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A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics

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ABSTRACT

Energy budget models for five marine ecosystems were compared to identify differences and similarities in trophic and community structure. We examined the Gulf of Maine and Georges Bank in the northwest Atlantic Ocean, the combined Norwegian/Barents Seas in the northeast Atlantic Ocean, and the eastern Bering Sea and the Gulf of Alaska in the northeast Pacific Ocean. Comparable energy budgets were constructed for each ecosystem by aggregating information for similar species groups into consistent functional groups. Several ecosystem indices (e.g., functional group production, consumption and biomass ratios, cumulative biomass, food web macrodescriptors, and network metrics) were compared for each ecosystem. The comparative approach clearly identified data gaps for each ecosystem, an important outcome of this work. Commonalities across the ecosystems included overall high primary production and energy flow at low trophic levels, high production and consumption by carnivorous zooplankton, and similar proportions of apex predator to lower trophic level biomass. Major differences included distinct biomass ratios of pelagic to demersal fish, ranging from highest in the combined Norwegian/Barents ecosystem to lowest in the Alaskan systems, and notable differences in primary production per unit area, highest in the Alaskan and Georges Bank/Gulf of Maine ecosystems, and lowest in the Norwegian ecosystems. While comparing a disparate group of organisms across a wide range of marine ecosystems is challenging, this work demonstrates that standardized metrics both elucidate properties common to marine ecosystems and identify key distinctions useful for fisheries management.

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1. Introduction

High latitude marine ecosystems have had some of the highest fishery production in the world's oceans (Cohen et al., 1982; Bax, 1991; Wassmann et al., 2006). High-latitude ecosystems may also experience significant changes in physical attributes of marine waters, such as temperature, stratification, currents, and sea ice, as a result of climate warming (e.g., Overland and Stabeno, 2004). While the effects of fishing on individual fish stocks have been studied for many years to promote sustainable harvests, the ecosystem-level effects of fishing and of climate change are increasingly of interest as well. There are many mechanisms by which physical oceanic changes affect biological resources, but one of the most basic ways is through alterations of energy flow within the ecosystem, by increasing or decreasing the amount of primary and secondary production available to planktivorous animals (e.g., Francis et al., 1998; Hunt et al., 2002). Similarly, many ecosystem-level fishing effects have been described, including redirection of energy flow from pathways involving heavily fished species to pathways involving unfished species (Fogarty and Murawski, 1998; Link and Garrison, 2002). The combined effects of changes in the physical environment and fishing may alter energy flow in complex ways, such as in the Black Sea where interacting eutrophication, overfishing, and invasive species have produced multiple shifts in ecosystem state (Daskalov et al., 2007). Resource management in these complex circumstances requires more and different information than has been historically used. Basic comparisons of structure and energy flow are an initial step in identifying the properties that exhibit important ecosystem-level responses to such changes and hence have important management implications.

In this paper, we compare energy budget models for five marine ecosystems to identify differences and similarities in trophic and

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community characteristics across ecosystems. We examined the Gulf of Maine (GOM) and Georges Bank (GB) systems in the northwest Atlantic Ocean, the combined Norwegian/Barents Seas (NorBar) systems in the northeast Atlantic Ocean, and the eastern Bering Sea (EBS) and the Gulf of Alaska (GOA) systems in the northeast Pacific Ocean (Fig. 1). For most analyses here, the Norwegian and Barents seas are combined because a single combined energy budget model exists for these systems. However, some primary production data will be shown separately where available. Conversely, the GOM and GB are combined for some primary production analyses due to data availability, but are separated for many comparisons here because separate energy budget models exist for those systems. The EBS and GOA are always kept distinct in this analysis. An overview of key physical and biological characteristics of each ecosystem, including a description of major predator and prey species, is detailed in Link et al. (in this issue) and Mueter et al. (in this issue). This work, as well as that presented in companion papers by Link et al. (in this issue), Megrey et al. (in this issue), Mueter et al. (in this issue), and Drinkwater et al. (in this issue), is part of the international Marine Ecosystems of Norway and the US (MENU) collaboration.

While all of these ecosystems are classified as “high latitude,” the areas and latitudes of the ecosystems studied differ somewhat. For example, the eastern Bering Sea, Gulf of Alaska, Gulf of Maine, and Georges Bank are almost entirely (80–95%) continental shelf ecosystems less than 200 m in depth as defined in this analysis, while the Norwegian Sea ecosystem is primarily (95%) slope/basin area over 200 m deep, and the Barents Sea is half shelf, half slope up to 500 m deep (Fig. 1). The systems rank from largest area and highest latitude (NorBar) through intermediate area and latitude (EBS and GOA) to smallest area and lowest latitude (GOM and GB). Areal differences were accounted for in this analysis by measuring biomass, production, and consumption on a per unit area basis for all systems.

This analysis uses a snapshot in time of energetic structure in these high latitude ecosystems to describe key attributes which are comparable across systems. The attributes we compare potentially indicate both ecosystem processes and fishing effects acting on each ecosystem. We make three basic types of energetic comparisons: first, of energy flow in the lower trophic levels of the food webs, second, of flow and food web structure or biomass ratios in the middle trophic levels of the food web, and finally, of flows at high trophic levels, with comparisons to fishery catches. While the environmental conditions prevalent in each ecosystem affect all levels, fishing is most likely to affect the middle and upper levels of the food web, through direct catch, biomass redistribution, and perhaps competition with other predators. Finally, we describe ecosystem structure more comprehensively, comparing the systems using network metrics calculated for each food web model.

2. Methods

2.1. Energy budget models and aggregations

Our comparisons are based primarily on existing energy budget models for each ecosystem. Energy budget models, also called mass balance or food web models, are fairly simple conceptually; they attempt to account for the standing stock, energy requirements, outputs, and connections between major biomass pools within the system at a particular instant in time. The energy budget models we used were all implemented within a common modeling framework based on the work of Polovina (1984), as extended by Walters et al. (1997) and Pauly et al. (2000) in the software package Ecopath with Ecosim (EwE). Ecopath is the portion of the software that implements a static mass balance model of the trophic relationships between species groups in a marine ecosystem; it is described in detail elsewhere (e.g., Christensen and Pauly, 1992; Pauly et al., 2000; Christensen and Walters, 2004), so we give only a brief overview here. Ecosim, the dynamic portion of the EwE model, was not used in this analysis.

The Ecopath mass balance model solves 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 (functional group) in a modeled food web. A single functional group (food web compartment) may be a single species or a set of trophically similar species. The master Ecopath equation is, for each functional group (i) with predators (j):

$$B_i\left(\frac{P}{B}\right)_i * EE_i + IM_i + BA_i = \sum_j \left[B_j * \left(\frac{Q}{B}\right)_j * DC_{ij}\right] + EM_i + C_i. \qquad (1)$$

The definition of the parameters in Eq. (1) and the general methods used to derive their group specific values are given in Table 1.

With the system of equations solved by matrix inversion, it is simple to calculate which predators are responsible for what portion of each species group’s mortality, and consumption for each

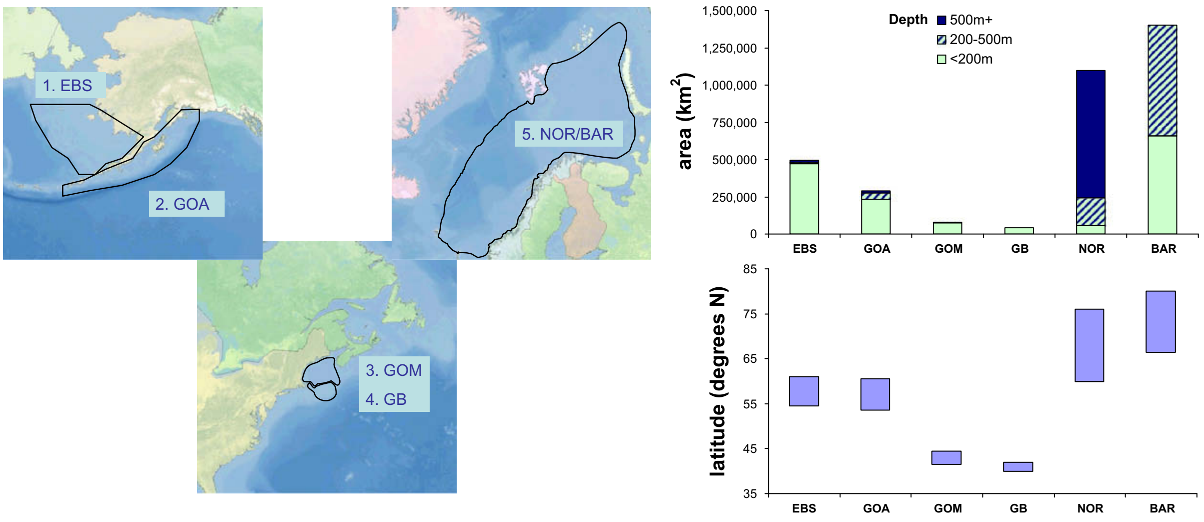

Fig. 1. Geographic and physical characteristics of ecosystems compared. Modelled areas are the Eastern Bering Sea (EBS) and the Gulf of Alaska (GOA) in the North Pacific, the Gulf of Maine (GOM) and Georges Bank (GB) in the Northwest Atlantic, and the combined Norwegian and Barents Seas (NOR/BAR) in the Northeast Atlantic.

Table 1
Parameters (input data) and parameter calculation methods for the Ecopath master equation.

Parameter	Abbreviation (units)	Parameter source
Biomass	B (t km^{-2})	Data or model estimate: survey estimates, sampling programs, stock assessments; estimated by fixing EE if no data available
Production/biomass	P/B (yr^{-1})	Data: mortality rates, growth rates, bioenergetics models
Consumption/Biomass	Q/B (yr^{-1})	Data: bioenergetics models, gut content analysis
Diet composition	DC (proportion of the prey *i* in the diet (by mass) of consumer *j*; dimensionless)	Data: gut content analysis
Fisheries catch	C (t km^{-2})	Data: fisheries statistics
Biomass accumulation	BA (t km^{-2})	Data: biomass trend (only used if energetic demand requires it)
Immigration and emigration	IM and EM (t km^{-2})	Data: used to specify annual net migration imbalance (not used in these models)
Ecotrophic efficiency	EE (proportion; dimensionless)	Model estimate or assumption: estimated by Ecopath; if no biomass data are available, EE is fixed at a standard level to estimate biomass

group. Trophic level is also calculated at this point; primary producers have a trophic level of one, and each successive consumer group has a trophic level equal to one higher than the average of the trophic levels of its prey, weighted by the proportion of prey in the diet.

We briefly outline the models here, but refer the reader to the detailed documentation available for each model (Aydin et al. (2007) for EBS and GOA, Link et al. (2006) for GOM and GB, and Skaret and Pitcher (in press) for NorBar). The mass balance models were built to represent annual snapshots based on averages from roughly comparable time periods in each ecosystem; The EBS and GOA models are based on data from the early 1990s (1991 and 1990–1993, respectively). The GOM and GB models were based on data from 1996 to 2000. The Norwegian/Barents sea model was balanced using data for the year 2000. The food web models were designed with the same annual timescale and broad, basin-wide spatial scale as the single species stock assessments currently applied in fishery management in each of these ecosystems. This represents both an advantage and a pitfall in that much of the data collected for single species population models can be used in food web modeling, but as in the single species stock assessment models, the available data generally do not allow modeling of seasonal dynamics and fine spatial resolution of food webs.

In all regions, access to impressive fishery independent and fishery dependent datasets made it possible to model trophically explicit age structured groups for major groundfish and pinnipeds, and substantial taxonomic detail in benthos, pelagic fish, seabirds, and marine mammals (Table 2). The Alaskan models were the most taxonomically disaggregated of the models compared. The EBS model included 121 consumer groups and 16 fishing fleets (defined by gear type, target species, and bycatch complex), the GOA model included 113 consumer groups and 14 fishing fleets, and each model had an additional 4 producer groups (large and small phytoplankton, macroalgae, and external production), 5 detritus groups (benthic and pelagic detritus, fishery discards, fishery offal, and external detritus) and 2 microbial loop groups (benthic and pelagic; Aydin et al., 2007). The GOM and GB models were based on similarly detailed information which was aggregated into 36 functional groups, including 29 consumer groups, 2 fisheries (pelagic and demersal), 1 producer group, 3 detritus groups (fishery discards, particulate organic carbon, and dissolved organic carbon), and 1 bacterial group (Link et al., 2006). The combined NorBar model was intermediate in taxonomic aggregation between the north Pacific and north Atlantic models. It included 55 consumer groups, 19 fishing fleets, 2 producer groups (phytoplankton and macroalgae), and 1 detritus group (Skaret and Pitcher, in press).

All of the models were aggregated to 17 common functional groups to facilitate ecosystem comparisons: fisheries, toothed whales, sharks, pinnipeds, baleen whales, seabirds, pelagics (fishes and squids), demersals (fishes and octopus), megabenthos (large commercial crustaceans), shrimps, macrobenthos (infauna and epifauna excluding shrimps), gelatinous zooplankton, carnivorous zooplankton, herbivorous zooplankton, phytoplankton, macroalgae, and bacteria. Table 2 lists the original groups in each model and shows our mappings of the original groups into common functional groups. The aggregation process summed the biomass of the original model groups into the functional group biomass, and calculated a biomass-weighted average of P/B and Q/B for the functional group from the original model groups. We did not compare estimates for detritus groups or groups outside the boundaries of the models in this analysis. We considered the toothed whales, sharks, pinnipeds, baleen whales, and seabirds to be the higher trophic level groups for analytical purposes. Mid-trophic level groups included pelagics, demersals, megabenthos, shrimps, and macrobenthos. Lower trophic level groups included zooplankton, primary producers, and bacteria.

2.2. Cross-system comparisons

We compared primary production in each ecosystem using multiple information sources. The aggregated energy budget models (described above) provided one annual total estimate of primary production in metric tons per square kilometer (t km^{-2}) for each system. We also examined the seasonal cycle in primary production between systems, as an annual snapshot of total production provides an incomplete characterization of production. Seasonal production was estimated from satellite data. Chlorophyll *a* concentrations were derived from the Sea-viewing Wide Field of View Sensor (SeaWiFS) onboard the SeaStar spacecraft. We used the level-3 processed data at a temporal resolution of 1 month (available at the NASA Ocean Color Website: http://oceancolor.gsfc.nasa.gov/) and confined our spatial sampling to the domains prescribed in Fig. 2. Estimates of net primary productivity are based on the vertically generalized production model (VGPM) of Behrenfeld and Falkowski (1997). This chlorophyll-based model uses a temperature dependent relationship for photosynthetic efficiency. These data are available via the Ocean Productivity Website (http://web.science.oregonstate.edu/ocean.productivity/index.php) and were also sampled at a temporal frequency of 1 month. We assumed that averages across years for the monthly observations represented monthly production in each ecosystem, and used this to describe an average seasonal cycle of production.

For all consumer groups, fisheries, and detritus pools, we limited our analysis to the annual snapshots estimated by the aggregated energy budget models, and did not attempt to include seasonal information. Annual biomass (t km^{-2}), production (t km^{-2}), and consumption (t km^{-2}) were summed by functional group. For fisheries, biomass and production were not applicable,

Table 2
Functional groups used for comparisons, with the corresponding model groups aggregated from each ecosystem. For living functional groups, biomass data quality ratings are: (no mark) biomass estimate based on direct fishery independent sampling data; (#) biomass estimate based on stock assessment model and/or commercial catch data; (∗) no data available or data-based estimate proved inadequate to balance energy flow, biomass estimate based on trophic demand or other ecosystem model-based analysis. Fishery catch data quality was considered high in all systems. In the EBS and GOA models, juvenile age groups are indicated by "juv" after a group name. In the NorBar model, numbers in parentheses refer to age classes for each model group.

Aggregate	EBS	GOA	GOM	GB	NorBar
Fisheries	Cod Longline Cod Pots Cod Trawl Crab Pots Flatfish Trawl Halibut Longline Herring Fishery Indigenous and Subsistence Oth. Groundfish Trawl Pollock Trawl Rockfish Longline Rockfish Trawl Sablefish Longline Salmon Fishery Turbot Longline Turbot Trawl	Cod Longline Cod Pots Cod Trawl Crab Pots Flatfish Trawl Halibut Longline Herring Fishery Indigenous and Subsistence Oth. Groundfish Trawl Pollock Trawl Rockfish Trawl Sablefish Longline Salmon Fishery Shrimp Trawl	Demersal Pelagic	Demersal Pelagic	EU/other purse EU/other trawl Iceland purse seiner Iceland trawl Nor div conventional Nor div trawlers Norgillnet8-21 m Nor industrial trawlers Nor longlining >28 m Nor longlining 8-21 m Nor ocean shrimp trawlers Nor purse seiners Nor seiners Nor shrimp trawlers 8-20 m Nor seine >21 m Nor seine 8-21 m Other vessels Russian trawl Whale Seal boats
Toothed whales	Belugas Porpoises Resident Killers Sperm Whales Transient Killers	Porpoises Resident Killers Sperm Whales Transient Killers	Odontocetes	Odontocetes	Killer whale Other toothed whales Sperm whale
Sharks	Sleeper shark	Dogfish Salmon shark Sleeper shark	Tuna$^{\#}$ Billfish$^{\#}$ Swordfish$^{\#}$ Sharks$^{\#}$	Tuna$^{\#}$ Billfish$^{\#}$ Swordfish$^{\#}$ Sharks$^{\#}$	Basking shark* Other sharks*
Pinnipeds	N. Fur Seal N. Fur Seal juv Resident seals Sea Otters Steller Sea Lion Steller Sea Lion juv Walrus and Bearded Seals Wintering seals	N. Fur Seal N. Fur Seal juv Resident seals Sea Otters Steller Sea Lion Steller Sea Lion juv	Pinnipeds	N/A	Harp seal (0) Harp seal (1+) Other seals (0) Other seals (1+)
Baleen whales	Bowhead Whales Fin Whales Gray Whales Humpbacks Minke whales Right whales Sei whales	Fin Whales Gray Whales Humpbacks Minke whales Right whales Sei whales	Baleen Whales	Baleen Whales	Minke whale Other baleen whales
Birds	Albatross Jaeger Auklets Cormorants Fulmars Gulls Kitti wakes Murres Puffins Shearwater Storm Petrels	Albatross Jaeger Auklets Cormorants Fulmars Gulls Kittiwakes Murres Puffins Shearwater Storm Petrels	Seabirds	Seabirds	Atlantic puffin Other seabirds
Pelagics	Bathylagidae* Capelin* Eulachon* Herring$^{\#}$ Herring juv$^{\#}$ Myctophidae* Oth. forage fish* Oth. pelagic smelt* Salmon outgoing* Salmon returning$^{\#}$ Sandlance* Squids*	Bathylagidae* Capelin* Eulachon* Herring$^{\#}$ Herring juv$^{\#}$ Myctophidae* Oth. forage fish* Oth. pelagic smelt* Salmon outgoing* Salmon returning$^{\#}$ Sandlance* Squids*	Larval-juv fish Medium Pelagics Small Pelagics: Commercial$^{\#}$ Squid$^{\#}$ Anadromous$^{\#}$ Other$^{\#}$	Larval-juv fish Medium Pelagics Small Pelagics: Commercial$^{\#}$ Squid$^{\#}$ Anadromous$^{\#}$ Other$^{\#}$	Atlantic salmon Blue whiting (0–1)$^{\#}$ Blue whiting (2+)$^{\#}$ Capelin (0)$^{\#}$ Capelin (1)$^{\#}$ Capelin (2+)$^{\#}$ Lumpsucker* Mackerel$^{\#}$ Mesopelagic fish Herring (0)$^{\#}$ Herring (1–2)$^{\#}$ Herring (3+)$^{\#}$ Polar cod Small pelagic fish* Squid$^{\#}$

Table 2 (*continued*)

Aggregate	EBS	GOA	GOM	GB	NorBar
Demersals	AK Plaice Alaska skate Arrowtooth Arrowtooth juv Atka mackerel# Atka mackerel juv# Dover Sole Dusky Rock# Eelpouts* FH. Sole FH. Sole juv Gr. Turbot Gr. Turbot juv Greenlings* Grenadiers Kamchatka fl. Kamchatka fl. juv Lg. Sculpins Misc. fish deep* Misc. fish shallow* Misc. Flatfish* N. Rock sole N. Rock sole juv Northern rockfish Octopi* Other sculpins* Other Sebastes* Other skates P. Cod# P. Cod juv# P. Halibut P. Halibut juv Pacific O. perch Rex Sole Rougheye rockfish Sablefish Sablefish juv Sharpchin rockfish* Shortraker rockfish Shortspine Thorns W. Pollock# W. Pollock juv# YF. Sole YF. Sole juv	AK Plaice Arrowtooth Arrowtooth juv Atka mackerel Atka mackerel juv Big skate Dover Sole Dusky Rock Eelpouts* FH. Sole FH. Sole juv Greenlings Grenadiers Lg. Sculpins Longnose skate Misc. fish deep* Misc. fish shallow* Misc. Flatfish N. Rock sole Northern rockfish Octopi* Other sculpins* Other Sebastes* Other skates P. Cod P. Cod juv P. Halibut P. Halibut juv Pacific O. perch Pacific O. perch juv Juv Rex Sole Rougheye rockfish S. Rock sole Sablefish Sablefish juv Sharpchin rockfish* Shortraker rockfish Shortspine Thorns Shortspine Thorns juv W. Pollock# W. Pollock juv# YF. Sole	Demersals: Benthivores# Omnivores# Piscivores#	Demersals: Benthivores# Omnivores# Piscivores#	Coastal cod (0–2)# Coastal cod (3+)# Deep-sea redfish (0–4)# Deep-sea redfish (5+)# Flatfishes and rays* Golden redfish (0–4)# Golden redfish (5+)# Greenland halibut (0–4)# Greenland halibut (5+)# Haddock (0–2)# Haddock (3+)# NE Arctic cod (0–2)# NE Arctic cod (3+)# Other benthic fish* Saithe (0–2)* Saithe (3+)* Wolffishes*
Megabenthos	Tanner crab Tanner crab juv* King crab King crab juv* Snow crab Snow crab juv*	Tanner crab* King crab	Megabenthos: Filter Feeders Other	Megabenthos: Filter Feeders Other	Edible crabs and lobster*
Shrimp	NP shrimp* Pandalidae*	NP shrimp* Pandalidae*	Shrimp et al.*	Shrimp et al.*	Prawns
Macrobenthos	Anemones Benthic Amphipods* Bivalves Brittle stars* Corals Hermit crabs* Hydroids* Misc. crabs* Misc. Crustacean* Misc. worms* Polychaetes Sea Pens Sea stars Snails* Sponges Urchins dollars cucumbers* Urochordata	Anemones Benthic Amphipods* Bivalves* Brittle stars Corals Hermit crabs* Hydroids* Misc. crabs* Misc. Crustacean* Misc. worms* Polychaetes* Sea Pens Sea stars Snails* Sponges Urchins dollars cucumbers Urochordata	Macrobenthos: Crustaceans Molluscs Polychaetes Other*	Macrobenthos: Crustaceans Molluscs Polychaetes Other*	Corals Other macrobenthos
Gelatinous zooplankton	Gelatinous filter feeders* Scyphozoid Jellies	Gelatinous filter feeders* Scyphozoid Jellies	Gelatinous zooplankton*	Gelatinous zooplankton*	Jellies
Carnivorous	Chaetognaths*	Chaetognaths*	Micronekton	Micronekton	Krill

(*continued on next page*)

Table 2 (*continued*)

Aggregate	EBS	GOA	GOM	GB	NorBar
zooplankton	Euphausiids* Fish Larvae* Mysids* Pelagic Amphipods* Pteropods*	Euphausiids* Fish Larvae* Mysids* Pelagic Amphipods* Pteropods*			Pelagic amphipods
Herbivorous zooplankton	Copepods*	Copepods*	Large Copepods Microzooplankton*	Large Copepods Microzooplankton*	Calanus Zooplankton 0-2 mm
			Small copepods	Small copepods	Zooplankton >2 mm
Phytoplankton	Lg Phytoplankton* Sm Phytoplankton*	Lg Phytoplankton Sm Phytoplankton	Phytoplankton	Phytoplankton	Phytoplankton
Macroalgae	Macroalgae*	Macroalgae*	N/A	N/A	Seaweeds
Bacteria	Benthic microbes* Pelagic microbes	Benthic microbes* Pelagic microbes*	Bacteria*	Bacteria*	N/A

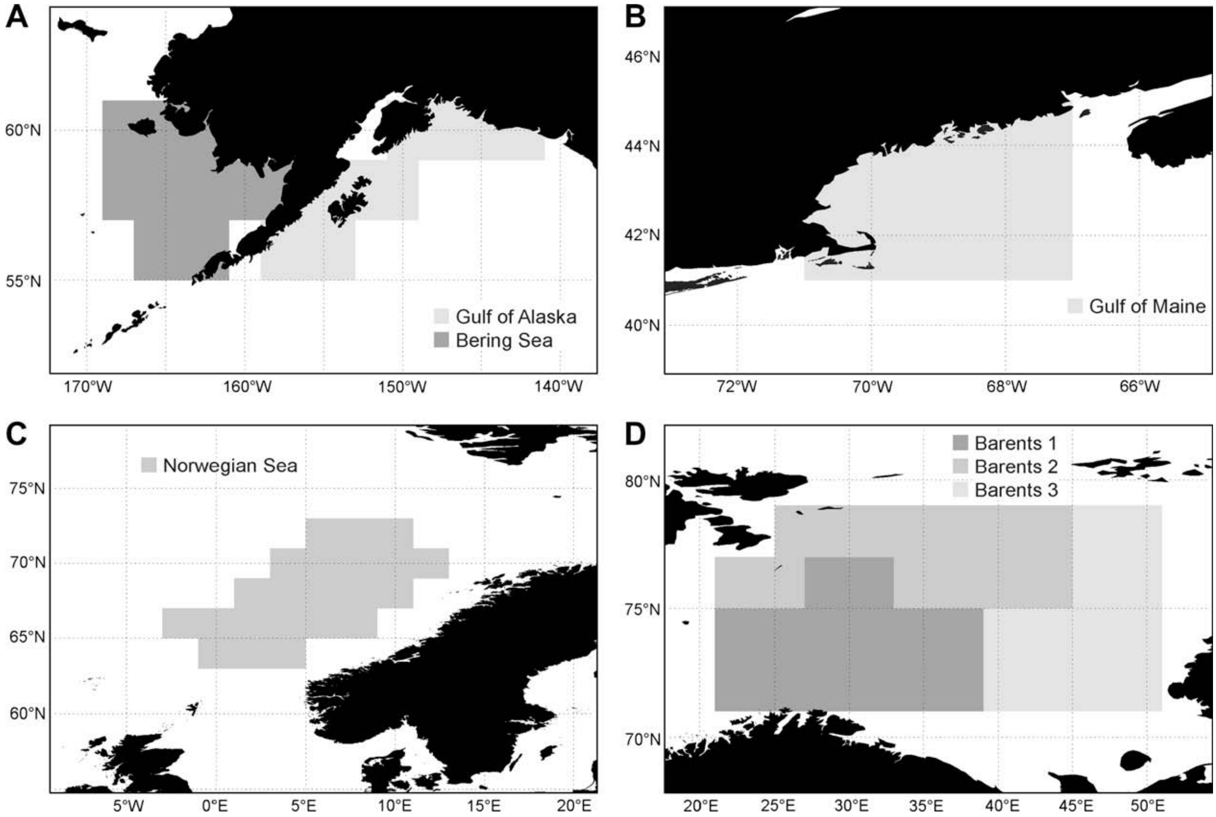

Fig. 2. Locations of sampling for chlorophyll *a* data.

but we included fisheries catch in comparisons with predator consumption. Biomass, production, and consumption were compared for each aggregate group across ecosystems, and were summed for additional comparisons (e.g., all invertebrates, all fish, all zooplankton) across systems. Comparing these attributes for broad functional groups will indicate the relative strengths of energy flow pathways in each ecosystem, and potentially the cumulative effects of fishing and environmental forcing (e.g., Fulton et al., 2005; Link, 2005; Link et al., 2008). Dimensionless ratios of certain attributes were also calculated for further comparisons. We calculated biomass ratios of pelagics to demersals, pelagics to zooplankton, demersals to benthos, benthos and zooplankton to all invertebrates, pelagics and demersals to all fish, sharks to all fish, zooplankton, shrimps, and benthos to phytoplankton, toothed whales to pelagics, baleen whales to zooplankton, and shrimp to zooplankton. Production ratios were calculated for zooplankton production to total primary production, and zooplankton plus bacterial production to primary production. Finally, we compared indices of catch to production and consumption for selected groups, including fishery catch to primary production, to zooplankton production, to fish production and biomass, and to high trophic level predator consumption.

2.3. Network metrics

The Ecopath diet matrix from each original, disaggregated energy budget model provides the fundamental food web information for the calculation of 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 diet matrix also provides important qualitative information about community structure, conveying trophic connections among species. Full diet matrices for each system are not reproduced here, but can be found in the detailed model documentation (Aydin et al., 2007 for EBS and GOA, Link et al., 2006 for GOM and GB, and Skaret and Pitcher, in press for NorBar). System-level metric calculations were taken directly from EwE or calculated according to methods described in Yodzis (1980), Briand and Cohen (1984), Briand (1985), Martinez (1991), Link (2002), Christensen et al. (2004), and Megrey and Aydin (2009).

Specifically, we calculated the number of functional groups (S) and the number of interactions (or links, L) in each disaggregated model, from which linkage density (L/S) was calculated. An undirected link is an interaction between species which does not distinguish predator from prey; species A and B share an undirected link whether A eats B or B eats A. In contrast, the directed link A eats B is different from the directed link B eats A. We calculated three connectance metrics: interactive connectance (IC), the realized proportion of all possible undirected, inter- and intra-specific trophic interactions (Briand, 1985); upper connectance (UC), the proportion of all possible interspecific trophic interactions plus number of competitive interactions (I) between predators that share at least one prey, (Yodzis, 1980); and directed connectance (DC), the proportion of links out of the maximum number of possible directed links in a food web, including cannibalism and predation (Martinez, 1991). Interactive connectance was calculated as

$$\mathrm{IC} = \frac{L}{\frac{[S\cdot(S-1)]}{2} + S}, \tag{2}$$

upper connectance as

$$\mathrm{UC} = \frac{L + I}{[S\cdot(S-1)]}, \tag{3}$$

and directed connectance as

$$\mathrm{DC} = \frac{L}{S^2}. \tag{4}$$

Upper connectance multiplied by number of functional groups (UC × S) gives linkage complexity. The stability proxy (Link, 2002) was calculated as the number of functional groups times connectivity ($S \times C$), where

$$C = \frac{L}{\frac{S(S-1)}{2}}. \tag{5}$$

Numbers of basal, top predator, intermediate, cannibalistic, two-cycle, and omnivorous groups were also calculated for each system. Basal groups were simply trophic level 1 groups, top predators were defined as groups with less than two predators exclusive of fisheries, and all other groups were defined as intermediate. Cannibalistic groups were those feeding on themselves, cycles were defined as pathways starting and ending at the same group, and omnivores were defined as groups feeding on multiple trophic levels.

3. Results

3.1. Overview

On a per unit area basis, the EBS had the highest total biomass, production, and consumption, as well as the highest fishery catch. The NorBar had the second highest total biomass, but the lowest production, consumption, and fishery catch of all the ecosystems compared. The GOA ranked third in total biomass and production, and fourth in consumption and fishery catch. The GB ranked fourth in total biomass, but second in production and consumption, and third in fishery catch. The GOM had the lowest total biomass, ranked fourth in production and third in consumption, but had the second highest fishery catch of all the ecosystems compared. Biomass, production, and consumption by aggregate group for each model are summarized in Table 3. Dimensionless ratios calculated for each model are presented in Table 4. Network metrics are summarized in Table 5. We focus on specific comparisons of interest below.

3.2. Gaps remaining after aggregation

Even aggregated, not all models had all groups for comparison. However, these small gaps were not considered critical impediments to making general ecosystem comparisons. For example, no macroalgae group was included in the GB and GOM models, due to low abundance. While all other models had this group, the contribution of macroalgae to total primary production was of relatively minor importance in those models, and the biomass of macroalgae was substantial only in the NorBar model (Table 3). Therefore, it is still possible to make reasonable comparisons of production despite this gap. Similarly, pinnipeds were not included in the GB model due to rare occurrence in the area (Link et al., 2006). This represents an estimate of zero for comparative purposes, rather than a data gap. Perhaps the most substantial gap was that no bacterial group was included in the NorBar model, but all other models had some basic microbial loop included. However, representing microbial loop processes in energy budget models with highly aggregated spatial and temporal scales is difficult and likely subject to high uncertainty; most of our compared models (aside from pelagic microbes in the EBS) used trophically-derived estimates for bacterial standing stock and production because direct information was lacking (Table 2). While comparisons of bacterial production, biomass, and consumption would be useful across all models (and we do present them for the EBS, GOA, GOM, and GB), they are more accurately and precisely estimated using different methods altogether. Therefore, we do not emphasize these comparisons in the present study.

3.3. Lower trophic level energetic comparisons

Lower trophic level comparisons included phytoplankton, zooplankton, and bacterial groups; we compare primary producers first. The annual total primary production derived from the energy budget models was similar across ecosystems, with the exception of a lower value for the combined Norwegian/Barents Sea (Fig. 3, upper). Annual values for the GOM, GB, GOA, and EBS ranged from 3600 to 4700 t km^{-2}, while the NorBar was 1770 t km^{-2} (Table 3). This difference may partially reflect the inclusion of much more low-productivity ocean basin area in the NorBar model relative to the other four, which contained primarily high-productivity continental shelf area (Fig. 1). However, the Norwegian systems are also highest in latitude, with associated lower seasonal light levels and temperature, as well as longer ice cover (see Link et al., in this issue; Drinkwater et al., in this issue; and Mueter et al., in this issue), all of which may contribute to lower primary productivity.

A similar pattern is apparent in the averaged seasonal primary production data (Fig. 3, lower), with the Norwegian ecosystems having lower annual production (less area under the curve) relative to the northeast Pacific and northwest Atlantic systems. However, the satellite data suggest higher overall production per unit area in the (combined) GOM/GB system than in the EBS and GOA systems, in contrast with the energy budget model results. The higher latitude Norwegian systems show an earlier May–June peak in primary productivity relative to the lower latitude GOM/GB systems, which had peak production in July–September. The intermediate latitude northeast Pacific systems show different patterns: the EBS had a late peak in August, while the GOA displayed a steady period of high primary production in May through August. These differing productivity patterns, along with the overall differ-

Table 3

Biomass, production, and consumption (t km^{-2}) by aggregate group for each model. See text for details on group definitions.

Aggregation	Biomass					Production					Consumption				
	EBS	GOA	GOM	GB	NorBar	EBS	GOA	GOM	GB	NorBar	EBS	GOA	GOM	GB	NorBar
Fisheries											4.082	1.438	2.300	2.145	0.867
Toothed whales	0.035	0.062	0.034	0.113	0.070	0.002	0.003	0.001	0.005	0.001	0.610	0.767	0.286	1.559	0.513
Sharks	0.053	0.142	0.009	0.048	0.038	0.005	0.014	0.003	0.007	0.007	0.160	0.531	0.016	0.032	0.113
Pinnipeds	0.195	0.033	0.063	0	0.107	0.013	0.004	0.004	0	0.009	4.054	1.232	0.306	0.000	1.578
Baleen whales	0.541	0.512	0.602	0.417	0.116	0.016	0.018	0.025	0.016	0.003	3.678	3.680	1.385	1.875	1.331
Birds	0.012	0.015	0.004	0.004	0.005	0.002	0.001	0.001	0.001	0.005	0.980	1.147	0.019	0.015	0.589
Pelagic fish	8.581	16.409	7.612	18.529	9.253	9.063	17.306	7.057	17.122	15.857	39.472	76.338	23.419	65.172	87.739
Demersal fish	44.852	26.500	7.387	10.260	1.549	26.224	10.408	3.787	4.698	1.079	114.569	64.514	7.106	12.015	6.234
Megabenthos	3.437	0.635	6.384	7.579	0.149	3.820	0.632	8.376	25.999	0.371	10.740	1.904	67.454	136.419	0.869
Shrimps	19.549	22.229	0.396	0.090	0.278	11.253	12.804	0.792	0.180	0.472	47.102	53.571	1.980	0.450	1.388
Macrobenthos	119.571	41.702	57.784	72.185	66.004	324.728	110.068	134.604	160.946	99.003	1,623.637	550.339	845.354	1,272.301	643.543
Gelatinous zooplankton	1.041	1.049	1.283	1.319	4.000	4.146	5.239	44.906	52.778	16.800	12.009	15.022	187.324	188.788	40.000
Carnivorous zooplankton	19.007	23.059	4.874	3.805	46.455	99.481	122.232	69.448	54.223	80.728	284.231	349.234	177.883	138.887	378.095
Herbivorous zooplankton	22.459	21.864	27.243	25.554	76.705	134.753	131.181	1,091.759	1,324.763	553.465	623.010	606.493	3,822.205	3,777.912	1,672.235
Phytoplankton	42.812	35.519	22.126	25.705	15.000	4,714.881	4,444.443	3,609.674	4,270.433	1,765.500					
Macroalgae	0.748	0.877			4.400	2.993	3.509			2.860					
Bacteria	66.942	19.507	5.484	6.518		2,443.376	712.018	500.411	594.759		6,981.072	2,034.338	2,085.047	2,478.163	
Total producers	43.560	36.396	22.126	25.705	19.400	4,717.874	4,447.952	3,609.674	4,270.433	1,768.360	0	0	0	0	0
Total consumers	239.333	154.211	113.673	139.902	204.727	613.507	409.911	1,360.764	1,640.738	767.801	2,764.253	1,724.770	5,134.735	5,595.427	2,834.227
Total inverts	185.065	110.537	97.964	110.533	193.590	578.181	382.156	1,349.885	1,618.889	750.840	2,600.729	1,576.563	5,102.200	5,514.758	2,736.130
Total vertebrates	54.269	43.673	15.709	29.370	11.138	35.325	27.755	10.879	21.849	16.961	163.524	148.207	32.536	80.669	98.097
Total zooplankton	42.507	45.972	33.399	30.679	127.160	238.380	258.652	1,206.113	1,431.765	650.993	919.251	970.749	4,187.412	4,105.588	2,090.330
Total benthos	142.558	64.565	64.565	79.854	66.430	339.801	123.504	143.772	187.125	99.847	1,681.478	605.813	914.788	1,409.170	645.800
Total fish	53.486	43.051	15.007	28.837	10.840	35.292	27.729	10.848	21.827	16.942	154.201	141.382	30.541	77.220	94.086
Total warm-blooded	0.783	0.622	0.702	0.533	0.297	0.033	0.026	0.032	0.021	0.019	9.323	6.825	1.995	3.450	4.011
Total low TL	153.009	101.875	61.009	62.901	146.560	7,399.630	5,418.622	5,316.198	6,296.957	2,419.353	7,900.323	3,005.087	6,272.459	6,583.750	2,090.330
Total mid TL	195.990	107.474	79.563	108.643	77.232	375.088	151.218	154.617	208.945	116.782	1,835.520	746.665	945.313	1,486.358	739.773
Total high TL	0.836	0.765	0.711	0.581	0.335	0.039	0.041	0.035	0.029	0.025	9.482	7.356	2.010	3.482	4.124

Table 4
Dimensionless ratios calculated for each model.

	EBS	GOA	GOM	GB	NorBar
Biomass ratio					
Benthos/inverts	0.770	0.584	0.659	0.722	0.343
Zoop/invert	0.230	0.416	0.341	0.278	0.657
Pelagics/demersals	0.191	0.619	1.030	1.806	5.972
Pelagics/total fish	0.160	0.381	0.507	0.643	0.854
Demersals/total fish	0.839	0.616	0.492	0.356	0.143
Sharks/total fish	0.001	0.003	0.001	0.002	0.003
Pelagics/zoops	0.202	0.357	0.228	0.604	0.073
Demersals/benthos	0.315	0.410	0.114	0.128	0.023
Zoops/producers	0.976	1.263	1.510	1.193	6.555
Toothed/pelagics	0.004	0.004	0.004	0.006	0.008
Baleen/zoops	0.013	0.011	0.018	0.014	0.001
Shrimp/zoops	0.460	0.484	0.012	0.003	0.002
Shrimp/producers	0.449	0.611	0.018	0.004	0.014
Benthos/producers	3.273	1.774	2.918	3.107	3.424
Production ratio					
Zooplankton/primary	0.051	0.058	0.334	0.335	0.368
Zoop + micro/primary	0.568	0.218	0.473	0.475	0.368
Benthic/primary	0.072	0.028	0.040	0.044	0.056
Fish/primary	0.007	0.006	0.003	0.005	0.010
Mid TL/primary	0.080	0.034	0.043	0.049	0.066
High TL/primary	0.000008	0.000009	0.000010	0.000007	0.000014
Catch ratio					
Catch/primary prod	0.00087	0.00032	0.00064	0.00050	0.00049
Catch/zoop prod	0.017	0.006	0.002	0.001	0.001
Catch/benthic prod	0.012	0.012	0.016	0.011	0.009
Catch/fish prod	0.116	0.052	0.212	0.098	0.051
Catch/fish bio	0.076	0.033	0.153	0.074	0.080
Catch/high TL cons	0.430	0.195	1.144	0.616	0.210

Table 5
Network metrics calculated for each model (based on original, disaggregated models). See text for metric definitions.

Metric	EBS	GOA	GB	GOM	NorBar
Number of species groups (S)	134	118	29	29	57
Number of links (L)	1915	1828	231	233	519
Number of competitive interactions (I)	9473	6994	427	427	1808
Linkage density (L/S)	14.29104	15.49153	7.965517	8.034483	9.105263
Interactive connectance	0.212	0.26	0.531	0.536	0.314
Upper connectance (UC)	0.639	0.639	0.81	0.813	0.729
Directed connectance $L/(S\char`^2)$	0.10665	0.131284	0.274673	0.277051	0.159741
Connectivity (w/o cannibalism)	0.214903	0.264812	0.568966	0.573892	0.325188
Stability proxy ($S \times C$)	28.79699	31.24786	16.5	16.64286	18.53571
Linkage complexity ($\mathrm{UC} \times S$)	85.626	75.402	23.49	23.577	41.553
Number of basal species	4	3	1	1	1
Number of top predators	38	19	4	5	15
Number of intermediate species	92	96	24	23	41
Basal species (%)	2.99	2.54	3.45	3.45	1.75
Top predators (%)	28.36	16.10	13.79	17.24	26.32
Intermediate species (%)	68.66	81.36	82.76	79.31	71.93
Number of cannibals	8	11	19	19	11
Cannibalism (%)	5.97	9.32	65.52	65.52	19.30
Number of 2 species cycles	22	14.5	36.5	35.5	10.5
Cycles (%)	16.42	12.29	125.86	122.41	18.42
Number of omnivores	93	83	26	26	44
Omnivores (%)	69.40	70.34	89.66	89.66	77.19

ences in primary production, may account for some of the other energetic differences between the ecosystems.

There was contrast across systems in the biomass of the other lower trophic level groups, zooplankton and bacteria. Biomass of zooplankton is comparable between Alaskan and northwest Atlantic systems, but is much higher in the Norwegian systems according to the energy budget models (Fig. 4). The estimate for the NorBar, 127 t km^{-2}, is three to four times higher than the estimates for the EBS, GOA, GOM, and GB, which range from 31 to 46 t km^{-2} (Table 3). Biomass of bacteria was highest in the EBS at 67 t km^{-2}, nearly 10 times the values for the GOM and GB ecosystems, and more than 3 times the bacteria biomass for the GOA (bacteria were not included in the NorBar model; Table 3). The total biomass at lower trophic levels was highest in the EBS at 153 t km^{-2}, where zooplankton and primary producers had approximately equal standing stocks and bacterial biomass was high; however, the NorBar system had nearly equivalent high biomass (147 t km^{-2}), composed almost entirely of zooplankton (Table 3). At 61–63 t km^{-2}, lower trophic level biomass in the GOM and GB was less than half that estimated for the EBS and NorBar, and was roughly composed of 50% zooplankton, 40% primary producers, and 10% bacteria. The GOA had a similar distribution of biomass by group, although the total lower trophic level biomass was 102 t km^{-2} (Table 3).

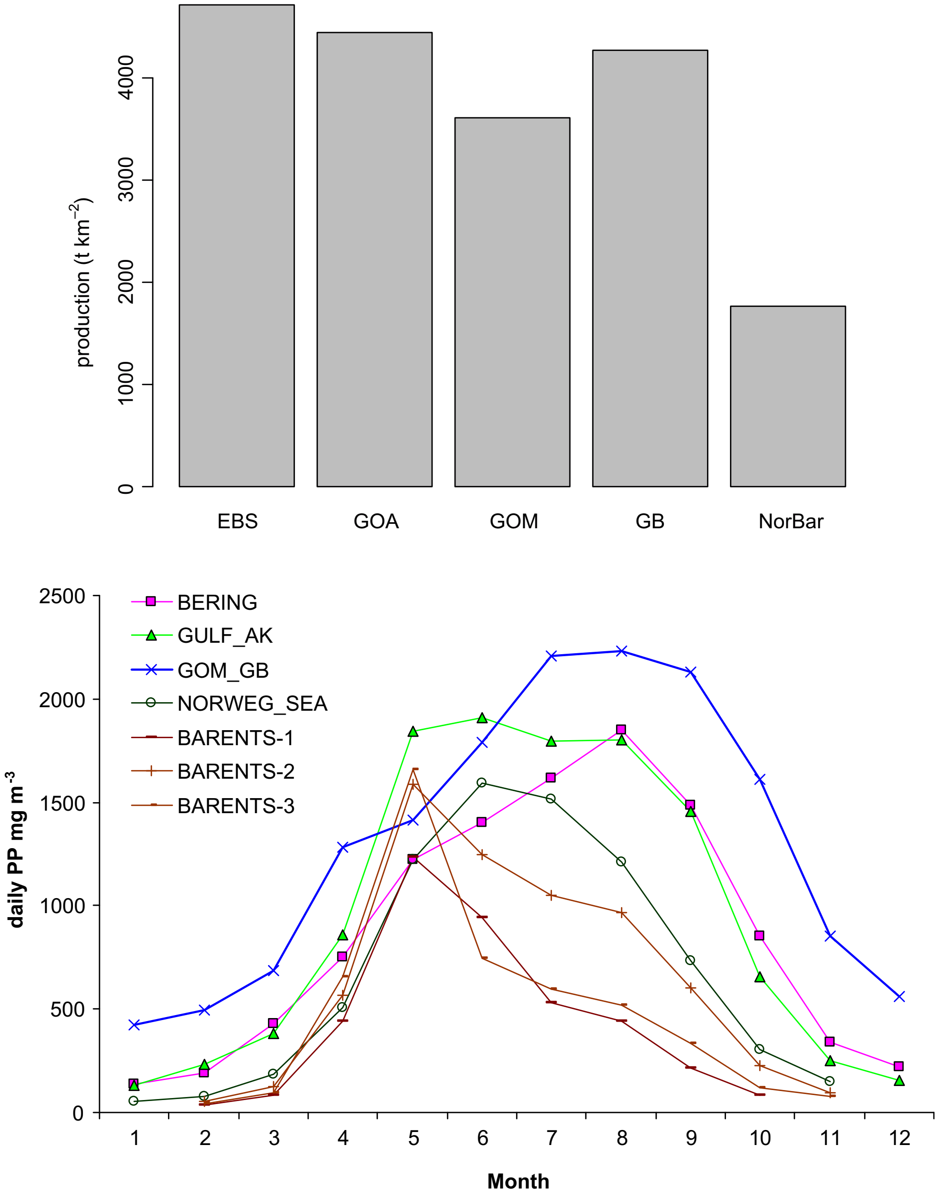

Fig. 3. Annual estimate of primary production for each system from energy budget models (upper) and average annual production cycle from satellite chlorophyll *a* analysis (lower). Lower panel time series refer to areas outlined in Fig. 2.

Comparing the zooplankton production to primary production ratios between each ecosystem shows contrasts between the northeast Pacific systems and all the others: EBS and GOA ratios are around 0.05, while ratios are between 0.30 and 0.40 in the other systems (Table 4, Fig. 5). While primary production was generally similar in the northeast Pacific and northwest Atlantic systems, zooplankton production in the GOM and GB was six times higher than that in the EBS and GOA (Table 3). Given that zooplankton biomass was similar between these systems, the difference in production arises from the P/B ratio for zooplankton between the areas. A similar pattern is apparent when comparing zooplankton consumption between models, suggesting a Q/B difference as well. NorBar zooplankton production was more than double that in the EBS and GOA (similar to the biomass), but the ratio of zooplankton to primary production in the Norwegian systems is nearly equivalent to that of the northwest Atlantic systems due to lower primary production in the NorBar (Tables 3 and 4; Fig. 5). Alaskan systems were also distinct in a further comparison of the ratios of combined zooplankton plus bacterial production to primary production. The high biomass of bacteria in the EBS corresponds to a much higher bacterial production in the EBS relative to the GOA, GOM, and GB systems. While microbial processes are likely not well captured by these models, the inclusion of both bacterial and zooplankton production in the ratio compared to primary production reduces the contrast between the systems somewhat, changing the range of ratios to 0.22–0.57 (Table 4).

3.4. Mid-trophic level comparisons

We included the pelagics, demersals, megabenthos, shrimps, and macrobenthos groups in mid-trophic level comparisons. In contrast with zooplankton biomass which was highest in the NorBar, biomass of benthos (megabenthos, shrimps, and macrobenthos combined) was highest in the EBS, and comparable between the Norwegian, northeast Atlantic, and Gulf of Alaska systems (Fig. 4). Overall, the group contributing the highest proportion of total mid-trophic level (mid-TL) biomass in all five ecosystems was macrobenthos (Table 3, Fig. 6). Biomass of this group ranged

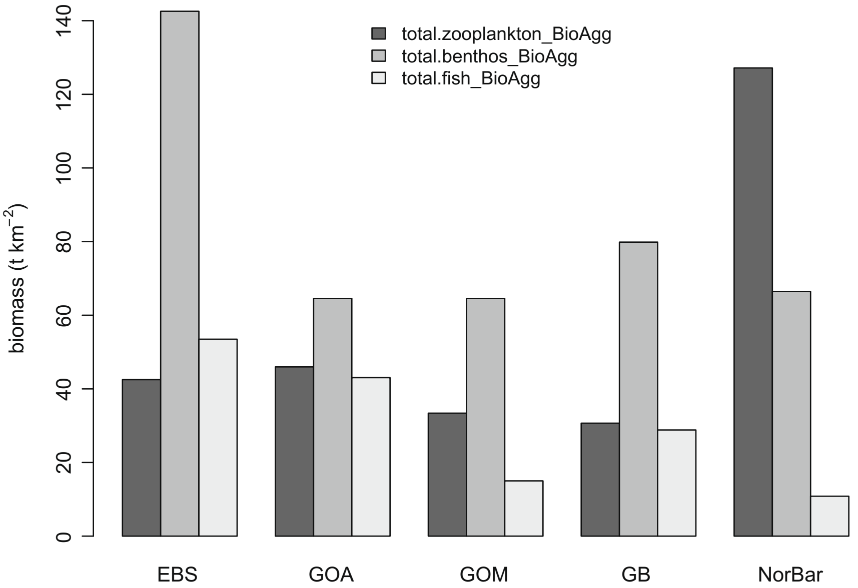

Fig. 4. Total zooplankton, benthic invertebrate, and fish biomass in t/km^2 from energy budget models.

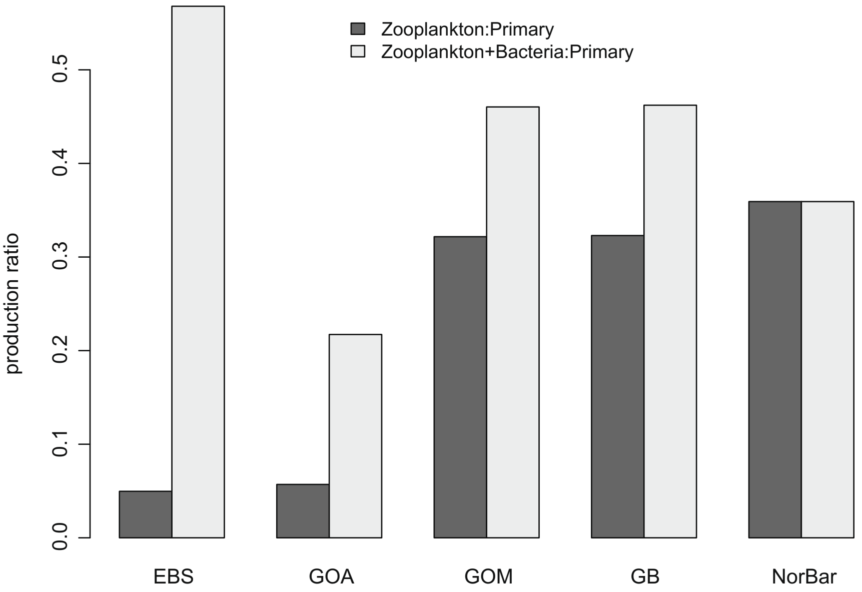

Fig. 5. Ratios of zooplankton production to primary production, and zooplankton + bacterial production to primary production for each ecosystem. Note that the NorBar model does not have a bacteria group.

from a high of 120 t km^{-2} (~60% of mid-TL biomass) in the EBS to a low of 42 t km^{-2} (~40% of mid-TL biomass) in the GOA. Macrobenthos made up the highest proportion of mid-TL biomass, over 85%, in the NorBar. Fish groups comprised the next largest proportion of mid-TL biomass in all ecosystems, from a low of 15% in NorBar to a high of 40% in the GOA. Total fish biomass ranged from highest in the northeast Pacific systems to intermediate on Georges Bank, and lowest in the Gulf of Maine and Norwegian systems (Fig. 4, Table 3). The remaining composition of mid-TL biomass differed greatly between the Pacific and Atlantic systems, with shrimp comprising 10–20% of mid-TL biomass in Alaskan systems, and megabenthos dominating the remaining biomass in the GOM and GB (Table 3). Both shrimp and megabenthos were low biomass groups in the NorBar (Fig. 6).

Differences in pelagic and demersal fish biomass apparent in Fig. 6 translate into a large contrast in pelagic to demersal fish biomass ratios, with a gradient from the EBS low of 0.19 to the Norwegian high of 5.97 (Table 4). Ratios of pelagic to total fish biomass were therefore lowest in Alaskan systems and highest in Norway; conversely, ratios of demersal to total fish biomass showed the opposite trend. Relationships between fish and invertebrates did not scale similarly across ecosystems. The EBS and GOA systems had the highest ratios of demersals to benthic biomass (0.31 and 0.41, respectively; all others <0.13; Table 4), despite the contrast in benthic biomass (EBS was highest, GOA was tied for lowest with GOM; Table 3). Ratios of pelagics to zooplankton biomass were highest in GB (0.60) and lowest in NorBar (0.07), with other systems ranging from 0.20 to 0.36 (Table 4).

The pelagic to demersal biomass ratio also drives fish production and consumption patterns across systems, with the exception of the GOA. While demersal fish biomass dominates in the GOA, pelagic production is higher than demersal production, and the consumption by pelagics and demersals is nearly equal, due to low demersal production rates and relatively high consumption rates for pelagics in that system (Table 3). Differences in production and consumption rates between systems are even more apparent for the commercially important megabenthos group. For example, despite a difference in biomass densities of only a factor of 2 for megabenthos in the EBS, GOM, and GB, the annual consumption by these groups is much higher (by a factor of 6 and 13, respectively) in the GOM and GB (Table 3), similar to the observations for zooplankton reported above.

3.5. Higher trophic level comparisons, including fisheries

We included toothed whales, sharks, pinnipeds, baleen whales, and seabirds in higher trophic level comparisons. Biomass of all high trophic level groups combined was highest in the Alaskan systems, lowest in the Norwegian, and intermediate in the northwest Atlantic systems. Total biomass ranged from a high of 0.84 t km^{-2} in the EBS to a low of 0.34 t km^{-2} in the NorBar (Table 3). Baleen whales were the highest biomass group in this category across all systems, representing 65–85% of total higher TL biomass in all systems except for the NorBar (34%). The GOM had the highest baleen whale biomass of all systems. Aside from baleen whales, different higher TL groups dominated in different systems. Pinniped biomass was highest in the EBS, followed by the NorBar. Shark biomass was highest in the GOA, and toothed whale biomass was highest in the GB (Table 3). Seabird biomass was higher in the Alaskan systems than in other systems.

In this section, we focus on the system-wide energetic demands imposed by higher trophic levels by examining consumption in detail. Consumption patterns by higher TL groups appear consistent with the biomass distribution of these species among systems, although there are some patterns which are magnified due to differences in consumption rates. We present higher TL group consumption alongside fishery catch (Fig. 7). The highest annual fishery catch of 4.08 t km^{-2} was in the EBS, which also had the highest consumption by pinnipeds and baleen whales of any system. In the EBS, fishery catch edges out pinniped consumption (4.05 t km^{-2}) as the highest removal (Table 3, Fig. 7). Baleen whale consumption was equally high in the GOA (3.68 t km^{-2}), but unlike in the EBS, was much higher than all other higher TL consumption, including fishery catch (1.44 t km^{-2}) and pinniped consumption (1.23 t km^{-2}). Fishery catch represented the highest consumption for this category in both the GOM and GB ecosystems (2.30 and 2.14 t km^{-2}, respectively; Fig. 7). Despite the high biomass of baleen whales in both systems, consumption rates were lower than for other systems, so the resulting baleen whale consumption in the GOM and GB (1.38 and 1.88 t km^{-2}, respectively) made up a lower proportion of the total for higher TL groups in the GOM and GB. Toothed whale consumption was highest in the GB, but lowest in the GOM. Consumption by seabirds was highest in the EBS, and GOA, intermediate in the NorBar, and lowest in the GOM and GB (Table 3). This pattern arose from high biomass in the EBS and GOA combined with high consumption rates in the EBS, GOA, and NorBar compared to the other systems. The NorBar has the lowest fishery catch, but otherwise displays a distribution of consumption among higher TL groups most similar to the EBS (Fig. 7).

We used ratios of catch to production at lower and mid-trophic levels, in addition to catch to consumption ratios for higher trophic levels to place fisheries catch within context of the energy budget for each ecosystem. Catch to primary production ratios were uniformly very small, with values ranging from a high in the EBS (8.7 10^{-4}) to a low in the GOA (3.2 10^{-4}) with other systems intermediate and roughly equal (Table 4). The ratio of catch to zooplankton production is also highest in the EBS (0.017, an order of magnitude higher than the Atlantic systems), the GOA is second highest and the remaining systems have comparably low ratios. Ratios of catch to benthic production differ by a factor of 2 between systems, ranging from 0.0087 (NorBar) to 0.016 (GOM; Table 4). There is a bit more contrast in ratios of catch to fish production and biomass across systems: the ratio of catch to both fish metrics was highest in the GOM at 0.21 for production and 0.15 for biomass, followed by the EBS and the GB which both had ratios approximately half that of the GOM (Table 4, Fig. 8). The GOA and NorBar had equally low ratios of catch to fish production (0.05) but ratios of catch to biomass differed substantially between these systems due to different productivity rates of fish. The NorBar ratio of catch to fish biomass (0.08) was slightly higher than that in the EBS, thus ranking second behind the GOM (Table 4). Ratios of catch to total higher TL predator consumption showed slightly different patterns. Although the GOM again had the high-

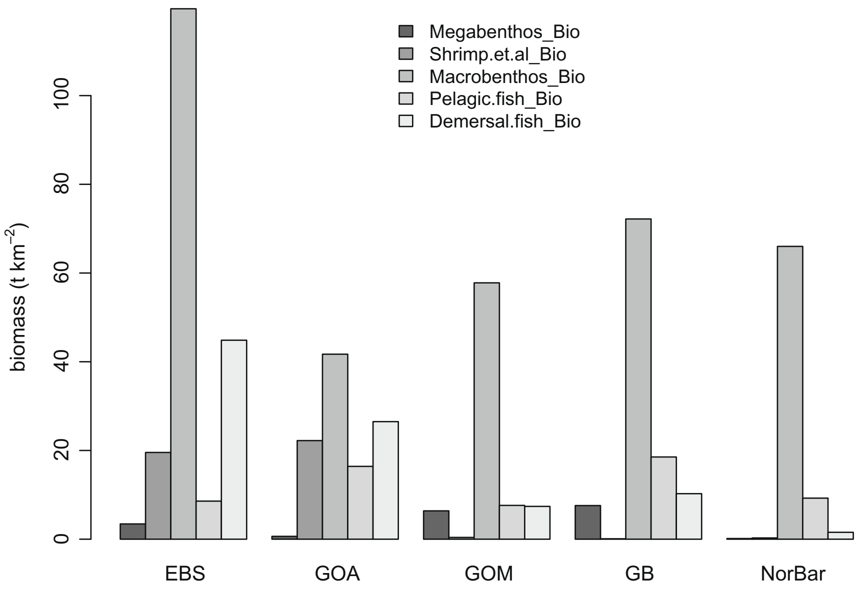

Fig. 6. Biomass of mid-trophic level groups in all systems, including megabenthos, shrimps, macrobenthos, pelagic fish, and demersal fish.

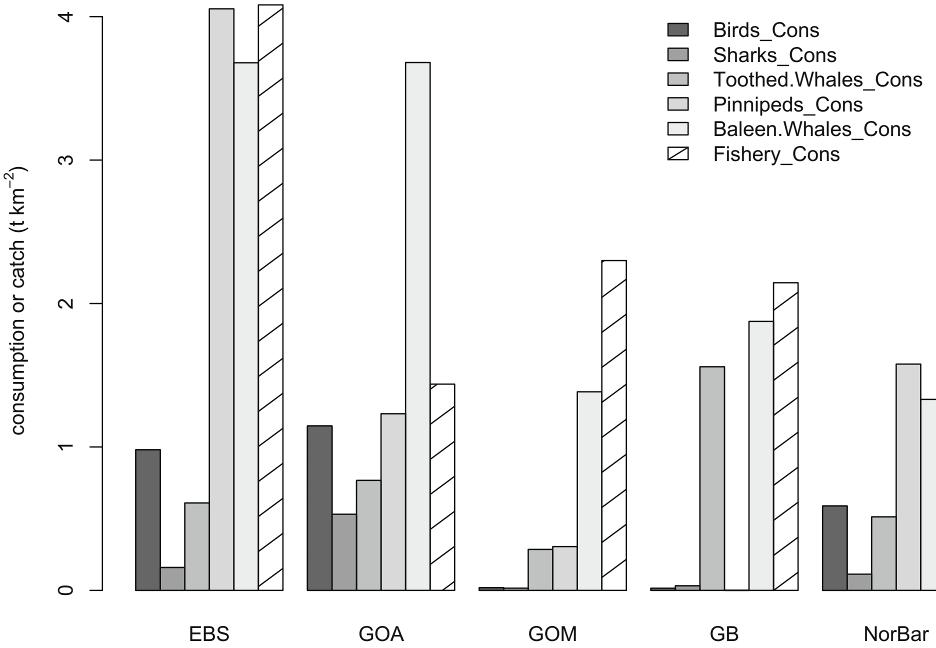

Fig. 7. Consumption of high trophic level functional groups birds, sharks, toothed whales, pinnipeds, and baleen whales, compared with fishery catch in all ecosystems. Pinnipeds are not found in the GB ecosystem.

est ratio (1.14), it was followed by the GB (0.62), and the EBS (0.43), with the GOA and NorBar again having the smallest ratios around 0.20 (Table 4, Fig. 8).

3.6. Network metric comparisons

Network metrics have the potential to reveal structural similarities and differences between the energy budget models, but here mainly reflect the disparate aggregation levels in the original models (Table 5). The level of aggregation inherent in the original models is clearly apparent in the number of species groups (*S*), where the EBS and GOA are highest because they were the most taxonomically disaggregated originally. The GB and GOM models were the most aggregated to begin with, therefore they have the fewest model groups, although these groups were intended to represent many species. The NorBar *S* value was intermediate, reflecting its aggregation level. Related to the number of functional groups is the number of interactions (*L*), which tends to increase with *S*. However, the linkage density (*L*/*S*) does show some contrast, with the Alaskan models having higher densities than the Atlantic models (14–15 vs. 8–9; Table 5). The less aggregated Alaskan models also have generally lower values of connectance (all types) com-

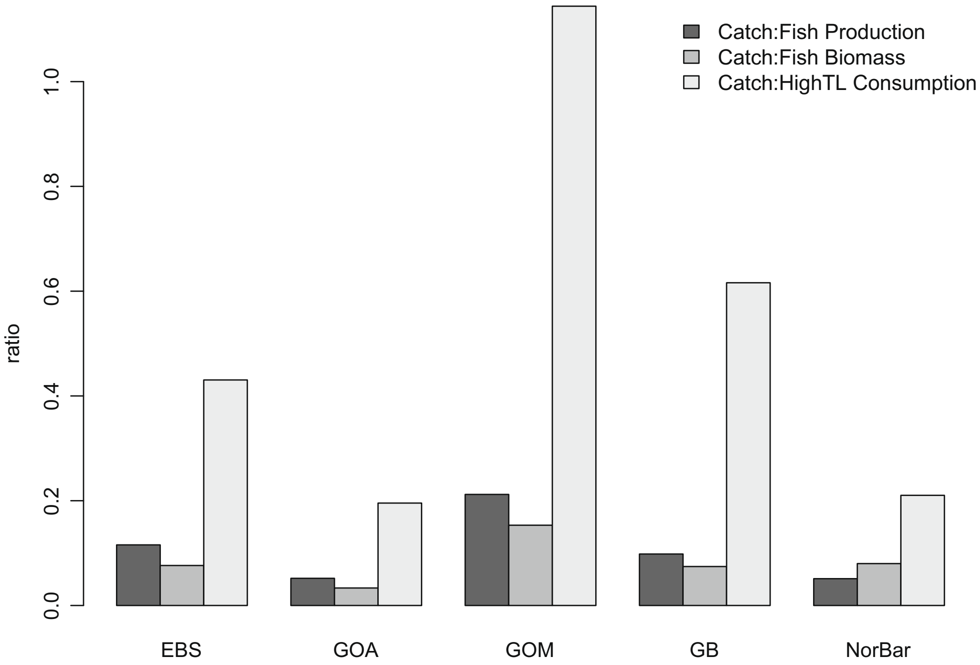

Fig. 8. Ratios of fishery catch to total fish production, total fish biomass, and total high TL predator consumption in each ecosystem.

pared with the more aggregated GOM, GB, and NorBar models, and higher values for the stability proxy and linkage complexity. Comparably aggregated models had nearly identical values of upper connectance, while there was some contrast between the EBS and GOA in interactive and directed connectance and connectivity without cannibalism; all values were higher in the GOA. The GOM and GB had very similar values for network metrics.

While counts of basal species, top predators, and intermediate species also reflect the level of model aggregation, the percentages by number of groups in each category appeared more comparable across differently constructed models. In particular, percentages of top predators and intermediate species show contrast between systems, with the EBS and NorBar having similarly higher top predators and lower intermediate species than the GOA, GOM, and GB (Table 5). The GOM had the lowest percentage of top predators, and the highest percentage of intermediate species. Highly aggregated models such as the GOM and GB are expected to have a high proportion of self-feeding groups, but there was similarity in the number of cannibalistic groups in the Alaskan systems and the NorBar (8–11) despite differences in aggregation level. Finally, the percentage of omnivores was similar across models despite differences in aggregation (Table 5).

4. Discussion

This comparison is based primarily on energy budget models which were built by different research groups for slightly different time periods, have had different levels of peer review and revision, and used different assumptions where data were missing. Comparing different time periods within a system or between systems has the potential to change our view of energy flow. For example, previous analyses suggest that the EBS energy balance was fundamentally different between the 1950s and the 1980s (Trites et al., 1999), and certainly there have been major changes documented in the Northwest Atlantic systems over the past several decades (e.g., Fogarty and Murawski, 1998). However, the models compared here differ by at most a single decade at the extreme ends of the timeframes for all of them (1990–2000). While we feel the time periods are generally comparable, we cannot rule out that methodological differences in the details of model construction may account for some of the results shown here. In particular, we found it challenging and perhaps counterproductive to compare network metrics for models with widely different aggregation levels, given that most of the standard metrics we calculated are highly correlated with the number of model groups (S). However, disaggregating each model to a similar species level was beyond the scope of this work. We still consider this set of network metrics valuable as an ecosystem comparison tool, so we have retained it here as an example of the method, but with the caveat that future work should focus on separating aggregation effects from ecosystem attributes in network analysis where possible.

Our results clearly demonstrate, however, that aggregating the mass balance models into the same broad functional groups for comparison greatly reduced the importance of individual details of model parameterization described above and allowed a reasonable view of the "big picture" energy flow and structure in each ecosystem. Overall, these high latitude ecosystems were similar in having seasonally cyclical but high primary productivity, high fishery catch, high biomass of baleen whales and macrobenthos, and apparent tradeoffs between benthic and pelagic energy pathways. The main differences between the systems were observed in four attributes: (1) biomass distributions of pelagic versus demersal fish groups, (2) biomass of shrimp versus megabenthos, (3) zooplankton biomass and production, and (4) the ratio of fishery catches to higher trophic level consumption.

Lower trophic level comparisons were perhaps most affected by the differences between models which remained after aggregation. Because the NorBar model did not include bacteria, we were unable to compare this component of the energy budgets between areas. Modeling microbial loop processes in full ecosystem energy budgets is a continuing challenge in many of the ecosystems which did include bacterial groups, so future research in all areas should focus on filling this gap. Habitat differences are another important consideration. While the EBS, GOA, GB and to a lesser extent the GOM were specifically defined to include the continental shelf region of highest fishery and primary production, the NorBar model encompasses both continental shelf and deep ocean basins, which include both high and low productivity habitats. Therefore, the generally lower production observed across trophic levels in the NorBar model may partially result from differences in model scope. However, seasonal patterns in primary production derived from independent satellite data show that the Norwegian and Barents Seas had generally lower monthly productivity than the other ecosystems, as well as a shorter productive season. This corroborates that there may be generally lower production in the NorBar relative to the other systems, even though the difference in habitats may bias productivity lower in the NorBar than in the other models. Additional work focused on energetic comparisons within distinct habitat types (i.e., smaller scales) would improve the general picture of relative productivity from this initial comparison.

Patterns observed in the low and mid-trophic level biomass and production comparisons suggest that there are different dominant energy pathways in each system. Overall, benthic and demersal pathways seem dominant in the EBS while pelagic energy seems dominant in the NorBar. The GOA, GB and GOM appear to have more mixed benthic and pelagic energy pathways, depending on the trophic level. One obvious indicator of pathway dominance is the pelagic to demersal fish biomass ratio, which is lowest in the EBS and highest in the NorBar. Biomass ratios of benthos and zooplankton to all invertebrates again appear to reflect the relative dominance of benthic versus pelagic energy flow pathways in each system, with EBS and GB having high benthic and low pelagic invertebrate (zooplankton) to total invertebrate ratios, the GOA and GOM intermediate, and the NorBar much lower benthic and higher pelagic invertebrate distributions. The extremely high standing stock of zooplankton in the NorBar relative to all other systems also suggests a strong pelagic pathway. These patterns may reflect bathymetry and habitat type to a certain extent; the EBS and GB are shallow shelves where benthic influences are likely to be strong, the NorBar may be dominated by the pelagic influence of the offshore Norwegian Sea ecosystem, and the GOA and GOM are shelf areas with deeper basins contained therein, leading to more mixed energy pathways in these spatially aggregated energy budget models (see the full ecosystem descriptions in Drinkwater et al., in this issue; Link et al., in this issue; and Mueter et al., in this issue). Comparisons within a single region have also shown this pattern reflecting habitat type; the Aleutian Islands ecosystem in Alaska, also a narrow shelf surrounded by deepwater oceanic ecosystem, has a clearly dominant pelagic energy pathway relative to the EBS and GOA (Aydin et al., 2007).

One system does not fit as well with the pattern described above based on bathymetry and habitat type alone. While there is a high biomass of benthos in the shallow shelf GB ecosystem, second only to the EBS value, the ratio of pelagic to demersal fish is also high, second only to the NorBar value. The combined effects of historical heavy exploitation of demersal fish, subsequent predation effects, and the environmental attributes of the GB may contribute to this mixed energetic picture, where the dominance of pelagic fish is a relatively recent phenomenon (Spencer and Collie, 1997; Fogarty and Murawski, 1998; Link et al., 2002; Collie et al., 2004). The high biomass of commercially important megabenthos in both the GOM and GB is also distinct from this region. Given the history of intensive whaling in all of these ecosystems, it was somewhat surprising that baleen whale biomass remained the largest component of higher TL biomass in all systems; if this represents relatively low whale stocks then the energy budgets of these systems may have looked substantially different with unexploited whale populations (Clapham and Link, 2006). Fishery removals are also important components of higher trophic level energetics in all five ecosystems, where they are at a similar scale to consumption by predators. The GOA and NorBar appear to be the most lightly fished systems in our comparison; they have the lowest ratios of catch to higher TL consumption, and are the only systems where at least one high TL group's consumption (baleen whales) exceeds fishery catch on a per unit area basis. In contrast, the GOM, GB, and EBS have the highest ratios of catch to higher TL consumption and to fish production, suggesting that fishing might be more likely to have obvious effects on energy flow here than in the GOA and NorBar, at least for the time periods modeled.

The pelagic to demersal biomass ratio was considered one of the most robust indicators of fishing effects in an exhaustive review and simulation analysis by Fulton et al. (2005). Based on experience in the GB and in other heavily exploited systems, Link (2005) suggests that a warning threshold has been crossed when pelagic fish biomass exceeds 75% or drops below 25% of total fish biomass. However, our results are somewhat counterintuitive with respect to this indicator and fishing in the ecosystems exhibiting extreme values of pelagic to demersal biomass. The NorBar pelagic to total fish biomass ratio is 0.85, despite the fact that fishery catch is lowest in this system relative to all the others. The EBS ratio is 0.16 according to our results (and catch per unit area is highest there, comprised almost entirely of demersal fish). While the extreme values of this ratio could be partially attributable to our original mappings of key species and age groups into pelagic and demersal functional groups, they were mapped consistently between ecosystems and so still clearly show a major contrast between the EBS and NorBar. What is unclear is whether the energetic indicator baselines and thresholds should be equivalent for all systems, especially when comparisons are based only on static snapshots, which may represent the results of multiple different or interacting processes. For example, while there is a strongly supported hypothesis that heavy fishing altered dominant energy pathways from benthic to pelagic in the GB, a climate-related biophysical hypothesis for shifts in energy pathways has been developed for the EBS (e.g., Hunt et al., 2002). Both bio-physical and predator-prey hypotheses have been posed for a recently observed shift from shrimp to groundfish dominance in the GOA as well (Anderson and Piatt, 1999; Bailey, 2000), although our results show that shrimp biomass and production are still higher in Alaskan systems compared with Atlantic systems. Given that multiple mechanisms may shift energy flow between major pathways in marine ecosystems, and that fishing is an important factor in all of these systems, it is important to remember that our results are snapshots summarizing multiple cumulative effects.

In summary, energy budget comparisons were relatively simple to complete yet provide valuable insights into basic ecosystem structure and function. While there are similarities between the systems in terms of high primary and fisheries production, there are also clearly differences between the ecosystems, in particular with respect to benthic and pelagic energy pathways, which may suggest different fishery management strategies. As climate warming becomes a more important factor in high-latitude ecosystems, energy may be redirected through different pathways, so this comparison may be viewed as baseline information. Therefore, these results represent the first step in continued comparisons which should ultimately include time series information for each system to develop system-appropriate indicators and management thresholds.

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References

Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189, 117–123.

Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., Friday, N., 2007. A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. US Department of Commerce. NOAA Tech. Memo, NMFS-AFSC-178, 298p.

Bailey, K.M., 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Marine Ecology Progress Series 198, 215–224.

Bax, N.J., 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals on six marine ecosystems. ICES Marine Science Symposium 193, 217–224.

Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42, 1–20.

Briand, F., 1985. Structural singularities of freshwater food webs. Internationale Vereingung für theoretische und angewandte Limnologie, Verhandlungen 22, 3356–3364.

Briand, F., Cohen, J.E., 1984. Community food webs have scale-invariant structure. Nature 307, 264–266.

Christensen, V., Pauly, D., 1992. Ecopath II – a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61, 169–185.

Christensen, V., Walters, C., 2004. Ecopath with Ecosim: methods, capabilities, and limitations. Ecological Modelling 172, 109–139.

Christensen, V., Walters, C.J., Pauly, D., 2004. Ecopath with Ecosim: a User's Guide. Fisheries Center Research Reports, vol. 12(4), University of British Columbia, Vancouver, 154p. Available from: <http://www.ecopath.org and http://www.fisheries.ubc.ca>.

Clapham, P.J., Link, J.S., 2006. Whales, whaling and ecosystems in the North Atlantic Ocean. In: Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M., Brownell, R.L. (Eds.), Whales, Whaling and Ecosystems. University of Chicago Press, pp. 314–323.

Cohen, E.B., Grosslein, M.D., Sissenwine, M.P., Steimle, F., Wright, W.R., 1982. Energy budget of Georges Bank. Canadian Special Publication of Fisheries and Aquatic Sciences 59, 95–107.

Collie, J.S., Richardson, K., Steele, J.H., 2004. Regime shifts: can ecological theory illuminate the mechanisms? Progress in Oceanography 60, 281–302.

Daskalov, G.M., Grishin, A.N., Rodionov, S., Mihneva, V., 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. PNAS 104, 10518–10523.

Drinkwater, K.F., Mueter, F.J., Friedland, K.D., Taylor, M., Hunt, G.L., Jr., Hare, J.A., Melle, W., this issue. Recent climate forcing and physical oceanographic changes in Northern Hemisphere regions: a review and comparison of four marine ecosystems. Progress in Oceanography, doi:10.1016/j.pocean.2009.04.003.

Fogarty, M.J., Murawski, S.A., 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecological Applications 8 (1), 6–22 (supplement).

Francis, R.C., Hare, S.R., Hollowed, A.B., Wooster, W.S., 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7, 1–21.

Fulton, E.A., Smith, A.D.M., Punt, A.E., 2005. Which ecological indicators can robustly detect the effects of fishing? ICES Journal of Marine Science 62, 540–551.

Hunt Jr., G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Research II 49, 5821–5853.

Link, J., 2002. Does food web theory work for marine ecosystems? Marine Ecology Progress Series 230, 1–9.

Link, J.S., 2005. Translation of ecosystem indicators into decision criteria. ICES Journal of Marine Science 62, 569–576.

Link, J.S., Garrison, L.P., 2002. Trophic ecology of Atlantic Cod *Gadus morhua* on the Northeast US Continental Shelf. Marine Ecology Progress Series 227, 109–123.

Link, J.S., Brodziak, J.K.T., Edwards, S.F., Overholtz, W.J., Mountain, D., Jossi, J.W., Smith, T.D., Fogarty, M.J., 2002. Marine ecosystem assessment in a fisheries management context. Canadian Journal of Fisheries and Aquatic Science 59, 1429–1440.

Link, J.S., Griswold, C.A., Methratta, E.T., Gunnard, J. (Eds.), 2006. Documentation for the Energy Modeling and Analysis eXercise (EMAX). US Dep. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 06–15. National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026, 166p.

Link, J.S., O'Reilly, J., Dow, D., Fogarty, M., Vitaliano, J., Legault, C., Overholtz, W., Green, J., Palka, D., Guida, V., Brodziak, J., 2008. Comparisons of the Georges Bank Ecological Network: EMAX in Historical Context. Journal of Northwest Atlantic Fishery Science 39, 83–101.

Link, J.S., Stockhausen, W.T, Skaret, G., Overholtz, W., Megrey, B.A., Gjøsæter, H., Gaichas, S.K., Dommasnes, A., Falk-Petersen, J., Kane, J., Mueter, F.J, Friedland, K.D, Hare, J.A., in this issue. A comparison of biological trends from four marine ecosystems: synchronies, differences, and commonalities. Progress in Oceanography, doi:10.1016/j.pocean.2009.04.004.

Martinez, N.D., 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecological Monographs 61 (4), 367–392.

Megrey, B.A., Aydin, K.Y., 2009. A macrodescriptor perspective of ecological attributes for the Bering and Barents Seas. Deep Sea Research II. in press, doi:10.1016/j.dsr2.2008.11.024.

Megrey, B.A., Hare, J.A., Stockhausen, W.T., Dommasnes, A., Gjøsæter, H., Overholtz, W., Gaichas, S.K., Skaret, G., Falk-Petersen, J., Link, J.S., Friedland, K.D., in this issue. A cross-ecosystem comparison of spatial and temporal patterns of covariation in the recruitment of functionally analogous fish stocks. Progress in Oceanography, doi:10.1016/j.pocean.2009.04.006.

Mueter, F.J., Broms, C., Drinkwater, K.F., Friedland, K.D., Hare, J.A., Hunt, G.L., Jr., Melle, W., Taylor, M., in this issue. Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems. Progress in Oceanography, doi:10.1016/j.pocean.2009.04.018.

Overland, J.E., Stabeno, P.J., 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? EOS Transactions American Geophysical Union 85, 309–312.

Pauly, D., Christiensen, V., Walters, C., 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science 57, 697–706.

Polovina, J.J., 1984. Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3, 1–11.

Skaret, G., Pitcher, T.J., in press. An ecosystem model of the Norwegian Sea and Barents Sea fitted to data Fisheries Centre Research Reports, Fisheries Centre, UBC, Vancouver, Canada.

Spencer, P.D., Collie, J.J., 1997. Effect of nonlinear predation rates on rebuilding the Georges Bank haddock (*Melanogrammus aeglefinus*) stock. Canadian Journal of Fisheries and Aquatic Sciences 54, 2920–2929.

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A.M., Pauly, D., 1999. Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. UBC Fisheries Centre Research Reports 7 (1), 106.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7, 139–172.

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D., Pavlova, O., 2006. Food webs and carbon flux in the Barents Sea. Progress in Oceanography 71, 232–287.

Yodzis, P., 1980. The connectance of real ecosystems. Nature 284, 544–545.