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A comparison of biological trends from four marine ecosystems: Synchronies, differences, and commonalities

Jason S. Link[a,*], William T. Stockhausen[b], Georg Skaret[c], William Overholtz[a], Bernard A. Megrey[b], Harald Gjøsæter[c], Sarah Gaichas[b], Are Dommasnes[c], Jannike Falk-Petersen[d], Joseph Kane[e], Franz J. Mueter[f], Kevin D. Friedland[e], Jonathan A. Hare[e]

[a] *National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543, USA*
[b] *National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA*
[c] *Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, Norway*
[d] *Polar Environmental Centre, University of Tromsø, N-9296 Tromsø, Norway*
[e] *National Marine Fisheries Service, Northeast Fisheries Science Center, 28 Tarzwell Drive, Narragansett, RI 02882, USA*
[f] *Sigma Plus Statistical Consulting, 697 Fordham Drive, Fairbanks, AK 99709, USA*

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ABSTRACT

Major features of four marine ecosystems were analyzed based on a broad range of fisheries-associated datasets and a suite of oceanographic surveys. The ecosystems analyzed included the Gulf of Maine/Georges Bank in the Northwest Atlantic Ocean, the Norwegian/Barents Seas in the Northeast Atlantic Ocean, and the eastern Bering Sea and the Gulf of Alaska in the Northeast Pacific Ocean. We examined survey trends in major fish abundances, total system fish biomass, and zooplankton biomasses. We standardized each time series and examined trends and anomalies over time, using both time series and cross-correlational statistical methods. We compared dynamics of functionally analogous species from each of these four ecosystems. Major commonalities among ecosystems included a relatively stable amount of total fish biomass and the importance of large calanoid copepods, small pelagic fishes and gadids. Some of the changes in these components were synchronous across ecosystems. Major differences between ecosystems included gradients in the magnitude of total fish biomass, commercial fish biomass, and the timing of major detected events. This work demonstrates the value of comparative analysis across a wide range of marine ecosystems, suggestive of very few but none-the-less detectable common features across all northern hemisphere ocean systems.

1. Introduction

The ecosystem approach to fisheries (EAF) requires a basic understanding of the important processes controlling marine ecosystem productivity. A necessary first step toward understanding any ecosystem is to determine its community structure and function, and associated variability. Obtaining such understanding has proved difficult because of the complexity of marine ecosystems and their many components. Ecosystem considerations in a marine scientific and management context have been extant for more than a century (e.g. Baird, 1873), but making them operational in the context of EAF has remained a key challenge. Research needs to be extended to encompass the full suite of structures and processes related to the functioning of ecological systems (production, consumption, respiration, energy flow and cycling) and their link to physical systems (advection, mixing, front genesis, stratification, light). Ultimately, we need to seek general relationships among patterns and processes in the world's marine ecosystems.

One method that has provided significant insights into understanding marine ecosystem functioning has been the comparative approach. This method has been used successfully to elucidate commonalities for particular species (for example cod,, c.f. ICES/GLOBEC Cod and Climate Change; Brander, 1994, 1995; Drinkwater, 2005; Dutil and Brander, 2003; Planque and Frédou, 1999; Rätz and Lloret, 2003) and for particular groups of species within ecosystems (for example small pelagics, c.f. GLOBEC Small Pelagic Fishes and Climate Change; Alheit and Eberhard, 1997; Hunter and Alheit, 1995; Kim and Kang, 2000; Mullon et al., 2003; Santos et al., 2007). Comparisons can also be made at the system-level (e.g. Hunt and Megrey, 2005; Moloney et al., 2005). In many respects, comparisons of similar ecosystems serve as *ad hoc* replicate responses akin to an experiment, highlighting common, unique and fundamental features, as well as important drivers that influence the processes in marine ecosystems. These comparative analyses allow the opportunity for taking a broader ecosystem perspective and permit the ability to draw generalizations important to successful implementation of EAF.

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[*] Corresponding author. Tel.: +1 508 4952340; fax: +1 508 4952258.
E-mail address: Jason.Link@noaa.gov (J.S. Link).

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Such generalizations will also be important in determining marine ecosystem responses to climate change.

Global fisheries landings (Garcia et al., 2003) are dominated by regions with a relatively high primary productivity, are usually found on continental shelves, and are often associated with prominent warmer or nutrient-laden physical oceanographic features (Bax, 1998; Sherman, 1991). Four example northern hemisphere marine ecosystems all match these conditions: the eastern Bering Sea, Gulf of Alaska, Georges Bank/Gulf of Maine, and the Barents/Norwegian Sea. Recognizing these commonalities, and based upon a shared expressed interest in bi-national cooperation and collaboration between the two countries, the Marine Ecosystems of Norway and the U.S. (MENU) project was established to execute a series of comparative studies.

The overall objectives of MENU were to: (1) compare time series of the environment, biota, and fisheries from these four northern hemisphere marine ecosystems; (2) elucidate pan-basin synchronies and differences, with a particular emphasis on climate change relationships, and (3) establish any correlative linkages between the environment and fish with the responding biota. This particular contribution addresses the first and second MENU objectives. Additionally, this contribution provides much of the background information upon which a series of related papers are based (Drinkwater et al.; Gaichas et al.; Megrey et al.; Mueter et al.; all this volume).

2. Ecosystem overviews

2.1. The Eastern Bering Sea

The eastern Bering Sea (EBS; Figs. 1 and 2) has a shallow (average depth of 70 m) and broad (500–800 km; Hunt and Megrey, 2005) continental shelf, with an abyssal Aleutian Basin in the southwest and the Aleutian Island chain to the south (Coachman, 1986; NRC, 1996). Current flow is generally cyclonic within the abyssal basin (NRC, 1996), with an easterly-flowing current along the Aleutian chain (the Aleutian North Slope Current; Reed and Stabeno, 1999) and a northwestwardly-flowing boundary current associated with the shelf edge (the Bering Slope Current; Schumacher and Reed, 1992). The principal sources of inflow are through passes between the Aleutian Islands, and through coastal riverine inputs (NRC, 1996; Stabeno et al., 2005). Outflow occurs through the Bering Strait northward into the Chukchi Sea (NRC, 1996). Tidal currents dominate the weak mean flow on the shelf (Coachman, 1986; Kowalik, 1999), where stratification is roughly a function of water depth (Kinder and Schumacher, 1981).

The EBS experiences seasonal ice cover that influences water temperatures, water column stratification, nutrient mixing, the fate of primary production and the structure and function of the pelagic and benthic communities (Grebmeier et al., 2006; Hunt et al., 2002). Overall, primary production on the shelf is high, but this varies spatially with the domain structure (Hansell et al., 1993; Sakshaug, 2004).

Currently this ecosystem supports about one-half of the annual US fish and shellfish harvest, including the largest single-species commercial fishery in the world, walleye pollock (*Theragra chalcogramma*; Napp and Hunt, 2001; NMFS, 2005). The walleye pollock constitutes approximately 50% the total biomass of assessed fish species in this ecosystem (NPFMC, 2004). Forage fish (e.g. Pacific herring *Clupea pallasi*, capelin *Mallotus villosus*, eulachon *Thaleichthys pacificus*, and juvenile walleye pollock) provide a prey base for marine mammals and seabirds, as well as for larger and commercially important piscivorous fish (Loughlin et al., 1999). Abundance of forage fishes show great interannual variation, as well as

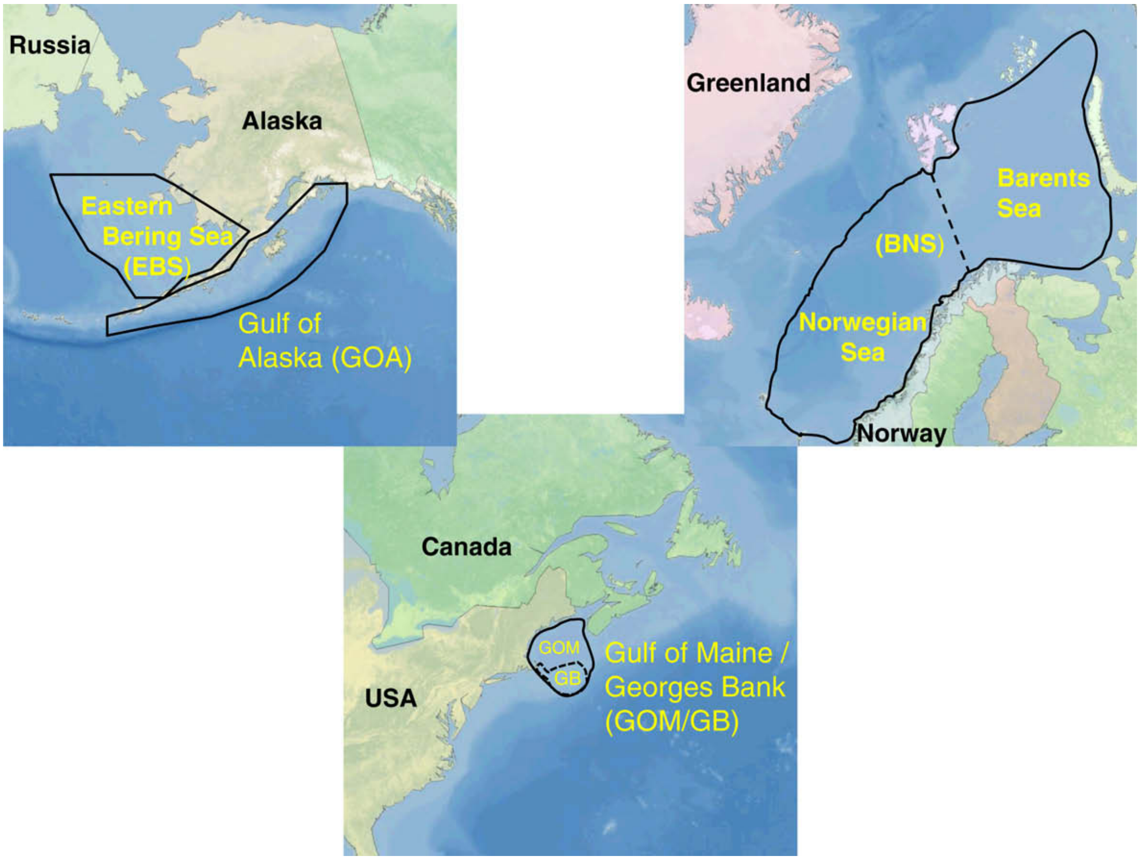


Fig. 1. Maps depicting the four marine ecosystems in this study.

longer term trends. Concurrent with a decline in forage fishes in the mid-1970's to mid-1980's, adult pollock, Pacific cod (*Gadus macrocephalus*), and several flatfish species increased in biomass and stabilized. Biomass of the two gadids and flatfish was three times higher in 1999 than it had been in 1975 (Hunt et al., 2002).

Large invertebrates are also important in the ecosystem. King (*Lithodes* and *Paralithodes* spp.) and tanner (*Chionoecetes* spp.) crabs are bottom-foraging omnivores found on the Bering Sea shelf that support (or have supported) important commercial fisheries. Several species of squid (*Berryteuthis* spp. and *Gonatus* spp.) inhabit the Bering Sea seasonally; juveniles play a role similar to that of forage fishes: providing an important food source for larger cephalopods, fish, birds, and marine mammals (NRC, 1996). Large jellyfish (e.g. *Chrysaora melanaster*) may be important predators on walleye pollock and other larval fishes (Brodeur et al., 2002).

Several species of seabirds and marine mammals occupy the top trophic levels of the EBS ecosystem. Declines in several seabird species indicate the carrying capacity of the region may have decreased (Hunt et al., 2002), while a few marine mammal species are regarded with concern (Loughlin et al., 1999).

2.2. The Gulf of Alaska

The Gulf of Alaska (GOA; Figs. 1 and 2) ecosystem occupies a similar geographic location and biological ecotone as the Bering Sea. The GOA has a narrow, deeper shelf (>200 m) and the system is more dynamic (i.e. faster and stronger currents); advection and cross shelf recirculation of nutrients are prominent features.

Freshwater input is a major determinant of salinities in the upper water column of the coastal GOA and is important to the timing and strength of stratification in the spring and summer (Weingartner et al., 2002). These distributed freshwater sources set up a buoyancy-driven coastal current that follows the perimeter of the GOA before entering the southeastern Bering Sea. Offshore of the coastal current, the swift subarctic current flows cyclonically around the GOA and frequently impinges upon the shelf, exchanging nutrients and biota across the shelf break.

The GOA fish fauna consist of a mix of temperate and subarctic species (Mueter and Norcross, 2002). Annual groundfish, salmon, herring and shellfish landings from the GOA average 360,000 metric tons (NPFMC, 2002). Marine mammal and bird populations are also important components of the upper trophic levels.

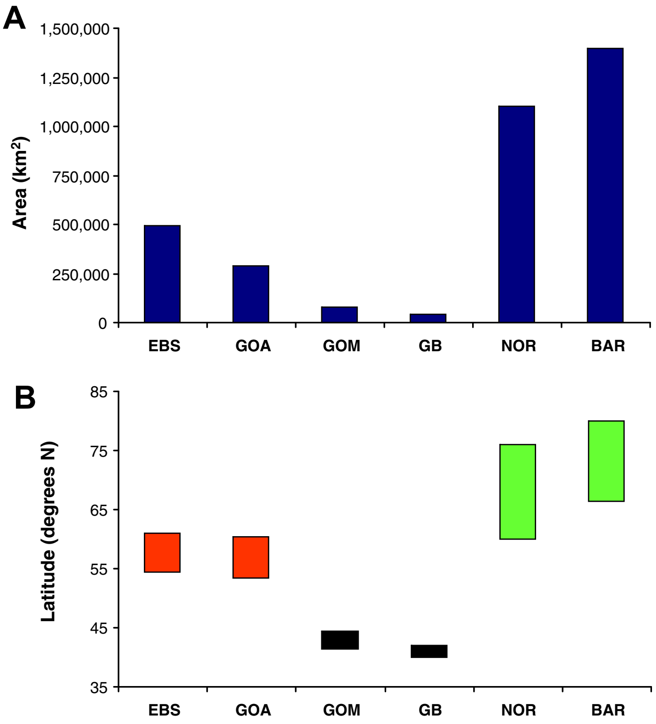


Fig. 2. (A) Surface area of each of the ecosystems in this study (km^2). (B) Latitudinal range of each of the ecosystems in this study (°N).

2.3. Gulf of Maine and Georges Bank

The Gulf of Maine and Georges Bank region are part of the northeast US continental shelf ecosystem (GOM-GB; Sherman, 1991; Figs. 1 and 2). The Gulf of Maine averages 150 m in depth. Georges Bank flanks the Gulf of Maine to the south and is a large topographic high, with an average depth of 70 m.

In general terms, the circulation in this ecosystem is predominantly from northeast to southwest. Water enters the Gulf of Maine from the Scotian Shelf and from the Northeast Channel. This flow travels counterclockwise around the Gulf of Maine. Some exits through the Great South Channel, while the remainder flows eastward along the northern flank of Georges Bank. This eastward flow contributes to the anti-cyclonic circulation on Georges Bank, with some of this flow recirculating at the Great South Channel, while some continues southwestward along the remainder of the northeast U.S. shelf. Tidal-scale forcing is also an important component of the physical dynamics, with the shallower portions of Georges Bank remaining well mixed even during periods of stratification over the deeper portions of Georges Bank and the Gulf of Maine. Flows onto and alongshore the Mid Atlantic Bight (the region south of Gulf of Maine and Georges Bank) have had some drastic effects on water mass properties, as has the changing influence of Labrador slope and Scotian Shelf waters into the Gulf of Maine (Mountain, pers. comm.; Drinkwater and Mountain, 1997). For more details about physical oceanographic factors, see Link and Brodziak (2002), Mountain (1989), and Taylor and Bascunán (2001).

These subregions are highly productive and have supported significant commercial fisheries for multiple centuries (Sissenwine et al., 1984). Georges Bank has remained remarkably consistent in its overall primary production, with production and standing stock biomass of phytoplankton relatively stable over the past few decades (O'Reilly and Zetlin, 1998; O'Reilly, pers. comm.).

The recent history of the component fish stocks has exhibited the classic cycles of excessive effort, stock declines, and iterations thereof until the point of sequential stock depletion (Fogarty and Murawski, 1998; Murawski et al., 1997; Serchuk et al., 1994). The fish community has shifted from dominance by groundfish species (e.g. cod, haddock; Table 1) to small pelagics (e.g. herring and mackerel; Table 1; Fogarty and Murawski, 1998; Link and Brodziak, 2002; Overholtz, 2002; Serchuk et al., 1994).

While the various fisheries and their effects were occurring, notable changes to protected, endangered and threatened species (e.g. many marine mammals) have also occurred, with many in more critical condition than 50 years ago (Waring et al., 2004). Additionally, shifts in non-targeted fauna (e.g. some benthos, some non-targeted fishes) occurred (Link and Brodziak, 2002), with some actually persisting at relatively stable levels or even increasing (Link and Brodziak, 2002; Link, 2005).

2.4. The Barents and Norwegian Sea Ecosystems

The Barents Sea (BAR) is a large marine ecosystem covering an area of ca. 1.4×10^6 km^2 (Carmack et al., 2006; Figs. 1 and 2). The complex bottom topography with isolated banks and deeper troughs strongly influences the circulation and distribution of water masses in the Barents (Carmack et al., 2006).

Table 1A
Functionally analogous fish species for the four different ecosystems.

	Eastern Bering Sea	Gulf of Alaska	Gulf of Maine/Georges Bank	Norwegian Sea/Barents Sea
Herring	Pacific herring		Atlantic herring	Atlantic herring
Mackerel			Atlantic mackerel	Atlantic mackerel
Cod	Pacific cod	Pacific cod	NW Atlantic cod	NE Arctic cod
Haddock			Haddock	Haddock
Medium Gadids	Walleye pollock	Walleye pollock	Silver hake	Blue whiting
Saithe			Pollock	Saithe
Pleuronectids	Greenland Turbot	Pacific halibut	Yellowtail flounder	Greenland halibut
Capelin	Capelin	Capelin		Capelin
Sebastes spp.	Rockfish	Rockfish	Redfish	Redfish

Table 1B
Taxonomy of functionally analogous species.

Common name	Family	Genus species name
Pacific herring	Clupeidae	*Clupea harengus pallasi*
Atlantic herring	Clupeidae	*Clupea harengus harengus*
Atlantic mackerel	Scombridae	*Scomber scombrus*
Pacific cod	Gadidae	*Gadus macrocephalus*
NW Atlantic cod	Gadidae	*Gadus morhua*
NE Arctic cod	Gadidae	*Gadus morhua*
Haddock	Gadidae	*Melanogrammus aeglefinus*
Walleye pollock	Gadidae	*Theragra chalcogramma*
Silver hake	Merlucciidae	*Merluccius bilinearis*
Blue whiting	Gadidae	*Micromesistius poutassou*
Pollock	Gadidae	*Pollachius virens*
Saithe	Gadidae	*Pollachius virens*
Greenland turbot	Pleuronectidae	*Reinhardtius hippoglossoides*
Pacific halibut	Pleuronectidae	*Hippoglossus stenolepis*
Yellowtail flounder	Pleuronectidae	*Limanda ferruginea*
Greenland halibut	Pleuronectidae	*Reinhardtius hippoglossoides*
Capelin	Osmeridae	*Mallotus villosus*
Rockfish	Sebastidae	*Sebastes* spp.
Redfish	Sebastidae	*Sebastes mentella/Sebastes marinus*

The Barents Sea is the deepest of the Arctic Ocean shelf-sea areas with an average depth of ca. 230 m (Carmack et al., 2006). Three water masses dominate in the Barents and are related to three different current systems (Loeng, 1991): the Norwegian Coastal current along the Norwegian coast, the Atlantic current, entering the central Barents from southwest, and the Arctic current system from the north. The massive flow of Atlantic water through the Barents Sea entering the Arctic Ocean makes it appropriate to speak of the Barents as a flow-through shelf (Wassmann et al., 2006). The variability in temperature and the amount of inflowing Atlantic water is considerable (Loeng et al., 1997; Ingvaldsen et al., 2004) and is a major influence on climatic variations and the biological production in the Barents Sea (Ottersen et al., 2000; Wassmann et al., 2006).

The areas north and east of the polar front of the Barents Sea are covered with ice during parts of the year. The retracting of ice cover is thought to play an important role for the primary and secondary production in the area, as well as for feeding of small pelagic fish (Falk-Petersen et al., 2000; Sakshaug and Skjoldal, 1989). The copepod, *Calanus finmarchicus*, dominates the zooplankton biomass and annual production in the Barents Sea (Melle and Skjoldal, 1998; Tande, 1991; Zenkevich, 1963).

The Barents Sea ecosystem is characterized as a highly variable system with a simple structure and is associated with one of the world's largest fisheries. The annual fish catch in the late 1970s was around 2.5 million metric tons, while at present the annual catches are considerably lower.

Many important fish species such as capelin, herring, and cod plus many marine mammals and sea birds use the Barents Sea as their nursery and feeding grounds (Bogstad and Mehl, 1997; Dalpadado et al., 2000; Mehlum and Gabrielsen, 1993). Three commercially important species play vital roles in the ecosystem: Northeast Arctic cod (*Gadus morhua*), Barents Sea capelin (*Mallotus villosus*) and Norwegian spring-spawning herring (*Clupea harengus*). Cod are resident in the Barents and are the most important predator on capelin which are also resident, whereas herring only have their nursery area in the Barents (Bogstad and Mehl, 1997; Bogstad et al., 2000; Bogstad and Gjøsæter, 2001; Huse et al., 2004; Johansen, 2002, 2003; Johansen et al., 2004). Some previous comparative studies of marine ecosystems between the Bering Sea and the Barents Sea have been undertaken (Hunt and Megrey, 2005; Sakshaug and Walsh, 2000).

The Norwegian Sea (NOR) to the south of the Barents, by definition ~1.1 million km^2, is a deep ocean basin with an average depth exceeding 2000 m (Skjoldal, 2004; Figs. 1 and 2). The Norwegian Sea is bordered by the Norwegian continental shelf to the east with average depth less than 300 m. Over the Norwegian Shelf, less saline coastal water flows northwards, ending in the Barents Sea (Skjoldal and Rey, 1989; Skjoldal et al., 1992).

The central Norwegian Sea is strongly influenced by the inflow of warm and saline Atlantic water from the North Atlantic. The location of oceanic fronts and the inflow of Atlantic water from south vary with large-scale atmospheric climate systems such as the NAO (Blindheim, 2004). To the west the Norwegian Sea contains Arctic water. Arctic water is characterized by its own fauna of zooplankton and fish, different from the sub-arctic species of Atlantic water (Melle et al., 2004). The northern Norwegian Sea is a major area for deep-water formation.

The southern gyre of the Norwegian Sea is a major area for production of *Calanus finmarchicus* and production of this copepod is forced by climate variability (Melle et al., 2004). Zooplankton from centers of production in the Norwegian Sea are advected with Atlantic water into the Barents, and strongly influence local zooplankton stocks there.

The fisheries in the Norwegian Sea are mainly pelagic; and the herring fishery (annually >1 million metric tons) and the fishery for mackerel, blue whiting and saithe are the most important.

The Norwegian shelf is the spawning area for large fish stocks such as cod and herring, and larvae and juveniles are brought to the Barents Sea nursery areas mainly with the coastal current. Thus, the ecosystem of the Norwegian and Barents Seas are closely connected and in some respects function as one system (Skjoldal, 2004).

3. Methods

3.1. Data sources

For each system, we examined survey (or as modeled by assessment) trends in abundances for major fish species abundances, total system fish biomass, and zooplankton, shrimp and krill biomasses. In the following subsections we provide a brief description and source of information for each of the ecosystems.

We also chose functionally analogous species from each ecosystem (Table 1). These species were chosen as representative of the main demersal, pelagic and commercially targeted fish species from each ecosystem and grouped according to their life histories, body shapes, and ecological functionality to facilitate cross-system comparisons. Where data were available we included comparisons among zooplankton and shrimp species across these ecosystems.

3.1.1. Gulf of Alaska and Eastern Bering Sea

The Alaska Fisheries Science Center conducts trawl surveys in three major ecosystems: the Eastern Bering Sea (EBS), the Aleutian Islands, and the Gulf of Alaska (GOA). These surveys take place during the summer season, starting between late May and early June and ending in late July or early August. Because each ecosystem has fundamentally different physical characteristics, the trawl survey methods vary slightly between areas. In addition, the length of the survey time series and the frequency of surveys differ between areas. In this section, we describe the major characteristics of the bottom trawl surveys of the EBS and GOA which provide much of the input information for the corresponding time series analyses.

The EBS shelf survey is the longest running continuous trawl survey in Alaskan offshore waters; it has been conducted annually since 1982 (Lauth and Acuna, 2007). The shelf survey design has fixed stations on a grid covering six sampling strata, and it ranges in depth from 50 m to 200 m. The overall area covered by the survey is 495,000 km^2. We used an estimated time series of spawning stock biomass for Pacific Ocean perch in the EBS from a stock assessment model (Spencer and Ianelli, 2006) rather than survey data because Pacific Ocean perch are poorly sampled by the shelf survey.

The GOA region was surveyed triennially between 1984 and 1999, alternating years with the Aleutian Islands survey and a U.S. West Coast survey in the intervening third year of each cycle (Britt and Martin, 2001). Starting in 2000, these surveys went on a biennial schedule. The GOA survey uses a stratified random design for selecting stations, and each station is towed for 15 min. The area covered by each survey is generally 291,840 km^2 in the GOA. Because surveys were conducted only bi- or triennially in the GOA, we used abundance time series estimated from stock assessment models for several species in place of survey data in this analysis (Pacific cod: spawning stock biomass from Model 1 from Thompson and Dorn, 2005; walleye pollock: spawning stock biomass from Dorn et al., 2006; Pacific Ocean perch: spawning stock biomass from Hanselman et al., 2005). We also characterized annual Pacific halibut abundance using abundance estimates from surveys conducted by the International Pacific Halibut Comm. (http://access.afsc.noaa.gov/reem/ecoweb/content/TrendsGroundfishBSr_halibut.xls) and annual capelin abundance using mean CPUE from small mesh pelagic trawl surveys conducted in Pavlof Bay by the Alaska Department of Fish and Game (http://access.afsc.noaa.gov/reem/ecoweb/content/GOASmallMeshSurvey.xls).

Regardless of differences in design, the general types of data collected from each of these surveys is the same. For each tow, the catch is sorted to species and the weight and number of each species caught is recorded. For commercially important species, length frequencies by sex are recorded. Other biological collections include otoliths for ageing, gonads for maturity and fecundity studies, samples for genetic work or other research, and stomach samples for food habits studies. There were no zooplankton, shrimp, or euphausiid data for either of these ecosystems.

3.1.2. Gulf of Maine and Georges Bank

Fish abundance and biomass data were obtained from the Northeast Fisheries Science Center bottom trawl survey program, which has been conducted annually since 1963 (Azarovitz, 1981; NEFC, 1988). These multi-species surveys are designed to monitor trends in abundance and distribution and to provide samples to study the ecology of the large number of fish and invertebrate species inhabiting the region. These broad-scale trawl surveys cover continental shelf waters from Cape Hatteras, North Carolina to Nova Scotia (approximately 290,000 km^2). All four seasons are sampled, but the major focus has been in spring (March–May) and fall (September–November), with winter and summer surveyed more sporadically. The surveys generally utilize a #36 Yankee (or similar) bottom trawl towed at approximately 6.5 km h^{-1} for 30 min at each station. Trawl stations are selected using a stratified random design. Within each depth-region stratum, stations are assigned randomly, and the number of stations allotted to a stratum are in proportion to its area. Within each stratum, 2′ latitude by 2.5′ longitude rectangular sampling units are randomly selected in proportion to the strata area (approximately one station per 200 square nautical miles or per 690 km^2). Once onboard, fish are sorted to species, weighed (0.1 kg), length measured (cm), sex and maturity determined, and subsamples of key species eviscerated for feeding ecology studies. Here we provide estimates of mean weight per tow for each of the main species as an index of abundance or assessment estimates of fish biomass derived from these surveys (NEFSC, 2002). Azarovitz (1981) or NEFC (1988) provide a more detailed description of the survey program. Ancillary stock assessment information can be viewed from the following webpage (http://www.nefsc.noaa.gov/sos/), but here we used survey indices.

Zooplankton and krill abundances were determined from plankton monitoring programs conducted by the Northeast Fisheries Science Center (Kane, 1993, 2007). Plankton samples have been collected seasonally on two types of cruises since 1974. First, broadscale surveys dedicated to plankton sampling were conducted with standard or randomly selected stations spaced approximately 8–35 km apart. Second, plankton surveys were piggybacked on trawl surveys (see above) with standard or randomly selected plankton stations at a subsample of trawl stations. All samples were collected with a 61-cm bongo frame fitted with a 0.333-mm mesh net towed obliquely to a maximum depth of 200 m or 5 m from the bottom and back to the surface. A flowmeter was suspended in the center of the bongo frame to measure volume of water filtered during the tow. Samples were preserved in 5% formalin. Plankton biomass was measured by displacement volume in the laboratory. Samples were then reduced to approximately 500 organisms by sub sampling with a modified box splitter. Zooplankton were sorted, counted, and identified to the lowest possible taxa. Abundances were then calculated based on the number of splits (aliquots) and the volume filtered. Similar to the Norwegian Sea (below), *Calanus finmarchicus* was the dominant copepod in this ecosystem. See Kane (1993, 2007) for further details of the zooplankton sampling protocols.

Finally, we employed an estimate of shrimp (*Pandalus borealis*) biomass based on limited beam trawl sampling in the Gulf of Maine region conducted for this purpose (NEFSC, 2001). These estimates are survey trends based on 30–60 stations per cruise in each summer.

3.1.3. Norwegian Sea and Barents Sea

Abundance estimates for fish and invertebrate species were obtained from both Norwegian and Russian surveys and stock assessments. Unlike the US ecosystems, surveys in these ecosystems tended to be focused on particular species rather than from a multi-species perspective. The duration and timing of these surveys has varied considerable across species. For further details see Stiansen and Filin (2007) and Skjoldal (2004).

Due to its short longevity, time series of adult capelin was estimated solely based on acoustic surveys carried out during autumn (Gjøsæter, 1998). The rest of the fish stock time series are from VPA-runs based on catch statistics. The VPA were tuned using fishery CPUE data and data from different scientific cruises (Skjoldal, 2004). The tuning of the VPA for Norwegian spring-spawning herring was based on eight scientific surveys. The blue whiting VPA was tuned with data from the Norwegian acoustic survey. Northeast Arctic cod estimates were tuned using three scientific surveys (Anon., 2006). The tuning of Northeast Arctic haddock VPA was done using Russian bottom trawl survey and Norwegian bottom trawl and acoustic surveys. Time series of Northeast Arctic saithe were tuned using CPUE data from the Norwegian trawl fisheries. Time series of Greenland halibut were tuned using experimental commercial fishery CPUE and Russian and Norwegian trawl survey indices. For golden redfish (*Sebastes marinus*), the VPA was tuned with quarterly length distributions and age-length keys from the Norwegian trawl and gillnet fleet and the Norwegian-Barents Sea bottom trawl survey. For mackerel, fishery independent data for the VPA-tuning was based on egg survey estimates of spawning stock biomass. Total fish biomass was calculated for the Barents Sea based on the four biomass-dominant populations: Northeast Arctic cod, Northeast Arctic haddock, capelin and Norwegian spring-spawning herring (<4 years old). For krill (Euphausiidae), Russian estimates from October/December were used (Drobysheva, 1994). These abundance indices were obtained using a net (opening diameter, 50 cm, sieve mesh, 564 μm) attached to the bottom trawl during the annual demersal fish survey. This net collects macrozooplankton in a layer 6–10 m above the bottom (Dalpadado and Bogstad, 2004).

Abundance estimates of shrimp (*Pandalus borealis*) were taken from annual Norwegian trawl surveys in the Barents Sea in spring and in the Spitsbergen area in summer/autumn (Skjoldal, 2004).

3.2. Analysis

Time series from various fisheries surveys (noted above) were collated to compare abundance by functionally analogous species (Table 1). These time series were normalized to the mean of each and are presented as anomalies. We use these anomalies to facilitate cross-system comparisons and to minimize differences due to absolute magnitude of abundance. All subsequent analyses were executed on the survey time series anomalies.

We executed four analyses on the time series of biomasses within and among functional groups and ecosystems. To evaluate similarity in recent trends, time series were grouped into increasing, decreasing, and variable patterns based on trends in a 10 year lowess smoother of the annual biomass anomalies from 1990 to the present. We limited this analysis to the more recent years of the time series to deemphasize long-term variability and cyclicity.

For each functionally analogous species group, we evaluated the general relationships among the fish or zooplankton groups by calculating cross-correlations among ecosystems. All correlations were adjusted for auto-correlation using Bartlett (1946) correction.

The time series were analyzed using dynamic factor analysis (DFA), which is a dimension-reduction technique used to detect common patterns in a set of time series (Zuur et al., 2003). The biomass time series were truncated to 1970 to the present to prevent dominance of the Norwegian and Barents Seas (which had longer data sets) time series in the DFA. For shorter time series, DFA is limited in the number of time series that can be analyzed simultaneously, thus DFA was applied separately to all species in an ecosystem and to each functional group across ecosystems. These preliminary analyses led to more explicit exploratory analyses examining common trends among ecosystems and functional groups. Any commonalities in pattern or synchronies of events were particularly highlighted.

We applied change-point analysis using the Sequential *T*-test Analysis of Regime Shifts algorithm (STARS; Rodionov, 2004; Rodionov and Overland, 2005) to time series of environmental indices and fish stock abundance from the four ecosystems to investigate whether the "regime shifts" identified by the algorithm occurred synchronously across the ecosystems and whether shifts occurred in similar patterns across ecosystems. STARS is one of several methods that have been developed to detect discontinuities ("change points" or "regime shifts") in time series (see reviews of other methods in Easterling and Peterson, 1995; and in Lanzante, 1996). It sequentially tests whether each subsequent data point in a time series differs significantly from the mean of previous data points belonging to the latest "regime". The identification of a discontinuity is tested using the "regime shift index" (RSI), which represents the cumulative sum of normalized deviations from the hypothetical mean level for the "new" regime; the difference between this and the mean level for the current regime is tested using a *t*-statistic. The main advantage of STARS over other methods is its ability to identify potential shifts in real time and to measure the changing confidence in evidence for a shift as additional data arrives (Rodionov and Overland, 2005).

We used the same set of environmental indices for each ecosystem. These indices consisted of time series covering 1948–2006 for the annual mean u- and v-components of surface wind speed ("u-winds" and "v-winds"), net heat flux ("netf") and sea surface temperature ("SST") (See Drinkwater et al., this volume, for a fuller description of those data). We also used the indices of abundance for the functionally analogous species in each ecosystem.

4. Results

All ecosystems have species with recently increasing stock biomasses (Table 2). Most groundfish stocks are increasing across ecosystems with the exception of cod, which is decreasing or variable in all ecosystems. Most pelagic stocks are variable or increasing, with the exception of decreasing stocks of walleye pollock in the Gulf of Alaska and blue whiting in the Norwegian and Barents Sea. Lower tropic levels are more variable with no clear pattern across ecosystems.

Total fish biomass was variable for all ecosystems over time (Fig. 3, Table 2). The NOR/BAR ecosystem exhibited the highest variability, followed by GOM/GB. The GOA and EBS were less variable over time, with the EBS showing a slight increasing trend in the more recent years. Total fish biomass was positively correlated between the GOA and EBS and the GOA and GOM (Fig. 3B, Table 3).

4.1. Invertebrates

The zooplankton time series were tightly varying about the mean except the Barents Sea, which was highly variable and exhibited an increase over time (Fig. 4, Table 2). All of the ecosystems or subsystems (for which we had data) were positively correlated (Fig. 4B, Table 3).

The shrimp time series were all variable about the long term means for each ecosystem (Fig. 5, Table 2). The most notable peak in anomalies was in the EBS during the early 1990s, most other ecosystems had anomalies ranging between ±1. The GOA and GOM were weakly negatively correlated, as were the GOA and NOR/BAR (Fig. 5B, Table 3), with the latter exhibiting an out of phase cycle.

Table 2
Trends detected using the dynamic factor analysis on biomass anomalies since 1990; *I*, increasing; *D*, decreasing; *V*, variable.

	EBS	GOA	GOM/GB	NOR/BAR
Cod	D	D	D/V	V
Haddock	–	–	I	I
Pleuronectidae	V	I	I	V
Sebastes spp.	I	V	I	D
Saithe	–	–	I	I
Medium gadids	V	D	V	I
Herring	I	V	I	I
Mackerel	–	–	I	D
Capelin	V	I	–	V
Krill	–	–	V/V	I
Shrimp	D	I	D	V
Zooplankton	–	–	V/V	I

Table 3
Summary of significant cross-correlations among the four ecosystems for each functionally analogous species. Emboldened values are where the correlations (corrected for auto-correlation) have a $p < 0.05$.

	–	+
Shrimp	–GOM:NOR/BAR, –GOA:GOM	
Krill		**++GB:NOR**
Zooplankton		**++GB:GOM**, +GB:BAR
Total Fish Biomass		**++GOA:EBS, ++GOA:GOM**
Cod	–GOA:GOM, – –**GB:NOR/BAR**	**++GOA:EBS**, +GB:GOM
Medium gadids	– –GOA:NOR/BAR	
Herring	– –**GOA:GOM/GB,** – –**GOA:NOR/BAR**	**++GOM/GB:NOR/BAR**
Mackerel	N/A	N/A
Haddock	N/A	N/A
Saithe/ Pollock	N/A	N/A
Sebastes spp.	–GOA:NOR/BAR, – –**EBS:NOR/BAR,** – –**GOM/GB:NOR/BAR**	**++GOM/GB:EBS, ++GOM/GB:GOA, ++GOA/EBS**
Pleuronectids	–EBS:NOR/BAR	**++GOA:EBS, ++GOM/GB:NOR/BAR**
Capelin	–GOA:NOR/BAR	

++ or – – 0.05
+ or – 0.05 < 0.10
N/A

Euphasiid biomass was notably variable in all ecosystems, with apparent increases after the early 1990s in the NOR/BAR and GB regions (Fig. 6, Table 2). Euphasiid biomass in the GB and NOR/BAR were positively correlated (Fig. 6B, Table 3).

4.2. Groundfish

Cod biomass was either decreasing or highly variable in all the ecosystems (Fig. 7, Table 2). The NOR/BAR cod had the longest time series and the most notable declines in biomass anomalies. Most cod stocks in these ecosystems, even if showing a more recent increase, had exhibited notable declines in biomass anomalies in the past. The GOA and GOM were negatively correlated, as was GB and NOR/BAR (Fig. 7B, Table 3). Conversely, the GOA and EBS were positively correlated, as were GB and GOM implying that the contiguous ecosystems were experiencing similar processes affecting cod.

The medium gadid biomass anomalies were also mostly decreasing or quite variable (Fig. 8, Table 2). Only blue whiting in NOR/BAR has exhibited a notable recovery, but even it is trending downward in more recent years. Silver hake in the GOM/GB exhibited the highest variability. Walleye pollock in EBS and GOA had a shorter time series but were also variable over time, albeit at lower amplitudes. The GOA and NOR/BAR medium gadids had a negative correlation (Fig. 8B, Table 3).

For the two ecosystems with haddock, both exhibited an increase in biomass anomlies in more recent years (Fig. 9, Table 2). In recent years both ecosystems approached the highest levels of anomalies observed for each time series. There was no significant cross-correlation for haddock between these two ecosystems (Fig. 9B, Table 3).

For the two ecosystems with saithe, both exhibited an increase in biomass anomlies in more recent years (Fig. 10, Table 2). Pollock had a very large peak in the late 1980s, with recent values approximately half of the peak. There was no significant cross-correlation for pollock between these two ecosystems (Fig. 10B, Table 3).

The pattern for *Sebastes* spp. biomass anomalies were dominated by Pacific ocean perch in the EBS (Fig. 11, Table 2). Although increasing in the EBS, redfish were also increasing to a lesser extent in the GOM/GB ecosystem. The other ecosystems *Sebastes* stocks were declining in more recent years. Of the six significant cross-correlations, all the negative ones with other ecosystems and NOR/BAR. were negative: GOA with NOR/BAR, EBS with NOR/BAR and GOM/GB with NOR/BAR (Table 3, Fig. 11B). The others were positively correlated.

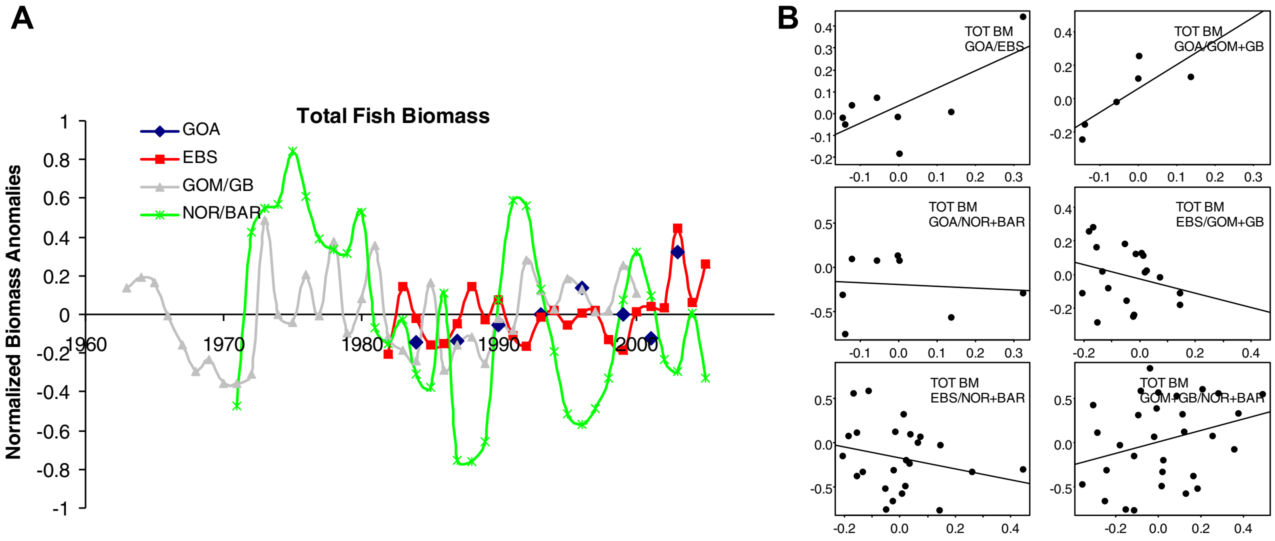


Fig. 3. (A) Normalized biomass anomalies for total surveyed finfish of the ecosystems in this study. (B) Cross-correlation plots for total surveyed finfish biomass of the ecosystems in this study.

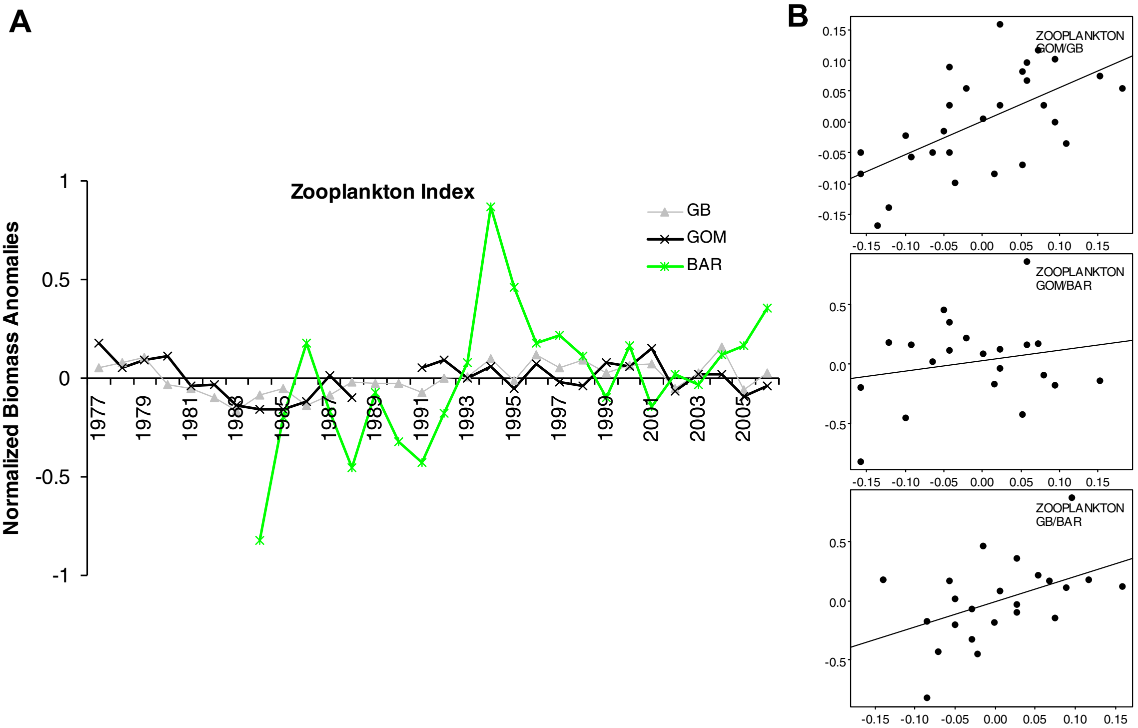


Fig. 4. (A) Normalized biomass anomalies for total zooplankton biomass in the ecosystems of this study. (B) Cross-correlation plots for total zooplankton biomass in the ecosystems of this study.

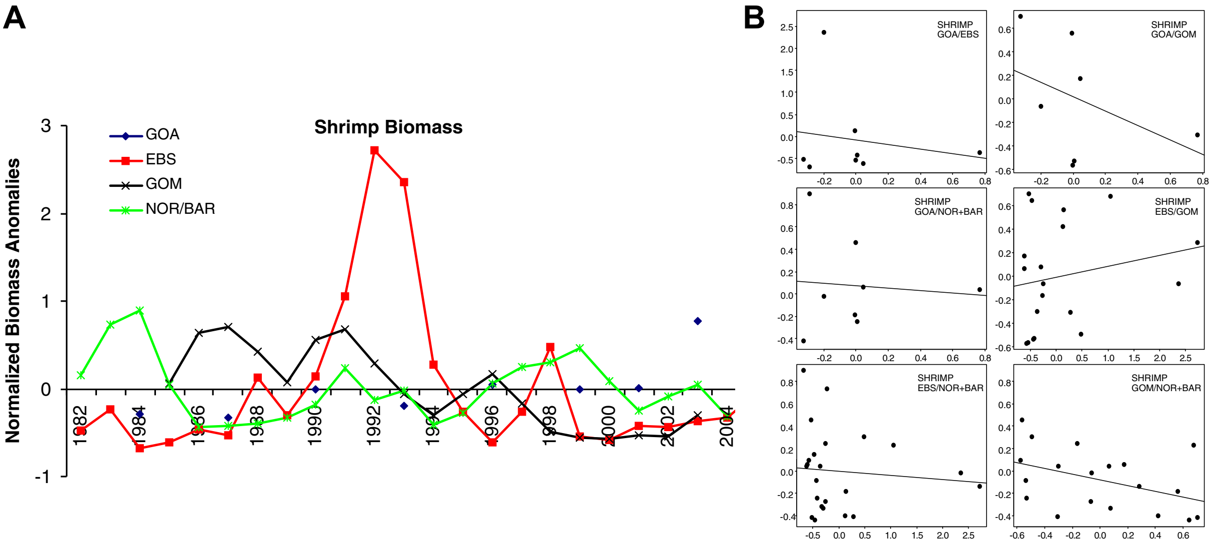


Fig. 5. (A) Normalized biomass anomalies for shrimp in the ecosystems of this study. (B) Cross-correlation plots for shrimp in the ecosystems of this study.

The flatfish (Pleuronectidae) biomass anomalies were mainly variable over time, with three of the four ecosystems (GOA, GOM/GB, NOR/BAR) exhibiting a notable increase in biomass in recent years (Fig. 12, Table 2). Both yellowtail flounder in GOM/GB and Greenland halibut in NOR/BAR exhibited biomass peaks early in the time period, followed by a notable decline with only recent years showing an increase in those stocks. Greenland turbot in the EBS had a peak in the mid 1990s followed by a subsequent decline in biomass. There was a negative correlation between EBS and NOR/BAR (Fig. 12B, Table 3). However, there was a positive correlation for GOA with EBS and one for GOM/GB with NOR/BAR. Greenland turbot was chosen in the Bering Sea for these comparisons, because it is the same species as in the Atlantic. However, it is a relatively minor contributor to flatfish biomass in the EBS and its biomass trend is the exception among Bering Sea flatfish. The biomass trends for all other flatfish have been increasing or stable over the last decade or more.

4.3. Small pelagics

Herring biomass anomalies were generally increasing (Fig. 13, Table 2). The EBS and GOA herring were more variable in recent

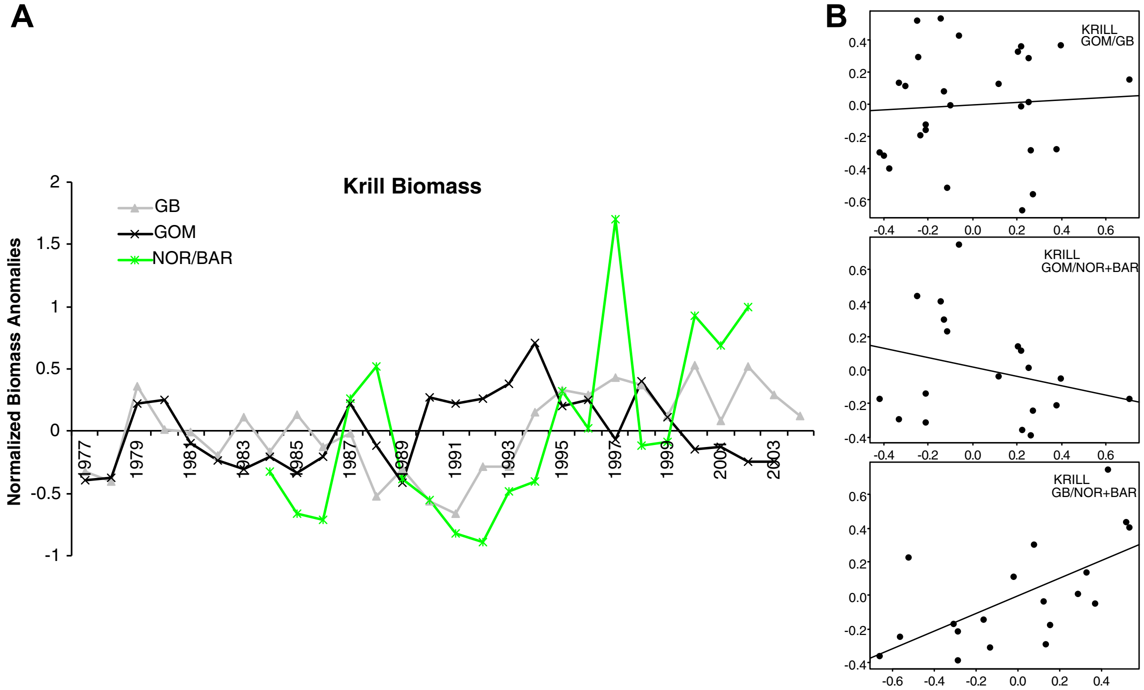


Fig. 6. (A) Normalized biomass anomalies for krill in the ecosystems of this study. (B) Cross-correlation plots for krill in the ecosystems of this study.

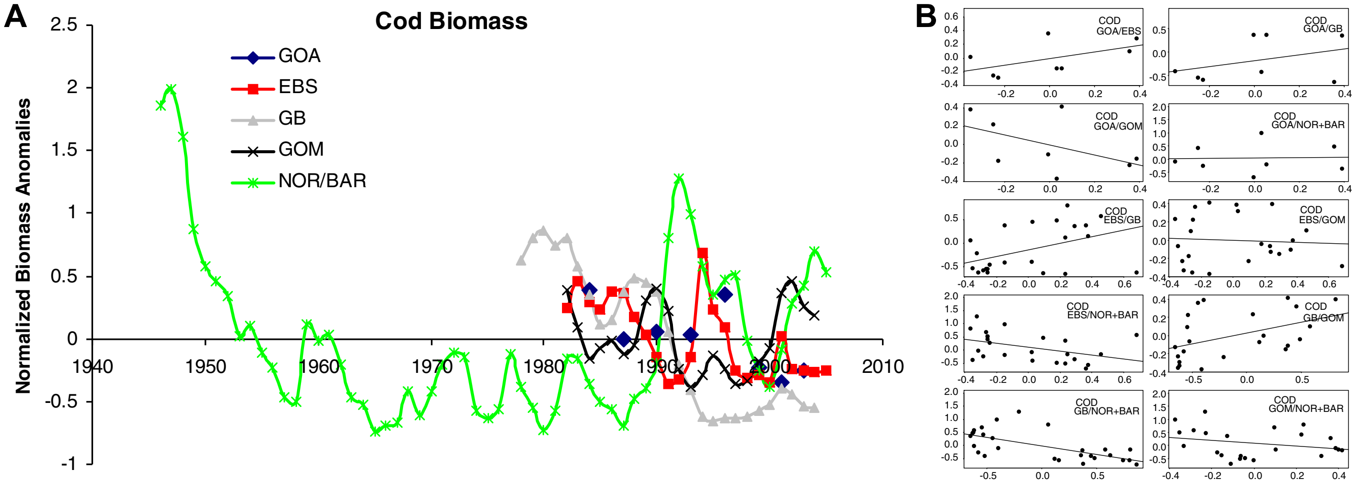


Fig. 7. (A) Normalized biomass anomalies for cod in the ecosystems of this study. (B) Cross-correlation plots for cod in the ecosystems of this study.

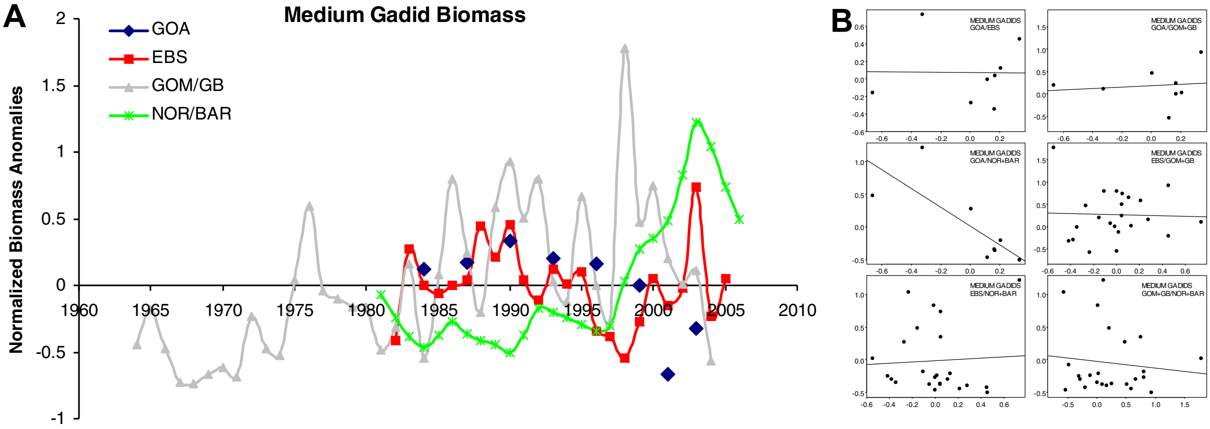


Fig. 8. (A) Normalized biomass anomalies for medium gadids in the ecosystems of this study. (B) Cross-correlation plots for medium gadids in the ecosystems of this study.

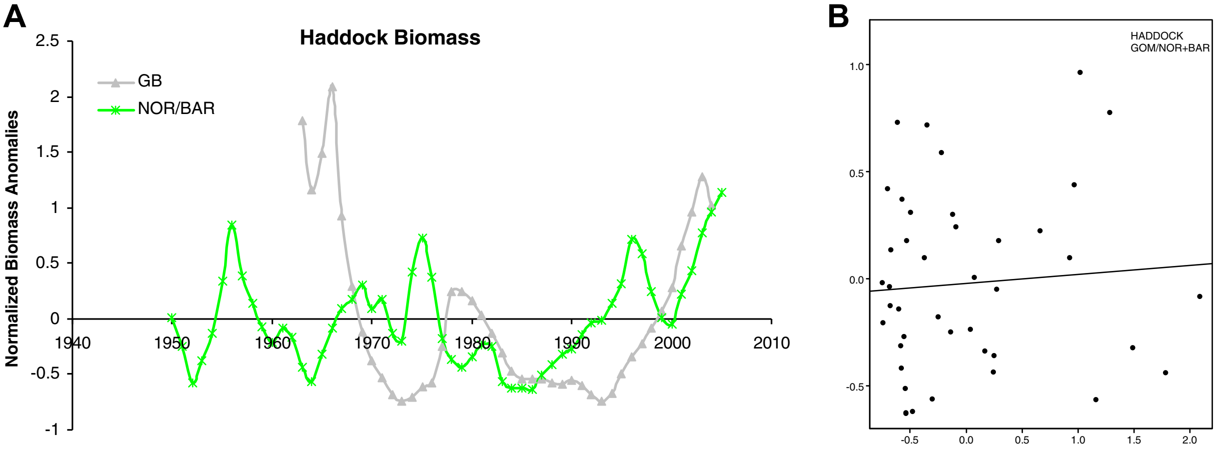


Fig. 9. (A) Normalized biomass anomalies for haddock in the ecosystems of this study. (B) Cross-correlation plots for haddock in the ecosystems of this study.

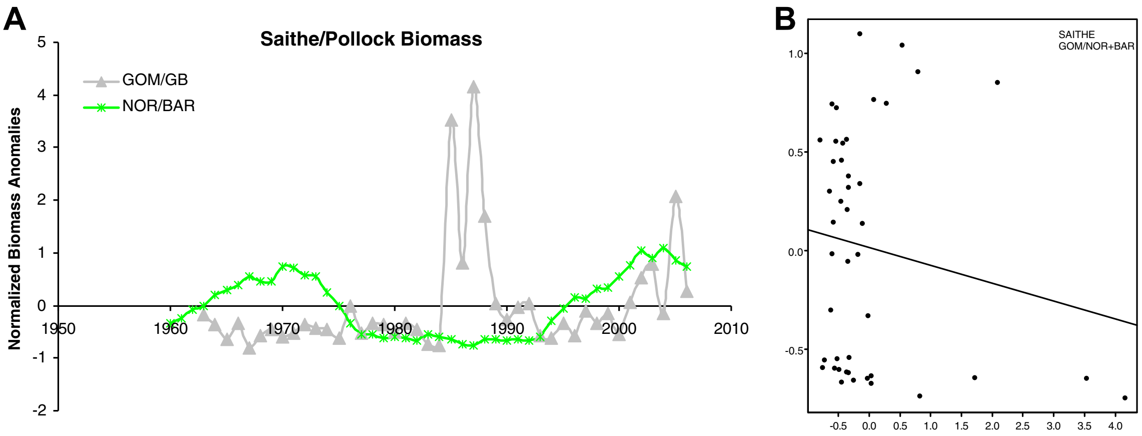


Fig. 10. (A) Normalized biomass anomalies for saithe in the ecosystems of this study. (B) Cross-correlation plots for saithe in the ecosystems of this study.

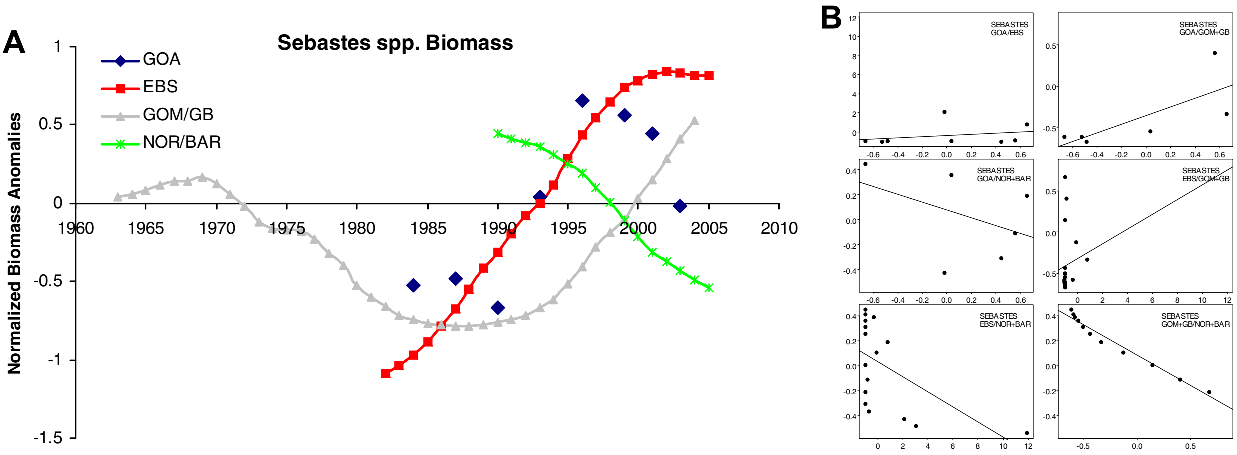


Fig. 11. (A) Normalized biomass anomalies for *Sebastes* spp. in the ecosystems of this study. (B) Cross-correlation plots for *Sebastes* spp. in the ecosystems of this study.

years, whereas the NOR/BAR and GOM/GB ecosystems exhibited a pattern of high anomalies followed by a notable decline leading up to the more recent increases in biomass. As expected, the GOM/GB and NOR/BAR had a significant positive correlation (Fig. 13B, Table 3). Conversely, the GOA herring biomass was negatively correlated with both the GOM/GB and NOR/BAR ecosystems.

For the two ecosystems with mackerel, GOM/GB exhibited an increase whereas NOR/BAR exhibited a decrease in biomass anomalies

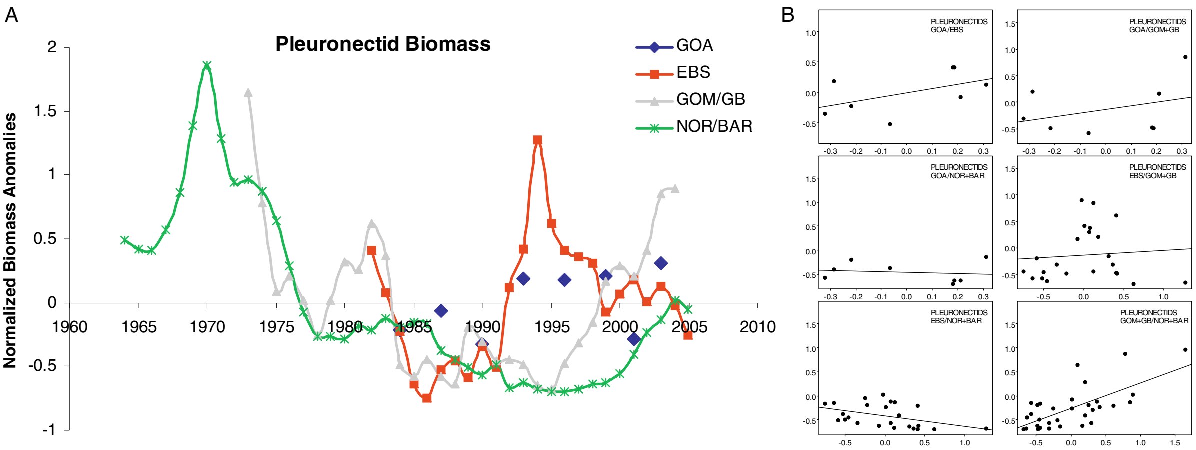


Fig. 12. (A) Normalized biomass anomalies for pleuronectids in the ecosystems of this study. (B) Cross-correlation plots for pleuronectids in the ecosystems of this study.

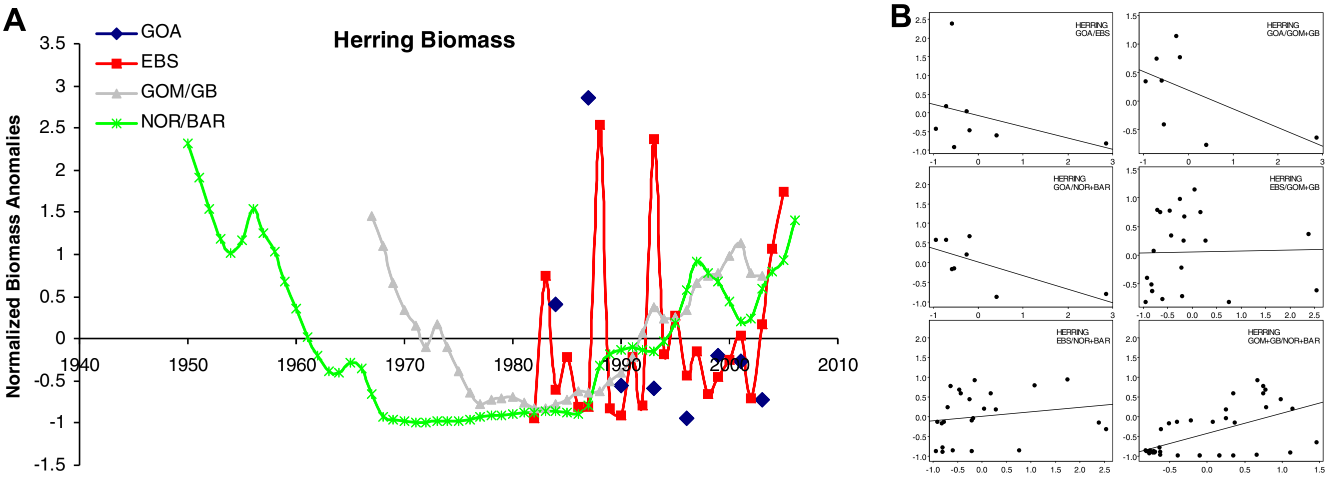


Fig. 13. (A) Normalized biomass anomalies for herring in the ecosystems of this study. (B) Cross-correlation plots for herring in the ecosystems of this study.

(Fig. 14, Table 2). Both ecosystems had a peak biomass in the early 1970s followed by a notable decline, but only the GOM/GB ecosystem has recently increased. There was no significant cross-correlation for mackerel between these two ecosystems (Fig. 14B, Table 3).

In the three ecosystems with capelin, the biomass anomalies were quite variable over time (Fig. 15, Table 2). Much of the variability in these ecosystems can be attributed to sampling variability because the trawl survey gear is not generally de-

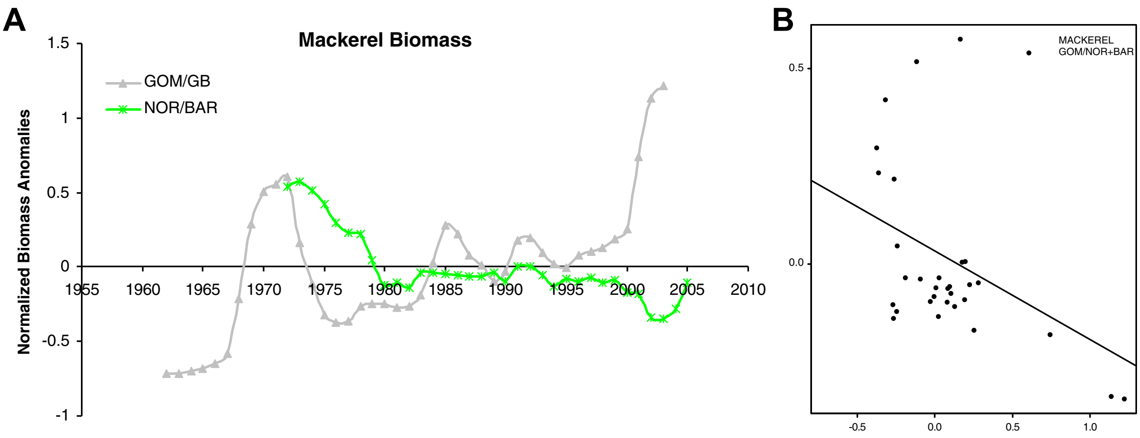


Fig. 14. (A) Normalized biomass anomalies for mackerel in the ecosystems of this study. (B) Cross-correlation plots for mackerel in the ecosystems of this study.

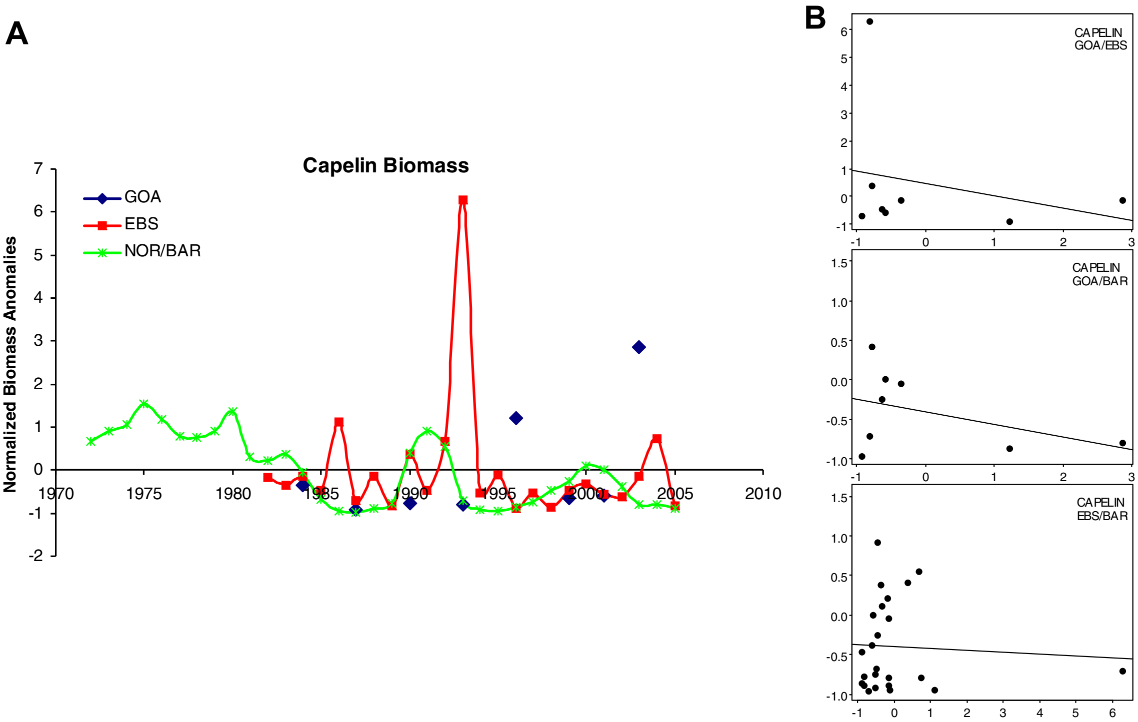


Fig. 15. (A) Normalized biomass anomalies for capelin in the ecosystems of this study. (B) Cross-correlation plots for capelin in the ecosystems of this study.

signed for small pelagics. If one removes the one peak year in the EBS, there is effectively no pattern for these stocks. There was a negative cross-correlation between the GOA and NOR/BAR.

4.4. Detecting commonalities and synchronies

Comparing all species across all ecosystems revealed very minimal commonalities. The one exception was that capelin and herring had opposite trends in the three ecosystems where they coexist. This pattern was very apparent in the Norwegian and Barents Sea (herring increasing and capelin decreasing; Fig. 16A) and in the Gulf of Alaska (herring decreasing and capelin increasing; Fig. 16B). The correlations of the species time series with the common trends (Fig. 16E) were opposite for these two species in these two ecosystems (Fig. 16F). The correlation of species time series with the common trends were lower for the Eastern Bering Sea ecosystem, but capelin and herring time series were still in opposition. The time series of herring in Georges Bank/Gulf of Maine was very similar to the Norwegian and Barents Sea herring, but capelin do not occur in the Gulf of Maine/Georges Bank.

Using the smoothed, summary RSI values from the environmental time series, we identified three broad scale regime shift periods: 1976–78, 1987–89, and 1998–1999 (Fig. 17a). Two earlier periods (1953–55, 1961–63) exhibited much smaller smoothed RSI values. For the EBS, the STARS algorithm detected significant regime shift indices in the environmental time series in 1972 (u-winds), 1977 and 1978 (SST and netf, respectively), and in 2002 (SST) (Table 4). The 1977–78 shifts, when taken together, exhibited the largest combined RSI. For the GOA, significant RSIs were detected in all four environmental indices during the 1976–1977 period, as well as in 1994 (v-winds) and 2003 (SST). The 1976–77 shifts again had the largest combined RSI. Significant RSIs were detected in the GOM/GB environmental time series only for net heat flux and SST: during 1954 (SST), 1974 (netf), 1988 (netf) and 1999 (netf and SST). The largest combined RSIs for the NOR/BAR occurred in 1963 (NOR and BAR netf), 1976 (NOR SST), 1988–89 (primarily NOR, BAR SST), and 1998 (NOR SST).

These results provide evidence for an almost synchronous environmental regime shift across three of the four ecosystems during the 1976–1978 time period. A substantial regime shift in the physical environment has been well-documented for the 1976–77 time period over the north Pacific (Rodionov and Overland, 2005). At smaller spatial scales, near-synchronous changes in net heat flux and SST were detected in the GOM/GB and the NOR/BAR during 1987–89 and again in 1998–99. Although no shifts were detected for the EBS and GOA during these latter periods in the environmental indices used here, regime shifts in other environmental indices have been detected across these ecosystems during these time periods (e.g. Rodionov and Overland, 2005).

For the forage fish time series, we identified four broad scale regime shift periods from smoothed, summary RSI values: 1957–59, 1979–82, 1988–92, and 1998–2001 (Fig. 17b). The first shift might be described as following a minor shift indicated in the environmental time series, although the environmental shift was detected in GOM/GB SST whereas the forage fish shift was detected in NOR/BAR herring (Table 4). The other three shifts identified in the smoothed, summary RSI values for forage fish appear to lag the broad scale shifts identified in the environmental indices by a year or two. This approach detected fewer regime shift indices in the forage fish time series for the EBS (1: herring, 2004) and the GOA (2: capelin, 1981; herring, 1998) in comparison with those detected for the GOM/GB (7 change points) and the NOR/BAR (9 change points) (Table 4).

For the groundfish time series, we identified four broad scale regime shift periods from smoothed, summary RSI values: 1966, 1973–76, 1980–84, and 1994–99 (Fig. 17c). These periods do not seem to be closely linked to corresponding broad scale shifts in the environmental indices, as was the case for forage fish (e.g. the 1994–1999 period either precedes the broad scale shift in

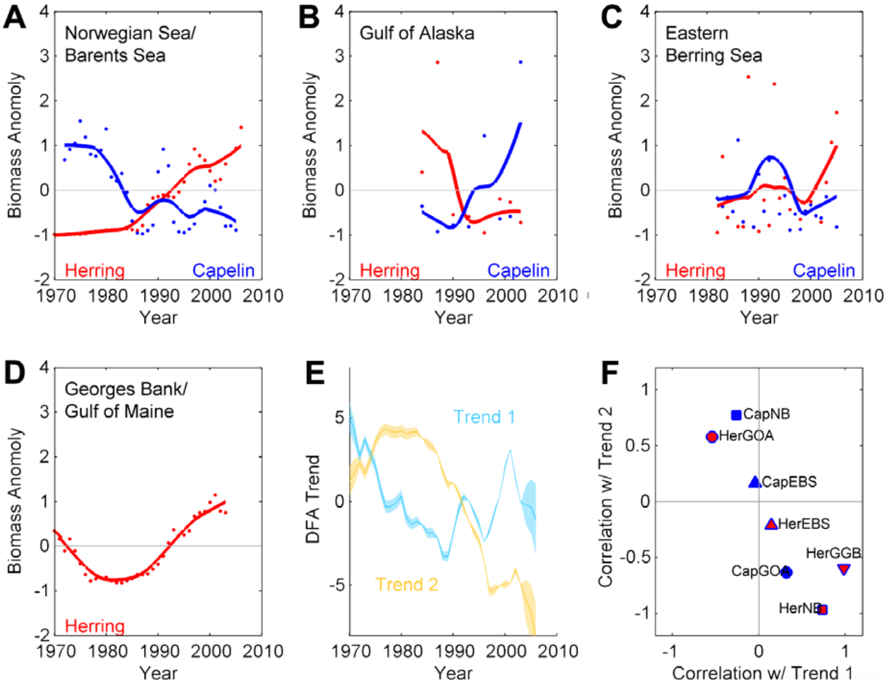
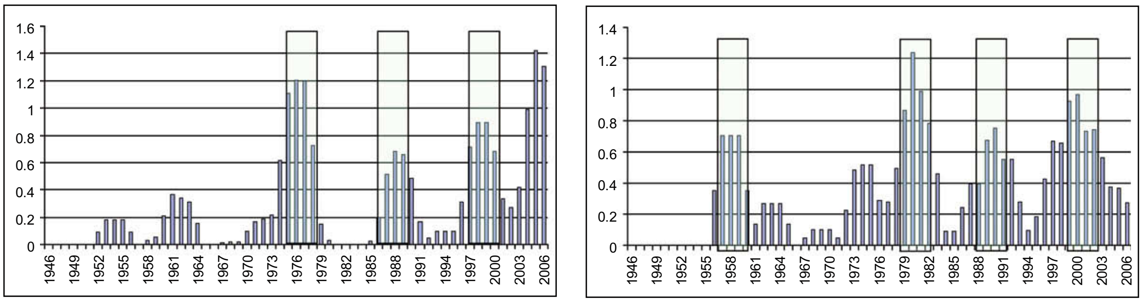


Fig. 16. Time series of herring and capelin from the four ecosystems compared in this study: (A) Norwegian Sea/Barents Sea, (B) Gulf of Alaska, (C) Eastern Bearing Sea, and (D) Georges Bank/Gulf of Maine. Points represent individual year estimates of biomass anomolies and line represents a 12 point lowess smoother. Capelin do not occur in the Georges Bank/Gulf of Maine system so only herring are plotted. (E) The results of a dynamic factor analysis (see text) showing two common trends from the herring and capelin series from the four ecosystems. (F) Correlation of the individual series to the common trends shown in (E).

environmental parameters during 1998–99 or follows one several years earlier in 1987–89). Numerous regime shifts were detected in the groundfish time series in all four ecosystems (Table 4). Although several synchronous or near-synchronous shifts were detected across several of the ecosystems, these generally involved species playing different roles in each ecosystem. For example, during 1994–1999 shifts were detected in cod in the EBS, medium gadids, cod and flatfish in the GOA, flatfish in the GOM/GB, and medium gadids in the NOR/BAR (as well as in *Sebastes* spp. stocks across all ecosystems, see below). Given the number of detected regime shifts in each ecosystem, this seems more likely to be the result of pure chance than an underlying "teleconnection". A somewhat more intriguing pattern across ecosystems concerns changes in *Sebastes* spp. abundance.


(a) Environmental indices

(b) Forage fish

(c) Groundfish

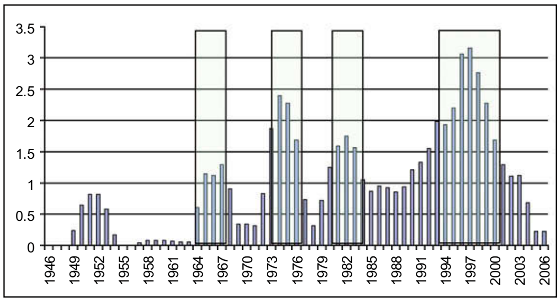


Fig. 17. Summary RSI values from STARS analysis after smoothing. Wide boxes highlight periods of major shifts.

Table 4

Summary of regime shift analyses for environmental, forage fish and groundfish time series. Environmental time series: u-winds, v-winds, net heat flux ("netf') and sea surface temperature (SST). Forage fish categories: herring, mackerel and capelin. Groundfish categories: cod, flatfish, hake (i.e. medium gadids), haddock, rockfish and saithe. Reported shifts were based on STARS analysis using a 10-year window, a *p*-value of 0.1 and a Huber range of 3. See Drinkwater et al. (this volume) for further descriptions of the physical variables.

Year	EBS			GOA			GOMBS			NORBAR			
	EnvData	Forage	Groundfish	EnvData	Forage	Groundfish	EnvData	Forage	Groundfish	NOR EnvData	BAR EnvData	Forage	Groundfish
1946													
1947													
1948													
1949													
1950													
1951									rockfish–				
1952													cod–
1953													
1954							SST–						
1955													
1956													
1957													
1958												herring–	
1959									rockfish–				
1960										SST+			
1961										netf+	netf+		
1962													
1963												herring–	cod–
1964													
1965													
1966			rockfish–			rockfish–							
1967													
1968													
1969								mackerel+	haddock–		netf–		
1970													
1971													
1972	u–winds+												
1973									rockfish–				
1974						hake+rockfish–	netf+	herring–					
1975								mackerel–	hake+				saithe– flatfish-
1976			rockfish-	u-winds- v-winds+ netf-						SST-			
1977	SST+			SST+									
1978	netf-												haddock-
1979												mackerel-	
1980									rockfish-				
1981			hake+		capelin-							cod-	
1982						flatfish+							
1983						cod+							
1984								mackerel+	flatfish-				
1985									saithe+				
1986									hake+				
1987						hake-	netf-						flatfish-
1988			rockfish+							SST+		herring+	
1989									saithe–	u-winds+ v-winds+	SST+		
1990													
1991								herring+					cod+haddock+
1992			flatfish+						cod–				
1993													
1994				v-winds–									saithe+
1995						rockfish+			rockfish+				
1996			rockfish+									herring+	
1997			cod–			hake–cod–flatfish+							
1998					herring+			herring+	flatfish*	SST+			hake+rockfish–
1999							netf+SST+		haddock*				
2000												mackerel–	
2001								mackerel*					saithe+
2002	SST+								hake–rockfish+				haddock* flatfish*
2003				SST+								capelin–	
2004		herring*									v-wind+		
2005											SST+	herring+	
2006											netf–		

5. Discussion

The value in this study, as in all comparative ecosystem studies, is that we can use the histories of the biota for each ecosystem to separate out localized phenomena from broader basin- or global-scale "teleconnections." Efforts such as these will become increasingly important as scientists continue to grapple with how climate change will affect marine ecosystems (Beaugrand et al., 2002; Perry et al., 2005; Stenseth et al., 2002). Certainly simulation models will also be important in evaluating the impacts of global scale phenomena (such as a changing climate) on marine ecosystems (Denman and Pena, 2002; Chai et al., 2003; Hashioka and Yamanaka, 2007; Megrey et al., 2007; Rose et al., 2007; Sakshaug and Walsh, 2000). Yet having actual time series of data will be critical to not only validate such models but also to detect common patterns in the world's marine biological communities. Often science is conducted in a reductionist, deductive approach; evaluating global scale phenomena is not conducive to such an experimental approach and using a comparative approach allows for ecosystems to serve as "replicates" in an hypothesis testing context.

The sum of our results – via cross-correlations, common pattern detection, and major event synchronies – all indicate that although there are some pan-basin and within-basin similarities, most of the dynamics that dominate these biological systems are at the local (i.e. region specific) scale. This is not to imply that there are no significant pan-basin or within-basin phenomena occurring. In fact, where commonalities and synchronies were detected implies that such factors are not likely to be trivial. More so, our results indicate that regional effects of global processes must be interpreted for each ecosystem in light of local histories, accounting for all the specific processes affecting a particular biological community. Particularly in systems which have received intense fishing pressure over the past century. The common mid- to late 1970s regime shift in environmental data detected here and in related MENU studies (Drinkwater et al.; Mueter et al., this volume) are good examples of a global phenomenon. Yet how that translates into common responses from the biota is less clear. Megrey et al. (this volume) explore both within basin recruitment responses and between basin inverse synchronies in recruitment events as possible examples of how these broad-scale changes are translated into responses exhibited by the biota. Further work on this "translation" topic is still needed (*sensu*, Beaugrand et al., 2002; Perry et al., 2005; Stenseth et al., 2002).

There were similarities for all of the four ecosystems examined in this study. For instance, the importance of small pelagics, gadids, and *Calanus* spp. in each ecosystem was apparent as we went through the process of collating our data sets. Additionally, total fish biomass was relatively stable in all systems, suggesting that although changes in species composition have occurred, the fundamental levels of overall system productivity have not been radically altered. Thus it appears that these marine systems have an inherent resilience to changes in overall fish biomass; these results also imply some form of approximate systemic carrying capacity. Conversely, the magnitudes of total fish biomass, fisheries removals, and biomasses of lower trophic levels were distinct across all ecosystems (Gaichas et al., this volume), suggestive of different levels and timing of the productivity among these ecosystems.

There were some significant pan-basin commonalities and synchronies. The GOA and GOM/GB total fish and *Sebastes* spp. biomass anomalies trended in similar directions and roughly at similar time frames. The only major commonality among EBS, NOR/BAR and GOM/GB was the opposite trends in herring and capelin. In the NOR/BAR system, Hjermann et al. (2004) indicated that the climatic regime of the region ultimately determines the balance between herring and capelin and that changes can have dramatic impacts on ecosystem function. Shifts from capelin to herring can also potentially impact piscivorous fishes, including cod (Rose and O'Driscoll, 2002). The coherence in the capelin-herring dynamics across ecosystems and the potential impact on fishery resources deserve further attention. Where the opposite patterns in herring and capelin occur is suggestive of potential competition, differential fishing or predation mortalities, and/or a shift in environmental conditions between these two species.

Although there were some commonalities among the four ecosystems, the majority of correlated and commonly-timed trends were within a basin. For example, comparing the GOA and EBS, total fish, cod, and pleuronectid biomass anomalies were all positively synchronous. Similarly, both positive and negative synchronicity in recruitment is evident in these systems and is much stronger within than between ecosystems (Mueter et al., 2007). Or comparing the GOM/GB and NOR/BAR, herring, krill and pleuronectid biomass anomalies were positively synchronous. There were far more similarly timed events or positively correlated time-series within an ocean basin than between them.

As a corollary, there were notably more negative correlations and asynchronous timing of events between the two ocean basins: 9 out of 12 significant negative correlations among biomass time series involved between-basin comparisons, whereas 9 out of 12 significant positive correlations involved within-basin comparisons (Table 3). For example, the GOA compared to NOR/BAR herring, medium gadids, *Sebastes* spp., and capelin biomass anomalies were negatively correlated and/or asynchronous. The same was true for GOA and GOM/GB herring biomass anomalies or the EBS and NOR/BAR *Sebastes* spp. and pleuronectid biomass anomalies. Granted, there were some within basin negative correlation and asynchronies, such as the GOM/GB and NOR/BAR cod and *Sebastes* spp. biomass anomalies, but the vast majority of asynchronous and negatively correlated trends were between the two ocean basins.

We found that 1976–78 constituted a period of shifts in the environmental indices across all four ecosystems. This shift is well-documented in other environmental indices across the North Pacific (e.g. Bond et al., 2003), reflecting the different manifestation of a shift of the Pacific Decadal Oscillation (PDO; Hare, 1996; Mantua and Hare, 2002) from a cold phase to a warm phase in a multitude of other environmental indices. An approximately synchronous, but less strong shift or transition in key North Atlantic atmospheric indices have also been noted (e.g. NAO; Hurrell et al., 2003; Jones et al., 1997). Two other periods were identified that involved near-synchronous shifts across multiple ecosystems: 1987–89 and 1998–99. Shifts in these periods were detected in both the GOM/GB and NOR/BAR. An apparent shift during 1987–89 has also been found in oceanographic and climatic variables for the North Sea (Beaugrand, 2004). Although shifts were not detected during the 1987–89 or 1998–99 time periods for the EBS or GOA in the suite of environmental indices we analyzed here, regime shifts have been detected in other environmental indices during these time periods for both ecosystems (EBS: e.g. Rodionov and Overland, 2005; GOA: Mantua et al., 1997; and Litzow, 2006).

We also found evidence that these shifts in environmental conditions were followed by shifts in stock abundance of forage fishes in the same ecosystems at lags up to several years. However, not all shifts in forage fish abundance were preceded by shifts in the environmental indices (e.g. GOM/GB mackerel in 1969). In contrast, we found little evidence suggesting that shifts in groundfish abundance in the four ecosystems correlated with previous shifts in environmental indices. Given that the groundfish species are typically longer-lived than the forage fishes, the "storage effects" associated with extended age structure seem likely to obscure the effects of abrupt environmental changes over multiple age classes and introduce lag effects that combine to obfuscate the impact of environmental regime shifts on groundfish biomass. Further, given the histories of fishing exhibited in these ecosystems, any future endeavor to tease apart global-scale climate studies will need to account for the fisheries removals of stocks within each of these or related ecosystems. Alternatively, time series of recruitment or survival rates may provide more direct indicators of environmental effects and show clear evidence of synchronous shifts in survival associated with both the 1976/77 and the 1988/89 environmental shifts in the GOA and EBS (Megrey et al., this volume; Mueter et al., 2007) as has been suggested in other studies (Beaugrand, 2004; Brander, 2005; Ottersen et al., 2000).

This work demonstrates the value of comparative analysis across a wide range of marine ecosystems, suggestive of few but none-the-less still detectable common features across all northern hemisphere ocean systems. The similarities between the Pacific and Atlantic are indicative of common global processes; e.g. the consistently detected regime shift in environmental data in the mid to late 1970s. The distinctions between the Atlantic and Pacific represent how those phenomena are uniquely expressed in each ocean. Additionally, the similarities within an ocean basin represent basin-scale factors that consistently impact the biota; e.g. herring in the Atlantic possibly in response to changes in a suite of NAO related physical oceanographic factors. But probably most commonly and most importantly, distinctions even within ocean basins represent how each regional ecosystem responds to these global or broad-scale phenomena in the context of the other processes acting more locally.

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