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2 **Spatial and year-to-year patterns in new and primary**

3 **productivity in sea ice melt regions of the eastern Bering Sea**

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Abstract

Four years of data on for new (nitrate), regenerated (ammonium) and primary (carbon) productivity (2007 through 2010) confirm the elevated productivity associated with the marginal ice zone (MIZ) of the eastern Bering Sea (EBS) in spring. The greatest levels of productivity were associated with ice melt regions along the western edge of the ice pack. Population seeding and the shallowing of the mixed layer depth near the ice edge were less important in the development of elevated MIZ productivity than was the amount of ice melt entering surface water, suggesting that ice contributed substances stimulating phytoplankton growth. Based on ice melt as an index of bloom development, primary productivity continued to increase after new productivity peaked. At the MIZ environments with optimum growth conditions, new productivity averaged $18.6 \text{ mmols N m}^{-2} \text{ d}^{-1}$, with a f -ratio of 0.61, and primary productivity averaged $492 \text{ mmols C m}^{-2} \text{ d}^{-1}$. Although these features were consistently recorded in late April/ early May, they varied with the dynamics of ice cover, whose retreat was later in 2008 relative to 2007 and 2009. The intense but localized MIZ blooms appear to be under-sampled in ocean color imagery. Under ice productivity was generally low (ave. $\text{pNO}_3 = 0.45 \text{ mmols N m}^{-2} \text{ d}^{-1}$; ave. primary prod. = $4.16 \text{ mmols C m}^{-2} \text{ d}^{-1}$), although larger values were measured under the western edge of the ice pack and in the St. Lawrence polynya region. The advection of ice and water may contribute to the large values under the western ice edge and the highly transparent, new ice may play a role in the polynya. New and primary

44 productivity rates of under-ice samples were significantly inhibited when exposed
45 to ice-free irradiance levels. *In situ* productivity could be estimated to +/- 35%
46 from rates measured on-deck after by adjusting for the impact of ice on
47 submarine light. The carbon to nitrate uptake ratio was closely related to specific
48 carbon production in the *in situ* incubations.

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1 Introduction

Sea ice has a number of direct and indirect impacts on the productivity of the ocean. Sea-ice provides a habitat for microbes in the brine channels that form as ice develops and ages (Hunke et al., 2011). The release of these organisms as ice melts may result in a significant flux of organic matter to deeper waters (Bauerfeind et al., 1994; Fortier et al., 2002). Sea ice also influences the plankton environment under ice and in nearby ice-free waters that receive ice melt (Mobley et al., 1998; Long et al., 2011). The relationship between sea ice and productivity therefore influences the nature and extent of production that is available for higher trophic levels as well as the biogeochemical fluxes of bioactive materials in ice impacted waters (Sigler et al., 2014; Manizza et al., 2013, Wassman, 2011). These relationships are important to a better understanding of the biological response of ice-covered oceans in the face of significant changes in the spatial patterns and duration of ice cover (Comiso 2008, Stroeve et al., 2012). These large-scale changes raise important questions regarding the biological impact that the ocean's new ice environment will have on its biology and geochemical fluxes.

Extensive, first-year, sea ice develops on the wide continental shelf of the eastern Bering Sea (EBS). Most productivity studies have focused on ice-free periods and the elevated productivity associated with features such as frontal regions and the flow through the Bering Strait (Iverson et al., 1979; Springer et al., 1993; Sambrotto et al., 2008). Rates compiled from multiple studies estimate

72 yearly primary productivity from 110-150 g C m⁻² yr⁻¹ in the various biogeographic
73 regions of the EBS shelf (Rho and Whitledge, 2007). This moderate level of
74 productivity takes place over a relatively short season, and elevated rates of new
75 and primary production continue through the summer on the northern shelf (Lee
76 et al., 2012). Productivity measurements in the ice-impacted regions of the EBS
77 in the March-May period are fewer however. Recent sampling in the EBS
78 included the period of the ice retreat and found primary productivity rates
79 exceeding 2 g C m⁻² d⁻¹ at several stations at the ice edge in each of 2 sampling
80 seasons (Lomas et al., 2012). These rates approach the extraordinary rates of
81 primary productivity recorded at the ice edge of the EBS in earlier sampling
82 (Niebauer et al., 1995). The present focus is on the productivity associated with
83 the ice edge in order to better characterize the factors associated with its
84 development and intensity. The analysis is based largely on the rates of nitrogen
85 (new and regenerated) productivity and primary (carbon) productivity from field
86 incubations. The addition of nitrogen productivity to the suite of available
87 measurements in the ice edge of the EBS provides an estimate of nitrate
88 productivity, a useful parameter for estimating the 'new' component of primary
89 production that is available for export or trophic consumption (Dugdale and
90 Goering, 1967). The link between nutrient supply and productivity is mediated by
91 physical processes and is relevant to a range of questions on how climate driven
92 changes in the EBS propagate to upper trophic levels.

93 Extensive sampling in other ice edge regions such as those in the Barents Sea
94 show predictable developmental sequences associated with ice retreat (Slagstad,
95 1985, Sakshaug, 1997) and a similar characterization in the EBS would support
96 an improved understanding of the role that this unique environment plays in the
97 regional ecology. In addition to intense productivity, the ice melt regions of the
98 EBS exhibit similarities to the Barents Sea system in their characteristic ice-edge,
99 phytoplankton communities (Schandelmier and Alexander, 1981). The current
100 results were obtained across the EBS from late winter to summer of 2007-2010
101 and capture the retreat of the ice edge in 2007-2009 and the late winter
102 conditions in 2010. Here, we report on the distributions in biomass, nitrogen (both
103 nitrate and ammonium) and primary (carbon) productivity. Specific goals
104 included a better description of the biological transition between the ice-
105 dominated and open water environments that are associated with the rapid
106 seasonal progression in ocean physical and chemical properties.

107 The large photoautotrophic biomass that develops in such sea ice environments
108 may have a significant impact on the tropho-dynamics and biogeochemical
109 transformations of the EBS shelf, but until recently, the relationship of ice to these
110 factors and its impacts on higher trophic levels has not been investigated with
111 detailed field observations (Hunt et al., 2010). Ice influenced production is critical
112 to benthic food webs (Grebmeier et al., 1988, Cooper et al., 2013) and the EBS
113 supports a rich benthic assemblage as well as demersal food webs of significant
114 economic importance (Vestfals et al., in press). A more detailed analysis of how

large-scale climate patterns interact with regional biology is crucial for any predictive capability for potential changes in the ecology of this economically important shelf (Stabeno et al., 2010) and for a better understanding of how arctic change influences the larger scale patterns of polar productivity (Bergeron and Tremblay, 2014).

2 Methods

Sampling included most of the EBS shelf, from the Alaskan Peninsula in the south, to the international boundary between the United States and Russia in the north (Figure 1). Most of the data were obtained from the USCGC *Healy* that sampled the eastern Bering Sea each spring from 2007-2009. In 2010, the earliest seasonal data were obtained from the USCGC Polar Sea during March and April and from the non-ice strengthened R/V *T.G. Thompson* cruise TN249 a month later. In addition, earlier *Healy* cruises were done in 2008 and 2009 (HLY0801 and HLY0901 respectively) that provided information on hydrography and ice conditions.

Core hydrographic data during each cruise included underway data measured continually on water pumped from just below the water line for temperature and salinity from a thermosalinograph, as well as for fluorescence. These variables were calibrated against discrete samples with a salinometer for salinity and extraction and analysis on a calibrated Turner 10 AU fluorometer (Parsons et al. 1984) for Chl *a*. The ships also recorded meteorological data (wind speed and direction, relative humidity and air temperature) continuously. In most cases,

137 measurements of surface photosynthetically available radiation (PAR, 400-700
138 nm wavelength) also were collected. At each station, profiles of temperature,
139 salinity, and chlorophyll fluorescence were collected with a SeaBird CTD system
140 and associated sensors. Water sample profiles were collected from these same
141 casts with a rosette of Niskin bottles. Discrete samples were collected for the
142 chemical analysis of nutrients (NO_3 , NO_2 , NH_4 , PO_4 and Si(OH)_4) by on-board
143 autoanalysis (Mordy et al., 2005) as well as for salinity and extracted Chl *a*
144 calibration samples. Typically, a productivity station was occupied each day as
145 soon as enough light was available to assess the depth of the euphotic zone. A
146 CTD cast was done prior to the productivity cast to establish physical, nutrient
147 and Chl *a* conditions and retrieve the submarine irradiance profile. The
148 attenuation coefficient of PAR was estimated from this profile and used to identify
149 the depths at which 55, 30, 17, 9, 5 and 1.5% of surface irradiance penetrated.
150 Together with a surface (100% irradiance) sample, this provided a 7-depth profile
151 for productivity rate incubations. All productivity incubations were done in 2.2 L
152 PET (poly(ethylene terephthalate)) bottles in one of two ways. Most rate
153 measurements were derived from simulated *in situ* incubations in which the
154 incubation bottles were covered with neutral density plastic screen to simulate
155 the various irradiance levels and incubated in on-deck incubators that were
156 flushed with surface seawater to maintain *in situ* temperature. Incubators were
157 monitored periodically with hand-held thermometers and never found to be more
158 than 1.5°C warmer than surface water (and usually less than 1°C). Productivity

rate incubations also were done *in situ* at ice stations (Figure 1). In this case, the un-screened bottles were suspended from a wire through a hole in the ice and incubated at the depth and presumably the irradiance and temperature conditions, from which they were originally collected.

Stable isotopic tracers were used to estimate rates of new productivity (using $^{15}\text{NO}_3$), regenerated productivity (using $^{15}\text{NH}_4$) and primary (carbon) productivity (using H^{13}CO_3). All tracer solutions were made from salts enriched to 99 atom% of the tracer element. The amount of the nitrogen tracers added was based on the preliminary measurement of their respective pool sizes. Typically, a nitrogen tracer concentration equal to about 10% of the initial pool was added to the incubation bottles. In the few cases in which surface nitrogen pools were exhausted, $0.1\ \mu\text{M}\ ^{15}\text{NO}_3$ or $0.05\ \mu\text{M}\ ^{15}\text{NH}_4$ was added. For carbon productivity experiments, $100\ \mu\text{M}$ of ^{13}C -bicarbonate solution was added. This resulted in ~ 5 atom% enrichment of the external dissolved inorganic carbon (DIC) pool. Typically, a dual-tracer incubation was done with $^{15}\text{NO}_3$ and ^{13}C in the same bottle and separate, and parallel incubations for $^{15}\text{NH}_4$. Incubation periods for the dual $^{15}\text{NO}_3$ and ^{13}C experiments were 24 hrs. Levels of ammonium were typically low in surface waters however, and incubations for this substrate were usually limited to 6 hours or less. Irradiance-response experiments were done for ammonium uptake in which the same water was incubated at different light levels. In addition, short-term, incubation experiments for ammonium uptake were done at different periods of the day and night. Based on the light response

and diurnal uptake experiments, we estimated daily ammonium uptake by multiplying the hourly rates from the morning incubations by 18.

At the end of the incubations, particulate material was collected on pre-combusted GF/F filters under gentle vacuum and dried on-board at 50°C for 24 hrs. and returned to the laboratory in a desiccator. Isotopic ratios of N and C and total N and C content of the samples were measured with a Europa 20-20 mass spectrometer in continuous flow mode with an automated ANCA combustion system. Uptake rates were calculated from the equations of Dugdale and Goering (1967). In the following text, we discuss the mass flux of N as new productivity (ρNO_3) or regenerated productivity (as ρNH_4) and primary productivity (ρC), all in units of moles element (N or C) $\text{vol}^{-1} \text{time}^{-1}$. The element specific uptake rates of each ($v\text{N}$ or $v\text{C}$) in units of time^{-1} , are used when we wish to discuss the physiological rate independent of the biomass. The nitrogen f -ratio [$\rho\text{NO}_3 / (\rho\text{NO}_3 + \rho\text{NH}_4)$] is used to describe the relative amount of new to total nitrogen production. Trapezoidal integration was done to estimate areal (m^2) productivity rates from productivity depth profiles. A mixed layer depth was estimated as the depth at which density (σ_t) increased by 0.02 units from the surface value. Sections were created using Ocean Data View (Schlitzer, 2012).

3 Results and Discussion

3.1 Plankton productivity under the ice

Fifteen *in situ* productivity experiments are available to estimate plankton productivity in the water under the ice (Table 1). Most *in situ* stations from 2007-2009 were sampled in April and those from 2010 (the PS1001 cruise) were

204 sampled a month earlier. New productivity ranged from 0.05 to 2.92 mmol N
205 m⁻² d⁻¹ with a median of 0.13 and only three stations had a value exceeding 1.
206 Primary productivity ranged from 0.1 to 20.6 mmol C m⁻² d⁻¹ and was also non-
207 normally distributed with the largest 2 values several times the median value of
208 2.64. The *in situ* experiments were dominated by locations in the inner (< 50 m)
209 and middle shelf (50 – 80 m) regions and only 1 station had a water depth
210 greater than 80 m. The March stations from cruise PS1001 had moderate levels
211 of under-ice productivity relative to the range of the April experiments from the
212 other years. The most inshore locations generally had the lowest under-ice
213 productivity and Chl *a* levels in April. The shallower stations also had lower
214 nitrate levels in surface water, a pattern that was similar in all years in spring.
215 The most productive under-ice waters were associated with some degree of ice
216 melt as reflected by surface salinity (Figure 2). At some stations (e.g. HLY0802-
217 42 & 116) this freshening was only a few hundredths relative to deeper water,
218 although at HLY0802-111 and HLY0902-93 the surface waters were more than
219 0.3 less salty than the deepest layer. The station with the greatest new
220 productivity and second greatest primary productivity (HLY0802-111) also had
221 some of the highest salinity in its deep layer, suggesting the influence of nutrient-
222 rich, slope water at depth. In contrast, several of the stations with the lowest
223 chlorophyll and productivity had a salinity maximum at the surface, suggesting
224 that ice formation was still occurring.

Overall, plankton productivity under the ice was greater at the deeper stations near the western edge of the ice field that exhibited the greatest evidence of melting. Melting ice releases ice algae that grow in the brine channels and these can contribute to the plankton (Cota et al., 1987). The presence of ice algae forms such as *Fragilariopsis cylindrus*, *Pseudo-nitzschia* sp., and *Achnanthes* spp. and their ingestion by copepods in the EBS in early spring indicated their presence and trophic importance (Durbin and Casas, 2014; Sukhanova et al., 2009). At the under-ice stations with greater algal biomass however, centric forms such as *Thalassiosira* spp. typically dominated. While there are no reports of *Thalassiosira* as a major component of the ice algae, it could be present in that environment in low numbers. Bauerfiend et al. (1994) recorded the genus throughout the winter in low numbers and an alternative interpretation is that it overwinters as a widely distributed component of the plankton that colonizes the MIZ on an opportunistic basis the following spring.

Advection also could contribute to the greater photoautotrophic biomass at the western edge of the ice field. Both the advection of phytoplankton laden, ice-free surface waters under the ice, or conversely the movement of ice over formerly ice-free waters could contribute to the observed patterns. For example, the ice pack expanded between March and April of 2009 and can move rapidly under the influence of winds (Zhang et al., 2010). Also, stations such as HLY0802-111 were close to the edge of the northern shelf such that is characterized by currents that transport nutrient-rich slope waters onto the shelf

and lead to an extensive region of elevated production into and beyond the Bering Strait (Sambrotto et al., 1986, Walsh et al., 1989). This flow could direct some of the water under the ice as it moves north and east, and account for some of the biomass observed under the ice.

In situ growth also may have contributed to the greater biomass at the western edge of the ice pack. Variation in ice thickness and snow cover impact irradiance reflection and absorption and make the estimation of the sub-ice light levels complex (Perovich, 1990). The relationship between sub-ice irradiance levels and the combined thickness of the overlying snow and ice during our spring sampling was fairly linear, however (data not shown) and suggests that sea ice during April reduced the submarine irradiance field in the EBS to between 1-6% of the incident irradiance, a reduction that is greater than those recorded by Gosselin et al. (1997) and Kirchman et al. (2009). Like the Bering Sea, the Chukchi Sea and southern Canada Basin sampled by Kirchman et al. (2009) were dominated by relatively thin first year ice. The lower sun angle during the March-April sampling in the present Bering Sea work as compared to the sampling period of Kirchman et al. (2009) may have contributed to the penetration of less irradiance. Surface melt pools also enhance the penetration of light through ice (Arrigo et al., 2012), but these were not common. In the Bering Sea in April, broken floes from which water drained readily dominated the ice field. Greater under ice irradiance in the region just south of St. Lawrence Island is likely however, because this is an active ice formation region (Zhang et

al., 2010) and was observed to have little to no snow cover. This results in greater penetration of light to surface waters similar to the conditions described in the Chukchi Sea (Lowry et al., 2014).

The large reduction of incident irradiance by the ice resulted in lower rates of both nitrate uptake and primary productivity when the incubations were done *in situ* as compared to on-deck (Figure 3 and Table 1). The areal uptake rates from the on-deck incubations were from ~2 to 15 and ~2 to 25 times greater than those *in situ* for new and primary productivity, respectively, and in both cases, the largest discrepancy was at the station with the greatest productivity and biomass (HLY0802, stn. 111). Excluding this station with elevated Chl *a*, the enhanced rates measured in the on-deck incubations were not strongly related to Chl *a* levels. There was a significant reduction in both new and primary productivity rates in most of the on-deck incubations above the 30% irradiance level. Productivity rates did not decrease at the surface irradiance levels in the *in situ* profiles however, and suggest that there was significant photoinhibition of both nitrate uptake and primary productivity rates at the greater PAR levels and altered spectral distribution of the on-deck incubations. Photoinhibition is often associated with nutrient replete arctic phytoplankton (McMinn and Hegseth, 2004) and the lower productivity rates at the high light level, on-deck incubations as compared to rates lower in the euphotic zone, were similar to the shape of rate profiles in the Ross Sea that also was attributed to this factor (Smith et al., 2000). In the Bering Sea MIZ region, it appears that the under ice community is

physiologically prepared to take advantage of the increased light levels the ice retreat will bring, and is similar to prior observations of greater $P_{\max}$ in surface waters dominated by large centric diatoms (Huot et al., 2013).

Prior approaches for correcting the estimates of productivity from on-deck incubations to *in situ* rates include adjustments for ice cover and irradiance attenuation by ice (e.g. Gosselin et al., 1997) such that:

$$P_{\text{cor}} = (P_{\text{uncor}} \times (100 - \phi) / 100) + (P_{\text{uncor}} \times \phi) / 100 \times E_s / E_0 \quad (1)$$

Where P_{cor} and P_{uncor} are the integrated rates of primary productivity corrected and uncorrected for ice, and ϕ is the percent ice cover. The ratio E_s/E_0 is the ratio of irradiance above and below the ice. This adjustment yielded estimates of *in situ* productivity that were within 20% and 50% of the measured nitrate and primary productivity respectively. The accuracy of the estimates was better at lower rates (<0.5 and $5 \text{ mmols m}^{-2} \text{ d}^{-1}$ for nitrate and primary production respectively). The increase in temperature experienced by the plankton during sampling and on-deck incubation may contribute to greater productivity rates. *In situ* experiments were labeled on the ice however, and warming of these samples was minimal. The Q_{10} for both photosynthesis and nitrogen uptake are large for ice algae in this temperature range (Priscu et al., 1989). The rapid change from *in situ* temperature to the on-deck conditions likely did not provide enough time for the full expression of temperature acclimation by the photosynthetic parameters of the phytoplankton, however (Geider et al., 1996; Coles and Jones, 2001), but could be a factor that enhanced rates by the end of the 24 hr.

incubations. Conversely, Net Community Production (NCP) declined with temperature for Barents Sea communities (Holding et al., 2013), but the experimental changes in that study exceed the warming measured in the on-deck incubators here. Thus, while the temperature of the on-deck incubations may have contributed to the observed enhancement of rates above *in situ* levels, it is likely that the greater PAR levels caused most of the observed differences in rates between the *in situ* and on-deck incubations.

The C/Chl *a* ratio explained 25% and 28% (R^2) of the increase in primary and new productivity rates respectively between *in situ* and on-deck incubations (linear model, Table 2). The specific C productivity values in the upper water column were significantly greater for the on-deck incubations than the *in situ* incubations and were within the range expected for ice edge temperatures (Behrenfield and Falkowski, 1997). While the *in situ*, specific C productivity rates were not a good predictor of the differences between *in situ* and on-deck measured rates, they explained over 60% of the variation in the C/NO₃ uptake ratio using an exponential model. The specific C productivity values from the on-deck experiments did not predict the C/NO₃ uptake ratios as well ($R^2 = 0.42$) and displayed no relationship to the uptake ratios.

3.2 Development of elevated productivity in the marginal ice zone

As the ice pack retreated in April, the greatest levels of Chl *a* in surface waters usually were found in the MIZ and, in 2009 an extensive band of elevated phytoplankton developed along the region of maximum ice extent (Figure 4).

This and future references to the MIZ refer to the region near the 15% ice cover as detected remotely. Many of the regions of greatest productivity were located near the 15% ice cover and ice cover changed within a relatively short distance on either side of this concentration to either ice-free or continuous coverage. The surface Chl *a* distributions in late April 2009 are characteristic of those observed from ocean color and ship sampling from 2007 through 2010 (Brown and Arrigo, 2013). The band of elevated Chl *a* in 2009 (Figure 4) exceeded 1000 km in length and maintained Chl *a* levels above several mg m⁻³ over a region of ~80,000 km² from late April to mid-May and was the most obvious biological feature in the MODIS imagery of the North Pacific at this time. The greatest Chl *a* levels were just inshore of the maximum western ice extent in early April and consistently associated with the initial retreat of ice from this position. Unlike the western ice edge that is constrained by the relatively warm surface waters of the Bering basin, the extent of sea ice to the south is more variable and dependent on atmospheric forcing of physical conditions on the southern shelf (Stabeno et al., 2012). Wind may push the southern ice edge north before any significant melting occurs (Sullivan et al., 2014) and the relationship between the ice edge and productivity is more variable in the south (Brown and Arrigo, 2013). These physical differences may account for the greater consistency of the MIZ bloom along the western ice edge as compared to the south.

The persistence of elevated Chl *a* along most of the original western MIZ even after the ice retreated in May indicated that exceptionally favorable conditions for

357 phytoplankton growth developed in the region of maximum ice extent that were
358 not present in subsequent positions of the retreating ice edge. Section data
359 consistently recorded the co-occurrence of MIZ blooms with surface pools of
360 relatively low salinity, ice melt water along the west edge of the original pack ice
361 (Figure 5). Although the horizontal salinity contrast is less obvious on the
362 shoreward side of the MIZ (Figure 5), there also was about a 0.1 salinity gradient
363 in this direction as well.

364 Profiles from three stations along the MN line in 2007 were selected to represent
365 typical productivity conditions seaward of the ice pack in basin waters (station
366 90), in the melt pool itself (station 98) and in the inner shelf region (station 110,
367 Figure 6). In the warmer waters of the deep basin, nitrate levels were over $26 \mu\text{M}$
368 (Figure 6 A) and new and primary productivity were less than 1 and $10 \text{ mmols m}^{-2} \text{ d}^{-1}$
369 respectively (Figure 6 D). Chl *a* levels, while well above winter values, were
370 among the lowest on the section (Figure 6 G). In contrast, station 98 exhibits
371 many features that were typical of the intense productivity in the MIZ including:
372 the drawdown of surface nitrate to less than $5 \mu\text{M}$ (from the initial levels of ~ 14
373 μM , Figure 6 B); the development of a large standing stock of phytoplankton with
374 particulate carbon levels exceeding $40 \mu\text{M}$ (Figures 6 B) and Chl *a* levels
375 routinely exceeding 10 mg m^{-3} (Figure 6 H); and the greatest rates of productivity
376 recorded during the study (Figure 6 E). New productivity at station 98 exceeded
377 $39 \text{ mmols m}^{-2} \text{ d}^{-1}$ and the *f*-ratio was 0.51 on an areal basis. Primary productivity
378 exceeded $800 \text{ mmols (>9 g) C m}^{-2} \text{ d}^{-1}$. A second productivity station taken in the

379 outer edge of the same melt pool in 2007 (station 94 at 131 m depth) had lower
380 (but still relatively large) rates of new productivity ($21.7 \text{ mmols m}^{-2} \text{ d}^{-1}$) and
381 primary productivity in comparison to station 98. The lower productivity at Station
382 94 in comparison to Station 98 may reflect either an earlier stage in bloom
383 development at station 94, or the lower influence of melt water there (Station 98
384 had a surface salinity of ~ 31.9 (Figure 6 H) in comparison to a surface salinity of
385 32.6 at station 94). While some of the greater salinity at station 94 can be
386 attributed to its more offshore location, the lower temperature at station 98 (-1.6
387 $^{\circ}\text{C}$, Figure 9 H) as compared to station 94 ($\sim 0^{\circ}\text{C}$) also suggested greater impact
388 of recent ice melt. The rates of productivity in the ice melt regions were
389 consistently the largest recorded during the BEST field work and compare
390 favorably to the areal rates of 2 to $4 \text{ g C m}^{-2} \text{ d}^{-1}$ for primary productivity reported
391 by Lomas et al. (2102) in these regions.

392 The representative productivity station for the inner shelf shows the low nitrate
393 levels typical of this region in April (station 110, Figure 6 C). Despite these low
394 nitrate concentrations, plankton biomass in the inner shelf remained relatively
395 large (with particulate carbon levels over $40 \mu\text{M}$ and Chl *a* levels over 6 mg m^{-3}
396 (Figure 6 C & I). Productivity rates, while not as great as those in the melt pool,
397 also were relatively large and exceeded $5 \text{ mmols NO}_3 \text{ m}^{-2} \text{ d}^{-1}$ (with a nitrogen *f*-
398 ratio of 0.61) and $120 \text{ mmols C m}^{-2} \text{ d}^{-1}$ (Figure 6 F). At the shallow depths typical
399 of the inner shelf, vertical properties of nutrients, temperature and salinity were
400 usually homogenous (Figure 6 C & I). The inner shelf region along the MN line in

401 April, 2007 also had an accumulation of particulate carbon and nitrogen at depth
402 (Figure 6 C). Although this was not a consistent feature of the inner shelf, such
403 deep particle maxima suggest the re-suspension of organic material that was
404 formed earlier in the year, or perhaps in prior years, by tidal currents. The C/Chl
405 *a* ratios also were significantly lower in the MIZ bloom regions, decreasing from
406 108 and 69 ug C/ ug Chl *a* in the surface waters of the outer and inner shelf
407 regions to less than 30 in the MIZ bloom. These differences were similar to those
408 in the particulate C/N ratio that decreased from 8 and 8.9 on a molar basis in the
409 outer and inner shelf regions, to 6.4 in the MIZ bloom.

410 Some of the rapid dynamics occurring at spatial scales of 10s of km for the
411 relationship between ice melt and productivity were captured in sequential
412 sections across the MIZ approximately 9 days apart in late April 2007 (Figure 7).
413 The changes in salinity and Chl *a* were compared between the re-occupation of
414 the same 7 stations. While this simple comparison does not account for
415 advection and mixing, the surface layer was strongly stratified and limited vertical
416 mixing, and estimates of horizontal advection are low and from the southeast, a
417 region with similar hydrography and thus weak horizontal gradients (Stabeno et
418 al, 2010). Over this time, the surface layer across this region freshened,
419 particularly near two stations where salinity decreased by over 0.3. The amount
420 of ice melt that would be required to produce the salinity decrease in the surface
421 mixed layer is shown in Figure 7A. The average ice thickness required was ~23
422 cm and was a reasonable rate of spring ice melt over this time (Perovich et al.,

2011). Importantly, the peak ice melt regions also exhibited the maximum increases in Chl *a* and suggest a causal link between the melt water plumes and phytoplankton growth response (Figure 7B). The enhancement of vertical stability in surface waters by ice melt is one factor that contributes to this growth response (Smith and Nelson, 1985). Freshening of surface waters causes much more vertical stability than is needed to initiate a phytoplankton bloom, however. By late April, much of the ice-impacted shelf exhibited at least a 0.02 σ_t density contrast in vertical density within 30 m of the surface, a feature that is sufficient to create favorable irradiance conditions for phytoplankton growth (Sambrotto et al., 1986, Arrigo et al., 1999). Variations in the mixed layer depth in fact, explained only 6% of the change in Chl *a* (Figure 8A). The intensity of ice melt as reflected by the decrease in surface salinity was a much better predictor for increases in surface Chl *a* (Figure 8B). The salinity decrease was calculated as the change in salinity between the end of winter to the time of sampling. The end of winter salinity was estimated from the surface-most sub-surface salinity maximum from CTD profiles that was a remnant of the winter surface water (Jennings et al., 1984; Sambrotto et al., 2003). Although this approach failed in shallow shelf regions that mixed to the bottom, a winter remnant layer could usually be identified in deeper waters. This approach suggests that 58% of the variations in Chl *a* can be attributed to the total amount of melt water, much more than was associated with changes in the depth of mixing. Both the salinity decrease and the mixed layer depth were combined into an ice melt index was constructed by

normalizing the measured salinity decrease to the depth of the mixed layer. This provided a way to gauge both the potentially positive effect of the ice melt and the negative effect of deep mixed layers. The specific rates of new and primary productivity had different responses to the ice melt index (Figures 8 C & D). Both rates increased rapidly in response to the initial ice melt. Specific rates of new productivity peaked below $\sim 0.02 \text{ m}^{-1}$ however, while specific rates of primary productivity remained large or even increased with greater inputs of melt water. The decrease in new productivity rates did not appear to be caused by nitrate depletion because these concentrations typically remained above $5 \mu\text{M}$. Ammonium concentrations increased with the ice melt index from 0.1 to $0.3 \mu\text{M}$ however, and ammonium and other regenerated nutrients could contribute to the reduction of new productivity despite continued elevated levels of photosynthesis (Dortch, 1990).

Although the seeding of photoautotrophic biomass to the MIZ as the ice melts and releases ice algae to the surface water has been suggested as a contributing factor to ice edge blooms (Lizotte, 2001), the dominant diatoms in the ice edge blooms of the EBS were not the same as those in the ice-algal assemblage. Also, even though there is ample ice algal biomass in dense layers near the bottom of coastal sea ice (Gradinger, 2009), much of this biomass sinks rapidly to depth as the ice melts (Garrison and Buck, 1986). This may contribute to the inability of the ice algae to establish a large planktonic population and allow the centric diatoms to dominate surface waters. Similar to the under-ice

467 phytoplankton, centric diatoms such as, *Thalassiosira* spp. were dominant in the
468 MIZ bloom, but the MIZ community was more diverse, with significant
469 representation of the genus *Chaetoceros*. Representatives of *Thalassiosira*
470 have also been observed as a dominant in the MIZ bloom in the East Greenland
471 Sea (Bauerfiend et al., 1994). This change from pennate ice algal communities
472 to largely centric diatom communities in open water is similar to floristic changes
473 seen in the Arctic where ice communities that supported dense algal growth were
474 dominated by pennates of the genera *Nitzschia*, *Fragillariaopsis* and *Navicula* but
475 were replaced by centrals in the plankton bloom (Rozanska et al., 2009; Gosselin
476 et al., 1997). The presence of *Thalassionema nitzschioides* together with
477 *Thalassiosira nordenskioeldii* and *gravida* in the sediment has been used as a
478 proxy to reconstruct the location of productive ice edges (Sancetta, 1982).
479 Finally, the isotopic mismatch between ice algae and the planktonic production at
480 the ice edge data also has been interpreted as an indication of the limited impact
481 of the ice algae on the planktonic bloom (Tremblay et al., 2006).

482 Ice melt may be a source of growth factors that stimulate productivity at the ice
483 edge. Iron has been suggested as one such factor for the MIZ bloom (Sedwick
484 and DiTullio, 1997). Much of the ice in the eastern Bering Sea is advected from
485 the north and east, both of which are shallow regions in which forming ice may
486 entrain particulate iron from the bottom or dissolved iron from the water itself.
487 Sea ice in the eastern Bering Sea contains large levels of both dissolved and
488 particulate iron (Aguilar-Islas et al., 2008). Brine drainage as ice melts enhances

the release of particulate and dissolved iron in to surface waters (Lannuzel et al., 2007), so that particulate iron may be released well before the ice has melted completely. Other factors released from ice include chelators that condition the environment by removing toxic metals and as yet uncharacterized organics (Apollonio et al., 2002). It is not possible identify which of these (or some other) component contributed to the development of the large productivity rates in the MIZ region of the EBS, but the release of one or more growth factors from the ice is compatible with the relationship of ice melt to both total biomass (*Chl a*; Figure 9 B) as well as to new and primary productivity (Figure 8 C & D).

3.3 Ice dynamics and the variability of the MIZ bloom

The integrated new (nitrate) and regenerated (ammonium) productivity measurements from 2007 – 2010 are shown in Figure 9. The analogous data for primary productivity are shown in Figure 10. The rates were derived from the on-deck rates for regions with less than 15% ice cover and the *in situ* rates at locations where they are available. At other locations with greater than 15% ice-cover (i.e. within the pack ice), the rates from the on-deck measurements were scaled with the relationship of Gosselin et al. (1997) as discussed in section 3.1. Ammonium uptake was scaled in a similar fashion to 0.5 at 100% ice cover assuming that it was less irradiance dependent than either nitrate or carbon uptake (Muggli and Smith, 1993). The surface nitrate concentrations in Figure 9 were interpolated from the discrete station measurements and the surface *Chl a*

concentrations in Figure 10 were interpolated from underway fluorometer readings.

Consistent features in these distributions include the greater nitrogen productivity rates associated with the MIZ along the western edge of the pack ice, as well as lower rates in the more ice covered and basin waters. The spatial coherence between the largest observed new productivity and the regional minima in surface nitrate concentrations is particularly evident in 2007 and 2009 (Figures 9 A & C) in which surface waters along the western ice edge had lower nitrate concentrations than more inshore waters. The slower development of bloom conditions at the western MIZ in 2008 is reflected by the lack of significant nitrate drawdown along the MIZ in April of this year. The 2008 and 2009 new productivity rates under the ice (Figures 9 B and C) suggest that the low rates found in this environment in March, 2010 (Figure 10 D) persist into April. Although the exact position of the maximum nitrogen productivity rates along the ice edge varied from year to year, it was never far from the maximum ice extent. A major exception to this pattern was the region southwest of St. Lawrence Island that often had large nitrogen productivity rates in the absence of the MIZ. As discussed for the *in situ* productivity results, the thin, transparent ice and frequent polynya likely played a role in maintaining higher productivity here than in the other ice-covered regions of the EBS.

Nitrogen *f*-ratios were generally large (0.5 – 0.95) in the MIZ environment, and similar to those measured in the ice edge regions of the high Arctic (Tremblay et

532 al., 2006). Lower f -ratios characterized the inner shelf region, reflecting the lack
533 of nitrate near-shore. Ship measured surface Chl a levels coincided with the
534 elevated production in the MIZ region and this match-up was apparent in 2007
535 (Figure 10 A), and locally in 2008 and 2009 (Figures 10 B & C). Moran et al.
536 (2012) also identified the western MIZ as the region of greatest net primary
537 production. The changes in surface nitrate during April in these regions produce
538 a nitrate consumption estimate of 200-350 mmols $\text{NO}_3 \text{ m}^{-2}$. This is similar to the
539 estimate by Niebauer et al. (1995) in this environment and compatible with new
540 productivity rates of 6-12 mmols $\text{m}^{-2} \text{ d}^{-1}$, within the range of rates measured here.
541 The present incubation rates suggest primary productivity in April of 25-45 g C m^{-2}
542 ². These rates are similar to rates measured in the northern EBS in May and
543 June by Lee et al. (2012). These estimates, as well as the spatial consistency of
544 the MIZ bloom in the EBS are similar to the impact of the receding ice edge in the
545 Barents Sea (Sakshaug et al, 1997). The MIZ bloom in the Barents Sea also is
546 important for benthic and pelagic food webs (Sakshaug, 2011), and it is likely that
547 the elevated productivity of the MIZ plays a similar role in the seasonal structure
548 of food webs in the EBS. Both new production rates and nitrogen f -ratios
549 indicate that a large amount of organic material is produced for either pelagic or
550 benthic consumption. The micro- and macro-grazing rates in April were
551 significantly less than phytoplankton growth rates (Sherr et al., 2013), suggesting
552 that much of the new production is exported to benthic and demersal food webs.
553 Trap measurements consistently show elevated levels of export flux in MIZ

regions during spring (Olli et al., 2002) and this flux is typically associated with enhanced benthic biomass (Cooper et al., 2013; Lalande et al., 2007).

The productivity rates are organized by the ice melt index developed in Section 3.2 and summarized in Figure 11. This index is a useful indicator of bloom development at the ice edge and when arranged in this way, the stations exhibit a progression from low to high rates of new and primary production (Figure 11 A & C). The different trajectories of new and primary productivity beyond the ice melt index of 0.03 m^{-1} is similar to the differences exhibited in the specific rates (Figure 8 C & D). In addition, Figure 11 shows that the changes in the *f*-ratio reflect those of new productivity (Figure 11B), while primary productivity continues to increase with Chl *a* (Figure 11D). The low *f*-ratio prior to the MIZ bloom may reflect the dependence of phytoplankton growth on under ice ammonium (Morales et al., 2014). The ice melt index therefore is useful for the interpretation of processes influencing new and primary productivity at the ice edge and is relevant to the interpretation and prediction of the biological response to climate variations in the EBS and other ice impacted regions.

The importance of the ice edge bloom to the yearly productivity is particularly significant because, excluding the shelf break region that maintains elevated productivity throughout the summer (Mathis et al., 2010), the yearly productivity of the EBS is not above the global mean, and the MIZ bloom contributes up to a third of the estimated annual productivity (Rho and Whitledge, 2007; Brown et al., 2011). This is comparable to the contribution of the MIZ bloom in the ice-

576 impacted Barents Sea (Loeng and Drinkwater, 2007) and emphasizes the
577 importance of this transient environment to regional ecology and material flow. In
578 the present data for example, the ice edge bloom in late April 2008 was later and
579 less spatially organized compared to those observed in 2007 and 2009 near 60°N
580 (Figure 9 B). The altered location and developmental stage of the ice edge
581 bloom in April 2008 relative to the other years may reflect colder conditions with
582 altered wind (Zhang et al., 2010) that resulted in significantly less ice melt by late
583 April than in the other years. Coupled atmosphere-ocean models predict that
584 while the year-to-year variability in sea ice conditions will continue in the EBS, a
585 40% decrease in maximum ice extent is expected in the next few decades (Wang
586 et al., 2012). In response, the MIZ dominated production cycle of the northern
587 self will shrink in proportion to the less predictable and less spatially organized
588 spring blooms of the southern region that are initiated by thermal stratification
589 (Stauffer et al., 2014).

590 On the basis of Chl *a* levels, Sigler et al. (2014) concluded that the open water
591 blooms that occur in early ice out years result in greater production over the
592 spring than do the MIZ initiated blooms. The new and primary productivity rates
593 recorded at the MIZ in this study however, equaled or exceed those of the ice—
594 free blooms typical of early ice retreat or ice free years (Sambrotto et al., 1986).
595 The present results are consistent with the notion that the impacts of the MIZ
596 bloom extend beyond the period of ice retreat by their impact on copepod
597 development and fisheries production (Sigler et al., 2014, Rey et al., 1987).

While the consistency of the spatial pattern of the bloom in the western ice pack were similar to the observations of ocean color made by Brown and Arrigo (2013), the timing of the ice edge bloom recorded here is 1-2 weeks earlier than its average appearance in the ocean color data. It is not clear how well the remotely-sensed estimates record the productive MIZ blooms because these events are localized in optically complex environments with frequent cloud cover that is difficult to record with current satellite technology (Perrette et al., 2011).

The intensity of the MIZ blooms in the high Arctic will be less than those in the EBS due to the low nutrient levels in arctic surface waters that are expected to control the productivity response to ice retreat (Niebauer et al., 1990). Ice-water interactions and eddy activity may contribute to vertical mixing and nutrient supply under proper conditions however (Niebauer and Smith, 1989). In addition, the current results emphasize the role of the ice melt in enhancing productivity, and the efficiency of export production increases in less productive conditions, a trend that would offset the reduction in productivity due to nutrient limitation (Tamelander et al., 2013). These factors suggest several complications in predicting the response of the high arctic productivity and biogeochemical flux in response to climate change.

4 Summary and Conclusions

Based on nitrogen and primary productivity data from April-May of 2007 through 2009 and March sampling in 2010 in the ice-impacted region of the EBS, we found:

- 1) Under ice phytoplankton exhibit significant light inhibition at surface irradiance levels and appear to be shade adapted for the under ice environment.
- 2) The specific C production values were a useful indicator of the C/ NO₃ uptake ratios of the under ice phytoplankton.
- 3) The conversion of on-deck measured rates to *in situ* estimates was prone to errors of 25-50%.
- 4) Under ice productivity was low except for regions of the western pack ice and the St. Lawrence Island polynya where factors such as advection, and increased under ice irradiance were significant.
- 5) The greatest new and primary productivity rates were associated with the extensive ice melt regions along the western edge of the ice pack in late April and early May.
- 6) The amount of melt water entering the surface layer, as estimated from its freshening through time, provided a more robust index of the development of the MIZ bloom than did MLZ and was compatible with ice melt as a source of growth factors for the developing MIZ bloom.
- 7) Under optimal growth condition in the MIZ, new productivity averaged 18.6 mmols N m⁻² d⁻¹, with a *f*-ratio of 0.61, and primary productivity averaged 492 mmols C m⁻² d⁻¹. The sequence was element specific, with peak new productivity rates appearing first, followed by maxima in primary productivity.

8) The MIZ bloom provides up to a third of the yearly production in the non-shelf break regions of the EBS and there was some variation in the timing of the bloom along the western pack ice. The intensity and timing of the MIZ bloom in this region do not appear to be accurately represented in ocean color data.

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List of figures

Figure 1. Map of study region showing locations of productivity stations in the eastern Bering Sea (EBS). Inset in lower left provides regional context. The 200 m isobaths is shown to suggest the extent of the broad shelf. Different symbols represent years and station types: Squares = spring 2007 (HLY0701, April 10-May 12, 2007; n=32), Triangles = spring 2008 (HLY0802, March 29-May 6, 2008; n=16), Crosses = spring 2009 (HLY0902, April 3-May 12, 2009; n=31), Stars = early spring 2010 stations (PS1001, March 8-April 6, 2010; n=6). Circled stations indicate in situ productivity incubations.

Figure 2. Representative under-ice profiles of A. Temperature ($^{\circ}\text{C}$), B. Salinity and C. Chl *a* (mg m^{-3}) at 4 stations where in situ productivity was measured. Note that no Chl *a* profile is available for station HLY0902-93.

Figure 3. Productivity profiles generated from on-deck and *in situ* methods of estimating productivity in surface water under 100% ice cover. A & B: On-deck and *in situ* profiles for the specific nitrate uptake rate (vNO_3 , hr^{-1}). C & D: On-deck and in-situ profiles for the specific carbon uptake rate (vC , hr^{-1}).

Figure 4. MODIS Terra composite of Chl *a* from April 25 through May 1, 2009 (color bar, mg m^{-3}). White regions are either clouds or sea ice. Also shown are the mean position of the ice edge in March, April and May by the different patterns of dashed line. The ice edge positions reflect the 15% ice concentration as recorded by Nimbus-7 SMMR and DMSP SSM/I Passive Microwave Data

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Figure 5. Results of multiple ship transits across the ice edge from April 30 through May 6, 2007. The locations of the 6 transits are shown in the small map on the left and the arrow indicates the direction of view for the figure. The sections depict salinity as shown by the labeled color bar. The contours show values of Chl *a* in volts from the CTD fluorometer. The location of the ice edge in April estimated from 15% ice cover is shown as a dashed line.

Figure 6. Profiles of particulate pools, nutrients and productivity at a station well seaward of the ice edge (S90), a station in the MIZ (S98), and a station well shoreward of the ice edge (S110). Panel columns are individual stations (i.e. panels A, D & G are S90; panels B,E & H are S98; and panels C, F, & I are S110). Panel rows show different variables: The top row of panels (A, B & C) show profiles of particulate nitrogen and particulate carbon as well as concentrations of nitrate and ammonium (all in units of micro-moles L⁻¹); The middle row of panels shows profiles of new (nitrate) productivity (ρNO_3), regenerated (ammonium) productivity (ρNH_4) and primary (C) productivity (ρC) (all in units of $\text{mmoles m}^{-3} \text{d}^{-1}$); The bottom row of panels shows profiles of salinity (large dashed line), temperature (°C, solid line) and Chl *a* (mg m^{-3} , small dashed line).

Figure 7. A. The changes in salinity and Chl *a* over 9 days (April 23 – May 4, 2007) along a section in the outer shelf region (see inset in lower left). A. Bar

graph of the estimated ice melt required to generate the observed freshening of the surface waters at the seven stations. B. Section of the salinity changes with depth according to the color bar at right. The Chl *a* changes are superimposed as isopleths in units of mg m^{-3} .

Figure 8. Relationships between biomass and rate measurements in surface waters and physical properties. A. Average Chl *a* in top 20 m vs. mixed layer depth (MLZ). B. Average Chl *a* in top 20 m vs. the estimated salinity decrease since the beginning of ice melt. C. The specific rate of nitrate productivity ($v\text{NO}_3$) in the upper euphotic zone and the salinity decrease normalized to the MLZ. D. The specific rate of primary productivity ($v\text{C}$) in the upper euphotic zone and the salinity decrease normalized to the MLZ.

Figure 9. New productivity rates mapped onto the surface nitrate distributions. The panels contain results for A. 2007 (HLY0701, $n=29$); B. 2008 (HLY0802, $n=14$); C. 2009 (HLY0902, $n=26$); D. 2010 (TT249, $n=5$). Results of on-deck incubations shown for years 2007-2009 and of *in situ* incubations for 2010. The column heights represent the integrated rates of nitrate productivity (ρNO_3 , purple) and ammonium productivity (ρNH_4 , gray), both linear and in units of $\text{mmoles N m}^{-2} \text{ d}^{-1}$. The surface nitrate distributions are the results of spline interpolations of the ship data. Note the smaller sampling region in 2010. The solid black line is the 200 m isobath. The average positions of the major ice edges for March through May are indicated by different dashed lines as labeled

in the figure legend. Note that the ice remaining in May is often present only in irregularly shaped filaments and plumes.

Figure 10. Primary productivity rates mapped onto the surface chlorophyll *a* (*Chl a*) distributions. The column heights represent the integrated rates of C productivity (ρC , gray), linear scale in units of $\text{mmoles C m}^{-2} \text{ d}^{-1}$. The surface *Chl a* distributions are the results of spline interpolations of the ship's underway fluorometer data. As in Figure 9: A. 2007 (HLY0701, $n=28$); B. 2008 (HLY0802, $n=13$); C. 2009 (HLY0902, $n=26$); D. 2010 (TT249, $n=5$). The years 2007-2009 are from on-deck incubations and those for 2010 are from *in situ*. The 200 m depth contour and ice distribution lines also are the same as those used in Figure 9.

Figure 11. Summary of nitrogen uptake, primary productivity and *Chl a* data organized along the ice melt index (amount of surface freshening relative to the winter remnant layer normalized to mixed layer depth). A. Sequence of new productivity in which stations have been organized into 4 ice melt index bins: 1) ice melt index less than 0.001 m^{-1} (ρNO_3 average = $1.24 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=19$); 2) index from 0.001 to 0.005 m^{-1} , (ρNO_3 average = $2.42 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=16$); 3) index from 0.005 to 0.03 m^{-1} , (ρNO_3 average = $18.57 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=29$); and 4) indexes greater than 0.03 m^{-1} , (ρNO_3 average = $11.76 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=6$). B. Same format as in A. but for the nitrogen *f*-ratio: 1) index less than 0.001 m^{-1} (*f*-ratio average = 0.35 , $n=11$); 2) index from 0.001 to 0.005 m^{-1} , (*f*-ratio average = 0.49 , $n=15$); 3) index from 0.005 to 0.03 m^{-1} , (*f*-ratio average = 0.61 , $n=23$); and

1060 4) indexes greater than 0.03 m^{-1} , (f -ratio average = 0.42, $n=6$). C. Same format
1061 as in A. but for primary productivity: 1) index less than 0.001 m^{-1} (ρC average =
1062 $22.73 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=19$); 2) index from 0.001 to 0.005 m^{-1} , (ρC average =
1063 $22.89 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=15$); 3) index from 0.005 to 0.03 m^{-1} , (ρC average =
1064 $190.75 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=27$); and 4) indexes greater than 0.03 m^{-1} , (ρC average
1065 = $491.97 \text{ mmols m}^{-2} \text{ d}^{-1}$, $n=6$). D. Same format as in A. but for the average Chl a
1066 levels in the surface layer: 1) index less than 0.001 m^{-1} (Chl a = $0.62 \text{ }\mu\text{g/L}$, $n=23$);
1067 2) index from 0.001 to 0.005 m^{-1} , (Chl a = $1.55 \text{ }\mu\text{g/L}$, $n=16$); 3) index from 0.005
1068 to 0.03 m^{-1} , (Chl a = $5.65 \text{ }\mu\text{g/L}$, $n=31$); and 4) indexes greater than 0.03 m^{-1} , (Chl
1069 a = $11.76 \text{ }\mu\text{g/L}$, $n=7$).

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Figure 1

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Tables

Table 1. Integrated rates of new (NO_3) and primary productivity from on-deck and *in situ* experiments.

Cruise	Stn.	Water depth (m)	[NO ₃]* (μM)	Chl <i>a</i> * (mg m^{-3})	← New productivity** >			← Primary productivity** >		
					On-deck	<i>in situ</i>	OD/IS ρNO_3	On-deck	<i>in situ</i>	OD/IS ρC
HLY0802	25	75	3		0.16	0.08	2.1	5.92	1.10	5.4
HLY0802	42	55	10	0.14	0.66	0.24	2.7	11.54	1.64	7.1
HLY0802	111	73	12	8.50	28.88	1.91	15.2	298.58	12.04	24.8
HLY0802	116	72	13	0.23	1.65	0.45	3.7	17.66	2.65	6.7
HLY0902	9	56	4	0.18		0.05			0.82	
HLY0902	29	113	18	0.16	0.20	0.10	2.0	5.44	3.09	1.8
HLY0902	45	28	4	0.22	0.15	0.02	7.6	8.03	3.55	2.3
HLY0902	50	38	1	0.18	0.05	0.01	4.3	6.01	1.73	3.5
HLY0902	92	74	11	0.17	0.40	0.21	1.9	7.86	1.70	4.6
HLY0902	93	57	8	1.48	3.20	0.67	4.8	67.19	17.16	3.9
PS1001	8	78	12	0.21		0.16			2.51	
PS1001	15	50	13	0.39		0.13			2.64	

* Average in upper 20 m.

** Rate units are $\text{mmoles m}^{-2} \text{d}^{-1}$

Table 2. Chl *a* normalized particulate C and primary productivity and the ratio of primary to new productivity in the on deck (OD) and *in situ* (IS) incubations.

Cruise-stn.	Chl <i>a</i> ¹	C/Chl ²	<- C spec. prod. ³ ->		C/NO ₃ (OD) ⁴	C/NO ₃ (IS) ⁴
			on deck	<i>in situ</i>		
HLY0802-25					8.6	0.8
HLY0802-42	0.14	634.3	2.7	0.57	13.6	6.7
HLY0802-111	8.50	45.2	1.9	0.04	10.0	4.4
HLY0802-116	0.23	391.3	3.3	0.87	15.0	9.5
HLY0902-9	0.18	1166.7		0.22		1.1
HLY0902-29	0.16	345.0	0.7	0.73	21.3	33.4
HLY0902-45	0.22	354.5	2.9	1.27	71.1	84.8
HLY0902-50	0.18	946.7	1.7	0.94	103.3	94.4
HLY0902-92	0.17	543.5	1.4	0.38	17.4	8.1
HLY0902-93	1.48	92.4	2.3	1.18	19.2	20.6
PS1001-8	0.21	691.4		0.95		18.2
PS1001-15	0.35	582.9		0.63		20.0

¹ – ug L⁻¹

² – ug C (ug Chl *a*)⁻¹

³ – ug C (ug Chl *a*)⁻¹ hr.⁻¹

⁴ – M:M