Alaska FISHERIES SCIENCE CENTER

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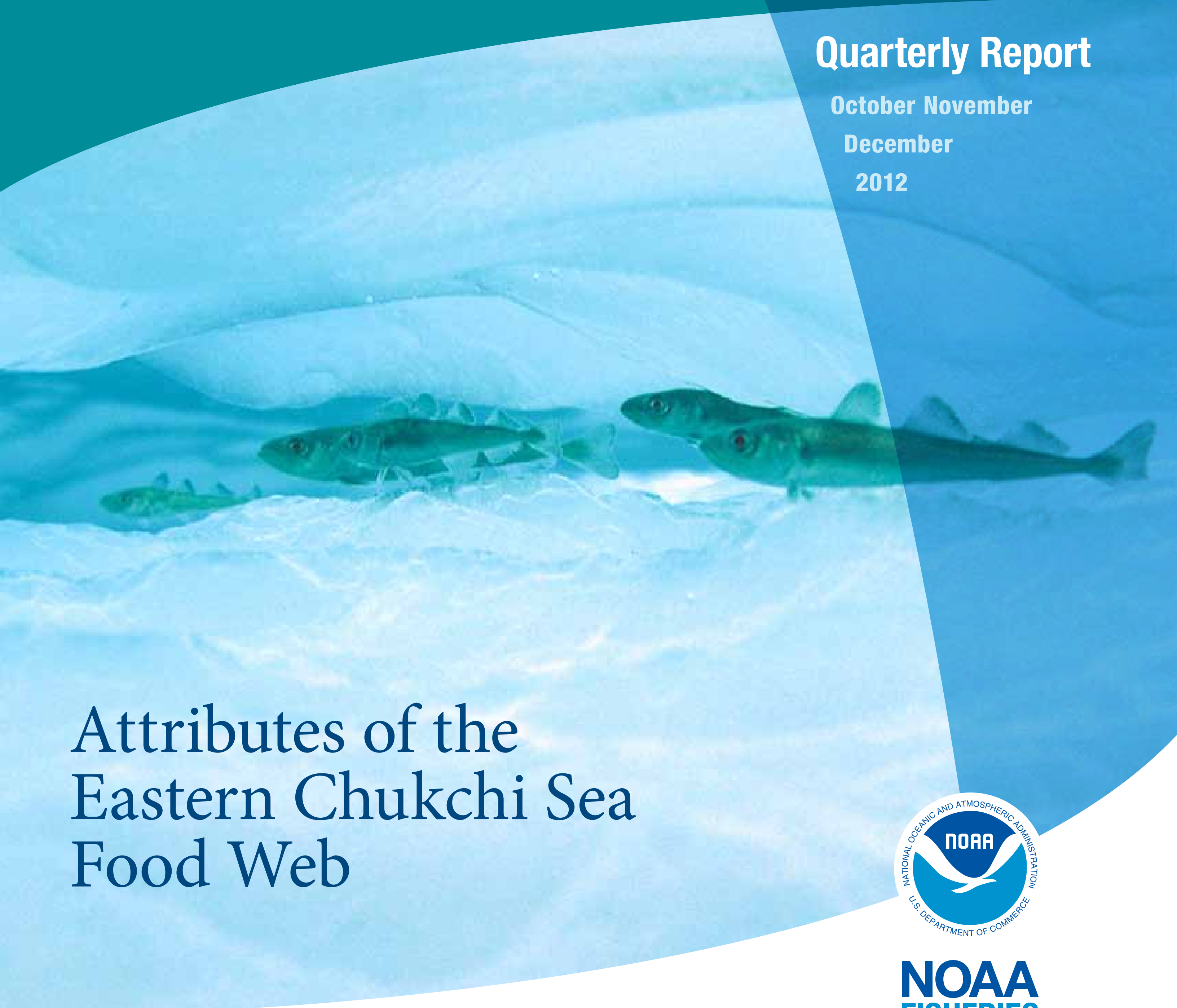

Attributes of the Eastern Chukchi Sea Food Web

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Attributes of the Eastern Chukchi Sea Food Web With Comparisons to Three Northern Marine Ecosystems

By Andy Whitehouse

There is growing recognition that the Arctic is threatened by multiple human impacts including climate change and increased activities resulting from greater access due to retreating sea ice. Arctic sea ice cover has declined about 3% per decade over the satellite record (1979-present), with the six lowest annual sea ice minima occurring in the last 6 years (2007-12). The Alaska Arctic contains large petroleum reserves, and human activities related to energy extraction are expected to increase in the near future. Continued reduction in the extent of Arctic sea ice could improve access for the oil and shipping industries and has spurred interest in understanding what changes in sea ice coverage could mean for future Arctic fisheries. The Alaska Arctic is presently home to several subsistence fisheries and marine mammal harvests. The development of new commercial fisheries in the Alaska Arctic is currently prohibited by the Arctic Fishery Management Plan until sufficient research has been conducted to allow for adequate evaluation of the ecological impact of commercial fishing. Thus, there is great need for the development of modeling and other decision-support tools that can synthesize existing knowledge of Arctic marine ecosystems and foster an improved understanding of ecosystem structure, function, and sensitivity to human activities.

Food web models describe the organization of a food web and the exchange of material (measured in biomass) between species in a food web through feeding interactions. These models can be used to study the structure and function of ecosystems and produce ecosystem metrics and indicators that can help to identify and clarify ecosystem properties. Scientists with the Alaska Fisheries Science Center's (AFSC) Resource Ecology and Ecosystem Modeling (REEM) program previously developed mass-balance food web models of large marine ecosystems (LME) in Alaska, including the eastern Bering Sea, Gulf of Alaska, and Aleutian Islands. These food web models are updated frequently and are used regularly in fishery management advice in annual Stock Assessment and Fishery Evaluation (SAFE) reports.

Food web models provide a convenient means to evaluate ecosystem structure and function by utilizing existing ecological knowledge to quantify the strength of linkages and interactions between predator and prey groups, including the role of humans in the food web via fisheries and marine mammal harvests. Knowledge of trophic interactions and ecosystem function is an important part of predicting and interpreting an ecosystem's response to expected changes related to climate change, extractive activities such as fishing, or other large mortality events such as an oil spill.

The Chukchi Sea is a seasonally ice-covered, peripheral sea of the western Arctic Ocean. It lies north of the Bering Strait off the northwestern coast of Alaska (Fig. 1). The Chukchi Sea is a broad and shallow continental shelf sea, with most depths less than 60 m and a total area of about 565,000 square kilometers. Ice covers the Chukchi Sea for about 6 to 8 months a year, with ice cover advancing southward beginning in October and retreating northward starting in June. From a management perspective, the Chukchi Sea falls within the territorial waters of the United States and Russia and is divided approximately in half by the U.S.-Russia maritime boundary.

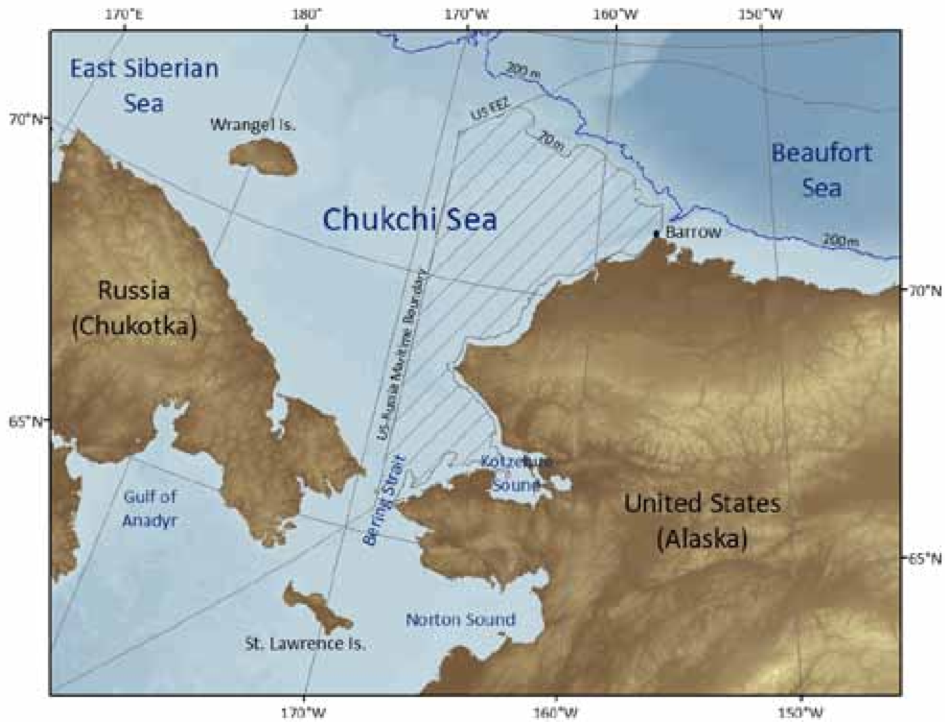

Figure 1. The Chukchi Sea, with the model area filled in with hatched lines. The model area is bounded by the U.S-Russia convention line in the west, Pt. Barrow to the east, Bering Strait to the south, and a combination of the 70-m isobath and the U.S. Exclusive Economic Zone (200-mile limit) in the north. Near shore, the model is bounded by the 20-m isobath. The blue contour is the 200-m isobath.

The eastern Chukchi Sea presents a unique opportunity to study the trophic ecology of a large marine ecosystem prior to the development of large-scale commercial fisheries or widespread energy extraction. The purpose of our study was to synthesize available data from published and unpublished sources in the construction of a food web model and to use this model to quantitatively compare the eastern Chukchi Sea to other northern marine ecosystems. The assembly of a preliminary food web model of the eastern Chukchi Sea provides important groundwork for improving our understanding of trophic relationships, produces a baseline for many ecosystem indicators, and provides a means of assessing the ecosystem-wide impacts of the removal of fish species by potential fisheries and possible environmental disturbances related to energy extraction and shipping.

A comparative approach to ecosystem analysis with a common modeling framework has been used previously to highlight similarities and differences in the structure and function of high latitude marine ecosystems. The comparative approach improves our understanding of ecosystem structure and function by revealing a number of contrasts that would otherwise not be apparent when studying a single ecosystem. The use of a common modeling framework improves these comparisons by removing the confounding effects of interpreting different metrics from different models and grants us the ability to make generalizations about ecosystem-scale processes.

In this article we summarize some of the early findings of our mass balance food web model, which describes the key attributes of the eastern Chukchi Sea food web. Specifically, we examined the distribution of biomass throughout the food web and sought to identify important prey groups linking production of lower trophic levels to mammals and seabirds. We also evaluated mass flows, which describe the exchange of mass between groups in a food web, mediated by feeding interactions, to describe the relative significance of benthic and pelagic trophic pathways. Using the same food web modeling framework, we then focused on a set of network metrics to draw comparisons with nearby subarctic ecosystems—the eastern Bering Sea and Gulf of Alaska, and a more distant Arctic ecosystem, the Barents Sea.

Methods

Study System

We developed a food web model for the eastern Chukchi Sea continental shelf between the 20- and 70-m isobaths covering approximately 192,000 km^2 (Fig. 1). Waters outside this depth range are beyond the range of existing trawl survey data and may incorporate nearshore or deep-water processes and taxa that are not modeled here. The base time period for the model is the late 1980s and early 1990s, as many of the data needed to parameterize the model were obtained during this time period. Data from other years were included as needed to improve parameter estimates. Temporal and spatial patterns (e.g., migration, primary production) were not explicitly modeled, though where data were available they were taken into consideration when developing model parameters. This is a static mass balance model that presents an annual average snapshot of the food web. The mass-balance assumption is a way of ensuring that the food web model does not represent a configuration where mass loss or mass gains are unaccounted for, such as predator groups with excessively high biomass consuming prey at rates much higher than prey can withstand. The mass-balanced model represents just one of many possible balanced states, but the mass-balance assumption assures that the balanced model obeys this basic conservation of mass principle.

Modeling Framework

The eastern Chukchi Sea food web was modeled using Ecopath with Ecosim (EwE) software (www.ecopath.org). Ecopath is a biomass compartment model describing the structure and material flows of a food web. Each compartment represents a model group and is comprised of a single species or suite of species that have similar habitat requirements, diets, and life histories (Fig. 2). Mass balance is achieved by solving a set of linear equations which quantify the exchange of biomass between the compartments in the food web. For each model group the basic model parameters are an estimate of biomass density (t km^{-2}) in wet weight, the diet composition of predators, fishery removals or subsistence harvests (t km^{-2}), production rate (yr^{-1}), consumption rate (yr^{-1}), and ecotrophic efficiency. Ecotrophic efficiency is the proportion of a model group's total production that is consumed by predation or removed by fisheries explicitly represented in the model and must have a value less than 1.

Ecopath mass balance is ensured by solving for one unknown parameter for each linear equation. Typically estimates of biomass, production, consumption, diet composition, and any fisheries removals are entered into the model and the equation is solved for ecotrophic efficiency. When reliable input estimates are not available, ecotrophic efficiency can be set equal to an arbitrary value and the equation solved for the missing parameter (usually biomass). Setting ecotrophic efficiency and solving for biomass is referred to as a "top-down balance" because it is estimating prey biomass based on estimated predator demand and fishery removals. Ecotrophic efficiency is difficult to accurately measure in nature, but is generally thought to be close

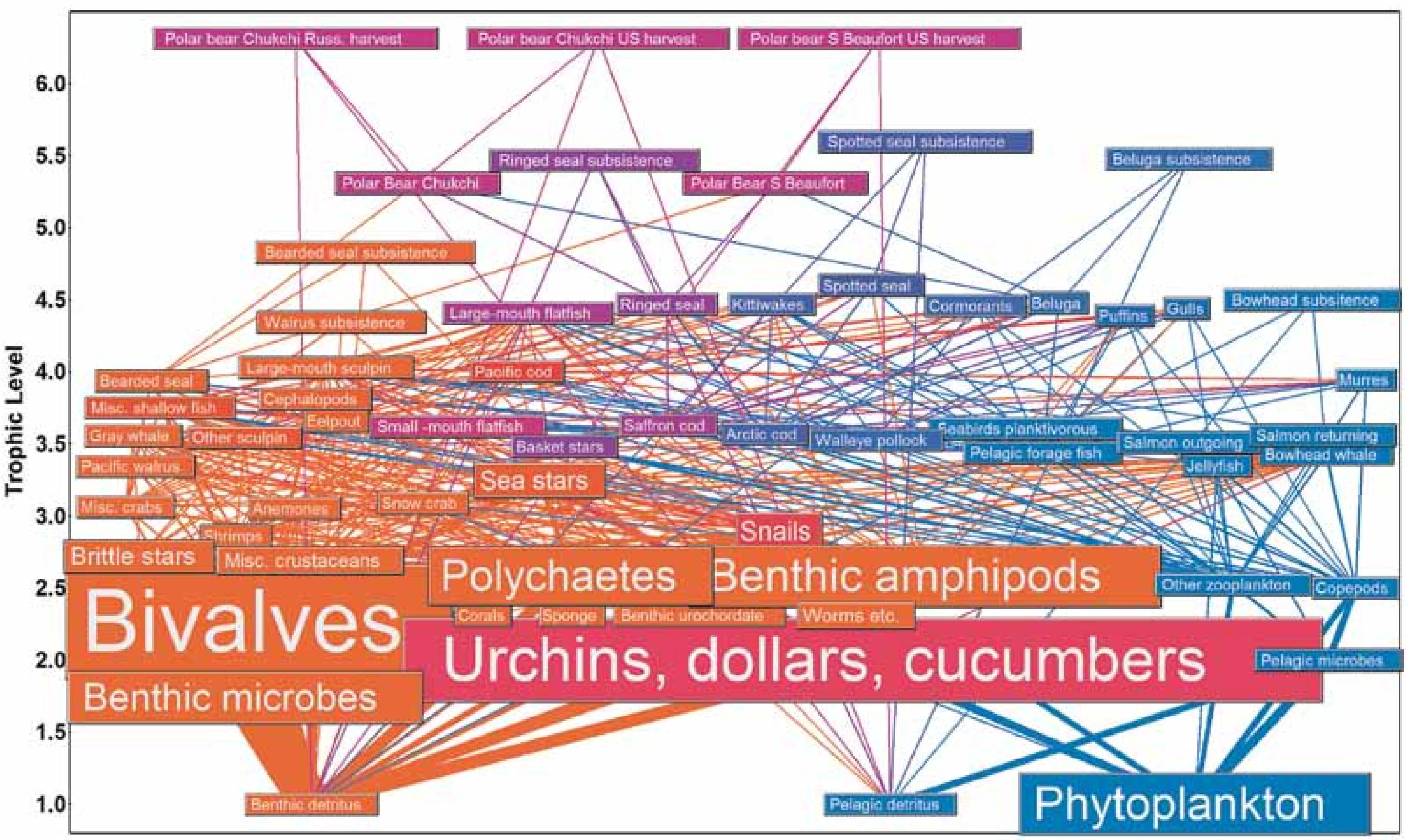

Figure 2. Visualization of the eastern Chukchi Sea food web. Each box represents a functional group, and the boxes are arranged vertically by their approximate trophic level. The size of the box is roughly proportional to the biomass of the group, and the width of the lines represents the magnitude of flows between the groups. Groups highlighted in blue have a pelagic orientation, while groups highlighted in red have a benthic orientation, with varying shades in between.

to 1 for groups subject to predation and exploitation and closer to 0 for top predators who experience little predation or exploitation.

The development of a mass-balance food web model and the necessary parameters for each functional group requires the synthesis of a large body of literature. Our model includes 54 functional groups consisting of 52 living groups and 2 detrital compartments. Additionally, 9 fishing and subsistence harvest groups were identified and parameterized separately. Many model parameters can be taken directly from the literature, while others require adjustment in order to accommodate the spatial and temporal restrictions of the model. Still other parameters may need to be calculated following empirical relationships. Our preferred method in this study was to obtain parameter estimates directly or calculate them from literature sources and unpublished reports. When parameter estimates were unavailable in the literature, they were obtained from other food web models or were computed following published empirical relationships. The full model and a detailed description of all model parameters can be found in Whitehouse (2011).

The relative strength of benthic and pelagic pathways was evaluated by examining the amount of total system throughput that is attributed to benthic- or pelagic-oriented functional groups. Total system throughput (TST) is a sum of total mass flows within the food web (t km^{-2} yr^{-1}) for consumption, respiration, flow to detritus, and export. Total consumption is the total food intake by a predator. Respiration flow is calculated as the fraction of assimilated food that does not lead to production. The flow to detritus from each group is a combination of the unassimilated portion of food that is egested and the portion of the group that is lost to other sources of mortality outside of the predation and fisheries mortality explicitly included in the model.

Fish occupy a central position in the food web connecting production on lower trophic levels to upper level piscivores and are potentially susceptible to future fishery exploitation. We examined the consumption of fish by mammals and seabirds in an effort to identify key fish prey species/functional groups. The total consumption of each fish group was summed across all piscivorous mammals and seabirds, yielding the total consumption of each prey by this collection of predators.

Table 1. Aggregate functional groups used in the comparative analyses of the four modeled food webs.

Aggregated functional groups
Phytoplankton
Microbes
Zooplankton
Jellyfish
Shrimp
Benthos
Snow crab
Arctic cod or walleye pollock*
Pelagic forage fish
Demersal fish
Seabirds
Baleen whales
Toothed whales
Polar bears and seals
Detritus

*The eastern Chukchi Sea and Barents Sea have an Arctic cod group and no walleye pollock group, while the eastern Bering Sea and Gulf of Alaska both have a walleye pollock group and no Arctic cod group.

Model comparisons

We compared our mass balance trophic model of the eastern Chukchi Sea to existing models of the nearby subarctic eastern Bering Sea, Gulf of Alaska, and to another polar system, the Barents Sea, to highlight similarities and identify differences in ecosystem structure and function. The basic model properties of these additional models are briefly reviewed. Each of the models presents an annual snapshot of its respective system during a similar base time period. For the eastern Bering Sea and Gulf of Alaska models, the base time period is 1990-94 and for the Barents Sea it is 1995. Initially, all the models had different numbers of functional groups, ranging from 149 in the eastern Bering Sea to 47 in the Barents Sea. Because differences in the level of trophic aggregation can make comparisons difficult to interpret and may confound some system indices, we aggregated all models to a common set of 15 functional groups (Table 1).

We computed system level metrics that describe total ecosystem production and biomass, enabling cross-ecosystem comparisons between the eastern Chukchi Sea and the selected ecosystems. Total ecosystem production is the sum of production (t km^{-2} yr^{-1}) from all functional groups, and total biomass density was calculated as the sum of biomass density estimates (t km^{-2}) of all functional groups (excluding detritus). Additionally, we calculated the ratio of total system production to total biomass density (P/B).

Results and Discussion

Model balancing

The primary diagnostic tool used to balance the eastern Chukchi Sea model was to identify groups with ecotrophic efficiency values greater than 1, which implies that the loss rates of these groups exceeded production rates. Eight of the 13 fish functional groups had ecotrophic efficiencies greater than 1 with the initial input parameter estimates. The initial estimates of biomass density for fish groups were calculated from the catch data of a single bottom trawl survey conducted in the northeastern Chukchi Sea during the summer of 1990. After re-examining the model parameters for all the fish groups, we concluded that the primary cause of this misbalance was underestimation of fish biomass in the trawl survey data. We therefore used a top-down balance approach, assuming an ecotrophic efficiency of 0.8 and estimated biomass for these groups. An ecotrophic efficiency of 0.8 implies the model explains 80% of the mortality of these groups via consumption by predators or fishery removals. As there are no large-scale fisheries targeting these fish groups we assume the model captures most of their mortality through consumption by predators. Other sources of mortality not explicitly represented in the model include disease, starvation, senescence, and possible outmigration. This non-predation mortality is not generally measurable; a uniform percentage of 20% for this other "unexplained" mortality allows a standardized analysis and is generally consistent with dynamic fits of unexplained mortality across a range of species. The top-down balance produced estimates of biomass density that were markedly larger than the survey-derived estimates (Fig. 3). The top-down balance results suggest that, based on the consumptive demands of predators, there are more fish present in this system than the survey-derived estimates indicate. The underestimation of the survey estimates may reflect low catchability of some groups to bottom-trawl gear, spatial limitations of survey coverage, patchy fish distribution, and high interannual variation in fish abundance. For example, Arctic cod were likely undersampled by the bottom trawl gear as they may be found in pelagic habitats in ice-free waters and also in association with sea ice in ice covered areas.

Fish have not been abundant in previous demersal trawl surveys of the eastern Chukchi Sea, but when present have been dominated by gadids. In particular, Arctic cod has been consistently identified as the most abundant fish species in the eastern Chukchi Sea, and it is identified as a species of potential commercial importance in the Arctic Fishery Management Plan. Arctic cod primarily prey on zooplankton and represent an important trophic pathway for pelagic predators. They were the primary fish prey of marine mammals and seabirds in the present food web model, accounting for nearly 46% of all consumed fish (Fig. 4). As modeled here, seabirds and marine mammals consume about 75% of total Arctic cod production. Ecological studies of the Beaufort Sea and Canadian High Arctic have indicated Arctic cod are similarly abundant and are of central importance in the transfer of energy from lower trophic levels to top predators including seabirds and marine mammals.

Model outputs

In the eastern Chukchi Sea food web, the total biomass flows (TST) amongst consumer groups (trophic level > 2) were dominated by benthic invertebrates. The dominant mass flows were concentrated near the bottom of the food web and were primarily the result of productive phytoplankton and microbial groups combined with a sizeable detrital pool. Because these mass flows dominate and obscure those occurring at higher trophic levels, we separately assessed the magnitude of trophic flows among consumer groups (trophic level > 2). When phytoplankton, microbes, and detritus are excluded, pelagic groups such as copepods and other zooplankton represent about 3.6% of the total system throughput, while benthic invertebrate groups account for approximately 94.5% (Fig. 5), emphasizing the dominance of the benthic trophic pathway. This is consistent with the distribution of biomass in this ecosystem as well. Benthic invertebrates collectively account for 81% of the total system biomass, while copepods, other zooplankton, and jellyfish together represent 1.1% of total biomass. Fish biomass and throughput was much less than that of benthic invertebrates. All fish groups combined accounted for 0.2% of total system throughput and only 1.1% of total system biomass.

Model comparisons

The system-level metrics revealed differences between the eastern Chukchi Sea and the other selected ecosystems. The eastern Chukchi Sea and eastern Bering Sea were nearly equal in terms of biomass density, while the Barents Sea had only a third of the biomass density of the eastern Chukchi Sea (Table 2). A similar relationship was observed in total production, with the eastern Chukchi Sea again having only half that of the eastern Bering Sea, but the eastern Chukchi Sea having more than 1.5 times the production observed in the Barents Sea. The subarctic Gulf of Alaska had the second highest total production. The production in all four study systems was dominated by production of phytoplankton and microbes, which together accounted for more than 75% of the total production in all systems.

Table 2. Summary of network metrics calculated by EwE along with the ratio of total production to total biomass (ECS=eastern Chukchi Sea, EBS=eastern Bering Sea, GOA=Gulf of Alaska, BAR=Barents Sea). See text for system metric definitions.

System metric	ECS	EBS	GOA	BAR
Sum of all production (t km^{-2} yr^{-1})	3,578.06	7,935.91	5,573.88	1,921.29
Total biomass (excluding detritus) (t km^{-2})	355.43	363.24	214.11	118.95
Total production/total biomass (P/B)	10.07	21.85	26.03	16.15

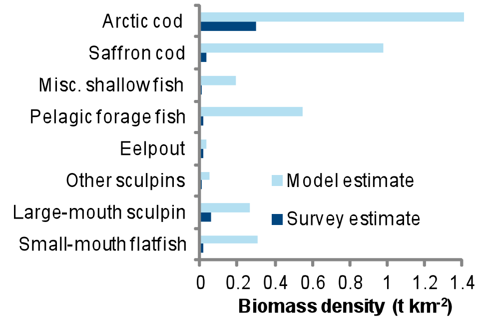

Figure 3. Biomass density estimates (t km^{-2}) of fish from the eastern Chukchi Sea. The survey estimates are derived from a 1990 bottom-trawl survey of the northeastern Chukchi Sea and the top-down estimates are from our Ecopath model, assuming an ecotrophic efficiency of 0.8. The large-mouth flatfish, walleye pollock, Pacific cod, salmon returning, and salmon outgoing groups are not included in this figure as the Ecopath model was not used to estimate their biomass density.

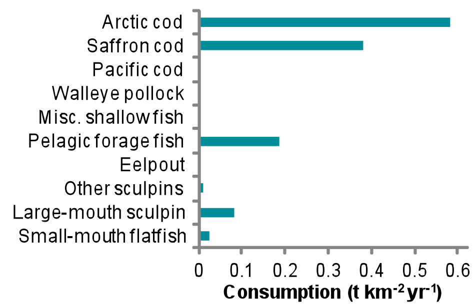

Figure 4. The estimated consumption (t km^{-2} yr^{-1}) of fish functional groups by seabirds and piscivorous mammals in the eastern Chukchi Sea.

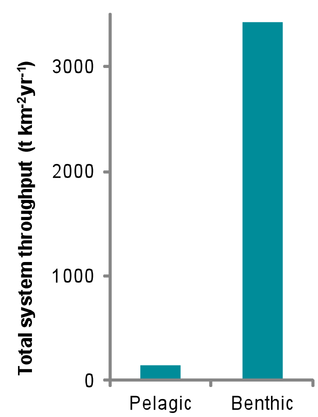

Figure 5. The distribution of total system throughput (t km^{-2} yr^{-1}) between pelagic and benthic oriented consumer groups in the eastern Chukchi Sea. Phytoplankton, microbes, and detritus are excluded from this figure. Total system throughput is a measure of mass flow between groups in a food web.

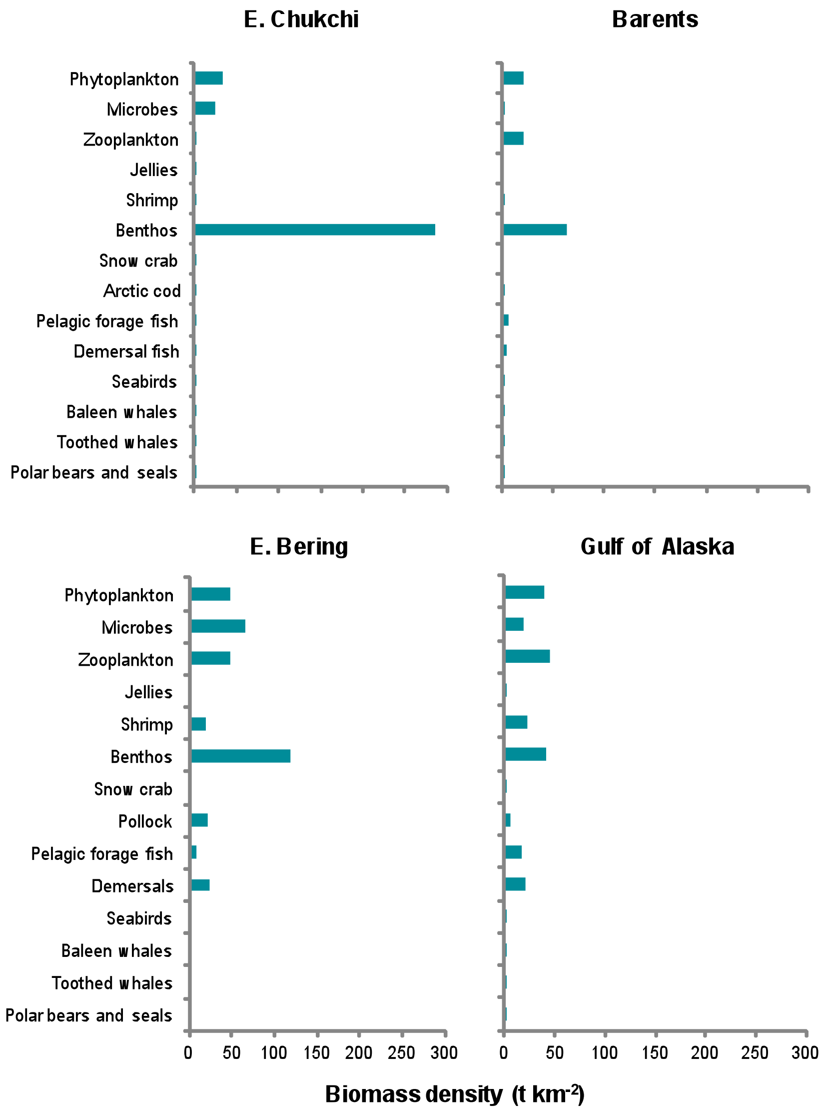

Figure 6. The biomass density of all living functional groups in the four modeled ecosystems.

Future food web modeling studies could also help address questions about the fragility and resilience of the eastern Chukchi Sea food web and its sensitivity to human activities.

Using the common set of aggregated functional groups, we examined structural differences among ecosystems in terms of the distribution of biomass density. In both polar systems the benthos comprised the majority of total system biomass (Fig. 6). This was especially pronounced in the eastern Chukchi Sea, where the benthos comprised 81% of the total biomass. The benthos accounted for 54% of the Barents Sea total biomass and only 33% and 19% in the eastern Bering Sea and Gulf of Alaska, respectively. Fish account for the smallest proportion of biomass in the two polar systems, representing only 1.1% of total biomass in the eastern Chukchi Sea and 9% in the Barents Sea, while in the subarctic systems fish comprised 15% of total biomass in the eastern Bering Sea and 20% in the Gulf of Alaska.

These comparisons bring attention to the dominant role of the benthos in food web structure and energy processing in the eastern Chukchi Sea. This is a structural and functional distinction between the Arctic and subarctic systems modeled here. Both subarctic systems have a much more even distribution of biomass between benthos, zooplankton, and fish. In the two Arctic systems, the high benthic component is in part attributed to tight pelagic-benthic coupling, where low grazing rates on phytoplankton by zooplankton, combined with shallow shelves, permit much of the primary production to eventually settle to the seafloor where it becomes available to support the benthos. Numerous ecological studies conducted over the last 50 years in the eastern Chukchi Sea have documented a diverse and abundant community of benthic invertebrates. The abundant benthos is an important prey resource for benthic-foraging marine mammals, such as bearded seals, Pacific walrus, gray whales, and for seabirds.

Comparison of the network metrics highlights distinctions that lead to the eastern Chukchi Sea having the lowest total production/biomass (P/B) ratio of the systems examined (Table 2). Both Arctic systems had lower P/B ratios than the subarctic systems. This is largely due to much higher levels of primary production in the subarctic systems, but is also augmented by higher production from zooplankton, fish, and shrimp groups. Total production in the eastern Chukchi Sea is diminished by the less productive benthos. In contrast to the eastern Chukchi Sea, the P/B of the nearby eastern Bering Sea was about double that of the eastern Chukchi Sea. In practical terms, this characteristic implies that the eastern Chukchi Sea is fundamentally different from the adjacent eastern Bering Sea – they have roughly comparable total biomass density but the total production of the Chukchi Sea is 45% that of the eastern Bering Sea. Thus, the standing biomass in the Chukchi Sea is not expected to be highly resilient to commercial fishing or other high-mortality events such as that which might be expected following a large-scale oil spill. Further research into the production of species/functional groups and their response to extraction or disturbance could be useful for evaluating the impact of future fisheries on the food web and predicting response to potential environmental disturbances related to energy extraction.

Future work

Our mass balance food web model of the eastern Chukchi Sea provides a general description of food web structure and function. Future updates to model parameters would not only improve its accuracy but would also affect the system metrics as well. Recently, the AFSC partnered with other federal and state agencies to conduct an integrated ecosystem assessment of the northern Bering and Chukchi Seas. As this assessment progresses and new data on the abundance, distribution, diet, and life histories of marine organisms becomes available, we intend to produce an updated version of our model, detailing the current state of the eastern Chukchi Sea food web. Future food web modeling studies could also help address questions about the fragility and resilience of the eastern Chukchi Sea food web and its sensitivity to human activities. Future food web studies employing dynamic simulations, can examine potential stressors, such as fishing and energy extraction, individually to explore the possible range of food web responses, and they can be modeled simultaneously to identify any interactive effects of multiple stressors occurring simultaneously. The present model represents just one of many possible mass balanced states and could be improved with updated parameters and more precise data specific to the study area. A number of assumptions and parameter adjustments were required to achieve mass balance, but despite these limitations this model provides an instructive broad-scale view of the structure and function of the eastern Chukchi Sea ecosystem.

Looking southward from high over the Arctic Ocean, NASA's Aqua satellite reveals coastal phytoplankton blooms in the Chukchi Sea along northern Alaska (foreground) stretching into the Bering Strait in September 2006. Credit: NASA

Additional Reading

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