



# A macrodescriptor perspective of ecological attributes for the Bering and Barents Seas

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## ARTICLE INFO

### Article history:

Accepted 11 November 2008

Available online 6 December 2008

### Keywords:

Ecosystem  
Macrodescriptors  
Metrics  
Barents Sea  
Bering Sea

## ABSTRACT

The eastern Bering Sea (EBS) and Barents Sea (BS) are both high-latitude, subarctic ecosystems that share many similar biophysical and trophic characteristics, and support valuable commercial fisheries. In this paper we compare system-level characteristics that make the Bering and Barents Sea ecosystems unique. We use Ecopath models and systems ecology macrodescriptor metrics applied to the two marine ecosystems to identify key areas of differences and similarities. Metrics calculated include number of species, number of interactions or trophic links, connectivity of the system, number of interactions per species, a measure of directed connectance, and an assessment of overall web interaction strength. In addition, number of basal species, number of top predators, total number of intermediate species, number of cannibals, number of cycles, number of omnivores, number of predators for a prey item, number of prey items for a predator, predator to prey ratio, and other indices were enumerated. Calculated food-web metrics for the eastern Bering and Barents Seas are compared between systems as well as with other similar metrics from published sources. We attempt to relate these observations to the questions of the uniqueness of marine food webs, implications for system stability, how climate impacts the physical environment, how the physical environment affects the structure of fish communities in each sea, and how changes in the physical environment affect the production of fish and the ability of the Bering and Barents Seas to support stable fisheries and productive ecosystems.

Results show that the average number of trophic steps from primary producers to predators is shorter in the EBS. In the EBS, trophic pathways are shorter and more linear, there are more benthic species (flatfish and crabs) and there are both pelagic and benthic food webs. The BS is mainly a pelagic ecosystem. More production flows to the detritus pool in the BS most likely due to its deeper average depth (EBS: 50 m, BS: 200 m deep). The EBS is more efficient at converting primary production into upper trophic level biomass since there are fewer trophic steps and primary production fuels both the pelagic and benthic food webs. Commercial fish species biomass is greater in the EBS (7.6 mt) compared with BS (3.8 mt). Many alternate pathways exist in the BS, thus there are no single critical species creating bottlenecks. Results suggest that the BS may be more stable than the EBS.

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## 1. Introduction

The eastern Bering Sea (EBS) and the Barents Sea (Fig. 1) share a number of common characteristics reviewed recently by Hunt and Megrey (2005) and Sakshaug and Walsh (2000). For example, both are high-latitude seas with broad shelf regions that are seasonally ice covered and contain ecosystems dominated by gadoid fishes. These two ecosystems also differ in many important aspects. In the Barents Sea, cod (*Gadus morhua*) is dominant and capelin (*Mallotus villosus*) is an important forage species, whereas in the eastern Bering Sea walleye pollock (*Theragra chalcogramma*)

and Pacific cod (*Gadus macrocephalus*) dominate and juvenile pollock, eulachon and capelin are important forage species. Comparisons between the two ecosystems have gone beyond simple physical and biological descriptions. Aydin et al. (2002) and Blanchard et al. (2002) used the Ecopath with Ecosim (EwE) software suite (Christensen et al., 2004) to describe and study the ecosystem characteristics of these two subarctic ecosystems.

Recent arguments for Ecosystem-Based Fisheries Management means moving from single-species population assessments to ecosystem or community-based assessments paying particular attention to community dynamics and species interactions. This will serve us well as we attempt to understand and quantify the impacts of climate variability on trophic transfer and ecosystem structure of the subarctic seas to improve the prediction of growth and recruitment of key fish species. This is a difficult task,

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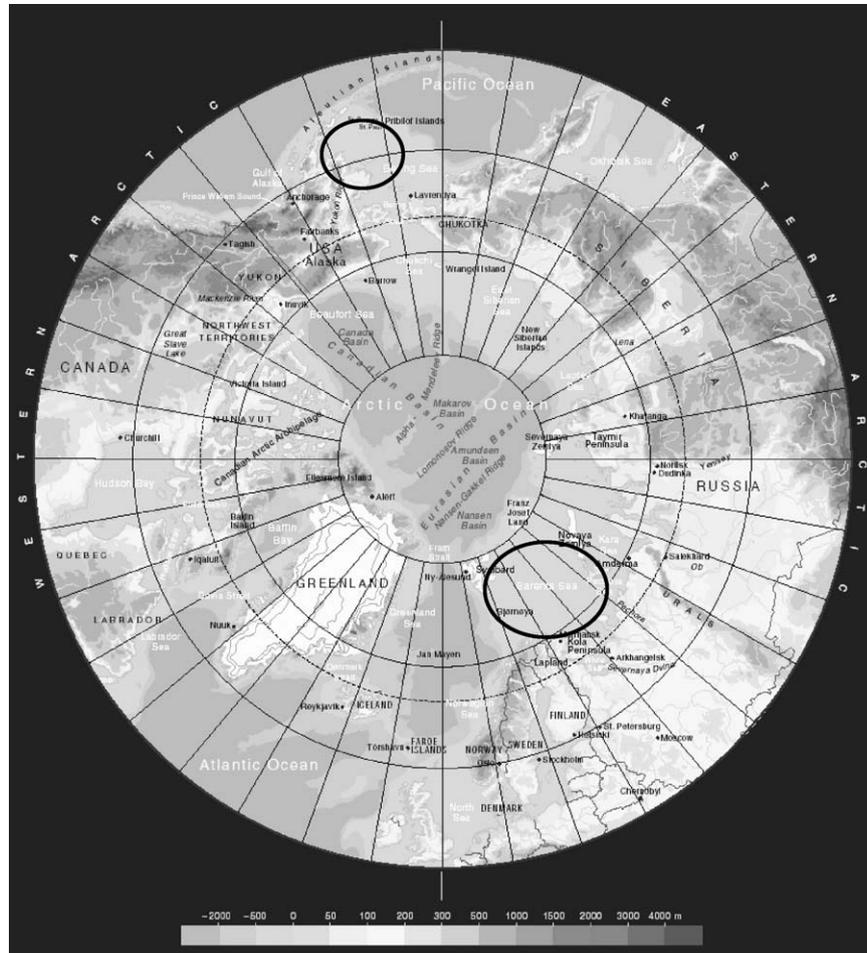


Fig. 1. Map indicating the geographical proximity of the Bering (top circle) and Barents Seas (bottom circle).

especially if only one ecosystem is being examined. A partial solution to this problem, and one recommended in GLOBEC's Ecosystems of the Subarctic Seas Science Plan (Hunt and Drinkwater, 2005), is to use modeling as the central approach for comparative analyses of ecosystems to examine if patterns of food-web structure and trophodynamics are similar in marine systems that occur in different regions.

The comparative approach is one method that has provided significant insights into ecosystem structure, function and variability (Hunt and Megrey, 2005; Moloney et al., 2005; Sakshaug and Walsh, 2000). Comparative analysis is a valuable scientific activity since the size and complexity of marine ecosystems precludes conducting controlled *in situ* experiments. Comparisons among and between ecosystems are powerful because they can take advantage of "natural experiments" that otherwise would not be feasible and can identify important similarities and differences between ecosystems. Comparisons allow a broad perspective and permit the ability to draw generalizations about fundamental aspects of marine ecosystems and unique aspects of specific ecosystems. Such generalizations are important for successful application of the ecosystem approach to fisheries, and help determine the response of marine ecosystems to both global warming and climate change.

Comparative analysis is often a fruitful approach to large-scale questions wherein data patterns are sought from different ecosystems and frequently assembled from unrelated studies (Dunne et al., 2004). Similar to many previous studies (Myers and Barrowman, 1996; Myers, 1998; Planque and Frédo, 1999;

Brander and Mohn, 2004; Stige et al., 2006), the approach of this study is focused on taking data from two ecosystems and performing a comparison in a unified analysis using a single modeling approach.

The objectives of this study are to use a common modeling approach, such as an Ecopath model, apply it to the eastern Bering and Barents Seas, two high-latitude ecosystems with important commercial fisheries, derive a set of system-level ecological macrodescriptor metrics to represent meaningful attributes of marine ecosystems, identify key areas of differences and similarities, and to compare our results to published results from other systems.

## 2. Material and methods

### 2.1. Data sets

The two main data sets for this study were taken from published Ecopath models. Aydin et al. (2002) provide an Ecopath model for the eastern Bering Sea continental shelf containing 41 species or functional groups (including two detritus groups) covering four trophic levels (1.0–4.76) based on data from 1980 to 1985. Blanchard et al. (2002) provided an Ecopath model for the Barents Sea (BS) containing 41 species or functional groups (dead carcasses and two detritus groups) and covering four trophic levels (1.0–4.85) based on data from 1995. Aydin et al. (2007) expanded the 41 functional groups of the published EBS model

into 136 functional groups (including two detritus groups) covering four trophic levels (1.0–4.76). For the purposes of calculating ecosystem metrics, the detritus functional groups were not included in calculating the number of species for either region. Thus the EBS and BS ecosystems we analyzed contain 39 and 38 species, respectively. For the eastern Bering Sea, we call the published model (39 functional groups) the “small” model and the expanded version (139 functional groups) the “big” model. Metrics calculated from the Ecopath model for the eastern Bering Sea ecosystem only used the small eastern Bering Sea model since the Ecopath with Ecosim software used in this analysis (Version 5.1) can only accommodate a finite number of functional groups.

Since capelin is an important component of the Barents Sea food web (Dolgov, 2002; Ciannelli and Bailey, 2005), an important diet item for cod, and a species whose abundance varies from year-to-year, the published BS Ecopath model was estimated using data from years of high and low-capelin abundance. However, capelin currently plays a relatively insignificant role in the food web dynamics of the EBS, making up only about 1% of the EBS cod diet (Mito, 1974, 1979; Livingston, 1991; Livingston and deReynier, 1996). To recognize the lack of importance of capelin in the EBS, the low-capelin BS model from 1995 was compared against the EBS model. Metrics from the EBS and BS were compared with other published metrics from the northwest Atlantic Shelf (NAS) (Link, 2002).

The Ecopath model (Christensen and Pauly, 1992; Pauly et al., 2000), which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represents the ecosystem as trophically linked biomass “pools”. The biomass pools consist of a single species, or species groups representing ecological guilds. Ecopath data requirements are relatively simple, and the data are generally available from stock assessments, ecological studies, the literature, biomass estimates, consumption estimates, diet compositions, and fishery catches.

### 2.1.1. Connectedness, interactions, and trophic links

The Ecopath diet matrix provides the fundamental food web information for the calculation of macrodescriptor metrics such as connectedness and interactions (often referred to as trophic links). The diet matrix tells us quantitatively who eats whom, what percentage of a predator species diet is made up of a prey species, and the number of species in the ecosystem. The undirected interaction matrix (consisting of zeros and ones) tells us qualitatively about community structure and trophodynamic interactions because it conveys which species is trophically connected to another species. Both are important pieces of ecosystem information.

For  $S$  number of species, the diet matrix has  $S \times S$  possible links. If predators and prey are assigned a column index ( $j = 1, \dots, S$ ) and a row index ( $i = 1, \dots, S$ ) of the diet matrix, respectively, then any cell entry  $A_{ij}$  shows there is a trophic connection between species  $i$  and species  $j$ , and by convention indicates that species  $j$  preys on species  $i$ , and  $A_{ij}$  is the percentage of prey  $i$  in the diet of predator  $j$  (Martinez, 1991). Note that  $0.0 \leq A_{ij} \leq 1.0$  and that  $\sum_{j=1}^S A_{ij} = 1.0$ .

Several biological interactions can be recognized from the diet matrix. Competition for prey species  $i$  is shown when more than one predator species shares a prey species. Predation cycles can be shown when, for example, species  $i$  preys on species  $j$  and vice versa. Cannibalism, an important process in the eastern Bering and Barents Sea, can be shown when  $A_{ij} \neq 0$ , for  $i = j$ .

The number of trophic interactions or links can be calculated in several ways (Martinez, 1991), after the diet matrix is transformed (undirected) into the interaction matrix by the following formula: if  $A_{ij} > 0.0$  in the diet matrix then  $I_{ij} = 1.0$  in the interaction matrix. The interaction matrix is used to compute the number of species

interactions.  $I_{ij}$  tells us that species  $i$  has a trophic connection with species  $j$ , where  $I_{ij} = 1.0$ . In an undirected interaction matrix, the direction of the interaction is not of any significance so  $I_{ij}$  and  $I_{ji}$  measure the same interaction. In a directed interaction matrix, the direction of the interaction is described by the value of  $I_{ij}$ :  $I_{ij} = 1.0$  if species  $i$  preys on species  $j$ ,  $I_{ij} = -1.0$  if species  $i$  is the prey for species  $j$ , and  $I_{ij} = 0.0$  if there is no interaction.

To calculate the necessary metrics we need to compare all links to the total number of potential links. Calculating total potential links is similar to the total number of links. Let  $S$  be the number of species represented in the interaction matrix. All potential links (including cannibalism) can be calculated with  $S^2$ . All links, regardless of direction, but not including cannibalism (i.e. the diagonal of the diet matrix) can be calculated with  $S(S-1)$ . We can count only  $\frac{1}{2}$  of all potential links, not including cannibalism, with  $[S(S-1)]/2$  if we assume  $I_{ij}$  and  $I_{ji}$  measure the same link. Finally we can count just  $\frac{1}{2}$  of all potential links, including cannibalism, with  $([S(S-1)]/2) + S$ .

The term links will be retained here and is synonymous with ecosystem interactions. The convention in this paper is to represent the total number of ecosystem links by including cannibalism, since it is prevalent in both the EBS and the BS, as well as to exclude redundant interactions. For example, as mentioned above, we assume that  $I_{ij}$  and  $I_{ji}$  measure the same trophic link.

In our tabulation of links and connectance, we calculate links as the bottom diagonal of the undirected interaction matrix, including the diagonal (i.e. cannibalism) relative to the total undirected potential links.

## 2.2. Macrodescriptor definitions

### 2.2.1. Ecological Macrodescriptors

Several of the definitions presented here are summarized after Martinez (1991). We review these briefly for the benefit of the reader.

“Species” refers to a group of organisms with generally or exactly similar sets of predators and prey. Species in the eastern Bering Sea and Barents Sea ecosystem food web description refer to functional guilds or ecological groups with similar food habits. The first summary macrodescriptor is simply the number of species ( $S$ ).

*Connectedness* is the degree to which components of a system are affected by each other (Allen and Starr, 1982). There are two measures. *Connectance* is the proportion of all possible connections within a system that are realized (Gardner and Ashby, 1970) and *connectivity* is the number of interactions per species (Levins, 1974; Allen and Starr, 1982; Gardner and Ashby, 1970). Connectedness increases if connectance or connectivity increases while the number of species stays the same.

There are three main connectance statistics: *interactive connectance* ( $IC$ ) or the realized proportion of all possible undirected, interspecific, trophic interactions (Briand, 1983), *upper connectance* ( $UC$ ), or the proportion of all possible interspecific trophic interactions plus number of competitive interactions between predators that share at least one prey, and *directed connectance* ( $DC$ ) is the proportion of links out of the maximum number of possible directed links in a food web, including cannibalism and predation (Martinez, 1991). Upper connectance measures interspecific food-web complexity including competitive interactions (Yodzis, 1980).

$IC$  is calculated by first creating the interaction matrix, accomplished by taking the square food-web diet matrix and replacing any  $A_{ij} > 0$  with a 1.0, including the diagonal, which includes cannibalism. Then the lower diagonal portion, including

the diagonal, is retained, which eliminates double counting (species A preys on species B and species B preys on species A). If the *number of links* ( $L$ ) for the lower diagonal of the interaction matrix (with cannibalism) is given by

$$L = \sum_{i=1}^S \sum_{j=1}^i I_{ij} \quad (1)$$

then interactive connectance is calculated as

$$IC = \frac{L}{([S(S-1)]/2) + S} \quad (2)$$

upper connectance by

$$UC = \frac{L}{[S(S-1)]} \quad (3)$$

and directed connectance by

$$DC = \frac{L}{S^2} \quad (4)$$

Connectivity has two associated statistics useful for ecosystem comparison. These are *linkage density* ( $LD$ ), or the total number of links divided by the number of species in the food web (Briand and Cohen, 1984). Linkage density indicates the average number of predators per species and is also known as the links-to-species ratio. Also useful is *linkage complexity* ( $LC$ ): upper connectance multiplied by the number of species (Briand, 1985). Linkage complexity multiplied by 2 describes the average number of undirected trophic and competitive interactions per species in a food web.

$$LD = \frac{L}{S} \quad (5)$$

$$LC = UCS \quad (6)$$

The final metric, suggested by Link (2002), is the *stability proxy* ( $SP$ ) calculated by

$$SP = SC \quad (7)$$

where  $C$  is connectivity given by

$$C = \frac{L}{S(S-1)/2} \quad (8)$$

and  $L$  is the number of links from Eq. (1)

In addition to the statistics described above, several other summary statistics are available. These include the *number of basal species*: no trophic levels support these species; *number of top predators*: species with <2 predators not including man; *number of intermediate species*: total – (basal + top predator); *number of cannibal species*: number of nonzero diagonal cells in the interaction matrix; *number of cycles*: linked pathways, starting from a group and returning to it (i.e.  $A \rightarrow B \rightarrow C \rightarrow A$ ); *number of omnivores*: species eating prey from more than one trophic level; *number of pathways in the food web connecting primary producers to a trophic level* (i.e.  $A \rightarrow B \rightarrow C$ ); and *mean path length*: total # trophic links/total # pathways.

### 2.3. Ecopath with Ecosim (EwE) metrics

The EwE software provides several system-level calculations and metrics that help characterize the ecosystem. A selection of these is briefly described below and more information and details can be found in Christensen et al. (2004).

#### 2.3.1. Summary statistics

*Total system throughput*: The sum of all flows in a system expressed as a flow in units of  $\text{t km}^{-2} \text{yr}^{-1}$  (tons in wet weight)

and represents the size of the entire ecosystem in terms of flow (Ulanowicz, 1986). It is the sum of total consumption, total export, total respiration, and total flow to detritus.

*Total primary production*: Total net primary production from all producers expressed as a flow in units of  $\text{t km}^{-2} \text{yr}^{-1}$ .

*System omnivory index*: An index to express the extent to which a system displays web-like features that overcome shortcomings of the connectance index, which only measures connectedness, see Christensen et al. (2004, p. 54) for a more detailed explanation. A smaller index indicates a more web-like system.

#### 2.3.2. Network analysis

*Finn's cycling index*: Finn (1976) expresses the fraction of an ecosystem's throughput that is recycled. This metric is assumed to increase for more mature ecosystems.

*Finn's mean path length*: The average number of groups that an inflow passes through, after Finn (1980). This metric is assumed to increase for more mature ecosystems.

#### 2.3.3. Cycles and pathways

*Cumulative number of pathways from primary producers to a trophic level*: Originally suggested by Ulanowicz (1986), it is the number of pathways implied by the food web representing the ecosystem that connects the primary producers to the higher trophic levels.

*Mean length of a pathway*: Calculated as the total number of trophic links divided by the number of pathways.

*Total number of all cycles*: All cycles in the system. Linked pathways, starting from a group and returning to it (i.e.  $A \rightarrow B \rightarrow C \rightarrow A$ ).

*Number of two species cycles*: Cycles that involve only two species.

*Mean length of a cycle*: Calculated as the total number of trophic links divided by the number of cycles.

*Sum of all consumption*: Sum of all consumption from all ecosystem components.

*Sum of flows to detritus*: Sum of all flows to detritus from all ecosystem components.

*Sum of all production*: Sum of all production from all ecosystem components.

*Total primary production/total respiration*: The ratio between total primary production and total respiration in a system is considered to be an important ratio describing the maturity of an ecosystem (Odum, 1971). In the early developmental stages of a system, production is expected to exceed respiration, leading to a ratio greater than 1; however, in mature systems, the ratio should approach 1.

*Total biomass (excluding detritus)*: The sum of all biomass, not including detritus in units of  $\text{t km}^{-2}$

*Throughput cycled (excluding detritus)*: The sum of biomass cycled through the ecosystem, excluding detritus, in units of  $\text{t km}^{-2} \text{yr}^{-1}$

*Throughput cycled (including detritus)*: The sum of biomass cycled through the ecosystem, including detritus, in units of  $\text{t km}^{-2} \text{yr}^{-1}$

## 3. Results

Trophic connections from Ecopath (Fig. 2) show some fundamental structural differences in the two ecosystems. Even though both systems cover the same trophic level range, 1–5, the Barents Sea appears to have a broader lower trophic base and is wider (i.e. has more species) at the upper trophic levels compared with the eastern Bering Sea.

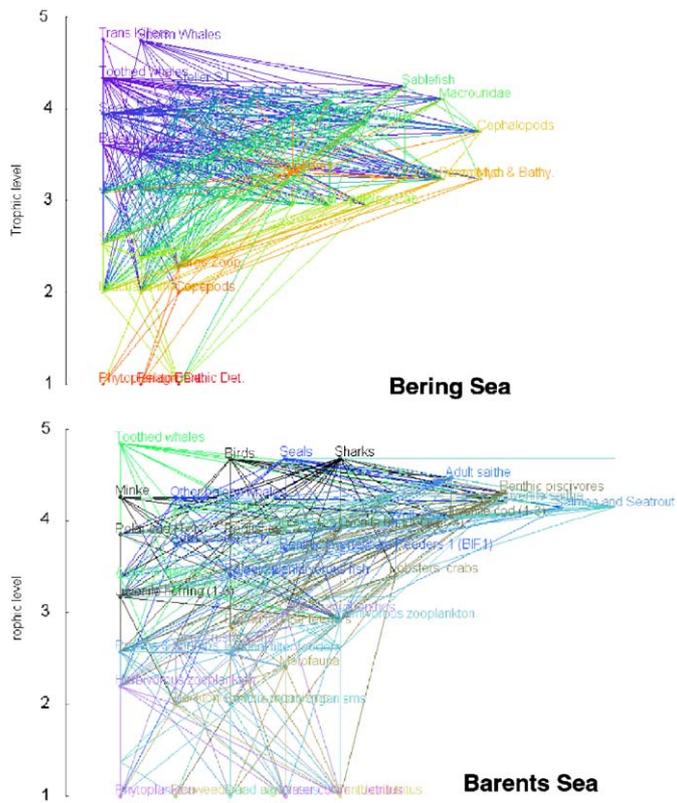


Fig. 2. Trophic connections for the Bering and Barents Sea. Horizontal space between species generated by Ecopath to maximize readability.

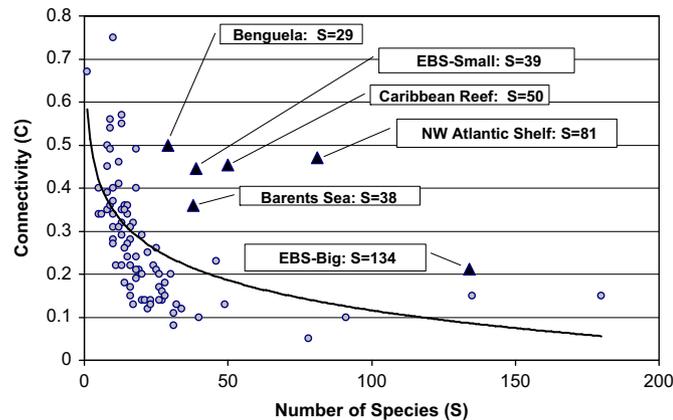


Fig. 3. Relationship between connectivity and number of species (adapted from Link, 2002). Grey dots are data from terrestrial systems presented in Link (2002). The black line shows the theoretical connectivity vs. number of species relationship for terrestrial systems. Connectivity for the eastern Bering Sea (EBS), Barents Sea (BS) and Northwest Atlantic (NAS) ecosystems are shown by the triangles. Data from the Benguela and Caribbean reef ecosystems are added for comparison (Data from Dunne et al., 2004).

The relationship between connectivity ( $C$ ) and number of species ( $S$ ) is presented in Fig. 3. Grey dots represent terrestrial systems after data presented in Link (2002). There are two eastern Bering Sea models—an aggregated (small) model and a disaggregated (big) model. Marine ecosystem data reported by Dunne et al. (2004) are also presented. There is a “controversial” balance

between  $C$  and  $S$ . As Link (2002) and Martinez (1992) point out, there is disagreement whether higher  $C$  increases, decreases, or has alternating effects on overall stability. As  $S$  goes down,  $C$  has to increase to maintain stability and vice versa. There are four main points to take away from this: (1) for a given connectance, the probability that a system will be stable goes down as  $S$  goes up (i.e. NAS is less stable than EBS-small); (2) for a given  $S$ , the probability that a system will be stable goes down as connectance goes up (i.e. BS vs. EBS-small); (3) within the same system, if  $S$  goes up, due to disaggregation, then  $C$  must come down (i.e. EBS-small vs. EBS-big); and (4) marine systems fall above the hypothetical  $C$  vs.  $S$  relationship, which is based mainly on terrestrial systems. These data suggest that marine ecosystems are “different” from terrestrial systems since the connectivity of marine systems is inherently greater than that of terrestrial systems, for the same number of species.

A summary and highlights of metrics from Table 1 and Table 2 are given below. The level of primary production and the number of species between the EBS (small) and BS are very similar (Table 1). Compared with the BS, the small EBS has a larger number of links and higher linkage density, linkage complexity, upper connectance, directed connectance, and interactive connectance. The EBS also has a slightly higher percentage of predators, lower percentage of intermediate species, higher percentage of omnivores, lower percentage of basal species, and a lower percentage of cannibalistic species. Overall the NAS ecosystem had almost 3 times the number of species compared to the EBS and BS and generally had higher metric values, except for lower values for linkage complexity and upper connectance. The NAS system had a larger percentage of cannibals and a smaller percentage of basal species and omnivores compared to EBS and BS.

Metrics from Ecopath with Ecosim (Table 2) show the EBS (small) has more consumption, less detritus, more throughput, more primary production, higher biomass (excluding detritus), and higher connectance, compared with the BS. The BS ecosystem appears to be more mature than the EBS based on the ratio of total production to total respiration. The EBS appears to be more connected and web-like compared with the BS based on a higher connectance index and a lower system omnivory index. Finn’s cycling index also shows the BS as the more mature of the two ecosystems and BS has a longer mean path length compared with the EBS. The BS system has about 2.5 times more cycles than the EBS and slightly large number of two species cycles. Consequently, the biomass recycled in the BS system is higher than it is in the EBS. The cumulative number of paths leading from primary producers to upper trophic levels is almost double in the BS compared with the EBS. The total amount of primary production flowing to upper trophic levels is over 4 times higher in the EBS compared with the BS.

The number of species per trophic level between the Eastern Bering Sea (EBS) and the Barents Sea (BS) is similar for trophic levels I and II, but the EBS has more species than the BS in trophic level III and the BS has more species than the EBS in trophic level IV (Fig. 4). The number of species affects the number of energy or material pathways connecting the food webs in the two systems. At trophic level II, the BS has almost 4 times the number of pathways compared with the EBS, even though both systems have a similar number of species. At trophic level III, the EBS has 25 times the number of pathways and more species compared with BS. The number of trophic pathways is higher in both systems in trophic level IV. The BS has more pathways compared with the EBS, corresponding to a larger number of species.

We see a different representation of this relationship in Fig. 5. The top panel shows that the cumulative number of pathways from primary producers for the EBS increases at a faster rate over

**Table 1**

Summary of ecological macrodescriptor metrics for the small and large eastern Bering Sea (EBS), the Barents Sea (BS), and the Northeast Atlantic Shelf (NAS) calculated from the Ecopath model diet matrix.

Metric	Small EBS	Large EBS	BS	NAS
Primary production ( $\text{gC m}^{-2} \text{yr}^{-1}$ )	120 <sup>a</sup>	120 <sup>a</sup>	100 <sup>a</sup>	~400
No. of Species ( <i>S</i> )	39	134	38	81 <sup>b</sup>
No. of links ( <i>L</i> ) (see Eq. (1))	347	1915	267	1562 <sup>b</sup>
Linkage density (see Eq. (5))	8.9	14.3	7.0	19.3
Linkage complexity (see Eq. (6))	9.13	14.39	7.21	19.52 <sup>b</sup>
Upper connectance (see Eq. (3))	0.23	0.11	0.19	0.15 <sup>b</sup>
Directed connectance (see Eq. (4))	0.23	0.11	0.18	0.24 <sup>b</sup>
Connectivity (see Eq. (8))	0.46	0.21	0.38	0.48
Interactive connectance with cannibalism (see Eq. (2))	0.47	0.21	0.36	Na
Stability proxy (see Eq. (7))	17.9	28.1	14.4	38.9 <sup>b</sup>
Top predators (#/% of <i>S</i> )	9/23.1	38/28.4	5/13.6	8/10.0 <sup>b</sup>
Intermediate species (#/% of <i>S</i> )	29/74.4	92/68.7	31/81.5	73/90.0 <sup>b</sup>
Omnivores (#/% of <i>S</i> )	36/92.3	124/92.5	31/81.5	49/61.0 <sup>b</sup>
Basal species (#/% of <i>S</i> )	1/2.56	4/3.0	2/5.26	2/2.4 <sup>b</sup>
Cannibalistic species (#/% of <i>S</i> )	8/20.5	8/5.9	12/31.6	25/31.0 <sup>b</sup>

For some metrics, results are given in absolute numbers (to the left of the /) and the percentage of the total number of species (to the right of the /). #—numbers. Na—not available.

<sup>a</sup> Data from Hunt and Megrey (2005).

<sup>b</sup> Data, or calculations based on data, taken from Table 1 of Link (2002).

**Table 2**

Summary of ecological metrics calculated for the small eastern Bering Sea (EBS) and Barents Sea (BS) ecosystems by the Ecopath with Ecosim model.

Metric	EBS	BS
Sum of all consumption ( $\text{t km}^{-2} \text{yr}^{-1}$ )	3129	2402
Sum of flows to detritus ( $\text{t km}^{-2} \text{yr}^{-1}$ )	1456	1699
Sum of all production ( $\text{t km}^{-2} \text{yr}^{-1}$ )	2724	1920
Total system throughput ( $\text{t km}^{-2} \text{yr}^{-1}$ )	6585	5201
Total net primary production ( $\text{t km}^{-2} \text{yr}^{-1}$ )	2000	1100
Total primary production/total respiration	1.214	1.034
Total biomass (excluding detritus) ( $\text{t km}^{-2}$ )	240.3	119.0
Connectance index	0.240	0.208
System omnivory index	0.128	0.228
Finns cycling index (% of total throughput)	8.5	13.6
Finns mean path length	3.3	4.7
Cumulative number of paths connecting primary producers to the upper trophic levels	1008548	1853629
Number of cycles	1419	3970
Number of two species cycles	11	13
Throughput cycled (excluding detritus) ( $\text{t km}^{-2} \text{yr}^{-1}$ )	18.17	26.7
Throughput cycled (including detritus) ( $\text{t km}^{-2} \text{yr}^{-1}$ )	56.2	70.7
Total flows from primary producers to upper trophic levels ( $\text{t km}^{-2} \text{yr}^{-1}$ )	1825	412

trophic levels 3.5–4.5, but that the cumulative number of pathways from primary producers in the BS system increases faster than the EBS at trophic levels higher than 4. The data plotted on the log scale both show a linear increasing trend, but the slopes are not significantly different from each other ( $p < 0.1$ ). This result indicates that, despite superficial differences, the systems are not statistically different with respect to the cumulative number of pathways from primary producers.

The amount of primary production consumed by predators ( $\text{t km}^{-2} \text{yr}^{-1}$ ) is larger at all trophic levels in the eastern Bering Sea compared with the Barents Sea (BS) (Fig. 6) except for TL 5.

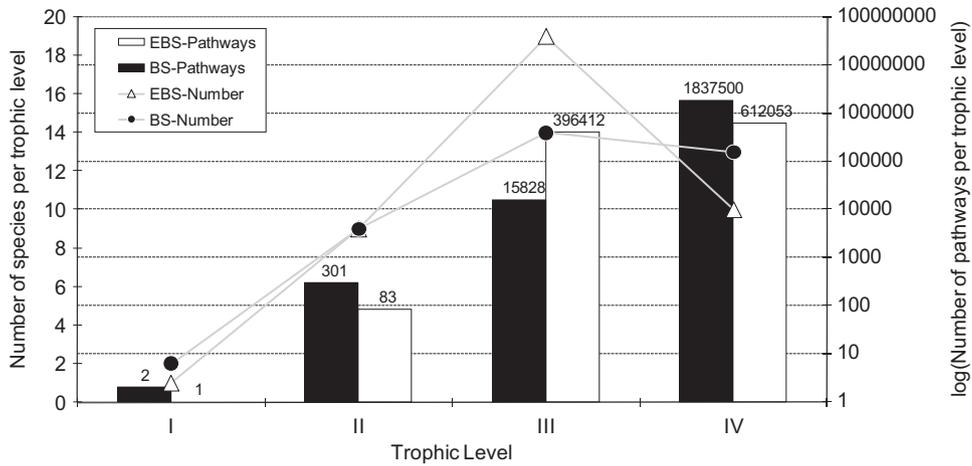
#### 4. Discussion

We demonstrate the benefit of using a common modeling approach to perform comparative analyses of marine ecosystem characteristics. While interesting similarities and differences were revealed, results from this analysis must be taken with some

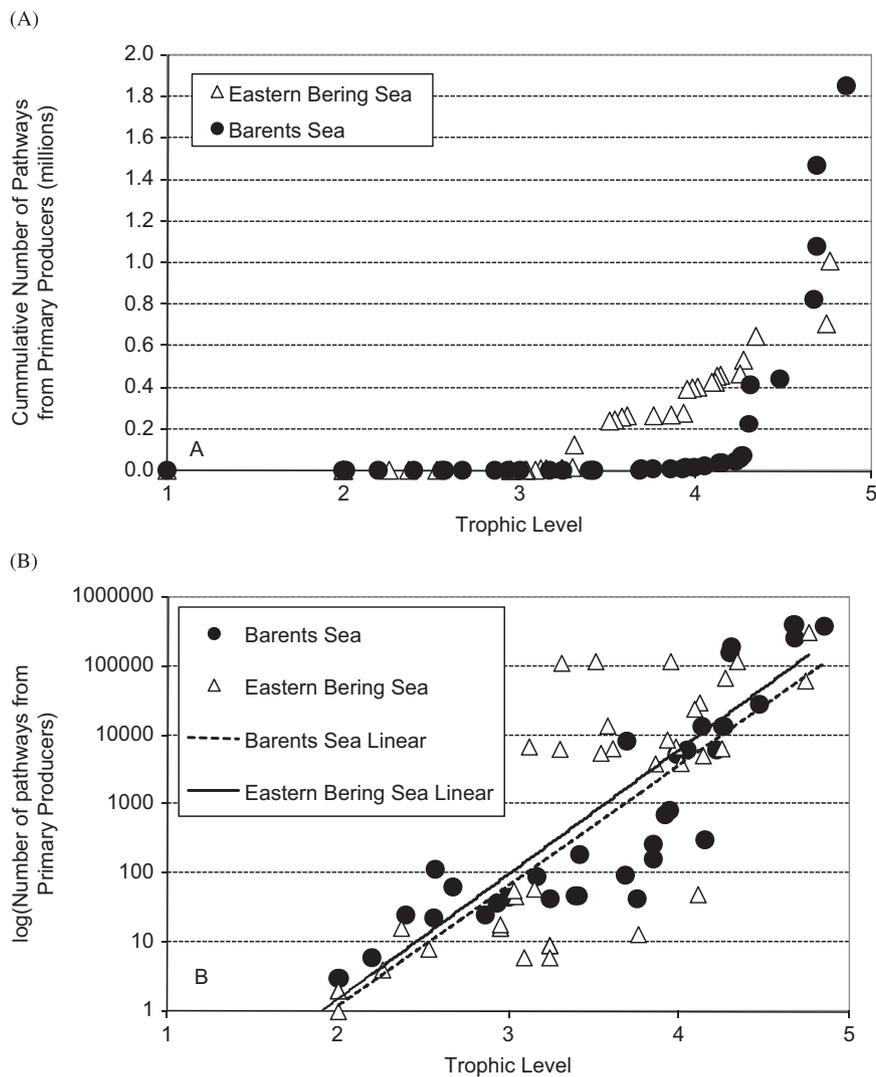
caution as the data collected from both systems do not represent the complete ecosystem. This is not unique to the two systems considered here. It is unlikely that any food web data set will specify all organisms and their interactions, and it is commonly accepted that most sampled marine ecosystems do not reflect all the pathways of energy transfer (Jennings et al., 2002). We must acknowledge that most data come from exploited systems and most published food webs are vertebrate centric. Finally, the modeler actively makes subjective decisions about the best way to aggregate data into functional groups to maximize the utility of the data at hand. Thus the number of species representing each ecosystem is somewhat artificial due to the limitations mentioned above as well as to some limitations in the Ecopath software (i.e. the ability to define a finite number of functional groups). In this study we compared model results which use data rather than comparing the data directly.

It must also be realized that building Ecopath models involve pragmatic model construction choices ( $n$  species groups;  $n$  basal species) that may not reflect the true biological characteristics of the ecosystem under study. These simplifying model decisions and available data directly affect the level of aggregation of the model's functional groups and artificially influence the number of species and any metric calculated that depends on the number of species. Thus, the metrics calculated from the number of species (i.e. in Table 1) all are directly influenced from the choices made when aggregating the biology in the Ecopath model. Consequently metrics based on the number of species may not be directly comparable. Martinez et al. (1999) discuss the difficulties of sampling ecosystems to characterize their structure. It is clear there is a connection between levels of sampling effort, accurate description of ecosystem structure, and the impacts of data availability as it relates to building realistic Ecopath models.

Results from these analyses do not consider any factors that would contribute to uncertainty. Moreover, the food habits data, which are isolated in time, may come from different time periods, do not reflect temporal changes in abundance and community composition, and lack historical data on temporal and spatial changes in trophic dynamics. Thus they ignore regime shifts and other quasi-decadal variability. The two ecosystems compared in this study are from different time periods. The EBS model was constructed with data from the 1980s while the BS model used data from 1995. Still, the diet matrices are comparable between



**Fig. 4.** Number of species per trophic level (lines and symbols) and the number (log scale) of material or energy pathways by trophic level (bars) for the eastern Bering Sea (EBS) and Barents Sea (BS). Numbers above the bars are presented on the arithmetic scale.



**Fig. 5.** The cumulative number of pathways from primary producers to trophic levels 1–5 (A) and the number (log scale) of pathways from primary producers to trophic levels 1–5 (B) along with linear fits, for the eastern Bering Sea (EBS) and Barents Sea (BS).

ecosystems because food-habits data collection methods used to characterize food web relationships are very standardized and consistent across ecosystems.

Ecosystem metrics calculated in this study indicate that the EBS is a more productive system, and that more of this production makes its way to upper trophic level ecosystems components and less is

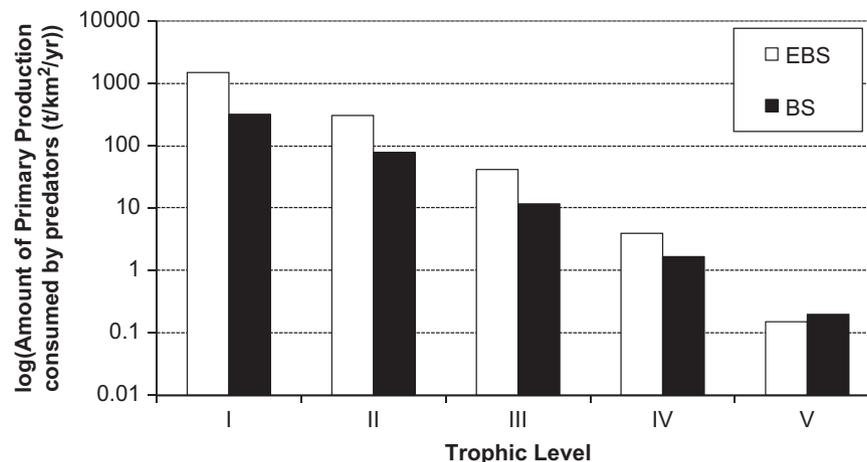


Fig. 6. Amount of Primary production (log scale) consumed by predators in each of five trophic levels, for the eastern Bering Sea (EBS) and Barents Sea (BS).

recycled. Fig. 6 illustrates this point by showing that more primary production is consumed by predators at every trophic level in the EBS compared to the BS. Trophic level V is the only exception.

In conclusion, ecosystem metrics calculated in this study indicate the average number of trophic steps from primary producers to predators is shorter in the EBS. In the EBS, trophic pathways are shorter and more linear, there are more benthic species (flatfish and crabs) and there are both pelagic and benthic food webs. The number of trophic pathways is greater between trophic levels 3.5 and 4.5 in the EBS, but there are more trophic pathways between trophic levels 4 and 5 in the BS. The BS food web is mainly pelagic. The greater depth of the Barents Sea and the longer water column (EBS: 50 m, BS: 200 m deep) result in a greater proportion of the sinking flux being remineralised by pelagic microbes, reducing the food supply to the benthos. Consequently, more production in the BS is unused and becomes detritus. The EBS is more efficient at converting primary production into upper trophic level biomass since there are fewer trophic steps and primary production fuels both the pelagic and benthic food webs. Commercial fish species biomass is presently greater in the EBS (7.6mt) compared with BS (3.8mt). Many alternate pathways exist in the BS; thus there are no single critical species creating bottlenecks. Results suggest that the BS may be more stable and more mature compared with the EBS.

Methods presented here show that it is possible to quantitatively compare whole communities and ecosystems with relatively modest data requirements and that comparative analyses can offer useful insights into similarities and differences among marine ecosystem structure and function. It appears that this modeling approach might have benefited from comparing subsystems rather than compressing the entire food web into one scheme. The subsystems could be the surface mixed layer, the deep water column and the benthos. Comparing the ecological attributes of these subsystems with each other within one ecosystem or at this level of detail between ecosystems may highlight the similarities and differences between them more effectively and enhance the explanatory power of this approach. We offer this observation in hindsight and recognize the more detailed subsystem analysis was not a planned part of the scope of the current work. We plan to explore these issues in more detail in the near future.

## Acknowledgements

Thanks to Steve Mackinson for supplying the Barents Sea Ecopath data files from which the Blanchard 2002 publication was

based. The authors thank two anonymous reviewers whose comments improved the manuscript. We also thank Sarah Gaichas and Ken Drinkwater for offering several insightful comments and for reading an early draft of the paper. This research is contribution FOCI-0568 to NOAA's Ecosystems Fisheries-Oceanography Coordinated Investigations (EcoFOCI).

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