Food Web Comparisons In the Eastern and Western Bering Sea

By Kerim Aydin and Pat Livingston

The Alaska Fisheries Science Center (AFSC) and the Russian Pacific Institute of Fisheries and Ocean Research (TINRO) each have conducted substantial ecosystem studies on their respective sides of the Bering Sea over the past 50 years. In a management context, the waters of the Bering Sea lie in both Russian and U.S. Exclusive Economic Zones (EEZs), with international waters in a section of the central basin commonly known as “the donut hole.”

The Bering Sea covers more than 2.3 million km^2 and supports high biological production and multiple fisheries. On one hand, the differences 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 the same commercially important fish species such as walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) in both areas may result in profound similarities.

In order to develop meaningful measures of large marine ecosystem (LME) function and health, a comparative study of ecosystems is required. One basis for comparison is the food web—the system of predator/prey relationships by which energy originating in sunlight is passed through plankton, fish, birds, marine mammals, and humans. The study of changes in the structure and function of food webs over time may reveal critical relationships between marine ecosystems, climate, and fishing.

Such comparisons require synthesizing large bodies of literature that exist in different locations and contain results in different contextual formats not readily adaptable for comparison. Our study aimed to synthesize data on 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 by combining data from fisheries agencies on both sides of the Bering Sea.

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. (See www.ecopath.org for the free software.) 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.

By using a common modeling framework, we hoped our efforts would serve two primary purposes:

1) The synthesis of predator and prey data from the western Bering Sea into a quantitative food web with a substantial literature review for comparison with the eastern Bering Sea;

2) The examination of the resulting food web models as a preliminary exploration and comparison of the ecosystem interactions which occur in both ecosystems.

The resulting models both highlight the dominant predator/prey processes as they can be gleaned from the data and help focus on major data gaps relative to their importance in the ecosystem as a whole. The full models resulting from this study were published in Aydin, K. Y., V. V. Lapko, V. I. Radchenko, and P. A. Livingston. 2002. A comparison of the eastern and western Bering Sea shelf and slope ecosystems through the use of mass-balance food web models. U.S. Dep.

Commer., NOAA Tech. Memo. NMFS-AFSC-130, 78 p. The publication is available on the AFSC web site at www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-130.pdf.

Methods

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 preyed upon more than they are produced (EE > 1.0), which is impossible under the mass-balance assumption.

A mass-balance model of the eastern Bering Sea (EBS) shelf and slope for the years 1979-85, including a substantial literature review of available data sources, was compared with a western Bering Sea (WBS) literature review of the data for the western model, not previously available in English. One of the main information sources was a series of stock assessment documents representing collective papers on all commercial fisheries in the Russian Far East, published annually by TINRO with limited distribution through Russian fisheries agencies. The documents are analogous to the NMFS Stock Assessment and Fisheries Evaluation report series.

The time period 1979-85 was used as the base time period. This time period represents the ecosystem immediately following the increase of walleye pollock biomass in the Bering Sea and thus captures some of the ecosystem changes resulting from this shift in dominant fish biomass over 30 years. For building the WBS model, the time period was extended to 1990 to increase the pool of available data.

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.

The EBS shelf consists of inner, middle, and outer shelf ecological zones separated by oceanographic fronts associated with the 50-, 100-, and 200-m isobaths, respectively. The EBS model was limited entirely to the area of the EBS south of 61°N and 20 km or more offshore, 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, with the exception of Pacific salmon (*Oncorhynchus* spp.), for which 75% of their diet was considered to come from outside the EBS. Marine mammal migration and off-the-shelf foraging was handled by lowering the average biomass of seasonal migrants. However, because 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 WBS. 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

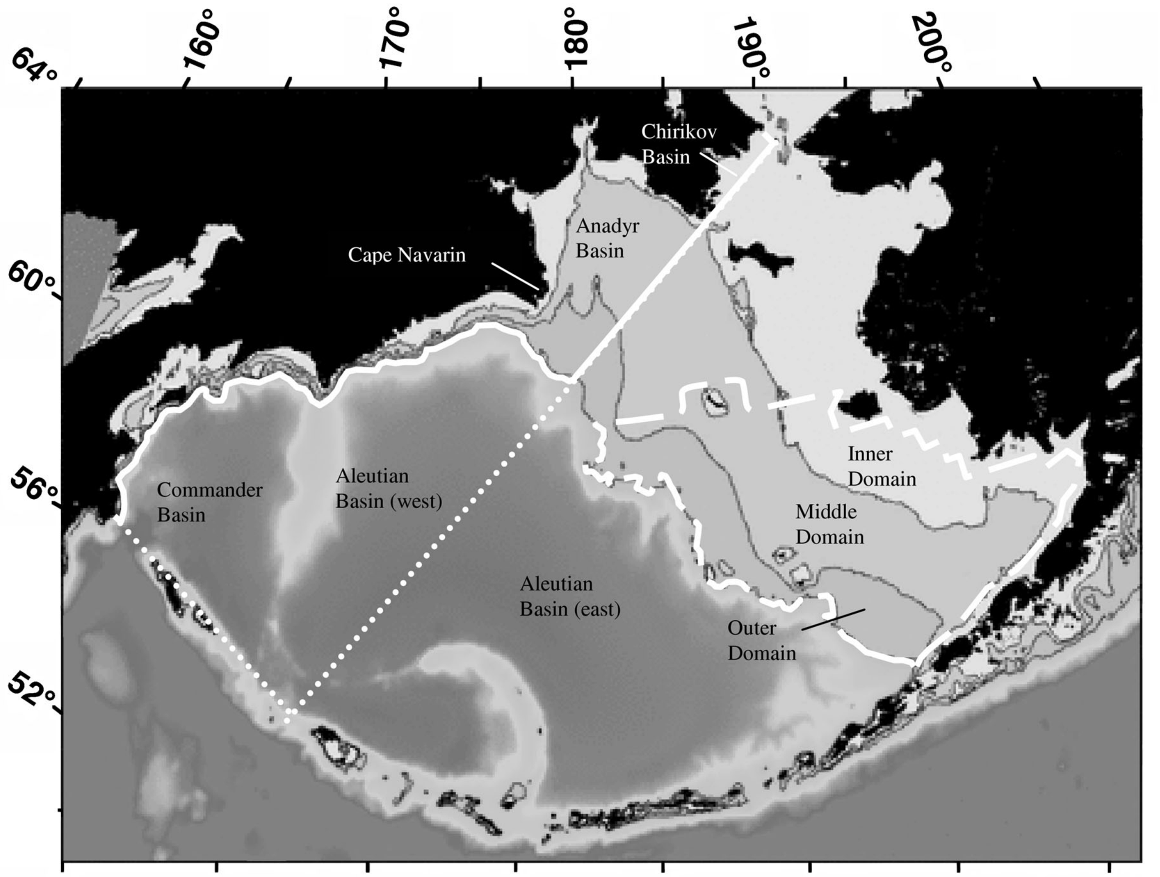

Figure 1. The Bering Sea, with boundaries of the EBS shelf model (eastern dashed line), the WBS shelf model (western solid line), and the WBS shelf+basin model (dotted line). Isobaths shown are 50 m (between inner and middle domains), 100 m (between middle and outer domains), and 200 m (between outer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

total western area (Fig. 1). South of Cape Navarin, the shelf (0-200 m) varies from less than 5 km to 50 km in width, but in general the whole shelf area is closer to shore than the inshore border of the EBS study area. While temperature and salinity may divide 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. North of Cape Navarin, the shallow (50-100 m) Anadyr Basin and the most northern Chirikov Basin are northward extensions of the EBS shelf.

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 the Russian EEZ. To reflect this, the initial WBS model was a combined shelf/basin model, bounded by the shore and the Russian EEZ boundary. Further details of the model-building process may be found in Aydin et al. (2002).

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 the WBS shelf model covers 254,000 km^2, while the EBS shelf model covers 485,000 km^2. 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 the difference in total areas, especially when considering the relative magnitudes of fishing with respect to overall stock size.

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). The resulting WBS shelf/slope model was compared with the EBS shelf/slope model as described in the Results section. An important step in future modeling should be to create refined subregional models for each distinct biogeographic area.

Results and Discussion

The components of the Bering Sea food webs were compartmentalized on several scales. For abundant commercial fish species such as walleye pollock, a single "compartment" represents a single species. On the other hand, for less-understood groups such as epifauna (sea stars, sea urchins, and snails) or infauna (clams and other burrowing invertebrates), a single box may represent hundreds of species.

The EBS and WBS food webs consist of hundreds of compartments divided into trophic levels, the distance in feeding steps between each organism and initial sunlight energy input. Trophic Level I consists of phytoplankton and detritus; Trophic Levels II-III are zooplankton and small benthic animals (clams, worms, echinoderms); Trophic Levels III-IV are most major fish, squid and crab species, baleen whales, and zooplanktivorous birds; Trophic Level V+ is carnivorous marine mammals (pinnipeds, porpoises, killer whales), large predatory fish (sharks, large halibut), and some larger birds. Overall, each food web was examined by trophic level, the density of biomass on each trophic level, and the throughput, or energy passed through each trophic level in a given year. In many compartments, especially plankton, the energy passed through in a single year could be several times the biomass density of the compartment overall.

The estimate of total density (biomass per unit area, excluding detritus) was 2.3 times higher in the WBS (568 t/km^2) than in the EBS (240 t/km^2). The total production density requirements from Trophic Level I (phytoplankton and detritus) to support all consumers were similarly scaled between the two systems, with 6,031 t/km^2/year required in the WBS and 2,566 t/km^2/year 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.

The throughput of each trophic level is defined as yearly input plus output, or in a

Table 1. Throughput (t/km^2/year), biomass density (t/km^2), throughput/biomass (1/year) and transfer efficiency (percentage) by trophic level in the EBS and WBS models.

Trophic Level	Throughput		Biomass Density		Throughput /Biomass		Transfer Efficiency	
	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	-	-

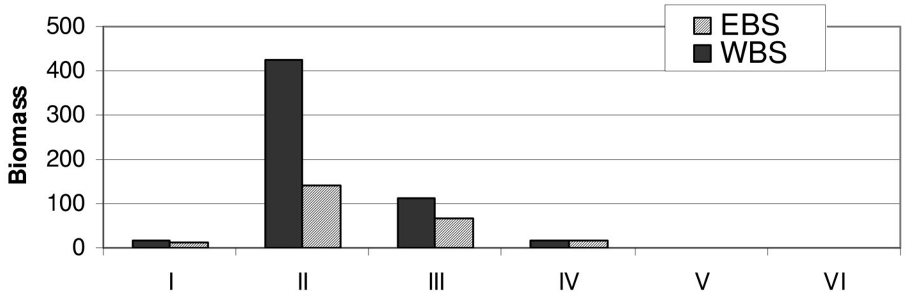

Figure 2. Biomass density (t/km^2) as a function of trophic level on the EBS and WBS shelves.

steady state, double the trophic level's production less production consumed within the trophic level. The throughput per unit area is consistently higher by a factor of two in the WBS for all levels between Trophic Levels I and VII (Table 1). The excess density, however, is not evenly spread: in the WBS, most of this excess occurs on Trophic Level II (Table 1; Fig. 2). The density of Trophic Levels IV-V are similar or higher in the EBS (Fig. 2). Further, the amount of throughput per unit biomass density shows that on all trophic levels except Trophic Level II, the EBS uses less throughput for each unit of supported biomass density (Table 1).

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 Trophic Level II to 2%-4% on Trophic Level VI. 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.

Density 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 density 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/km^2) and the WBS (15.0 t/km^2). However, estimates of pelagic zooplankton—copepods and large zooplankton—have a 2-3 times higher density in the WBS than in the EBS (Fig. 3). Within large zooplankton, euphausiid densities are comparable between the two systems (35 t/km^2 in the EBS and 38 t/km^2 in the WBS), while the WBS literature reports a large density of chaetognaths, pelagic amphipods, and gelatinous zooplankton, each of which have estimated densities 5-10 times higher in the WBS.

The overall density of pelagic forage species is comparable between the two systems, with a total of 24 t/km^2 in the EBS and 30 t/km^2 in the WBS. The largest proportion of this density 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 estimates were available for these species in either system, so the biomass levels indicated are the minimum requirement to satisfy the measured demands of predators in the system—the actual density of forage fish could be considerably higher in both systems.

The estimates of infaunal density are higher in the WBS (126 t/km^2 vs. 47 t/km^2 in the EBS), while the epifaunal density is almost 20 times higher in the WBS (115 t/km^2 vs. 6 t/km^2 in the EBS). The large majority of the WBS epifaunal biomass was due to a high estimated density (96 t/km^2) of sea urchin populations.

On the other hand, the density of higher trophic-level benthic species is greater in the

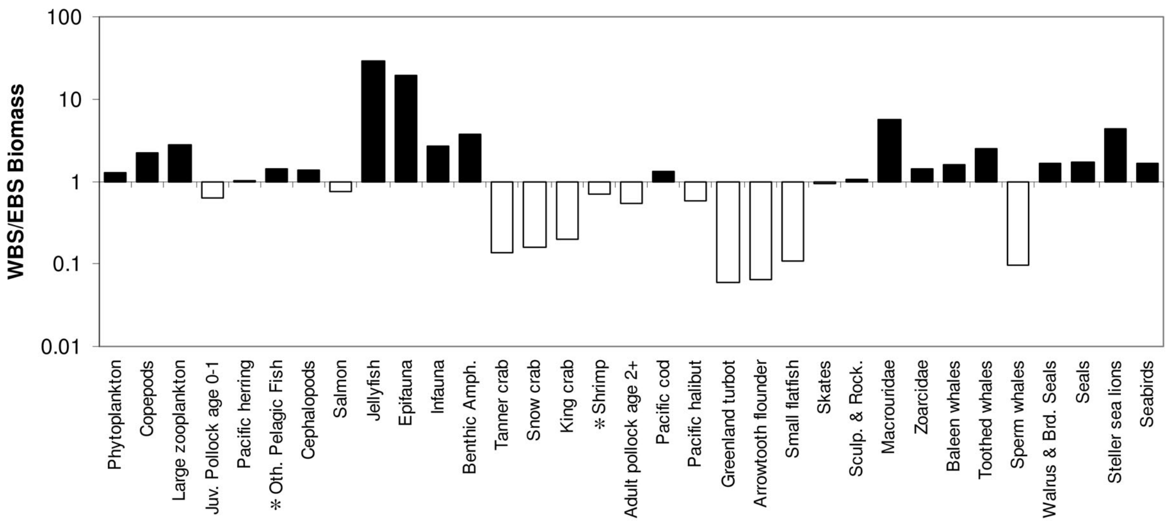

Figure 3. WBS/EBS biomass density (t/km^2), log scale. A black bar indicates a higher value in the WBS (WBS/EBS value greater than 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value less than 1.0). (*)species biomass set by top-down balance (demand).

EBS. Tanner crab (*Chionoecetes bairdi*), snow crab (*C. opilio*), and king crabs (*Paralithodes* spp.) have density 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 density estimates of flatfish species—Greenland turbot (*Reinhardtius hippoglossoides*), arrowtooth flounder (*Atheresthes stomias*), Pacific halibut (*Hippoglossus stenolepis*), and especially the small flatfish community as a whole—was considerably higher in the EBS.

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

Groundfish species other than flatfish showed similar densities between the two systems (Fig. 3). Toothed whales and Steller sea lions (*Eumetopias jubatus*) have a higher density in the WBS, while estimates of sperm whale (*Physeter macrocephalus*) presence is higher in the EBS. The density 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.

In both the EBS and the WBS, the same top seven groups produce 95% of the detritus in the system (Fig. 4): all of these except pollock are below Trophic Level 2.5. (Note: trophic level has two distinct but related definitions depending on whether one is speaking of the flows through compartments or the biomass of compartments. In this report, flow trophic level or pathway level is represented in Roman numerals, while the traditional trophic level of each functional group may be a weighted, fractional average of pathway levels and for clarity is reported in Arabic numerals.)

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 (nonpredation) mortality.

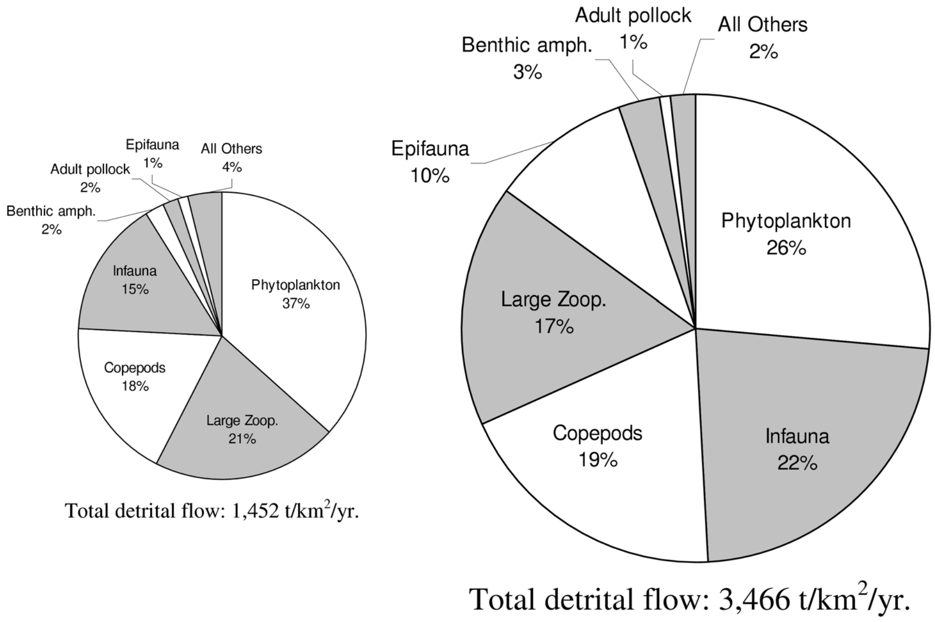

Figure 4. The amount of material flowing from "living" boxes per unit area into detritus in the EBS (left small circle) and the WBS (right large circle). The area of each circle is proportional to the total detrital flow of the system.

For each compartment, the PPR value is the amount of Trophic Level I production required to support the density of biomass of that compartment and, in an iterative fashion, to support its prey and its prey's prey and so on. The PPR value for all of the compartments in the system will sum to greater than the actual Trophic Level I production, as the "required" energy is counted for a prey species itself and for all of its predators.

Normalizing the PPR values per unit supported biomass by total ecosystem primary production (Fig. 5) 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 density. Overall, the standing stocks in the EBS utilize a larger percentage of their primary production per unit area than those in the WBS.

The EBS shelf model contains 320 described predator/prey (diet) links between distinct functional groups, compared to 235 links in the WBS. 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.

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 III and above in the EBS than it does in the WBS (Fig. 6). This is despite the fact that demand for benthic detrital production is a greater proportion of the overall total production per unit area in the WBS than in the EBS (37% vs. 24%).

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 density are modeled in the WBS ecosystem (biomass 115 t/km^2 in the WBS vs. 6 t/km^2 in the EBS).

Moreover, epifauna is the dominant predator of infauna in the WBS: in the EBS, the larger proportion of infaunal biomass passes

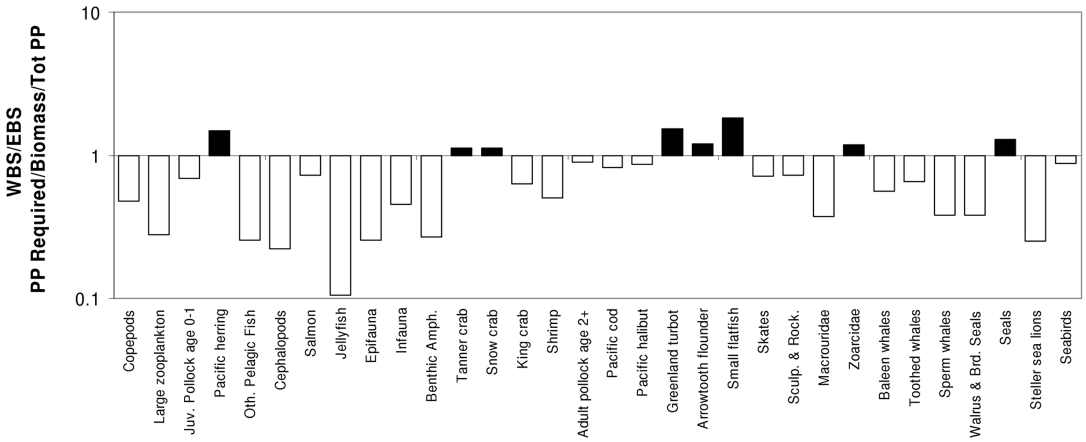

Figure 5. Primary Production Required (PPR)/Total Ecosystem Primary Production (PP) to support a unit biomass each indicated predator, taking into account the energy required to support the prey of each predator (PPR/Tot PP/t predator; WBS/EBS, log scale). A black bar indicates a higher value in the WBS (WBS/EBS value above 1.0); a white bar indicates a higher value in the EBS (WBS/EBS value below 1.0).

Table 2. Trophic level (TL), biomass density (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 Group	TL	Biomass density	TL 3+ Prod.%	WBS Group	TL	Biomass density	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 TL. 3.0+ prod.			96.7%	Total Percent of TL. 3.0+ prod.			96.7%

upwards into crab and fish species. The small flatfish community has approximately a 10 times higher biomass density in the EBS in comparison to the WBS. 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 2 lists the functional groups that 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. Three major routes through Trophic Levels 3.0-3.5 are evident in the EBS and WBS: 1) forage fish and cephalopods; 2) pollock (adult and juvenile combined); and 3) benthic components such as crabs and small flatfish.

As noted above, the benthic web plays a much smaller role in the WBS than in the

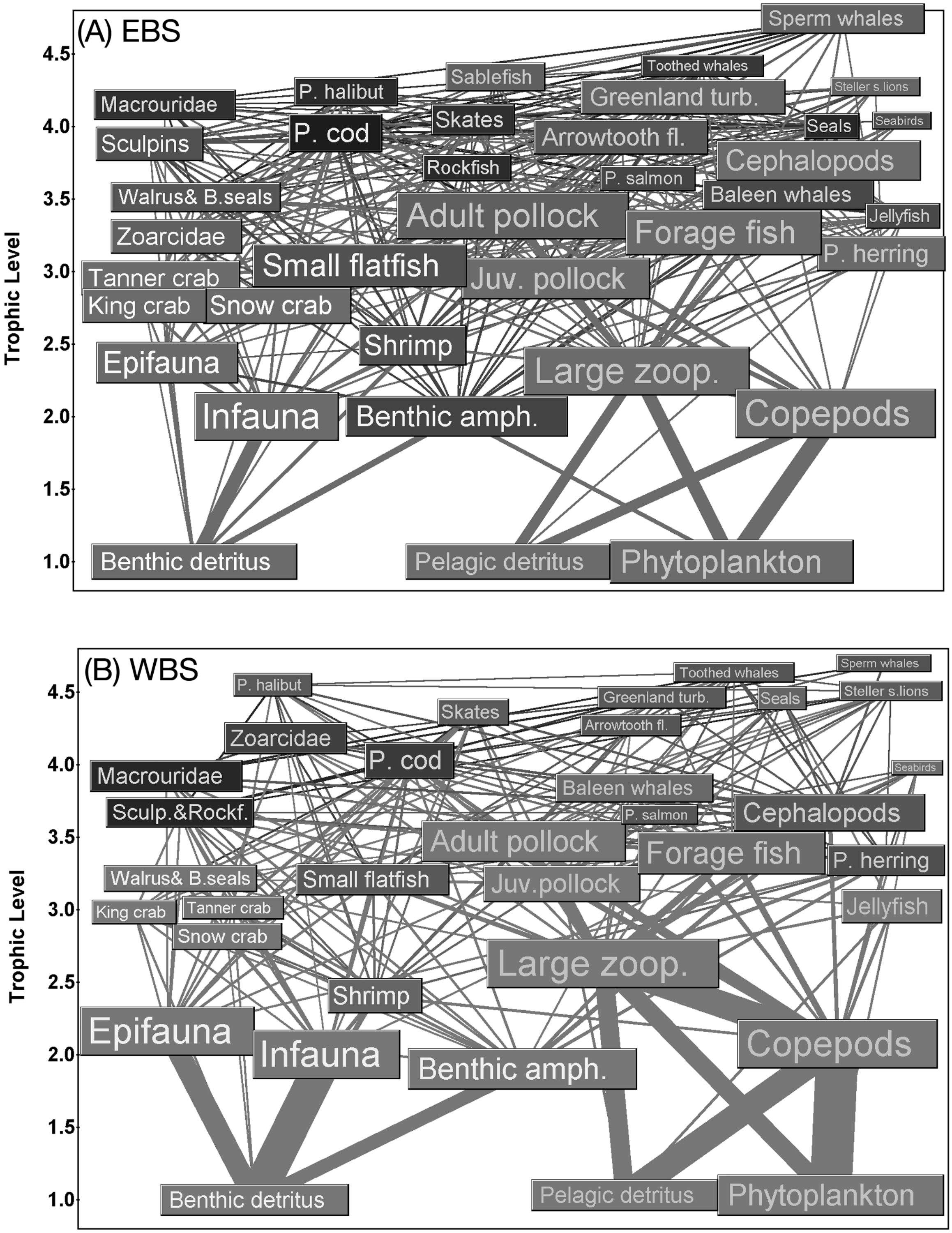

Figure 6. The proportion of energy flow into each compartment above Trophic Level 1 ultimately deriving from pelagic sources (phytoplankton and pelagic detritus; lighter gray) or benthic sources (benthic detritus; darker gray). (A) eastern Bering Sea shelf; (B) western Bering Sea shelf. Box and text size is proportional to log(biomass) of each compartment, while the area of each connection link is proportional to the volume of flow.

EBS. Pollock are more dominant as prey of upper trophic level fish in the EBS, especially large flatfish (arrowtooth flounder and Greenland turbot). Small pelagic animals, especially 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 pathways mentioned above, although seals feed on a higher trophic level. Baleen whales and seals do not have a benthic component in their diet in the WBS.

Two other species groups in Table 2, 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 is more important as a prey item in the WBS than in the EBS (Figs. 7a,b) with a diet that includes a high degree of cannibalism. Pacific cod, as shown in Figure 6 and in Figures 7c and d, is a “bridge species” between benthic and pelagic components in the EBS, while in the WBS the fish feeds primarily on pollock.

Conclusion and Future Work

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 per unit area (Table 1; Figs. 2-4) 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.

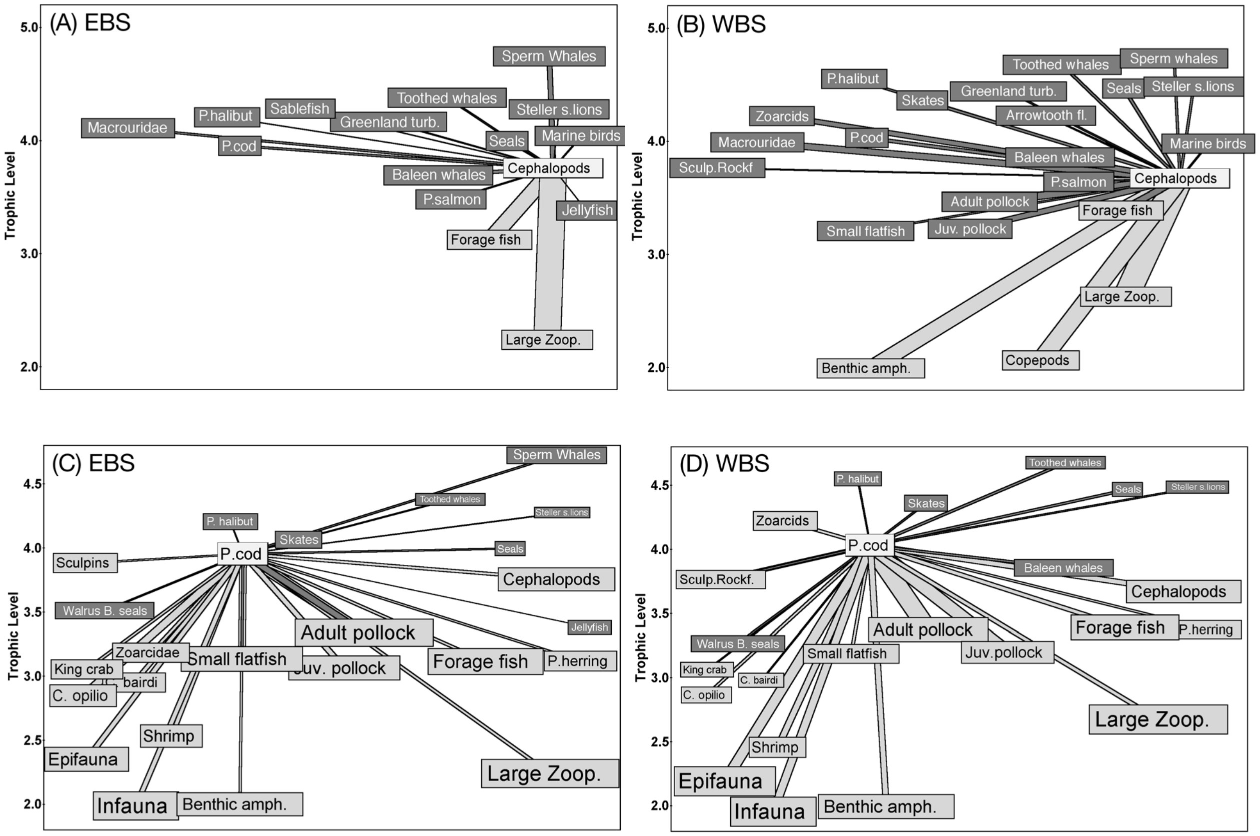

Figure 7. Predator and prey of cephalopods (A,B) and Pacific cod (C,D) in the EBS and the WBS. Light gray boxes indicate prey; dark gray indicate predators. The width of the connecting flow lines is proportional to the volume of flow ($t/km^2/year$).

However, this large energy supply does not translate into higher supported biomass densities 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 (Figs. 5-6).

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 density, as seen from examining PPR values (Fig. 5) 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 is worth further investigation. Specifically, it is not clear if estimation methods for epibenthic biomass densities 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 million t to 3.0 million t overall. Their role in both ecosystems is an important area for future research.

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 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 development of subregional 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.