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The Barents and Chukchi Seas: Comparison of two Arctic shelf ecosystems

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ABSTRACT

This paper compares and contrasts the ecosystems of the Barents and Chukchi Seas. Despite their similarity in a number of features, the Barents Sea supports a vast biomass of commercially important fish, but the Chukchi does not. Here we examine a number of aspects of these two seas to ascertain how they are similar and how they differ. We then identify processes and mechanisms that may be responsible for their similarities and differences.

Both the Barents and Chukchi Seas are high latitude, seasonally ice covered, Arctic shelf-seas. Both have strongly advective regimes, and receive water from the south. Water entering the Barents comes from the deep, ice-free and “warm” Norwegian Sea, and contains not only heat, but also a rich supply of zooplankton that supports larval fish in spring. In contrast, Bering Sea water entering the Chukchi in spring and early summer is cold. In spring, this Bering Sea water is depleted of large, lipid-rich zooplankton, thus likely resulting in a relatively low availability of zooplankton for fish. Although primary production on average is similar in the two seas, fish biomass density is an order of magnitude greater in the Barents than in the Chukchi Sea. The Barents Sea supports immense fisheries, whereas the Chukchi Sea does not. The density of cetaceans in the Barents Sea is about double that in the Chukchi Sea, as is the density of nesting seabirds, whereas, the density of pinnipeds in the Chukchi is about double that in the Barents Sea. In the Chukchi Sea, export of carbon to the benthos and benthic biomass may be greater. We hypothesize that the difference in fish abundance in the two seas is driven by differences in the heat and plankton advected into them, and the amount of primary production consumed in the upper water column. However, we suggest that the critical difference between the Chukchi and Barents Seas is the pre-cooled water entering the Chukchi Sea from the south. This cold water, and the winter mixing of the Chukchi Sea as it becomes ice covered, result in water temperatures below the physiological limits of the commercially valuable fish that thrive in the southeastern Bering Sea. If climate change warms the Barents Sea, thereby increasing the open water area via reducing ice cover, productivity at most trophic levels is likely to increase. In the Chukchi, warming should also reduce sea ice cover, permitting a longer production season. However, the shallow northern Bering and Chukchi Seas are expected to continue to be ice-covered in winter, so water there will continue to be cold in winter and spring, and is likely to continue to be a barrier to the movement of temperate fish into the Chukchi Sea. Thus, it is unlikely that large populations of boreal fish species will become established in this Arctic marginal sea.

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1. Introduction

Comparative studies of marine ecosystems provide the opportunity to identify ecosystem components or processes that play a critical role in determining ecosystem productivity (Drinkwater et al., 2009; Hunt and Megrey, 2005; Megrey and Aydin, 2009). In turn, identification of

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the mechanisms that control productivity facilitates understanding of the critical vulnerabilities of the ecosystems to global change (Mueter et al., 2009).

Carmack and Wassmann (2006) presented a broad overview of the marginal seas of the Arctic Ocean, noting that some were more productive than others. The Barents and Chukchi Seas have their southern extremes at 70°N and 66°N, respectively, while their northern borders extend to the edge of the continental shelf of the Arctic Ocean (Fig. 1). Despite this geographic similarity, the two seas differ remarkably in the productivity of their fisheries, even when expressed on a per unit area basis. However, it is not known whether these differences in fisheries are the result of differences in: 1) the standing stocks of fish populations; 2) local rates of primary and secondary production; 3) the pathways of energy and material through the ecosystems; or 4) the heat, nutrient and plankton content of waters advected into these seas. This paper investigates these questions by comparing factors hypothesized to be responsible for the major differences in fish productivity in these two areas. In addition, the standing stocks of other upper trophic levels, including marine mammals and seabirds, are examined to determine if they can provide insight into the overall productivity of the two regions. Finally, we briefly discuss mechanisms whereby future climate warming may affect the productivity of these Arctic marginal seas.

We begin by providing a brief overview of the salient geographic features of the Barents and Chukchi Seas (Section 1.1), their physical oceanography (Section 1.2), and their fisheries productivity (Section 1.3). In Section 2, we proceed, from fish (Section 2.1), seabirds (Section 2.2) and marine mammals (Section 2.3) down through the food web to primary production (Sections 2.4–2.6) to compare and contrast standing stocks and productivity in the two seas. In Section 3, we compare water depths and export of carbon to the benthos (Section 3.1), migratory behaviors of top predators (Section 3.2), and advection (Section 3.3) in the two regions. In Section 4, we provide some preliminary speculations as to how the Chukchi Sea and Barents Sea ecosystems may respond to global warming. Lastly, in Section 5, we summarize our findings and offer some conclusions on this comparative examination of two marginal Arctic seas.

1.1. Geography of the Barents and Chukchi Seas

1.1.1. Location and size

The Barents and Chukchi Seas are marginal Arctic seas that are located at similar latitudes (Fig. 1). They both are inflow shelf seas (Carmack et al., 2006) for waters entering the Arctic Ocean, albeit from different oceans: the Barents Sea is one of the routes for Atlantic water into the Arctic, and the Chukchi Sea is the only route for Pacific water into the Arctic. For the extent of the Barents and Chukchi Seas, we use the International Hydrographic Office definitions as modified by Jakobsson (2002), which include the continental shelf in the northern Chukchi out to the edge of the continental slope. Accordingly, both seas have their northern limits at the slope of the Arctic Basin. The area of the Barents Sea is 1.5×10^6 km², nearly 2.5 times that of the Chukchi's 0.620×10^6 km² (Jakobsson, 2002).

1.1.2. Bathymetry

The areal distributions of bottom depths are strikingly different between the Barents and Chukchi Seas (Figs. 1, 2). In the Barents Sea (average depth 230 m), only around 10% of the sea is less than 50 m deep, whereas in the Chukchi Sea (average depth 80 m), about 50% of the bottom area is less than 50 m deep, and most is less than 100 m. The Barents Sea consists of deep basins (~300–400 m deep) and banks, with a major trough (~450 m deep) in the west between Bear Island and the Norwegian mainland. In contrast, the southern Chukchi Sea is almost flat, with a very gentle slope to the edge of the Arctic Basin. In the north, the Chukchi Sea has shallow gullies running more or less south to north, with the deepest being Barrow Canyon in the northeast, and Herald Canyon in the west (Fig. 3).

1.2. Physical oceanography

The Barents Sea is one place where Atlantic and Arctic waters meet (Loeng, 1991; Loeng and Drinkwater, 2007). Warm and salty Atlantic Water, with relatively high concentrations of nutrients, enters

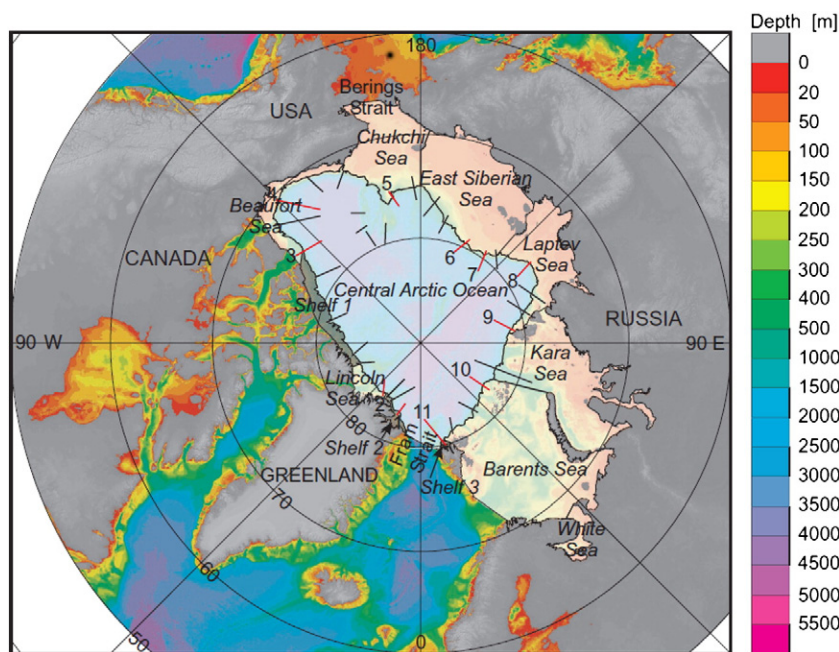


Fig. 1. Map of the Arctic marginal seas with depth contours and outlines of boundaries as modified by Jakobsson (2002) from the IHO definitions. The black and red lines indicate where Jakobsson developed bathymetric profiles that were used in the process of delineating the shelf break from a slope model (see Fig. 2). From Jakobsson, 2002. Hypsometry and volume of the Arctic Ocean and its constituent seas. *Geochem. Geophys. Geosyst.* 3(5) 10.1029/2001GC000302, ISSN: 1525–2027. Copyright 2002 American Geophysical Union. Reproduced/modified by permission of American Geophysical Union.

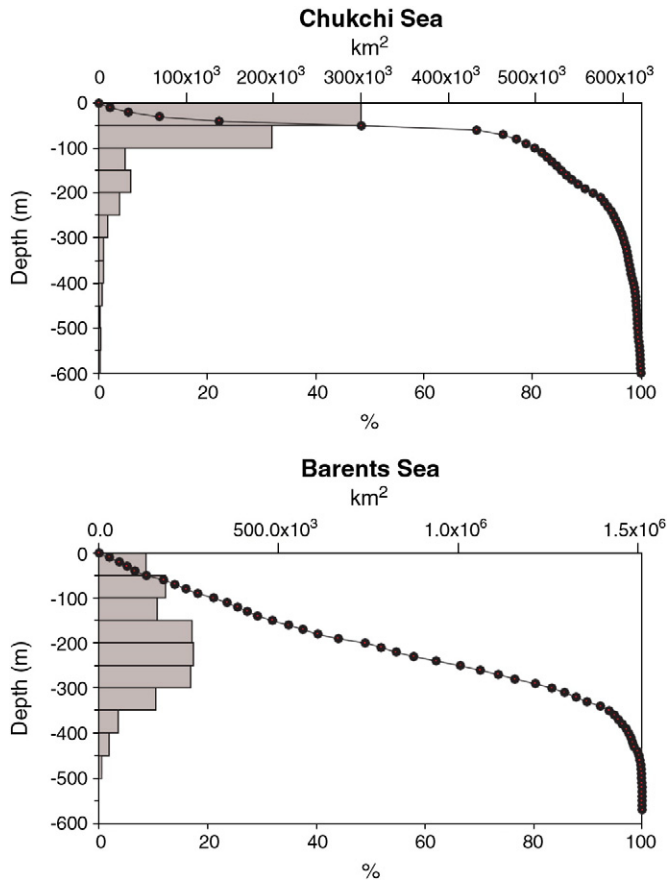


Fig. 2. Areal distribution by depth in the Chukchi and Barents Seas. Although maximal depths are similar, 50% of the Chukchi Sea is less than 50 m deep. From Jakobsson, 2002. Hypsometry and volume of the Arctic Ocean and its constituent seas. *Geochem. Geophys. Geosyst.*, an Electronic J Earth Sci. 3(5) 10.1029/2001GC000302, ISSN: 1525–2027. Copyright 2002 American Geophysical Union. Reproduced/modified by permission of American Geophysical Union.

the Barents Sea primarily through its western entrance and influences the southern region. Cold, low salinity Arctic Water, with low nutrients, penetrates from the east and north and dominates the northern Barents Sea (Fig. 3). The two regions are separated by the Polar Front (Harris et al., 1998; Parsons et al., 1996).

Atlantic Water originates from the North Atlantic Current and flows northward through the Norwegian Sea. Forty percent (annual average $1.8 \text{ Sv} \pm 1 \text{ Sv}$) of this flow enters the Barents Sea through its western entrance (Ingvaldsen, 2005; Ingvaldsen et al., 2004; Skagseth et al., 2011), of which an average of 0.7 Sv recirculates near the entrance back into the Norwegian Sea (Fig. 3; Skagseth, 2008). The remainder of the transport (1.1 Sv) flows eastward with generally weak mean currents ($<0.05 \text{ m s}^{-1}$; Ozhigin et al., 2011; Skjoldal and Rey, 1989). Tidal currents in the Barents Sea typically exceed these weak mean currents and are especially strong over some of the shallow banks. The Atlantic Water that traverses the Barents Sea is modified *en route* through mixing and atmospheric heat exchanges and eventually exits through the St. Anna Trough into the Arctic Ocean (Schauer et al., 2002).

Some of the Atlantic Water that flows northward past the Barents Sea enters the Arctic Ocean through Fram Strait and continues eastward north of Spitsbergen (Beszczynska-Möller et al., 2011). Part of this flow enters the Barents Sea at depth between Spitsbergen and Franz Josef Land; reliable estimates of this transport are not available (Lind and Ingvaldsen, 2012).

Coastal waters, which are carried northward along the Norwegian Shelf by the Norwegian Coastal Current, originate from the Baltic Sea outflow and southern North Sea; they are augmented by freshwater

runoff from Norwegian rivers and mix with offshore waters off the Norwegian shelf *en route* to the Barents Sea (Sætre, 2007). These waters enter the Barents Sea on the southern side of the western entrance (Loeng, 1991). A total volume flux of 2.6 Sv was estimated for this flow at the entrance to the Barents Sea (Skagseth et al., 2011), but part of this transport overlaps with the Atlantic inflow estimates. Accounting for this overlap, the annual averaged total volume flux through the western entrance is roughly 3 Sv with an estimated uncertainty of around ± 0.5 . Estimates of the total outflow in the eastern entrance between Franz Josef Land and Novaya Zemlya are of the order of $2 \text{ Sv} \pm 0.6 \text{ Sv}$, but are highly uncertain due to limited observations (Gammelsrød et al., 2009).

Cold Arctic waters enter the Barents Sea through the eastern entrance of the Barents Sea as well as from the north between Spitsbergen and Franz Josef Land (Gammelsrød et al., 2009; Lind and Ingvaldsen, 2012). These waters generally flow southwestward, eventually exiting the Barents Sea via the western entrance (Blindheim, 1989; Loeng, 1991). In deeper areas of the northern regions, Atlantic Water underlies the cold, relatively fresh Arctic Water (Lind and Ingvaldsen, 2012).

In winter, the northern and eastern regions of the Barents Sea are ice-covered. Minimum ice extent occurs in August/September, when in some years there is no ice present, while the maximum occurs in March or April, when approximately 60% of the Barents Sea is ice covered (Loeng, 1979; Vinje and Kvambekk, 1991). In contrast, the southwestern region remains ice free throughout the winter as a result of the inflow of the warm Atlantic Water.

In the northern Barents Sea, there is a strong seasonal cycle in stratification, with homogenization of the upper layer in late autumn and late spring, a result of strong wind mixing and convective cooling, and strong stratification in summer caused by ice-melt (Loeng and Drinkwater, 2007; Sakshaug et al., 2009; Rey and Loeng, 1985). In the Atlantic (southern) region of the Barents Sea, seasonal stratification is dominated by solar heating, resulting in a slowly developing thermocline (Sakshaug et al., 2009; Skjoldal and Rey, 1989).

The southern Chukchi Sea is strongly influenced by waters entering through the Bering Strait (Coachman et al., 1975; Pantelev et al., 2010; Spall, 2007; Woodgate et al., 2005c). The Bering Strait volume transport averages about 0.8 Sv northwards over the year (Roach et al., 1995; Woodgate et al., 2006), being strongest in summer and weakest in winter. Occasionally, there are wind-driven reversals to southward transport between November and March (e.g., Woodgate et al., 2005b). Thus, the mean flow from the south into the Arctic via the Chukchi Sea appears to be 2–3 times less than that of the Barents Sea through-flow.

The water masses entering the southern Chukchi Sea are generally classed into two types (Coachman et al., 1975), Alaskan Coastal Water and Bering Sea Water. Alaskan Coastal Water is strongly influenced by the Alaska Coastal Current, which originates south of the Aleutian Islands and is augmented by river runoff from western Alaska. In the Chukchi Sea, it generally flows northward along the Alaskan Coast to Barrow Canyon (Fig. 3) (Aagaard and Carmack, 1989; Walsh et al., 1989) with a volume transport of $\sim 0.1 \text{ Sv}$ (Woodgate and Aagaard, 2005). It is present from May to about the end of December in the eastern Chukchi Sea (Fig. 3; Paquette and Bourke, 1974; Woodgate and Aagaard, 2005) and provides a swift transit (a few months) from the Bering Strait to Barrow Canyon (Woodgate et al., 2005c and the references therein). Alaskan Coastal Water is relatively warm, of low salinity, and with low nutrient concentrations post spring bloom.

The bulk of the water transiting the Chukchi Sea ($\sim 0.7 \text{ Sv}$, $>80\%$) is Bering Sea Water, which is a mixture of the nutrient-rich Anadyr Water from the west and Bering Shelf Water (Coachman et al., 1975). These waters are saltier and richer in nutrients than Alaskan Coastal Water (Springer et al., 1989). Topographic shoals in the northern Chukchi Sea split the northward flow of Bering Sea Water into 3 branches (Ahlñäs and Garrison, 1984;

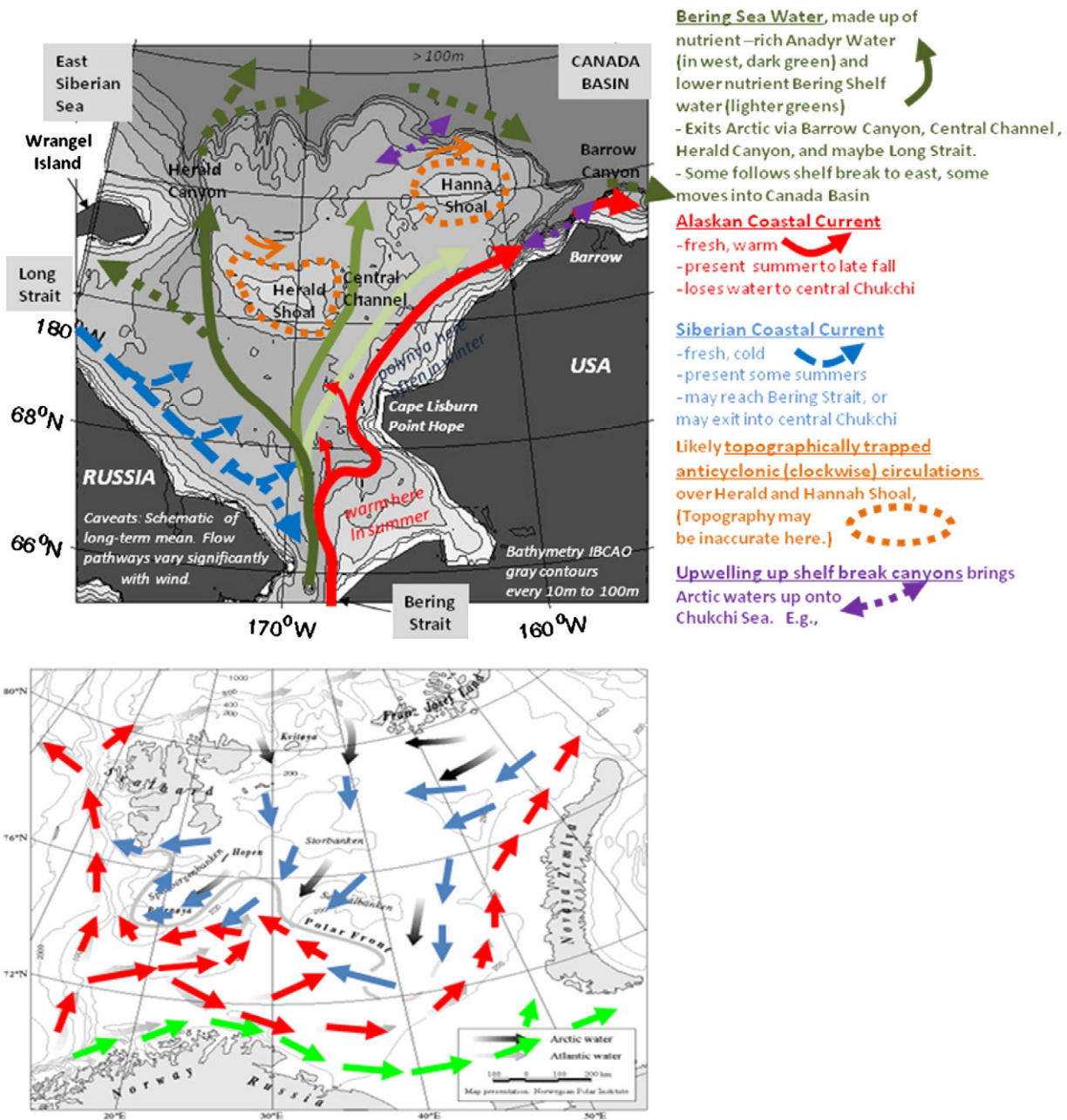


Fig. 3. Flows into and within the Chukchi (upper) and Barents Seas (lower). In the Barents Sea, the black arrows denote the flow of Arctic water, the blue arrows the flow of mixed water, and the red arrows the flow of Atlantic Water; green arrows indicate the flow of Coastal water. The Barents Sea figure is courtesy of Institute of Marine Research, Bergen.

Paquette and Bourke, 1981; Weingartner et al., 2005; Woodgate et al., 2010). One branch flows east of Hanna shoal and continues to Barrow Canyon, one is west of Herald Shoal through Herald Canyon, and other is between the shoals via what is called the Central Channel (Fig. 3; Panteleev et al., 2010; Spall, 2007; Weingartner et al., 2005; Woodgate et al., 2005c). Although the volume flows through these different branches are comparable, their seasonal variability is somewhat different (Woodgate et al., 2005c). The Herald Canyon outflow contains higher nutrient concentrations because of a greater proportion of Anadyr Water. These flows respond strongly to winds, with flow reversals being common, especially in the eastern side of the Chukchi Sea (Woodgate et al., 2005c), and there is episodic wind-driven upwelling of waters along the canyons on the continental slope (e.g.,

Aagaard and Roach, 1990; Bourke and Paquette, 1976; Mountain et al., 1976; Woodgate et al., 2005a).

In the extreme western Chukchi Sea, the seasonal Siberian Coastal Current (~0.1 Sv) flows southward along the coast in some years (Fig. 3; Weingartner et al., 1999). This cold fresh current, on occasion, may reach the Bering Strait, but usually is deflected into the central Chukchi Sea. There is also believed to be an outflow of similar magnitude to the Siberian Sea from the Chukchi Sea, but few measurements of this exist (Woodgate et al., 2005c).

In summer, the northward flows through the Bering Strait, including especially the Alaskan Coastal Current, transport heat into the Chukchi Sea (Woodgate et al., 2010), and beyond (Shimada et al., 2006). However, because flows through the Bering Strait must cross

the seasonally ice-covered northern Bering Sea, water entering the Chukchi Sea in winter is near-freezing, and the entire Chukchi remains ice-covered from late fall to spring (Woodgate et al., 2005c). Thus, there is a seasonal cycle of stratification, with strong stratification in summer, and a cold, well-mixed water column from fall through spring when the ice melt releases fresh water.

1.3. Fishery catches

Fisheries catches in the Barents Sea are large compared to those from the Chukchi Sea (Fig. 4), even on a catch-per-unit-area basis. Combined commercial catches by Norway and Russia in the Barents Sea during the period 2000–2009 were around 900,000 metric tonnes (mt) annually, although they increased in 2010 to close to 1 million mt (ICES, 2011). Combined, the Norwegian fisheries catches are presently worth well over \$500 million (USD) annually (Fishery Statistics, Directorate of Fisheries, Norway, 2011); additionally, Russia accounts

for an equally high value of fish taken (ICES, 2011). Catches in the Barents Sea are dominated by Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*) and haddock (*Melanogrammus aeglefinus*). In addition, there are important commercial catches of redfish (*Sebastes mentella* and *Sebastes marinus*), Greenland halibut (*Reinhardtius hippoglossoides*), Arctic cod (*Boreogadus saida*), wolffish (*Anarhichas* spp.), saithe (*Pollachius virens*), blue whiting (*Micromesistius poutassou*), deep sea shrimp (*Pandalus borealis*), and the introduced red king crab (*Paralithodes camtschaticus*) (ICES, 2011). It must be pointed out that there is high variability in the total catches as indicated by the range from a high of around 3.5 million mt to a low of less than 0.5 million mt between 1950 and 2006 (Fig. 4). This variability is largely determined by fluctuations in the capelin stock.

In contrast to the Barents Sea, there are and have been virtually no commercial fisheries in the Chukchi Sea since the days of commercial whaling (NPFMC, 2009). Total landings from the eastern Chukchi Sea have rarely exceeded \$50,000 to \$100,000 per annum; only

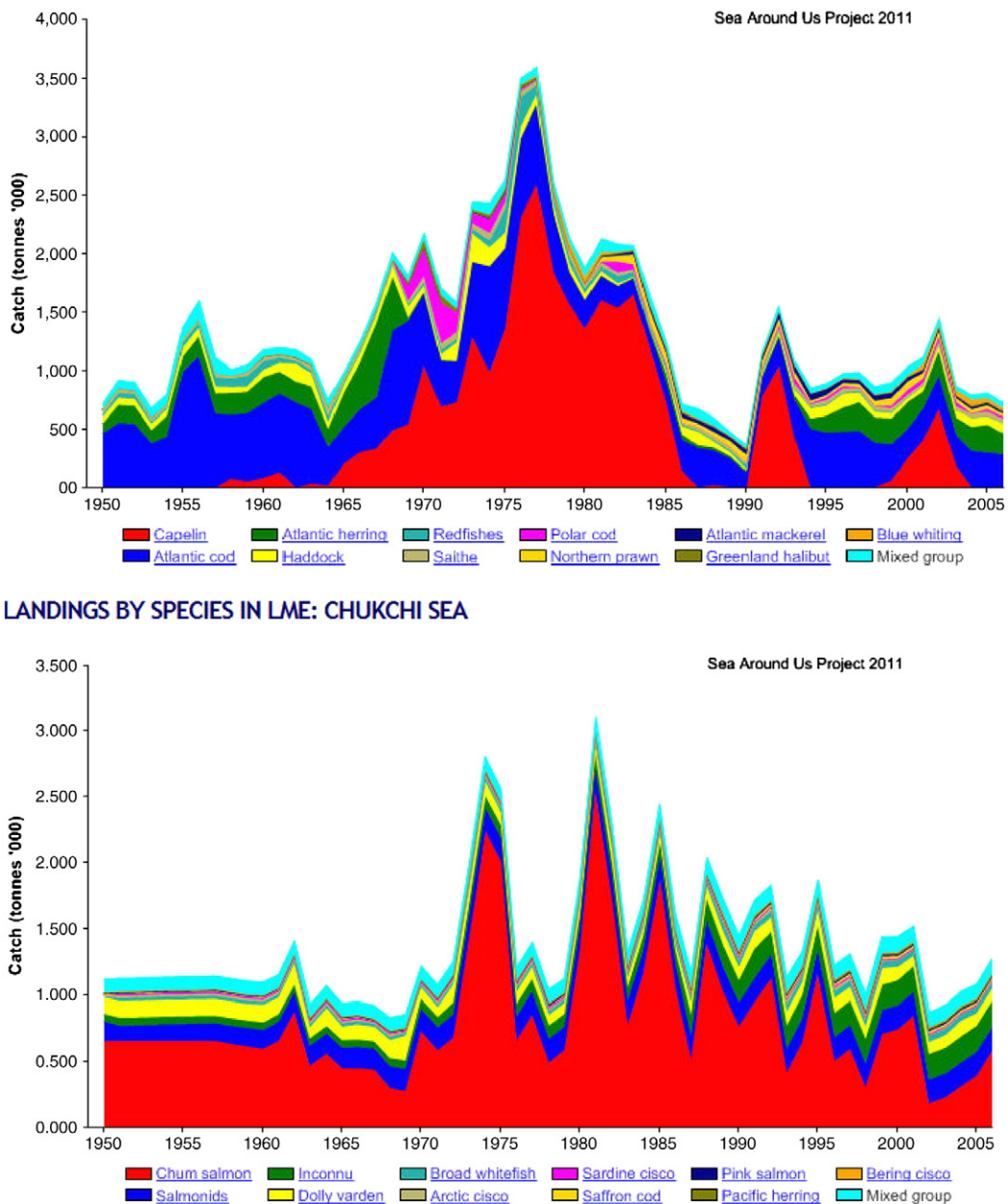


Fig. 4. Fisheries catch (thousands mt) in the Barents Sea (top) and Chukchi Sea (bottom), 1950–2006. Note that the scales differ between the panels as do the species codes and colors. From the Sea Around Us Project (2011).

1300 mt were landed in 2010 (Booth and Zeller, 2008; Sea Around Us Project, 2011). Fish landings in the Chukchi Sea are primarily for local consumption (NPFMC, 2009). The most important species are salmonids, especially chum salmon (*Oncorhynchus keta*), and inconnu (also known as sheefish, *Stenodus leucichthys*), though about 15 species are exploited (Fig. 4; Sea Around Us Project, 2011). Although the Chukchi Sea is now closed to commercial exploitation (NPFMC, 2009), the lack of extensive trawling in the past reflects a lack of commercial species at densities or sizes that would make them economically viable, as well as the long distances to fishing ports (Barber et al., 1997; Norcross et al., 2010; NPFMC, 2009). For example, snow crab (*Chionoecetes opilio*), a species of commercial interest elsewhere, are abundant in the Chukchi Sea, but individuals of marketable size have seldom been observed there (Bluhm et al., 2009; Fair and Nelson, 1999; Paul et al., 1997; Wolotira et al., 1977).

2. Comparisons of standing stocks and productivity

In this section we provide information on the abundance or biomass of stocks of fish, seabirds, marine mammals, benthos, zooplankton and phytoplankton in the Barents and Chukchi Seas. Where data are available, we report on fluxes and production rates, including primary production. We take a top-down approach, starting with the fish, seabirds and marine mammals, and the benthos, and then examine the available data on zooplankton, chlorophyll and primary production to determine the base on which the upper trophic levels depend.

2.1. Standing stocks of fish

Not surprisingly, the fish stocks of the Barents Sea, with its major commercial fisheries, have been well surveyed. Based on 2008 surveys, the five fish species with the highest estimated biomasses were: capelin, 4.4×10^6 mt; Atlantic cod, 2.3×10^6 mt; saithe, $> 1.1 \times 10^6$ mt; Atlantic haddock, 0.9×10^6 mt; and age-1 + 2 Atlantic herring (*Clupea harengus*), 0.25×10^6 mt, for a total of almost 9×10^6 mt or about 5.9 mt km^{-2} (ICES, 2008a; Stiansen et al., 2009). A major portion of this fish biomass, especially the demersal species, is located in the relatively warm and boreal southern Barents Sea, an area approximately the size of the entire Chukchi Sea.

In contrast, data on fish biomass in the Chukchi Sea are very sparse; bottom trawl surveys have been conducted in United States waters only in 1976 (Wolotira et al., 1977), 1990 and 1991 (Barber et al., 1997) and in 2004 (Norcross et al., 2010). Based on the 1990 and 1991 surveys, the five fish species with the highest biomasses in the eastern Chukchi Sea survey area in order were Arctic cod, sculpin sp. (*Myoxocephalus* sp.), saffron cod (*Eleginus gracilis*), Bering flounder (*Hippoglossoides robustus*), and Pacific herring (*Clupea pallasii*), which together accounted for approximately 0.41 mt km^{-2} (Barber et al., 1997). Extrapolating the density estimates of these top five species from 1990 and applying them to the entire area of the Chukchi result in a combined estimated biomass of about 254,200 mt. Of these stocks, only Arctic cod and Pacific herring might have been of commercial interest if their biomasses had been sufficient to support a fishery.

Arctic cod alone accounted for 61% of the entire Chukchi fish catch in 1990 and 47% in 1991, but other sources suggest that there may be more Arctic cod in the Chukchi Sea than found by Barber et al. (1997). For example, Quast (1974) estimated that there were 434,000 mt of Arctic cod in the Chukchi Sea, and Whitehouse (2011), using a mass balance Ecopath model, estimated that there must be about 874,000 mt of Arctic cod in the Chukchi Sea to satisfy the needs of the cod predators.

When adjusted for differences in area, the biomass of the top five species in the Barents Sea was about 13 times that of the top five in the Chukchi Sea, when using the estimates for the Chukchi Sea based on Barber et al. (1997). If we use the estimate for Arctic cod in the Chukchi Sea developed by Whitehouse (2011), then the Barents Sea may have about 3.8 times the fish biomass of the Chukchi

Sea and 1.6 times the biomass per unit area. Thus, not only does the Barents Sea support larger fish populations on an area adjusted basis, but those commercially exploited species in the Barents are thought to be more productive than the fish stocks in the Chukchi, given that the catches in the Barents Sea are about 3 orders of magnitude greater than those in the Chukchi.

2.2. Standing stocks of seabirds

The avifauna of the Barents Sea is dominated by the planktivorous little auk (*Alle alle*), the mostly piscivorous black-legged kittiwake (*Rissa tridactyla*) and Atlantic puffin (*Fratercula arctica*), and murre, one species of which, the common murre (*Uria aalge*), is primarily piscivorous, while the other, the thick-billed murre (*Uria lomvia*) is more planktivorous, with large amphipods and euphausiids constituting a substantial part of its diet (Table 1) (Anker-Nilssen et al., 2000; Mehlum and Gabrielsen, 1993). As a general pattern, the planktivorous seabird species dominate in the north and northwestern Barents Sea, whereas the piscivorous species are more abundant in the southern Barents Sea (Wassmann et al., 2006b).

Planktivorous (small auklets, *Aethia* spp.) and murre (*Uria* spp.) are the most abundant breeding seabirds in the Chukchi Sea, though the biomass of murre is much greater than that of the auklets. If seabirds nesting on the Diomed Islands in the Bering Strait were included in the Chukchi total, the number of small planktivorous auklets would be increased by about 2 million (USF&WS, 2003). The available data suggest that for much of the breeding season, these auklets forage south of Bering Strait (Piatt and Springer, 2003), and therefore they have not been included in our compendium of Chukchi breeding birds.

The number of nesting seabirds in the Barents Sea (~8 million) is more than 3.2 times greater than that in the Chukchi Sea (1.8 million, Table 1). On a per-unit-area basis, the Barents supports 1.3 times more nesting seabirds than the Chukchi Sea. Some of the difference between the two seas can be attributed to a lack of suitable nesting sites for

Table 1

Numbers of breeding seabirds. Data sources: Russian Chukchi: (north of Big Diomed Island), Konyukhov et al., 1998; Kondratyev et al., 2000; Alaskan Chukchi, USF&WS, 2003; Barents Sea: (individuals = pairs \times 2), Wassmann et al., 2006b.

Species	Chukchi Sea, Russian side individuals	Chukchi Sea, Alaskan side individuals	Barents Sea individuals
Northern Fulmar <i>Fulmarus glacialis</i>	0	0	54,000
Large Gulls spp. <i>Larus</i> spp.	15,500	4300	24,000
Black-legged Kittiwake <i>Rissa tridactyla</i>	275,000	119,300	1,118,000
Common Murre <i>Uria aalge</i>	20,000	82,500	292,000
Thick-billed Murre <i>Uria lomvia</i>	250,000	152,300	3,133,000
Murre, spp. <i>Uria</i> spp.		435,300	
Razorbill <i>Alca torda</i>	0	0	34,000
Black/Pigeon Guillemot <i>Cephus</i> spp.	5000	??	72,000
Atlantic/Horned Puffin <i>Fratercula</i> spp.	3000	19,700	1,826,000
Little Auk <i>Alle alle</i>	0	0	1,160,000
Small Auklets spp. <i>Aethia</i> spp.	0	446,000	0
Other	200	500	329,000
Total	568,700	1,259,900	8,042,000

cliff-nesting species along the shores of the Chukchi Sea, particularly on the western side (Piatt and Springer, 2003). When non-breeding resident individuals are accounted for, the Barents Sea is estimated to support 16×10^6 seabirds (Wassmann et al., 2006b), whereas the Chukchi Sea supports approximately 3.6×10^6 seabirds using the same reasoning as Wassmann et al. (2006b) (breeding birds $\times 2$).

The Chukchi Sea also supports numerous migrants, including red phalaropes (*Phalaropus fulicarius*) and short-tailed shearwaters (*Puffinus tenuirostris*, Piatt and Springer, 2003), both of which are planktivores. To determine post-breeding seabird use of the Chukchi Sea in August and September, we extracted all records of auklets, phalaropes (*Phalaropus* spp.), and shearwaters (*Puffinus* spp.) observed in the eastern Chukchi Sea (see area included in Sigler et al., 2011) from the North Pacific Pelagic Seabird Database (J. Piatt, USGS and G. Drew USFWS, Pers. Com), calculated the mean density of each species and then multiplied by the sea-area to obtain an estimate of the numbers present. From these calculations, we estimate approximately 1.1×10^6 post-nesting auklets, 2.0×10^6 phalaropes, and 3.0×10^6 migrant shearwaters use the Chukchi Sea in August and September. These species are planktivores that take advantage of the large, lipid-rich copepods and euphausiids advected northward in Bering Sea Water. By including phalaropes and shearwaters, as well as post-breeding auklets, we estimate that the total number of seabirds using the Chukchi Sea in late summer is on the order of 9.6×10^6 individuals. No comparable data are available for late season use of the Barents Sea by migrant seabirds.

2.3. Standing stocks of marine mammals

The pinniped and cetacean biotas of the Barents Sea are dominated by pelagic-foraging piscivorous species or, for the latter, zooplanktivores (Table 2). Walruses (*Odobenus rosmarus*) and bearded seals (*Erignathus barbatus*) concentrate their feeding on benthic fauna, but they are outnumbered considerably by pelagic-foraging harp seals (*Pagophilus*

groenlandicus), hooded seals (*Cystophora cristata*), ringed seals (*Phoca hispida*), etc. Thus, the dominant pathway of energy flow to marine mammals in the Barents Sea is through the pelagic food web.

In contrast, the marine mammal fauna of the Chukchi Sea has a large complement of benthic-foraging species (Dehn et al., 2007), in particular walrus, bearded seal, and gray whale (*Eschrichtius robustus*) (Highsmith et al., 2006), which is the dominant cetacean in the Chukchi Sea (Tables 2, 3). Even bowhead whales (*Balaena mysticetus*) take epibenthic prey, sometimes in very shallow (<20 m) water (Moore et al., 2010). For the bearded seal, the shallow eastern Bering Sea and Chukchi continental shelves represent the largest continuous expanse of their preferred habitat in the world (Burns, 1981; Burns and Frost, 1979).

Beluga whales (*Delphinapterus leucas*) spend part of the summer in the Chukchi Sea, though most migrate through the Chukchi to summering areas that are located to the east (Carroll et al., 1987; Moore et al., 1993, 2000). Similarly, bowhead whales, for the most part, migrate through the Chukchi Sea with little or no feeding in spring. However, both beluga and bowhead whales spend some time feeding in the Chukchi Sea in late summer and fall (Clarke et al., 1993; Moore et al., 1995; Quakenbush et al., 2010a, 2010b). Pelagic-foraging spotted (*Phoca largha*), ringed, and ribbon seals (*Histiophoca fasciata*) feed mostly on fish and large zooplankton (Dehn et al., 2007).

Depth affects the species composition and abundance of predators feeding at the seafloor. Thus, relatively shallow-feeding mammals such as walrus, bearded seals and gray whales are much more abundant in the shallow Chukchi Sea than in the Barents Sea, where pelagic-feeding marine mammals (e.g., harp seals, hooded seals, minke whales (*Balaenoptera acutorostrata*)) are more abundant (Loeng and Drinkwater, 2007). Some of this pattern, however, may be due in part to historical human harvesting of pinnipeds and cetaceans, which has been suggested to have heavily restructured the Barents Sea food web (Węśławski et al., 2000), as well as that of the Chukchi Sea (e.g., Mizroch et al., 2009).

Table 2
Estimated numbers of polar bears and pinnipeds in the Chukchi and Barents Seas.

Species/group	Chukchi sea Season present/estimate quality	References	Barents Sea season present/estimate quality	References
Polar bear <i>Ursus maritimus</i>	2000 R, P	Lunn et al., 2002	2650 R, E (95% CI: 1900–3600)	Aars et al., 2009
Walrus <i>Odobenus rosmarus</i>	200,000 S, F	Gilbert et al., 1992	5000 R, G Svalbard: 2629 (95% CI: 2318–2998)	Lydersen et al., 2008
Ringed seal <i>Phoca hispida</i>	230,000 (AK only, similar # on Russian side?) J, G	Bengtson et al., 2005	100,000 R, F	Luken et al., 2006
Bearded seal <i>Erignathus barbatus</i>	27,000 J, G 110,000 S, F	Cameron et al., 2010 P. Boveng, unpublished. ^a	10,000 R, P	Kovacs et al., 2009
Ribbon seal ^b <i>Histiophoca fasciata</i>	13,000 S, G	P. Boveng, unpublished.	0	
Harbor/Spotted seal ^c <i>Phoca vitulina</i> <i>Phoca largha</i>	84,000 S, F	P. Boveng, unpublished.	2500 R, G	Lydersen and Kovacs, 2001 Nilssen et al., 2010 Zynyanov, 2000
Harp seal <i>Pagophilus groenlandicus</i>	0		861,700R, E	ICES, 2008b
Hooded seal <i>Cystophora cristata</i>	0		82,400 R, E (95% CI: 65,200–99,600)	ICES, 2008b
Gray seal <i>Halichoerus grypus</i>	0		4500 R, G	Nilssen and Haug, 2007

R = resident year round; S = summer only; J = June only; Estimate quality: P = poor, F = fair; G = good; E = full survey.

^a P. Boveng (unpublished) based on Cameron et al. (2010), and an assumption that the 55,000 bearded seals estimated for the central Bering Sea by Ver Hoef (in review), represents about one-half (by area) of the bearded seal population that migrates north for the summer in the Chukchi Sea.

^b Ribbon seals: Assumes a central and eastern Bering Sea breeding population of 62,000 (Ver Hoef et al., in review) and that about 21% go north into the Chukchi Sea (Boveng et al., 2008); and recent unpublished telemetry studies.

^c Spotted seals: Based on central and eastern Bering Sea breeding population of 146,000 (Ver Hoef et al., in review) plus an unknown but fairly large number breeding in the Gulf of Anadyr, together making a population of about 200,000, 42% of which go north into the Chukchi Sea for the summer (unpublished telemetry studies).

Table 3
Estimates of numbers of cetaceans in the Chukchi and Barents Seas.

Species	Chukchi	References	Barents	References
Blue whale <i>Balaenoptera musculus</i>	0		222–979 ^a S, E for N. Atlantic	Pike et al., 2009
Fin whale <i>Balaenoptera physalus</i>	Low tens	Stafford and Esch, 2010	~1800 S, E for N. Atlantic	Øien, 2009
Humpback whale <i>Megaptera novaeangliae</i>	Low tens	RUSALCA, 2009; Stafford and Esch, 2010	NE Atlantic 1450 (including the Barents Sea)	Øien, 2009
Bowhead whale <i>Balaena mysticetus</i>	12,600+	Reeves et al., 2011	10–100 R, E	Christensen et al., 1992
Minke whale <i>Balaenoptera acutorostrata</i>	Ten or fewer	Stafford and Esch, 2010; Stafford and Mussoline, 2011	62,592 R, E	Skaug et al., 2004
Gray whale <i>Eschrichtius robustus</i>	19,100 total population- of which Highsmith and Coyle (1992) estimate 70% (13,370) forage in the Chukchi in summer	Laake et al. 2009 Moore et al., 2000; Bluhm et al., 2009	0	
Beluga <i>Delphinapterus leucas</i>	3710 S, minimum estimate for eastern Chukchi stock	Allen and Angliss, 2012	10,000 R, P	Kovacs et al., 2009
Killer whale <i>Orcinus orca</i>	Low tens	Stafford and Esch, 2010; Stafford and Mussoline, 2011	???	
Sperm Whale <i>Physeter macrocephalus</i>	Present	Stafford and Mussoline, 2011	???	
Narwhal <i>Monodon monoceros</i>	Occasional sighting???		1000 R, P	Kovacs et al., 2009
White-beaked dolphin <i>Lagenorhynchus albirostris</i>	0		60,000–70,000 R, G	Øien, 1993

R = resident year round; S = summer only; J = June only; Estimate quality: P = poor, F = fair; G = good; E = full survey.

^a High interannual variability.

Based on the available evidence, the abundance of pinnipeds may be quite similar for the Barents and Chukchi Seas (Table 2), whereas seasonally-resident cetaceans appear to be 4 to 5 times more abundant in the Barents Sea than in the Chukchi Sea (Table 3). Adjusted for area, the density of pinnipeds is likely 2 times greater in the Chukchi Sea than in the Barents. In contrast, the density of cetaceans is on the order of 2 times greater in the Barents Sea than in the Chukchi Sea.

2.4. Standing stocks of marine benthos

It is difficult to compare the standing stocks of benthic macro-invertebrates between the Barents and Chukchi Seas because of the scarcity of data in both regions, as well as the uneven sampling with respect to shallow versus deep areas (Fig. 5). The Chukchi Sea is much shallower on average than the Barents Sea (Fig. 2), and in both seas the biomass of benthic organisms varies with depth in a similar manner, increasing with depth up to between 125 m (Barents) and 190 m (Chukchi), then decreasing at greater water depths (Fig. 5).

Some authors (e.g., Feder et al., 1994, 2007; Renaud et al., 2007) have suggested that depth may be more important than specific water mass characteristics in generating broad-scale biomass patterns in both seas, perhaps due, in part, to influences on high-biomass epifaunal assemblages. Depth serves as a proxy for multiple covariates including increased decomposition of production with greater water depth, water mass and current changes, stratification, water temperature and salinity, and interactions with topography and water mass movements. The importance of depth and associated covariates complicates interpretations of theoretical and empirical data suggesting quantitative and qualitative differences in food supply to the benthos under productive versus less productive water masses (reviewed in Grebmeier et al., 2006a; Wassmann et al., 2006a).

In the Barents Sea, higher primary production in the Atlantic Water results in more food (on an annual basis) going to the benthos in Atlantic Water regions (the southwestern Barents) than in the less productive Arctic Water-dominated northern regions. However in the

northern regions, a higher percentage of the overall production reaches the bottom and the majority of the export to the benthos occurs over a comparatively short period due to the intense ice-edge bloom in spring (Reigstad et al., 2008). For the Barents Sea, Wassmann et al. (2006a) estimate that between 44% and 67% of primary production is available to benthic communities.

Barents Sea benthic community biomass (Carroll et al., 2008; Cochrane et al., 2009) and carbon cycling (Renaud et al., 2008) are generally coupled to the patterns of primary production and vertical flux to the sea floor. Heterogeneity in water depth (and related covariates described above), however, is substantial, and is also reflected in benthic communities. High tidal activity over the shallowest of the banks (Svalbard Bank, western Barents Sea, at 30–40 m depth) results in both very high primary production ($>200 \text{ g C m}^{-2} \text{ yr}^{-1}$) and rich communities of epifaunal suspension feeders (Idelson, 1930; M. Kędra and P. Renaud, pers. obs.; Reigstad et al., 2011).

Flows in the Chukchi Sea that derive from Anadyr Water (the western portion of the water passing through the Bering Strait) are rich in nutrients and zooplankton and support high benthic biomass (average wet biomass = $461.6 \text{ g m}^{-2} \pm 113.3 \text{ g m}^{-2}$ (SE)) compared to regions under the Alaskan Coastal Water in the east (average wet biomass = $198.3 \text{ g m}^{-2} \pm 26.6 \text{ g m}^{-2}$ (SE)) (using data from Fig. 5, see also Feder et al., 1994; Grebmeier et al., 2006a). In the Chukchi, benthic macrofaunal survey data are predominately from the eastern areas, thus potentially creating a bias in our sampling of the benthos (Feder et al., 1994; Grebmeier, 2012; Grebmeier et al., 2006a).

In the Chukchi Sea, maximum macrobenthic biomass values occur within depths up to about 190 m on the continental shelf margin and decline to lower maxima at greater depths (Fig. 5). Based on available data, biomass in areas that are less than 100 m deep is not significantly different from that in areas that are deeper than 100 m due to the greater variability of biomass in deeper depths associated with sites of high production along the shelf margin (Table 7 and Fig. 5). The high benthic biomass in the northern Chukchi Sea results from reduced meso- and micro-zooplankton grazing, which consumes only 44% of summer primary production, leaving more than half of the primary production for export to the benthos (Campbell et al.,

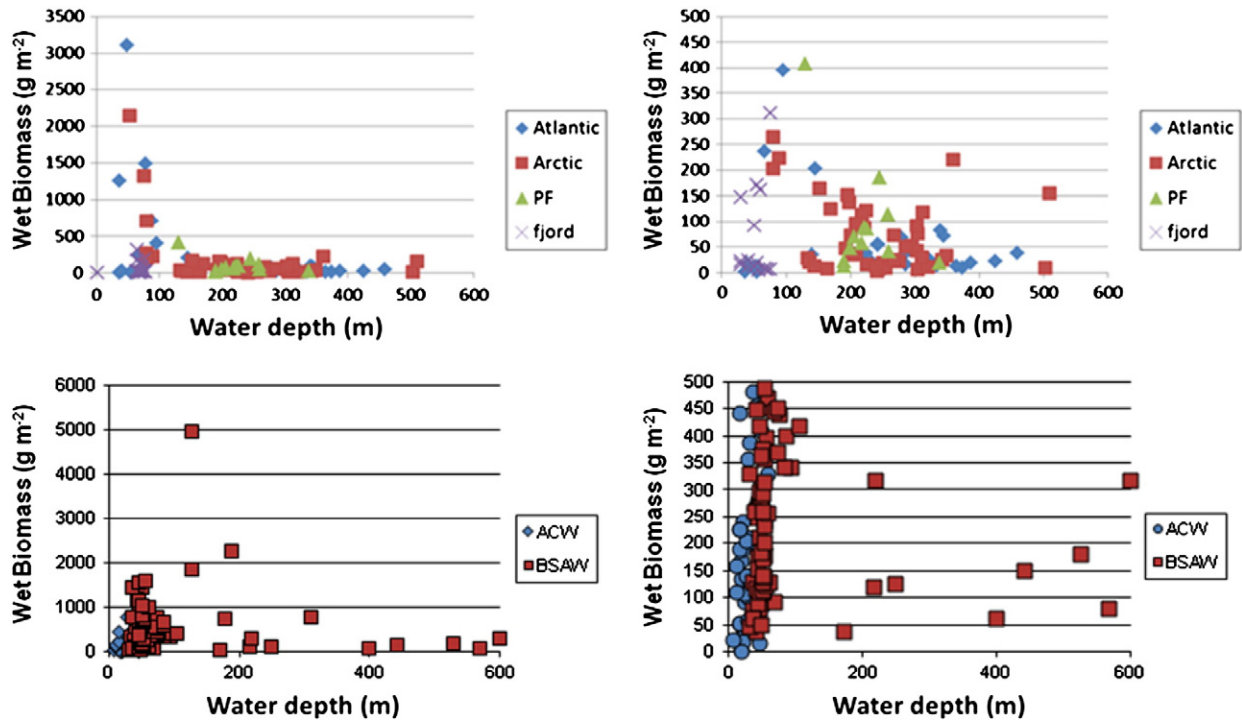


Fig. 5. Wet biomass (g m^{-2}) of benthic macrofauna by depth for the Barents Sea (top panels) and for the Chukchi Sea (bottom panels), color coded by the overlying water masses. For the Barents Sea, Atlantic refers to Atlantic Water; PF to the region of the Polar Front; Arctic, to Arctic Water; and Fjord to samples taken from fjords. For the Chukchi, ACW refers to Alaskan Coastal water, BSAW refers to Bering Shelf/Anadyr Water. Note the differences in scales on the x axes in the left two and right two panels. Data from: Idelson (1930); Feder et al. (1994); Piepenburg et al. (1995); Włodarska-Kowalczyk et al. (1998); Grebmeier et al. (2006a); Carroll et al. (2008); S. Cochrane et al. (unpub. data).

2009). Working in the northeastern corner of the Chukchi Sea and near Barrow Canyon, Moran et al. (2005) estimated that, in 2002, between 19% (spring) and 37% of primary production was exported to the benthos, and Lepore et al. (2007) estimated that, in 2004, 24% (spring) and 15% (summer) of primary production was exported. They also concluded that up to ~20% of primary production was exported off the shelf into the Canada Basin. Very high benthic biomass occurs in the southwestern Chukchi Sea, and in the northeastern Chukchi Sea at Barrow Canyon and Hanna Shoal (Dunton et al., 2005; Grebmeier et al., 2006a).

The Chukchi Sea has never been subject to extensive, heavy trawling by a large commercial fishing fleet, whereas the Barents Sea has been subjected to extensive trawling by large fleets of commercial fishing vessels since the 1950s (Wassmann et al., 2006a). Trawling has been suggested to be, at least in part, responsible for an estimated 60% reduction in benthic biomass in the Barents Sea between the time periods 1924–1932 and 1968–1970 (Fig. 6) (Wassmann et al., 2006a). However, warmer conditions and an expansion of the Atlantic benthic fauna into the Barents Sea took place during the former period, while the latter period encompasses a cooler period that was dominated by Arctic species (see discussion in Drinkwater, 2005).

Given the available data (see Fig. 5), it appears that the Barents Sea has, on average, a lower macrobenthic biomass (166.5 g m^{-2} wet mass $\pm 41.9 \text{ g m}^{-2}$ SE, $N=105$) than the Chukchi Sea (380.5 g m^{-2} $\pm 40.8 \text{ g m}^{-2}$, wet biomass, $N=163$), though, because of the non-random sampling in both seas and highly skewed depth distributions of the data we had available, the uncertainty around these estimates may be greater than suggested by the SE alone. In both seas, shallow, high-biomass areas are dominated by epifaunal organisms, predominantly echinoderms, whereas infaunal polychaetes and mollusks are more important at deeper sites (see references for Fig. 5).

2.5. Standing stocks of zooplankton

In both the Barents Sea and the Chukchi Sea, the species composition and biomass (Tables 4 and 5) of zooplankton species, or species groups, are greatly influenced by year, season and water mass composition, which in turn is related to local wind conditions. These features make obtaining an accurate average challenging.

The zooplankton dry mass biomass in the Barents Sea has varied between about 1 and 10 g m^{-2} , being commonly in the upper part of this range, $5\text{--}10 \text{ g m}^{-2}$. Summer investigations in the cold period from 1979 to 1982 showed high dry biomass values in the central Barents Sea, in the range of $5\text{--}30 \text{ g m}^{-2}$ with means of $10\text{--}18 \text{ g m}^{-2}$ (0–200 m; Blindheim and Skjoldal, 1993; Rey et al., 1987; Skjoldal et al., 1992). The biomass in the upper 50 m was particularly low in 1983 and 1984, with values $<1 \text{ g m}^{-2}$ in the central Barents Sea. This low biomass reflected a low abundance of *Calanus finmarchicus*, with a 50-fold decline in the numbers of copepodites between the summers of 1982 and 1983 (Skjoldal et al., 1987, Fig. 10). The low followed a major inflow of Atlantic Water during the winter 1982/83 that left the central Barents Sea with winter water devoid of *C. finmarchicus* (Blindheim and Skjoldal, 1993; Skjoldal and Rey, 1989; Skjoldal et al., 1992). For the period from the 1980s through 2000, the average zooplankton biomass for the Barents Sea ranged from 4.5 g m^{-2} in 1991 to a maximum of about 13 g m^{-2} in 1994 (Dalpadado et al., 2000, 2003). Since 2000, Barents Sea zooplankton biomass has remained fairly stable at around $6\text{--}8 \text{ g m}^{-2}$ (Dalpadado et al., 2012a), with the highest values in Atlantic Water ($8\text{--}11 \text{ g m}^{-2}$), and lower values in the Arctic Water (5 g m^{-2}) (Table 5) (Knutsen and Dalpadado, 2011).

In the Barents Sea, the richest source of zooplankton is the Atlantic Water, which transports the copepod *C. finmarchicus* and other zooplankton from the Norwegian Sea to the Barents Sea. This circa

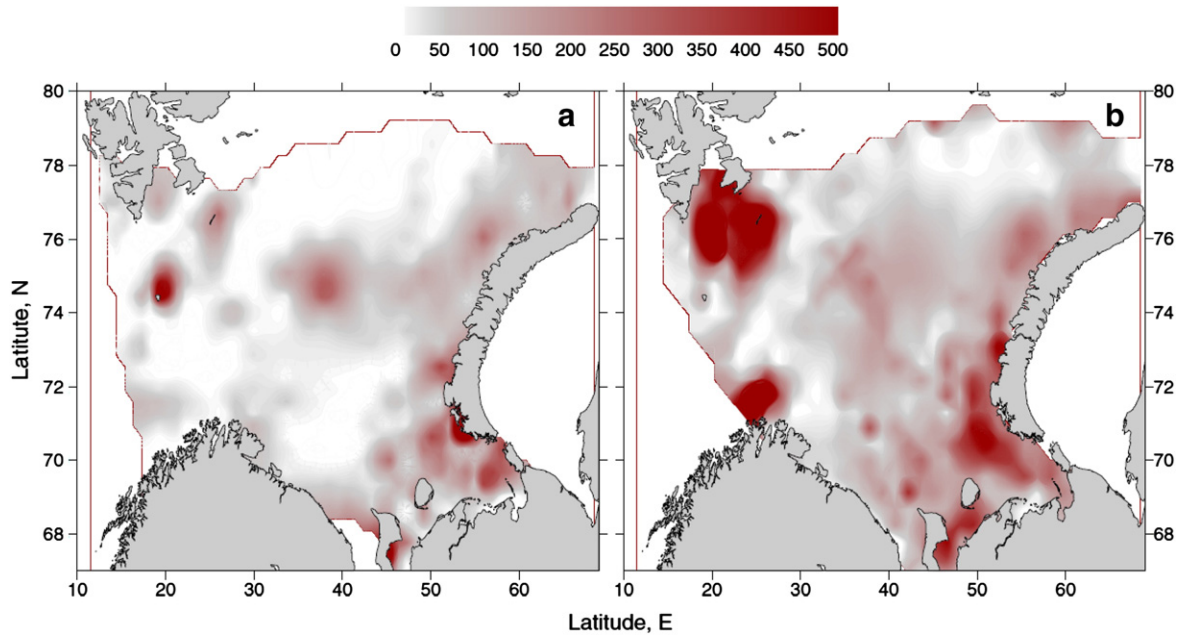


Fig. 6. Comparison of the distribution and biomass of macrobenthos ($\text{g wet biomass m}^{-2}$) in the Barents Sea before (b: 1924–1932) and after (a: 1968–1970) extensive bottom trawling in the 1960s. From Wassmann et al. (2006a), with permission.

3-mm-long, lipid-rich species is an important food resource for juvenile Atlantic cod, herring, capelin and other small fishes in the southern Barents Sea (Dalpadado and Bogstad, 2004; Pedersen and Fossheim, 2008; Sundby, 2000). Atlantic boreal krill species such as *Meganyctiphanes norvegica* and *Thysanoessa* spp. are also advected into the Barents Sea in the Atlantic Water, most likely in large quantities (Dalpadado and Mowbray, in press). The high biomass of zooplankton present in the mid 1990s was associated with Atlantic Water, as has been the case since 2000. Dalpadado et al. (2012a) estimated the transport of zooplankton in Atlantic Water into the Barents Sea to be 8×10^6 mt wet mass (or 1.6×10^6 mt dry mass) per

year, with interannual variation from 7 to 9.2×10^6 mt. They estimated that the advective input of zooplankton could contribute up to 1/3 of the zooplankton production in the Atlantic part of the Barents Sea (Dalpadado et al., 2012a).

In the Barents Sea, Arctic Water is also an important source of zooplankton. The large lipid-rich species of Arctic zooplankton, *Calanus glacialis* and *Calanus hyperboreus*, are abundant in this water mass (Blachowiak-Samolyk, 2008; Dvoretzky and Dvoretzky, 2011, and the references therein; Melle and Skjoldal, 1998). The copepods are advected southward and westward, eventually exiting the Barents Sea south of Svalbard (Karnovsky et al., 2003; Stempniewicz et al., 2007). A peak in the zooplankton biomass in the central and northern Barents Sea in 1986, a cold year, was associated with Arctic Water (Dalpadado et al., 2003). *C. glacialis* is a shelf species, and is observed overwintering on the northern, ice-covered shelf of the

Table 4

Zooplankton species or groups that accounted for the top ten most abundant and the top ten with the highest dry biomass from collections made in the Chukchi Sea in August 2004 (Hopcroft et al., 2010) and in Fugløy-Bear Island section at the western entrance to the Barents Sea in August 2004. Barents Sea abundance data are based on WP2 net samples. Biomass data for the Barents Sea are approximate estimated values.

Chukchi zooplankton species	Num m^{-3}	mg m^{-3}	Barents zooplankton species	Num m^{-3}	mg m^{-3}
<i>Acartia longiremis</i>	199.1	0.41	<i>Acartia longiremis</i>	33.8	0.06
<i>Calanus glacialis/marshallae</i>	36.1	6.71	<i>Calanus glacialis</i>	3.5	0.65
<i>Centropages abdominalis</i>	190.8	0.74	<i>Calanus finmarchicus</i>	87.1	11.32
<i>Eucalanus bungii</i>	14.4	1.31	Copepod nauplii	77.1	0.06
<i>Metridia pacifica</i>	39.7	1.45	<i>Metridia</i> spp.	40.0	2.40
<i>Neocalanus christatus</i>	0.9	6.38	Mollusca larvae	160.2	0.16
<i>Neocalanus flemingeri</i>	7.1	4.50	<i>Temora longicornis</i>	43.0	0.60
<i>Neocalanus plumchrus</i>	2.1	1.42	<i>Oithona similis</i>	1345.7	1.88
<i>Oithona similis</i>	703.4	0.77	<i>Pseudocalanus</i> spp.	72.3	0.26
<i>Pseudocalanus</i> spp.	1807.6	6.46	Ostracods	6.9	0.34
<i>Oikopleura vanhoeffeni</i>	255.9	4.12	Appendicularia	151.0	1.50
<i>Parasagitta elegans</i>	5.7	4.77	Cheatoagnatha	0.9	0.46
<i>Aglantha digitale</i>	5.4	0.95	<i>Aglantha digitale</i>	0.5	0.09
Barnacle cypris	226.7	–	<i>Centropages</i> spp.	6.5	0.20
Barnacle nauplii	1008.9	–			
Bivalvia larvae	148.3	–			
Echinodermata larvae	795.1	–			

Table 5

Dry biomass of crustacean zooplankton in various water masses of the Chukchi and Barents Seas.

Chukchi Sea water mass	Chukchi Sea dry biomass (g m^{-2})/SD (number of stations) ^a	Barents Sea water mass	Barents Sea 2008 dry biomass (g m^{-2})/SD (number of stations) ^b	Barents Sea 2009 dry biomass (g m^{-2})/SD (number of stations) ^b
Alaskan Coastal Water	<0.5/0.7 (3)	Coastal Water	3.90/2.57 (3)	13.5/9.12 (4)
Anadyr Water	2–4 (12) 4.3 (19)	Arctic Water	4.52/3.50 (6)	5.34/4.73 (28)
Bering Shelf Water	0.2–1.2/1.6 (6)	Atlantic Water	8.49/7.01 (41)	7.32/4.21 (73)
Overall	2.1	Polar Front Water	5.99/2.35 (8)	5.78/6.79 (58)

^a Data from Piatt and Springer (2003), Hopcroft et al. (2010), and unpublished.

^b Updated from Knutsen and Dalpadado (2011)—note that the biomass data are from the autumn period.

Barents Sea (Hirche and Kosobokova, 2011). In contrast, *C. hyperboreus* is more confined to deeper waters, overwinters at 500 m or more, and is likely advected into the Barents Sea from the Arctic Ocean (Auel et al., 2003). Arctic Water is also an important source of ice-associated amphipods (Hyperiididae and Gammaridae), and *Themisto libellula*, a large, predatory amphipod that is an important component of the zooplankton fauna in these seasonally ice-covered waters.

In the Chukchi Sea, most zooplankton taxa sampled in August 2004 by Hopcroft et al. (2010) were derived from Pacific waters advected through the Bering Strait (for the most abundant species by number or biomass, see Table 4). The zooplankton biomass in the Bering Sea Water was dominated by copepods, especially *Calanus* spp. and *Neocalanus* spp. (Hopcroft et al., 2010). Euphausiids are also transported through the Bering Strait, and aggregations are often found in the area of Barrow Canyon, after a transit time of 4 to 20 months depending on the point of origin, the route taken, and the time of year they start moving (Ashjian et al., 2010; Berline et al., 2008, and the references therein). During September 2007, a time of record ice retreat in the Arctic, relatively high abundances of early stage euphausiids (juvenile *Thysanoessa raschii* and Euphausiacea spp. furcilia) were observed in Bering Sea Water (Bering Shelf Water and Anadyr Water) on the south Chukchi Sea shelf (Eisner et al., in review). Springer et al. (1989) estimated that 1.8×10^{12} g C in the form of zooplankton was advected from the Bering Sea to the Chukchi Sea in the summer of 1985.

Within the two water masses transiting the Bering Strait, there are substantial differences in the transport of zooplankton (Table 5). Bering Sea Water (Bering Shelf Water plus Anadyr Water) is relatively rich in zooplankton, in particular the large, lipid-rich copepods (*Calanus marshallae/glacialis* and *Neocalanus* spp.) when compared to the Alaskan Coastal Water, which is depauperate in zooplankton (Eisner et al., in review; Hopcroft et al., 2010; Piatt and Springer, 2003). *C. glacialis* and *C. marshallae* are sister species that are difficult to distinguish. Adding to the confusion, there may be two separate populations of *C. glacialis*, one that occurs in the northern Bering Sea and the Chukchi Sea, and one that originates in the Arctic (Nelson et al., 2009), with the current view being that *C. marshallae* is uncommon in the Chukchi Sea. Although *C. glacialis* reproduces in the northern Bering and Chukchi Seas (Frost, 1974; Matsuno et al., 2011; Nelson et al., 2009; Plourde et al., 2005), it is unclear what differences in overwintering or reproductive strategies might exist between the two populations.

Water entering the Chukchi Sea from the Bering Sea in spring is depleted of large crustacean zooplankton given the required transit time from the northern Bering Sea or the Gulf of Anadyr to the southern Chukchi Sea (Pacific species are absent from cold Bering Sea winter water, Hopcroft et al., 2010). Springer et al. (1989) estimated that these oceanic zooplankton reach peak numbers on the northern Bering Sea shelf in early July and therefore likely have peak numbers in the Chukchi Sea in late July or early August. The large sub-arctic zooplankton species found in the Chukchi Sea require over-wintering at depths of 500 m or more (e.g., *Eucalanus bungii*, *Neocalanus* spp.), and it is likely that they were advected from the Aleutian Basin (Matsuno et al., 2011), probably in the year that they were sampled, given the transit time in spring from Anadyr Strait by St. Lawrence Island to the Bering Strait.

At the shelf edge of the Arctic Basin, Lane et al. (2008) found that the zooplankton fauna was almost entirely Arctic in origin. There is little evidence for transport of Arctic zooplankton species onto the Chukchi shelf, except near the shelf edge (Ashjian et al., 2003; Plourde et al., 2005), where localized upwelling (e.g., Aagaard and Roach, 1990; Mountain et al., 1976; Woodgate et al., 2005a) may transport zooplankton from the Arctic Basin. In the western Chukchi Sea, the Siberian Coastal Current is apparently not a conduit for large-bodied zooplankton from the central Arctic Basin (Hopcroft et al., 2010; Kulikov, 1992; Pavshchikov, 1984).

The recent data suggest that all of the water masses in the Barents Sea have greater biomass densities of zooplankton than those in the Chukchi (Table 5). Neither of the water masses entering the Chukchi Sea from the south is as rich in zooplankton as the Atlantic Water that enters the southern Barents Sea (Table 5), though older data suggest greater fluxes of zooplankton into the Chukchi (1.8×10^6 mt C, July to September; Springer et al., 1989) than into the Barents Sea in the Atlantic Water (0.8×10^6 mt C, May to October; Dalpadado et al., 2012a; Edvardsen et al., 2003, similar to the estimates of Pedersen (1995) and Pedersen et al. (1995) of 0.7×10^6 mt C). Advected zooplankton arrive earlier in the Barents Sea (April) than in the Chukchi Sea (July/August). In the Barents Sea, *C. finmarchicus* reproduces in the southern Barents Sea in April, thus providing prey for larval and forage fish early in the season (Pedersen and Fosheim, 2008; Tande, 1991).

2.6. Nutrients, chlorophyll, and primary production

Comparison of annual primary productivity in the Barents and Chukchi Seas is compromised by the spatial and temporal variability in these systems, the striking differences in nutrient availability in the water masses present, and seasonal shifts from sea-ice production to pelagic production (Gradinger, 2009). For chlorophyll-based estimates of primary production, there are issues of grazing pressure from zooplankton that reduces standing stocks of chlorophyll (e.g., Campbell et al., 2009; Vernet, 1991), and amount of sub-surface chlorophyll, which may be missed by satellite observations. Recently, Arrigo et al. (2011) have addressed the latter issue and suggest that the expected error in satellite-based estimates is, at a maximum, less than twenty percent.

2.6.1. Nutrients

The amount of nutrients available to support primary production varies spatially and temporally. In the Barents Sea, the Atlantic Water has a winter content of $10\text{--}13 \mu\text{g l}^{-1} \text{NO}_3^-$ (Kristiansen et al., 1994; Reigstad et al., 2002). In contrast, on the northern Bering Sea shelf in winter, water in the western area has $20\text{--}25 \mu\text{g l}^{-1}$ of NO_3^- while waters to the east have between 0 and $5 \mu\text{g l}^{-1}$ of NO_3^- (Clement et al., 2004). These are likely close to the late winter values in the Chukchi Sea. In the Alaskan Coastal Waters in summer, nitrate values are $<1.0 \mu\text{g l}^{-1}$ of NO_3^- (Eisner et al., in review; Walsh et al., 2005). Walsh et al. (2005), in developing their numerical model for Chukchi primary production, used a value of $20 \mu\text{g l}^{-1}$ of NO_3^- for the Anadyr Water in spring and $10 \mu\text{g l}^{-1}$ of NO_3^- in the eastern sector. Thus, in spring, nutrients are more abundant in the Chukchi Sea than in the Barents. This is because of the higher nutrient concentrations in the source waters of the North Pacific than in the North Atlantic.

2.6.2. Chlorophyll

In the Barents Sea, phytoplankton biomass as chlorophyll *a* rarely exceeds $10 \mu\text{g l}^{-1}$ during bloom situations. Extensive studies covering Atlantic water and the marginal ice zone in the central Barents Sea during the years 1979–1984 showed chlorophyll *a* values typically in the range of $2\text{--}10 \mu\text{g l}^{-1}$ for bloom situations, and $1\text{--}6 \mu\text{g l}^{-1}$ in the chlorophyll maximum layer (at 20–30 m depth) post-bloom (Skjoldal et al., 1987). Integrated chlorophyll *a* in the water column was typically $100\text{--}300 \text{mg m}^{-2}$ in bloom situations with a maximum of about 450mg m^{-2} (Rey et al., 1987). Similar chlorophyll *a* concentrations have been found also in other studies in the central Barents Sea (Kristiansen et al., 1994; Reigstad et al., 2002; Wassmann et al., 1999, 2006b).

Chlorophyll *a* concentrations can also be calculated based on the drawdown of nitrogen (N). Applying the N/Chl *a* ratio of $0.6 \mu\text{g}\text{--}\mu\text{g}^{-1}$, as used by Walsh et al. (2005) for the Chukchi Sea, gives a maximum chlorophyll *a* concentration of $18 \mu\text{g l}^{-1}$ in the Barents Sea,

assuming a starting value of 11 $\mu\text{g-at N}$ nitrate, and no extraneous losses. Rey et al. (1987) used a N/Chl *a* ratio of 1.2 (based on empirical data on phytoplankton C and chlorophyll *a* in bloom situations in the Barents Sea), which would give a maximum of about 9 $\mu\text{g chlorophyll } a\text{ l}^{-1}$ for a consumption of 11 $\mu\text{g-at N l}^{-1}$. However, there are a few cases where values in the range of 10–15 $\mu\text{g chlorophyll } a\text{ l}^{-1}$ have been observed in the deeper layer of developing blooms (where shade adaptation and sinking may contribute to higher levels; Reigstad et al., 2002; Skjoldal et al., 1987; Wassmann et al., 1999).

In the Chukchi Sea, Walsh et al. (2005) assumed a mean chlorophyll *a* concentration of the Anadyr Water in the Bering Strait of 10 $\mu\text{g l}^{-1}$. Springer and McRoy (1993) reported chlorophyll *a* values in the southern Chukchi Sea up to 1000 mg m^{-2} in a small area of extraordinarily high productivity where Anadyr Water exited the Bering Strait. In the same set of studies, Hansell et al. (1993) recorded a maximum nitrate deficit of 1100 mg m^{-2} , which corresponds to a maximum phytoplankton biomass of about 1800 $\text{mg Chl } a\text{ m}^{-2}$ (if there were no extraneous losses). These values are not typical of the Chukchi Sea as a whole. Inspection of Figs. 2 and 7 in Wang et al. (2005) indicates that satellite-derived chlorophyll *a* values of $<3 \mu\text{g l}^{-1}$ were common over most of the Chukchi Sea from June through August in 1998 and from July through September in 2001. Higher values, on the order of 5 to 10 $\mu\text{g l}^{-1}$ were widespread in September 1998 and June 2001 (Wang et al., 2005) and September, 2007 (Eisner et al., in review).

In the northern Chukchi Sea, chlorophyll *a* concentrations in the surface layer rarely exceed 1 $\mu\text{g l}^{-1}$ due to nutrient exhaustion (Cota et al., 1996; Eisner et al., in review; Hill et al., 2005; Wang et al., 2005). The summer situation is characterized by a pronounced sub-surface maximum in chlorophyll *a* (Cota et al., 1996; Hameedi, 1978; Hill and Cota, 2005; Hill et al., 2005) located at the upper nutricline, where nutrients become available from the deeper layer. The maximum chlorophyll *a* values reported (up to 40 $\mu\text{g l}^{-1}$) are found typically at 20–40 m, at or below the strong pycnocline (Codispoti et al., 2005; Hameedi, 1978; Hill et al., 2005).

Dunton et al. (2005) compiled information on integrated chlorophyll *a* in the water column in the context of benthic–pelagic coupling and the role of advection across the Chukchi shelf. They found an overall pattern of high chlorophyll values of $>150 \text{ mg m}^{-2}$ to $>300 \text{ mg m}^{-2}$ north from the Bering Strait toward Wrangel Island and eastward across the northern shelf to Hannah Shoal and Barrow Canyon. The high chlorophyll values corresponded broadly to the flow pattern of the productive Anadyr Water and were distinctly different from the low chlorophyll content of the less productive Alaskan Coastal Water (Dunton et al., 2005).

2.6.3. Primary production

The available maps of primary productivity in the Barents suggest that there is a large area of modest productivity in the south and east, a northern area with low productivity, and some small areas of extremely high productivity primarily over banks, where tidal mixing continually replenishes nutrient concentrations in surface waters (Fig. 7). Stratification of the southern Barents Sea usually takes place in June, which is when the main spring phytoplankton bloom commonly develops (Olsen et al., 2003; Skjoldal et al., 1987). There is considerable inter-annual variation, however, in stratification and spring bloom development. In the south, a relatively large portion of the annual primary production occurs in the summer and autumn, whereas in the Arctic Water, most production is associated with the spring bloom, and this shorter growing season results in production there that is only about one third of that in Atlantic Water (Loeng and Drinkwater, 2007). Ice algae are also important in Arctic waters, as they extend the period of food availability by several months (Leu et al., 2011).

The total annual primary production for the Barents Sea as a whole has been estimated to range from 69 g C m^{-2} (Rey et al., 1987, using ^{14}C uptake) to 103 g C m^{-2} (Ellingsen et al., 2008, using a 3-D model), with an average of 93 g C m^{-2} (Sakshaug, 2004; Wassmann et al., 2006b). Most recently, Reigstad et al. (2011) estimated an average primary production for the Barents Sea of 102 g C m^{-2} for the years 1995–2007. Arrigo et al. (2008), using a satellite-based approach, estimated that annual primary production for the Barents Sea as a whole was 109 Tg C yr^{-1} , or about 72 $\text{g C m}^{-2}\text{yr}^{-1}$ for the period 1998–2002. Arrigo et al.'s estimate was for a wedge-shaped area that extends to the North Pole. However, because most of the production accounted for by their study occurs in the southern portions of this wedge, over the shelf regions, it is reasonable to use their estimate for the Barents Sea as defined in this paper.

The highest rates of primary production in the Barents Sea are found in the Atlantic waters of the southwestern entrance area with rates of 120–160 g C m^{-2} , while the lowest rates are associated with ice-covered waters of the northern Barents Sea, where the annual production may be as low as 18–30 g C m^{-2} including the contribution from ice algae (Hegseth, 1998; Wassmann and Slagstad, 1993; Wassmann et al., 2010, though more recently Reigstad et al. (2011) have provided an estimate of 54–67 g C m^{-2}). The overall estimates for the Barents Sea are largely based on modeling studies and have been shown to be associated with substantial inter-annual variation (Wassmann et al., 2006a, 2006b).

The southern Chukchi Sea is known for extraordinarily high levels of primary production and standing stocks of chlorophyll (Fig. 7). Mixing occurs in relation to the islands in the center of the Bering Strait (Woodgate and Weingartner, pers. comm.), and intense blooms occur north of the Strait in the southern Chukchi Sea, in regions fed by Anadyr water. There, rates of primary production as high as 4.1 $\text{g C m}^{-2}\text{d}^{-1}$ in June (McRoy et al., 1972), $>3.0 \text{ g C m}^{-2}\text{d}^{-1}$ in July (Hameedi, 1978), and 4.8–6.0 $\text{g C m}^{-2}\text{d}^{-1}$ (Hansell et al., 1993) have been observed. Hansell et al. (1993) estimated a maximum primary production of 720 $\text{g C m}^{-2}\text{yr}^{-1}$ using the most extreme gradient in nitrate deficit. However, others working in these same waters have obtained lower estimates of primary production, e.g., Sambrotto et al. (1984) 2.7 $\text{g C m}^{-2}\text{d}^{-1}$ (or 270 $\text{g C m}^{-2}\text{yr}^{-1}$ assuming a 100-day growing season), and Lee et al. (2007) 145 $\text{g C m}^{-2}\text{yr}^{-1}$. These high levels of production are maintained by the continual replenishment and mixing to the surface of nutrients advected in the Anadyr Water. It is assumed that the nutrient content of Anadyr Water remains steady throughout the production season. High levels of primary production also occur in the northeast corner near the head of Barrow Canyon, which is subject to upwelling and sometimes supports high standing stocks of chlorophyll (Ashjian et al., 2010; Grebmeier et al., 2006a).

Efforts to assess the average annual primary productivity for the Chukchi Sea as a whole have resulted in much lower estimates of annual primary production. Zeeman (1992) sampled much of the southern Chukchi Sea, including western (Russian) waters, and estimated an annual mean primary production of 96 $\text{g C m}^{-2}\text{yr}^{-1}$ based on measurements of 1.6 $\text{g C m}^{-2}\text{d}^{-1}$ and a growing season of 60 days. If this were extended to a 100-day growing season, the result would be 160 $\text{g C m}^{-2}\text{yr}^{-1}$. Additional field estimates include 90 $\text{g C m}^{-2}\text{yr}^{-1}$ (Hill et al., 2005) and 55 $\text{g C m}^{-2}\text{yr}^{-1}$ (Lee et al., 2007). Walsh et al. (2005), using a numerical model, estimated annual Chukchi primary production at 100 $\text{g C m}^{-2}\text{yr}^{-1}$. Two estimates based on satellite observations are 27 Tg C or about 43 $\text{g C m}^{-2}\text{yr}^{-1}$ (Arrigo et al., 2008; Arrigo, pers. comm.) and 55 $\text{g C m}^{-2}\text{yr}^{-1}$, assuming a 100-day growing season (Vetrov and Romankevich, 2011). However, recent field work suggests that we may have grossly underestimated the primary production in the Chukchi Sea, where, in 2010 and 2011, Arrigo et al. (2012) discovered an immense phytoplankton bloom under first-year ice, which may add greatly to our estimates of primary production in this region. Additionally, there is some indication from a trophic mass-balance

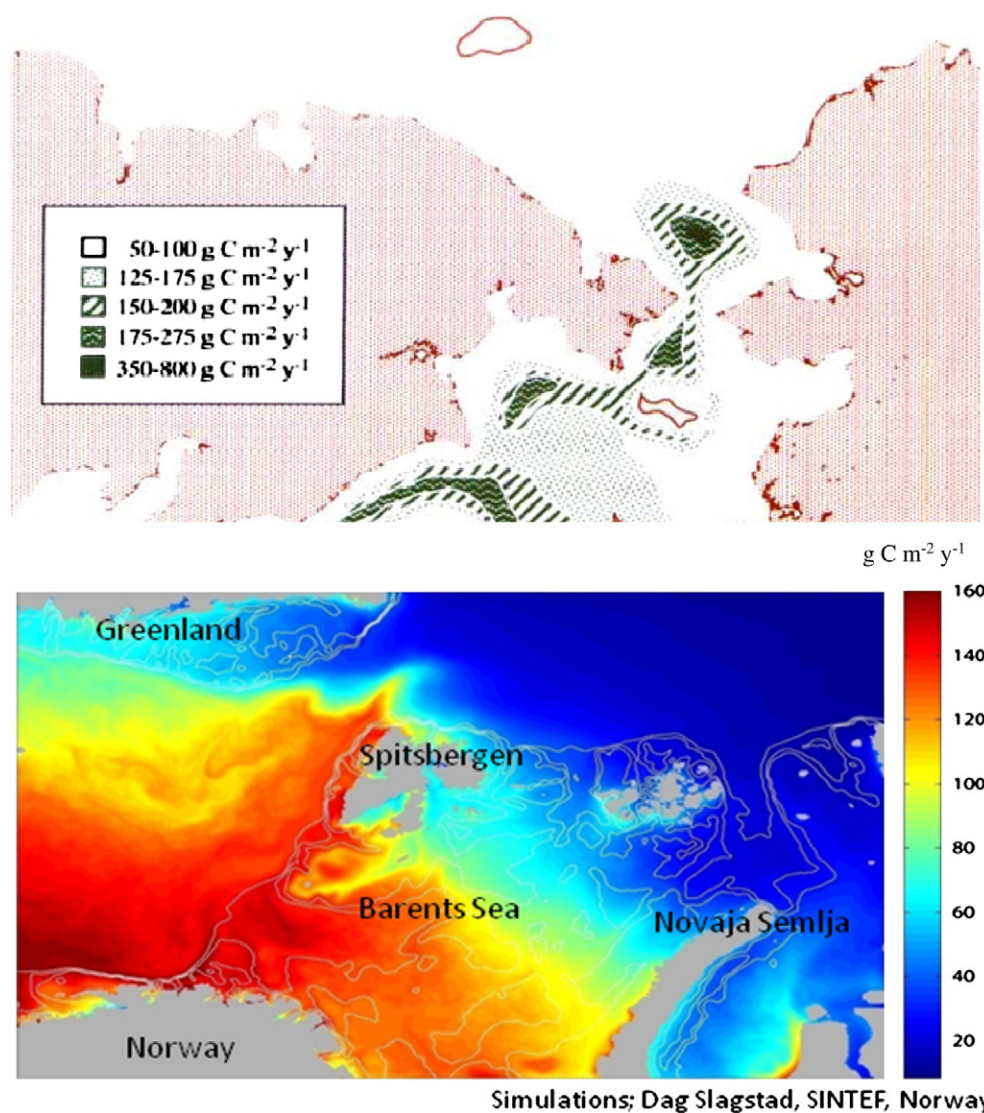


Fig. 7. Top: Chukchi Sea mean annual primary productivity, from Springer et al. (1996); Bottom: Barents Sea mean annual primary productivity, 1995–2007, as modeled by Dag Slagstad, SINTEF, Norway. From Reigstad et al. (2011), with permission.

model of the eastern Chukchi Sea that elevated levels of primary production and export to the benthos may be required if there is to be sufficient phytodetritus to support the abundant benthic food web (Whitehouse, 2011).

Thus, despite the very high levels of primary production in the southern Chukchi Sea, the present, highest model-based estimate of annual sea-wide primary production for the Chukchi Sea at $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ is remarkably similar to that for the Barents Sea at $102 \text{ g C m}^{-2} \text{ yr}^{-1}$. In both seas, there is apparently considerable interannual variability, at least some of which is dependent on the timing of ice-melt, which affects the length of the growing season. In addition, inter-annual variability in wind mixing will affect the availability of nutrients in the upper mixed layer of stratified waters.

2.7. Summary of standing stocks and productivity

Overall, when we examine the fishery production and the standing stocks of fish, cetaceans and nesting seabirds in the Barents and Chukchi Seas, it is difficult to see how the higher fish stocks and fisheries yields of the Barents Sea can be accounted for on the basis of autochthonous primary productivity. Primary production in the

Barents Sea is similar to that in the Chukchi Sea (Table 7), yet fisheries landings are between two and three orders of magnitude higher in the Barents Sea. The higher fish landings of the Barents Sea do not appear to be driven by a lesser provision of carbon to seabirds, marine mammals and the benthos. Although it would be desirable to estimate the biomass and consumption of marine mammals in both systems, at present the data available are too sparse to have tight estimates of numbers and days of occupancy. It is noteworthy, that in the Barents Sea, all cetaceans and virtually all pinnipeds (except for small populations of walrus and bearded seals) forage in the water column, whereas in the Chukchi Sea, gray whales, walrus and bearded seals, all of which are abundant there, are primarily benthic and epibenthic foragers. However, based on the available data, at depths $<100 \text{ m}$, the Barents Sea supports about 671 g m^{-2} of benthic wet biomass, whereas the Chukchi Sea supports, on average only 355 g m^{-2} of benthic wet biomass at depths $<100 \text{ m}$ (Table 7). It is apparently the shallowness of the Chukchi Sea that makes it a better habitat for benthic-foraging marine mammals. Thus, we need to examine other aspects of the oceanography of the Chukchi and Barents Seas to understand why the Barents Sea supports a significantly greater biomass and productivity of fish, nesting

seabirds and marine mammals, primarily in its southern (Atlantic Water) half.

3. Potential mechanisms responsible for differences between the Barents and Chukchi Seas

In this section we synthesize data relevant to some of the possible mechanisms that may be responsible for the differences between the marine ecosystems of the Barents and Chukchi Seas. The most striking difference between these ecosystems may be the enormous fisheries and fish resources of the Barents Sea as compared to those of the Chukchi Sea. A number of possible mechanisms might be responsible for these differences, some of which can be eliminated quickly. It is unlikely that top-down control of fish in the Chukchi Sea is responsible for the difference in fish resources, as there are fewer piscivorous marine mammals and birds in the Chukchi Sea than in the Barents Sea, and some of those in the Chukchi Sea linger only briefly on their way to foraging areas elsewhere. Likewise, it is unlikely that differences in primary production are responsible for the difference in fish biomass and fisheries, as the best estimates suggest that annual rates of primary production are either similar in the two systems or somewhat greater in the Chukchi Sea. Thus, we must look to mechanisms that involve differences in pathways of carbon through the ecosystems, differences in the behavior of the fish using these systems, and differences in advective inputs. Thus, below, we investigate the roles of: 1) shallow depths and export of carbon to the benthos, 2) migration of fish and other upper trophic level species to alternate regions, and 3) differences in the advection of heat and zooplankton.

3.1. Water depth and export of carbon to the benthos

Shallow depths may promote enhanced pelagic–benthic coupling in two ways. In shallow water, there is less opportunity for material to be consumed by zooplankton before it reaches the bottom (Grebmeier et al., 1988, 2006a), and there is less opportunity for material to decompose as it sinks. Secondly, in shallow water, such as at Hannah and Harold shoals in the Chukchi Sea, phytoplankton becomes directly available for benthos, especially filter feeders. Indeed, “hot spots” of benthic biomass accumulation and oxygen consumption occur in shallow areas of both the Barents and Chukchi Seas (Figs. 5, 6) (Antipova, 1975; Grebmeier and McRoy, 1989; Grebmeier et al., 1989, 2006a; Piepenburg et al., 1995).

The amount of production that is consumed in the pelagic realm depends not only upon the depth, but also upon the strength of the vertical stratification of the water column as well (Hargrave et al., 1985; Smetacek, 1980). Stronger stratification acts to retain more of the production in the near surface layers, with less primary production making it to the benthos under such conditions. Thus, over most of the northern Barents Sea during summer when there is strong stratification after ice melt, primary production is low and little of it reaches the sea floor, even over many of the shallow banks (Reigstad et al., 2008).

Because of the greater depths of the Barents Sea and assumed higher zooplankton grazing, more of the primary production is believed to be captured by the pelagic food web, especially in the southern Barents Sea, and thus is more available to pelagic-feeding fish, birds and mammals compared to the Chukchi Sea. The high pelagic grazing in the southern Barents Sea region can be seen in the generally low fraction of primary production exported to the benthos. Reigstad et al. (2008) found that 34% of total annual primary production was exported to the benthos based on sediment traps in this region, whereas 47% was exported to the benthos in the northern Barents Sea. In the Chukchi Sea, Campbell et al. (2009) estimated that 56% of primary production was available for export to the benthos, and Whitehouse (2011), using a trophic mass-balance

model, estimated that export of 65% of primary production to the benthos was needed to support the benthic food web in the eastern Chukchi Sea.

When we examine how much of the primary production is consumed in the upper water column, we find that approximately $36 \text{ g C m}^{-2}\text{yr}^{-1}$ is consumed in the Arctic waters of the Barents Sea, and $86 \text{ g C m}^{-2}\text{yr}^{-1}$ is consumed in the Atlantic waters (Reigstad et al., 2008). In contrast, somewhere between $56 \text{ g C m}^{-2}\text{yr}^{-1}$ (Walsh et al., 2005; Campbell et al., 2009) and $7.5 \text{ g C m}^{-2}\text{yr}^{-1}$ (using a top-down forced ecopath model, Whitehouse, 2011) is consumed by the pelagic component of the Chukchi Sea marine ecosystem. Thus, there appears to be a larger amount of the primary production that is taken up by the pelagic component (by a factor of maximum of ~2–10) in the southern Barents compared to the Chukchi Sea. It is thus possible to make a case for differences in export rates to be a contributor to the order of magnitude difference in biomass of fish in the Barents Sea compared to the Chukchi Sea.

3.2. Migratory behavior of top predators

Although many fish species remain in the Barents Sea throughout the year, some species make seasonal migrations to alternative feeding sites or spawning areas (Fig. 8). Capelin follow the ice-edge bloom north, and forage on both the Arctic and Atlantic zooplankton fauna associated with this bloom, and Atlantic cod make feeding migrations northward to intercept the capelin in summer. In addition, both adult Atlantic cod and Norwegian spring-spawning herring have spawning migrations to the west coast of Norway, whereby they provide their eggs and larvae with more favorable rearing conditions than would be available in the Barents Sea (Loeng and Drinkwater, 2007). In winter, many of the marine birds and cetaceans either move to the southern Barents Sea, or out of the Barents Sea entirely.

The Chukchi Sea also supports upper trophic level migrants in summer and fall, though apparently not in spring, when most migrating beluga whales (a few spend part of the summer in the Chukchi; Suydam et al., 2001) and bowhead whales move through the area on their way to foraging areas elsewhere in the Arctic (Carroll et al., 1987). However, in the fall, migrating bowhead and beluga whales linger in the Chukchi to forage (Clarke et al., 1993; Moore et al., 1995; Quakenbush et al., 2010a, 2010b), and millions of planktivorous seabirds enter the Chukchi to forage on large, lipid rich copepods and euphausiids, the bulk of which have been advected into the Chukchi from the Bering Sea (see sections above). As winter approaches, some pinnipeds (e.g., Burns, 1970, 1981; Fay, 1982; Johnson et al., 1966; Lowry et al., 1998), most cetaceans (e.g., Braham, 1984; Brueggeman, 1982; Richard et al., 2001) and virtually all seabirds leave the Chukchi Sea for warmer seas with open water. In contrast, most fish species do not migrate out of the Chukchi Sea in winter, despite the very low water temperatures, perhaps because migrating against the strong currents in the Bering Strait and northern Bering Sea would be energetically too expensive. Thus, at present, only fish with the physiological mechanisms that allow existence in sub-zero waters are able to overwinter in the Chukchi Sea (Sigler et al., 2011). Temperate and boreal fish species in the southern Barents Sea do not need to migrate out of the Barents to escape freezing, as the southern Barents remains at 2°C or above year round (Fig. 10) (Drinkwater, 2005).

3.3. Water inputs and their sources

The influence of water inputs to the Chukchi and southern Barents Seas on fish productivity depends on conditions to the south (Ottersen et al., 2010; Sundby, 2000). Importantly, there are significant differences in the properties of the water masses entering the seas from the south and in the amount of water that is advected south from the northern edges of these seas. We hypothesize that the differences in the

Barents Sea Fish Movements

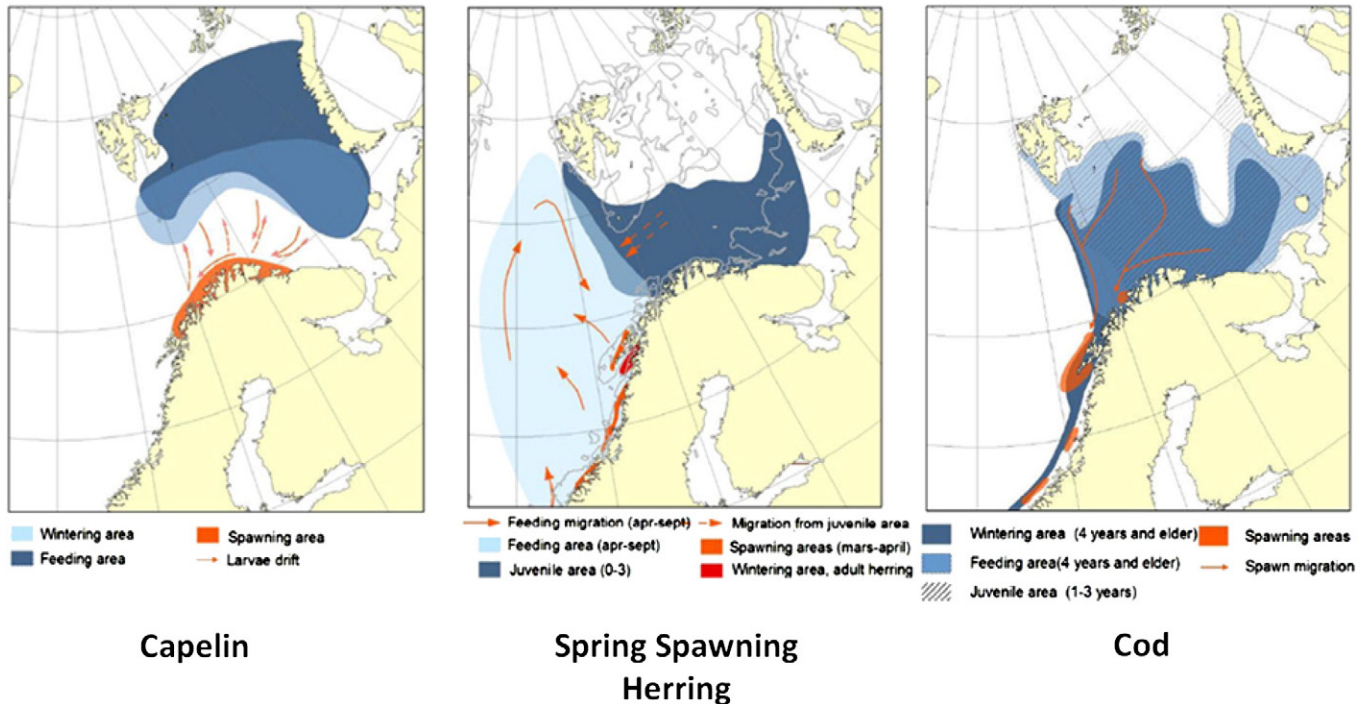


Fig. 8. Schematics of fish movements in the Barents Sea.

Figure from Stiansen et al. (2009), with permission, J.E Stiansen, Institute of Marine Research, Bergen, Norway.

timing and amounts of heat and plankton advected in the inflows of water from the south of the Barents and Chukchi Seas play critical roles in determining the differences in the upper trophic levels of these two seas, and in the differences between their northern and southern portions.

3.3.1. Advection of heat

The water entering the southern Barents Sea originates in the North Atlantic Ocean and in particular, the Norwegian Sea. This water supplies heat to the southern Barents Sea throughout the year (Smedsrud et al., 2010). A long time-series from the Kola Section, north of Murmansk, Russia, shows that monthly mean temperatures in the southwestern Barents Sea remain above 2 °C all year, as do temperatures at depth throughout much of the Barents Sea (Fig. 9). These temperatures are well within the tolerance ranges of numerous species of groundfish including Atlantic cod (Drinkwater, 2005), haddock, and saithe among others (Bogstad et al., 1998; Rose, 2007; Sonina, 1969; Stiansen et al., 2009). These comparatively “warm” temperatures also promote higher feeding and growth rates of zooplankton and fish than would be expected in waters with sub-zero temperatures.

In the Chukchi Sea, and in the waters passing through the Bering Strait, there is a pronounced seasonal signal in heat content (Fig. 10) (Woodgate et al., 2005b, 2010). In most years, water temperatures in the Chukchi Sea dip below 0 °C in October or November and remain below 0 °C until May or June. Thus, like the northern Barents Sea (Fig. 11), the Chukchi Sea remains mostly ice-covered through much of May (Fig. 12), which results in a delay in the onset and expansion of the spring bloom there (Fig. 13). The spring melting of Chukchi Sea ice generally occurs when warmer (>0 °C) waters appear in Bering Strait (Woodgate et al., 2010) and the open water bloom is delayed until May or June (Fig. 13).

The temperature of the waters advected into the southern portions of the Barents and Chukchi Seas (Figs. 10, 11) have a major

influence not only on water temperature within the seas, but also on the timing of ice retreat (Figs. 11, 12) and thus the length of the productive season. In most years, the warm Atlantic Water in the southwestern Barents Sea causes the area to remain ice-free throughout the year. In exceptionally cold years, or in years with strong prevailing northerly winds, ice extends into the southern Barents Sea. The comparatively warm Atlantic Water then melts this ice, leading to a stratified water column, which in turn promotes an early spring bloom (Olsen et al., 2003) (Fig. 13). The spring bloom in the Barents Sea starts in April, and continues into June, and even July in the northern regions (Fig. 13), but due to heterogeneous ice conditions, blooms and high primary production can be observed in the Barents Sea also in July (Hodal and Kristiansen, 2008).

In winter and spring, water entering the Chukchi Sea from the south is cold, having crossed the shallow, ice-covered, northern Bering Sea. These cold waters do nothing to warm the cold, well-mixed waters of the winter ice-covered Chukchi Sea. Water temperatures less than 0 °C are below the tolerance of fish species that do not have antifreeze in their blood. Thus, most temperate fish species are excluded from the Chukchi Sea and northern Bering Sea in winter and spring (Sigler et al., 2011). It is possible that some sub-arctic fish species entering the Arctic Ocean may develop mechanisms to cope with extreme cold. For example, in the Atlantic Ocean, Atlantic cod generally migrate offshore in winter to avoid freezing temperatures. However, some populations are able to remain inshore in sub-zero waters because they have developed glycoprotein antifreeze (Fletcher et al., 1987; Goddard et al., 1999; Ruzzante et al., 1996).

3.3.2. Advection of plankton

Nutrients and phytoplankton are advected into the southern Barents Sea in the warm Atlantic Water and result in the Atlantic-influenced portion of the Barents Sea being its most productive

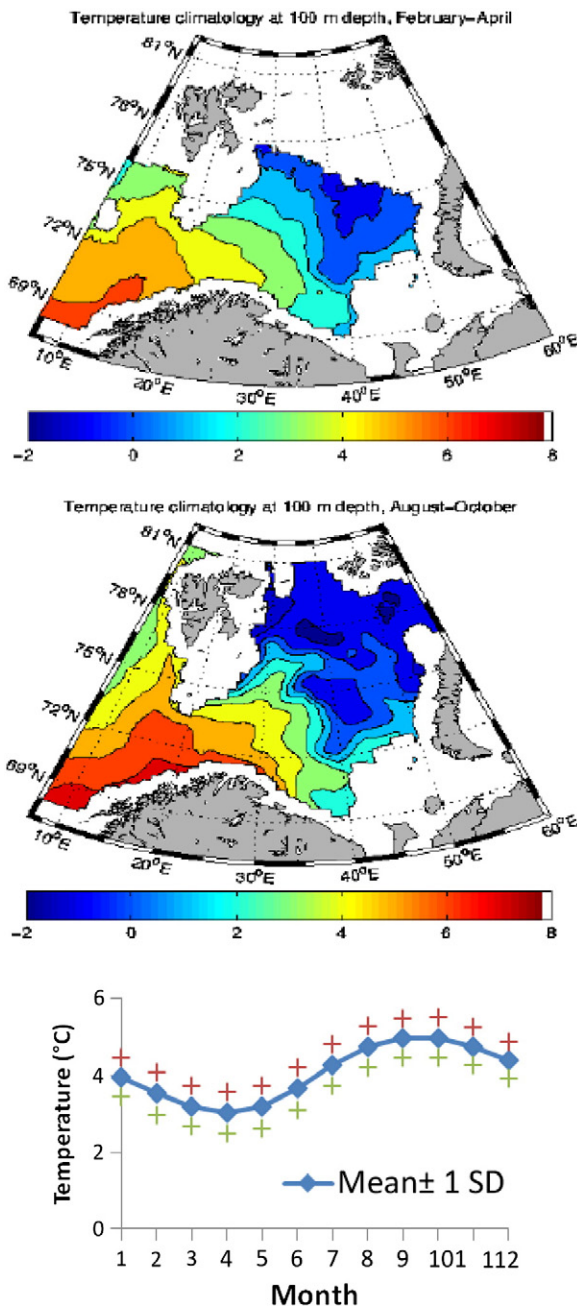


Fig. 9. Winter (February–April) (top) and summer (August–October) (middle) mean temperatures at 100 m in the Barents Sea, 1977–1996. Bottom: Seasonal changes in the 0–200 m averaged temperature for the Kola Line. Data courtesy of PINRO ("Polar Research Institute of Marine Fisheries and Oceanography", http://www.pinro.ru/index_e.htm).

region on an annual basis (Figs. 7, 13) (Sakshaug et al., 2009; Wassmann et al., 2010). Phytoplankton blooms there are often dominated by taxa of Atlantic affinity, emphasizing the importance not only of the nutrients but also the biomass of phytoplankton that is advected from the south (Sakshaug et al., 2009).

The available data suggest that all of the water masses in the Barents Sea have greater standing stocks of zooplankton biomass than those in the Chukchi Sea (Table 5). As discussed above, in the Barents Sea, the richest source of zooplankton is the Atlantic Water, which transports the copepod *C. finmarchicus* from the Norwegian Sea to

the Barents Sea. The Barents Sea also receives zooplankton from the north. Arctic Water from the shelf regions farther east may be an important source of large lipid-rich *C. glacialis* as well as ice-associated amphipods (Hyperiididae and Gammaridae) that support large seabird colonies on Svalbard (Karnovsky et al., 2003; Kovacs and Lydersen, 2006), and are important for maintenance of capelin throughout the Barents Sea (Orlova et al., 2010).

As discussed above, in the Chukchi Sea, Bering Sea Water (Bering Shelf Water plus Anadyr Water) is relatively rich in large, lipid-rich copepods (*Calanus* spp. and *Neocalanus* spp.), whereas the Alaskan Coastal Water is depauperate in zooplankton (Hopcroft et al., 2010; Piatt and Springer, 2003). *Neocalanus* spp. overwinter at depth in the basin of the Bering Sea, and re-enter the upper water column in the southeastern Bering Sea in early spring, with peak numbers occurring in April or May (Smith and Vidal, 1986). If these copepods are not present in waters over the outer portion of the northern shelf until May, it is likely that they will not reach peak numbers in the Chukchi Sea until August. The lack of large-bodied species in plankton samples from the southern Chukchi Sea in early summer (Hopcroft et al., 2010) may indicate reduced foraging opportunities for planktivorous fish, seabirds, and marine mammals there in spring (Hopcroft et al., 2010; Piatt and Springer, 2003). This may be too late in the season to support juvenile fish, breeding of planktivorous auklets or early season foraging by planktivorous cetaceans in the Chukchi Sea. It is telling that planktivorous seabirds nest primarily to the south of Bering Strait, whereas in the Barents Sea planktivorous seabirds are abundant nesters on the shores of Svalbard, in the northern Barents Sea, as well as in the southern Barents Sea on mainland Norway and coastal islands.

The importance of the advection of nutrients and zooplankton, e.g. *C. marshallae*/*glacialis*, *Neocalanus* spp. (Hopcroft et al., 2010) and euphausiids (Eisner et al., in review), for late-season production in the Bering Sea Water areas of the Chukchi is evidenced by late summer/early fall concentrations of bowhead whales along the western Chukchi (Chukotka) coast (Quakenbush et al., 2010a,b). The western Chukchi Sea also has a rich benthic fauna that is supported by high primary production and the advection of plankton in the Bering Sea Water that dominates the western Chukchi. Concentrations of gray whales (Miller et al., 1985; Nerini, 1984) forage there, and most of the walrus in the Chukchi Sea are located on Wrangel Island and the northern Chukotka coast (Gilbert et al., 1992). The Chukchi Sea was also a historically important foraging ground for large, planktivorous cetaceans, which were hunted in the Chukchi Sea in August and September, when zooplankton advected in the Bering Sea Water would have been plentiful (Mizroch et al., 2009). Thus, the western Chukchi, due to the advection of both nutrients and zooplankton in Bering Sea Water, supports a considerable number of both pelagic and benthic foragers.

Advection of zooplankton from the Arctic occurs in both the Barents and the Chukchi Seas. In the northern Barents Sea, Arctic zooplankton are available to support Arctic cod, capelin and other planktivorous fish (Gjøsæter, 1998; Orlova et al., 2010) and seabirds (Hunt et al., 1996; Mehlum and Gabrielsen, 1993; Mehlum et al., 1996, 1998) and some marine mammals (e.g., Falk-Petersen et al., 2004; Nilssen et al., 1995). They support particularly large colonies of little auks in Storfjorden and on the west coast of Svalbard (Karnovsky et al., 2003; Kovacs and Lydersen, 2006). In contrast, in the Chukchi Sea, Arctic zooplankton are primarily concentrated along the shelf edges and in canyons where they are upwelled onto the shelf. They are too far from breeding colonies to be important to nesting seabirds, and they are not accessible until late summer when the ice has melted back to the Arctic Basin.

To summarize this section, the advection of heat in Atlantic Water plays a pivotal role in allowing boreal species of fish to exist in the Barents Sea. Additionally, the advection of large, lipid-rich

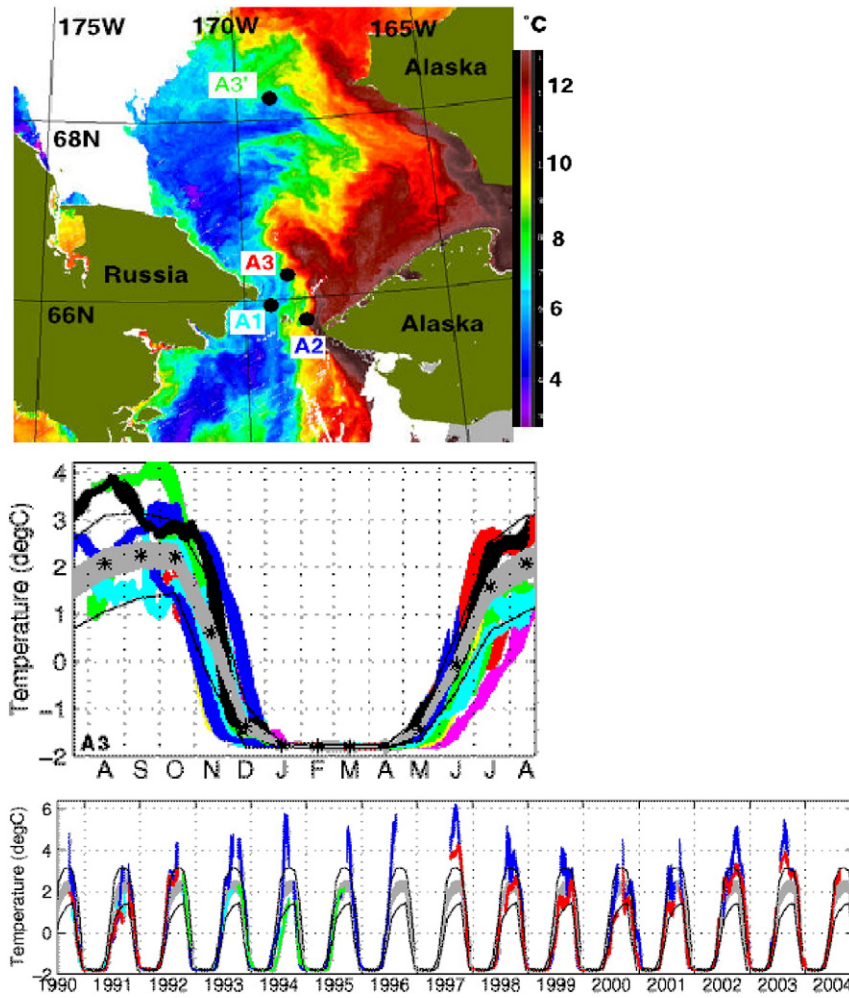


Fig. 10. Top: Bering Strait and Chukchi Sea surface temperature on 26 August 2004. (MODIS/Aqua level 1 image courtesy of Ocean Color Data Processing Archive, NASA/Goddard Space Flight Center, courtesy of M. Schmidt) indicating sites (A1, A2, A3, A3') of year-round moorings in the Bering and Chukchi (see e.g., Woodgate et al., 2005b). Middle: Temperatures at 9 m above the bottom at mooring A3. Colors indicate different years. Gray region with stars represents monthly climatology from Woodgate et al. (2005b). Bottom: Temperatures at 9 m above the bottom at four moorings in Bering Strait and the Chukchi Sea. Colors indicate mooring as per the top panel. All from Woodgate, Aagaard and Weingartner, 2005b, 2005c. Monthly temperature, salinity, and transport variability of the Bering Strait throughflow. *Geophysical Research Letters*, 32: L04601, doi:10.1029/2004GL021880 Copyright 2005 American Geophysical Union. Reproduced/modified by permission of American Geophysical Union.

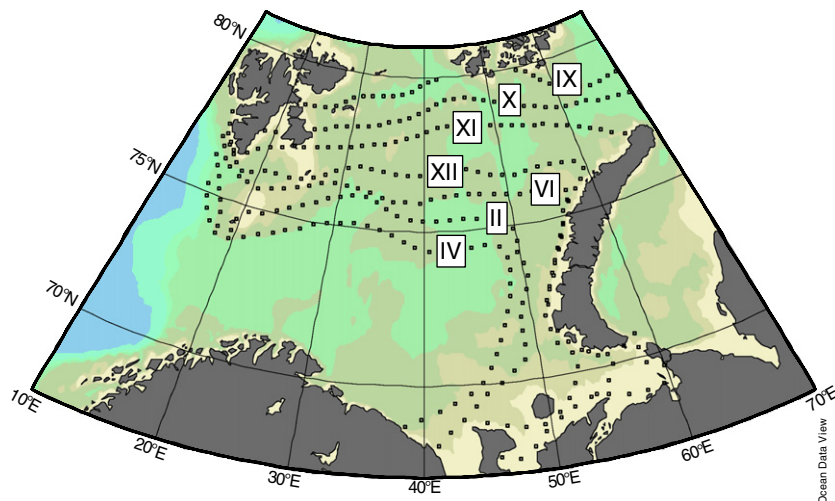


Fig. 11. Monthly climatology of ice edge position in the Barents Sea 1940 to 1975 using AARI (Murmansk Branch) data published in 1980. From Titov and Ozhigin (2005), with permission.

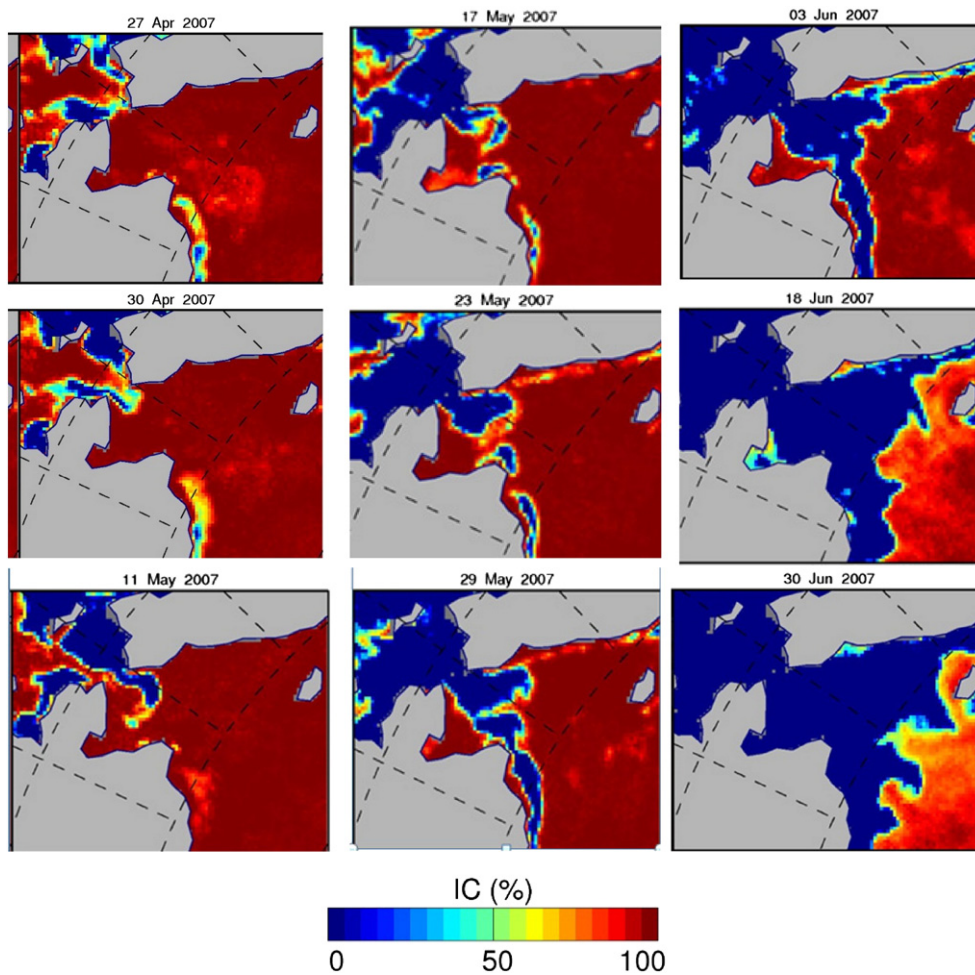


Fig. 12. Ice cover (%) in the Chukchi Sea 17 April 2007 to 30 June 2007. The Chukchi Sea is to the right of each cell, and the gray areas are the land masses. AMSR-E data are from the National Snow and Ice Data Center (Cavalieri et al., 2004). Figure by Ron Lindsay (see also Woodgate et al., 2010).

C. finmarchicus into the Barents Sea in spring provides an important source of prey that supplements the locally-reproducing stocks of *C. finmarchicus*. Finally, the migratory habits of several of the Barents Sea fish species allow them to utilize the high food concentrations available in the north after the main bloom in the south, as well as to escape harsh winter conditions and a late start to spring production by spawning well to the south along the coast of Norway. In contrast, the Chukchi Sea is cold and well mixed from fall through spring, and the water entering from the Bering Sea is also cold and inhospitable to boreal fish species. Out migration through the Bering Strait of juvenile fishes is challenged by the strong northward currents present throughout spring, summer and fall. Although zooplankton are advected to the Chukchi from the Bering Sea in great abundance, their arrival in July and August may be too late for them to support seabirds and cetaceans, except for late-season migrants.

4. Future changes

4.1. Climate warming

Climate warming has already had a marked impact on the Arctic, with increasing areas of ice-free waters in the summer and fall, a later freeze-up in the fall and earlier retreat of the seasonal sea-ice cover in spring (Markus et al., 2009). There has also been a marked decline in ice thickness and in the amount of multi-year sea ice, a factor contributing to an earlier beginning of the ice-melt season

(Kwok, 2007; Kwok and Rothrock, 2009; Nghiem et al., 2007). Effects of the changing ice conditions are already being documented throughout the ecosystem, from the distributions and abundances of benthic organisms to marine mammals (e.g. Grebmeier, 2012; Kovacs et al., 2011). In this brief section, we try to identify some of the major ways that climate warming might affect the ecosystems of the Barents and Chukchi Seas.

4.1.1. Mechanisms suggesting increases in productivity

A warming of the global climate (including the Arctic) and a reduction in Arctic sea ice will result in a warming of the Barents and the Chukchi Seas and a reduction in the length of the ice-covered season. This in turn will produce longer growing seasons, increased primary production, and warming of surface waters (e.g., Ellingsen et al., 2008; Slagstad and Wassmann, 1997). As Arrigo et al. (2012) have shown, thinning ice with melt ponds may permit large under-ice phytoplankton blooms. The timing and intensity of these blooms may be such that more of the annual primary production may sink to the benthos than at present. This will most likely benefit the benthos at the expense of the pelagic food web in those areas that retain sea ice.

Climate warming may allow northward expansion of boreal species, as has recently been observed in the North Atlantic and the Barents Sea (Berge et al., 2005) and as was documented following the warming period in the 1930s and 1940s (reviewed in Drinkwater, 2005). Recent evidence suggests that some fish species, including

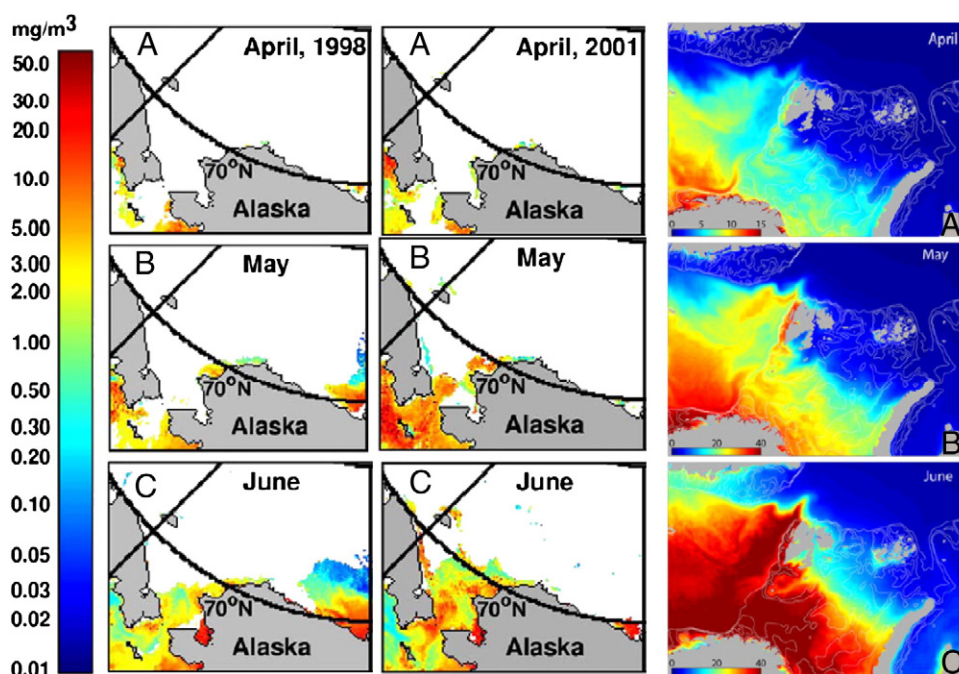


Fig. 13. Two columns on the left: Monthly maps of chlorophyll concentration in April, May, and June, 1998, an “average year” and 2001, a “warm year” in the Chukchi Sea (mg Chl-a m^{-3}) (see scale to the left) (from Wang et al., 2005), with permission. The white areas are ice covered, and the gray areas are land masses. Column on the right: Monthly average gross primary production in the Barents Sea for the period 1995–2007 in April (a), May (b) and June (c) ($\text{g C m}^{-2} \text{month}^{-1}$), see scale in lower left of each panel. From Wassmann et al., 2010, with permission. Note differences in timing of the bloom in the Barents and Chukchi Seas.

Atlantic mackerel (*Scomber scomber*) and blue whiting, are increasing in abundance in the Barents Sea during the current warming period (Anon, 2004, 2005). In the Barents Sea, it is also possible that warming will lead to increased biomasses of zooplankton and upper trophic level fish, seabirds and marine mammals that are not ice-associated species (Drinkwater, 2005; Stenevik and Sundby, 2007; Sættersdal and Loeng, 1987). Estimates of future mesozooplankton production in the Barents Sea, given increased air temperatures, suggest an increased secondary production at moderate warming, but a decrease if the temperature in the northern Barents Sea reduces the dominance of the larger Arctic copepods (Slagstad et al., 2011).

Likewise, in the Chukchi Sea warming could lead to range expansions of fish species presently confined to waters considerably farther south. Although cold winter temperatures and coverage by sea ice will continue in the northern Bering Sea and Chukchi Sea (Wang et al., 2012), temperatures in the future may become sufficiently high that temperate and boreal fish species could overwinter in the intermediate layers in the Canada Basin should these become sufficiently warm (Fig. 3) (Jackson et al., 2011; Mclaughlin et al., 2011). At present, Bering flounder in the northeastern Chukchi Sea are thought to be maintained there by the northward advection of larvae in Alaskan Coastal Water (Wyllie-Echeverria et al., 1997). Summer ichthyoplankton assemblages connect through the Bering Strait, indicative of a northward flow in the eastern Chukchi Sea (Norcross et al., 2010). Temperate species like walleye pollock (*Theragra chalcogramma*) and yellowfin sole (*Limanda aspera*) may move northward in summer, particularly in warm surface waters, even though at present, the Chukchi Sea is not an important feeding area for these species (Barber et al., 1997; Norcross et al., 2010). Likewise, juvenile pollock have been captured in trawls north of Barrow, Alaska, suggesting that they may have a mechanism for overwintering there (NPFMC, 2009; Rand and Logerwell, 2011). Changes in distributions of demersal fish species will result in restructuring of fish assemblages and possibly impact benthic invertebrate communities (Norcross et al., 2010).

4.1.2. Mechanisms suggesting decreases in productivity

In the Barents Sea, a decrease in the amount of multi-year ice at its northern boundary may impact the availability of ice-associated (sympagic) organisms (Hop et al., 2000), thereby affecting those fish, seabirds and marine mammals that forage on this community (e.g., Falk-Petersen et al., 2000). The ice-edge blooms and associated zooplankton are important for capelin, and if the ice edge retreats sufficiently far north, it has been hypothesized that capelin might switch their spawning grounds from the north coast of Norway to areas farther north and east (Huse and Ellingsen, 2008). Capelin serve as both a bottom-up and a top-down control in the “wasp-waist” structure of the Barents Sea (Ottersen et al., 2010), and any impact of climatic change on capelin will affect both lower and upper trophic level species that interact with capelin.

Recent investigations in the Barents Sea indicate a marked decrease in the area of Arctic waters in the last decade, as well as a decline in the abundance of the Arctic amphipod, *T. libellula* (Dalpadado et al., 2012a, 2012b). Additionally, Ottersen et al. (2010) discuss the potential for impacts on interactions among species resulting from species' adaptations to climate change. Thus, changes in community composition that accompany these potential changes in biomass must also be considered. For example, climate impacts on cod and herring are observed as bottom-up, with lower trophic levels a major influence on higher levels (Skern-Mauritzen et al., 2011). The climate impacts on capelin, however, show indirect effects with a delayed bottom-up effect (Hjermann et al., 2007). Although fish may be able to acclimatize to warming temperatures, such adaptation comes with a cost in lost metabolic performance and growth (Drinkwater et al., 2010; Pörtner, 2010; Pörtner and Knust, 2007).

In the Chukchi Sea, climate warming may result in a reduction of the input of large crustacean zooplankton, because the large *Calanus* copepods in the Bering Sea Water are vulnerable to warming sea temperatures and the loss of sea ice (Baier and Napp, 2003). During the warm period in the Bering Sea from 2001 to 2005, ice retreat

came early and the production of *C. marshallae/glacialis* was limited (Hunt et al., 2011). If these copepods, and the euphausiid *Thysanoessa raschii* are, as is believed, dependent on sea ice or at least a bloom in cold water (Baier and Napp, 2003; Drobysheva, 1994; Ressler et al., 2012), then warming of the northern Bering Sea sufficient to remove seasonal ice cover might result in failure of pollock recruitment, as happened in the southeastern Bering Sea during the warm period of 2001–2005 (Coyle et al., 2011; Hunt et al., 2011).

Water temperature variations and possible changes in fluxes of primary production to the bottom will be primary influences of climate warming on the benthos in the Chukchi Sea. Macrobenthic assemblages are responsive to climate variations and spatial distributions of organisms will change due to differential survival and recruitment of pelagic larval stages with varying water temperatures (Blanchard et al., 2010; Grebmeier, 2012; Sirenko and Kolutin, 1992). Hence, climate warming will contribute to changes in the spatial distributions of species (Grebmeier et al., 2006b; Sirenko and Kolutin, 1992).

4.2. Effects of climate change on seabirds and marine mammals

All ice-associated Arctic seals, whales, and polar bears are likely to be heavily negatively impacted by climate change (e.g., Cameron et al., 2010; Kovacs et al., 2011, 2012). The severity of the impacts will depend largely on the breadth of their range and whether they are generalist or specialist feeders (Laidre et al., 2008; Moore and Huntington, 2008), but ultimately also on the degree to which plastic responses to new environmental conditions will be possible for individual species (e.g., Bradbury et al., 2010; Ruzzante et al., 2005). In contrast, decreased ice cover will allow cetacean species now concentrated in boreal regions to penetrate farther into the Arctic and to remain there longer, thereby competing with (or consuming) Arctic species heretofore free of their presence (Kovacs et al., 2012; Moore and Huntington, 2008). Impacts on seabirds are somewhat more difficult to predict, but again, ice-associated feeders such as ivory gulls (*Pagophila eburnea*) may find the commutes between their nest sites and where they find food for their young too long for successful nesting (Kovacs et al., 2012).

5. Summary and conclusions

The marine ecosystems of the Barents and Chukchi Seas are similar in a number of aspects and strikingly different in others. Both seas are at similar latitudes, and both have remarkably similar average annual rates of primary production (Tables 6, 7). This latter similarity is surprising, in that nitrate concentrations in the Bering Sea Water that enters the Chukchi Sea are almost twice those of the Atlantic Water entering the Barents Sea (Table 6). Two factors that likely contribute to the similarity of annual rates of primary production are the longer growing season in the Barents Sea (by about a month), because of less ice, and the greater volume of water entering the Barents Sea from the south, which provides as much or more nitrate

over the growing season compared to the more nitrate-rich Bering Sea Water in the Chukchi Sea.

Populations of various biotic components in the marine ecosystems of these two seas may vary by up to a factor of two. These include, on an area adjusted basis, the numbers of: nesting seabirds (Barents 2× the Chukchi), all foraging seabirds (Chukchi 2× the Barents), cetaceans (Barents 2× the Chukchi), pinnipeds (Chukchi 2× the Barents), and the wet biomass of benthic macro-invertebrates (Chukchi 2× the Barents) (Table 7). Virtually all of these groups are under-sampled, with the possible exception of the numbers of nesting seabirds, and more thorough surveys may yield quite different results. There is a need for additional surveys, not only with more extensive spatial coverage of both seas, but also better seasonal coverage, so that annual average days of use can be calculated for the seabirds and marine mammals. From such information, estimates of prey consumption could be developed, based on the total biomass and age structure of populations within each species, and their metabolic demands. Prey consumption would be a useful measure of the relative ability of these two seas to support seabirds and marine mammals.

The two seas differ strikingly in the fisheries that they support (Barents 3 orders of magnitude greater than the Chukchi), the biomass of the five most abundant fish species (Barents 1 order of magnitude greater than the Chukchi), and in the standing stocks of zooplankton (Barents 3× the Chukchi) (Table 7). The remarkably higher fisheries removal rates in the Barents Sea imply that the fish stocks of this region must be much more productive than those in the Chukchi Sea. Likewise, zooplankton populations in the Barents Sea must be more productive or fish must be more efficient in converting zooplankton into fish biomass, as there is only a three-fold difference in zooplankton standing stocks compared to the orders-of-magnitude difference in standing stocks of fish. Additionally, there seems to be a better match in time and space between fish and the availability of their most important prey species for harvested fish stocks in the Barents Sea compared to the Chukchi Sea, which allows a longer and more efficient growing season for the migrating pelagic fish stocks in the Barents Sea.

At least two other differences between the seas contribute to the greater biomass of fish in the Barents Sea. Firstly, the heat content of the Atlantic Water entering the Barents Sea is much greater than that of the Bering Sea Water entering the Chukchi Sea and secondly, the greater depth of the Barents Sea allows for the formation of a deep layer of salty, warm Atlantic Water. This Atlantic Water occupies the southern portion of the Barents Sea, and also exists as a deep layer that extends through much of the northern Barents. This warmer water promotes higher feeding and growth rates in both zooplankton and fish, and permits fish to survive year-around in the Barents Sea. In contrast, the shallow Chukchi Sea is ice covered from November through June, with a well-mixed sub-zero water column. The water entering the Chukchi Sea from the south has passed over the shallow northern Bering Sea, which is also well-mixed and ice-covered from November to May, with the result that the waters entering the Chukchi Sea are below zero for about eight months of the year. Thus, in both the northern Bering Sea and the Chukchi Sea, fish lacking adaptations for sub-zero temperatures are unlikely to thrive. The cold water temperatures of the Chukchi Sea slow the feeding and growth of the zooplankton and fish. We suggest that the differences in water temperatures between the southern Barents and the Chukchi Sea are a critical factor in explaining the differences between the fisheries and fish stocks of the two seas.

The Chukchi Sea is a fully Arctic sea, whereas only the northern Barents Sea is Arctic in its seasonal ice cover and cold temperatures. By contrast, the southern Barents is essentially a boreal sea. In the Arctic Barents and Chukchi Seas, the water column becomes stratified in spring via ice melt, and there is a strong ice-associated algal bloom in cold water, much of which sinks to the benthos. Nutrients are exhausted in these strongly stratified waters, and post ice-edge

Table 6
Primary productivity, and nitrate availability in the Chukchi and Barents Seas.

		Chukchi Sea	Barents Sea
Primary Productivity 1998–2006 ^a (g C m ⁻² yr ⁻¹)	Min.	20	<20
	Max.	>400	200
	Mean	100	102
Means are from Walsh et al. (2005), and Reigstad et al. (2011)			
Nitrate ^b (μM)	ACW	5	Atlantic water
	BSW	20–25	12

^a Sakshaug, 2004; Ellingsen et al., 2008; Walsh et al., 2005; Hill et al., 2005; Lee et al., 2007.

^b ACW—Alaskan Coastal Water; BSW—Bering Sea Water; Sakshaug, 2004; Walsh et al., 2005.

Table 7

Summary of differences in standing stocks and productivity of the Barents and Chukchi Seas. For sources of data, see the individual sections on standing stocks and productivity. Chukchi area adjusted estimates account for the Barents Sea being 2.5 times the size of the Chukchi Sea.

Stock or production measured	Barents Sea	Chukchi Sea raw data	Chukchi Sea area-adjusted data
Fisheries removals (2010)	1.0×10^6 mt yr ⁻¹	0.0013×10^6 mt yr ⁻¹	
Fish stocks (5 most abundant species)	5.9×10^6 mt		0.25×10^6 mt
Nesting Seabirds (individuals)	8.0×10^6	1.8×10^6	4.6×10^6
Total seabirds (nesting plus non-breeding individuals)	16×10^6	9.6×10^6	24×10^6
Pinnipeds (individuals)	1.1×10^6	0.88×10^6	2.2×10^6
Cetaceans (individuals)	0.14×10^6	0.03×10^6	0.07×10^6
Benthos <100 m depth (Barents–no fjords)	671.8 ± 212.2 g m ⁻² wet biomass \pm SE	354.7 ± 57.4 g m ⁻² wet biomass \pm SE	
Benthos > 100 m depth	61.6 ± 7.9 g m ⁻² wet biomass \pm SE	510.1 ± 401.5 g m ⁻² wet biomass \pm SE	
Benthos, overall mean, wet biomass	166 g m ⁻²	381 g m ⁻²	
Crustacean zooplankton dry biomass	$6\text{--}7$ g m ⁻²	2.1 g C m ⁻²	
(Dalpadado et al., 2012a, 2012b; Hopcroft et al., 2010)			
Primary production (Walsh et al., 2005; Reigstad et al., 2011)	102 g C m ⁻² yr ⁻¹	100 g C m ⁻² yr ⁻¹	
Primary production (Arrigo et al., 2008)	109 Tg C yr ⁻¹	27 Tg C yr ⁻¹	66 Tg C yr ⁻¹
Export to benthos	$34\text{--}47\%$	56%	
% Total annual primary production			
(Reigstad et al., 2008; Campbell et al., 2009)			

bloom production is weak. In contrast, in the southern Barents Sea, stratification results from solar warming of ice-free Atlantic Water, and the spring bloom is more prolonged due to the relatively weak stratification that promotes nutrient availability. Following the spring-bloom, primary production is enhanced by storms that mix the surface waters down through the pycnocline, thereby re-infusing the upper mixed layers with nutrients. These differences within the Barents Sea and between the Barents Sea and the Chukchi Sea also contribute to the higher rates of fish production in the former, much of which occurs in the southern Atlantic portion of the Barents. The feeding migrations of fish into the northern Barents Sea in summer and the spawning migrations of fish out of the Barents to productive areas along the west coast of Norway also promote the productivity of Barents Sea fish stocks.

The Barents and Chukchi Seas are responding, and will continue to respond, to global warming. Both seas are likely to have shorter periods of ice cover and thinner ice. With the reductions in ice cover, both in terms of duration and thickness, there is likely to be an increase in the length of the productive season, though concomitant increases in primary production will depend not only on the availability of light, but also on availability of nutrients. If there is increased storm activity or weaker pycnoclines, then there may be more available nutrients, but there is no obvious reason to expect changes in the amounts of nutrients advected into these seas. In the Barents Sea, fish biomass may increase, as it has in the past. But in winter and spring, in the Chukchi Sea and the northern Bering Sea, the waters will likely remain cold. These cold waters are expected to remain a barrier to the northward movement of boreal fish species presently of commercial interest in the southeastern Bering Sea.

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References

- Aagaard, K., Carmack, E.C., 1989. The role of sea ice and other fresh water in the Arctic circulation. *J. Geophys. Res.* 94, 14485–14498.
- Aagaard, K., Roach, A.T., 1990. Arctic Ocean-shelf exchange: measurements in Barrow Canyon. *J. Geophys. Res.* 95, 18163–18175.
- Aars, J., Marques, T.A., Buckland, S.T., Andersen, M., Belikov, S., Boltunov, A., Wiig, Ø., 2009. Estimating the Barents Sea polar bear subpopulation size. *Mar. Mamm. Sci.* 25, 35–52.
- Ahlnäs, K., Garrison, G.R., 1984. Satellite and oceanographic observations of the warm coastal current in the Chukchi Sea. *Arctic* 37, 244–254.
- Allen, B.M., Angliss, R.P., 2012. Beluga whale (*Delphinapterus leucas*): Eastern Chukchi Sea stock. Alaska Marine Mammal Stock Assessments, 2011. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-234, pp. 70–74.
- Anker-Nilssen, T., Bakken, V., Strøm, H., Golovkin, A.N., Bianki, V.V., Tatarinkova, I.P. (Eds.), 2000. The status of marine birds breeding in the Barents Sea region: Norsk Polarinstittutt Rapportserie No., 113. Tromsø. 213pp.
- Anon, 2004. Survey Report from the joint Norwegian/Russian ecosystem survey in the Barents Sea in August–October 2004. IMR/PINRO Joint Report Series, No 3/2004, vol. 1. ISSN 1502–8828, 68pp.
- Anon, 2005. Survey Report from the joint Norwegian/Russian ecosystem survey in the Barents Sea in August–October 2005 (vol. 1). IMR/PINRO Joint Report Series, No 3/2005. ISSN 1502–8828, 99 pp.
- Antipova, T.V., 1975. Benthos biomass distribution of the Barents Sea. *Tr. PINRO* 35, 121–124 (in Russian).
- Arrigo, K.R., Matrai, P.A., Sudeshna Pabi, S., 2008. Impact of a shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.* 35, L19603. <http://dx.doi.org/10.1029/2008GL035028>.
- Arrigo, K.R., van Dijken, G., van Dijken, G.L., 2011. Primary productivity in the Arctic Ocean: impacts of complex optical properties and subsurface chlorophyll maxima on large-scale estimates. *J. Geophys. Res.* 116, C11022. <http://dx.doi.org/10.1029/2011JC007273>.
- Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., et al., 2012. Massive phytoplankton blooms under Arctic sea ice. *Science* 333, 1408. <http://dx.doi.org/10.1126/science.1215065>.
- Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., Van Keuren, D., 2003. Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep Sea Res.* 50, 1235–1261.
- Ashjian, C.J., Braund, S.R., Campbell, R.G., George, J.C., Kruse, J., Maslowski, W., Moore, S.E., Nicolson, C.R., Okkonen, S.R., Sherr, B.F., Sherr, E.B., Spitz, Y.H., 2010. Climate variability, oceanography, bowhead whale distribution, and Inupiat subsistence whaling near Barrow, Alaska. *Arctic* 63, 179–194.
- Auel, H., Klages, M., Werner, I., 2003. Respiration and lipid content of the Arctic copepod *Calanus hyperboreus* overwintering 1 m above the seafloor at 2300 m water depth in the Fram Strait. *Mar. Biol.* 143, 275–282.
- Baier, C.T., Napp, J.M., 2003. Climate-induced variability in *Calanus marshallae* populations. *J. Plankton Res.* 25, 771–782.
- Barber, W.E., Smith, R.L., Vallarino, M., Meyer, R.M., 1997. Demersal fish assemblages of the northeastern Chukchi Sea, Alaska. *Fish. Bull.* 95, 195–209.
- Bengtson, J.L., Hiruki-Raring, L.M., Simpkins, M.A., Boveng, P.L., 2005. Ringed and bearded seal densities in the eastern Chukchi Sea, 1999–2000. *Polar Biol.* 28, 833–845.
- Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B., Slagstad, D., 2005. Ocean temperature oscillations enforce the reappearance of blue mussels in Svalbard after 1000 years of absence. *Mar. Ecol. Prog. Ser.* 303, 167–175.

- Berline, L., Spitz, Y.H., Ashjian, C.J., Campbell, R.G., Maslowski, W., Moore, S.E., 2008. Euphausiid transport in the western Arctic Ocean. *Mar. Ecol. Prog. Ser.* 360, 163–178.
- Beszczynska-Möller, A., Woodgate, R.A., Lee, C., Melling, H., Karcher, M., 2011. A synthesis of exchanges through the main oceanic gateways to the Arctic Ocean. *Oceanography* 24, 82–99.
- Blachowiak-Samolyk, K., 2008. Contrasting zooplankton communities (Arctic vs. Atlantic) in the European Arctic Marginal Ice Zone. *Oceanologica* 50, 363–389.
- Blanchard, A.L., Feder, H.M., Hoberg, M.K., 2010. Temporal variability of benthic communities affected by a large earthquake and anthropogenic stressors, 1971–2007. *Mar. Environ. Res.* 69, 95–107.
- Blindheim, J., 1989. Cascading of Barents Sea bottom water into the Norwegian Sea. *Rapp. P.V. Reun. Cons. Int. Explor. Mer* 188, 49–58.
- Blindheim, J., Skjoldal, H.R., 1993. Effects of climate changes on the biomass yield of the Barents Sea, Norwegian Sea, and West Greenland Large Marine Ecosystems. In: Sherman, K., Alexander, L.M., Gold, B.D. (Eds.), *Large Marine Ecosystems: Stress, Mitigation and Sustainability*. AAAS, Washington D.C., U.S.A., pp. 185–198.
- Bluhm, B.A., Iken, K., Mincks-Hardy, S., Sirenko, B.I., Holladay, B.A., 2009. Community structure of epibenthic megafauna in the Chukchi Sea. *Aquat. Biol.* 7, 269–293.
- Bogstad, B., Ottersen, G., Michalsen, K., Nakken, O., 1998. Ambient temperature and distribution of north-east Arctic cod. *ICES J. Mar. Sci.* 55, 67–85.
- Booth, S., Zeller, D., 2008. Marine fisheries catches in Arctic Alaska. Fisheries Centre Research Report, University of British Columbia, 16. 59 pp.
- Bourke, R.H., Paquette, R.G., 1976. Atlantic water on the Chukchi shelf. *Geophys. Res. Lett.* 3, 629–632.
- Boveng, P.L., Bengtson, J.L., Buckley, T.W., Cameron, M.F., Dahle, S.P., Megrey, B.A., Overland, J.E., Williamson, N.J., 2008. Status review of the ribbon seal (*Histiophoca fasciata*). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-191. 115 pp.
- Bradbury, I.R., Hubert, S., Brent Higgins, B., Borza, T., Bowman, S., et al., 2010. Parallel adaptive evolution of Atlantic cod on both sides of the Atlantic Ocean in response to temperature. *Proc. R. Soc. B* 277, 3725–3734. <http://dx.doi.org/10.1098/rspb.2010.0985>.
- Braham, H.W., 1984. Distribution and migration of gray whales in Alaska. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), *The Gray Whale, Eschrichtius robustus*. Academic Press, Orlando, FL, pp. 249–266.
- Brueggeman, J.J., 1982. Early spring distribution of bowhead whales in the Bering Sea. *J. Wildl. Manage.* 46, 1036–1044.
- Burns, J.J., 1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi seas. *J. Mammal.* 51, 445–454.
- Burns, J.J., 1981. Bearded seal – *Erignathus barbatus* Erxleben, 1777. In: Ridgway, S.H., Harrison, R.J. (Eds.), *Handbook of Marine Mammals. : Seals, vol. 2*. Academic Press, New York, pp. 145–170.
- Burns, J.J., Frost, K.J., 1979. The Natural History and Ecology of the Bearded Seal, *Erignathus barbatus*. Alaska Department of Fish and Game. 77 pp.
- Cameron, M.F., Bengtson, J.L., Boveng, P.L., Jansen, J.K., Kelly, B.P., Dahle, S.P., Logerwell, E.A., Overland, J.E., Sabine, C.L., Waring, G.T., Wilder, J.M., 2010. Status review of the bearded seal (*Erignathus barbatus*). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-211. 246pp.
- Campbell, R.G., Sherr, E.B., Ashjian, C.J., Plourde, S., Sherr, B.F., Hill, V., Stockwell, D.A., 2009. Mesoplankton prey preference and grazing impact in the western Arctic Ocean. *Deep Sea Res. II* 56, 1274–1289.
- Carmack, E., Wassmann, P., 2006. Food webs and physical–biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. *Prog. Oceanogr.* 71, 446–477.
- Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B., Sakshaug, E., 2006. Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. *Prog. Oceanogr.* 71, 145–181.
- Carroll, G.M., George, J.C., Lowry, L.F., Coyle, K.O., 1987. Bowhead whale (*Balaena mysticetus*) feeding near Point Barrow, Alaska, during the 1985 spring migration. *Arctic* 40, 105–110.
- Carroll, M.L., Denisenko, S., Renaud, P.E., Ambrose, W.G., 2008. Benthic infauna of the seasonally ice-covered western Barents Sea: patterns and relationships to environmental forcing. *Deep Sea Res. II* 55, 2340–2351.
- Cavalieri, D., Thorsten, M., Comiso, J., 2004. Updated daily/AMSR-E/Aqua Daily L3 12.5 km Brightness Temperature, Sea Ice Concentration, & Snow Depth Polar Grids V002/. National Snow and Ice Data Center, Boulder, Colorado USA. Digital media.
- Christensen, I., Haug, T., Øien, N., 1992. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. *ICES J. Mar. Sci.* 49, 341–355.
- Clarke, J.T., Moore, S.E., Johnson, M.M., 1993. Observations on Beluga fall migration in the Alaskan Beaufort Sea, 1982–87, and northeastern Chukchi Sea, 1982–91. Reports of the International Whaling Commission, 43, pp. 387–396 (SC/44/SM2).
- Clement, J.L., Cooper, L.W., Grebmeier, J.M., 2004. Late winter water column and sea ice conditions in the northern Bering Sea. *J. Geophys. Res.* 109, C03022. <http://dx.doi.org/10.1029/2003JC002047>.
- Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The Regional Physical Oceanography. University of Washington Press, Seattle. 175pp.
- Cochrane, S.J.K., Denisenko, S.G., Renaud, P.E., Emblowa, C.S., Ambrose Jr., W.G., Ellingsen, I.H., Skarðhamar, J., 2009. Benthic macrofauna and productivity regimes in the Barents Sea – ecological implications in a changing Arctic. *J. Sea Res.* 61, 222–233.
- Codispoti, L.A., Flagg, C., Kelly, V., et al., 2005. Hydrographic conditions during the 2002 SBI process experiments. *Deep Sea Res. II* 52, 3199–3226. <http://dx.doi.org/10.1016/j.dsr2.2005.10.007>.
- Cota, G.F., Pomeroy, L.R., Garrison, W., Jones, P., Peters, F., Weingartner, T., 1996. Nutrients, primary production and microbial heterotrophy in the southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy. *Mar. Ecol. Prog. Ser.* 135, 247–258.
- Coyle, K.O., Eisner, L.B., Janout, M.A., Farley, E.V., Cieciel, K., 2011. Climate change in the southeastern Bering Sea: refining the oscillating control hypothesis. *Fish. Oceanogr.* 20, 139–156. <http://dx.doi.org/10.1111/j.1365-2419.2011.00574.x>.
- Dalpadado, P., Bogstad, B., 2004. Diet of juvenile cod (age 0–2) in the Barents Sea in relation to food availability and cod growth. *Polar Biol.* 27, 140–154.
- Dalpadado, P., Mowbray, F., in press. Comparative analysis of feeding ecology of capelin from two shelf ecosystems, off Newfoundland and in the Barents Sea. *Prog. Oceanogr.*
- Dalpadado, P., Ellertsen, B., Melle, W., et al., 2000. Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES J. Mar. Sci.* 57, 843–857. <http://dx.doi.org/10.1006/jmsc.2000>.
- Dalpadado, P., Ingvaldsen, R., Hassel, A., 2003. Zooplankton biomass variation in relation to climatic conditions in the Barents Sea. *Polar Biol.* 26, 233–241. <http://dx.doi.org/10.1007/s00300-002-0470-z>.
- Dalpadado, P., Ellertsen, B., Melle, W., Skjoldal, H.R., 2012a. Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the Nordic Seas. *Sarsia* 83, 103–116.
- Dalpadado, P., Ingvaldsen, R.B., Stige, L.C., Bogstad, B., Knutsen, T., Ottersen, G., Ellertsen, B., 2012b. Climate effects on Barents Sea ecosystem dynamics. *ICES J. Mar. Sci.* 69. <http://dx.doi.org/10.1093/icesjms/fss063>.
- Dehn, L.A., Sheffield, L.L., Follmann, E.H., Duffy, L.K., Thomas, D.L., O'Hara, D.M., 2007. Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biol.* 30, 167–181.
- Drinkwater, K.F., 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES J. Mar. Sci.* 62, 1627–1637.
- Drinkwater, K.F., Mueter, F., Friedland, K., Taylor, M., Hunt Jr., G.L., Hare, J., Melle, W., 2009. Recent climate forcing and physical oceanographic changes in Northern Hemisphere regions: a review and comparison of four marine ecosystems. *Prog. Oceanogr.* 81, 10–28.
- Drinkwater, K., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., 2010. On the processes linking climate to ecosystem changes. *J. Mar. Syst.* 79, 374–388.
- Drobysheva, S.S., 1994. The Barents Sea euphausiids and their role in the formation of fishing biological production. PINRO Press, Murmansk. 139 pp. (in Russian).
- Dunton, K.H., Goodall, J.L., Schonberg, S.V., Grebmeier, J.C., Maidment, D.R., 2005. Multi-decadal synthesis of benthic–pelagic coupling in the western arctic: role of cross-shelf advective processes. *Deep Sea Res. II* 52, 3462–3477.
- Dvoretzky, V.G., Dvoretzky, A.G., 2011. Copepod communities off Franz Josef Land (northern Barents Sea) in late summer of 2006 and 2007. *Polar Biol.* 34, 1231–1238. <http://dx.doi.org/10.1007/s00300-011-0977-2>.
- Edvardsen, A., Tande, K.S., Slagstad, D., 2003. The importance of advection on production of *Calanus finmarchicus* in the Atlantic part of the Barents Sea. *Sarsia* 88, 261–273.
- Eisner, L., Hillgruber, N., Martinson, E., Maselko, J., in review. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics 1 in the 2 northern Bering and southeast Chukchi Seas. *Polar Biol.*
- Ellingsen, I.H., Dalpadado, P., Slagstad, D., Loeng, H., 2008. Impact of climatic change on the biological production in the Barents Sea. *Clim. Change* 87, 155–175.
- Fair, L.F., Nelson, A., 1999. Southeast Chukchi Sea and Kotzebue Sound trawl survey, 1998. Regional Information Report No. 3A99-34. Alaska Dept. of Fish and Game, Commercial Fisheries Division, AYK Region, Anchorage, AK. 106 pp.
- Falk-Petersen, S., Hop, H., Budgell, W.P., Hegseth, E.N., Korsnes, R., Løyning, T.B., Ørbæk, J.B., Kawamura, T., Shirasawa, K., 2000. Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. *J. Mar. Syst.* 27, 131–159.
- Falk-Petersen, S., Nilssen, K.T., Wold, A., Dahl, T.M., 2004. Lipids and trophic linkages in harp seal (*Phoca goenlandica*) from the eastern Barents Sea. *Polar Res.* 23, 43–50.
- Fay, F.H., 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *North Am. Fauna* 74, 1–279.
- Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., Whitedge, T.E., 1994. The north-eastern Chukchi Sea: benthos–environmental interactions. *Mar. Ecol. Prog. Ser.* 111, 171–190.
- Feder, H.M., Jewett, S.C., Blanchard, A.L., 2007. Southeastern Chukchi Sea (Alaska) macro-benthos. *Polar Biol.* 30, 261–275.
- Fletcher, G.L., King, M.J., Kao, M.H., 1987. Low temperature regulation of antifreeze glycoprotein levels in Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 49, 516–522.
- Frost, B.W., 1974. *Calanus-marshallae*, a new species of *Calanus* copepod closely allied to sibling species *Calanus finmarchicus* and *Calanus glacialis*. *Mar. Biol.* 26, 77–99. <http://dx.doi.org/10.1007/BF00389089>.
- Gammelsrød, T., Leikvin, Ø., Lien, V., Budgell, W.P., Loeng, H., Maslowski, W., 2009. Mass and heat transports in the NE Barents Sea: observations and models. *J. Mar. Syst.* 75, 56–69.
- Gilbert, J.R., Fedoseev, G.A., Seagars, D., Razlivalov, E., LaChugin, A., 1992. Aerial census of Pacific walrus, 1990. USFWS R7/MMM Technical Report 92. 33 pp.
- Gjøseøter, H., 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia* 83, 453–496.
- Goddard, S.V., Kao, M., Fletcher, G.L., 1999. Population differences in antifreeze production cycles of juvenile Atlantic cod (*Gadus morhua*) reflect adaptations to overwintering environment. *Can. J. Fish. Aquat. Sci.* 56, 1991–1999. <http://dx.doi.org/10.1139/cjfas-56-11-1991>.
- Gradinger, R., 2009. Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. *Deep Sea Res. II* 56, 1201–1212.
- Grebmeier, J.M., 2012. Shifting patterns of life in the Pacific Arctic and Sub-Arctic seas. *Ann. Rev. Mar. Sci.* 4, 63–78.
- Grebmeier, J.M., McRoy, C.P., 1989. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. *Mar. Ecol. Prog. Ser.* 53, 79–91.

- Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. *Mar. Ecol. Prog. Ser.* 48, 57–67.
- Grebmeier, J.M., Feder, H.M., McRoy, C.P., 1989. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. *Mar. Ecol. Prog. Ser.* 51, 253–268.
- Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006a. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog. Oceanogr.* 71, 331–361.
- Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006b. A major ecosystem shift in the Northern Bering Sea. *Science* 311, 1461–1464. <http://dx.doi.org/10.1126/science.1121365>.
- Hameedi, J.M., 1978. Aspects of water column primary productivity in the Chukchi Sea during summer. *Mar. Biol.* 48, 37–46. <http://dx.doi.org/10.1007/BF00390529>.
- Hansell, D.A., Whitley, T.E., Goering, J.J., 1993. Patterns of nitrate utilization and new production over the Bering–Chukchi shelf. *Cont. Shelf Res.* 13, 601–627.
- Hargrave, B.T., Harding, G.C., Drinkwater, K.F., Lambert, T.C., Harrison, W.G., 1985. Dynamics of the pelagic food web in St. Georges Bay, southern Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.* 20, 221–240.
- Harris, C.L., Plueddemann, A.J., Gawarkiewicz, G.G., 1998. Water mass distribution and polar front structure in the western Barents Sea. *J. Geophys. Res.* 103 (C2), 2905–2917.
- Hegseth, E.N., 1998. Primary production of the northern Barents Sea. *Polar Res.* 17, 113–123.
- Highsmith, R.C., Coyle, K.O., 1992. Productivity of arctic amphipods relative to gray whale energy requirements. *Mar. Ecol. Prog. Ser.* 83, 141–150.
- Highsmith, R.C., Coyle, K.O., Bluhm, B.A., Konar, B., 2006. Gray whales in the Bering and Chukchi Seas. In: Estes, J., DeMaster, D.P., Doak, D.F., Williams, T.M., Brownell, R.L. (Eds.), *Whales, Whaling and Ocean Ecosystems*. University of California Press, Berkeley, California, pp. 303–313.
- Hill, V., Cota, G., 2005. Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002. *Deep Sea Res. II* 52, 3344–3354.
- Hill, V., Cota, G., Stockwell, D., 2005. Spring and summer phytoplankton communities in the Chukchi and Eastern Beaufort Seas. *Deep Sea Res. II* 52, 3369–3385.
- Hirche, H.J., Kosobokova, K.N., 2011. Winter studies on zooplankton in Arctic seas: the Storfjord (Svalbard) and adjacent ice-covered Barents Sea. *Mar. Biol.* 158, 2359–2376.
- Hjermann, D.Ø., Stenseth, N.C., Ottersen, G., 2007. Indirect climate forcing of the Barents Sea capelin: a cohort effect. *Mar. Ecol. Prog. Ser.* 273, 229–238.
- Hodal, H., Kristiansen, S., 2008. The importance of small-celled phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea. *Deep Sea Res. II* 55, 2176–2185.
- Hop, H., Poltermann, M., Lønne, O.J., Falk-Perersen, S., Korsnes, R., Budgell, W.P., 2000. Ice-amphipod distribution relative to ice density and under-ice topography in the northern Barents Sea. *Polar Biol.* 23, 357–367.
- Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A., 2010. Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep Sea Res. II* 57, 27–39.
- Hunt Jr., G.L., Megrey, B.A., 2005. Comparison of the biophysical and trophic characteristics of the Bering and Barents Seas. *ICES J. Mar. Sci.* 62, 1245–1255.
- Hunt Jr., G.L., Bakken, V., Mehllum, F., 1996. Marine birds in the marginal ice zone of the Barents Sea in late winter and spring. *Arctic* 49, 53–61.
- Hunt, G.L., Coyle, K.O., Eisner, L.B., Farley, E.V., Heintz, R.A., Mueter, F., Napp, J.M., et al., 2011. Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the oscillating control hypothesis. *ICES J. Mar. Sci.* 68, 1230–1243.
- Huse, G., Ellingsen, I., 2008. Capelin migrations and climate change – a modeling analysis. *Clim. Chang.* 87, 177–197.
- ICES (International Council for the Exploration of the Sea), 2008a. Report of the Arctic Fisheries Working Group 21–29 April 2008, Copenhagen, Denmark. *ICES CM 2008/ACOM: 01*. 531 pp.
- ICES (International Council for the Exploration of the Sea), 2008b. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals, 27–30 August 2008, Tromsø, Norway. *ICES CM 2008/ACOM 17*. 59 pp.
- ICES (International Council for the Exploration of the Sea), 2011. Report of the Arctic Fisheries Working Group. *ICES C. M.* 2011/ACOM: 05. 659 pp.
- Idelson, M.S., 1930. A preliminary quantitative evaluation of the bottom fauna of Spitsbergen Bank. *T. Morsk. Nauchn. Inst.* 4, 26–46 (in Russian).
- Ingvaldsen, R.B., 2005. Width of the North Cape Current and location of the Polar Front in the western Barents Sea. *Geophys. Res. Lett.* 32, L16603. <http://dx.doi.org/10.1029/2005GL023440>.
- Ingvaldsen, R.B., Asplin, L., Loeng, H., 2004. The seasonal cycle in the Atlantic transport to the Barents Sea during the years 1997–2001. *Cont. Shelf Res.* 24, 1015–1032.
- Jackson, J.M., Allen, S.E., McLaughlin, F.A., Woodgate, R.A., Carmack, E.C., 2011. Changes to the nearsurface waters in the Canada Basin, Arctic Ocean from 1993–2009: a basin in transition. *J. Geophys. Res.* 116, C10008. <http://dx.doi.org/10.1029/2011JC007069>.
- Jakobsen, M., 2002. Hypsometry and volume of the Arctic Ocean and its constituent seas. *Geochem. Geophys. Geosyst. Electron. J. Earth Sci.* 3 (5). <http://dx.doi.org/10.1029/2001GC000302> ISSN: 1525–2027. 18 pp.
- Johnson, M.L., Fiscus, C.H., Ostenson, B.T., Barbour, M.L., 1966. Marine mammals. In: Wilimovsky, N.J. (Ed.), *Environment of the Cape Thompson Region, Alaska*. U.S. Atomic Energy Commission, Division of Technical Information Exchange, Oak Ridge, Tennessee, pp. 887–924.
- Karnovsky, N.J., Kwasniewski, S., Weslawski, J.M., Walkuz, W., Beszcyska-Moller, A., 2003. Foraging behavior of little auks in a heterogeneous environment. *Mar. Ecol. Prog. Ser.* 253, 289–303.
- Knutsen, T., Dalpadado, P., 2011. Secondary production in the Barents Sea. *Fisken Havet* 1–120, 86–88 ISSN 0802 0620 1, (In Norwegian).
- Kondratyev, A.Ya., Litvinenko, N.M., Shibaev, Y.V., Vyatkin, P.S., Lubov, F., Kondratyeva, L.F., 2000. The breeding seabirds of the Russian Far East. In: Kondratyev, A.Ya., Litvinenko, N.M., Kaiser, G.W. (Eds.), *Seabirds of the Russian Far East. Special Publication*. Canadian Wildlife Service, Ottawa, pp. 37–81.
- Konyukhov, N.B., Bogoslovskaya, L.S., Zvonovi, B.M., van Pelt, T.I., 1998. Seabirds of the Chukotka Peninsula, Russia. *Arctic* 51, 315–329.
- Kovacs, K.M., Lydersen, C. (eds.), 2006. *Birds and mammals of Svalbard*. Polarhåndbok No. 13, Norwegian Polar Institute, Tromsø, Norway, Grafisk Nord AS, Finnsnes. 203 pp.
- Kovacs, K.M., Haug, T., Lydersen, C., 2009. Marine mammals of the Barents Sea. In: Sakshaug, E., Johnsen, G., Kovacs, K.M. (Eds.), *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim, pp. 453–496.
- Kovacs, K.M., Moore, S., Overland, J.E., Lydersen, C., 2011. Impacts of changing sea ice conditions on Arctic marine mammals. *Mar. Biodivers.* 41, 181–194.
- Kovacs, K.M., Michel, C., Bluhm, B., Gaston, T., Gradinger, R., Hunt, G.L., Moore, S., Renaud, P., Rysgaard, S., 2012. Chapter 9.3 – biological impacts of changes to sea ice. *Arctic Climate Change and the Cryosphere: Snow, Water, Ice, and Permafrost in the Arctic (SWIPA)*. AMAP, Oslo, pp. 32–51.
- Kristiansen, S., Farbot, T., Wheeler, P.A., 1994. Nitrogen cycling in the Barents Sea Seasonal dynamics of new and regenerated production in the marginal ice zone. *Limnol. Oceanogr.* 39, 1630–1642.
- Kulikoff, A.S., 1992. Characteristics of zooplankton communities. In: Nagel, P.A. (Ed.), *Results of the Third Joint US-USSR Bering and Chukchi Seas Expedition (BERPAC), Summer 1988*. U.S. Fish and Wildlife Service, Washington, pp. 161–172.
- Kwok, R., 2007. Near zero replenishment of the Arctic multiyear sea ice cover at the end of 2005 summer. *Geophys. Res. Lett.* 34, L05501. <http://dx.doi.org/10.1029/2006GL028737>.
- Kwok, R., Rothrock, D.A., 2009. Decline in Arctic sea ice thickness from submarine and ICES at records: 1958–2008. *Geophys. Res. Lett.* 36, L15501. <http://dx.doi.org/10.1029/2009GL039035>.
- Laake, J., Punt, A., Hobbs, R., Ferguson, M., Rugh, D., Breiwick, J., 2009. Re-analysis of grey whale southbound migration surveys 1967–2006. NOAA Technical Memorandum: NMFS-AFSC 203. 55 pp.
- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jorgensen, M.P., Ferguson, S.F., 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecol. Appl.* 18, S97–S125.
- Lane, P.V.Z., Llinás, L., Smith, S.L., Pilz, D., 2008. Zooplankton distribution in the western Arctic during summer 2002: hydrodynamic habitats and implications for food chain dynamics. *J. Mar. Syst.* 70, 97–133.
- Lee, S.H., Whitley, T.E., Kang, S.H., 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. *Cont. Shelf Res.* 27, 2231–2249.
- Lepore, K., Moran, S.B., Grebmeier, J.M., et al., 2007. *J. Geophys. Res. Oceans* 112 (C10), C10024. <http://dx.doi.org/10.1029/2006JC003555>.
- Leu, E., Soeride, J.E., Hessen, D.O., Falk-Petersen, S., Berge, J., 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Prog. Oceanogr.* 90, 18–32.
- Lind, S., Ingvaldsen, R.B., 2012. Variability and impacts of Atlantic Water entering the Barents Sea from the north. *Deep Sea Res. I* 62, 70–88.
- Loeng, H., 1979. A review of the sea ice conditions of the Barents Sea and the area west of Spitsbergen. *Fisken Havet* 2–1979, 29–75 (in Norwegian, abstract in English).
- Loeng, H., 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Res.* 10, 5–18.
- Loeng, H., Drinkwater, K., 2007. Climate variability and the ecosystems of the Barents and Norwegian Seas. *Deep Sea Res. II* 54, 2478–2500.
- Lowry, L.F., Frost, K.J., Davis, R., DeMaster, D.P., Suydam, R.S., 1998. Movements and behavior of satellite-tagged spotted seals (*Phoca largha*) in the Bering and Chukchi Seas. *Polar Biol.* 19, 221–230.
- Luken, L.P., Ogetov, G.N., Boyko, N.S., 2006. Ringed Seal Ecology in the White Sea. *UrO.RAN, Ekaterinburg*. 165 pp. (in Russian).
- Lunn, N.J., Schliebe, S., Born, E.W. (Eds.), 2002. *Polar bears: Proceedings of the 13th Working Meeting of the IUCN/SSC Polar Bear Specialist Group*. IUCN, Gland, Switzerland and Cambridge, UK. Vii + 153 pp.
- Lydersen, C., Kovacs, K.M., 2001. The world's northernmost population of harbour seals. *Ottar* 5, 34–40 (in Norwegian).
- Lydersen, C., Aars, J., Kovacs, K.M., 2008. Estimating the number of walrus in Svalbard from aerial surveys and behavioral data from satellite telemetry. *Arctic* 61, 119–128.
- Markus, T., Stroeve, J.C., Miller, J., 2009. Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. *J. Geophys. Res. Oceans* 114, C12024.
- Matsuno, K., Yamaguchi, T., Hirawake, T., Imai, I., 2011. Year to year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1993, and 2007, 2008. *Polar Biol.* 34, 1349–1360.
- McLaughlin, F., Carmack, E., Proshutinsky, A., Krishfield, R.A., Guay, C., Yamamoto-Kawai, M., Jackson, J.M., Williams, B., 2011. The rapid response of the Canada Basin to climate forcing: from bellwether to alarm bells. *Oceanography* 24 (3), 146–159. <http://dx.doi.org/10.5670/oceanog.2011.66>.
- McRoy, C.P., Goering, J., Shields, W., 1972. Studies in primary productivity in the eastern Bering Sea. In: Takenouti, A., et al. (Ed.), *Biological Oceanography of the Northern North Pacific Ocean*. Motoda Commemorative Volume. Idemitsu Shoten, Tokyo, pp. 199–216.
- Megrey, B.A., Aydin, K.Y., 2009. A macro descriptor perspective of ecological attributes for the Bering and Barents Seas. *Deep Sea Res. II* 56, 2132–2140.
- Mehlum, F., Gabrielsen, G.W., 1993. The diet of High-Arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. *Polar Res.* 12, 1–20.
- Mehlum, F., Hunt Jr., G.L., Klusek, Z., Decker, M.B., Nordland, N., 1996. The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard. *Polar Biol.* 16, 537–547.

- Mehlum, F., Hunt Jr., G.L., Decker, M.B., Nordlund, N., 1998. Hydrographic features, cetaceans and the foraging of thick-billed murres and other marine birds in the northwestern Barents Sea. *Arctic* 51, 243–252.
- Melle, W., Skjoldal, H.R., 1998. Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. *Mar. Ecol. Prog. Ser.* 169, 211–228. <http://dx.doi.org/10.3354/meps169211>.
- Miller, R.V., Johnson, J.H., Doroshenko, N.V., 1985. Gray whales (*Eschrichtius robustus*) in the Western Chukchi and East Siberian seas. *Arctic* 38, 58–60.
- Mizroch, S.A., Rice, D.W., Zwiefelhofer, D., Waite, J., Perryman, W.L., 2009. Distribution and movements of fin whales in the North Pacific Ocean. *Mamm. Rev.* 39, 193–227.
- Moore, S.E., Huntington, H.P., 2008. Arctic marine mammals and climate change: Impacts and resilience. *Ecol. Appl.* 18 (2 supplement), S157–S165. <http://dx.doi.org/10.1890/06-0571.1>.
- Moore, S.E., Clarke, J.T., Johnson, M.M., 1993. Beluga distribution and movements offshore northern Alaska in spring and summer, 1980–84. Reports of the International Whaling Commission, 43, pp. 375–386 (SC/44/SM1).
- Moore, S.E., George, J.C., Coyle, K.O., Weingartner, T.J., 1995. Bowhead whales along the Chukotka Coast in autumn. *Arctic* 48, 155–160.
- Moore, S.E., DeMaster, D.P., Dayton, P.K., 2000. Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic* 53, 432–477.
- Moore, S.E., George, J.C., Sheffield, G., Bacon, J., Ashjian, C.J., 2010. Bowhead whale distribution and feeding near Barrow, Alaska, in late summer 2005–06. *Arctic* 63, 195–205.
- Moran, S.B., Kelly, R.P., Hagstrom, K., et al., 2005. Seasonal changes in POC export flux in the Chukchi Sea and implications for water column–benthic coupling in Arctic shelves. *Deep Sea Res. II* 52, 3427–3451. <http://dx.doi.org/10.1016/j.dsr2.2005.09.011>.
- Mountain, D.G., Coachman, L.K., Aagaard, K., 1976. On the flow through Barrow Canyon. *J. Phys. Oceanogr.* 6, 461–470.
- Mueter, F.J., Broms, C., Drinkwater, K.F., Friedland, K.D., Hare, J.A., Hunt Jr., G.L., Melle, W., Taylor, M., 2009. Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems. *Prog. Oceanogr.* 81, 93–110.
- Nelson, R.J., Carmack, E.C., McLaughlin, F.A., Cooper, G.A., 2009. Penetration of Pacific zooplankton into the western Arctic Ocean tracked with molecular population genetics. *Mar. Ecol. Prog. Ser.* 381, 129–138.
- Nerini, M., 1984. A review of gray whale feeding ecology. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), *The Gray Whale, Eschrichtius robustus*. Academic Press, Inc., Orlando, FL, pp. 423–450.
- Nghiem, S.V., Rigor, I.G., Perovich, D.K., Clemente-Colon, P., Weatherly, J.W., Neumann, G., 2007. Rapid reduction of Arctic perennale sea ice. *Geophys. Res. Lett.* 34, L17501. <http://dx.doi.org/10.1029/2006GL027198>.
- Nilssen, K.T., Haug, T., 2007. Status of grey seals (*Halichoerus grypus*) in Norway. *NAMMCO Sci. Publ. Ser.* 6, 23–31.
- Nilssen, K.T., Haug, T., Potelov, V., Timoshenko, Y.K., 1995. Feeding habits of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents Sea. *Polar Biol.* 15, 485–493.
- Nilssen, K.T., Skavberg, N.-E., Poltermann, M., Haug, T., Härkönen, T., Henriksen, G., 2010. Status of harbour seals (*Phoca vitulina*) in mainland Norway. *NAMMCO Sci. Public Ser.* 8, 61–70.
- Norcross, B.L., Holladay, B.A., Busby, M.S., Mier, K.L., 2010. Demersal and larval fish assemblages in the Chukchi Sea. *Deep Sea Res. II* 57, 57–70.
- NPFMC (North Pacific Fishery Management Council), 2009. Fishery Management Plan for Fish Resources of the Arctic Management Area. North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK, 99501. 158 pp.
- Øien, N., 1993. *Lagenorhynchus* species in Norwegian waters as revealed from incidental observations and recent sighting surveys. Paper SC/48/SM15 to the IWC Scientific Committee, Aberdeen.
- Øien, N., 2009. Distribution and abundance of large whales in Norwegian and adjacent waters based on ship surveys 1995–2001. *NAMMCO Sci. Publ.* 7, 31–47.
- Olsen, A., Johannessen, T., Rey, F., 2003. On the nature of the factors that control spring bloom development at the entrance to the Barents Sea and their inter-annual variability. *Sarsia* 88, 379–393.
- Orlova, E.L., Rudneva, G.B., Renaud, P.E., Eiane, K., Savinov, V., Yurko, A.S., 2010. Climate impacts on feeding and condition of capelin (*Mallotus villosus*) in the Barents Sea: evidence and mechanisms from a 30-year data series. *Aquat. Biol.* 10, 105–118.
- Ottersen, G., Kim, S., Huse, G., Polovina, J., 2010. Major pathways by which climate may force marine fish populations. *J. Mar. Syst.* 79, 343–360.
- Ozhigin, K.O., Ingvaldsen, R.B., Loeng, H.L., Boitsov, V.D., Karsakov, A.I., 2011. Introduction to the Barents Sea. In: Jakobsen, T., Ozhigin, V.K. (Eds.), *The Barents Sea. Ecosystem, Resources, Management: Half a Century of Russian–Norwegian Cooperation*. Tapir Press, Trondheim, Norway, pp. 39–76.
- Panteleev, G., Nechaev, D.A., Proshutinsky, A., Woodgate, R., Zhang, J., 2010. Reconstruction and analysis of the Chukchi Sea circulation in 1990–1991. *J. Geophys. Res.* 115, C08023. <http://dx.doi.org/10.1029/2009JC005453>.
- Paquette, R.G., Bourke, R.H., 1974. Observations on the coastal current of Arctic Alaska. *J. Mar. Res.* 32, 195–207.
- Paquette, R.G., Bourke, R.H., 1981. Ocean circulation and fronts as related to ice melt-back in the Chukchi Sea. *J. Geophys. Res.* 86 (C5), 4215–4230.
- Parsons, A.R., Bourke, R.H., Muench, R.D., Chiu, C.S., Lynch, J.F., Miller, J.H., Plueddemann, A.J., Pawlowicz, R., 1996. The Barents Sea Polar Front in summer. *J. Geophys. Res.* 101 (C6), 14201–14221.
- Paul, J.M., Paul, A.J., Barber, W.E., 1997. Reproductive biology and distribution of the snow crab from the northeastern Chukchi Sea. In: Reynolds, J. (Ed.), *Fish Ecology in Arctic North America*. American Fisheries Society Symposium, 19. American Fisheries Society, Bethesda, Maryland, pp. 287–294.
- Pavshitsk, E.A., 1984. Zooplankton of the Chukchi Sea as indices of water origins. *Tr. Arkt. i Antarkt. Nauch-Issled. Int.*, 368, pp. 140–153 (in Russian).
- Pedersen, G., 1995. Factors influencing the size and distribution of the copepod community in the Barents Sea with special emphasis on *Calanus finmarchicus* (Gunnerus). Dr. Sci thesis, Norwegian College of Fishery Science, University of Tromsø, 89 pp.
- Pedersen, T., Fosshem, M., 2008. Diet of 0-group stages of capelin (*Mallotus villosus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) during spring and summer in the Barents Sea. *Mar. Biol.* 153, 1037–1046.
- Pedersen, G., Tande, K.S., Nilssen, E.M., 1995. Temporal and regional variation in the copepod community in the central Barents Sea during spring and early summer 1988 and 1989. *J. Plankton Res.* 17, 263–282.
- Piatt, J.F., Springer, A.M., 2003. Advection, pelagic food webs and the biogeography of Beringia. *Mar. Ornithol.* 31, 141–154.
- Piepenburg, D., Blackburn, T.H., von Dorrien, C.F., Gutt, J., Hall, P.O.J., Hulth, S., Kendall, M.A., Opalinski, K.W., Rachor, E., Schmid, M.K., 1995. Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea). *Mar. Ecol. Prog. Ser.* 118, 199–213.
- Pike, D., Vikingsson, G., Gunnlaugsson, T., Øien, N., 2009. A note on the distribution and abundance of blue whales (*Balaenoptera musculus*) in the Central and Northeast North Atlantic. *NAMMCO Sci. Publ. Ser.* 7, 19–29.
- Plourde, S., Campbell, R.G., Ashjian, C.J., Stockwell, D.A., 2005. Seasonal and regional patterns in egg production of *Calanus glacialis/marshallae* in the Chukchi and Beaufort Seas during spring and summer, 2002. *Deep Sea Res. II* 52, 3411–3426.
- Pörtner, H.-O., 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* 213, 881–893.
- Pörtner, H.-O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97. <http://dx.doi.org/10.1126/science.1135013>.
- Quakenbush, L.T., Citta, J.J., George, J.C., Small, R.J., Heide-Jørgensen, M.P., 2010a. Fall and winter movements of bowhead whales (*Balaena mysticetus*) in the Chukchi Sea and within a potential petroleum development area. *Arctic* 63, 289–307.
- Quakenbush, L.T., Small, R.J., Citta, J.J., 2010b. Satellite Tracking of Western Arctic Bowhead Whales. OCS Study BOEMRE 2010–033. 118 pp.
- Quast, J.C., 1974. Density distribution of juvenile Arctic cod, *Boreogadus saida*, in eastern Chukchi Sea in fall of 1970. *Fish. Bull.* 72, 1094–1105.
- Rand, K.M., Logerwell, E.A., 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. *Polar Biol.* 34, 475–488. <http://dx.doi.org/10.1007/s00300-010-0900-2>.
- Reeves, R., Rosa, C., George, J.C., Sheffield, G., Moore, M., 2011. Implications of Arctic industrial growth and strategies to mitigate future vessel and fishing gear impacts on bowhead whales. *Mar. Policy* 36, 454–462.
- Reigstad, M., Wassmann, P., Wexels Riser, C., Øygarden, S., Rey, F., 2002. Variations in hydrography, nutrients and chlorophyll *a* in the marginal ice zone and the central Barents Sea. *J. Mar. Syst.* 38, 9–29.
- Reigstad, M., Wexels Riser, C., Wassmann, P., Ratkova, T., 2008. Vertical export of particulate organic carbon: attenuation, composition and loss rates in the northern Barents Sea. *Deep Sea Res. II* 55, 2308–2319.
- Reigstad, M., Carroll, J., Slagstad, D., Ellingsen, I., Wassmann, P., 2011. Intra-regional comparison of productivity, carbon flux and ecosystem composition within the northern Barents Sea. *Prog. Oceanogr.* 90, 33–46.
- Renaud, P.E., Morata, N., Ambrose, W.G., Bowie, J.C., Chiuchio, A., 2007. Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. *J. Exp. Mar. Biol. Ecol.* 349, 248–260.
- Renaud, P.E., Morata, N., Carroll, M.L., Denisenko, S.G., Reigstad, M., 2008. Benthic–pelagic thtthcoupling in the western Barents Sea: processes and time scales. *Deep Sea Res. II* 55, 2372–2380. <http://dx.doi.org/10.1024/j.dsr2.2008.05.017>.
- Ressler, P.H., De Robertis, A., Warren, J.D., Smith, J.N., Kotwicki, S., 2012. Developing an acoustic survey of euphausiids to understand trophic interactions in the Bering 1998 sea ecosystem. *Deep Sea Res. II* 65–70, 184–195.
- Rey, F., Loeng, H., 1985. The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. In: Gray, J.S., Christiansen, M.E. (Eds.), *Marine Biology of Polar Regions and the Effects of Stress on Marine Organisms*. John Wiley, Chichester, pp. 49–63.
- Rey, F., Skjoldal, H.R., Slagstad, D., 1987. Primary production in relation to climatic changes in the Barents Sea. In: Loeng, H. (Ed.), *The Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea*. Bergen, Institute of Marine Research, pp. 29–46.
- Richard, P.R., Martin, A.R., Orr, J.R., 2001. Summer and autumn movements of belugas of the Eastern Beaufort Sea stock. *Arctic* 54, 223–236.
- Roach, A.T., Aagaard, K., Pease, C.H., Salo, S.A., Weingartner, T., Pavlov, V., Kulakov, M., 1995. Direct measurements of transport and water properties through the Bering Strait. *J. Geophys. Res.* 100 (C9), 18443–18457.
- Rose, G.A., 2007. *Cod: The Ecological History of North Atlantic Fisheries*. Breakwater Books, St. John's, NL, Canada. 587 pp.
- RUSALCA, 2009. Report on the execution of marine research in the Bering Strait, East Siberian and the Chukchi Sea by the Russian–American expedition under the program “RUSALCA” during the period from 23 August through 30 September, 2009. Accessed May 24, 2012, at: http://www.arctic.noaa.gov/aro/russian-american/2009/RUSALCA_2009_report.pdf.
- Ruzzante, D.E., Taggart, C.T., Cook, D., Goddard, S., 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. *Can. J. Fish. Aquat. Sci.* 53, 634–645.
- Ruzzante, D.E., Wroblewski, J.S., Taggart, C.T., Smedbol, R.K., Cook, D., Goddard, S.V., 2005. Bay-scale population structure in coastal Atlantic cod in Labrador and Newfoundland, Canada. *J. Fish Biol.* 56, 431–447.

- Sætersdal, G., Loeng, H., 1987. Ecological adaptation of reproduction in northeast Arctic cod. *Fish. Res.* 5, 253–270.
- Sætre, R. (Ed.), 2007. *The Norwegian Coastal Current – Oceanography and Climate*. Tapir Academic Press, Trondheim. 159 pp.
- Sakshaug, E., 2004. Primary and secondary production in the Arctic Seas. In: Stein, R., Macdonald, R.M. (Eds.), *The Organic Carbon Cycle in the Arctic Ocean*. Springer-Verlag, Heidelberg, pp. 57–81.
- Sakshaug, E., Johnsen, G., Kristiansen, S., von Quillfeldt, C., Rey, F., Slagstad, D., Thingstad, F., 2009. Phytoplankton and primary production. In: Sakshaug, E., Johnsen, G., Kovacs, K.M. (Eds.), *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim, pp. 167–207.
- Sambrotto, R.N., Goering, J.J., McRoy, C.P., 1984. Large yearly production of phytoplankton in the western Bering Strait. *Science* 225, 1147–1150. <http://dx.doi.org/10.1126/science.225.4667.1147>.
- Schauer, U., Loeng, H., Rudels, B., Ozhigin, V.K., Dieck, W., 2002. Atlantic Water flow through the Barents and Kara Seas. *Deep Sea Res.* 1 49, 2281–2298.
- Sea Around Us Project, 2011. <http://www.seaaroundus.org/lme/default.aspx> accessed on April 3, 2011.
- Shimada, K., Kamoshida, T., Itoh, M., Nishimo, S., Carmack, E., McLaughlin, F., Zimmermann, S., Proshutinsky, A., 2006. Pacific Ocean inflow: influence on catastrophic reduction of sea ice in the Arctic Ocean. *Geophys. Res. Lett.* 33, L08605. <http://dx.doi.org/10.1029/2005GL025624>.
- Sigler, M.F., Renner, M., Danielson, S.L., Eisner, L.B., Lauth, R.R., Kuletz, K.J., Logerwell, E.A., Hunt Jr., G.L., 2011. Fluxes, fins, and feathers: relationships among the Bering, Chukchi, and Beaufort Seas in a time of climate change. *Oceanography* 24, 250–265. <http://dx.doi.org/10.5670/oceanog.2011.77>.
- Sirenko, B.I., Kolutin, V.M., 1992. Characteristics of benthic biocoenoses of the Chukchi and Bering Seas. In: Nagel, P.A. (Ed.), *Results of the Third Joint US-USSR Bering & Chukchi Seas Expedition (BERPAC), Summer 1988*. US Fish and Wildlife Service, Washington DC, pp. 251–258.
- Skagseth, Ø., 2008. Recirculation of Atlantic Water in the western Barents Sea. *Geophys. Res. Lett.* 35, L11606. <http://dx.doi.org/10.1029/2008GL033785>.
- Skagseth, Ø., Drinkwater, K.F., Terrile, E., 2011. Wind- and buoyancy-induced transport of the Norwegian Coastal Current in the Barents Sea. *J. Geophys. Res.* 116, C08007. <http://dx.doi.org/10.1029/2011JC006996>.
- Skaug, H.J., Øien, N., Schweder, T., Bøthun, G., 2004. Abundance of minke whales (*Balaenoptera acutorostrata*) in the Northeastern Atlantic. *Can. J. Fish. Aquat. Sci.* 61, 870–886.
- Skern-Mauritzen, M., Johannessen, E., Børge, A., Oien, N., 2011. Baleen whale distributions and prey associations in the Barents Sea. *Mar. Ecol. Prog. Ser.* 426, 289–301.
- Skjoldal, H.R., Rey, F., 1989. Pelagic production and variability of the Barents Sea ecosystem. In: Sherman, K., Alexander, L.M. (Eds.), *Biomass Yields and Geography of Large Marine Ecosystems*. : AAAS selected Symposium, 111. Westview Press, Inc., Colorado, USA, pp. 241–286.
- Skjoldal, H.R., Hassel, A., Rey, F., et al., 1987. Spring phytoplankton development and zooplankton reproduction in the central Barents Sea in the period 1979–1984. In: Loeng, H. (Ed.), *The Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea*. Proceedings of the Third Soviet–Norwegian Symposium, Murmansk, 26–28 May 1986, pp. 59–89.
- Skjoldal, H.R., Gjøsæter, H., Loeng, H., 1992. The Barents Sea ecosystem in the 1980s – ocean climate, plankton, and capelin growth. *ICES Mar. Sci. Symp.* 195, 278–290.
- Slagstad, D., Wassmann, P., 1997. Climate change and carbon flux in the Barents Sea: 3D simulations of ice distribution, primary production and vertical export of particulate organic matter. *Mem. Natl. Inst. Polar Res. Spec. Issue* 51, 119–141.
- Slagstad, D., Ellingsen, I.H., Wassmann, P., 2011. Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. *Prog. Oceanogr.* 90, 117–131.
- Smedsrud, L.H., Ingvaldsen, R., Nilssen, J.E.Ø., Skagseth, Ø., 2010. Heat in the Barents Sea: transport, storage, and surface fluxes. *Ocean Sci.* 6, 219–234.
- Smetacek, V., 1980. Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight. *Ophelia* 1, 65–76 (Suppl.).
- Smith, S.L., Vidal, J., 1986. Variations in the distribution, abundance, and development of copepods in the southeastern Bering Sea in 1980 and 1981. *Cont. Shelf Res.* 5, 215–239.
- Sonina, M.A., 1969. Biology of the Arcto-Norwegian haddock during 1927–1965. *Trudy polyar. naucho-issled. Inst. morsk. ribb. Kohz. Okeanogr.*, 26: 3–111 and 115–124. *Fish. Res. Board. Can. Transl. Ser.*, 1924.
- Spall, M.A., 2007. Circulation and water mass transformation in a model of the Chukchi Sea. *J. Geophys. Res. Oceans* 112 (C5), C05025. <http://dx.doi.org/10.1029/2006JC003364>.
- Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea. 3. Patterns of Primary Production. *Cont. Shelf Sci.* 13, 575–599. [http://dx.doi.org/10.1016/0278-4343\(93\)90095-F](http://dx.doi.org/10.1016/0278-4343(93)90095-F).
- Springer, A.M., McRoy, C.P., Turco, K.R., 1989. The paradox of pelagic food webs in the northern Bering Sea—II. Zooplankton communities. *Cont. Shelf Res.* 9, 359–386.
- Springer, A.M., McRoy, C.P., Flint, M.V., 1996. The Bering Sea Green Belt: shelf-edge processes and ecosystem production. *Fish. Oceanogr.* 5, 205–223.
- Stafford, K., Esch, C., 2010. Report from the whale observation team. In: Woodgate, R. (Ed.), *RUSALCA 2010—Bering Strait Mooring Cruise Report*, pp. 29:44–32:44. Accessed on May 24, 2012 at: http://www.arctic.noaa.gov/aro/russian-american/2010/CruiseReportKhromov2010_verAug10.pdf.
- Stafford, K., Mussoline, S., 2011. Marine mammal and bird sightings RUSALCA 2011. In: Woodgate, R. (Ed.), *RUSALCA – Bering Strait AON 2011 Mooring Cruise Report*, pp. 40–49. Accessed on May 24, 2012 at: <http://www.arctic.noaa.gov/aro/russian-american/2011/Khromov2011CruiseReport.pdf>.
- Stempniewicz, L., Blachowiak-Samolyk, K., Węśławski, J.M., 2007. Impact of climate change on zooplankton communities, seabird populations and arctic terrestrial ecosystem—a scenario. *Deep Sea Res.* 54, 2934–2945.
- Stenevik, E.K., Sundby, S., 2007. Impacts of climate change on commercial fish stocks in Norwegian waters. *Mar. Policy* 31, 19–31.
- Stiansen, J.E., Korneev, O., Titov, O., Arnberg, P., Filin, A., Hansen, J.R., Høines, Å., Marasæv, S. (Eds.), 2009. *Joint Norwegian–Russian Environmental Status 2008. Report on the Barents Sea ecosystem. Part II—Complete Report: IMR/PINRO Joint Report Series, 2009 (3)*. 375 pp.
- Sundby, S., 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* 85, 277–298.
- Suydam, R.S., Lowry, L.F., Frost, K.J., O’Corry-Crowe, G.M., Pikok Jr., D., 2001. Satellite tracking of eastern Chukchi Sea beluga whales into the Arctic Ocean. *Arctic* 54, 237–243.
- Tande, K.S., 1991. *Calanus* in north Norwegian fiords and in the Barents Sea. *Polar Res.* 10, 389–407.
- Titov, O., Ozhigin, V., 2005. Climate variability, frontal zones, and recruitment to commercial fish stocks in the Barents Sea. In: Shibanov, V. (Ed.), *Ecosystem Dynamics and Optimal Long-term Harvest in the Barents Sea Fisheries*. Proceedings of the 11th Russian–Norwegian Symposiums. Murmansk, 15–17 August 2005. PINRO Press, Murmansk, pp. 31–41.
- USF&WS (U.S. Fish and Wildlife Service), 2003. *Beringian Seabird Colony Catalog—Computer Database*. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska, 99503. Beringian Seabird Colony Catalog Website: <http://alaska.fws.gov/mbsp/mbm/seabirds/colony/colony.htm>.
- Ver Hoef, J.M., Cameron, M.F., Boveng, P.L., London, J.M., Moreland, E.M., in review. A spatial hierarchical model for abundance of three ice-associated seal species in the Eastern Bering Sea. *Stat. Methodol.*
- Vernet, M., 1991. Phytoplankton dynamics in the Barents Sea estimated from chlorophyll budget models. *Polar Res.* 10, 129–145.
- Vetrov, A.A., Romankevich, E.A., 2011. Primary production and fluxes of organic carbon to the seabed in the Russian Arctic seas as a response to the recent warming. *Oceanology* 51, 255–266.
- Vinje, T., Kvambekk, Å.S., 1991. Barents Sea drift ice characteristics. *Polar Res.* 10, 59–68.
- Walsh, J.J., McRoy, C.P., Coachman, L.K., et al., 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter effecting AOU demands of the Arctic Ocean. *Prog. Oceanogr.* 22, 277–359.
- Walsh, J.J., Dieterle, D.A., Maslowski, W., Grebmeier, J.M., Whitley, T.E., Flint, M., Sukhanova, I.N., Bates, N., Cota, G.F., Stockwell, D., Moran, S.B., Hansell, D.A., McRoy, C.P., 2005. A numerical model of seasonal primary production within the Chukchi/Beaufort Seas. *Deep-Sea Res.* 52, 3541–3576.
- Wang, J., Cota, G.F., Comiso, J., 2005. Phytoplankton in the Beaufort and Chukchi Seas: distribution, dynamics, and environmental forcing. *Deep Sea Res.* 52, 3355–3368.
- Wang, M., Overland, J.E., Stabeno, P., 2012. Future climate of the Bering and Chukchi seas projected by global climate models. *Deep Sea Res.* 57, 46–57. <http://dx.doi.org/10.1016/j.dsr2.2012.02.022>.
- Wassmann, P., Slagstad, D., 1993. Seasonal and annual dynamics of particulate carbon flux in the Barents Sea. *Polar Biol.* 13, 363–372.
- Wassmann, P., Ratkova, T., Andreassen, I., et al., 1999. Spring bloom development in the marginal ice zone and the central Barents Sea. *Mar. Ecol. – Publ. Stn. Zool. Napoli* 20, 321–346. <http://dx.doi.org/10.1046/j.1439-0485.1999.2034081.x>.
- Wassmann, P., Reigstad, M., Haug, T., et al., 2006a. Food webs and carbon flux in the Barents Sea. *Prog. Oceanogr.* 71, 232–287.
- Wassmann, P., Slagstad, D., Wexels Riser, C., Reigstad, M., 2006b. Modeling the ecosystem dynamics of the marginal ice zone and central Barents Sea. II. Carbon flux and climate variability. *J. Mar. Sys.* 59, 1–24.
- Wassmann, P., Slagstad, D., Ellingsen, I., 2010. Primary production and climatic variability in the European sector of the Arctic Ocean prior to 2007: preliminary results. *Polar Biol.* 33, 1641–1650.
- Weingartner, T.J., Danielson, S., Sasaki, Y., Pavlov, V., Kulakov, M., 1999. The Siberian Coastal Current: a wind- and buoyancy-forced Arctic coastal current. *J. Geophys. Res.* 104, 29697–29713. <http://dx.doi.org/10.1029/1999JC00161>.
- Weingartner, T.J., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., Cavalieri, D., 2005. Circulation on the north central Chukchi Sea shelf. *Deep Sea Res.* 52, 3150–3174.
- Węśławski, J.M., Hacquebord, L., Stempniewicz, L., Malinga, M., 2000. Greenland whales and walrus in the Svalbard food web before and after exploitation. *Oceanologia* 42, 37–56.
- Whitehouse, A., 2011. Modeling the eastern Chukchi Sea food web with a mass-balance approach. Master’s thesis, School of Aquatic and Fishery Sciences, Univ. of Washington, Seattle, Washington, USA, 159 pp.
- Włodarska-Kowalczyk, M., Węśławski, J.M., Kotwicki, L., 1998. Spitsbergen glacial bays macrobenthos – a comparative study. *Polar Biol.* 20, 66–73.
- Wolotira, R.J., Sample, T.M., Morin Jr., M., 1977. Demersal fish and shellfish resources of Norton Sound, the southeastern Chukchi Sea, and adjacent waters in the baseline year 1976. U.S. Department of Commerce, NOAA-NMFS-NWAFRC Processed Report.
- Woodgate, R.A., Aagaard, K., 2005. Revising the Bering Strait freshwater flux into the Arctic Ocean. *Geophys. Res. Lett.* 32, L02602. <http://dx.doi.org/10.1029/2004GL021747>.
- Woodgate, R.A., Aagaard, K., Swift, J.H., Falkner, K.K., Smethie, W.M., 2005a. Pacific ventilation of the Arctic Ocean’s lower halocline by upwelling and diapycnal mixing over the continental margin. *Geophys. Res. Lett.* 32, L18609. <http://dx.doi.org/10.1029/2005GL023999>.
- Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005b. Monthly temperature, salinity, and transport variability of the Bering Strait throughflow. *Geophys. Res. Lett.* 32, L04601. <http://dx.doi.org/10.1029/2004GL021880>.
- Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005c. A year in the physical oceanography of the Chukchi Sea: moored measurements from autumn 1990–1991. *Deep Sea Res.* 52, 3116–3149.
- Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2006. Interannual changes in the Bering Strait fluxes of volume, heat and freshwater between 1991 and 2004. *Geophys. Res. Lett.* 33, L15609.

- Woodgate, R.A., Weingartner, T.J., Lindsay, R.W., 2010. The 2007 Bering Strait Oceanic Heat Flux and anomalous Arctic Sea-ice Retreat. *Geophys. Res. Lett.* 37, L01602. <http://dx.doi.org/10.1029/2009GL041621>.
- Wyllie-Echeverria, T., Barber, W.E., Wyllie-Echeverria, S., 1997. Water masses and transport of age-0 Arctic cod and age-0 Bering flounder into the Northeastern Chukchi Sea. In: Reynolds, J. (Ed.), *Fish Ecology in Arctic North America*: American Fisheries Society Symposium, 19, pp. 60–67. Bethesda, Maryland.
- Zeeman, S.F., 1992. The importance of primary production and CO₂. In: Nagel, P.A. (Ed.), *Results of the Third Joint US-USSR Bering and Chukchi Seas Expedition (BERPAC), Summer 1988*. U.S. Fish and Wildlife Service, Washington, DC, pp. 218–224.
- Zynyanov, S.V., 2000. Harbour seal (*Phoca vitulina*) of the Russian coast of the Barents Sea – contemporary status and population state. *Marine Mammals of the Holarctic*, 21–23 September 2000, Arkhangelsk, pp. 135–138.