

# Comparison of the biophysical and trophic characteristics of the Bering and Barents Seas

George L. Hunt Jr. and Bernard A. Megrey

Hunt, G. L., and Megrey, B. A. 2005. Comparison of the biophysical and trophic characteristics of the Bering and Barents Seas. — ICES Journal of Marine Science, 62: 1245–1255.

The eastern Bering Sea and the Barents Sea share a number of common biophysical characteristics. For example, both are seasonally ice-covered, high-latitude, shelf seas, dependent on advection for heat and for replenishment of nutrients on their shelves, and with ecosystems dominated by a single species of gadoid fish. At the same time, they differ in important respects. In the Barents Sea, advection of Atlantic Water is important for zooplankton vital to the Barents Sea productivity. Advection of zooplankton is not as important for the ecosystems of the southeastern Bering Sea, where high levels of diatom production can support production of small, neritic zooplankton. In the Barents Sea, cod are the dominant gadoid, and juvenile and older fish depend on capelin and other forage fish to repackage the energy available in copepods. In contrast, the dominant fish in the eastern Bering Sea is the walleye pollock, juveniles and adults of which consume zooplankton directly. The southeastern Bering Sea supports considerably larger fish stocks than the Barents. In part, this may reflect the greater depth of much of the Barents Sea compared with the shallow shelf of the southeastern Bering. However, walleye pollock is estimated to occupy a trophic level of 3.3 as compared to 4.3 for Barents Sea cod. This difference alone could have a major impact on the abilities of these seas to support a large biomass of gadoids. In both seas, climate-forced variability in advection and sea-ice cover can potentially have major effects on the productivity of these Subarctic seas. In the Bering Sea, the size and location of pools of cold bottom waters on the shelf may influence the likelihood of predation of juvenile pollock.

© 2005 International Council for the Exploration of the Sea. Published by Elsevier Ltd. All rights reserved.

Keywords: Barents Sea, Bering Sea, capelin, cod, ecosystem productivity, herring, walleye pollock.

Received 5 November 2004; accepted 10 April 2005.

G. L. Hunt: *Ecology and Evolutionary Biology, University of California-Irvine, Irvine, CA 92697-2525, USA.* B. A. Megrey: *National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA.* Correspondence and present address to G. L. Hunt: *School of Aquatic and Fishery Sciences, University of Washington, Seattle WA, 98195, USA; tel: +1 949 824 6322; fax: +1 949 824 2181; e-mail: geohunt2@u.washington.edu.*

## Introduction

Recent, unprecedented changes in the Subarctic marine ecosystems of the eastern Bering Sea and Barents Sea underscore the need to understand how global change may impact ecosystem structure and productivity (Napp and Hunt, 2001; Ottersen *et al.*, 2001; Hunt *et al.*, 2002; ACIA, 2004). These high-latitude seas are especially sensitive to climate change as they bridge the transition region between Arctic and north temperate ecosystems. The last few decades of modern ocean observations have recorded significant year-to-year variations in features such as ice cover, insolation, sea surface temperature, advective processes, and

ecological dynamics. Since the Bering and Barents Sea support the northern hemisphere's largest and most valuable commercial fisheries [walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*)/cod (*Gadus morhua*), respectively], it is also relevant to ask how climate change may influence fish stocks found in northern temperate waters. Unfortunately, the critical processes linking climate change to marine and fisheries production are not well known.

Attempts to understand how marine ecosystems react to climate and human influences pose huge sampling problems for analysis at the scale of whole ecosystems. However, comparative studies of marine ecosystems may provide key insights into how they respond to climate

change, insights that could not be achieved by studying one region in isolation. The objective of this paper is to compare, in a general way, the characteristics that make the Bering Sea and Barents Sea ecosystems unique, to identify key areas of differences and similarities, and to attempt to relate these observations to the questions of how climate impacts the physical environment, how the physical environment affects the structure of fish communities in each sea, and how changes in the physical environment affect the production of fish and the ability of the Bering and Barents Seas to support stable fisheries and productive ecosystems. Earlier efforts to compare these two ocean systems (Sakshaug and Walsh, 2000; Sakshaug, 2004) did not have the advantage of the information and the Ecopath modelling results provided by Aydin *et al.* (2002) and Blanchard *et al.* (2002).

In the following sections, the Bering and Barents Seas are compared with respect to their physical setting, climate and advective processes, productivity, biomass, ecosystem structure, and fisheries yield.

## Comparison

### Physical setting

The entire Bering Sea lies at a lower latitude than the relative to the Barents Sea. For example, the southernmost point of the Barents Sea is at a higher latitude than Bering Strait, the northernmost point of the Bering Sea (Figure 1). Latitude has a major impact on the light field, determining the length of the growing season, the daily distribution of light and the angle at which light impinges on the water's surface, and thus the proportion of the light that penetrates into the water column. Latitude, through proximity to Arctic winds and through daylength in winter, also influences the prevalence of cold temperatures. However, the Barents Sea is warmer than might be expected for its latitude because of the advection of heat in the inflowing Atlantic Water.

The bathymetries of the Bering and Barents Shelves differ. The Barents Sea has a shelf composed of deep basins (400–500 m) and intervening shallow banks (100–200 m), whereas the southeastern Bering Sea has a broad, flat, shallow shelf that gradually increases in depth from the coast to the continental shelf edge at a depth of about 180 m. The eastern Bering Sea is separated into three bathymetrically fixed oceanographic provinces, an inner, middle, and outer shelf domain on the basis of hydrographic structure in summer (Kinder and Schumacher, 1981; Coachman, 1986; Stabeno *et al.*, 1999). In contrast, the Barents Sea has two major hydrographic domains: Atlantic and Arctic, which differ in the sources of their water masses (Loeng, 1991). These differences in topography result in the Barents Sea having a smaller area of shallow shelf (<200 m; Table 1), and a greater average depth (230 m vs. 70 m) than the southeastern Bering Sea.

Circulation patterns also differ strongly between the two seas (Figure 2). In the Barents Sea, Arctic Water flows southwards onto the shelf and meets north and east-flowing Atlantic Water, creating a strong Polar Front (Loeng, 1991). The location and strength of the front depends on variation in the strength of the two currents, but it is relatively distinct and stable in the southwest Barents Sea, at about 76°N. In the Bering Sea, there is little inflow of Arctic Water, and inflows of water are primarily from the Alaska Coastal Current and the Alaska Stream, both of which enter the Bering Sea through the passes of the Aleutian Islands (Stabeno *et al.*, in press), and from riverine inputs along the coast.

Most nutrients for primary production are delivered by deep ocean circulation and brought into the photic zone by dynamic processes occurring along the continental slope and frontal regions. Advection of nutrients is likely more important in the Barents than the Bering Sea, but for both regions, little is known about the relative importance of advection vs. remineralization of nutrients in bottom sediments. In the Bering Sea, winter nutrient levels, especially nitrate, are about twice those in the Barents Sea (Table 1), mainly due to the longer period available during which the Pacific deep water can become enriched with nutrients from decaying organic matter (Sakshaug and Walsh, 2000; Sakshaug, 2004). Levels of phosphate are similar in the two systems, but the Bering Sea has higher concentrations of silicate, which support a larger standing stock of diatoms.

Seasonal sea-ice cover is an important and common characteristic of both seas. Because of its proximity to the Arctic Ocean, the northern edge of the Barents Sea is permanently covered in ice, whereas in the Bering Sea, ice is present only during winter. In both systems, the southern extent of the ice edge is related to the prevailing annual temperature conditions and the southern edge seasonally expands and contracts. It is believed that the extent of ice cover in the Barents Sea is governed by variability in the inflow of warm Atlantic Water, which is influenced by variation in the North Atlantic Drift Current, and is regulated by variation in the North Atlantic atmospheric circulation (Ådlandsvik and Loeng, 1991; Orvik and Skagseth, 2003). Also in both systems, ice dynamics affect the vertical circulation of water masses, through brine rejection during ice formation and release of freshwater during melting, and influence water temperature, biological production, and the formation of fronts. Melt water increases the stratification of the water column and therefore increases the energy required to mix the water vertically. The underside of the sea-ice provides a substrate for an epontic flora and fauna, while the surface is used as a platform by marine mammals, birds, and human predators. The formation, melt, and retreat of sea-ice provide physical conditions that also influence the structure and function of pelagic and benthic communities.

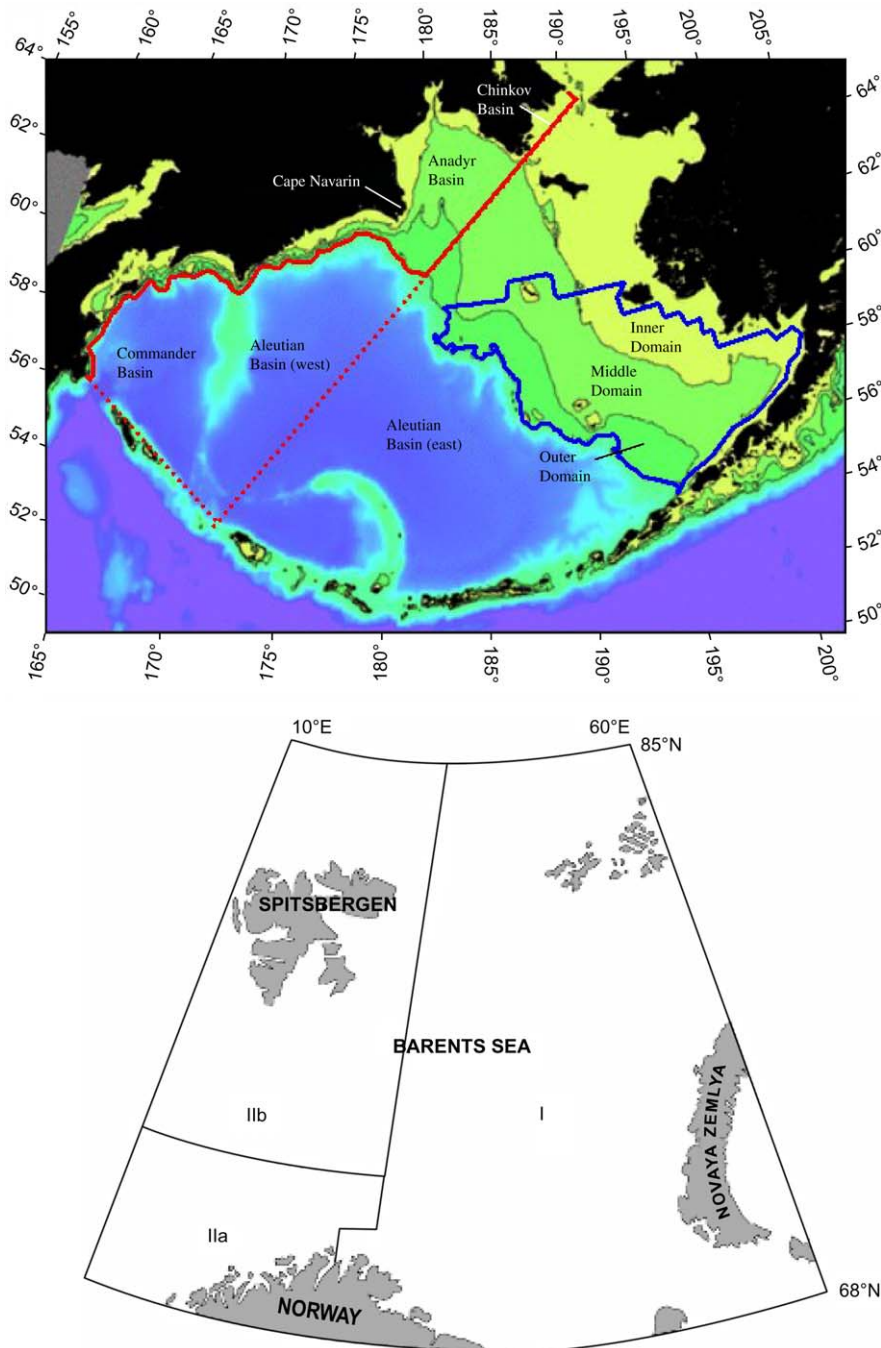


Figure 1. Geographic regions defining the eastern Bering Sea Shelf (top panel, Aydin *et al.*, 2002) and the Barents Sea system (bottom panel, Blanchard *et al.*, 2002).

### Climate processes

High-latitude seas come under the influence of the large-scale atmospheric patterns. In the North Atlantic region, the leading mode of atmospheric variability is the North Atlantic Oscillation (NAO) (Hurrell *et al.*, 2003). The NAO, which essentially is an indication of the relative

strengths of the Icelandic Low and the Azores High, is the principal factor controlling air–sea interaction in the region. For example, changes in the Barents Sea reflect changes in the NAO index (Ottersen *et al.*, 2001) (Figure 3). Typically, 40–50% of the variance in oceanographic variables such as sea temperatures and

Table 1. Comparison of the physical characteristics of the Bering and Barents Sea ecosystems.

Parameter	SE Bering Sea	Barents Sea
Latitude	54–60°N*	68–85°N†
Area > 200 m (km <sup>2</sup> )	21.1 × 10 <sup>3</sup> *	533.2 × 10 <sup>3</sup> †
Area < 200 m (km <sup>2</sup> )	463.4 × 10 <sup>3</sup> *	472.9 × 10 <sup>3</sup> †
Advection	~1 Sv‡	~2–2.5 Sv§
Nitrate (mM m <sup>-3</sup> )	10–30	12
Phosphate (mM m <sup>-3</sup> )	1.0–2.0	0.85
Silicate (mM m <sup>-3</sup> )	25–60	6–8

\*Aydin *et al.* (2002).

†Dommasnes *et al.* (2001).

‡Sakshaug and Walsh (2000).

§Ingvaldsen *et al.* (2004).

||Sakshaug (2004).

sea-ice in this region can be accounted for by the NAO index, including the strong decadal variability since the 1960s. The strengthening of the Icelandic Low associated with a high NAO index results in an increase in south-westerly winds in the Barents Sea, which brings warmer conditions. This climate forcing strongly impacts advection of Atlantic Waters into the Barents Sea. It is less clear how atmospheric forcing affects water flow in the southeastern Bering Sea and Gulf of Alaska (the source of water for the Bering Sea). Flows through Bering Strait are often reversed by winter atmospheric pressure systems (Roach *et al.*, 1995; Overland *et al.*, 1996), but flow through Bering Strait only impacts the northern shelf and Arctic Ocean and has little influence on the southeastern shelf (Stabeno *et al.*, 1999) (Figure 2). Little is known about how climate influences flow through the passes of the Aleutian Archipelago.

In the North Pacific region, wintertime physical climate indices include the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO) (Figure 4). The AO is defined as the leading mode of sea level pressure variability north of 20°N, including over the North Atlantic, and consists of a pattern of zonally symmetric variability in the strength of the polar vortex (Thompson and Wallace, 1998). The AO has its largest variance in winter (January–March). The AO influences the Bering Sea through its effect on the Aleutian Low Pressure System, which reflects the strength and distribution of storm tracks in the southern Bering Sea and Subarctic Pacific Ocean (Overland *et al.*, 1996). The PDO is defined as the leading mode of sea surface temperature variability in the North Pacific (north of 20°N) (Trenberth and Hurrell, 1995; Mantua *et al.*, 1997).

In conjunction with indices of biological responses in marine ecosystems, the AO and PDO have been used to identify abrupt shifts in climatic forcing and ecosystem response at decadal time scales (Francis *et al.*, 1998; Hare and Mantua, 2000; McFarlane *et al.*, 2000; Hollowed *et al.*, 2001). Two of these regime shifts have been identified in

the past 30 years. One followed the winter of 1976–1977, in which the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO) both shifted (Figure 4). A second shift, of just the AO, occurred after the winter of 1988–1989 (Ebbesmeyer *et al.*, 1991; Hare and Francis, 1995; Sugimoto and Tadokoro, 1998; Beamish *et al.*, 1999; Brodeur *et al.*, 1999; Hare and Mantua, 2000). There is some evidence of a third shift in the winter of 1998–1999 (Schwing and Moore, 2000; Peterson *et al.*, 2002), or possibly a mode shift (Bond *et al.*, 2003). Although the *El Niño*-Southern Oscillation (ENSO) appears to alternate between two states that are repeatedly visited, that is not the case for regime shifts in the southeastern Bering Sea, where the few regimes documented so far each have had unique characteristics (Overland *et al.*, 2001). The influences of the North Pacific and AO modes in spring have resulted in an increase in southerly winds over the Bering Sea. Atmospheric teleconnections also result in influences from more distant regions, such as the equatorial Pacific Ocean (e.g. ENSO; see Overland *et al.*, 2001).

In the northeastern Pacific Ocean, as the wintertime Aleutian low-pressure system deepens, the winds driving circulation patterns strengthen, more nutrients are brought to the surface, and ocean productivity increases. Under these circumstances, zooplankton biomass increases (Brodeur and Ware, 1992). Many fish stocks have shown strong recruitment during the years when the Aleutian low was deep and extensive, and poor recruitment when it was shallow and limited.

Within the Bering and Barents Seas, currents transport biological material in addition to influencing nutrients, heat, and salt. For example, in the Barents Sea, zooplankton, especially *Calanus finmarchicus*, are transported by the Atlantic inflow, with added influx of zooplankton-rich water from the Norwegian Sea into the Barents Sea in years of higher inflows (Ottersen and Sundby, 1995; Sundby, 2000). Also, the distribution of capelin (*Mallotus villosus*), the single most important food species for Arcto-Norwegian cod, is (at least during some seasons) known to vary from year to year in response to the inflow of Atlantic Water (Sakshaug *et al.*, 1992). In the Bering Sea, wind-driven cross-shelf advection of surface waters influences year-class strength in flatfish and possibly pollock (Wespestad *et al.*, 2000; Wilderbuier *et al.*, 2002).

The Bering and Barents Seas also export water to the neighbouring ocean basins. Important during the transport within the Bering and Barents Seas is the modification of water masses as they move to or from the Arctic. In the southern Barents Sea and the eastern Bering Sea, the currents transport relatively warm, salty water to the Arctic from the Atlantic and the Pacific, respectively. For example, the transformation of Atlantic Water as it passes through the Barents Sea is important for the ventilation of the Arctic Ocean. The Barents Sea also provides intermediate water to the Arctic Ocean to a depth of 1200 m (Schauer *et al.*, 1997, 2002). The northern Barents Sea

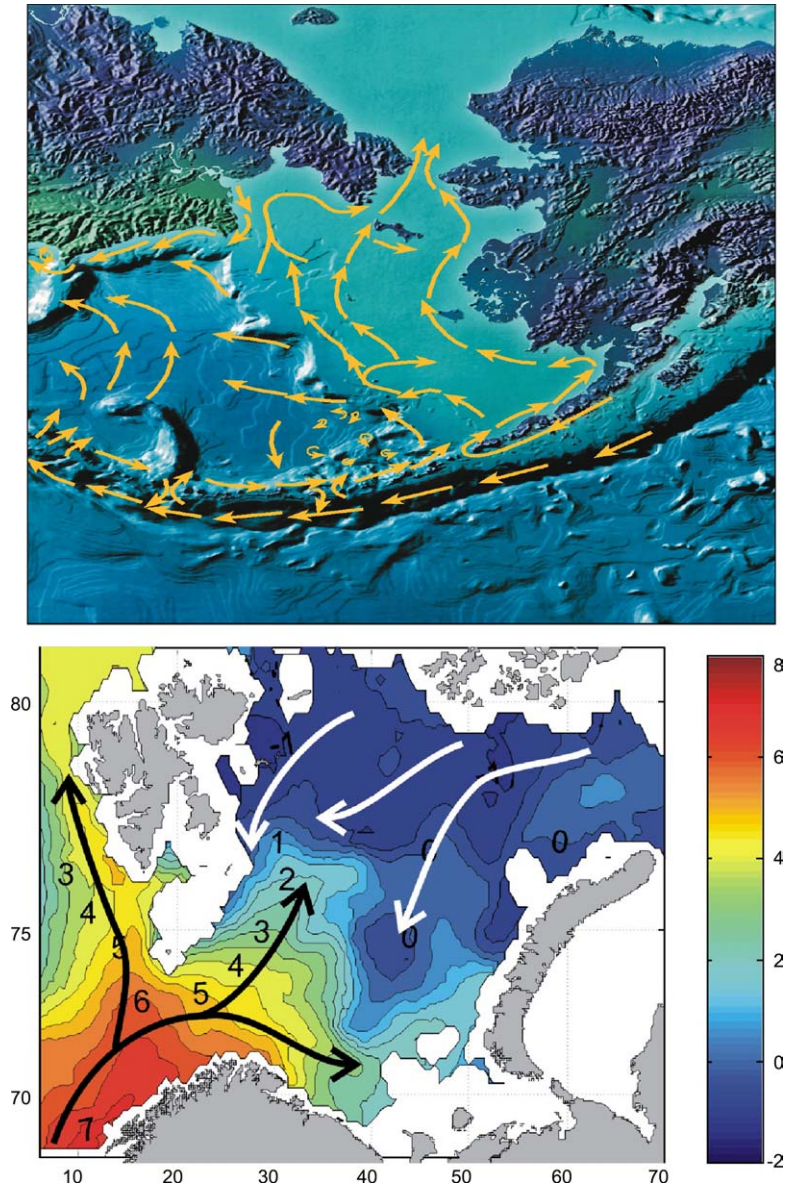


Figure 2. Circulation patterns for the Bering Sea (top panel, Aydin *et al.*, 2002) and the Barents Sea (bottom panel, H. Loeng and R. B. Ingvaldsen, Institute of Marine Research, Bergen, pers. comm.). Numbers in the bottom panel are sea surface temperatures.

contains currents that carry Arctic Water towards the North Atlantic (Figure 2).

### Productivity

Overall primary production in the Bering Sea is similar to that in the Barents Sea (Table 2), though recent estimates by Sakshaug (2004) suggest that production over the eastern Bering Sea Shelf is higher than in the Barents Sea.

The seasonal primary production in the Bering and Barents Seas is generally governed by nutrients and light as modified by ice cover and vertical mixing of the water

column. Nutrients are supplied to the surface layers by mixing and upwelling of deep water. Production can be separated into two components. New primary production is based on new nutrients brought into the mixed layer by physical processes. Regenerated production is a result of the biological recycling of nutrients within the euphotic zone.

There is considerable variability in the concentrations of nutrients available in the Bering and Barents Seas, and advection plays an important role in determining the regional abundance of nutrients, and the resultant levels of new production. For example, because North Atlantic Waters are richer in nutrients than Arctic Waters, the waters

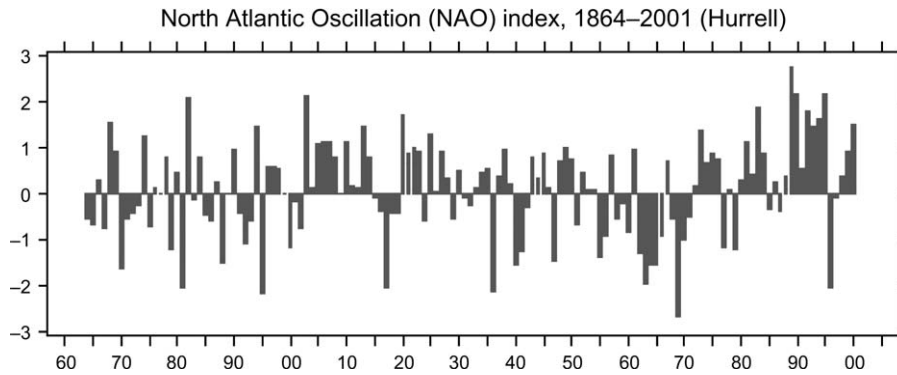


Figure 3. The North Atlantic Oscillation index time-series of Hurrell (jhurrell@ra.cgd.ucar.edu).

of the warmer, southern regions of the Barents Sea contain higher initial nutrient concentrations than do the more northern regions. In addition, mixed-layer depths in southern regions are generally deeper than those generated by ice-melt induced stratification in northern regions. In warmer regions of the Barents Sea, the phytoplankton blooms are also more prolonged than in its Arctic Waters. Thus, the Arctic Waters of the Barents Sea support an annual primary production of  $66 \text{ g C m}^{-2} \text{ y}^{-1}$ , with  $42 \text{ g C m}^{-2} \text{ y}^{-1}$  fuelled by nitrate (new nitrogen) vs. ammonia (recycled nitrogen), while for the Atlantic Waters the corresponding rates are 174 and  $83 \text{ g C m}^{-2} \text{ y}^{-1}$ , respectively (Sakshaug and Walsh, 2000). For the south-eastern Bering Sea, annual primary production rates of 160 and  $175 \text{ g C m}^{-2} \text{ y}^{-1}$  have been reported for the outer and middle domains, respectively (Sakshaug and Walsh, 2000). More recently, Sakshaug (2004) provided an estimate of  $>230 \text{ g C m}^{-2} \text{ y}^{-1}$  for total primary production on the southeastern Bering Sea Shelf.

On the Bering Sea Shelf, zooplankton levels are higher in its warmer regions (Smith and Vidal, 1986), so that a higher proportion of the phytoplankton in these regions is grazed than in the colder regions, and less sinks out. This is not necessarily the case in the Barents Sea (Tande *et al.*, 2000), since the interannual variation in summer copepod biomass may be governed primarily by the over-wintering biomass found in the deep basins and by advection in the inflowing Atlantic Water. The organic material that is grazed will be retained as zooplankton biomass or recycled within the surface layers, although some proportion will still sink to the bottom as faecal pellets.

A non-diatom bloom species, the prymnesiophyte, *Phaeocystis pouchetii*, is possibly more important as a component of the primary producers in the Barents Sea than in the Bering Sea (Sakshaug and Walsh, 2000). This species can exist in a unicellular flagellated form (ca.  $3 \mu\text{m}$  in diameter), but when in blooms, it is in its colonial form with groups of cells embedded in a gel-like matrix.

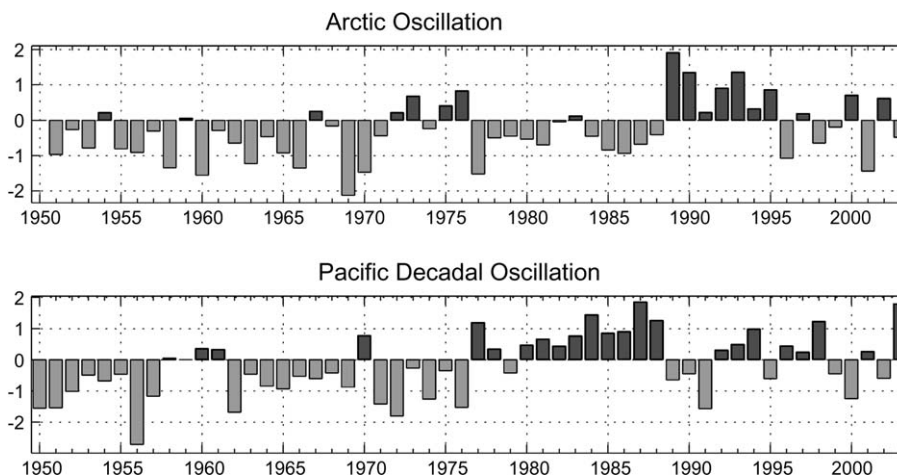


Figure 4. Time-series of the Arctic Oscillation (top panel) and the Pacific Decadal Oscillation (bottom panel), courtesy of J. Overland, NOAA, PMEL, Seattle.

Table 2. Comparison of lower trophic level productivity between the Bering and Barents Seas ecosystems and between regions within each location.

	Bering Sea			Barents Sea	
	Inner	Middle	Outer	Arctic	Atlantic
Total primary production* (g C m <sup>-2</sup> y <sup>-1</sup> )	50–70	150–175	160	<90	<200
New productivity	<20	30–50	?	<40	70–100
Secondary production	2–6	8–30	16–50	1–18	3–17
Dominant taxa		Diatoms		<i>Phaeocystis</i>	

Data sources: Sakshaug and Walsh (2000); Sakshaug (2004).

\*Sakshaug (2004) now estimates >230 g C m<sup>-2</sup> y<sup>-1</sup> for the eastern Bering Sea Shelf.

Conditions that favour the proliferation of *Phaeocystis* are thought to include low silicate:nitrate ratios and low light levels. *Phaeocystis* blooms sometimes occur in areas with deep mixed layers or in unstratified waters. *Phaeocystis* colonies may accumulate because they are not readily grazed by meso- or microzooplankton. *Phaeocystis* is not readily grazed by most copepods in the Bering and Barents Seas, and the predominance of *Phaeocystis* in the Barents Sea may result in a less efficient throughput of energy from the primary producers to the tertiary consumers (Sakshaug and Walsh, 2000). How changing climate will affect the role of *Phaeocystis* in these Subarctic seas and its impact on secondary production remains a question of interest.

On the Bering Sea Shelf, ecological models of carbon flow predict that roughly 40% of the annual carbon production in the outer (warm) domain is consumed by zooplankton, while only 20% is consumed in the middle (cool) domain (Walsh and McRoy, 1986). Primary production is more or less the same in both areas (160 g C m<sup>-2</sup> y<sup>-1</sup>) and the difference in secondary production is driven mainly by differences in zooplankton biomass and composition, i.e. the middle domain has lower biomass and lower grazing potential.

In the Barents Sea, the vertical flux of carbon in spring was found to be more or less the same in Arctic (cold) and Atlantic (warm) Waters (ca. 200 mg C m<sup>-2</sup> d<sup>-1</sup>) (Olli *et al.*, 2002). Ungrazed phytoplankton accounted for up to 50% of the flux and zooplankton faecal pellets, a very variable but sometimes large proportion. In summer, the flux was reduced by a factor of 1.7 probably due in part to increased recycling within the near-surface layers: microzooplankton grazing consumed up to 97% of phytoplankton production (Verity *et al.*, 2002). Despite the apparent similarity of vertical fluxes of organic material in Arctic and Atlantic Waters, it appears that benthic biomass in warm areas of the Barents Sea is higher than that found in cold areas.

In the southeastern Bering Sea, the timing of the sea-ice retreat is directly related to the timing of the spring phytoplankton bloom (Stabeno *et al.*, 2001; Hunt *et al.*, 2002). During years when ice is present after mid-March, there is an early, ice-associated phytoplankton bloom that

consumes the available nutrients in the upper mixed layer. During years of no ice cover after mid-March, the spring bloom does not occur until May or June with the onset of insolation-driven upper layer stratification (Eslinger and Iverson, 2001; Stabeno *et al.*, 2001). Because maximum zooplankton growth is delayed until later in the season when ocean temperatures are warmer, primary production from an early ice-associated bloom generally falls to the bottom and supports the benthic communities, while a later bloom favours the pelagic ecosystem.

Topographic differences between the Bering and Barents Seas appear to influence the fate of primary production. In the Bering Sea much, if not most, sinks to the bottom and is not utilized in the pelagic zone, while in the Barents Sea the deeper water column ensures that less production settles to the bottom (Coyle and Cooney, 1988; Sakshaug *et al.*, 1994).

## Biomass

Comparisons between biomass for the Bering and Barents Seas are given in Table 3. For the Barents Sea, comparisons are given for years of high and low capelin abundance, as the abundance of capelin strongly affects the system. The Barents Sea supports a larger biomass of phytoplankton and zooplankton per unit area than the Bering Sea. Currently, the southeastern Bering Sea has almost no capelin, and has a smaller biomass of herring than is found in the Barents Sea. The benthic community of the southeastern Bering Sea is larger than that in the Barents Sea. In the Bering Sea, benthic crustaceans have about double the biomass, and flatfish abundance is an order of magnitude greater than in the Barents Sea. The Bering Sea has a pollock biomass per km<sup>2</sup> that is 30 times larger than that of cod in the Barents Sea. However, the Barents Sea has a larger biomass of piscivorous pinnipeds.

Production-to-biomass ratios and measures of productivity (Table 4) show some striking differences. The Bering Sea has somewhat higher primary production, lower production by copepods, but higher production of large zooplankton. Production-to-biomass ratios and production

Table 3. Biomass estimates\* (tons km<sup>-2</sup>), from the literature, of components of the Bering and Barents Seas used as inputs for Ecopath models of these ecosystems. Comparisons for the Barents Sea are given for years of high (1990) and low (1995) capelin abundance.

Taxon	Barents 1990 high capelin	Barents 1995 low capelin	E. Bering Sea 1980s
Phytoplankton	20	20	11.8
Crustacean zooplankton	58	58	26
Capelin	4.17	0.14	—
Herring	1.34	3.33	0.78
Benthic crustaceans	1.43	1.38	>2.2
Flatfish	1.1	1.1	11.3
Gadids	1.2	2.6	35.9
Pinnipeds	0.87	0.87	0.22
Whales	0.20	0.20	0.26

Sources: Blanchard *et al.* (2002) (Barents Sea) and Aydin *et al.* (2002) (Bering Sea).

\*In parameterizing the Ecopath model Blanchard *et al.* (2002) used a wide variety of data sources. For some species or trophic compartments, he had no precise data and used best estimates, as in the case of phytoplankton and zooplankton. There were no separate estimates for 1990 and 1995 for these. For pinnipeds and whales, there were assessments of biomass, but not on an annual basis. Thus, their biomass do not vary for 1990 and 1995, which, for long-lived species may well have been the case. Capelin, herring, and cod biomass data were from fisheries assessments. Biomass estimates for other fish were obtained from ICES MSVPA results.

are similar between the two systems for forage fish and herring. Cod has a higher production-to-biomass ratio in the Barents Sea than pollock in the Bering Sea, but the size of the pollock population makes the production estimate for the Bering Sea much higher than the Barents Sea. The production of small flatfish in the Bering Sea is higher than

Table 4. Comparison of production-to-biomass ratios and productivity of the Bering and Barents Seas ecosystems.

Taxon	Bering Sea		Barents Sea	
	P/B (y <sup>-1</sup> )	P	P/B (y <sup>-1</sup> )	P
Phytoplankton	170	2000	117.73	1765
Copepods	6	330	10	500
Large zooplankton	5.5	242	4	67.5
Forage fish	0.8	—	1	1.13
Herring	1.0	0.78	0.38	1.24
Adult pollock/Atlantic cod	0.5	13.73	1.2	0.54
Small flatfish	0.4	3.67	1	0.7
Benthic infauna	1.37	63.84	1.5	99

Data source: Blanchard *et al.* (2002) (Barents Sea) and Aydin *et al.* (2002) (Bering Sea).

the Barents Sea, even though the production-to-biomass ratio is higher in the Barents Sea.

### Fisheries yield

The fisheries yields from the Barents and Bering Seas are dramatically different (Table 5). Data from the top five species over the most recent 5-year interval (1998–2002) show that the yield of pollock from the Bering Sea was almost three times the yield of cod from the Barents Sea. Also, flatfish, namely yellowfin sole (*Limanda aspera*) and rock sole (*Pleuronectes bilineatus*), contribute to the Bering Sea yield. In 2003, these primary benthic flatfish made up 26% of the total groundfish of the Bering Sea (North Pacific Fisheries Management Council, 2003). The list from the Barents Sea contains no flatfish, and benthic production is harvested as prawns. Prawns are not in the top five commercial species harvested from the Bering Sea, whereas flatfish are.

### Discussion

The comparisons between the Bering and Barents Seas that we present must be taken with some caution. When developing the Ecopath model for the Bering Sea, from which we have drawn many of the statistics presented, Aydin *et al.* (2002) used as their study area the southeastern Bering Sea Shelf (Figure 1), the richest and most productive area of the Bering Sea. In contrast, Blanchard *et al.* (2002) included in their Ecopath model a large portion of the Barents Sea north of the Polar Front (Figure 1). This cold, deep northern region of the Barents Sea is much less productive than the smaller southern region where warmer Atlantic Water predominates. Thus, if only the most productive regions of each sea were compared, the differences might not be as great as they appear here.

Overall, there are many similarities in the interaction of the physical processes of the two systems. They are both influenced by advection, formation, and retreat of sea-ice and by large-scale atmospheric and climatic forcing. However, the biological systems are quite distinct, and different mechanisms influence the processes underlying variation in fish production.

We have shown that nutrients and primary production are similar, and that diatoms dominate the phytoplankton in the Bering Sea while *Phaeocystis* is common in the Barents Sea. Both systems are sensitive to the timing of the spring bloom, large zooplankton are more abundant and productive in the Bering Sea, and the Bering Sea has a higher fisheries yield. Primary production in the Bering Sea supports a large and more diverse benthic community, suggesting that some significant fraction of the production that takes place in the mixed layer reaches the demersal habitat. This is not the case in the Barents Sea. Differences



Table 5. Comparison of fish catch of the top five species from each ecosystem summed over the past 5 years (1998–2002).

Bering Sea		Barents Sea	
Species	Catch (t)	Species	Catch (t)
Pollock	6091 077	Cod	1 784 718
Cod	764 767	Herring	1 077 166
Yellowfin sole	388 766	Capelin	558 692
Atka mackerel	268 974	Haddock	343 767
Rock sole	194 005	Northern prawn	290 617

Data sources: The Sea Around Us Project, <http://saup.fisheries.ubc.ca/lme/SummaryInfo.aspx?LME=20#> (Barents Sea) and Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions, 2003. <http://www.afsc.noaa.gov/refm/stocks/assessments.htm> (Bering Sea). North Pacific Fisheries Management Council, Anchorage, Alaska, November 2003.

in water depth between the shallow Bering Sea and deeper Barents Sea have been identified as the cause of this contrast (Sakshaug and Walsh, 2000).

An intriguing question is, why does the Bering Sea have a pollock biomass 30 times that of cod in the Barents Sea? Pollock in the Bering Sea are 25 times more productive than cod in the Barents Sea. One reason may be that the foodweb is shorter in the Bering Sea than in the Barents Sea. Indeed, it is evident that cod forage at a higher trophic level (4.3) than pollock (3.3) (Aydin *et al.*, 2002; Blanchard *et al.*, 2002). In the Bering Sea, pollock eat zooplankton directly, and the consumption of forage fish such as capelin is not great. They are, however, cannibalistic. In contrast, in the Barents Sea, capelin are essential for cod. Thus, pollock in the eastern Bering Sea are at a trophic level more similar to that of Barents Sea adult capelin (3.7) or adult herring (3.4) than they are to cod (Blanchard *et al.*, 2002). Additionally, predation pressure from seals is higher in the Barents Sea.

There have been large changes in fish abundance in both systems. For example, pollock, which currently account for 56% of the Bering Sea groundfish biomass, increased nearly 400% after the 1978 regime shift (Hunt *et al.*, 2002). After a period of high abundance, the spawning biomass of Norwegian spring-spawning herring in the Barents Sea collapsed towards the end of the 1960s (Dragesund *et al.*, 1980; Jakobsson, 1980). During the 1970s and early 1980s, the stock was gradually rebuilt, and the first strong year class after the collapse came in 1983. By the early 1990s the stock had regained much of its previous distribution area, was found feeding in the Norwegian Sea, and the stock has since been rebuilding (Dommasnes *et al.*, 2004). Toresen and Ostvedt (2000) hypothesized that the herring responded to changes in temperature, which in turn were related to the variability in the inflow of Atlantic Water, and associated with changes in the NAO.

Are these large changes in fish biomass a primary effect of climate-driven, bottom-up influences? Or are they secondary effects mainly attributable to the influence of climate change on species interactions? Since the early

1990s, evidence has been accumulating that climate variability strongly affects fish stocks. In the southeastern Bering Sea, four mechanisms connect fish to climate: (i) winter winds appear to be important for forcing transport of nutrients onto the shelf from the deep Bering Sea basin (Stabeno *et al.*, 1999); (ii) the extent and timing of sea-ice retreat influences the timing and fate of the spring phytoplankton bloom (Stabeno *et al.*, 2001; Hunt *et al.*, 2002); (iii) a cold pool generated by the melting ice influences the distribution of adult and juvenile pollock and thus the potential for cannibalism (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995); and (iv) wind-driven, cross-shelf advection of fish eggs and larvae has been shown to affect recruitment of pollock at interannual time scales and flatfish at decadal time scales (Wespestad *et al.*, 2000; Wilderbuer *et al.*, 2002). The first two mechanisms suggest that bottom-up effects of climate on production forces the system. The latter two mechanisms involve climate effects influencing fish populations through species interactions, via altered exposure to predators. In the Bering Sea, advection of copepods does not appear to be a major source of interannual variability in fish recruitment.

In the Barents Sea, variability in the transport of heat, nutrients, and zooplankton in Atlantic Water appears to be extremely important for determining the productivity of the Barents Sea (Nakken, 1994; Ottersen *et al.*, 1994). Not only do changes in the influx of Atlantic Waters affect cod directly through the effects of water temperature and zooplankton availability on growth, but these factors also affect the abundance of both capelin and herring, fish that are both prey and competitors for prey (Nakken, 1994; Hamre, 2003). The maximal extent of sea-ice and the timing of its retreat may also affect the productivity of the Barents Sea, but we are unaware of information that focuses on this issue. Thus, the climate-driven variability identified so far in the Barents Sea appears to act through bottom-up forces driven by advection. Overall, there is little doubt that climate has strong effects on the productivity of the fish stocks of the Bering and Barents Seas, but the pathways by which climate affects these systems differ.

## Acknowledgements

We thank K. Drinkwater, P. Stabeno, and E. Sakshaug for comments on an earlier draft of this manuscript. GLH acknowledges the support of National Science Foundation Grants OPP-09617287, OPP-9819251, and OPP-0226371 and the NOAA, Coastal Ocean Program, Southeastern Bering Sea Carrying Capacity Program (SEBSCC), and Bering Sea FOCI. This research is contribution of FOCI-0532 to NOAA's Fisheries-Oceanography Coordinated Investigations.

## References

- ACIA. 2004. Impacts of a Warming Climate: Arctic Climate Impact Assessment. Cambridge University Press. 140 pp.
- Ådlandsvik, B., and Loeng, H. 1991. A study of the climatic system in the Barents Sea. *Polar Research*, 10: 45–49.
- Aydin, K. Y., Lapko, V. V., Radchenko, V. I., and Livingston, P. A. 2002. A comparison of the Eastern Bering and Western Bering Sea Shelf and Slope ecosystems through the use of mass-balance food web models. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-130. 78 pp.
- Beamish, R. J., Noakes, D. J., McFarlane, G. A., Klyashtorin, L., Ivanov, V. V., and Kurashov, V. 1999. The regime concept and natural trends in the production of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 516–526.
- Blanchard, J. L., Pinnegar, J. K., and Mackinson, S. 2002. Exploring marine mammal–fishery interactions using 'Ecopath with Ecosim': modelling the Barents Sea ecosystem. Science Series Technical Report, CEFAS Lowestoft, 117. 52 pp.
- Bond, N. A., Overland, J. E., Spillane, M., and Stabeno, P. 2003. Recent shifts in the state of the North Pacific. *Geophysical Research Letters*, 30: 2183, doi:10.1029/2004GL019756.
- Brodeur, R. D., Mills, C. E., Overland, J. E., Walters, G. E., and Schumacher, J. D. 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fisheries Oceanography*, 8: 296–306.
- Brodeur, R. D., and Ware, D. M. 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fisheries Oceanography*, 1: 32–38.
- Coachman, L. K. 1986. Circulation, water masses and fluxes on the southeastern Bering Sea shelf. *Continental Shelf Research*, 5: 23–108.
- Coyle, K. O., and Cooney, R. T. 1988. Estimating carbon flux to pelagic grazers in the ice-edge zone of the eastern Bering Sea. *Marine Biology*, 98: 187–196.
- Dommasnes, A., Christensen, V., Ellertsen, B., Kvamme, C., Melle, W., Nøttestad, L., Pedersen, T., Tjelmeland, S., and Zeller, D. 2001. An Ecopath model for the Norwegian and Barents Sea. Fisheries impacts on North Atlantic ecosystems: models and analyses. University of British Columbia Fisheries Center Research Report, 9(4): 213–240.
- Dommasnes, A., Melle, W., Dalpadado, P., and Ellertsen, B. 2004. Herring as a major consumer in the Norwegian Sea. *ICES Journal of Marine Science*, 61: 739–751.
- Dragesund, O., Hamre, J., and Ulltang, Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. The Assessment and Management of Pelagic Fish Stocks Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 43–71.
- Ebbesmeyer, C. C., Cayan, D. R., Milan, D. R., Nichols, F. H., Peterson, D. H., and Redmond, K. T. 1991. 1976 step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1984. In Proceedings of the Seventh Annual Climate (PACLIM) Workshop, April 1990, pp. 115–126. Ed. by J. L. Betancourt, and V. L. Tharp. California Department of Water Resources. Interagency Ecological Studies Program Technical Report 26.
- Eslinger, D. L., and Iverson, R. L. 2001. The effects of convective and wind-driven mixing on spring phytoplankton dynamics in the southeastern Bering Sea middle shelf domain. *Continental Shelf Research*, 21: 627–650.
- Francis, R. C., Hare, S. R., Hollowed, A. B., and Wooster, W. S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, 7: 1–21.
- Hamre, J. 2003. Capelin and herring as key species for the yield of northeast Arctic cod. Results from multispecies model runs. *Scientia Marina*, 67(Suppl. 1): 315–323.
- Hare, S. R., and Francis, R. C. 1995. Climate change and salmon production in the northeast Pacific Ocean. In *Climate Change and Northern Fish Populations*, pp. 357–372. Ed. by R. J. Beamish. Canadian Special Publication in Fisheries and Aquatic Sciences, 121.
- Hare, S. R., and Mantua, N. J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47: 103–146.
- Hollowed, A. B., Hare, S. R., and Wooster, W. S. 2001. Pacific Basin climate variability and patterns of northeast Pacific marine fish production. *Progress in Oceanography*, 49: 257–282.
- Hunt Jr., G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., and Bond, N. A. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep Sea Research Part II*, 49: 5821–5853.
- Hurrell, J. W., Kushnir, Y., Ottersen, G., and Visbeck, M. 2003. The North Atlantic Oscillation: climatic significance and environmental impact. *Geophysical Monograph* 134. American Geophysical Union, Washington. 279 pp.
- Ingvaldsen, R. B., Aspline, L., and Loeng, H. 2004. The seasonal cycle in the Atlantic transport to the Barents Sea during the years 1997–2001. *Continental Shelf Research*, 24: 1015–1032.
- Jakobsson, J. 1980. The North Icelandic herring fishery and environmental conditions, 1960–1968. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 177: 460–465.
- Kinder, T. H., and Schumacher, J. D. 1981. Hydrographic structure over the continental shelf of the southeastern Bering Sea. In *The Eastern Bering Sea Shelf: Oceanography and Resources*, pp. 31–52. Ed. by D. Hood, and J. Calder. University of Washington Press, Seattle.
- Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research*, 10: 5–18.
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C. 1997. A Pacific interdecadal oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78: 1069–1079.
- McFarlane, G. A., King, J. R., and Beamish, R. J. 2000. Have there been recent changes in climate? Ask the fish. *Progress in Oceanography*, 47: 147–169.
- Nakken, O. 1994. Causes of trends and fluctuations in the Arcto-Norwegian cod stock. *ICES Marine Science Symposia*, 198: 212–228.
- Napp, J. M., and Hunt Jr., G. L. 2001. Anomalous conditions in the south-eastern Bering Sea, 1997: linkages among climate, weather, ocean, and biology. *Fisheries Oceanography*, 10: 61–68.
- North Pacific Fisheries Management Council, 2003. Stock Assessment and Fishery Evaluation Report.
- Ohtani, K., and Azumaya, T. 1995. Influence of interannual changes in ocean conditions on the abundance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. In

- Climate Change and Northern Fish Populations, pp. 87–95. Ed. by R. J. Beamish. Canadian Special Publication in Fisheries and Aquatic Sciences, 121.
- Olli, K., Riser, C. W., Wassmann, P., Ratkova, T., Arashkevich, E., and Pasternak, A. 2002. Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea. *Journal of Marine Systems*, 38: 189–204.
- Orvik, K. A., and Skagseth, Ø. 2003. The impact of the wind stress curl in the North Atlantic on the Atlantic inflow to the Norwegian Sea toward the Arctic. *Geophysical Research Letters*, 30(17): 1884, doi:10.1029/2003GL017932.
- Ottersen, G., Loeng, H., and Raknes, A. 1994. Influence of temperature variability on recruitment of cod in the Barents Sea. *ICES Marine Science Symposia*, 198: 471–481.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., and Stenseth, N. C. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia*, 128: 1–14.
- Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. *Fisheries Oceanography*, 4: 278–292.
- Overland, J. E., Bond, N. A., and Adams, J. M. 2001. North Pacific atmospheric and SST anomalies in 1997: links to ENSO. *Fisheries Oceanography*, 10: 69–80.
- Overland, J. E., Stabeno, P. J., and Salo, S. A. 1996. Direct evidence for northward flow on the northwestern Bering Sea Shelf. *Journal of Geophysical Research*, 101: 8971–8976.
- Peterson, W. T., Kister, J. E., and Feinberg, L. R. 2002. The effects of the 1997–1999 *El Niño-La Niña* events on the hydrography and zooplankton off the central Oregon coast. *Progress in Oceanography*, 54: 381–398.
- Roach, A. T., Aagaard, K., Pease, C. H., Salo, S. A., Weingartner, T., Pavlov, V., and Kulakov, M. 1995. Direct measurements of transport and water properties through Bering Strait. *Journal of Geophysical Research*, 100: 18443–18457.
- Sakshaug, E. 2004. Primary and secondary production in the Arctic seas. *In The Organic Carbon Cycle in the Arctic Ocean*, pp. 57–81. Ed. by R. Stein, and R. W. Macdonald. Springer, New York. 363 pp.
- Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H., and Mehlum, F. 1994. Structure, biomass, distribution and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. *Polar Biology*, 14: 405–411.
- Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H., and Mehlum, F. (Eds). 1992. *Økosystem Barentshavet*, Lillehammer. 304 pp. (In Norwegian)
- Sakshaug, E., and Walsh, J. M. 2000. Marine biology: biomass, productivity distributions and their variability in the Barents and Bering Seas. *In The Arctic: Environment, People, Policy*, pp. 163–196. Ed. by M. Nuttall, and T. V. Callaghan. Harwood Academic Press, Australia. 647 pp.
- Schauer, U., Loeng, H., Rudels, B., Ozhigin, V. K., and Dieck, W. 2002. Atlantic water flow through the Barents and Kara Seas. *Deep-Sea Research I*, 49: 2281–2298.
- Schauer, U., Muench, R. D., Rudels, B., and Timokhov, L. 1997. The impact of eastern Arctic Shelf waters on the Nansen Basin intermediate layers. *Journal of Geophysical Research*, 102: 3371–3382.
- Schwing, F. B., and Moore, C. S. 2000. A year without summer for California: or a harbinger of a climate shift. *Transactions of the American Geophysical Union*, 81: 301.
- Smith, S. L., and Vidal, J. 1986. Variations in the distribution, abundance and development of copepods in the southeast Bering Sea in 1980 and 1981. *Continental Shelf Research*, 5: 215–239.
- Stabeno, P. J., Bond, N. A., Kachel, N. B., Salo, S. A., and Schumacher, J. D. 2001. On the temporal variability of the physical environment of the south-eastern Bering Sea. *Fisheries Oceanography*, 10: 81–98.
- Stabeno, P. J., Kachel, D. G., and Sullivan, M. E. Observations from moorings in the Aleutian passes: temperature, salinity and transport. *Fisheries Oceanography*, in press.
- Stabeno, P. J., Schumacher, J. D., and Ohtani, K. 1999. The physical oceanography of the Bering Sea. *In Dynamics of the Bering Sea: a Summary of Physical, Chemical, and Biological Characteristics, and a Synopsis of Research on the Bering Sea*, pp. 1–28. Ed. by T. R. Loughlin, and K. Ohtani. University of Alaska Sea Grant, AK-SG-99-03.
- Sugimoto, T., and Tadokoro, K. 1998. Interdecadal variations of plankton biomass and physical environment in the North Pacific. *Fisheries Oceanography*, 7: 289–299.
- Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, 85: 277–298.
- Tande, K. S., Dobrysheva, S., Nesterova, V., Nilssen, E. M., Edvardsen, A., and Tereschenko, V. 2000. Patterns in the variations of copepod spring and summer abundance in the northeastern Norwegian Sea and the Barents Sea in cold and warm years during the 1980s and 1990s. *ICES Journal of Marine Science*, 57: 1581–1591.
- Thompson, D. W. J., and Wallace, J. M. 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters*, 25: 297–1300.
- Toresen, R., and Ostvedt, O. J. 2000. Variation in abundance of Norwegian spring-spawn herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries*, 1: 231–256.
- Trenberth, K. E., and Hurrell, J. W. 1995. Decadal coupled atmospheric-ocean variations in the North Pacific Ocean. *In Climate Change and Northern Fish Populations*, pp. 15–24. Ed. by R. J. Beamish. Canadian Special Publication in Fisheries and Aquatic Sciences, 121.
- Verity, P. G., Wassmann, P., Frischer, M. E., Howard-Jones, M. H., and Allen, A. E. 2002. Grazing of primary production by microzooplankton in the Barents Sea during early summer. *Journal of Marine Systems*, 38: 109–123.
- Walsh, J. J., and McRoy, C. P. 1986. Ecosystem analysis in the southeastern Bering Sea. *Continental Shelf Research*, 5: 259–288.
- Wespestad, V. G., Fritz, L. W., Ingraham, W. J., and Megrey, B. A. 2000. On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). *ICES Journal of Marine Science*, 57: 272–278.
- Wilderbuer, T. K., Hollowed, A. B., Ingraham Jr, W. J., Spencer, P. D., Conners, M. E., Bond, N. A., and Walters, G. E. 2002. Flatfish recruitment response to decadal climate variability and ocean conditions in the eastern Bering Sea. *Progress in Oceanography*, 55: 235–247.
- Wyllie-Echeverria, T. 1995. Sea-ice conditions and the distribution of walleye pollock (*Theragra chalcogramma*) on the Bering and Chukchi shelf. *In Climate Change and Northern Fish Populations*, pp. 131–136. Ed. by R. J. Beamish. Canadian Special Publication in Fisheries and Aquatic Sciences, 121.