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A comparison of the Eastern and Western Bering Seas as seen through predation-based food web modeling

by

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Abstract

We present a comparison of two quantitative food web models of the eastern and western Bering Sea Shelf/Slope areas. Food webs were created from independent estimates of production, consumption, biomass and diet from each region for multiple predator and prey species. The results highlight the differences in the trophic structure of the two food webs from the top predators' point of view, and also provide substantial insights into the relative strengths of different methods for measuring predator-prey linkages.

The pelagic community of the western Bering Sea showed a higher production in the lower trophic levels. The benthic community of the western Bering Sea shelf is dominated by epibenthos, with little or no transfer of energy into higher trophic levels. In the eastern Bering Sea, a complex flatfish community may compete with the epibenthos and provide an important pathway for energy flow into high trophic-level fish. Direct estimation of food consumption rates from the stomach contents of larger fish (cod and pollock), tended to estimate consumption rates which were not sustainable within the system: bionergetics models provided estimates that were more consistent with system productionlevels.

Introduction

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. Unfortunately, there have never been any joint integrative studies looking at the ecosystem production of the Bering Sea as a whole.

As an initial step in this process, two mass-balance ecosystem models were constructed of portions of the eastern and western Bering Sea shelf and slope areas. The eastern Bering Sea shelf model (EBS) covered an area of 485,000 km^2 between Alaska and the continental slope, south of 61°N latitude. The western Bering Sea shelf model (WBS) covered 254,000 km^2 of shelf area off the coast of Russia, including all shelf area south of Cape Navarin and the Anadyr and Chirikov Basins to the north. The models were constructed by researchers at the two institutions, with significant communication between researchers to compare methods of model construction and data estimation.

The models were “predation-based” in that the most detailed data were gathered on the biomass, and yearly production rates, consumption rates, and diet composition of the upper trophic levels, especially fish. The model was balanced to determine the amount of primary production and detritus required to “fuel” the standing stock of predators within the modeled regions.

The analyses of the models were conducted with two goals in mind: (1) the comparison of the ecosystem models and the implied differences in the structure and function of the eastern and western Bering Sea shelf ecosystems, and (2) the assessment of differing techniques of estimating predator/prey relationships in the context of the food web as a whole.

Methods

Two mass-balance food-web models of the eastern and western continental shelf/slope ecoregions of the Bering Sea were made using the Ecopath food web modeling software (Christensen and Pauly 1993). Ecopath has become a popular method for constructing food web models: identical model formulations were used to aid in cross-ecosystem comparisons.

Estimation of biomass, production/biomass (P/B), consumption/biomass (Q/B) and diet composition of over 50 fish, marine mammal, bird and plankton species were collected from an extensive review of North American and Asian literature and data sources. Much of the fish biomass data came from yearly stock assessments conducted by AFSC and TINRO. The data used for the model was averaged over the time period 1980-85. Production and consumption estimates for predators were derived from a combination of feeding studies and bioenergetics models.

Initial species groups were derived from an earlier Ecopath model of the eastern Bering Sea (Trites et al. 1998). These groups were refined into 38 species groupings that were used in both systems (Table 1). Some of the groups represented aggregations of many individual species.

Because information on primary production rates and detrital recycling were the most variable, the model was balanced using a “top-down” approach: primary production and detrital recycling were set to match the total demand of the predators. In intermediate trophic levels, in cases where the demand for a particular consumer was higher than its production, adjustments of appropriate production, consumption, or biomass estimates were documented and placed in the model. The final models were compared in terms of individual parameters and overall trophic structure.

Results

On a per-unit-area basis, the estimate of total biomass in the WBS was 1.5 times higher than in the EBS (Table 2). Moreover, the higher biomass in the WBS seemed to require primary production and detritus consumption rates out of proportion to its higher biomass, requiring 1.8 times more primary production, 2.6 times more pelagic detritus recycling and 3.5 times more benthic detritus recycling than the EBS.

Higher biomasses were estimated for the WBS pelagic community, including pelagic zooplankton (large and small), small pelagic fish, and cephalopods. The greatest biomass difference between the two models occurred in the infaunal and epifaunal species (Table 1a,b). Estimates of epifaunal biomass were over 19 times higher in the WBS than in the EBS.

Conversely, the estimates of biomass of groundfish are higher in the EBS (Table Id,e). The largest differences were in small flatfish species (10 times higher in the EBS than in the WBS). Biomass estimates of walleye pollock, Greenland turbot, and arrowtooth flounder were also higher in the EBS.

Epifauna and small flatfish are two of the largest consumers of infaunal biomass in both systems and, through infauna, the two major consumers of benthic detritus. In the WBS, much of the biomass of benthic detritus is consumed and respired by epifauna, while in the EBS a greater proportion is eaten by flatfish and enters the higher trophic levels of fish. Epifauna represented a major sink of biomass at trophic level 3 in the WBS (Figure 1).

The number of energy pathways between primary production and upper trophic levels was generally 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 (Table 3). This difference is due to the multiple energy cycles parameterized in the diet matrix of the EBS food web. These cycles appear as the result of including detailed cross-connections between fish, which arise as adults of many species eat each others’ juveniles.

On trophic levels 5-6, cephalopods were an important nexus of energy flow in the WBS model: the flow through these trophic levels in the EBS is distributed through a greater variety of fish, although the high biomass of pollock tends to dominate these trophic levels in the EBS.

The primary production required to support the standing stock of each species (Table 3) shows that estimates of consumption rates in the WBS were higher than in the EBS for some dominant species such as pollock and cod, despite the fact that pollock biomass was higher in the EBS. Much of the difference is the result of higher consumption/biomass estimates of fish in the WBS.

Discussion

Because production levels were set by demand, it is not clear if the overall high production of the WBS is due to higher calculated demand or actual high production: however, the biomass estimates of zooplankton species indicate that standing stocks in the WBS are higher for pelagic species. It is possible that this higher biomass arises because a greater proportion of the WBS model area occupies the “Green Belt” area of high production on the continental slope (Springer et al. 1996).

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 4) 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 0.53 million mt: their role in both ecosystems is an important area for future research.

The high consumption rates seen in pollock and cod in the WBS may be an artifact of the estimation method. Estimates of consumption/biomass in the WBS model were made using direct estimates of feeding rates from stomach contents, while the EBS model used bioenergetics models. Initial consumption rates in the WBS were considerably higher than those used in the final model, and had to be adjusted downward to fit the supply of lower trophic-level consumers. It is possible that the direct diet estimation methods may overestimate food consumption in predators if they are extrapolated over the entire age-structure of a population: bionenergetics model estimates were more consistent with the food supply of the system as a whoie.

Finally, the greater complexity of interactions between fish in the EBS, seen by the length of energy pathways, may be due to the larger shelf area's ability support a greater range of habitat and community structures: however, it may also be due to data processing methodology. EBS diet data includes a considerable range of life-history stages for many of the fish and includes predation on juveniles. The importance of juvenile predation on competition between species may be assessed in the future through detailed, age- or habitat-structured fisheries models.

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Table 1. Species groupings of consumers used in Ecopath models of the western and eastern Bering seas, and biomass estimates for each group (t/km*). Production groups were phytoplankton, pelagic detritus, and benthic detritus (not shown).

(A) Pelagic consumers

	EBSh	*WBSh*
Cephalopods	*3.50*	*4.83*
0. pelagic fish	*13.46*	19.08
Jellyfish	0.05	*1.40*
Pacific herring	*0.78*	*0.79*
Salmon	0.05	*0.04*
LARGE ZOOP	*44.00*	*120.74*
Copepods	*55.00*	*122.62*
Total	*116.84*	*269.49*

(B) Lower trophic level benthos

	EBSh	*WBSh*
Epifauna	5.9	*115.0*
Infauna	*46.5*	*125.7*
Benthic Amph.	3.6	13.8
Total	56.0	254.5

(C) Benthic particulate feeters

	EBSh	*WBSh*
C. bairdi	0.60	0.08
C. opilio	1.60	0.25
King crab	0.60	0.12
Shrimp	3.00	2.10
Total	5.80	2.55

(D) Misc. groundfish

	EBSh	*WBSh*
Small Flaffish	9.18	0.99
Skates	0.29	*0.27*
Sculpins	*0.56*	(*)0.68
Sablefish	0.11	
Rockfish	0.09	
Macrouridae	*0.20*	*1.16*
Zoarcidae	*0.64*	*0.90*
Total	11.07	*3.32*

(*) rockfish are included with sculpins in the WBSh

- no biomass assessed (minimal)

(E) Larger commercial groundfish

	EBSh	*WBSh*
Adult pollock2+	27.45	15.00
Juv. pollock0-1	6.00	3.76
Pacific cod	2.42	3.19
Pacific halibut	0.14	0.08
Greenland turb.	0.96	0.06
Arrowtooth fl.	0.80	0.05
Total	37.77	22.14

(F) Birds and marine mammals

	EBSh	*WBSh*
Baleen whales	0.25	0.39
Toothed whales	0.02	0.04
Sperm Whales	0.21	0.02
Walrus & Bearded seals	0.16	0.26
Seals	0.06	0.10
Stellars	0.01	0.04
Pisc. birds	0.01	0.01
Total	0.70	0.86

Table 2. Total biomass, primary production, and detrital flow estimates for both models.

	EBSh	WBSh	Units
TOTAL BIOMASS	275	410	t/km²
Total system throughput	7,671	18,060	t/km²/year
Sum of all respiratory flows	1,645	3,486	t/km²/year
Sum of all flows into detritus	1,452	3,466	t/km²/year
Calculated total net primary production	2,000	3,510	t/km²/year
Sum of all production	3,822	5,659	t/km²/year
Phytoplankton consumed	1,468	2,590	t/km²/year
Pelagic Detriius consumed	474	1,225	t/km²/year
Benthic Detritus consumed	624	2,214	t/km²/year

Table 3. Primary production required to support the standing stock of each biomass (PPR), trophic level, and number of distinct pathways leading from primary production or detritus to each indicated species. Species are listed in descending order by PPR.

EASTERN BERING SEA

Group Name	Paths	TL	PPR
LARGE ZOOP	4	2.6	1673
Copepods	2	2.2	1210
Adult pollock2+	44	3.6	876
Cephalopods	13	4.1	724
0. pelagic fish	9	3.5	576
INFAUNA	1	3.0	523
Pacific cod	748	4.6	512
Toothed whales	19376	4.8	440
SMALL FLATFISH	213	4.0	388
Juv. pollock0-1	6	3.3	339
Seals	6426	4.5	172
Shrimp	8	3.4	164
Sperm Whales	3764	5.1	158
Sculpins	334	4.8	146
Walrus & Beard.seals	6373	4.4	145
EPIFAUNA	12	3.4	144
Arrowtooth fl.	732	4.3	125
Greenland turb.	143	4.4	118
Skates	1470	4.6	99
C. opilio	14	4.0	93
Benthic Amph.	2	2.8	80
Baleen whales	151	4.0	70
Pacific halibut	1471	4.6	49
Marine birds	369	4.4	45
C. bairdi	14	4.0	35
King crab	14	4.0	35
Sablefish	137	4.5	34
Pacific herring	9	3.5	33
Macrouridae	48	4.6	27
Zoarcidae	51	4.1	25
Rockfish	895	4.1	20
Steller SeaLions	3819	4.6	11
Salmon	47	3.9	8
Jellyfish	6338	3.7	4

WESTERN BERING SEA

Group Name	Paths	TL	PPR
Copepods	2	2.3	3053
LARGE ZOOP	4	3.0	3023
EPIFAUNA	3	3.2	1748
INFAUNA	1	3.0	1510
Pacific cod	790	4.6	1304
Adult pollock	53	3.8	1229
Toothed whales	8832	5.0	549
Cephalopods	14	4.1	522
0. pelagic fish	7	3.8	461
Juv. pollock0-1	21	3.7	343
Seals	976	4.9	255
Baleen whales	918	4.2	240
Sculpins & rockfish	341	4.5	226
Walrus & Beard.seals	911	4.1	212
SMALL FLATFISH	177	4.1	194
Benth. Amph	1	3.0	193
Skates	916	4.8	182
Shrimps	5	3.3	136
Macrouridae	143	4.6	135
Steller sea lion	3118	5.0	122
Pacific herring	22	3.8	116
Zoarcidae	108	4.7	98
Halibut	1538	5.0	66
Marine birds	136	4.4	42
C.opilio	1 1	4.0	38
Greenland turbot	848	4.9	28
Arrowtooth flounder	97	4.7	25
Jellyfish	29	3.5	23
Sperm whales	1102	5.2	20
C.bairdi	11	4.0	13
King crab	11	4.0	10
Salmon	36	4.2	10

Table 4. Biomass (t/km^2), P/B (l/year), and Q/B (l/year) for components of small **flatfish** and epibenthic groups in the eastern and western Bering Sea shelf models.

	EBS			WBS		
Epifauna	**B**	**PB**	**QB**	**B**	**PB**	**QB**
Hermits & o.decapods	1.00	1.80	8.00	2.07	0.82	8.00
Snail	0.52	1.80	8.00	1.25	1.81	8.00
Brittlestar	3.00	1.50	**5.00**	14.49	1.21	5.00
Starfish	1.34	1.50	5.00	0.96	1.23	5.00
Urchins		•		36.34	1.15	5.00
Holoturia				6.1	0.61	5.00
Barnacles		•		26.24	0.26	5.00
Ascidia				10.57	3.58	8.00
Actinia		•		4.45	•	•
Spingia				2.27	•	•
Total	5.86	1.58	5.78	114.96	1.16	5.09

	EBS			WBS		
Small Flatfish	**B**	**PB**	**QB**	**B**	**PB**	**QB**
Flathead sole	0.45	0.40	2.56	0.20	0.37	4.70
Yellowfin sole	6.11	0.40	**2.96**	0.20	0.26	**9.80**
Rock sole	1.34	0.40	3.60	0.23	0.24	6.50
Alaska plaice	1.29	0.40	**2.49**	0.22	0.25	6.80
O.sm.flatfishes	0.00	0.00	0.00	0.14	0.35	6.50
Total	9.18	0.40	**2.97**	**0.99**	**0.29**	6.85

- • not assessed/unavailable

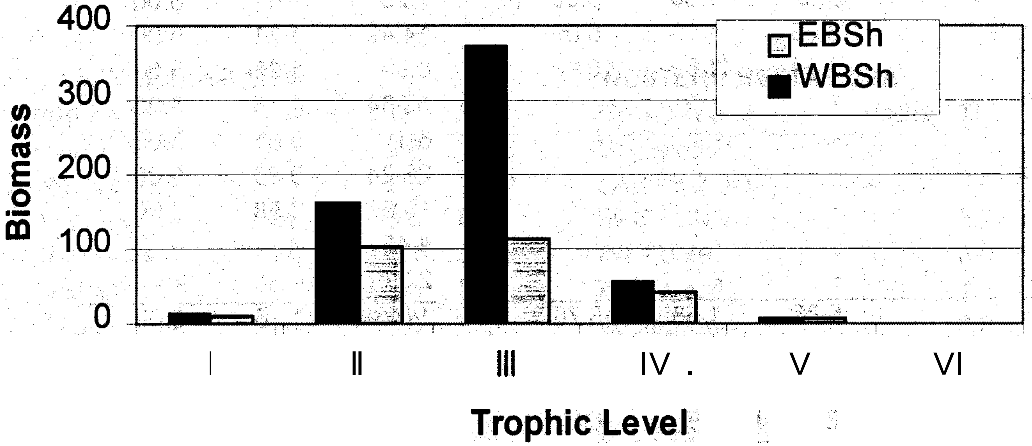

Figure 1. Biomass per unit area (t/km^2) by trophic level in the western and eastern Bering Sea shelf models.