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Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean

Zachary W. Brown* and Kevin R. Arrigo

Department of Environmental Earth System Science, Stanford University, 473 Via Ortega, Stanford, CA 94305, USA

**Corresponding author: tel: +1 650 7360688; fax: +1 650 7257344; e-mail: zwbrown@stanford.edu*

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Satellite remote sensing data were used to examine recent trends in sea-ice cover and net primary productivity (NPP) in the Bering Sea and Arctic Ocean. In nearly all regions, diminished sea-ice cover significantly enhanced annual NPP, indicating that light-limitation predominates across the seasonally ice-covered waters of the northern hemisphere. However, long-term trends have not been uniform spatially. The seasonal ice pack of the Bering Sea has remained consistent over time, partially because of winter winds that have continued to carry frigid Arctic air southwards over the past six decades. Hence, apart from the "Arctic-like" Chirikov Basin (where sea-ice loss has driven a 30% increase in NPP), no secular trends are evident in Bering Sea NPP, which averaged 288 ± 26 Tg C year^{-1} over the satellite ocean colour record (1998–2009). Conversely, sea-ice cover in the Arctic Ocean has plummeted, extending the open-water growing season by 45 d in just 12 years, and promoting a 20% increase in NPP (range 441–585 Tg C year^{-1}). Future sea-ice loss will likely stimulate additional NPP over the productive Bering Sea shelves, potentially reducing nutrient flux to the downstream western Arctic Ocean.

Keywords: Arctic Ocean, Bering Sea, primary production, remote sensing, sea-ice loss.

Introduction

Since the mid-20th century, the Arctic Ocean has experienced unprecedented sea-ice loss that has accelerated in recent years (Walsh and Chapman, 2001; Stroeve *et al.*, 2007). Declines are underway in all months of the year, but have been most severe in the boreal summer (Walsh and Chapman, 2001; Serreze *et al.*, 2007), potentially culminating in a seasonally ice-free Arctic well before the mid-21st century (Wang and Overland, 2009). A combination of factors appears to drive the attrition of the Arctic sea-ice pack, including increased flux of warm water into the Arctic Ocean (Maslowski *et al.*, 2001; Mizobata *et al.*, 2010), rising Arctic air temperatures (Lindsay and Zhang, 2005), and greater wind-driven advection of sea-ice out of Fram Strait (Serreze *et al.*, 2007). In turn, by reducing surface ocean albedo, diminished sea-ice cover allows greater penetration of shortwave solar radiation, thereby promoting enhanced melt in a positive feedback loop (Lindsay and Zhang, 2005; Perovich *et al.*, 2007). The recent observed decline in Arctic sea-ice extent has outpaced all global climate models participating in the Intergovernmental Panel on Climate Change Fourth Assessment Report (IPCC AR4; Stroeve *et al.*, 2007). This rapid sea-ice loss perturbs the Arctic Ocean's freshwater budget and large-scale circulation (ACIA, 2005; Peterson *et al.*, 2006), facilitates ocean-atmosphere flux of CO_2 (Bates and Mathis, 2009; Cai *et al.*, 2010), and erodes a crucial platform for the reproduction, foraging, and migration of many Arctic seabird and mammal species (Moline *et al.*, 2008).

Sea-ice dynamics are especially influential to the primary productivity regime of Arctic marine habitats. Over much of the Arctic Ocean's vast shallow continental shelf, brine rejection during sea-ice formation triggers convective mixing that replenishes nutrients into surface waters (Stabeno *et al.*, 2010). These nutrients are consumed in spring, when freshwater input from melting sea-ice stabilizes the surface ocean, leading to higher average mixed-layer light levels and the onset of the spring phytoplankton bloom at the ice-edge (Niebauer *et al.*, 1990). Sea-ice loss may disrupt these patterns of primary productivity, including the timing and magnitude of the spring bloom (ACIA, 2005). It also removes the platform for the growth of sea-ice algae, which may act as a seed population for the phytoplankton bloom as the ice-edge retreats north each spring (Spindler, 1994).

On the other hand, sea-ice loss creates additional open-water habitat for phytoplankton, whose growth is traditionally thought to be light-limited under the sea-ice cover (Hill and Cota, 2005; Loeng *et al*., 2005; Smetacek and Nicol, 2005). Area-normalized rates of CO_2 fixation in the ice-free zone are generally far higher than in adjacent sea-ice habitats (Arrigo, 2003), so sea-ice loss potentially leads to a more productive Arctic Ocean. For example, Arrigo *et al*. (2008a) demonstrated that pan-Arctic net primary production (NPP) in 2007, a year of exceptionally low sea-ice cover, was 23% greater than the 1998–2002 mean. This increase was attributed both to a protracted growing season (70% of change) and to the opening of new waters that were historically perennially ice-covered (30% of change). The implications of a more productive Arctic Ocean are still unclear, but shifts in surface productivity may affect pelagic–benthic coupling (Michel *et al*., 2006), foodweb structure (Piepenburg, 2005), and CO_2 uptake in Arctic waters (Bates and Mathis, 2009).

Whereas sea-ice loss and enhanced productivity have characterized the Arctic Ocean over recent years, counterintuitively, the Bering Sea has not conformed to this pattern. Brown *et al*. (2011) showed that the seasonal ice pack of the Bering Sea has not contracted since 1979, with warming generally limited to summer when the Bering Sea is ice-free. This fact has enormous economic implications, because the Bering Sea currently provides nearly half the US fishery annual take (Overland and Stabeno, 2004), the bulk being walleye pollock (*Theragra chalcogramma*), a species with great dependence on climate conditions (Hunt *et al*., 2002, 2011). Furthermore, Brown *et al*. (2011) showed that unlike the Arctic Ocean, primary production in the Bering Sea has not increased during recent years.

In their studies of trends in sea-ice and primary production, Arrigo and van Dijken (2011) and Brown *et al*. (2011) considered the Arctic Ocean and Bering Sea separately. In reality, these regions share at least two vital connections: the first is the predominantly northward flow of ~0.8 Sv from the Bering Sea into the Arctic Ocean, controlling the fluxes of heat, salt, and nutrients into the western Arctic (Woodgate and Aagaard, 2005). Without the nutrient-rich Anadyr stream flowing through western Bering Strait, productivity in the Chukchi Sea and, to a lesser extent, the East Siberian and Beaufort Seas, would be much reduced (Springer and McRoy, 1993; Codispoti *et al*., 2005). The second connection is the cold northerly Arctic winter winds that generally oppose the oceanic flow through Bering Strait (Woodgate *et al*., 2005) and drive sea-ice formation in the Bering Sea (Stabeno *et al*., 2007). Hence, these two seasonally productive, seasonally ice-covered regions can influence each other greatly, and trends in both should be considered when assessing northern hemispheric ecosystem change.

Here, we utilize satellite and reanalysis data to compare and contrast recent trends of sea-ice and NPP in the Arctic Ocean and Bering Sea. Recent work suggests basic differences in their behaviour, namely that the Bering Sea has heretofore resisted much of the rapid change currently gripping the Arctic (Arrigo and van Dijken, 2011; Brown *et al*., 2011). We explore this puzzling geographic difference in greater detail, examining regional winds as a possible explanation for the lack of Bering Sea ice loss. We define various geographic sectors and assess whether any part of the Bering Sea has conformed to the Arctic pattern of secular sea-ice loss and enhanced productivity. For those that have not, we examine interannual variability in sea-ice and NPP, asking whether these areas are likely to become more productive if sea-ice is lost in the future. Finally, given that the Bering Sea is a key source of nutrients to the western Arctic Ocean, we assess whether Bering Sea productivity is connected to productivity downstream, with particular attention given to the transition regions: the Chirikov Basin south of the Bering Strait and the Chukchi Sea to the north. The overarching goal is to clarify where sea-ice has changed and how it affects phytoplankton productivity in the ice-covered seas of the northern hemisphere.

Methods

Daily maps of NPP for the Bering Sea (all waters between the Aleutian Arc and the Bering Strait) and Arctic Ocean (all waters north of the Arctic Circle; Figure 1) were produced from satellite-derived chlorophyll *a* (hereafter Chl *a*), sea surface temperature (SST), and sea-ice cover using the algorithm of Arrigo *et al*. (2008b) as modified by Pabi *et al*. (2008).

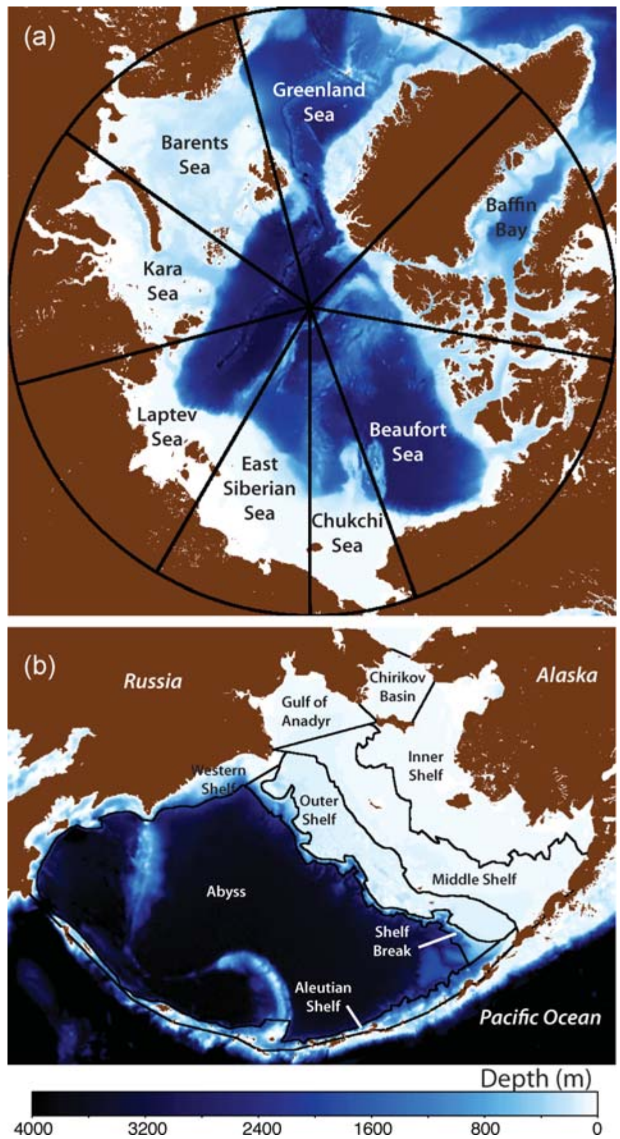

Figure 1. Bathymetric map of the study area delineating geographical sectors of (a) the Arctic Ocean, defined as all waters north of the Arctic Circle, and (b) the Bering Sea.

To characterize spatial differences, the Arctic Ocean was subdivided into eight geographic sectors demarcated by longitude, as described in Arrigo and van Dijken (2011), including the Chukchi (180–160°W), Beaufort (160–100°W), Baffin (100–45°W), Greenland (45°W to 15°E), Barents (15–55°E), Kara (55–105°E), Laptev (105–150°E), and Siberian sectors (150°E to 180°; Figure 1a). Similarly, the Bering Sea was subdivided into nine geographic sectors, as described in Brown *et al*. (2011). These included the Western Shelf, Abyss, Aleutian Shelf, Eastern Shelfbreak, Outer Shelf, Middle Shelf, Inner Shelf, Gulf of Anadyr, and Chirikov Basin sectors (Figure 1b).

NCEP/NCAR reanalysis data

Daily 2-m surface air temperatures (SATs) and the *u* and *v* components of 10 m wind velocities at 2.5° resolution were obtained from the NCEP/NCAR Reanalysis project (NOAA-ESRL, Boulder, CO, USA; http://www.esrl.noaa.gov/psd/data/reanalysis/) for the period 1948–2009. NCEP/NCAR reanalysis 10-m wind data have been validated in the Bering Sea and accurately reproduce offshore windspeed and direction to within 5% (Ladd and Bond, 2002).

Algorithm input data

Chlorophyll a

For the years 1998 through 2007, surface Chl *a* concentrations were determined from Level 3 (8-d binned, 9 km resolution) of the most recently reprocessed SeaWiFS ocean colour data (Reprocessing R2009.1) using the OC4v6 algorithm (http://oceancolor.gsfc.nasa.gov/REPROCESSING/R2009/ocv6/), a modified version of the OC4v4 algorithm (O'Reilly *et al*., 1998). For the years 2008 and 2009, surface Chl *a* concentrations were determined from Level 3 MODIS Aqua ocean colour data (Reprocessing R2009.1) using the OC3Mv6 algorithm (O'Reilly *et al*., 2000). Despite the recent reprocessing of both SeaWiFS and MODIS ocean colour data, which brought the global mean Chl *a* retrieval from the two sensors closer together, an analysis of the mean Chl *a* concentrations in Arctic waters between 2003 and 2007 (for which both SeaWiFS and MODIS Aqua data are available) shows that SeaWiFS-derived Chl *a* concentrations still exceed those from MODIS Aqua by ~2.6%. Therefore, to construct a 12-year time-series of NPP that was based on both SeaWiFS and MODIS Aqua data, daily NPP was calculated using SeaWiFS Chl *a* data for the years 1998 through 2007. Then, for 2008 and 2009 (for which limited SeaWiFS data are available), we used MODIS Aqua Chl *a* data as the algorithm input, but adjusted the resulting NPP estimates using region-specific correction factors based on the linear regression relating MODIS to SeaWiFS during the period of sensor overlap (2003–2007).

Nearshore Chl *a* pixels suspected of being contaminated by sediment or CDOM from river discharge, as identified by their anomalously high concentration of Chl *a* (relative to coastal pixels not influenced by rivers) or high remote-sensing reflectance in the red and near-infrared wavelengths, were removed for Arctic waters, which reduced the pan-Arctic NPP by <10%. For Bering Sea waters, suspect Chl *a* pixels were replaced by the daily mean of valid pixels within the same region of interest (Brown *et al*., 2011).

It should be noted that utilizing satellite-derived Chl *a* neglects algal production within and under sea-ice, which is not visible to ocean colour sensors, and whose prevalence and contribution to annual NPP is not currently well understood. Hence, NPP values reported herein should be considered conservative.

Sea surface temperature

Daily SST is based on the Reynolds Optimally Interpolated SST Version 2 product (Reynolds *et al*., 2002) obtained from NOAA (http://www.emc.ncep.noaa.gov/research/cmb/sst_analysis/).

Sea-ice cover

For Bering Sea waters, daily sea-ice concentrations at 25 km gridded resolution over the period 1979–2009 were obtained from the National Snow and Ice Data Center (NSIDC), which were derived from the Scanning Multichannel Microwave Radiometer and the Special Sensor Microwave/Imager (SSM/I) using the NASA Team algorithm (Cavalieri *et al*., 2008). For Arctic waters, sea-ice cover was estimated from SSM/I 37 and 85 GHz bands using the Polynya Signature Simulation Method (PSSM) algorithm (Markus and Burns, 1995), which allows determination of sea-ice presence/absence at 6.25 km resolution. According to this algorithm, a given pixel is defined as being ice-covered wherever the sea-ice concentration is >10%.

The date of sea-ice retreat was defined as the date when open-water area in a specified region of interest rose above a given threshold: in the Bering Sea and its regions of interest, this threshold was 90% of the total area, but for the Arctic Ocean and its regions of interest, this threshold was 50% of the average annual open-water amplitude for that region (see Arrigo and van Dijken, 2011). Similarly, the date of sea-ice advance was defined as the date when open-water area fell back below that threshold. The length of the open-water season (or phytoplankton growing season) is defined as the number of days elapsed between the date of sea-ice retreat and the date of sea-ice advance. Winter was defined as January–March, spring as April–June, summer as July–September, and autumn as October–December.

Results

Trends in open water

The mean annual open-water area has undergone no significant long-term changes in the Bering Sea since 1979 ($p = 0.51$; Figure 2a). Although there has been pronounced interannual variability over the satellite record, the mean annual open-water area averaged 2.11×10^6 km^2, equivalent to >90% of the Bering Sea's total area, reflecting the fact that the Bering Sea becomes completely ice-free each summer. Therefore, the length of the open-water season has also remained constant in the Bering Sea at 231 ± 27 d ($p = 0.56$; Figure 2b). This pattern is driven mainly by trends over the broad eastern continental shelf, which harbours >60% of the Bering Sea's ice-cover each year. We observed no significant long-term changes in the length of the open-water season in the inner ($p = 0.84$), middle ($p = 0.27$), or outer shelf sectors ($p = 0.16$). However, the Chirikov Basin, located north of St Lawrence Island, did exhibit a significant trend of reduced sea-ice. Since 1979, the mean open-water area in the Chirikov Basin has increased significantly by >1300 km^2 decade^{-1} ($p < 0.01$; Figure 2c). There was a corresponding increase in the length of the open-water season of >8 d decade^{-1} ($p = 0.01$; Figure 2d), driven mainly by the timing of sea-ice advance, which was delayed by 4.6 ± 2.1 d decade^{-1} ($p = 0.03$), indicating a later autumn transition in the Chirikov Basin.

In the Arctic Ocean to the north, trends in open water were more striking. In the Chukchi Sea north of Bering Strait, the mean annual open-water area increased by ~10^4 km^2 year^{-1} between 1998 and 2009 ($p = 0.01$; Figure 3a). Meanwhile, the

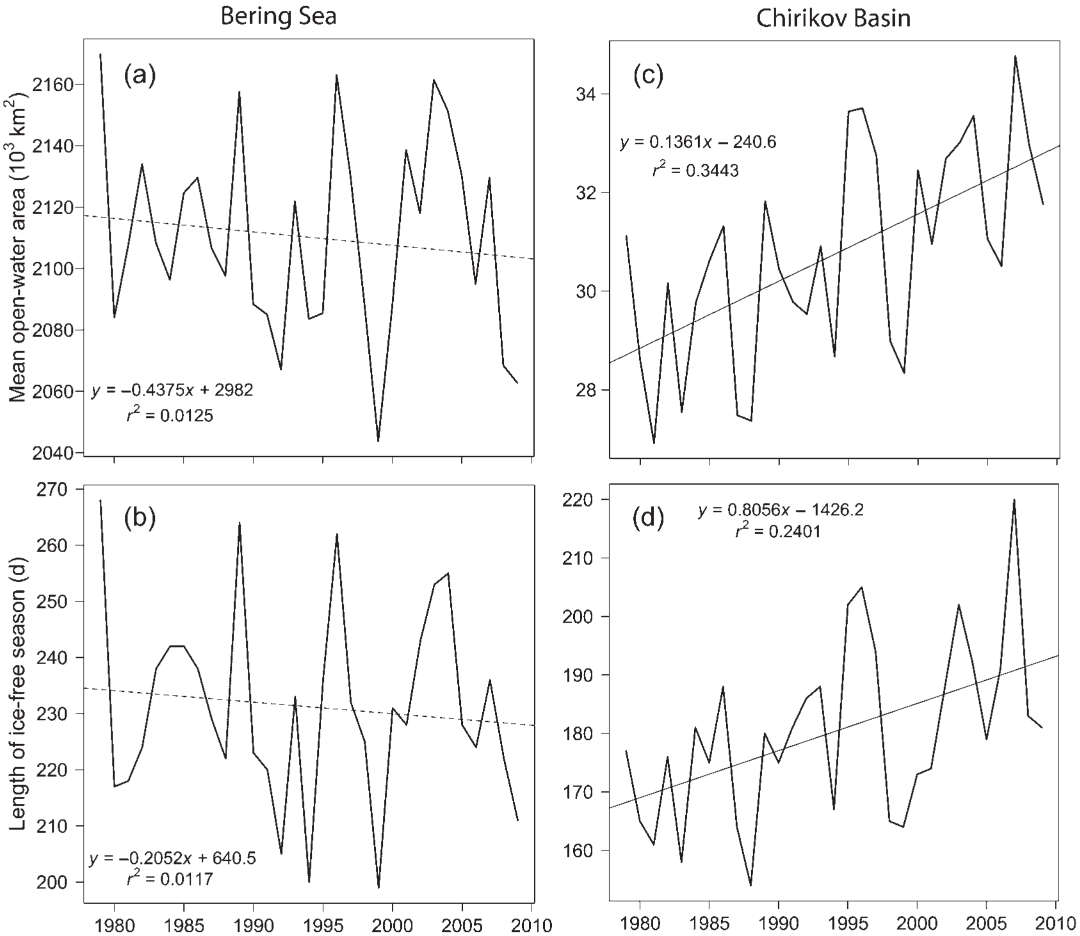

Figure 2. Long-term trends in the mean annual open water area and the length of the ice-free season in (a and b) the Bering Sea and (c and d) the Chirikov Basin over the satellite sea-ice record (1979–2009). Solid regression lines indicate significance at the $p = 0.05$ level, and dashed lines indicate a lack of significance.

open-water season expanded by ~4.5 d year^{-1}, more than five times the rate of change in the Chirikov Basin ($p = 0.03$; Figure 3b, Table 1). Overall, we observed a significant trend towards longer open-water season in five of the eight sectors of the Arctic Ocean, also including the Barents, Kara, East Siberian, and Baffin sectors (but not the Greenland, Laptev, or Beaufort sectors). The largest of these was in the Barents sector, where the open-water season was prolonged by a remarkable 12.5 d year^{-1} ($p = 0.01$).

As a whole, the Arctic Ocean has seen an annual increase in the mean open-water area of ~80 000 km^2 between 1998 and 2009, with $>1.1 \times 10^6$ km^2 more annual mean open-water area in 2007 than in 1998 (Figure 3c, Table 2). This rapid shift in open-water area was accompanied by shifts in the timing and duration of the open-water season: sea-ice retreated 2.4 d earlier each year ($p < 0.01$) and advanced 1.4 d later ($p < 0.01$), expanding the phytoplankton growing season at the unprecedented rate of nearly 4 d year^{-1} between 1998 and 2009 (Figure 3d). The earliest sea-ice retreat (26 June), latest advance (8 November), and longest growing season (135 d) in the Arctic Ocean over this period came in the extreme low-ice year of 2007 (Figure 3d, Table 1).

Given the difference in recent open-water trends between the Bering Sea and Arctic Ocean, it is perhaps unsurprising that there was no relationship between open-water area in the Bering Sea and that in either the neighbouring Chukchi Sea or the pan-Arctic Ocean (Figure 4a and b). Even 2007, a year of extreme sea-ice loss in the Arctic, was not an abnormally low-ice year in the Bering Sea (Figure 4a). Open water in the Chirikov Basin, however, was significantly related to open water in both the Chukchi Sea and the pan-Arctic Ocean (Figure 4c and d).

Atmospheric forcing in the Bering Sea

To assess why the trend in open water area in the Bering Sea is so different from that of the Arctic Ocean, we examined regional winds, which are known to drive sea-ice formation in the Bering Sea (Pease, 1980; Stabeno *et al.*, 2007). Sea-ice extent was a strong function of wind direction: during years when winds were more northerly (i.e. more Arctic in nature), sea-ice concentrations over the Bering Sea middle shelf sector were up to fourfold greater than in years when winds were more easterly ($p < 0.01$; Figure 5a). Similarly, wind direction exerted strong control over SAT. Years with northerly winter winds were associated with winter SATs that were as much as 10°C colder (indicating the presence of frigid Arctic air) than years with easterly winter winds ($p < 0.01$; Figure 5b). However, despite high inter-annual variability, winter winds have not changed direction since 1948, generally being east-northeasterly (oriented at ~205° from due east on average; $p = 0.75$; Figure 5c). An extremely rapid

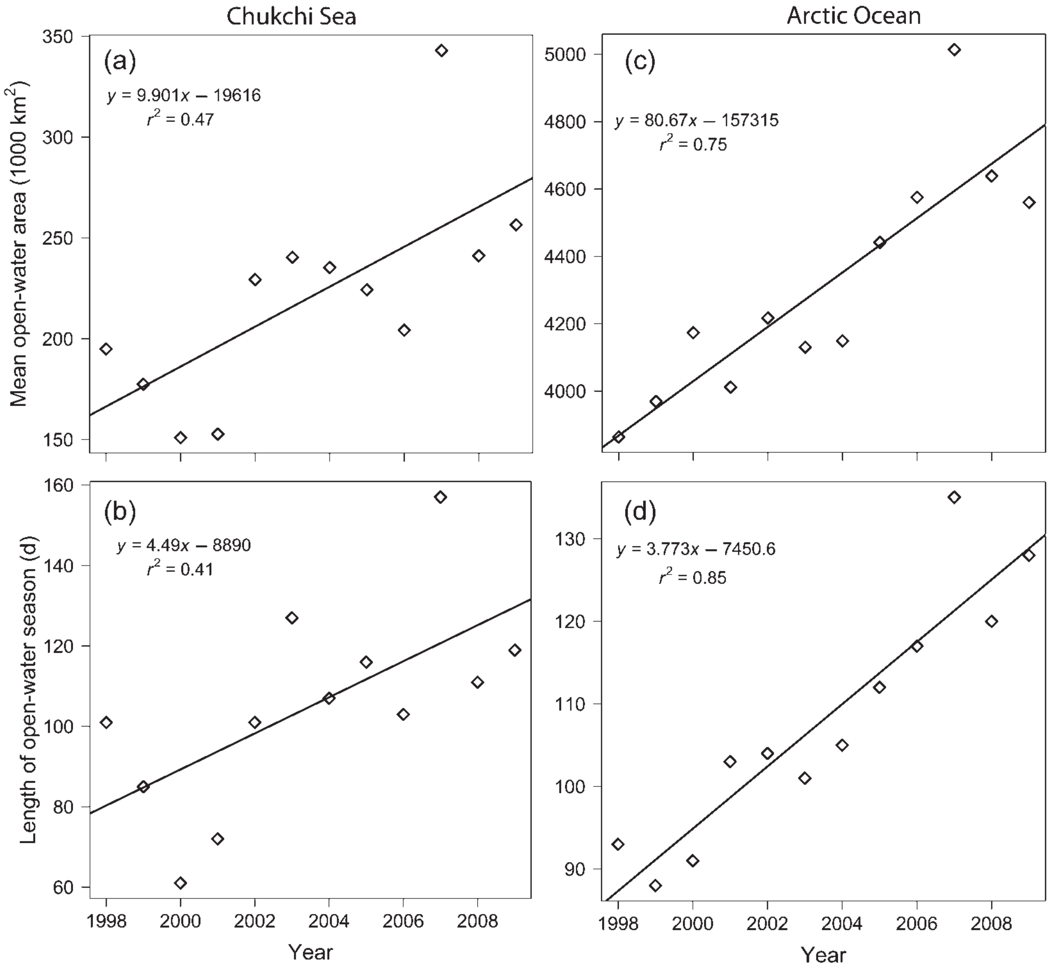

Figure 3. Long-term trends in the mean annual open water area and the length of the ice-free season in (a and b) the Chukchi Sea and (c and d) the Arctic Ocean over the ocean colour record (1998–2009). Solid regression lines indicate significance at the $p = 0.05$ level.

Table 1. Length of open water season (d) in different geographic sectors of the Arctic Ocean.

Year	Greenland	Barents	Kara	Laptev	Siberian	Chukchi	Beaufort	Baffin	Arctic
1998	134	129	56	52	13	101	140	102	93
1999	147	171	68	79	34	85	85	108	88
2000	115	210	117	77	33	61	56	123	91
2001	138	193	124	35	27	72	50	119	103
2002	162	152	76	65	88	101	76	141	104
2003	142	143	75	90	83	127	108	144	101
2004	176	177	104	29	56	107	79	120	105
2005	96	253	112	96	91	116	90	124	112
2006	136	312	120	91	71	103	93	148	117
2007	115	314	127	92	115	157	143	131	135
2008	145	270	129	64	71	111	133	135	120
2009	150	223	133	97	79	119	106	133	128
Mean	138.0	212.3	103.4	72.3	63.4	105.0	96.6	127.3	108.1
s.d.	21.6	63.3	27.1	23.5	30.9	25.2	30.6	14.0	14.7

transition from northerly (Arctic) to easterly winds is apparent in the 1970s, reflecting the North Pacific "regime shift" of 1976/1977 that was accompanied by a drastic reduction in Bering Sea ice extent (Ebbesmeyer *et al*., 1991; Hunt *et al*., 2002), although this shift was clearly not part of a long-term trend (Figure 5c). The constancy of winter wind direction over time implies that sea-ice extent in that region has not contracted in the past six decades.

Accordingly, winter SATs have not warmed in any sector of the Bering Sea since 1948 (Figure 6a). In fact, in the Abyss, the largest sector of the Bering Sea, winter SATs have cooled significantly at a rate of -0.12 ± 0.05°C decade^{-1} ($p = 0.03$) over this period. In

Table 2. Mean annual open water area (10^6 km^2) in different geographic sectors of the Arctic Ocean.

Year	Greenland	Barents	Kara	Laptev	Siberian	Chukchi	Beaufort	Baffin	Arctic
1998	1.60	0.99	0.17	0.10	0.05	0.19	0.34	0.43	3.86
1999	1.68	1.09	0.21	0.16	0.08	0.18	0.20	0.38	3.97
2000	1.65	1.23	0.33	0.17	0.08	0.15	0.14	0.42	4.17
2001	1.63	1.21	0.35	0.08	0.07	0.15	0.13	0.40	4.01
2002	1.69	1.15	0.25	0.14	0.14	0.23	0.18	0.45	4.22
2003	1.69	1.03	0.20	0.17	0.17	0.24	0.20	0.45	4.13
2004	1.71	1.16	0.31	0.07	0.12	0.24	0.16	0.39	4.15
2005	1.64	1.21	0.40	0.22	0.19	0.22	0.16	0.41	4.44
2006	1.68	1.34	0.37	0.18	0.14	0.20	0.17	0.48	4.58
2007	1.64	1.30	0.42	0.25	0.34	0.34	0.29	0.44	5.01
2008	1.67	1.23	0.43	0.13	0.18	0.24	0.35	0.42	4.64
2009	1.65	1.23	0.43	0.21	0.15	0.26	0.21	0.42	4.56
Mean	1.66	1.18	0.32	0.16	0.14	0.22	0.21	0.42	4.31
s.d.	0.03	0.10	0.09	0.06	0.08	0.05	0.08	0.03	0.34

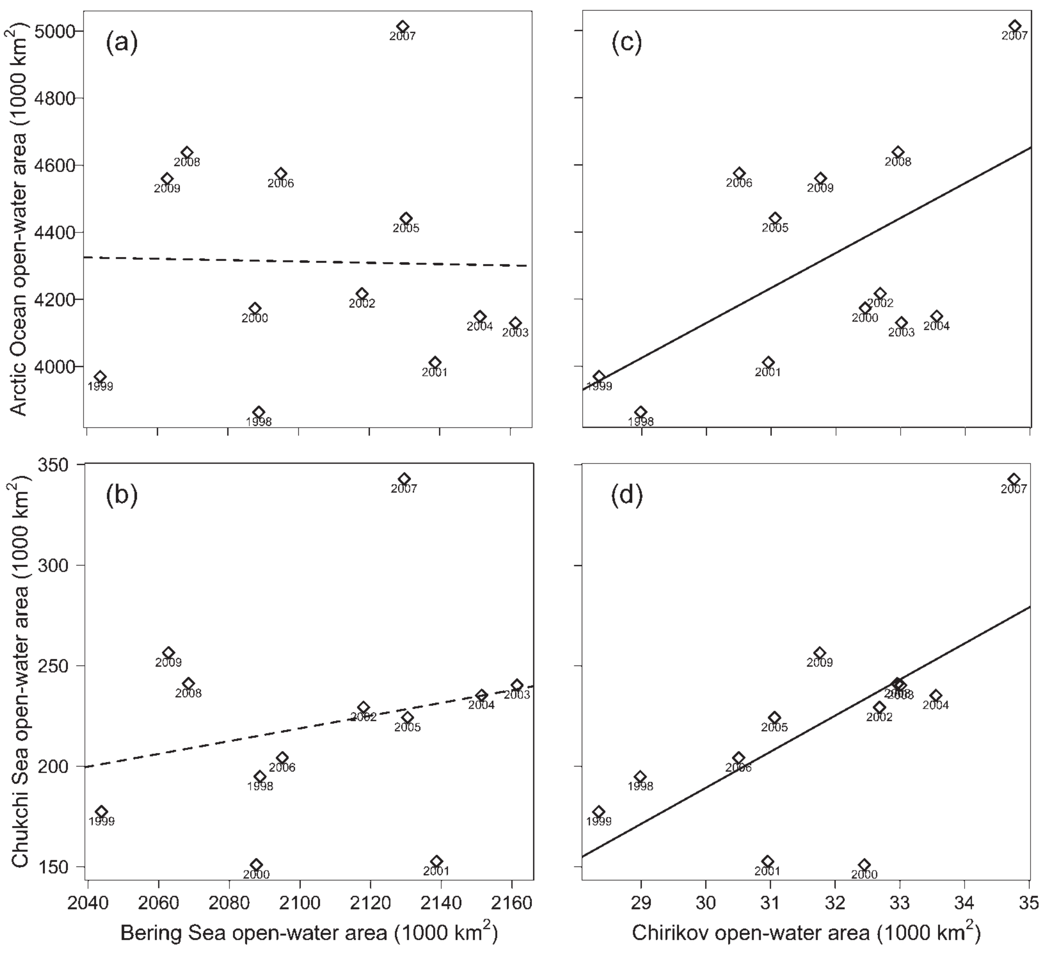

Figure 4. Comparison of the mean annual open-water extent in the Pacific Arctic and Subarctic seas, 1998–2009. (a) Arctic Ocean vs. Bering Sea; (b) Chukchi Sea vs. Bering Sea; (c) Arctic Ocean vs. Chirikov Basin; (d) Chukchi Sea vs. Chirikov Basin. Solid regression lines indicate significance at the $p = 0.05$ level, and dashed lines indicate a lack of significance.

stark contrast, summer SATs have warmed significantly over the entire Bering Sea except the southernmost sector, the Aleutian Shelf (Figure 6b). In many sectors, this summer warming appeared modest until the onset of an extremely warm period in the early 2000s; however, particularly dramatic summer warming is evident in the northern reaches of the Bering Sea, specifically the

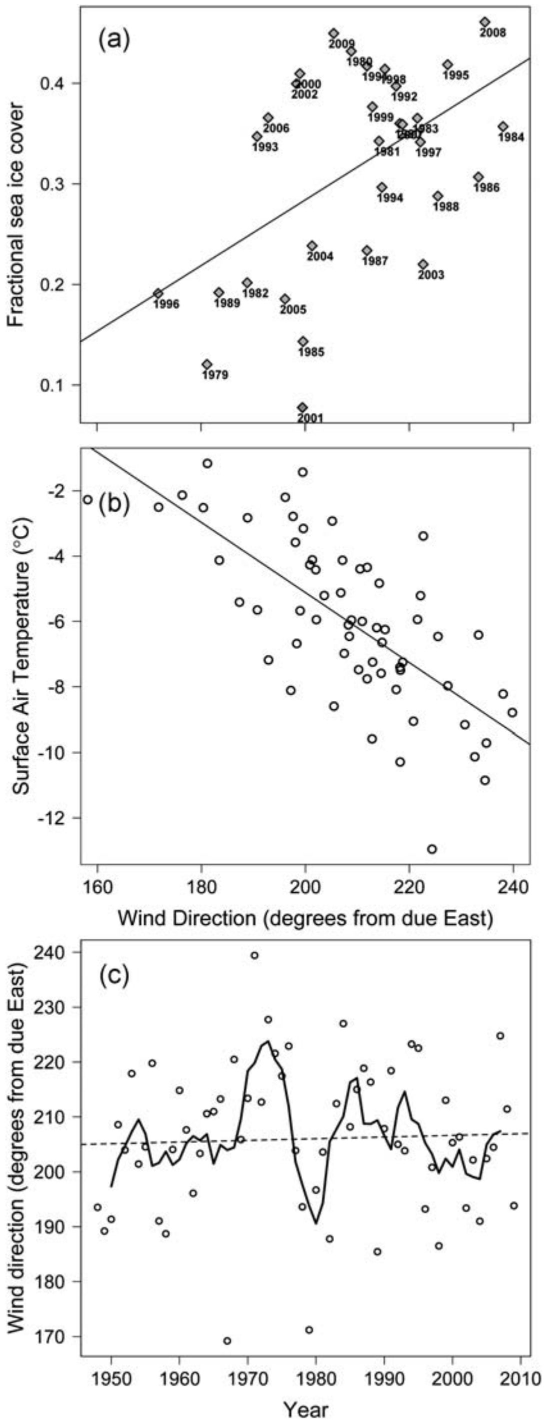

Figure 5. Mean winter wind direction vs. (a) mean fractional sea-ice cover, 1979–2009, and (b) mean winter SAT, 1948–2009. (c) Mean winter/spring wind direction over time, superimposed with a 5-year running mean. Wind direction increases anticlockwise from due east, such that 90° indicates due north (southerly winds), 180° due west (easterlies), and 270° due south (northerlies). Solid regression lines indicate significance at the $p = 0.05$ level, and dashed lines indicate a lack of significance. All data are from the Bering Sea middle-shelf sector, representative of the Bering Sea's broad eastern shelf which harbours >60% of the Bering Sea's ice cover each year.

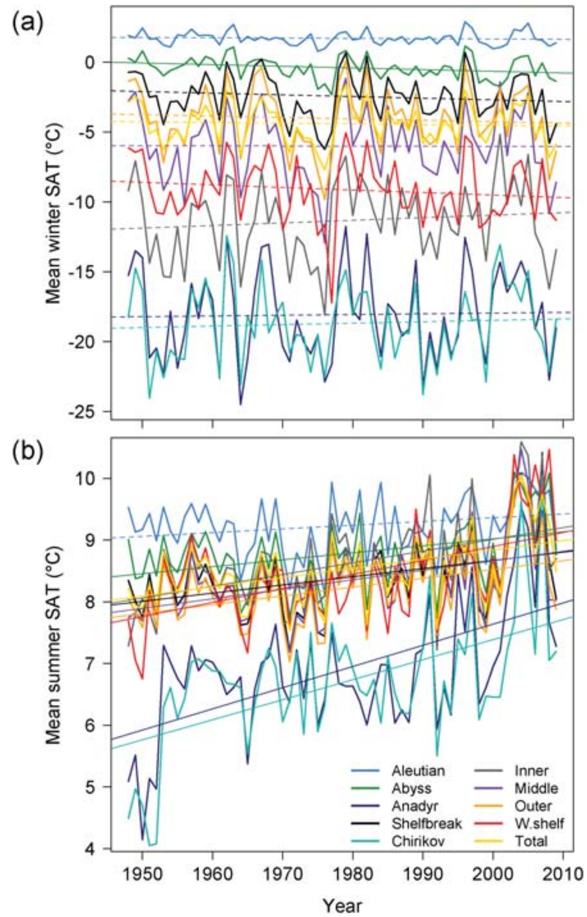

Figure 6. Mean NCEP/NCAR reanalysis 2 m SATs for (a) winter (January–March) and (b) summer (July–September). Solid regression lines indicate significance at the $p = 0.05$ level, and dashed lines indicate a lack of significance.

Gulf of Anadyr and the Chirikov Basin. Whereas the Bering Sea as a whole has warmed by only 0.15 ± 0.03°C decade^{-1} in summer ($p < 0.01$), the Gulf of Anadyr and Chirikov Basin have experienced more than double this rate of warming (0.34 ± 0.03°C decade^{-1}, $p < 0.01$; 0.32 ± 0.06°C decade^{-1}, $p < 0.01$, respectively). In 1950, summer temperatures in the Gulf of Anadyr and Chirikov Basin were >3°C cooler than all other sectors of the Bering Sea, but in summer 2007, these were two of the three warmest sectors in the Bering Sea, with temperatures >10°C (Figure 6b).

Open water and NPP

Although there is no long-term trend in the duration of the Bering Sea open-water season, interannual variations influenced annual NPP significantly. For example, the open-water season was 56 d longer in 2004 than in 1999, which increased Bering Sea annual NPP by 42%, from 233 to 331 Tg C (Figure 7). Open-water season and NPP are correlated in the Bering Sea (largely driven by these two years), with each additional day of open water promoting ~1 Tg C more NPP ($p = 0.03$; Figure 7). There is a similar correlation between sustained open water and enhanced NPP in nearly all sectors of the Bering Sea, including the

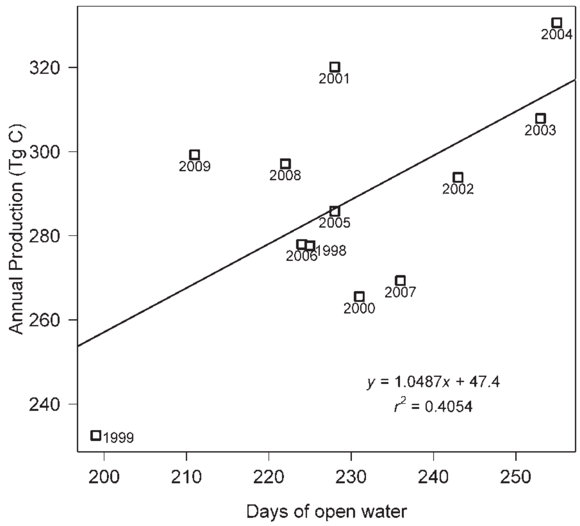

Figure 7. Annual NPP vs. the length of the open-water season in the Bering Sea over the satellite ocean colour record, 1998–2009.

Western Shelf ($p < 0.01$), the Shelf Break ($p = 0.04$), the Inner ($p = 0.03$), Middle ($p < 0.01$), and Outer Shelf regions ($p < 0.01$), and the Chirikov Basin ($p < 0.01$). Ignoring the Abyss and Aleutian Shelf sectors (whose open-water seasons last the entire year), the only sector where the length of the open-water season had no significant impact on NPP was the Gulf of Anadyr ($p = 0.15$).

Similar to the Bering Sea, the duration of the open water season was also significantly correlated with annual NPP in nearly all Arctic Ocean sectors (Figure 8), illustrating the primary dependence of pan-Arctic NPP on the amount of time available for phytoplankton growth. The relationship between annual NPP and open-water season was strongest in the three sectors influenced by Pacific inflow from the Bering Strait: the Chukchi, Siberian, and Beaufort sectors. Meanwhile, this relationship was weakest in the three sectors on the Atlantic side of the Arctic: the Greenland, Barents, and Baffin sectors (Figure 8). Baffin Bay and the Greenland Sea were the only Arctic sectors where the duration of the open-water season was not significantly correlated with annual NPP (Figure 8). This is likely because of the large expanse of perennially open water in the Atlantic Arctic sectors, which allowed them to dominate in terms of total production (the Greenland, Barents, and Baffin sectors accounted for 64% of pan-Arctic NPP; Table 3), but also meant that sea-ice loss had relatively little impact on NPP in these sectors.

Pacific Arctic NPP comparison

In addition to the impact of open water, we also assessed the impact that Bering Sea NPP has on NPP downstream in the Arctic Ocean. If high NPP in the Bering Sea deprives the western Arctic of essential nutrients flowing through the Bering Strait, western Arctic productivity should be diminished, resulting in a negative relationship between Bering Sea and Arctic NPP. However, there was no significant relationship between NPP in the Bering Sea and NPP in the Chukchi Sea or pan-Arctic Ocean (Figure 9a and b). NPP in the Chirikov Basin also did not conform to this hypothesis, being positively correlated with NPP in the downstream Chukchi Sea and Arctic Ocean (Figure 9c and d).

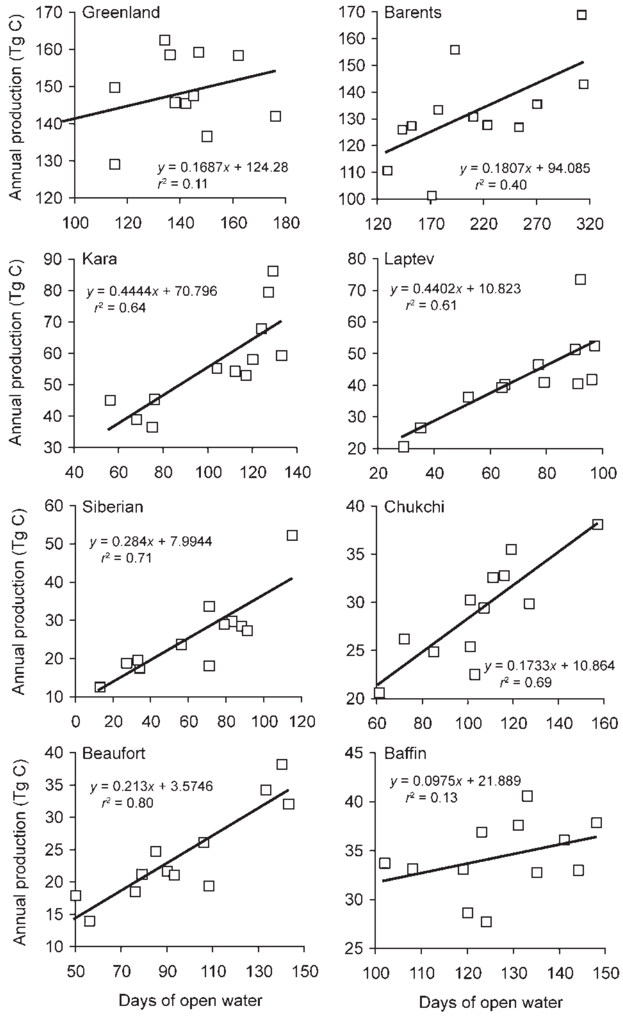

Figure 8. Regressions of annual NPP vs. the length of the open water season in each of the eight geographic sectors of the Arctic Ocean. The relationship is significant at the $p = 0.05$ level in all but the Greenland and Baffin sectors.

Secular trends in NPP

Secular trends in NPP tended to be driven by trends in the duration of the open-water season. For example, in the Bering Sea, where there was no significant change in the duration of the open-water season, there was also no trend in annual NPP over the 12-year ocean-colour record ($p = 0.34$; mean 288 ± 26 Tg C year^{-1}; Figure 10a). Conversely, in the Chirikov Basin where the growing season lengthened significantly, annual NPP also rose by >2 Tg C, an increase of 33% (Figure 10b).

Trends were similar in the Arctic Ocean, where the secular trend of sea-ice loss was positively correlated with a secular rise in NPP in the Chukchi (Figure 10c), Kara, and East Siberian Seas, as well as the pan-Arctic Ocean (Figure 10d). The largest secular increases in NPP came in the Kara and Siberian sectors (+2.7 and +1.9 Tg C year^{-1}, respectively), with the Siberian change amounting to a remarkable 135% increase from 1998 to 2009 (Arrigo and van Dijken, 2011). With a mean value of 493 ± 42 Tg C year^{-1}, annual pan-Arctic NPP rose by 8.1 Tg C each year, producing a 20% total increase in pan-Arctic NPP over this 12-year period (Figure 10d; Table 3).

Table 3. Annual net primary production (Tg C year^{-1}) in different geographic sectors of the Arctic Ocean.

Year	Greenland	Barents	Kara	Laptev	Siberian	Chukchi	Beaufort	Baffin	Arctic
1998	162.7	110.9	45.3	36.5	12.6	25.4	38.2	33.8	465.5
1999	159.4	101.4	39.1	41.1	17.6	24.9	24.7	33.2	441.5
2000	149.8	130.9	53.0	46.7	19.7	20.7	14.0	36.9	471.8
2001	145.8	156.1	68.1	26.6	18.9	26.3	18.0	33.1	492.9
2002	158.5	127.5	45.6	40.4	28.6	30.3	18.6	36.1	485.5
2003	145.7	126.1	36.7	51.4	29.8	29.9	19.5	33.0	472.2
2004	142.2	133.7	55.4	20.7	23.8	29.5	21.3	28.7	455.2
2005	134.4	126.9	54.5	42.0	27.4	32.9	21.7	27.8	467.6
2006	158.7	169.1	58.2	40.6	18.2	22.6	21.2	37.9	526.4
2007	129.1	143.2	79.5	73.5	52.4	38.2	32.1	37.6	585.6
2008	147.6	135.6	86.2	39.4	33.8	32.7	34.3	32.8	545.7
2009	136.7	127.9	59.4	52.6	29.1	35.6	26.2	40.6	509.5
Mean	147.6	132.4	56.8	42.6	26.0	29.1	24.1	34.3	493.3
s.d.	10.8	18.0	15.1	13.3	10.4	5.3	7.3	3.8	41.7

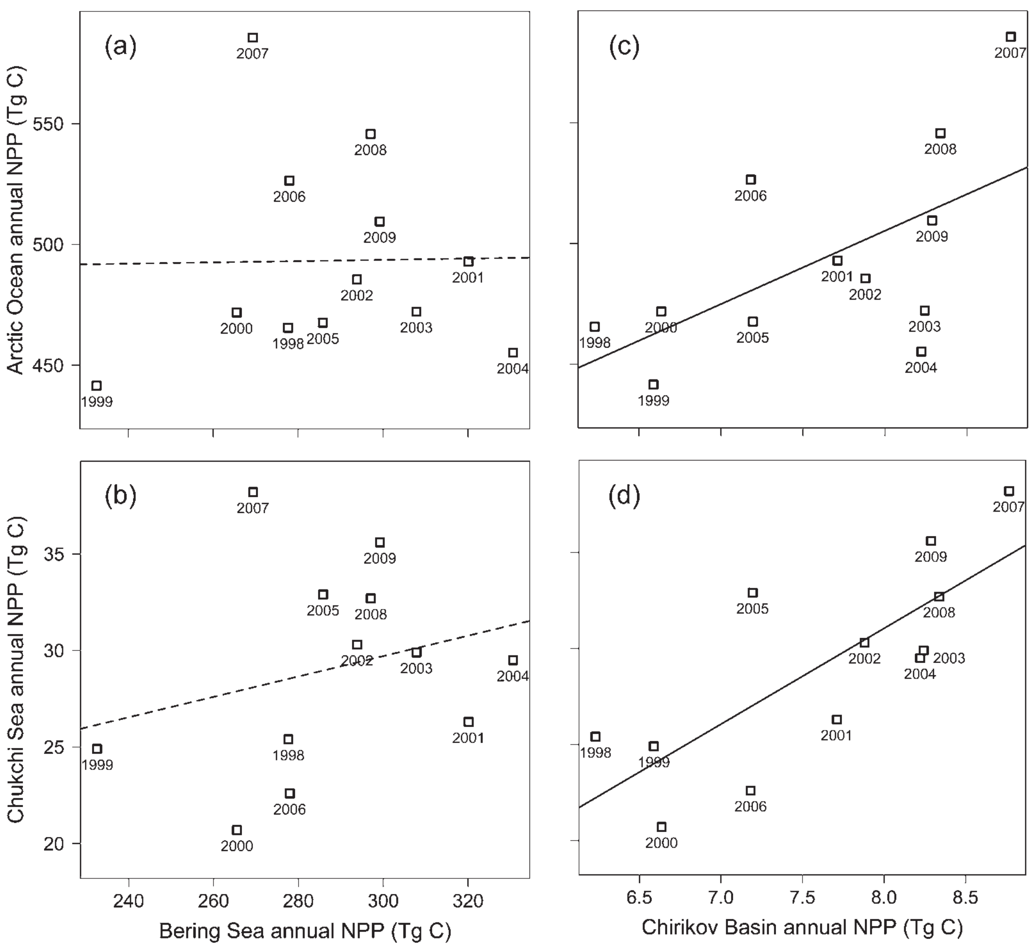

Figure 9. Comparison of annual NPP in Pacific Arctic and Subarctic seas, 1998–2009. (a) Arctic Ocean vs. Bering Sea; (b) Chukchi Sea vs. Bering Sea; (c) Arctic Ocean vs. Chirikov Basin; (d) Chukchi Sea vs. Chirikov Basin. Solid regression lines indicate significance at the $p = 0.05$ level, and dashed lines indicate a lack of significance.

However, although secular changes in NPP generally corresponded to open-water changes, this was not true in all sectors. First, the Greenland sector was anomalous in having a small but significant decline in NPP over time ($p = 0.03$), despite there being no significant change in the duration of the open-water season. This is likely because in the Greenland Sea, ice-cover is generally low and therefore has little impact on annual NPP. Second, the Gulf of Anadyr experienced a large secular rise in NPP (50% over the period 1998–2009; $p < 0.01$; Figure 10b), also with no change in the duration of the open-water season ($p = 0.14$). The reason for this change is unclear, but it may have to do with changes in the high-nutrient Anadyr Stream

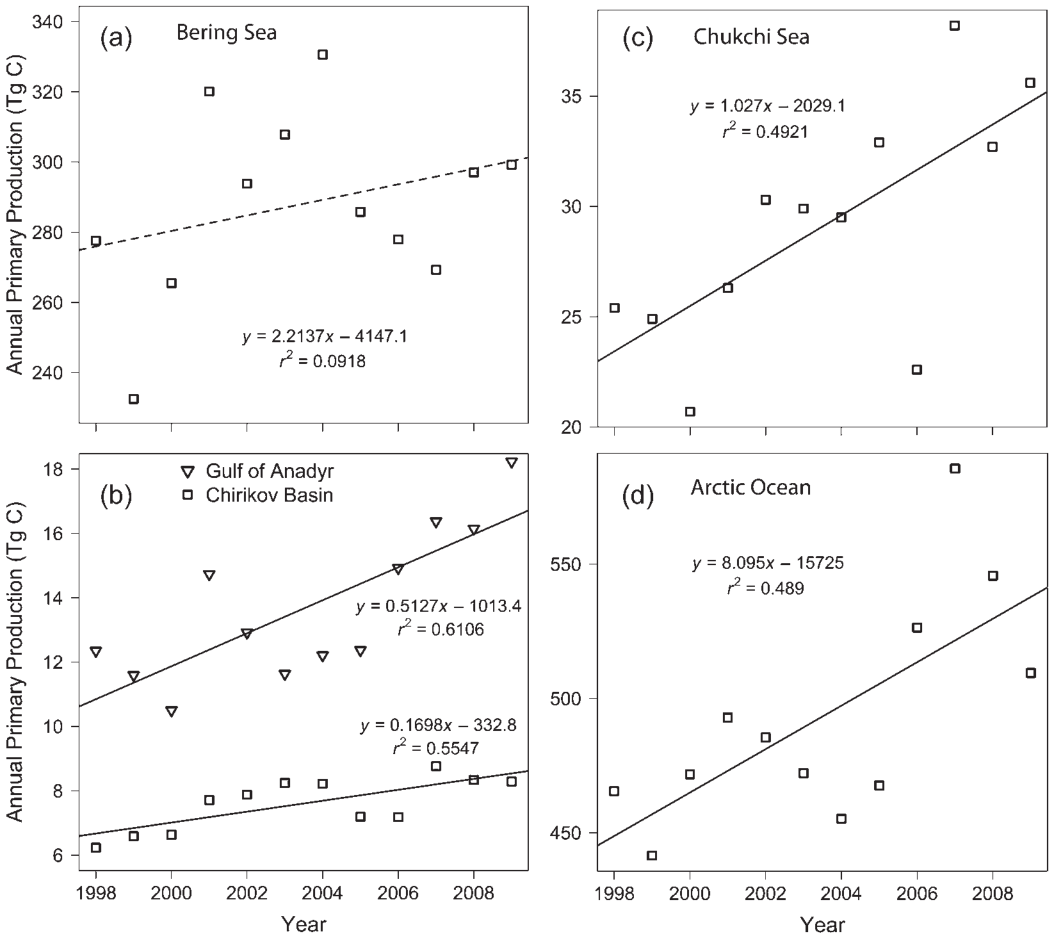

Figure 10. Secular trends in annual NPP in (a) the Bering Sea, (b) the Chirikov Basin and Gulf of Anadyr, (c) the Chukchi Sea, and (d) the Arctic Ocean. Solid regression lines indicate significance at the $p = 0.05$ level, and dashed lines indicate a lack of significance.

flowing through the region. These exceptions demonstrate that although the open water available to phytoplankton appeared to be of primary importance in determining annual NPP, other processes are also influential.

Discussion

Together, the Bering Sea and Arctic Ocean encompass the vast majority of the ice-covered seas of the northern hemisphere. They are connected via both the atmosphere, in which winds carry cold Arctic air south where it forms the Bering Sea's annual ice cover, and the ocean, in which nutrient-rich waters flow north to fuel production in the western Arctic seas. Both are highly productive seasonally, largely owing to their exceptionally large proportion of shallow continental shelf waters (>40%), which favour additional nutrient-loading through episodic advection and vertical mixing events (Tremblay *et al.*, 2008). Both regions are, however, also light-limited by sea-ice cover for much of the year (Loeng *et al.*, 2005). For this reason, in nearly all sectors examined, in both the Bering Sea and the Arctic Ocean, a longer open-water season was significantly correlated with greater annual NPP. Both regions are also experiencing rapid change, but in different ways. Whereas the Arctic Ocean has warmed in all seasons (Bekryaev *et al.*, 2010) and its annual mean open-water area has increased by 27% from 1998 to 2009 (Arrigo and van Dijken 2011), warming in the Bering Sea has been mainly limited to summer and its open-water area has held steady (Brown *et al.*, 2011).

It is somewhat surprising that the Bering Sea has experienced no secular loss of sea-ice, given that SAT and SST have increased dramatically in summer (Brown *et al.*, 2011) and sea-ice cover has plummeted in the adjoining Chirikov Basin and Chukchi Sea. Open-water extent in the Bering Sea appears uncoupled from that of seas to the north, and is instead tightly coupled to wind direction (Figures 4 and 5a). The Bering Sea ice cover has long been known to be driven by atmospheric circulation, and has been compared with a "conveyor belt", in which sea-ice forms in the northern Bering Sea in coastal lees and is then pushed south by northerly winds, where it contacts warm shelf waters, melting and cooling the water column, and facilitating further sea-ice advance (Pease, 1980). The mean winds in a given winter reflect the location of storms associated with the Aleutian low-pressure system. When storm tracks are displaced to the east, winds over the Bering Sea shelf are more northerly, driving expanded sea-ice extent (Overland and Pease, 1982; Wyllie-Echeverria and Wooster, 1998). This is consistent with our results showing that ice cover on the eastern shelf is strongly influenced by the direction of winter winds (Figure 5a). Because the direction of winds has undergone no secular change in recent decades (Figure 5c), winter sea-ice cover in the Bering Sea has also remained steady at ∼465 000 km^2 over the satellite record. However, it is not only wind direction that influences sea-ice extent, but also the frigid air temperatures typical of Arctic-origin winds, which are necessary to cool the water column and form ice (Stabeno *et al.*, 2007). Although winter SATs in the Bering Sea have been steady, winter SATs in the Arctic are warming more rapidly than in any other season (Bekryaev *et al.*, 2010). Therefore, if Arctic air entering the Bering Sea in winter warms significantly, this may limit sea-ice formation, illustrating one key connection between the Pacific sectors of the Arctic Ocean and the Bering Sea.

A second key connection is the northward flow of Pacific-origin water, particularly the nutrient-rich Anadyr Stream, through the Bering Strait into the Chukchi Sea. This influx of nutrients may help explain the fact that the Chukchi Sea has the longest sustained phytoplankton bloom of any Arctic region, and that it is the only "early bloomer" of the western Arctic, the others being the three Atlantic sectors where early production is likely favoured by their large perennially open water area (Arrigo and van Dijken, 2011). This nutrient source may also account for the fact that NPP was most responsive to increases in the length of the open-water season in the three Arctic regions most directly downstream (the Chukchi, Beaufort, and East Siberian Seas; Figure 8). Codispoti *et al.* (2005) conclude that without the Bering Strait inflow, annual NPP in the western Arctic would be much lower. It is possible, however, that future sea-ice loss in the Bering Sea could fuel additional NPP (as illustrated by Figure 7), leading to more complete utilization of available nutrients south of the Bering Strait and in turn, reducing their northward flux. Reduced nutrient flux through the Bering Strait may already be underway because of the rising NPP in the Gulf of Anadyr and Chirikov Basin (Figure 10b). However, the results here suggest that over the 12-year ocean-colour record, sea-ice decline, rather than changing nutrient fluxes, was paramount in driving the NPP trend in the western Arctic.

We would expect that if elevated NPP in the northern Bering Sea indeed limits NPP downstream, NPP in the Chukchi Sea should fall when NPP in the Chirikov Basin rises, i.e. a negative relationship. Instead, NPP has risen in both sectors over time as a result of sea-ice loss, resulting in a positive relationship (Figures 9d and 10b and c). One possible explanation is that nutrient flux has indeed been reduced, but the remaining nutrient flux is still sufficient to fuel enhanced annual NPP in the Chukchi Sea because it is continuous over a longer growing season. Another possibility is that the flow through the Bering Strait has increased over time, providing ample nutrients to fuel enhanced annual NPP in both the Chirikov and Chukchi sectors. Woodgate *et al.* (2006) observed stronger northward flow through the Bering Strait between 2001 and 2004, and although they did not measure nutrient fluxes, the flow consisted mainly of the nutrient-rich Anadyr Stream. The flux of nutrients through the Bering Strait should be monitored closely in the future to ascertain how changing patterns of productivity in the northern Bering Sea will be felt in the downstream western Arctic Ocean.

The Chirikov Basin appears the most "Arctic-like" of the Bering Sea sectors. Like the Arctic Ocean, it has undergone strong and significant increases in the mean open-water area, the duration of the growing season, and annual NPP. Because of its hydrography, it is not surprising that annual NPP in the Chirikov Basin has responded rapidly to a longer growing season, increasing by >30% in just 12 years. The western portion of the Chirikov Basin harbours the Anadyr Stream, a plume of cold, nutrient-rich water that upwells in the northern Bering Sea and flows northwards through the western Bering Strait. Because of this continuous nutrient input, the western Bering Strait has been likened to a laboratory "continuous culture" (Sambrotto *et al.*, 1984), whose high productivity is maintained in a nearly continuous bloom throughout the ice-free season (Hansell *et al.*, 1993; Springer and McRoy, 1993). Although satellite-based measurements show that productivity of the Anadyr Stream actually begins to decline before the advance of sea-ice (Brown *et al.*, 2011), a longer growing season still greatly enhances annual NPP in this nutrient-rich zone. Although the Chirikov Basin is small relative to the Bering Sea or Arctic Ocean, it is an important part of the Pacific Subarctic ecosystem, both as an overwintering location for bowhead whales (*Balaena mysticetus*) and as a prime summer foraging habitat for grey whales (*Eschrichtius robustus*; Moore *et al.*, 2003; Moore and Laidre, 2006). The secular increase in NPP in the Chirikov Basin does not support the hypothesis that a reduced prey base in this region is enhancing the mortality of grey whales (LeBoeuf *et al.*, 2000).

In the Arctic Ocean, sea-ice loss has been even more rapid than in the Chirikov Basin. Probably the most influential change for the ecosystem is the timing of annual sea-ice retreat, which was 3 weeks earlier in 2009 (1 July) than in 1998 (22 July; Arrigo and van Dijken, 2011). The primary productivity in the Arctic Ocean is currently understood to be dominated by ubiquitous spring blooms along the retreating ice-edge, where a favourable light environment is coupled with plentiful surface nutrients replenished over winter (Alexander and Niebauer, 1981; Loeng *et al.*, 2005; Perrette *et al.*, 2011). As sea-ice retreats earlier, phytoplankton are also blooming earlier (Kahru *et al.*, 2011). Altering the timing of phytoplankton production may result in a mismatch with calanoid copepods, the dominant Arctic Ocean grazers (Loeng *et al.* 2005), whose reproductive strategies have evolved over thousands of years to ensure that juveniles are at the right stage of development at the right time to exploit the spring bloom (Conover and Huntley, 1991). In turn, reduced copepod production would be expected to impact negatively the many upper-trophic level predators that time their migrations and/or breeding to coincide with maximal Arctic production. Moreover, any phytoplankton–zooplankton mismatch is likely to increase pelagic–benthic coupling (Wassmann *et al.*, 1996). Greater flux of organic matter to the benthos potentially can fuel additional benthic productivity (Grebmeier *et al.*, 1995) and increased rates of denitrification, reducing nutrient availability on the already N-limited shelf. Arctic copepod communities should be monitored closely in the future to determine whether continued sea-ice loss and earlier phytoplankton production is indeed altering the capacity of zooplankton to graze the spring bloom and transfer carbon within the pelagic environment.

In addition to disparities between long-term sea-ice trends, a second basic difference between Arctic and Subarctic seas is that the latter lose their sea-ice cover completely every year. This means that all possible phytoplankton habitat in the Bering Sea is already being utilized for at least a portion of the year: future sea-ice loss cannot expose new waters for phytoplankton growth, it can only lengthen the growing season. A longer growing season strongly stimulates production in the Bering Sea (Figure 7), raising NPP by a striking 42% over the range of open-water seasons observed since 1998. This is likely because essentially all sea-ice in the Bering Sea overlies continental shelves, shallow areas where a longer growing season facilitates additional nutrient-loading through episodic advection and wind and tidal mixing events (Sambrotto *et al.*, 1986; Tremblay *et al.*, 2008). However, it should be noted that a future trend towards longer growing seasons in the Bering Sea will likely proceed with diminishing NPP returns. That is, extremely long open-water seasons will no longer contribute much additional NPP because of eventual nutrient exhaustion and, more important, diminished solar input very early and very late in the growing season (i.e. winter). Primary production in ice-free portions of the Bering Sea is an order of magnitude less in winter than in summer (McRoy *et al.*, 1972). Therefore, although currently each extra open-water day stimulates ~1 Tg C of additional NPP in the Bering Sea, because all regions are already ice-free when solar input is maximal, and because no new phytoplankton habitat is available, the amount of additional NPP that can be expected with future sea-ice loss in the Bering Sea is limited.

Conversely, the Arctic Ocean retains a large area of potential phytoplankton habitat that is currently untapped because of its perennial sea-ice cover. This area is eroding rapidly, making these waters more suitable for phytoplankton growth. This is particularly true of the catastrophic ice loss of 2007, when 1.7×10^6 km^2 of Arctic Ocean (an area roughly the size of Alaska) were exposed for the first time in recorded history (Arrigo *et al.*, 2008a). Hence, secular increases in Arctic Ocean NPP are attributable not only to a longer growing season, but also to more total area over which to grow. Arrigo *et al.* (2008a) showed that in 2007, these newly exposed waters contributed only some 30% of the additional NPP compared with 2006, because they were mainly in the deep Arctic basins with intense salinity stratification and low surface nutrient levels year-round. A longer growing season was responsible for the bulk (70%) of the NPP increase, particularly over the already productive continental shelves (Arrigo *et al.*, 2008a).

The generally low productivity of the deep Arctic basins, even when sea-ice loss increases light exposure, probably explains why the Greenland and Baffin sectors did not exhibit the significant correspondence between growing season and annual NPP observed in all other sectors (Figure 8). Along with the Barents sector, Greenland and Baffin contain the greatest proportion of relatively deep (>220 m) ice-free waters, which may limit nutrient resupply and therefore temper their response to a longer growing season compared with the shallower sectors of the Arctic Ocean. In addition, along with the Barents sector, Greenland and Baffin already have the longest open-water seasons (Table 1), and as noted above, greatly extended growing seasons may support relatively little additional production. However, NPP in the Barents sector was correlated with the open-water season despite also having an expansive pelagic zone and long growing season (Figure 8), perhaps because, unlike the Greenland or Baffin sectors, it also contains a large proportion of nutrient-rich shelf waters that are more productive during warm years (Sakshaug, 1997). Recent work corroborates our finding that productivity in the Barents Sea is responsive to sea-ice loss, but also points to the importance of the location of storm tracks in creating additional mixing to fuel nutrient replenishment (Drinkwater, 2011).

Concluding remarks

The Pacific Arctic Ocean and Bering Sea are marked by greater productivity when less sea-ice is present, consistent with a predominantly light-limited system (Walsh *et al.*, 2005). However, despite pronounced summer warming, the Bering Sea as a whole has not lost seasonal sea-ice cover, nor has it become more productive over time. This is partially because winter winds have continued to bring frigid Arctic air southwards over the past six decades. The notable exception is the "Arctic-like" Chirikov Basin, where accelerated sea-ice retreat and delayed advance have led to greater productivity in the nutrient-rich waters. Moving polewards, the Arctic Ocean has experienced much more severe sea-ice loss, highlighted by a 45-d longer growing season in just 12 years, a much greater change than the Chirikov Basin experienced in three decades. Thus far, the longer growing season and new phytoplankton habitat have made that region substantially more productive, but it is unclear whether these gains are sustainable in the face of future climate change in the Arctic Ocean, where sun angles and surface nutrients are generally low. Moreover, ice-retreat is likely to progress in the context of changing wind-fields, warming sea temperatures, more extensive cloud cover, and increasing freshwater input from precipitation and runoff (Peterson *et al.*, 2006), all of which may alter the response of primary producers to wider, more persistent open water (Loeng *et al.*, 2005).

Future warming and sea-ice loss will likely extend the ice-free season over the Bering Sea shelves, which should initially make them substantially more productive. This may reduce the northward flux of nutrients through the Bering Strait, potentially depriving the western Arctic Ocean of a crucial source of fixed N. These nutrient fluxes, along with other potential nutrient sources such as enhanced shelf break upwelling, should be closely monitored in the future to determine whether the productivity of Arctic seas will continue to rise in a changing climate.

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