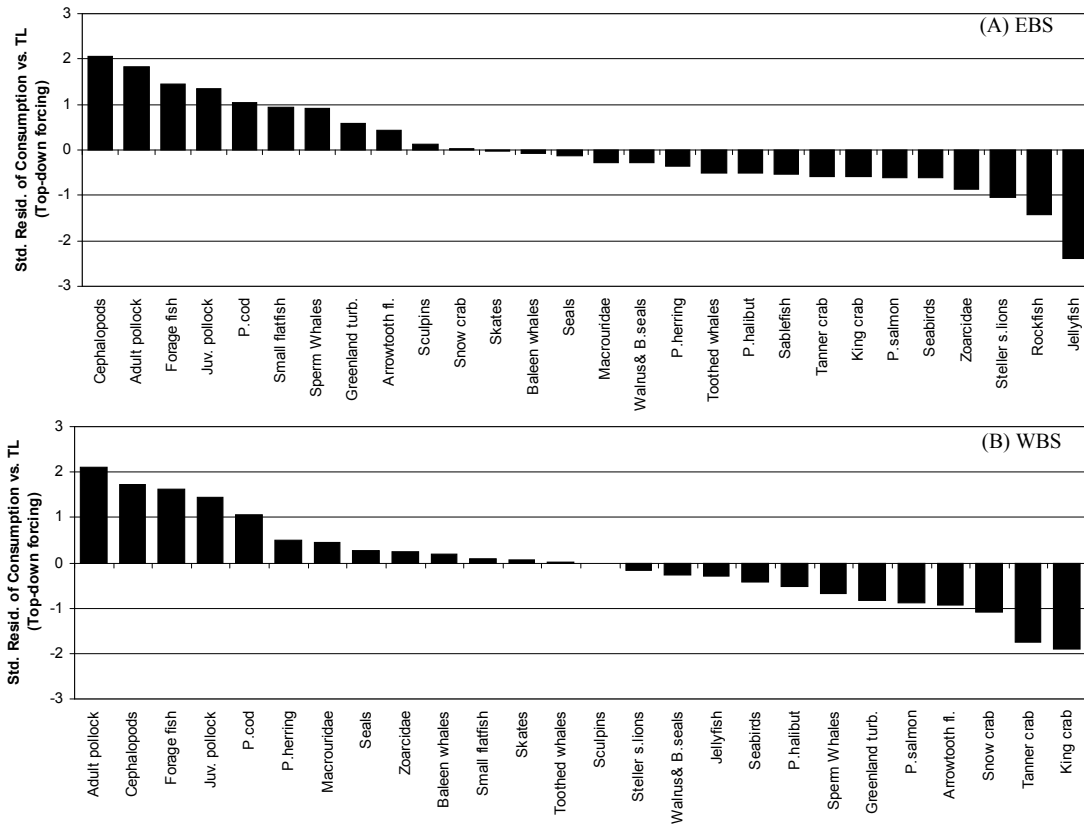


Figure 27. Standardized residuals from the fit $\ln(\text{consumption}) = TL_0 + m \cdot TL$ for (A) EBS and (B) WBS. Functional groups are sorted in order of decreasing residuals. Positive values indicate relatively strong top-down control for a group’s trophic level; negative values indicate relatively weak top-down control.

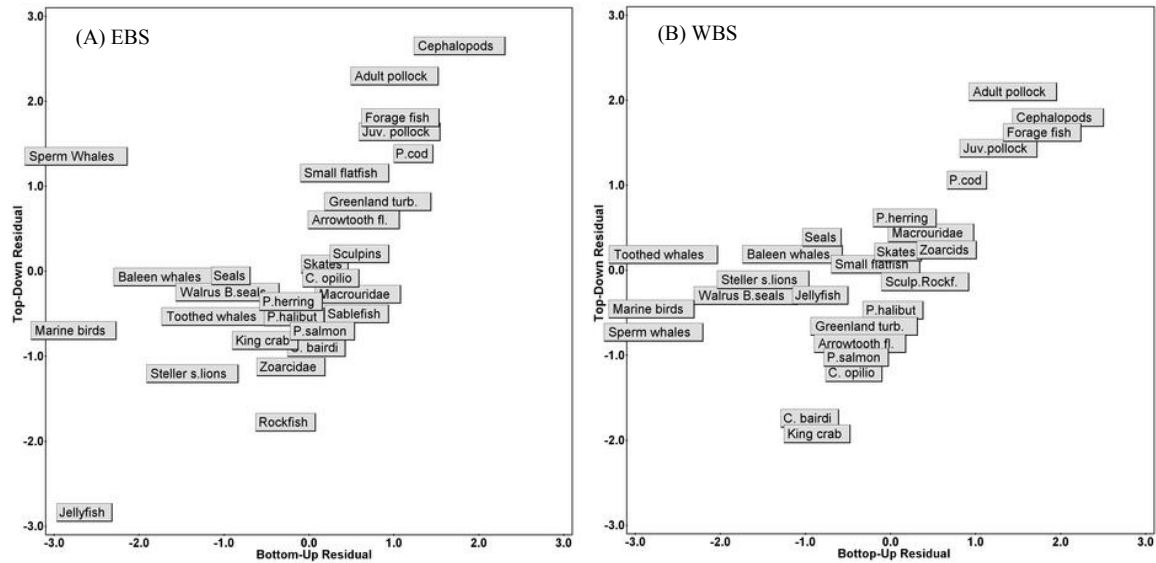


Figure 28. Standardized residuals by functional group of the regression $\ln(\text{utilized production}) = TL_0 + m \cdot TL$ (bottom-up residual) and $\ln(\text{consumption}) = TL_0 + m \cdot TL$ (top-down residual), where regression is performed for all groups with a trophic level of 3.0 and above. (A) EBS; (B) WBS.

A final method of examining top-down vs. bottom-up forcing is the trophic impact graph, described in Christensen and Pauly (2000). The graph shows the normalized, expected linear perturbation in one component, the “impacted” group (up or down) given a proportional increase in production and consumption of a second component, the “impacting” group. This calculation is performed for every pair of functional groups in each system: the fishery (total catch) may be similarly treated.

The results for each pairwise interaction of trophic impact are shown in Figure 29 (EBS) and Figure 30 (WBS). The grid shows the effect of the impacting species (shown in the left-hand column) on the impacted species (shown on the top). Black circles indicate a positive effect (an increase in the impacting species leads to an increase in the impacted species) while white circles indicate a negative effect (an increase in the impacting species leads to a decrease in the impacted species). Effect size is proportional to circle area, with the largest circles indicating effects of ± 1.0 and no circle indicating effects near zero.

The bars along the left and top of Figures 29 and 30 are the sums of the absolute values of each impact value in the row or column respectively, divided by the number of species in each system. This gives a measure of how much a species impacts all other species in the system (left bars) or is impacted by all other species in the system (top bars). The diagonal line of white circles on both Figures 29 and 30 indicates the self-limiting (density-dependent) effect of each species on itself. Groups below this diagonal, tending to be lower trophic levels, show a large number of black circles indicating general bottom-up forcing and an overall high upward impact.

The fishery creates a strong negative effect on most fished species—this is largest in salmon in the EBS (Bristol Bay salmon fishery) and is also large for marine mammals due to their low growth rates relative to indigenous harvest. Some positive effects of the fishery are due to the removal of competitors.

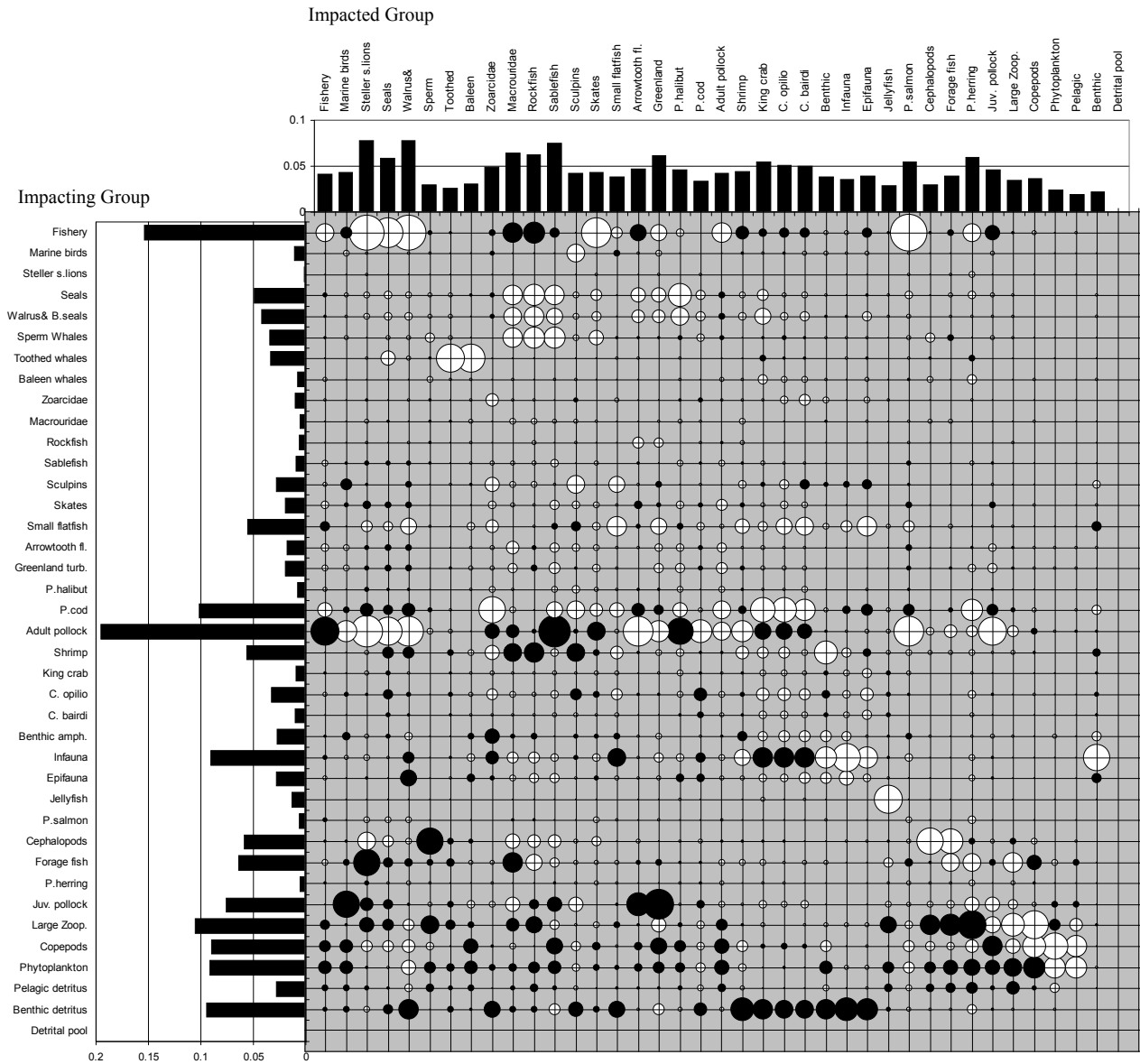


Figure 29. Trophic impact graph and impacting/impacted indices for each species in the EBS. See text for explanation of figure.

Aside from the fishery, the groups producing the most impact (left hand bars in Figs. 29-30) are adult pollock in both models. The effect of adult pollock is mixed but generally negative on many species, as they act as a competitor rather than a food source. Juvenile pollock, on the other hand, have a positive effect on a wide range of species in both ecosystems, particularly seabirds, arrowtooth flounder, and Greenland turbot.

Next to pollock, Pacific cod have one of the highest degrees of impact on both systems, comparable in effect to that of the lower aggregated trophic levels (benthic and pelagic bottom-up production). Most of the effects caused by Pacific cod are negative: this highlights Pacific cod's role as a top, structuring predator in both ecosystems.

The impacting graphs (top bars in Figures 29-30) indicate that while impacts are caused by a few keystone groups, the effects of these impacts are spread more evenly across the groups in both systems. The most sensitive (impacted) species are those with the highest fishing mortality in proportion to their total mortality (Table 6). Figures 29-30 also indicate the importance of a small amount of predation on groups with slow life-histories: for example, in the WBS, a small proportion (0.1%) of toothed whales' diet consists of Steller sea lions, and this shows up as a large negative effect—it is unclear if this interaction is overemphasized through the rounding up of this diet interaction to measurable levels. In addition to predation pressure, some secondary competitive effects may occur. For example, jellyfish experience a positive effect from fisheries; this may result from fisheries removing the jellyfish's competition for food.

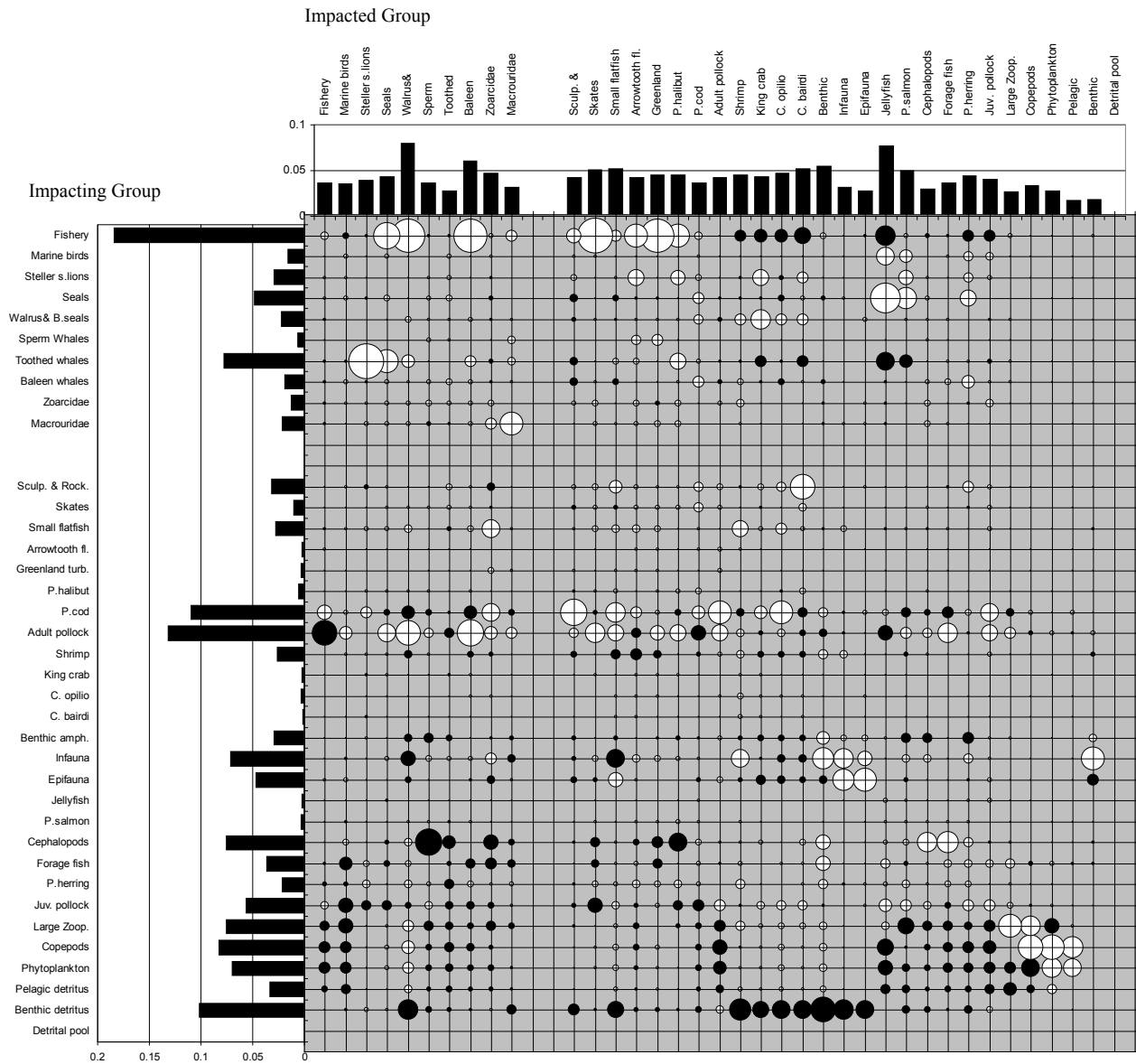


Figure 30. Trophic impact graph and impacting/impacted indices for each species in the WBS. See text for explanation of figure.

CONCLUSIONS

Ecosystem maturity and development is not always straightforward to calculate between systems. Clearly, the EBS and WBS shelf/slope areas are dominated by differing production regimes. The WBS, with higher production (Tables 2-3) is a more active ecosystem on the lower trophic levels, with higher primary and secondary production. This is probably due to having a larger percentage of its area associated with the “green belt” of high production along the shelf break.

However, this large energy supply does not translate into higher supported biomass for upper trophic levels. Our results point to the complexity of the broad shelf habitat in the EBS as supporting a more “mature” system, perhaps due to the relative stability of the oceanographic frontal structures in the EBS and sheer area of benthic habitat.

This maturity is visible in the number of interconnections within the web, even if this is considered to be a sampling artifact, the suggestion of maturity is further supported by the relatively high proportion of its production that actually “supports” biomass, as seen from examining PPR values (Fig. 8) and the average transfer efficiency above Trophic Level 2 (13.5% in the EBS vs. 12.1% in the WBS).

One fundamental difference in flow between the two systems occurs in the benthic web at Trophic Level 3: in the WBS, a tremendous amount of detrital energy is consumed by epifaunal species and passed out of the system through respiration, while in the EBS the small flatfish community provides a pathway between detritus and larger fish. If this pattern is not a data artifact, it may indicate that competition between small flatfish and epifauna has a strong structuring effect on the benthic community. The species composition of both groups (Table 5) is worth further investigation. Specifically, it is not clear if estimation methods for epibenthic biomass were comparable between the two systems.

The other large area of uncertainty in the models is in the cephalopod groups: it is not clear if their dominant position in the WBS is due to the accounting of off-shelf (deep basin) food consumption; furthermore, estimates of their biomass in the EBS vary from 0.5-3 million t overall. Their role in both ecosystems is an important area for future research.

The high consumption rates in some fish species in the WBS may be an artifact of the estimation method. It is possible that this is an accounting dichotomy: the estimates of consumption in the WBS were taken from daily ration estimations using field observations of stomach weight and evacuation rates while the EBS estimations generally came from bioenergetics models assessing minimum food requirements for observed growth. On the other hand, the low impact of jellyfish relative to their trophic level in the EBS suggests that jellyfish ration in the EBS may have been underestimated.

Some of the differences in consumption rate estimation may simply shift the balance of the loss to the “balancing” loss term, Ecotrophic Efficiency (or “unexplained” mortality). The relative apportionment of dissipative characteristics of energy flow within the food webs into metabolic costs (respiration, including reproductive costs), unassimilated food, “other” mortality (disease, etc.), and bacterial recycling are difficult

to compare between the two systems as they primarily represent the “balancing” terms in the population level mass-balance.

As such their measure is subject to considerable noise: this noise may create order of magnitude differences in estimates of “true” respiration or other loss which may not be captured in the Ecopath accounting methods. Particularly, it is not possible at this juncture to partition food web dissipation between detrital flows, recycled (bacterial) nutrients, and heat loss accurately. Considerably more work with bioenergetics is required as a next step.

The appropriate apportioning of a species’ loss terms between respiration and unexplained mortality is one of the more important unexplored areas of Ecopath at this moment. While the accounting difference has little effect on the overall mass-balance of a “snapshot” of energy flows, the difference in apportionment will have a strong effect in dynamic simulations such as Ecosim—it is thought that the accounting methods used for many current Ecopath models may cause overoptimistic compensation in fished species when applied to dynamic predictions (Aydin and Friday 2001). On the other hand, it is possible that if the WBS is a more productive system overall, greater feeding levels may exist even if those are not translated into fish growth.

Five functional groups: adult pollock, juvenile pollock, cephalopods, forage fish, and Pacific cod are important keystone predator and prey species in both systems. Two of these groups, forage fish and cephalopods, are aggregations of many species and existing data on their actual production rates are very poor. Investigating the dynamics of these forage species is a high priority for examining future fluctuations in predator stocks. Pacific cod are an important predator of both the benthic and pelagic food webs, and thus as a keystone species they represent a “uniting” of the two food webs. Overall, top fish predators (Greenland turbot, arrowtooth flounder and Pacific cod in particular) show indications of exerting more top-down control on pollock and other fish, when compared to with marine mammals.

The most important next step in this work is the further geographical refinement of the models, especially with regard to basin versus shelf processes. In particular, until the keystone forage fish and cephalopod groups are broken into shelf and basin components in the predators’ diets, it will be hard to gauge the relative contributions of the many different regional environmental forcing factors. The develop of sub-regional ecosystem models using this common framework, with the addition of migration and relative area utilization across the Bering Sea basin and north shelf areas would lend greatly to continued investigations.

APPENDICES

APPENDIX A: WESTERN BERING SEA MODEL

This Appendix describes the sources for all of the data used to construct the western Bering Sea shelf+slope+basin combined model covering all of the Bering Sea within the Russian EEZ (702,000 km², dotted line in Fig. 1). A similar data summary for the eastern Bering Sea model may be found in Appendix 2 of Trites et al. 1999. The main input biological parameters for the western Bering Sea shelf+slope+basin combined model are presented in Appendix Table B3, and the diet matrix for the shelf+slope+basin model is shown in Appendix Table B5. Appendix Tables C1 and C2 show the conversion factors used to convert from the shelf+slope+basin model to the shelf+slope model described in the main body of the text.

Table A1 shows the summary statistics, produced by Ecopath, calculated for the shelf+slope+basin. A more detailed treatment of the statistics for the shelf+slope only model is found in the Results and Discussion section of this report.

Appendix Table A1. Basic output parameters calculated by Ecopath for the WBS Shelf+Slope+Basin combined model.

Parameter	Value	Units
Sum of all consumption	8319	t/km ² /year
Sum of all exports	123	t/km ² /year
Sum of all respiratory flows	2451	t/km ² /year
Sum of all flows into detritus	4522	t/km ² /year
Total system throughput	15415	t/km ² /year
Sum of all production	5163	t/km ² /year
Mean trophic level of the catch	3.6	
Gross efficiency (catch/net prim. prod)	0.000367	
Input total net primary production	-	t/km ² /year
Calculated total net primary production	2,574	
Unaccounted primary production	-	
Total prim. prod./total respiration	1.05	
Net system production	123.14	t/km ² /year
Total prim. prod./total biomass	6.39	
Total biomass/total throughput	0.026	
Total biomass (excluding detritus)	403	t/km ² /
Total catches	0.945	t/km ² /year
Connectance Index	0.168	
System Omnivory Index	0.203	

Parameter Sources by Functional Group

For the groups listed below, all of the estimates of fishes include all age classes (ages 0+ and above). In the case of pollock, juvenile pollock consist of fish age 0+ to 1+, while adult pollock are age 2+ and older. The biomass of marine mammals includes all age groups; seabirds include all age groups excluding chicks; and benthic crustaceans include all age groups excluding planktonic larvae stages.

Fisheries catch statistics, including best estimates of discards, are presented in Appendix Table B3. It was difficult to estimate the bycatch of species that were completely discarded. Much of the catch of less valuable species is processed to produce a fish meal and are considered landings. Some groups (such as myctophids, skates, small sculpins) are often thrown overboard and not recorded. As a preliminary estimate, about half of “other small flatfishes” catch was considered discarded (0.001 t/km²), “other pelagic” discards were set at 0.001 (mainly myctophids and capelin). For “skates”, the whole catch is discarded (0.021); for “sculpin and rockfishes”, 10% discard (0.004) was assumed for 90% landings (0.032). For “Macrouridae” and “Zoarcidae”, about one-third of each catch discarded: 0.014 landings and 0.007 discard for Macrouridae; and 0.013 and 0.007 for Zoarcidae, respectively.

Literature sources and estimation procedures for individual groups are as follows:

Marine Mammals and Seabirds

Baleen whales: This group of marine animals consists mainly of bowhead whales (*Balaena glacialis*), gray whales (*Eschrichtius robustus*), minke whales (*Balaenoptera acutorostrata*), fin whales (*Balaenoptera physalus*), and humpback whales (*Megaptera novaeangliae*). The basic parameters for baleen whales as well as for other mammals were found in Sobolevsky (1983); however, the estimates contained therein were for the whole Bering Sea. We used one-third of Sobolevsky’s estimations according to the proportion of areas of Russian EEZ and whole Bering Sea, approximately equal to 1:3 (702.2 / 2304). The diet and annual consumption were obtained from the same source, but the species composition of diet was reconstructed from reports on food supply structure changes (Borets and Dulepova 1985; Efimkin and Radchenko 1991; Radchenko 1992, 1994a; Shuntov and Dulepova 1995; Shuntov et al. 1990). The P/B ratio was taken from Trites et al. (1999).

Toothed whales: The toothed whale compartment is composed of killer whales (*Orcinus orca*), other toothed whales (e.g., *Delphinapterus leucas*), dolphins and porpoises (mainly *Phocoenoides dalli* and *Phocoena phocoena*) and beaked whales (*Mesoplodon stejnegeri* and *Berardius bairdii*) after Sobolevsky (1983). The estimated whale and dolphin abundance was compared with data from sea observations (Shuntov 1993). All other parameters were extracted from Sobolevsky (1983), as were data for the separately grouped sperm whales (*Physeter macrocephalus*, with an addition from Bersin 1971).

Pinnipeds: Pinnipeds were placed in three functional groups: Steller sea lions (*Eumetopias jubatus*); Pacific walrus and bearded seals (*Odobenus rosmarus divergens* and *Erignathus barbatus*); and all other seals including northern fur seals (*Callorhinus ursinus*), *Phoca vitulina*, *Phoca larga*, *Phoca fasciata*, and *Phoca hispida*.

The diet compositions of seals and sea lions were difficult to obtain. Sobolevsky (1983) writes: “...Fur seals feed mainly on lower value fishes such as pollock, sand lance, lanternfishes and Atka mackerel. At the same time, there were found Pacific salmon in the stomachs of the seals killed on Commander Islands. In several seasons

weight share of salmon in the seals's stomachs can reach 24.5%. However, as supposed by Panina (1970), these fishes look to be a temporary item in the seal's diet...".

Finally, Sobolevsky concluded that annual ration of fur seals consists of fishes (80%) and cephalopods (20%). Unfortunately, there were not any quantitative data regarding composition of "fishes" group in his paper, excluding presented above citation. Data of Panina (1970) were collected near Commander Islands in 1965-1968 and, thus, do not satisfy the necessary time limits. The most recent monograph of Kuzin (1999) contains only general information about seals diet composition in the WBS. He mentioned that the proportion of fish in the seals' ration amounts to 75% of the wet weight without any comments regarding species composition of prey and proportion of their weights. For this model, seal diet was spread among several candidate fish groups.

A similar situation arose regarding sea lion diet composition. Sobolevsky noted that sea lions feed mainly on pollock, herring, large flatfishes, Atka mackerel and in several years, salmon. Overall he reports a diet composed of fishes (about 80%), cephalopods (17%) and other prey items (decapods < 3%). We could not find more accurate and detailed information.

Seabirds: This group consists of both migrating and settled species. Seabird abundance was calculated by assuming a time of residence for each species in the western Bering Sea by averaging the individual weight and number of birds separately for cold and warm seasons. Food consumption was similarly weighted by residence time. Basic parameters we applied were taken from Artyukhin (1991), Kondratiev (1992), Schneider and Shuntov (1993), Shuntov (1988a, 1988b, 1998), Smirnov and Velizhanin (1986), Springer and Byrd (1989), Vyatkin (1986), Vyatkin and Artyukhin (1994); P/B ratios – from Trites et al. (1999).

Fish and Cephalopods

Adult pollock and juvenile pollock: Walleye pollock (*Theragra chalcogramma*) were the most common groundfish in the Bering Sea during the 1980s. The basic characteristics came from Shuntov (1991), Shuntov et al. (1993), Radchenko (1994a), with some information from Balykin (1992), Kachina and Savicheva (1987), Livingston (1989), Mito (1990), Markina (1987), Okada (1986), Volkov et al. (1990). However to balance a model we had to decrease Q/B for adult and juveniles from 13 and 20 as in Shuntov et al. (1993) to 10 and 13, respectively.

Pacific cod: In the 1980s, Pacific cod (*Gadus macrocephalus*) was the most numerous demersal fish and main consumer of pollock and benthos on the Bering Sea shelf (Borets 1997). Borets (1990, 1997) estimated cod biomass in Russian EEZ as 900,000 metric tons (t). Diet composition and annual consumption were taken from the same source with corrections from Moiseev (1953) and Tokranov (1986), P/B came from Dulepova and Borets (1994).

Pacific halibut: The biomass (0.049) and catches (0.005 t/km²) of Pacific halibut (*Hippoglossus stenolepis*) were obtained from TINRO (1986-97) P/B came from Dulepova et al. (1984). Daily ration was estimated as 1.95% body weight/day (Chuchukalo, personal communication) in the fall, but we decreased it because of winter

abatement in feeding intensity (Novikov 1974). The final annual Q/B was assessed as 3.5/year.

Arrowtooth flounder and Greenland turbot: Data on biomass and catches of *Atheresthes stomias* and *Reinhardtius hippoglossoides* were obtained from TINRO (1986-97) with corrections from Fadeyev (1986). P/B was calculated by Dulepova et al. (1984). Diet composition was found in Novikov (1974) with corrections by Chuchukalo (personal communication).

Small flatfish: Biomasses of flathead sole (*Hippoglossoides elassodon*), yellowfin sole (*Pleuronectes asper*), rock sole (*P. bilineatus*) and Alaska plaice (*P. quadrituberculatus*) were obtained from Borets (1990, 1997) with corrections from TINRO (1986-97) and Lapko et al. (1999). We applied Q/B after Borets (1990), and P/B after Dulepova et al. (1984). Other small flatfishes consisted mainly of *Pleuronectes sakhalinensis* and *P. proboscideus*. Basic parameters for these species were taken from the same source. As the EE of small flatfishes was calculated to be near 1.0 in the initial model, we set EE = 0.95 and got B other small flatfishes = 0.049 t/km².

Pacific herring: According to Radchenko (1994a), in the 1980s Pacific herring (*Clupea pallasii*) biomass in the Russian EEZ of the Bering Sea was near 200,000 t. Taking into account coastal waters inside of 12-miles zone and Naumenko's estimations (Naumenko et al. 1990), we increased biomass of herring up to 250,000 t. Diet composition, Q/B, and P/B we also took from Radchenko (1994a) with achievement data from Kachina (1981).

Pacific salmon: This group consists of pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*). For estimation of the average biomass of these fish, we assumed that 120,000-140,000 t of pink salmon were resident in the western Bering Sea for 4 months, 60,000 t of chum salmon were resident for 6 months and 50,000 t of other salmon were resident for 6 months. Data on Pacific salmon abundance and the Bering Sea residence were received from Karpenko (1998); Radchenko (1994b); Sobolevsky et al. (1994). So, average annual biomass can be calculated as following: $140 \times 1/3 + 60 \times 1/2 + 50 \times 1/2 \approx 100,000$ t. We estimated P/B and Q/B from Radchenko (1994a). Salmon food composition and diet ration estimations were taken from the same sources with addition of information from Ito (1964), Pearcy et al. (1988), and Volkov (1994).

Skates: Data about skate (Rajidae) biomass and diets were obtained from Borets (1990, 1997), Dulepova and Borets (1984), and P/B from Trites et al. (1999).

Sculpins and rockfishes: Such widely distributed and relatively numerous species as *Myoxocephalus polyacanthocephalus*, *M. jaok*, *Hemilepidotus gilberti*, *H. jordani*, *Gymnacanthus* spp., *Sebastes* spp. compose this group. According to Borets (1990, 1997) the total biomass of these fishes was about 250,000 t, with a Q/B = 3.5. We used P/B ratio from Trites et al. (1999). There was no targeted fishery on these groups (except for rockfishes); they were usually caught as bycatch (TINRO 1986-97).

Macrouridae and Zoarcidae (grenadier and eelpouts): Mainly deepwater and locally abundant fishes. *Albatrossia pectoralis*, *Coryphaenoides cinereus*, *Lycodes* spp.,

Lycogramma spp. make up the majority of these groups. We used the data regarding abundance from Borets (1997) and TINRO 1986-97. Q/B ratios were calculated using daily rations determined by Chuchukalo et al. (1989, 1990). P/B is assumed to be equal to 0.3 based on Dulepova et al. (1984).

Forage fish (“other pelagic fish”): This forage fish group contained both pelagic and mesopelagic species, including capelin (*Mallotus villosus*), sandlance (*Ammodytes hexapterus*), Atka mackerel (*Pleurogrammus monopterygius*), Polar cod (*Boreogadus saida*), lanternfish (Myctophidae) and bathylagids (Bathylagidae). The main portion of total group biomass is composed of mesopelagic fishes – approximately 6 million t (Shuntov et al. 1988, 1993). Information on their diet composition was taken from Balanov and Ilyinsky (1992), Balanov et al. (1994), Gorbatenko and Ilyinsky (1991). Data about other fishes’ biomasses were also taken from Radchenko (1994a) and TINRO 1986-97. As the EE of other pelagics was above 1.0 initially, we set EE = 0.95 and got B (other pelagics) = 9.685 t/km².

Cephalopods: Biomass, P/B, Q/B and diet information were obtained from Radchenko (1992, 1994a) with some corrections from TINRO 1986-97. As assumed in Trites et al. (1999), we considered the Gonatidae squids, especially *Berryteuthis magister* as the most abundant squid in the Bering Sea overall.

Benthic Invertebrates

Crabs: The main sources of information regarding commercially valuable crabs (*Chionoecetes opilio*, *C. bairdi*, *Paralithodes platypus*) were the results of three trawl surveys conducted in 1985-1988 by RVs *Tamga*, *Gornyi*, and *Donchak*, for which data are contained in the TINRO (1986-97) documents. Composition of the diet was obtained from Tarverdieva (1979, 1981) and Nadtochyi et al. (1999). P/B and Q/B ratios were used from Dulepova et al. (1984), Borets and Dulepova (1985) and Trites et al. (1999).

Shrimp: The most numerous species that made up this group were *Pandalus goniurus* and *P. borealis*. It is very difficult to estimate these species’ biomass precisely by trawl surveys because of the wide range of vertical migration and interannual stock fluctuations. Besides, demersal shrimps such as *Sclerocrangon* spp., *Crangon* spp., and *Nectocrangon* spp. were also included into this group, for which biomass information is poorly known. So, we accepted the biomass to be equal to about 0.974 t/km² to balance the WBS model (with EE = 0.95 for this group).

Infauna: As in Trites et al. (1999), we accepted an infauna to be composed of clams, polychaetes and other worms (Appendix Table A2). Estimation of clam and polychaete biomass was made according to Volkov (1986), other worms – Lus and Kuznetsov (1961), Sagaydachnyi and Chistikov (1987). There are not any precise data regarding P/B and Q/B ratios of the Bering Sea’s infauna. Approximate estimates of P/B for clams were made from Warwick and Price (1975), Banse and Mosher (1980), Zaika (1983), Asmus (1987), for polychaetes – Warwick and Price (1975), Bagheri and McLusky (1982), Zaika (1983), Asmus (1987), Rainer (1991), for other worms – Banse and Mosher (1980), Bagheri and McLusky (1982), Asmus (1987) taking into account species composition of these hydrobionts and a latitude of their habitat. We also used

Q/B ratios from Trites et al. (1999). Diet of these animals consists of detritus (100%). No commercial fishery is known in the western Bering Sea concerning these groups.

Epifauna: The groups assessed by Trites et al. (1999) as epifauna (hermit crabs, snails, brittlestars and starfishes), accounted for only 13% of the epifauna biomass in the western Bering Sea (Appendix Table A2). The other 87% consists of barnacles (27%), sea urchins (37%), holoturias (6%), ascidias (11%), actinias (5%) and spongiar (2%). Biomass of these hydrobionts, excluding hermit crabs, has been estimated according to Volkov (1986). Hermit crab abundance was roughly assessed after Filatova and Barsanova (1964).

Appendix Table A2. Detailed information on ECOPATH parameters for benthic infauna and epifauna “In” – Infauna; “Epi” - Epifauna.; “?” – no data. Bold fonts indicates groups included by Trites et al. (1999) into the eastern Bering Sea model.

*	Group	B (t/km ²)	P/B (1/year)	Q/B (1/year)	Catch (t/km ²)
In	Clams	118.59	1.47	12.00	0.0000
In	Polychaetes	55.5	2.97	12.00	0.0000
In	Other worms	3.42	2.23	12.00	0.0000
Epi	Hermit crabs	1.37	0.82	8.00	0.0000
Epi	Snail	0.86	1.81	8.00	0.0023
Epi	Brittlestar	9.99	1.21	5.00	0.0000
Epi	Starfish	0.66	1.23	5.00	0.0000
Epi	Urchins	36.34	0.61	5.00	0.0019
Epi	Holoturia	6.10	0.26	5.00	0.0000
Epi	Barnacles	26.24	0.95	8.00	0.0000
Epi	Ascidia	10.57	3.58	?	0.0000
Epi	Actinia	4.45	?	?	0.0000
Epi	Spongia	2.27	?	?	0.0000

We could not locate exact data for production, P/B and Q/B, for the Bering Sea epifauna. Rough estimates of P/B for hermits were made by Volvenko (1995), Dulepov (1995), for urchins – by Banse and Mosher (1980), Zaika (1983), for barnacles – by Zaika (1983), Asmus (1987), for snails, sea stars and ascidias – by Asmus (1987), for brittlestars and holoturias – by Zaika (1983), taking into account species composition of these hydrobionts and a latitude of their habitat. P/B of actinias and spongiar are unknown. Q/B of all crustaceans composing epifauna may be accepted to be equal to 8.0, and all Echinodermata equal to 5.0, as in Trites et al. (1999). There are not ideas regarding ascidias, actinias, and spongiar. The food habits of snails, brittlestars, holoturias and hermits was assessed from Sokolova (1957), Tabunkov and Chernysheva (1985), Volvenko (1994), and Tsyhon-Lukanina (1982). Data for the fisheries catch of snails and urchins were obtained from TINRO (1986-97); other groups were not fished.

To balance the shelf/basin model from these initial estimates, a weighting of the overall model area by shallow and deep-sea regions in the western Bering Sea resulted in decreasing the biomass of clams and polychaetes by a factor of 3. The biomass of urchins, holoturias, barnacles, ascidias, actinias, and spongiar was grouped into “other benthos”, and the initial biomass estimate (85.97 t/km²) was decreased by 25%. This adjustment was made due to the following consideration: Assessment of the benthos

biomass was made over the shelf and continental slope area only. Shelf+slope area composes about one-third of the WBS region (if to be precise, 254,200 km² from 702,200 km² is 36%). So, we assumed that such groups as clams and polychaetes are very scarce in deep basins and took a third of their abundance. On the other hand, the groups forming “other benthos”, especially holoturias and spongiars, are known to inhabit a deep-sea zone and they may be even quite abundant there (although there are no proper quantitative data). Therefore, we decreased a biomass by 25%, although to take a half is also looking appropriate, as deep-basin processes are not fully detailed in this model.

Zooplankton

Copepods, euphausiids, and chaetognaths are the most abundant zooplankton in the Bering Sea. Amphipods (mainly hyperiids), mysids, ostracods, cladocerans, jellyfish, comb jellies, tunicates, pteropods and heteropods all play an important role in trophic structure of planktonic communities due to high abundance and wide distribution (Raymont 1988). Additionally, about 70-80% of benthic animals have a pelagic larvae, the so-called meroplankton (Mileykovsky et al. 1977).

Total plankton biomass per square meter in the western Bering Sea (for the upper 200 m of the water column), amounts to 62 g/m² in winter; 135 g/m² in spring; 179 g/m² in summer; and 125 g/m² in autumn (Shuntov et al. 1993). A seasonal maximum of zooplankton biomass in the upper pelagic layer was usually observed in May – June owing to planktonic animals’ reproduction and their lifting from mesopelagic layers (Tseytlin et al. 1994). For the 1980s, total zooplankton biomass was assessed at 103–401 million t for different seasons in the Bering Sea epipelagic layer, and at 453–601 million t for the water column overall (Shuntov et al. 1993, Shuntov and Dulepova 1995). The average annual zooplankton biomass was estimated at 500 million t (Radchenko 1994a).

Production was calculated for euryphagous and predatory zooplankton based on data on planktonic communities composition and generalized P/B – ratios for these groups. Chaetognaths (mainly *Parasagitta elegans*), hyperiids (mainly *Themisto japonica*, *T. libellula*) and gelatinous zooplankton have been regarded as predatory group (Dulepova 1993, 1994; Shuntov et al. 1993; Shuntov and Dulepova 1995).

Copepods: Copepods constituted the major portion of planktonic crustaceans – 102.18 t/km² (Efimkin and Radchenko 1991, Shuntov et al. 1988, Volkov and Efimkin 1990, Dulepova 1993). Diet composition was taken from Raymont (1988), Pavlutin (1987), Beklemishev (1954). Although this group’s biomass composed of mainly such large species as *Neocalanus plumchrus* and *N. cristatus*, a significant portion of the produced organic substance is contributed by small copepods (*Oithona similis*, *Pseudocalanus minutus*), species with a high growth rate and therefore high P/B ratios (Kozhevnikov 1979, Andreeva 1977). So we accepted P/B = 9.5.

Euphausiids: Euphausiid abundance has been regularly estimated during marine surveys (Efimkin and Radchenko 1991, Shuntov et al. 1988, Volkov and Efimkin 1990). Taking into account the square of whole Russian EEZ and that these crustaceans inhabit not only in the epipelagic layer but also deeper, we assumed a biomass of 30.44 t/km².

The P/B ratio for euphausiids was calculated by Pogodin (1990) as 1.55 in the Tatarsky Strait (Sea of Japan). However, it was not enough to balance the model, so we set $EE = 0.95$, which increased the annual P/B up to 3.129. Diet composition of this group was taken from Ponomareva (1990). Total Q/B was determined to be 17 using a $K2 = 0.35$, $U=0.5$.

Mysiids: Mysiids composed a small portion of zooplankton in the western Bering Sea. For its parameters, both euphausiids (P/B) and chaetognaths (Q/B) were used as a rough estimate.

Amphipods and Chaetognaths: The amphipods group consists of planktonic and bottom amphipods. The biomass of planktonic amphipods varied considerably by season: in fall – 0.4–18.3 t/km², in winter – 0.3-6.5, in spring-summer – 0.6-17.8 (Efimkin and Radchenko 1991, Shuntov et al. 1988, Volkov and Efimkin 1990). Overall the biomass averaged 15.22 t/km². The abundance of bottom amphipods was taken for shelf region from Belyaev (1960) and Lus (1970) – 14 t/km² and decreased down to 5 t/km² because of deep-sea areas (as was the case with clams and polychaetes). Thus, total biomass of amphipods was estimated to be 20.22 t/km².

The P/B ratio varies from 1.5 for pelagic amphipods (Dulepova 1991) to 7.4 for bottom ones (Dulepov 1995) and averaged 2.5/year. Diet composition was determined by Raymont (1988) and Shearer and Evans (1975). The annual consumption of food was calculated using net growth efficiency ($K2 = 0.35$) and digestion efficiency ($U = 0.5$) in equation $C = P/K2/U$, where C – ration, P – production.

Chaetognaths were very abundant in the plankton data – the second after copepods (Efimkin and Radchenko 1991, Shuntov et al. 1988, Volkov and Efimkin 1990, Dulepova 1993, Kotori 1976), though its portion varied from 0.6% in summer to 40% in fall of the average zooplankton biomass. Chaetognaths are typical predators (Terazaki 1998, Slabinsky 1982, Kosihina 1982) and feed on abundant planktonic animals. Ration was determined as 10% of body weight while feeding one time per 3 days (Fraser 1969, Wimpenny 1937), so daily diet is about 3.3%, annual Q/B – 12/year.

It is known that chaetognaths, especially *Sagitta* spp., are often mentioned as eating fish eggs and larvae and it has been assumed that chaetognaths predate on pollock juveniles. However, accurate analysis revealed no direct records of predation on pollock juveniles by chaetognaths or amphipods. Such fish juveniles as anchovy, herring, sardine and simply “fish larvae” are recorded as prey, but never pollock. Furthermore, fish larvae are always noted as secondary and temporary preys in the food of chaetognaths in comparison to copepods. So, we presumed that chaetognaths should be considered as competitors rather than predators for juvenile pollock, and removed pollock from the list of food items to balance the model. Furthermore, amphipods usually feed on the dead bodies of hydrobionts including fishes: no predation on live fish juveniles is recorded.

Gelatinous plankton: This group contains comb jellies (Ctenophora) and hydroid medusae, with the latter (mainly *Aglanta digitale*) composing a major portion. The total averaged biomass of this group is about 10.5 t/km². Because of high rate of growth (Timokhina 1968) we accepted P/B = 5. Diet composition was taken from Bamsted (1990). For annual consumption estimation, we applied the method shown under amphipods.

Jellyfish: Estimation of jellyfishes' biomass has been made based on both pelagic and bottom trawl survey results (Shuntov et al. 1996). The most abundant species among jellies is *Chrysaora melanaster*. The total biomass of jellyfishes according to our data reaches 0.5 t/km^2 , P/B ratio is about 1.5 (Zaika 1983). We have calculated an annual consumption and diet composition with the help of our own data (using production and K2) and literature sources (Mironov 1987, Raymont 1988, Fancet 1988).

Protozoa

This group was composed of bacteria and protozoa. Bacterial bioactivity was considered to include tripton (suspended particulate organic matter, or POM), dissolved organic matter, and bottom sediments resulting from planktonic ecosystem metabolism (Sorokin 1985). Bacteria also synthesize primary production through the oxidation of inorganic matter (chemosynthesis). Bacterioplankton of Far-Eastern seas remains poorly studied. Available data were primarily collected during the summer and autumn. Biomass of bacteria was estimated from Sorokin et al. (1995) and averaged as 15 g/m^2 .

The decline of bacterial production during the winter and early spring undoubtedly occurs. The vertical distribution of bacterial biomass is characterized by three peaks: in the surface layer, near the pycnocline and on the bottom. In the summer, the maximal bacterial productivity occurs above the thermocline. In the cold intermediate layer, the bacterial bioactivity is low despite the average level of their biomass there. We presume that 80% of bacterial primary production is synthesized during the summer and autumn, 5% - during winter, 15% - during spring. Daily P/B does not exceed 0.1, so annual P/B is about 36.5.

The microzooplankton group is formed by protozoa (zooflagellates, infusoria, amoebas, etc.) and small pluricellular zooplankton (rotifers, early stages of appendicularians and crustaceans). Infusoria and zooflagellates absolutely predominate in microzooplankton composition in quantitative ratio (Raymont 1988). In ecosystem structures, protozoa can be regarded as an important intermediate trophic link between bacteria and small phytoplankton fractions, from one side, and mesozooplankton, from the other side. Fish larvae and predatory zooplankton, also feed on protozoa.

Protozoa biomass including zooflagellates varied from $4 \text{ to } 6 \text{ g/m}^2$, daily P/B = 0.2-0.6 (Sorokin 1995). So the total biomass of the whole group was about 20 t/km^2 , annual P/B = 47. Protozoa have close trophic linkages to bacteria and their distribution is rather similar. Usually, the protozoa concentrated near the sea surface and thermocline layer to depths of about 30 m (Sorokin 1995, Moiseev 1987). Annual Q/B was calculated as $2,848 \text{ t/km}^2$ assuming $K2 = 0.55$, $U = 0.6$.

Phytoplankton

Many issues of phytoplankton biology and ecology remain poorly studied due to methodological and technical difficulties of the research. Not only nanoplankton (cell size at $2 - 30 \text{ }\mu\text{m}$) but also larger algae filter through the planktonic nets used in marine expeditions. Until recently, the smallest and most active fraction of phytoplankton (so

called picoplankton) remained beyond the view of researchers.. However, these smallest algae fractions include many systematic groups (blue-green, yellow-green, cryptomonadic, and diatom algae, dinoflagellates, etc.) that play an exceptionally important role in the primary production of organic matter due to their high abundance and growth rate (Raymont 1988; Vinogradov and Shushkina 1987).

The most important Bering Sea phytoplankton species is *Thalassiosira nordenskioldii*, which can contribute up to 70% of the total phytoplankton biomass in the spring (Semina 1981). Additional important species include: *Thalassiosira gravida*, *T. rotula*, *Fragilaria oceanica*, *Chaetoceros furcellatus*, *C. socialis*, *Bacterosira fragilis*, *Amphiprora hyperborea*, *Biddulphia sinensis*, and *Rhizosolenia* spp.

During late autumn and winter, phytoplankton is not abundant in the Bering Sea (Geinrikh 1959, Lapshina 1998). However, biological processes do not tail away completely even in these northern latitudes. Glacial forms of algae that develop on the ice underside mainly consist of diatom species. Chlorophyll A concentrations range from 7-60 mg/m³ here, considerably higher than winter pelagic phytoplankton. Glacial algae contribution is estimated at 9-10% from annual primary production in the Bering Sea, whereas winter phytoplankton contributes 2% only (McRoy and Goering 1976).

The phytoplankton bloom begins in the western Bering Sea immediately near the ice break in April. At this time, developing vertical water stratification, significant nutrient supply, longer day-time duration, and decreasing salinity in the upper layers make favorable conditions for planktonic algae growth (Mordasova 1994, Sapozhnikov et al. 1995a). Primary phytoplankton production totaled 25 gC/m² for the algae bloom period in the outer shelf and upper continental slope regions (e.g., in Karaginsky and Oljutorsky Bays). In the Bering Sea offshore waters, primary production is noticeably less – 1-5 gC/m² in spring. Later, nutrients concentrations are rather depleted. About 20% of primary production are originated owing to nutrients re-cycling.

Vertical phytoplankton distribution must be considered for the correct assessment of primary productivity. Studies of 1987-1990 show that summer penetration of large diatom phytoplankton in deeper layers can be regarded as a rule for the Bering Sea. In the upper layers, it is replaced by small diatoms and dinoflagellates, and sometimes by yellow-green and other algae groups. However, large diatoms save photosynthetic bioactivity in deeper layers (20-70 m). These aggregations on the pycnocline board produce 20-25% from total primary production of phytoplankton (Sapozhnikov 1995; Sapozhnikov et al. 1995a, 1995b).

Most published estimations of daily and annual phytoplankton primary production range between 0.4-1.0 gC/m² per day and 1.9-4.8×10⁸ metric tons of C per year (McRoy and Goering 1976, Tsyban et al. 1987, Tsyban and Korsak 1987, Nezlin et al. 1997). Ivanenkov (1961) has found from diurnal dynamics of oxygen concentrations that daily primary production varies in limits of 1.2-9.5 gC/m² in spring and 1.1-3.5 gC/m² in summer. Total primary production amounts to 387 gC/m², or 8.74×10⁸ tC. These estimations are confirmed by results of modern hydro-chemical research, which estimate annual primary production levels between 276-336 gC/m², or 6,4-7,8×10⁸ tC (Sapozhnikov and Naletova 1995). Shuntov and Dulepova (1995) concluded that the

annual primary production in the Bering Sea could be characterized as near 420 gC/m² when the contributions of macrophytobenthos and periphyton are included.

To convert phytoplankton biomass from gC to wet weight, we applied a proportion from Trites et al. (1999): "...assuming 0.4 g C per g dry weight and 0.5 g dry weight per g wet weight" (p. 86), that in total results this ratio to be equal to about 5. Russian scientists usually use greater values. For example, Sorokin (1999) used a ratio of 16.5 (averaged), Shushkina and Vinogradov (1988) used 16.7, while Moiseev (1989) and Gershanovich and Muromtsev (1982) used a ratio of 20. Detailed information was found in the last cited paper only (Appendix Table A3). Using these tables, it can be concluded that about 0.5 g C is in 1g of dry weight and 0.1 g of dry weight is in 1 g of wet weight, which results in a ratio of 20.

Appendix Table A3. Reference values for phytoplankton conversions.

(A) Composition (%) of wet substance according to Bogorov (1974).

	Phyto-plankton	Phyto-benthos	Zoo-plankton	Zoo-benthos	Nekton
Water	80	80	80	63	73
Organic substance	11	15	18	14	24
Ashes	9	5	2	23	3

(B) Elemental composition of some water plants (% of de-ashed substance) found in Muromtsev (1982).

<i>Groups</i>	C	H	O	N	P
Diatoms	50.54	10.21	28.83	7.0	1.55
Peridiniias	48.12	7.50	33.85	10.40	0.80
Green algae	54.55	7.54	31.21	7.7	2.94
Zostera spp.	46.11	7.12	43.26	3.4	0.50

Phytoplankton biomass can be calculated from Lapshina's (1998) data on seasonal dynamics of "net" fraction (i.e., microalgae kept by planktonic nets). Averaged value of "net" phytoplankton amounts to 14.7 g/m² for shelf and slope areas and 5.0 g/m² for offshore waters. Maximal averaged estimations of phytoplankton biomass have been given for June as 100 and 15 g/m² for shelf and offshore areas, respectively (Ventzel et al. 1995). In this paper, the portion of microalgae from total phytoplankton biomass is estimated at 98% in shelf and slope areas and 53% for deepwater basins. It allows assessing of annual value of averaged phytoplankton biomass as 15.0 and 9.3 g/m² for the two regions, or 11.0 g/m² for the western Bering Sea overall. If the mean estimation of primary production is about 306 gC/m² (Naletova and Sapozhnikov 1995), it means about 1,530 t/km² (wet weight) per year. In this case, P/B – ratio for phytoplankton reached 210/year. We increased this value by about 11% to 234/year to balance the model with a phytoplankton EE of 0.85—the extra 0.15 of "lost" production was required to satisfy benthic detrital demands.

APPENDIX B: ALL MODEL INPUT TABLES

Appendix Table B1. ECOPATH input parameters describing the 38-functional group 1980s eastern Bering Sea (EBS) shelf+slope ecosystem (485,000 km²). See Trites et al. (1999) for parameter references. Biomass and catch estimates are in t/km², Production/Biomass (P/B) and Consumption/Biomass (Q/B) are rates (1/year); Ecotrophic Efficiency (EE), Conversion Efficiency (PC) and Unassimilated Consumption (Unassim) are proportions. Blank cells were estimated by the model: gray cells are not applicable to the given group.

Group	Biomass	P/B	Q/B	EE	PC	Unassim	Catch
1 Baleen whales	0.245	0.02	8.032			0.2	0
2 Toothed whales	0.017	0.02	13.753			0.2	0
3 Sperm whales	0.208	0.02	4.553			0.2	0
4 Walrus & bearded seals	0.159	0.06	10.687			0.2	0.009
5 Seals	0.056	0.06	17.278			0.2	0.001
6 Steller sea lions	0.008	0.06	12.703			0.2	0
7 Seabirds	0.006	0.8	60			0.2	0
8 Adult pollock	27.451	0.5	2.64			0.2	2.08
9 Juvenile pollock	6	2.5			0.3	0.2	0
10 Pacific cod	2.421	0.4	2.04			0.2	0.151
11 Pacific halibut	0.14	0.4	2.49			0.2	0.003
12 Greenland turbot	0.96	0.4	2.04			0.2	0.077
13 Arrowtooth flounder	0.8	0.4	2.92			0.2	0.021
14 Small flatfish	9.181	0.4	2.968			0.2	0.326
15 Skates	0.288	0.4	2.56			0.2	0.018
16 Sculpins	0.555	0.4	2.56			0.2	0.017
17 Sablefish	0.11	0.4	2.49			0.2	0.005
18 Rockfish	0.094	0.4	2.49			0.2	0.003
19 Macrouridae	0.203	0.4	2.49			0.2	0.006
20 Zoarcidae	0.64	0.6	2.49			0.2	0.006
21 Tanner crab	0.6	1	5			0.2	0.019
22 Snow crab	1.6	1	5			0.2	0.049
23 King crab	0.6	0.6	5			0.2	0.042
24 Shrimp			10.2	0.9	0.2	0.2	0
25 Epifauna	5.858	1.578	5.777			0.4	0
26 Infauna	46.5	1.373	11.226			0.4	0
27 Benthic amphipods		3.5	22	0.9		0.4	0
28 Pacific herring	0.779	1	3.65			0.2	0.055
29 Pacific salmon	0.052	2.4	20			0.2	0.094
30 Cephalopods	3.5	3.2			0.3	0.2	0.007
31 Forage fish		0.8	3.65	0.9		0.2	0
32 Jellyfish	0.048	0.875	2			0.2	0
33 Large Zooplankton	44	5.5	22			0.2	0
34 Copepods	55	6	22			0.2	0
35 Phytoplankton	11.765	170					0
36 Pelagic detritus							0
37 Benthic detritus							0
38 Detrital pool(*)							0

(*) 100% of all detritus from living groups flowed into Group 38, the Detrital pool. From this pool, detritus moved to either benthic or pelagic detritus depending on demand for each group: 43.2% went to pelagic, 56.8% to benthic.

Appendix Table B2. ECOPATH input parameters describing the 36-functional group 1980s western Bering Sea (WBS) shelf+slope ecosystem (254,000 km²). See Appendix A for parameter references. Biomass and catch estimates are in t/km², Production/Biomass (P/B) and Consumption/Biomass (Q/B) are rates (1/year); Ecotrophic Efficiency (EE), Conversion Efficiency (PC) and Unassimilated Consumption (Unassim) are proportions. Blank cells were estimated by the model: gray cells are not applicable to the given group.

Group	Biomass	P/B	Q/B	EE	PC	Unassim	Catch
1 Baleen whales	0.391	0.02	8.312			0.2	0.007
2 Toothed whales	0.042	0.02	17.5			0.2	0
3 Sperm whales	0.02	0.02	9.8			0.2	0
4 Walrus & bearded seals	0.262	0.06	13.9			0.2	0.006
5 Seals	0.097	0.06	13.34			0.2	0.002
6 Steller sea lions	0.035	0.06	18			0.2	0
7 Seabirds	0.01	0.8	87			0.2	0
8 Adult pollock	15	0.5	10			0.2	1.051
9 Juvenile pollock	3.757	2.5	13			0.2	0
10 Pacific cod	3.187	0.521	3.3			0.2	0.226
11 P.halibut	0.083	0.25	3.5			0.2	0.01
12 Greenland turbot	0.058	0.2	3.6			0.2	0.01
13 Arrowtooth flounder	0.052	0.32	4.5			0.2	0.007
14 Small flatfish	0.992	0.288	6.849			0.2	0.041
15 Skates	0.271	0.4	4			0.2	0.041
16 Sculpins & Rockfish	0.677	0.4	3.5			0.2	0.07
17 Macrouridae	1.156	0.3	3.7			0.2	0.041
18 Zoarcidae	0.9	0.3	2.52			0.2	0.039
19 Tanner crab	0.083	0.8	5			0.2	0
20 Snow crab	0.249	0.8	5			0.2	0.006
21 King crab	0.119	0.6	2.7			0.2	0.008
22 Shrimp		2.04	10.2	0.9		0.2	0.002
23 Epifauna	114.962	1.159	5.087			0.4	0.004
24 Infauna	125.687	1.97	12			0.4	0
25 Benthic amphipods	13.812	2.5	14			0.4	0
26 Pacific herring	0.787	0.7	14.6			0.2	0.055
27 Pacific salmon	0.039	4	16			0.2	0.012
28 Cephalopods	4.83	3.2	10.67			0.2	0.02
29 Forage fish		0.95	3.5	0.9		0.2	0.001
30 Jellyfish	1.4	1.5	3			0.2	0
31 Large Zooplankton	120.74	4.399	14.457			0.2	0
32 Copepods	122.62	9.5	26.2			0.2	0
33 Phytoplankton	15	234					0
34 Pelagic detritus							0
35 Benthic detritus							0
36 Detrital pool(*)							0

(*) 100% of all detritus from living groups flowed into Group 38, the Detrital pool. From this pool, detritus moved to either benthic or pelagic detritus depending on demand for each group: 35.6% went to pelagic, 64.4% to benthic.

Appendix Table B3. ECOPATH input parameters describing the 1980s western Bering Sea shelf+slope+basin ecosystem (702,000 km²) with 48 functional groups. Biomass and catch estimates are in t/km², Production/Biomass (P/B) and Consumption/Biomass (Q/B) are rates (1/year); Ecotrophic Efficiency (EE) is a proportion. All EE values are estimated by Ecopath except for underlined values which were input. All trophic levels (T.L.) are estimated from the diet consumption matrix (Appendix Table B6).

	Group	T.L.	Biomass	P/B	Q/B	Catch	EE
1.	Baleen whales	3.8	0.283	0.02	8.312	.005	0.942
2.	Toothed whales	4.7	0.019	0.02	17.5		0
3.	Sperm whales	4.8	0.012	0.02	9.8		0
4.	Walrus & Bearded	3.4	0.095	0.06	13.9	.002	0.409
5.	Seals	4.6	0.044	0.06	13.34	.001	0.631
6.	Steller sea lion	4.6	0.016	0.06	18		0.346
7.	Seabirds	4	0.006	0.8	87		0
8.	Adult pollock	3.4	8.47	0.5	10	.634	0.772
9.	Juvenile pollock	3.3	1.7	2.5	13		0.517
10.	Cod	4.1	1.282	0.521	3.3	.091	0.411
11.	Halibut	4.6	0.043	0.25	3.5	.005	0.908
12.	Greenland turbot	4.5	0.03	0.2	3.6	.005	0.931
13.	Arrowtooth flounder	4.3	0.021	0.32	4.5	.003	0.996
14.	Flathead sole	3.6	0.074	0.37	4.7	.001	0.939
15.	Yellowfin sole	3.2	0.071	0.26	9.8	.009	0.885
16.	Rock sole	3.2	0.083	0.24	6.5		0.888
17.	Alaska plaice	3	0.081	0.25	6.8	.003	0.648
18.	Other small flatfishes	3.5	0.05	0.35	6.5	.002	0.94
19.	Herring	3.5	0.356	0.7	14.6	.025	0.912
20.	Salmon	3.8	0.142	4	16	.043	0.397
21.	Other pelagics	3.5	<u>9.685</u>	0.95	3.5	.001	<u>0.95</u>
22.	Skates	4.4	0.14	0.4	4	.021	0.375
23.	Sculpins, rockfish	3.9	0.35	0.4	3.5	.036	0.808
24.	Macrouridae	4	0.598	0.3	3.7	.021	0.731
25.	Zoarcids	4.1	0.427	0.3	2.52	.020	0.843
26.	Cephalopods	3.8	2.3	3.2	10.67	.009	0.98
27.	Tanner crab	3.1	0.03	0.8	5		0.94
28.	Snow crab	3.1	0.09	0.8	5	.002	0.975
29.	King crab	3.2	0.043	0.6	2.7	.003	0.936
30.	Shrimps	2.5	<u>0.974</u>	2.04	10.2	.001	<u>0.95</u>
31.	Clams	2	38.75	1.47	12		0.133
32.	Polychaetes	2	18.496	2.97	12		0.658
33.	Other worms	2	3.42	2.23	12		0.116
34.	Hermits, other decapods	2.5	1.43	0.82	8		0.966
35.	Snail	2.6	0.86	1.81	8	.002	0.954
36.	Brittlestar	2	9.99	1.21	5		0.071
37.	Starfish	2.8	0.66	1.23	5		0.163
38.	Other benthos	2.2	66.33	1.15	5		0.236
39.	Jellyfish	3.2	0.535	1.5	3		0.374
40.	Amphipods	3	20.22	2.5	14		0.808
41.	Gelatinous plankton	3	10.87	5	17		0.462
42.	Euphausiids	2.3	30.44	3.129	17		0.956
43.	Copepods	2.2	102.18	9.5	26.2		0.901
44.	Mysiids	2.1	1.09	3	12.5		0.842
45.	Chaetognaths	3.1	39.06	6	12		0.217
46.	Protozoa	2	20	47	142		0.583
47.	Phytoplankton	1	11	234	-		0.852
48.	Detritus	1	-	-	-		0.973

Table B4. Diet matrix (proportion of prey for each predator) for eastern Bering Sea shelf + slope ECOPATH model (2 pages).

Prey	Predator																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Baleen whales		0.002															
2 Toothed whales		0.001															
3 Sperm Whales																	
4 Walrus & B.seals		0.001															
5 Seals		0.002															
6 Steller s.lions																	
7 Seabirds																	
8 Adult pollock	0.041	0.081	0.012	0.02	0.037	0.063				0.295	0.503	0.236	0.16		0.646		0.707
9 Juv. pollock	0.042	0.081	0.013	0.02	0.115	0.185	0.604	0.13		0.074	0.055	0.707	0.48	0.018	0.034	0.017	0.236
10 P. cod		0.033	0.031	0.012	0.029	0.019		0.007		0.003	0.015			0.002	0.005		
11 P. halibut		0.004		0.001	0.003												
12 Greenland turb.		0.027		0.01	0.023	0.002								0.001			
13 Arrowtooth fl.		0.022		0.008	0.019	0.001		0.001									
14 Small flatfish		0.053		0.02	0.046	0.003				0.109	0.075		0.015	0.011	0.044	0.379	
15 Skates		0.004	0.004	0.001	0.003	0.002											
16 Sculpins		0.008	0.007	0.003	0.007	0.004	0.106			0.005	0.017		0.003	0.001	0.007	0.018	
17 Sablefish		0.014	0.014	0.005	0.012												
18 Rockfish		0.012	0.012	0.005	0.011												
19 Macrouridae		0.026	0.02	0.01	0.02							0.002	0.003				
20 Zoarcidae		0.009	0.008	0.003	0.008	0.005				0.03	0.021		0.002		0.01	0.037	0.01
21 Tanner crab	0.006	0.017		0.026	0.028					0.045	0.036			0.004	0.01	0.002	
22 Snow crab	0.015	0.046		0.069	0.074					0.146	0.035			0.007	0.063	0.15	
23 King crab	0.006	0.017		0.026	0.028					0.02							
24 Shrimp	0.028	0.085		0.129	0.14			0.031		0.055	0.026	0.009	0.071	0.044	0.064	0.358	0.01
25 Epifauna	0.06			0.25				0.001		0.067	0.111		0.001	0.084	0.049	0.02	
26 Infauna				0.342			0.001	0.016		0.064	0.008		0.002	0.637	0.01	0.004	
27 Benthic amph.	0.039	0.006			0.032		0.07	0.02		0.011		0.001	0.003	0.1	0.025	0.003	0.001
28 P. herring	0.005	0.009	0.001	0.002	0.009	0.035				0.01		0.004			0.001		0.01
29 P. salmon		0.001			0.001	0.002											
30 Cephalopods	0.161	0.247	0.854		0.007	0.08	0.053			0.022	0.006	0.008					0.022
31 Forage fish	0.079	0.152	0.024	0.038	0.148	0.599	0.05	0.013		0.02	0.083	0.03	0.059	0.006	0.018	0.011	
32 Jellyfish																	
33 Large Zoop.	0.245	0.04			0.2		0.116	0.431	0.33	0.024	0.009	0.003	0.201	0.085	0.002	0.001	0.004
34 Copepods	0.273							0.35	0.67								
35 Phytoplankton																	
36 Pelagic detritus																	
37 Benthic detritus															0.012		
38 Detrital pool																	
Import																	
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B4 (Cont.)

Prey	Predator																
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1 Baleen whales																	
2 Toothed whales																	
3 Sperm Whales																	
4 Walrus & B. seals																	
5 Seals																	
6 Steller s. lions																	
7 Seabirds																	
8 Adult pollock																	
9 Juv. pollock	0.1														0.001		
10 P. cod															0.001		
11 P. halibut															0.001		
12 Greenland turb.	0.04														0.001		
13 Arrowtooth fl.	0.04														0.001		
14 Small flatfish															0.004		
15 Skates															0.001		
16 Sculpins															0.001		
17 Sablefish															0.001		
18 Rockfish															0.001		
19 Macrouridae															0.001		
20 Zoarcidae			0.015												0.001		
21 Tanner crab			0.029					0.001							0.04		
22 Snow crab			0.039					0.001							0.04		
23 King crab															0.04		
24 Shrimp	0.36	0.322	0.021				0.01	0.002				0.001			0.011		
25 Epifauna		0.02	0.144	0.118	0.118	0.118		0.009									
26 Infauna			0.525	0.792	0.792	0.792	0.24	0.303			0.005			0.005			
27 Benthic amph.	0.01	0.002	0.227				0.15	0.051			0.005	0.05		0.005	0.04		
28 P. herring											0.004			0.001			
29 P. salmon																	
30 Cephalopods		0.232									0.03	0.2		0.001			
31 Forage fish		0.423									0.05	0.2		0.001			
32 Jellyfish														0.001			
33 Large Zoop.	0.45	0.001					0.1				0.9	0.065	0.6	0.9	0.65	0.01	
34 Copepods											0.09	0.05		0.09	0.15	0.25	
35 Phytoplankton										0.2						0.5	0.8
36 Pelagic detritus															0.01	0.24	0.2
37 Benthic detritus				0.09	0.09	0.09	0.5	0.633	1	0.8							
38 Detrital pool																	
Import												0.75					
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B5. Diet matrix (proportion of prey for each predator) for western Bering Sea shelf + slope ECOPATH model (2 pages).

Prey	Predator																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Baleen whales		0.001															
2 Toothed whales																	
3 Sperm Whales																	
4 Walrus & B.seals		0.001															
5 Seals		0.002															
6 Steller s.lions		0.001															
7 Seabirds																	
8 Adult pollock	0.04	0.15		0.01	0.18	0.17				0.386	0.19	0.45	0.5		0.37	0.25	
9 Juv. pollock	0.06	0.1		0.01	0.15	0.2	0.25	0.005		0.2	0.17		0.1	0.021	0.2	0.13	
10 P. cod	0.02	0.1		0.01	0.05	0.03					0.06				0.033	0.02	
11 P. halibut		0.01				0.005											
12 Greenland turb.			0.005														
13 Arrowtooth fl.	0.005	0.005			0.005												
14 Small flatfish	0.02					0.01				0.01	0.02	0.01				0.015	
15 Skates																	
16 Sculp. & Rockf.						0.02				0.015	0.005	0.01				0.005	
17 Macrouridae		0.03	0.09										0.01				0.04
18 Zoarcidae										0.01	0.005	0.05		0.01			0.01
19 Tanner crab				0.001		0.01				0.001	0.005				0.002	0.01	
20 Snow crab				0.005						0.01	0.005			0.002	0.005	0.01	
21 King crab		0.01		0.005		0.02				0.001						0.001	
22 Shrimp	0.045			0.1				0.005		0.05	0.015	0.07	0.15	0.145	0.02	0.08	0.02
23 Epifauna				0.319						0.126				0.07	0.06	0.209	0.1
24 Infauna				0.435			0.03			0.075				0.534	0.01	0.14	0.2
25 Benthic amph.				0.1						0.04				0.059		0.05	0.05
26 P. herring	0.02	0.1			0.07	0.05	0.04			0.005							0.02
27 P. salmon		0.012			0.017	0.015	0.01										
28 Cephalopods	0.1	0.26	0.9		0.2	0.25	0.05	0.01	0.02	0.03	0.5	0.3	0.2	0.01	0.2	0.01	0.3
29 Forage fish	0.13	0.045			0.075	0.01	0.19	0.04		0.021	0.025	0.1		0.006	0.1	0.005	0.16
30 Jellyfish					0.02		0.01										
31 Large Zoop.	0.315			0.005	0.01		0.32	0.495	0.505	0.02			0.05	0.094		0.045	0.12
32 Copepods	0.27						0.1	0.445	0.45					0.049			
33 Phytoplankton																	
34 Pelagic detritus									0.025								
35 Benthic detritus																	
36 Detrital pool																	
Import		0.153			0.228	0.205											
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B5 (Cont.)

Prey	Predator														
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Baleen whales															
1 Toothed whales															
2 Sperm Whales															
3 Walrus & B.seals															
4 Seals															
5 Steller s.lions															
6 Seabirds															
7 Adult pollock	0.05														
8 Juv. pollock	0.1												0.01		
9 P. cod															
10 P. halibut															
11 Greenland turb.															
12 Arrowtooth fl.															
13 Small flatfish															
14 Skates															
15 Sculp. & Rockf.															
16 Macrouridae															
17 Zoarcidae															
18 Tanner crab															
19 Snow crab															
20 King crab															
21 Shrimp	0.07	0.1	0.1	0.09					0.03	0.04					
22 Epifauna	0.09	0.33	0.33	0.38		0.047			0.03	0.025					
23 Infauna	0.07	0.37	0.37	0.33	0.2	0.095									
24 Benthic amph.		0.1	0.1	0.1	0.1	0.002		0.005	0.15	0.095	0.14	0.055			
25 P. herring															
26 P. salmon															
27 Cephalopods	0.35									0.095	0.12	0.02			
28 Forage fish	0.15								0.03	0.12	0.15				
29 Jellyfish															
30 Large Zoop.	0.12								0.41	0.525	0.39	0.525	0.3	0.079	
31 Copepods					0.1				0.35	0.1	0.2	0.4	0.6	0.484	0.05
32 Phytoplankton													0.04	0.196	0.7
33 Pelagic detritus													0.05	0.241	0.25
34 Benthic detritus		0.1	0.1	0.1	0.6	0.856	1	0.995							
35 Detrital pool															
36 Import															
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B6. Diet matrix (proportion of prey for each predator) for western Bering Sea shelf + slope+basin ECOPATH model (3 pages).

Prey	Predator																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1 Baleen whales		0.001																
2 Toothed whales																		
3 Sperm whales																		
4 Walrus & Bearded		0.001																
5 Seals		0.002																
6 Steller sea lion		0.001																
7 Marine birds																		
8 Adult pollock	0.04	0.15		0.01	0.18	0.17				0.386	0.19	0.45	0.5					
9 Juv. pollock	0.06	0.1		0.01	0.15	0.2	0.25	0.005		0.2	0.17		0.1	0.1				
10 Cod	0.02	0.1		0.01	0.05	0.03					0.06							
11 Halibut		0.01				0.005												
12 Greenland turbot			0.005															
13 Arrowtooth flounder		0.005	0.005			0.005												
14 Flathead sole		0.005								0.004								
15 Yellowfin sole		0.005				0.005				0.001								
16 Rock sole		0.005				0.005				0.002								
17 Alaska plaice		0.005								0.002								
18 O. sm. flatfishes										0.001	0.02	0.01						
19 Herring	0.02	0.1			0.07	0.05	0.04			0.005								
20 Salmon		0.12			0.17	0.13	0.01											
21 Other pelagics	0.13	0.09			0.15	0.1	0.19	0.04		0.021	0.025	0.1		0.03				
22 Skates																		
23 Sculpins & rockfish						0.02				0.015	0.005	0.01						
24 Macrouridae		0.03	0.09									0.01						
25 Zoarcids										0.01	0.005	0.05		0.05				
26 Cephalopods	0.1	0.26	0.9		0.2	0.25	0.05	0.01	0.02	0.03	0.5	0.3	0.2	0.05				
27 Tanner crab				0.001		0.01				0.001	0.005							
28 Snow crab				0.005						0.01	0.005			0.01				
29 King crab		0.01		0.005		0.02				0.001								
30 Shrimps	0.045			0.1				0.005		0.05	0.015	0.07	0.15	0.35	0.16	0.15		
31 Clams				0.31						0.03				0.35	0.2	0.2	0.3	
32 Polychaetes				0.065			0.02			0.04					0.4	0.35	0.65	
33 Other worms				0.06			0.01			0.005								
34 Hermits & o.decapods				0.07						0.06								
35 Snail				0.149						0.005								
36 Brittlestar				0.01						0.005			0.05	0.14	0.1	0.04		
37 Starfish																		
38 Other benthos				0.09						0.056								
39 Jellyfish					0.02		0.01											
40 Amphipods	0.065			0.1	0.01		0.05	0.065	0.05	0.04					0.1	0.1	0.01	
41 Gelatinous plankton							0.02	0.05	0.01									
42 Euphausiids	0.25						0.25	0.34	0.43	0.01			0.01		0.05		0.05	
43 Copepods	0.27						0.1	0.445	0.45									
44 Mysiids				0.005				0.015	0.01	0.01			0.05			0.05		
45 Chaetognaths								0.025	0.005									
46 Protozoa									0.005									
47 Phytoplankton									0.02									
48 Detritus																		
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B6 (Cont.)

Prey	Predator																
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1 Baleen whales																	
2 Toothed whales																	
3 Sperm whales																	
4 Walrus & Bearded																	
5 Seals																	
6 Steller sea lion																	
7 Marine birds																	
8 Adult pollock					0.37	0.25		0.05									
9 Juv. pollock					0.2	0.13		0.1									
10 Cod					0.033	0.02											
11 Halibut																	
12 Greenland turbot																	
13 Arrowtooth flounder																	
14 Flathead sole						0.005											
15 Yellowfin sole																	
16 Rock sole						0.005											
17 Alaska plaice																	
18 O. sm. flatfishes						0.005											
19 Herring						0.02											
20 Salmon																	
21 Other pelagics		0.03	0.12		0.1	0.005	0.16	0.15	0.15								
22 Skates																	
23 Sculpins & rockfish						0.005											
24 Macrouridae							0.04										
25 Zoarcids							0.01										
26 Cephalopods			0.095	0.02	0.2	0.01	0.3	0.35	0.12								
27 Tanner crab					0.002	0.01											
28 Snow crab					0.005	0.01											
29 King crab						0.001											
30 Shrimps	0.05	0.03	0.04		0.02	0.08	0.02	0.07		0.1	0.1	0.09					0.01
31 Clams					0.01	0.02	0.2	0.07		0.14	0.14	0.2	0.1				0.01
32 Polychaetes						0.11				0.1	0.1	0.08	0.1				0.06
33 Other worms						0.01				0.13	0.13	0.05					0.06
34 Hermits & o.decapods		0.03	0.025		0.01	0.09											0.04
35 Snail						0.03				0.12	0.12	0.2					0.01
36 Brittlestar						0.01	0.05	0.03		0.19	0.19	0.15					0.03
37 Starfish						0.005	0.05			0.02	0.02	0.03					
38 Other benthos					0.05	0.074		0.06									0.08
39 Jellyfish																	
40 Amphipods	0.1	0.15	0.095	0.055		0.05	0.05		0.14	0.1	0.1	0.1	0.1				0.1
41 Gelatinous plankton	0.1	0.02	0.235	0.14		0.005	0.03		0.04								
42 Euphausiids	0.35	0.35	0.26	0.35		0.02	0.02	0.04	0.3								
43 Copepods	0.35	0.35	0.1	0.4					0.2				0.1				
44 Mysiids	0.02	0.02	0.01	0.005		0.02	0.07	0.08	0.025								
45 Chaetognaths	0.03	0.02	0.02	0.03					0.025								
46 Protozoa																	
47 Phytoplankton																	
48 Detritus										0.1	0.1	0.1	0.6	1	1	1	0.6
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B6 (Cont.)

Prey	Predator												
	35	36	37	38	39	40	41	42	43	44	45	46	
1 Baleen whales													
2 Toothed whales													
3 Sperm whales													
4 Walrus & Bearded													
5 Seals													
6 Steller sea lion													
7 Marine birds													
8 Adult pollock													
9 Juv. pollock					0.01								
10 Cod													
11 Halibut													
12 Greenland turbot													
13 Arrowtooth flounder													
14 Flathead sole													
15 Yellowfin sole													
16 Rock sole													
17 Alaska plaice													
18 O.sm.flatfishes													
19 Herring													
20 Salmon													
21 Other pelagics													
22 Skates													
23 Sculpins & rockfish													
24 Macrouridae													
25 Zoarcids													
26 Cephalopods													
27 C.bairdi													
28 C.opilio													
29 King crab													
30 Shrimps													
31 Clams	0.4		0.6										
32 Polychaets				0.1									
33 Other worms													
34 Hermits & o.decapods													
35 Snail	0.1		0.1										
36 Brittlestar													
37 Starfish													
38 Other benthos				0.05									
39 Jellyfish						0.001							
40 Amphipods					0.05	0.005						0.05	
41 Gelatinous plankton						0.05							
42 Euphausiids					0.25	0.01	0.03	0.005					0.04
43 Copepods					0.6	0.5	0.5	0.2	0.05				0.71
44 Mysiids													
45 Chaetognaths						0.1	0.1						
46 Protozoa						0.1	0.1	0.1	0.15	0.1	0.1		
47 Phytoplankton					0.04	0.054	0.07	0.545	0.7	0.7			
48 Detritus	0.5	1	0.3	0.85	0.05	0.18	0.2	0.15	0.1	0.2	0.1		1
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1

APPENDIX C: WBS SHELF/BASIN PARTITIONING

Appendix Table C1. Biomass, Production/Biomass (PB), and Consumption/Biomass (Q/B) partitioned between western Bering Sea shelf/slope and basin. Biomass estimates are per-unit-area, and thus were used directly as Ecopath inputs.

	Shelf/Slope			Basin		
	B (t/km ²)	P/B (1/year)	Q/B (1/year)	B (t/km ²)	P/B (1/year)	Q/B (1/year)
Phytoplankton	15.0	234		9.3	234	
Protozoa	30	47	142	15	47	142
Copepods	122.62	9.5	26.2	91.96	9.5	26.2
L. Zoop. (amph., euph., chaet.)	107.7	4.24	14.15	76.23	4.24	14.15
Gel. Plankton	13.04	5.0	17.0	9.785	5.0	17.0
Sm. Pelagics	5.81	0.95	3.5	11.62	0.95	3.5
Cephalapods	4.83	3.2	10.67	1.04	3.2	10.67
Jellyfish	1.4	1.5	3.0	0.1	1.5	3.0

Appendix Table C2. Proportion of total assessed stock size for each functional group(tons) resident in the Western Bering sea shelf+slope and Basin, respectively. Since proportional estimates were provided in tons, densities (t/km²) were calculated by dividing the total tons calculated in each area by the total shelf+slope or basin area shown in Table 2.1.

Group	Shelf/ slope		Group	Shelf/ slope	
	Basin	Basin		Basin	Basin
Pacific salmon	0.1	0.9	Seabirds	0.6	0.4
Pacific herring	0.8	0.2	Steller sea lions	0.8	0.2
O. small flatfishes	1.0	0	Seals	0.8	0.2
Alaska plaice	1.0	0	Walrus & brd. seals	1.0	0
Rock sole	1.0	0	Sperm whales	0.6	0.4
Yellowfin sole	1.0	0	Toothed whales	0.8	0.2
Flathead sole	0.9	0.1	Baleen whales	0.5	0.5
Arrowtooth flounder	0.9	0.1			
Greenland turbot	0.7	0.3	Epifauna	0.7	0.3
Pacific halibut	0.7	0.3	Shrimps	0.6	0.4
Pacific cod	0.9	0.1	Snow crab	1.0	0
Juvenile pollock	0.8	0.2	Tanner crab	1.0	0
Adult pollock	0.6	0.4	King crabs	1.0	0

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