Climate forcing multiplies biological productivity in the coastal Arctic Ocean

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1. Introduction

[2] As the declining thickness and seasonal persistence of Arctic sea-ice challenges the organisms that use it for reproduction, foraging or refuge, the greater penetration of solar irradiance into the water column could stimulate photosynthetic carbon production (P) and the herbivorous food web sustaining harvestable resources. Modest, scattered increases in satellite-based P estimates (PS) support this scenario [Arrigo et al., 2008] although their cause, biogeochemical significance and sustainability are uncertain [e.g., Cai et al., 2010].

[3] Biogeochemical interpretations of change in Arctic productivity should consider two components of P. New production (PN) drives net increases in plant biomass from nitrogen (N) inputs (e.g., nitrate from deep waters, NO3) to the euphotic zone and sets the maximum quantity of carbon that can be harvested from the marine ecosystem without collapsing it. Regenerated production (PR) is fueled by local recycling of the byproducts of biological activity (e.g., NH4) and has little impact on net productivity. Current PS algorithms do not formally resolve PN and PR.

[4] While rivers and the Pacific Ocean bring allochthonous N to the Beaufort Sea and initially affect PN at the periphery, they also deliver low-density water that resides ca. 10 years in the interior. This water stratifies the upper ocean [Yamamoto-Kawai et al., 2009] and opposes the upward renewal of NO3 [Li et al., 2009; Tremblay et al., 2008]. Sediment denitrification compounds the NO3 shortage [Chang and Devol, 2009], which ultimately limits the positive influence of irradiance at the basin scale. A transient rise in PN is expected where multi-year ice withdraws and unused plant nutrients linger. Once ice-free conditions recur annually, however, phytoplankton deplete NO3 from the euphotic zone each summer and PN should rapidly level out in the absence of incremental N inputs [Tremblay and Gagnon, 2009].

[5] Here we verify the hypotheses that upward shifts of PN in the Beaufort Sea require additional N supply [Tremblay and Gagnon, 2009] and that upwelling can provide this N when the central ice pack recedes beyond the shelf break [Carmack and Chapman, 2003] by comparing time series of wind forcing, ice cover and PN for 2002–2008 with in situ measurements of salinity (moorings), nutrients, PN, biological stocks and biogenic fluxes obtained during overwintering surveys in 2003–2004 and 2007–2008 (Figure 1).

2. Methods

[6] The along-shelf component of wind velocity (u-wind) squared at 10 m above sea surface was calculated with data from the NCEP Re-analysis II project and used as an index of wind stress. Ice concentration was estimated using the AMSR-E/Aqua level-3 product from NSIDC. Vertically-resolved sampling was performed with a CTD-Rosette. Nutrients were determined on fresh samples and PN was estimated by multiplying NO3 drawdown by a molar C:N ratio of 7:1 [Tremblay et al., 2008]. Drawdown was estimated by difference between observed concentrations and expected ones based on NO3–salinity relationships from (a) the upwelling core for 2007/2008 and (b) the winter nutrient maximum for 2004 [Tremblay et al., 2008], after correcting for dilution. Extracted chl a concentrations and estimates of photosynthetic performance (FV/FM) were obtained as per Martin et al. [2010]. Satellite-based estimates of total primary production (PS) were derived using a semi-analytical approach for optically-complex waters (see auxiliary material).1 Ice algae were collected with an ice corer
and analysed for chl $a$ [e.g., Rozanska et al. 2008]. Procedures for sampling and counting zooplankton, deploying free-drifting sediment traps to estimate vertical fluxes of organic matter, collecting surface sediment, measuring sedimentary pigments and assessing the carbon demand of benthic organisms are given by Forest et al. [2011].

3. Upwelling and Its Consequences on $P_N$ in Autumn

[7] Prior to overwintering, the Canadian icebreaker CCGS Amundsen made a survey of the Canadian Beaufort Shelf (CBS) on 14 October 2007. Sampling began on the central shelf, where the legacy of upwelling was seen in the high salinity of surface waters near the coast (Figure 1a). These showed positive salt anomalies of $+7$ to $10\%$ relative to previous years [Mucci et al., 2010]. The upwelling core was encountered when the ship moved eastward and surface salinity increased to a maximum of $33.7\%$ off Cape Bathurst, consistent with model predictions of topographically-enhanced upwelling in this area [Williams and Carmack, 2008]. There, surface waters matched the temperature, salinity and nutrient characteristics of those normally locked beneath 175 m in central Amundsen Gulf. The highest surface NO$_3$ concentration (16.8 $\mu$M) ever observed in the region matched the highest salinity on 23 October (Figure 1b); in previous years when easterly winds were relatively mild, surface NO$_3$ concentrations were low ($<0.5\mu$M) and relatively uniform across the entire region [Simpson et al., 2008].

[8] Phytoplankton consumed up to a third of the upwelled nutrients before the ice took hold in November 2007. The NO$_3$ drawdown was initially small near Cape Bathurst but increased westward with chl $a$ (Figures 1b and 1c), as expected from the general surface circulation during upwelling [Williams and Carmack, 2008]. On the central shelf, the high photosynthetic performance of phytoplankton ($F_{\text{PS}} = 0.60 \pm 0.07$) and the ratio of NO$_3$ depletion (260 $\pm$ 66 mmol N m$^{-2}$) to chl $a$ accumulation (289 $\pm$ 130 mg m$^{-2}$) were consistent with a recent $P_N$ pulse. In western Franklin Bay, NO$_3$ deficits were relatively small in October (35 $\pm$ 17 mmol N m$^{-2}$) but had risen to 100 mmol N m$^{-2}$ during a repeat visit on 17 November (not shown). This post-upwelling consumption of NO$_3$ amounted to $P_N$ equivalents ranging from 8.5 g C m$^{-2}$ in Franklin Bay to 22 g C m$^{-2}$ on the central shelf, matching or exceeding previous estimates of annual $P_N$ [MacDonald and Carmack, 1991; Tremblay et al., 2008]. A large portion (11 $\mu$M) of the upwelled NO$_3$ remained unused when the ship headed offshore to overwinter in central Amundsen Gulf.


[9] In the two months preceding sampling in autumn 2007, a strong rise in sea-level pressure began over the northern Beaufort Sea in association with a positive phase of the Arctic Dipole Anomaly (DA) [Wang et al., 2009]. Winds pushed ice into the North Atlantic and conspired with solar heating to increase basal and lateral ice melt via the advection of warm water under the remaining pack ice [Perovich et al., 2008; Wang et al., 2009]. These processes produced the lowest September ice extent on record since 1979 and seriously deteriorated the multiyear ice cover, with feedbacks continuing into following years [Barber et al., 2009]. The central ice pack retreated far north of the shelf break between August and October 2007 and throughout summer 2008.

[10] Clockwise airflow along the southern edge of the anticyclone brought exceptionally strong, frequent and sustained easterlies over the CBS from August 2007 to July 2008 (Figure 2a). By delaying ice formation or causing ice divergence, wind forcing added 6 weeks to the open water period in fall 2007 and initiated the planktonic growth season a month early in spring 2008 (Figure 2b). As expected from inter-annual differences in upwelling-favorable wind forcing, salinities at the mooring location were much higher than in previous years [Mucci et al., 2010].
higher in 2007/08 than in 2003/04 under ice-free conditions (Figure 2c).

5. Upwelling and Its Consequences on PN in Spring-Summer 2008

[11] Most of the NO₃ not taken up by phytoplankton in late fall 2007 was present when the ship returned to Franklin Bay on 15 May 2008 (Figure 3). Surface concentrations beneath the fast ice (9.5 µM) were nearly 3 times higher than the maximum values observed throughout winter 2003–2004 in the same region [Tremblay et al., 2008] and offshore during winter 2007–2008 [Forest et al., 2011]. These differences were reflected in the seasonal build-up of ice-algae, whose final chl a biomasses in central (49.5 mg m⁻²; site 3 in Figure 1a) and eastern (102.2 mg m⁻²) Franklin Bay were 4–8 times higher than in Amundsen Gult (not shown) and 2–4 times higher than those observed in the Bay during 2004 [Rozanska et al., 2009].

[12] On 15 May, chl a concentrations in the upper 15 m of the water column in central Franklin Bay were 20-fold higher in 2008 than in 2004 and were associated with high NO₃ consumption under decaying landfast ice and, later, in the subsurface chlorophyll maximum (SCM) (Figure 3). Cumulative seasonal PN on 21 June was 6 times greater in 2008 (48 ± 4 g C m⁻²) and consistent with large accumulations of chl a in the nitracline (Figure 3). The bay was not revisited in 2008, but since PN was only 14 g C m⁻² on 6 August 2004, we conservatively estimate that seasonal PN was at least 3.4-fold higher in 2008.

[13] The CBS showed three conspicuous pulses of PS in 2008, each one lagging close behind an upwelling-favorable wind event (Figures 4a and 4b). Low and almost invariant PS at the nearby off-shelf control site confirmed that strong winds failed to erode the vertical stratification and that upwelling caused the incremental productivity on the shelf (Figure 4c). In Franklin Bay, the ice cleared relatively late and useful PS estimates could not be obtained before early June (Figure 4d). Weak PS pulsing afterward suggests that most of the newly upwelled NO₃ was used on the CBS before the “normal” eastward circulation resumed, which contrasts with the fall when low irradiance precluded prompt NO₃ drawdown on the eastern shelf.

[14] Annual PS on the shelf was nearly 2-fold greater in 2008 than in 2004 (Figure 5) and the mean for 2002–2007 (47 ± 11 g C m⁻²; not shown). Such a difference was not visible for Franklin Bay due to the inability of orbiting sensors to detect chl a through ice and at the SCM. The same limitation probably caused Ps to underestimate P for the shelf in spring 2008 but in situ validation was not possible at that time. Our Ps values should thus be considered as minimum estimates of the productivity upshift of 2008 relative to other years. These patterns cannot be explained by changing inorganic N supply from the Mackenzie River since this N is consumed in 4-m deep water within 20 km of

Figure 2. August-to-August time series of (a) the zonal component of wind velocity squared as an index of surface stress (negative = along-shelf and upwelling-favourable), (b) AMSR-E ice concentration on the eastern shelf, and (c) salinity recorded at 35-m by the mooring on the shelf slope. Colours distinguish the mean for 2002–2007 (Figures 2a and 2b only) from the years 2003/2004 and 2007/2008 (see Figure 1 for locations). A 5-day running average was applied to all data to remove high-frequency fluctuations and bring significant events into focus. The insets in Figure 2b show the spatial distribution of ice relative to land masses (black) on 17 November 2007 and 10 May 2008, with concentrations ranging from 0 (blue) to 100% (red).

Figure 3. Vertical profiles of NO₃ (µM) and chl a (µg l⁻¹) in Franklin Bay on (left) 15 May and (right) 21 June for 2004 (data from Tremblay et al. [2008]) and 2008 (this study). The location corresponds to site 3 in Figure 1a.

Figure 4. Detailed spring-summer time series of (a) wind activity on the eastern shelf and Ps for (b) the eastern shelf, (c) the offshore control site and (d) Franklin Bay during 2008 versus the mean (±0.5 standard deviation) for 2002–2007. See Figure 1 for locations.
explained by differential export of organic matter from the surface. In June 2008, the sinking flux of particulate organic carbon at 100 m in western Franklin Bay was 3.3 times higher than the mean for 11 other sites outside the Bay (see auxiliary material) and 2.9 times higher than in summer 2004 at the same location [Juul-Pedersen et al., 2010]. A substantial part of this material reached the benthos intact in 2008, judging by elevated sedimentary chl a:phaeopigment ratios (see auxiliary material).

7. Ecological Significance and Implications

[17] The CBS and adjacent bays make up a small part of the Arctic Ocean but are of prime social, economical and cultural importance for coastal communities as hotspots of marine productivity and staging and feeding areas for large aggregations of resident and migrant marine birds and mammals [Carmack and MacDonald, 2002]. When upwelling occurs in the fall, it drives a moderate $P_N$ pulse that supplies extra food to boost the maturation of the year’s cohort of $C. glacialis$. Because dwindling irradiance rapidly curtails $P$, unused nutrients persist through winter and precondition productivity for the next spring. This explains why ice-algal crops, whose maximum biomass responds positively to nutrient availability [Gradinger, 2009], can increase despite early ice melt. Fall upwelling will likely mitigate the adverse impacts of a somewhat early melt on ice algae and their consumers since 70% of the extension in the ice-free period is caused by late freeze-up in the region [Markus et al., 2009] and upwelling-favorable winds are strongest from October to December [Yang, 2009]. In summer, upwelling-driven $P_N$ pulses provide early and repeated access to new food for consumers and promote the recruitment of $C. glacialis$ and, presumably, carnivores higher up the food web. The paradigm that Arctic consumers must rely on a single $P$ outburst no longer holds.

[18] We showed that strong upwelling-favorable winds multiply the production of ice algae and phytoplankton by 2 to 4 fold in the coastal Beaufort Sea but so far fail to erode the freshwater stratification immediately offshore. Inshore-offshore gradients in $P_N$ thus become much steeper and the

![Figure 5](image108x547to253x731)

**Figure 5.** Spatial distribution of annual $P_N$ during 2004 and 2008 in the southeast Beaufort Sea, showing rates for the three locations described in Figures 1 and 4.

the delta [Emmerton et al., 2008], far south of the elevated production zone in Figure 5.

6. The Response of Secondary Producers

[15] The herbivorous copepod $Calanus glacialis$ is the key link between diatom production and apex consumers on Arctic shelves [Soreide et al., 2010]. In the areas influenced by upwelling in 2007–2008, the total abundance of $C. glacialis$ was 3 to 33 times higher than in 2003 during mid-fall and 1.6 to 13 fold higher than in 2004 during early summer (Figure 6a). Copepodites of stages III and IV made up most of the incremental abundance in fall 2007, especially in western Franklin Bay and on the central shelf where $P_N$ was highest and supplied the extra food for enhanced survival and maturation of the year’s cohort. The response of $C. glacialis$ was strongest on the central shelf in early summer 2008 but this time was due to early and successful recruitment of larvae into early stages CI and CII (Figure 6b). The 3-fold increase in the ratio of CI to females suggests high fecundity. At locations where the ice was still present (e.g., timing of $P_S$ in Figure 4d), early recruitment was not evident and the incremental abundance was due to CIV and CV individuals that matured from the CIIIs and CIVs of late 2007.

[16] On the central shelf, sedimentary chl a was over 20-fold higher than at any station not influenced by upwelling and benthic carbon demand (200.9 ± 66.3 mg C m$^{-2}$ d$^{-1}$) was among the highest ever observed in the Arctic Ocean [Clough et al., 2005] (see auxiliary material), reflecting a 3–4 fold increase in food availability relative to 2004 [Morata et al., 2008]. Benthic carbon demand in Franklin Bay was 1.9 times higher than the mean (21.2 ± 6.4 mg C m$^{-2}$ d$^{-1}$) for 10 other stations dispersed across the southeast Beaufort Sea. Surprisingly, this rate did not differ markedly from that of 2004 although sediment chl a inventories were higher in 2008 (9 mg m$^{-2}$) than in 2004 (2–4 mg m$^{-2}$) [Morata et al., 2008]. This apparent lack of response might be due to shifts in the composition of epifaunal, infaunal or microbial communities but comparative datasets are not available. Spatial and temporal patterns in sediment pigments were

![Figure 6](image336x151to528x266)

**Figure 6.** Inter-annual comparisons of $Calanus glacialis$ inventories for matching dates (±5 days) on the central shelf (35-m deep), the eastern shelf (45-m deep), western Franklin Bay (176-m deep), central Franklin Bay (250-m deep) and eastern Franklin Bay (95-m deep) for (a) 2007 vs. 2003 during early fall and (b) 2008 vs. 2004 during early summer. Numbers above bars give the percent contribution of stage III copepodites to total abundance in Figure 6a and the ratio of stage I copepodites to females in Figure 6b.
temporal feeding window of secondary producers extends considerably on the shelf, making it a conspicuous oasis for higher consumers that can successfully adjust to the changing environment. This situation is likely to prevail with the increasingly deep and frequent seaward retreat of the central ice pack and the greater incidence of upwelling-favorable winds [Yang, 2009]. The resultant P_N is also bound to rise as winds gain in intensity and upwelling draws deeper into the nutrient-rich, upper Pacific halocline. These portents of enhanced productivity do not assuage threats to biodiversity from ocean acidification, warming and ice loss, whose long-term impacts on the marine ecosystem are unknown.

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