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Seasonal distribution of dissolved inorganic carbon and net community production on the Bering Sea shelf

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Abstract

The southeastern shelf of the Bering Sea is one of the ocean's most productive ecosystems and sustains more than half of the total US fish landings annually. However, the character of the Bering Sea shelf ecosystem has undergone a dramatic shift over

- the last several decades, causing notable increases in the dominance of temperate features coupled to the decline of arctic species and decreases in the abundance of commercially important organisms. In order to assess the current state of primary production in the southeastern Bering Sea, we measured the spatio-temporal distribution and controls on dissolved inorganic carbon (DIC) concentrations in spring and
- ¹⁰ summer of 2008 across six shelf domains defined by differing biogeochemical characteristics. DIC concentrations were tightly coupled to salinity in spring and ranged from ~1900 µmol kg⁻¹ over the inner shelf to ~2400 µmol kg⁻¹ in the deeper waters of the Bering Sea. In summer, DIC concentrations were lower due to dilution from sea ice melt and primary production. Concentrations were found to be as low ~1800 µmol kg⁻¹ over
- the inner shelf. We found that DIC concentrations were drawn down 30–150 μmol kg⁻¹ in the upper 30 m of the water column due to primary production between the spring and summer occupations. Using the seasonal drawdown of DIC, estimated rates of net community production (NCP) on the inner, middle, and outer shelf averaged 28±10 mmol C m⁻² d⁻¹. However, higher rates of NCP (40–47 mmol C m⁻² d⁻¹) were observed in the "Green Belt" where the greatest confluence of nutrient-rich basin water
- and iron-rich shelf water occurs. We estimated that in 2008, total productivity across the shelf was on the order of $\sim 105 \text{ Tg C yr}^{-1}$. Due to the paucity of consistent, comparable productivity data, it is impossible at this time to quantify whether the system is becoming more or less productive. However, as changing climate continues to modify
- the character of the Bering Sea, we have shown that NCP can be an important indicator of how the ecosystem is functioning.

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1 Introduction

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The southeastern shelf of the Bering Sea (Fig. 1) is one of the oceans' most productive ecosystems, home to over 450 species of fish, 50 species of seabirds, and 25 species of marine mammals (NRC, 1996). This expansive shelf area sustains almost half of the total US fish landings annually through massive pollock (*Theragra chalcogramma*) and salmon populations, the majority of the US nesting seabird population, and some of the highest benthic faunal biomass in the world's ocean (Grebmeier et al., 2006).

Over the past several decades, the physical controls and biological character of the Bering Sea shelf ecosystem have undergone a shift, including notable increases in
the dominance of temperate features coupled to the decline of arctic characteristics, changes in pelagic and benthic ecosystem structure, and decreases in the abundance of commercially important organisms (e.g., Grebmeier et al., 2006; Macklin et al., 2002; Stabeno et al., 1999; Overland and Stabeno, 2004; Hunt et al., 2002; Bond et al., 2003; Stockwell et al., 2001). While most of these changes have been observed on
the southeastern shelf, there is some evidence of change on the northern shelf as well (Overland and Stabeno, 2004; Grebmeier et al., 2006).

Recent ecosystem variability in the Bering Sea has been partly linked to global climate change and recent fluctuations in sea ice extent (e.g., Francis et al., 1998; Springer, 1998; Hollowed et al., 2001; Hunt et al., 2002; Rho and Whitledge, 2007).

- ²⁰ Due to amplification of the global warming signal in Arctic and Subarctic regions (Bryan and Spelman, 1985; Roots, 1989; Serreze and Francis, 2006; Turner et al., 2007), further changes to the physical forcing on the shelf will likely result in continued ecosystem change in the Bering Sea (Stabeno et al., 1999; Schumacher and Alexander, 1999; Hunt and Stabeno, 2002; Schumacher et al., 2002). Of particular concern is the pos-
- sibility that the ecosystem may transition to an alternative state, which could be less economically viable for current fisheries (e.g., Hunt and Stabeno, 2002; Parsons, 1996; Scheffer et al., 2001; Kruse, 1998; Napp and Hunt, 2001).

In addition to impacting the distribution and abundance of higher trophic levels, cli-

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mate change could be affecting pelagic phytoplankton primary production (PP) and food web dynamics (Hunt et al., 2002; Hunt and Stabeno, 2002). In order to assess the current state of PP in the southeastern Bering Sea, we describe the spatio-temporal distribution and controls on dissolved inorganic carbon (DIC) concentrations across

- six domains defined by differing biogeochemical characteristics. We then use the seasonal drawdown of DIC in the mixed layer to estimate rates of net community production (NCP), which can be used as an indicator of ecosystem functionality (e.g., Bates et al., 2005; Mathis et al., 2009). Because a number of processes impact the cycling and fate of carbon in the ecosystem including the timing of sea ice retreat, water temperature, attratification, and anaging obundance (Hunt and Stahana, 2002). NCP is a valuable
- ¹⁰ stratification, and species abundance (Hunt and Stabeno, 2002), NCP is a valuable tool in assessing net ecosystem production (NEP; Andersson et al., 2004).

2 Background

2.1 Hydrography of the Bering Sea shelf

2.1.1 Geographic domains and frontal systems

¹⁵ Physical processes and seasonal sea ice cover in the Bering Sea play a major role in controlling water mass properties and shaping the ecosystem (e.g., McRoy and Goering, 1974; Wyllie-Echeverria and Ohtani, 1999; Stabeno et al., 1999, 2002; Grebmeier et al., 2006). During the winter, sea-ice covers much of the Bering Sea shelf, but the advance is constrained by the presence of relatively warm water in the central and southern Bering Sea. During winter, water-masses are confined to a small range of temperature-salinity through mixing and homogenization by ventilation, brine rejection and mixing. During the summertime, sea-ice retreats into the Chukchi Sea and Canada Basin of the Arctic Ocean (Fig. 1).

The >500 000 km² of the Bering Sea shelf is split into roughly six regions (Fig. 1). The entire shelf can be divided into northern and southern sections at approximately





60° N based on the relative influence of sea ice on bottom water temperatures (e.g., Stabeno et al., 2002; Ohtani and Azumaya, 1995; Wyllie-Escheveria, 1995; Wyllie-Escheveria and Wooster, 1998; Coachman, 1986). Summertime bottom water temperatures north of 60° N tend to be lower than bottom water temperatures to the south. Three along-shelf domains also exist, differentiated by frontal features imparted by strong horizontal property gradients during summer (e.g., Coachman, 1986; Kinder and Coachman, 1978; Coachman and Charnell, 1979; Stabeno et al., 2002; Kachel et al., 2002). The Inner Front, overlying the 50 m isobath (Kachel et al., 2002), di-vides the "Coastal Domain" from the "Middle Domain" (Figs. 1, 2). The "Central Front",

¹⁰ a broad transitional zone between the 80 m and 100 m isobaths (Coachman, 1986), separates the middle and outer domains. The "Shelf-Break Front", between the 170 m and 250 m isobaths (Schumacher and Stabeno, 1998), divides the outer shelf from basin waters (Fig. 2). In summer, these fronts inhibit most cross-shelf advection and mixing (Stabeno and Hunt, 2002; Coachman, 1986; Kachel et al., 2002).

15 2.1.2 Hydrographic structure

The annual formation and melting of sea-ice is one of the greatest contributors to water column structure in the Bering Sea. The ~1700 km advance and retreat of sea ice over the Bering Sea shelf is the largest in any of the Arctic or Subarctic regions (Walsh and Johnson, 1979), making it a significant source and sink for freshwater over the shelf.

- Increases in freshwater content caused by melting modify the water column density gradients, contributing to the maintenance of the summer stratification necessary for production (see Optimum Stability estimates by Coyle et al., 2008). Prior to melting, the advance and persistence of sea-ice over the shelf also has a distinct impact on hydrographic structure, especially over the northern portion of the shelf. Because sea-
- ice retreat begins in the south (Pease, 1980; Neibauer et al., 1990), ice persists longer over the northern shelf and northern bottom water temperatures in summer and fall are lower, leading to the division of the cross-shelf domains at ~60° N. Sea-ice persistence also plays a role in the formation of a cold water mass (<2°C; Maeda, 1977; Khen,</p>





1998) isolated by thermal stratification in the Middle Domain (Stabeno et al., 2002; Wyllie-Escheveria, 1995; Wyllie-Escheveria and Wooster, 1998).

The other major contributor to hydrographic structure in this region is tidal mixing. As the dominant source of total kinetic energy flow across the shelf (Coachman, 1986;

- Stabeno et al., 2006), tidal forces typically mix the water column to about 40 m, creating a well-mixed bottom layer in each domain. Because the Coastal Domain averages a depth of less than 50 m, tidal energy and wind mixing completely overturn the water column and prevent the formation of strong stratification in summer. However, tidal energy mixes only the bottom portion of the Middle (50–100 m) and Outer (100–180 m)
- domains, creating distinct upper and lower layers. Wind forcing mixes the surface layer in both regions, and in the deeper Outer Domain the wind-mixed surface layer and tidally-mixed bottom layer are separated by a sharp pycnocline (Stabeno et al., 2006). Summertime stratification is typically strongest in the Middle Domain and weakest in the Coastal Domain.

15 2.1.3 Nutrients

Inorganic nitrogen is widely considered to be the limiting nutrient to primary production over the Bering Sea shelf because concentrations are usually depleted to undetectable levels by late spring or early summer (Niebauer et al., 1995; Hattori and Goering, 1981; Whitledge et al., 1988; Whitledge and Luchin, 1999; Wong et al., 2002). Although
²⁰ cross-shelf advection and diffusion are largely prohibited by strong stratification and frontal systems, post-production inorganic nitrogen stocks can sometimes be minimally renewed by the interaction of deep basin water with Bering shelf water to produce brief summer-time blooms. In addition, storms during the summer can mix nitrate from the bottom layer into the surface to support short-term blooms over the Middle and

Outer Domains. Shelf-break topography, mesoscale eddies and summer storms can contribute small amounts of inorganic nitrogen as far as the Coastal Domain through shelf-slope exchange, but nutrient content and renewal is typically higher near the shelf break and slope due to proximity to basin waters (e.g., Mizobata and Saitoh, 2004;





Stabeno et al., 1999; Whitledge and Luchin, 1999; Sambrotto et al., 1986; Schumacher and Reed, 1992; Stabeno and van Meurs, 1999; Schumacher and Stabeno, 1994, 1998; Mizobata et al., 2002; Bond and Overland, 2005; Rho et al., 2005; Whitledge et al., 1986).

⁵ 2.2 Primary production, the ¹⁴C method, and annual rates of PP for the Bering Sea shelf

Because of the importance of Bering Sea shelf fisheries, there have been numerous studies of pelagic primary production over the southeast shelf (Table 1). The first efforts in this region began in the early 1960s, using the abundance of fish supported by the ecosystem to infer the necessary amount of primary production (900 mg C m⁻² d⁻¹; 10 Graham and Edwards, 1962). By the 1970s, the most common method for measurement of primary production (PP) became the in situ ¹⁴C technique developed by Sorokin (1960), which is still widely used today (e.g., Koblentz-Mishke et al., 1970; Motoda and Minoda, 1974; McRoy and Goering, 1976; Saino et al., 1979; Tsiban and Korsak, 1987; Sorokin, 1999; Rho and Whitledge, 2007). While this method pro-15 vides "short-term" rates of primary production sufficiently accurate in some systems and within a single trophic level, variations in species composition (Krupatkina et al., 1987) can introduce significant errors to the estimation of primary production. Further, because PP rates range so widely throughout the growing season and fluctuate differently across the shelf, it is difficult to extrapolate these measurements across both 20 time and space. Even recent extrapolations show annual PP rate error estimates of \sim 60% (Rho and Whitledge, 2007). Without continuous, year-round measurements made across the entire shelf, an accurate annual shelf PP value estimated by the C¹⁴ method is difficult to quantify (Rho and Whitledge, 2007).

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2.2.1 Primary production variability within the different Bering Sea shelf domains

Outer Domain. Although nitrate is present in sufficient concentrations on the outer domains of the Bering Sea shelf, production is low in this region compared to the middle
shelf. This is likely due to iron limitation: in general, iron concentrations tend to be highest nearer the coast, and decrease off the shelf where iron-deficient basin waters have a greater influence on the water column (Fujishima et al., 2001; Takata et al., 2005; Suzuki et al., 2002). Over the Outer Domain, iron is not present in high enough concentrations to allow complete drawdown of macronutrients, and some classify this area as a High-Nutrient, Low-Chlorophyll system as a result (Aguilar-Islas et al., 2007; Banse and English, 1999; Fung et al., 2000; Moore et al., 2002). Other work suggests that in iron-limited HNLC systems, particularly those dominated by basin waters, a secondary silicic acid limitation arises (Hutchins and Bruland, 1998; Koike et al., 2001). This silicate limitation may further restrict phytoplankton biomass in the Outer

15 Domain.

Middle Domain. Macro- and micronutrient concentrations trend inversely to each other, and sufficiently high concentrations of each seem to coincide at approximately the central front where a highly productive region known as the "Green Belt" spans parts of both the Middle and Outer Domains and the slope (Springer et al., 1996;

- Okkonen et al., 2004). Here, the confluence of coastally derived iron from weak crossshelf flows, bioavailable sedimentary iron from Middle and Coastal Domain sediments mixed into the water column through tidal currents during winter, and basin-derived nutrients from upwelled deep water supports a large accumulation of biomass in summer (Simpson and McRoy, 1999; McRoy et al., 2001). Unique fluid dynamics occurring at
- the Central Front may also trap phytoplankton in this idealized regime (Sorokin and Mikheev, 1979; Mackas et al., 1985; Coachman et al., 1986; Franks, 1992; Springer et al., 1996), contributing to the high primary production signal of the area. Annual PP rates here are further bolstered by the supply of both nutrients and iron throughout the

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summer by eddies and mixing, which prolong the production season (e.g., Whitledge et al., 1986; Rho et al., 2005; Springer et al., 1996).

Coastal Domain. Frontal systems block the Coastal Domain from extensive influence of high-nutrient basin water. Nutrient concentrations here are lower to begin the

- ⁵ production season, and mechanisms of nutrient resupply are limited, except along the Inner Front where nutrients can be introduced from the nutrient rich bottom layer of the Middle Domain. In contrast to the Middle and Outer Domains, the shallow, coastally influenced waters of the Coastal Domain are iron-replete (Aguilar-Islas et al., 2007). High iron concentrations permit the rapid maximization of production rates early in the
- season, but nutrient exhaustion in the euphotic zone typically prohibits extended periods of PP (e.g., Whitledge et al., 1986; Rho et al., 2005; Bond and Overland, 2005; Sambrotto and Goering, 1983; Sambrotto et al., 1986; Hansell et al., 1993; Springer and McRoy, 1993).

2.2.2 Other physical and biogeochemical controls on PP

- Primary production in the Bering Sea tends to occur in two phases. Early in the season, the melting of sea-ice and decreased wind mixing forces the water column to stratify in the marginal ice-edge zone. This fosters an intense bloom at the ice edge. However, following ice retreat, wind mixing may be enough to break down the density stratification imparted by the fresh meltwater (e.g., Lovvorn et al., 2005; Niebauer et al.,
- 1995) and limit continued open water PP. The second phase of PP occurs when solar radiation stabilizes the water column enough to support an open-water bloom. Both pulses in the production cycle are dependent on the timing of sea ice retreat. When sea-ice retreats early, light levels are insufficient for production, and the bloom is delayed. During this lag, solar radiation increases and heats the water column, providing
- ideal temperature conditions for zooplankton growth. By the time the bloom develops, zooplankton biomass is high and heavy grazing pressure likely reduces the amount of organic carbon exported to the benthos (Saitoh et al., 2002; Lovvorn et al., 2005). When ice retreat comes later in the season, stratification and solar radiation do not limit





primary production. Additionally, colder water temperatures persist and limit zooplankton development. With minimal grazing pressure on the bloom, the amount of carbon export to the benthos increases. When sea-ice does not extend over a given area, solar radiation alone imparts stratification much later in the season and production is ⁵ consequently grazed heavily by copepods, lending to a greater pelagic character.

2.2.3 Organic carbon export on the Bering Sea shelf

The organic matter produced in the surface layer in both spring and summer is consumed by copepods and ultimately exported to benthic regions, although this export and the higher trophic levels it supports has a slightly different character in each domain (e.g., Cooney, 1981; Cooney and Coyle, 1982; Springer et al., 1989; Vidal and Smith, 1986; Wyllie-Escheveria and Wooster, 1998; Walsh and McRoy, 1986; Hunt and Stabeno, 2002). Because of the proximity to fronts and unique flows at the shelf edge, approximately 48% of Outer Domain biomass is exported over the shelf break (Walsh and McRoy, 1986). Copepods are generally very large outside the central front, where they presumably consume this exported biomass (e.g., Cooney, 1981; Springer and 15 Roseneau, 1985; Coyle et al., 1996). Direct carbon flux to the benthos from primary production is highest over the Middle and Coastal Domains (Grebmeier and McRoy, 1989; Haflinger, 1981), where smaller species of copepods typical of the region inshore of the central front are incapable of completely grazing the prodigious volume of production in the "Green Belt" (Cooney, 1981) and the rapid volume of production of 20 the inner shelf.

Total organic matter export to the benthos is greatest over the Outer and Middle Domains of the shelf where combined primary and secondary biomass is highest. Because copepod biomass is enhanced with warmer temperatures (Huntley and Lopez,

1992), export may be higher in the southern region of the shelf where water temperatures warm earlier in the season (Pease, 1980; Neibauer et al., 1990). Studies of the fate of total organic matter export in highly productive polar seas (Mathis et al., 2009) have shown that the majority of it is exported from the mixed layer as sinking particles,

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with only a small amount retained in the mixed layer. It is likely that similar conditions exist in the southeastern Bering Sea and most of the organic matter is remineralized in bottom waters and in sediments (Grebmeier and McRoy, 1989; Sambrotto et al., 2008).

2.3 Net community production

- An alternative approach to direct-rate estimates of annual production uses the seasonal 5 consumption or production of the reaction products of photosynthesis (e.g. dissolved inorganic carbon, inorganic nitrogen, or dissolved oxygen, DO) to determine the net drawdown of inorganic matter or the accumulation of organic matter (e.g., Weiss et al., 1979; Codispoti et al., 1982, 1986; Karl et al., 1991; Chipman et al., 1993; Yager et al., 1995; Bates et al., 1998a; Lee, 2001; Lee et al., 2002; Bates et al., 2006). Here, 10 the cumulative change in surface layer concentrations of oxygen, inorganic nitrogen, or inorganic carbon is calculated by measurement of pre-bloom and post-bloom (early spring and midsummer) concentrations. Dividing this seasonal decrease in inventory
- by the amount of time between observations provides an integrated geochemical estimate of the rate of NCP which is conceptually equivalent to new production (Williams, 1993) estimated using NPP rates and f-ratios (Eppley and Peterson, 1979; Hansell et al., 1993; Springer et al., 1996; Varela and Harrison, 1999). Geochemical estimates of NCP can also be extrapolated across time and space, making high-resolution basinwide estimates of ecosystem production possible.
- Few estimates of NCP have been conducted in the Bering Sea region, but there 20 are historical studies of dissolved oxygen, inorganic nitrogen, and inorganic carbon drawdown (e.g., oxygen: Ivenakov, 1961; Azova, 1964; Sapohznikov and Naletova, 1995; inorganic nitrogen: Hansell et al., 1993; inorganic carbon: Codispoti et al., 1982, 1986). Estimation of NCP using oxygen and inorganic carbon drawdown have given
- the highest and lowest production rates, respectively (Table 2).

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3 Methods

3.1 Field sampling

Physical, biogeochemical and biological measurements were made from the USCGC Healy during two cruises to the eastern Bering Sea in 2008. During the spring (April-May) and summer (June–July) cruises CTD stations were occupied on three east to 5 west transect lines and one north-south transect line (Fig. 1). The SL line was the northern most transect extending from near shore across the broad northern part of the shelf to a depth of ~90 m. The central line (MN) extended roughly from the southern tip of Nunivak Island across the shelf south of St. Matthew Island out to the shelf break (2000 m). The southern line (NP) extended from the southern tip of Nunivak Island 10 southwest past the 150 m isobath. The north-south line followed the 70 m isobath for the length of the shelf southward from the SL line and ended southeast of the NP line. At the beginning of the spring cruise, sea ice cover was near 100% at all stations with the exception of some minor leads. During sampling of the SL, MN, and NP lines significant sea ice was present. Towards the end of the spring cruise, sea ice started to diminish. The southern half of the 70 m isobath line was ice free when sampled at the end of the cruise. During summer, the entire Bering Sea shelf was sea-ice free.

At each CTD station, a suite of biological and chemical measurements were collected, including salinity, inorganic nutrients (ammonium, nitrate, nitrite, phosphate, reactive silicon, and urea), DIC, and DO.

3.2 Laboratory analysis

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All DIC samples were collected as suggested by the Guide to Best Practices for Ocean CO_2 measurements (Dickson et al., 2007). Accordingly, seawater samples for DIC were drawn from Niskin bottles into pre-cleaned ~300 mL borosilicate bottles. After collection, all samples were poisoned with 200 µL of saturated aqueous mercuric chloride (HgCl₂) solution to halt biological alteration of DIC concentrations, sealed, and

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returned to the lab for analysis.

DIC samples were analyzed using a highly precise and accurate gas extraction/coulometric detection system (~0.02%, <1 μ mol kg⁻¹; Bates, 2001). The analytical system consists of a VINDTA 3C (Versatile Instrument for the Detection of Total Alkalin-

ity) coupled to a CO₂ coulometer (model 5012; UIC Coulometrics). Routine analyses of Certified Reference Materials (CRMs, provided by A.G. Dickson, Scripps Institution of Oceanography) and repeat sampling ensured that the accuracy of the DIC measurements was within 0.05% and was stable over time.

3.3 Estimates of NCP

- In our approach, we exploit seasonal changes in biological reactants and products (e.g., DIC), to estimate rates of NCP and identify minor factors such as gas exchange and remineralization that can introduce errors. NCP is calculated from the observed seasonal drawdown of DIC attributed to primary production over time, according to the following equation (Williams, 1993):
- ¹⁵ NCP = $DIC_{spring} DIC_{summer} = \Delta DIC$ (moles C per unit volume or area).

However, Eq. (1) reflects all seasonal modifications to DIC, while only a portion of the seasonal drawdown can be attributed to biological production in the Bering Sea. Seaice melt and terrestrial inputs can impact DIC concentrations in the upper mixed layer. The addition of water with low concentrations of DIC effectively dilutes the surface layer,

- decreasing concentrations of DIC. Because NCP also decreases DIC concentrations in the upper 30 m, ice melt and low DIC terrestrial runoff can cause a false amplification of the NCP signal. These effects on DIC concentrations can be corrected by normalizing DIC to a constant salinity of 35, thus rendering NCP the only significant process affecting seasonal changes in DIC concentrations (Mathis et al., 2009; Bates et al.,
- ²⁵ 2005). The effects of air-sea CO_2 flux and vertical diffusion on ΔDIC are discussed in Sect. 5.3.

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(1)



4 Results

4.1 Frontal systems and hydrographic structure

Temperature, salinity and density were used to identify frontal systems in both spring and summer. In spring, closely packed vertical isopycnals indicated the presence of
a front approximately overlying the 50 m isobath, where lower coastal densities began to increase offshore. Temperature and salinity, in addition to density, identified a front at the 100 m isobath. Along the coast, waters were largely vertically mixed, exhibiting uniform temperature and salinity from the surface to the bottom. At the 50 m isobath front, waters transitioned to a two-layer system. Density frontal structure was least clearly defined along the SL line due weak tidal flows and resultant lack of mixing, and was most developed along the MN line. Density frontal structure was apparent between 58° N and 60° N along the 70 m line, with fresher surface water and colder bottom temperatures to the north.

Summertime frontal systems were more clearly developed than in spring. Two-layer stratification was evident in all three properties (temperature, salinity, and density). A front overlying the 50 m isobath was clearly defined by temperature throughout the entire water column along all lines. In contrast to spring, where well mixed coastal waters transitioned to a two layer system much further seaward, the summertime transition to a two layer system occurred approximately at this inshore front. Rapidly chang-

ing temperature gradients identified a second front at approximately the 90 m isobath along the MN and NP lines, although this structure was not apparent along the SL line and was much broader than the inshore front. Summertime variance along the 70 m isobath was minimal, although a broad transitional zone in temperature was apparent between 58.5° N and 59.5° N, and isohalines showed a front occurring at approximately 61° N.

Stratification isolated a layer of cold bottom water between the inner front and the middle front during summer. This cold pool extended from the bottom to approximately 25 m below the surface on the MN and NP lines. A low salinity feature was also ap-

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parent in the summer surface layer seaward of the inner front and centered over the central front, likely due to the influences of fresh water from ice which melted in May and June. With the weak winds of late spring, this fresher surface water is not mixed vertically and thus a fresh water lens (~20 m deep) contributes to the vertical structure over the northern shelf.

4.2 Spatial and seasonal distributions of inorganic nitrogen and oxygen

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Spatially, changes in inorganic nutrients and DO concentration coincided with frontal transition zones. In particular, nitrate concentrations followed isohalines very closely in spring, and isothermal lines in summer. In general, DO concentrations followed density structure, but did not adhere to isohalines or isothermals as clearly as inorganic nitrogen concentrations.

Three broad zones were apparent in both seasons, separated by the fronts. In spring, inorganic nitrogen concentrations inshore of the innermost front were lowest (~7.5 μmol kg⁻¹), while DO concentrations were highest in this region (~355 μmol kg⁻¹). Inorganic nitrogen increased off the shelf, seaward of this front and peaked in bottom waters of the outer domain at ~28 μmol kg⁻¹, where DO concentrations were lowest (~300 μmol kg⁻¹). Springtime inorganic nitrogen concentrations were fairly uniform with depth, while oxygen concentrations exhibited a two-layer system seaward of the 100 m isobath front. Along the shelf, inorganic nitrogen concentrations concentrations decreased to the south (~15 μmol kg⁻¹ to ~10 μmol kg⁻¹) while oxygen concentrations increased (~325 μmol kg⁻¹ to ~415 μmol kg⁻¹), as was apparent both on the 70 m line and in the variability between concentrations along the cross-shelf lines (NP, MN, and SL). There were two low-nitrate (~5 μmol kg⁻¹) features in the surface layer along the 70 m line, at approximately 59° N and 56° N.

²⁵ Summertime inorganic nitrogen concentrations were consistently lower than springtime concentrations. Inshore of the innermost front, inorganic nitrogen concentrations were completely depleted throughout the entire water column. Seaward of this front, nitrate concentrations were still depleted in the surface layer, although higher con-



centrations (~15 μmol kg⁻¹ to 30 μmol kg⁻¹) of nitrate were observed in bottom waters. In summer, subsurface zones (~15 m to 50 m) of high oxygen concentration (~400 μmol kg⁻¹) were present across the entire shelf on the SL and MN lines. Along the NP line, oxygen concentrations were highest throughout the water column in the Coastal Domain (~380 μmol kg⁻¹). In general, oxygen concentrations were higher in summer in the upper 50 m compared to spring, but were lower relative to spring concentrations in the bottom waters over the shelf.

4.3 Spatial and seasonal distributions of DIC

Figure 3 shows the spatial distribution of spring DIC concentrations averaged over the upper 30 m of the shelf. The highest surface layer concentrations were found in the inner domain and the northern regions of the Middle Domain (~2100–~2150 μ mol kg⁻¹). The lowest surface layer concentrations occurred in the Middle and Outer Domains to the south (~2025 μ mol kg⁻¹). Comparison of the variation of DIC concentrations with depth along the three sampling lines (Fig. 4a–d) shows that concentrations throughout the water column were highest in the northern region of the shelf (~2130 μ mol kg⁻¹). Concentrations along the 70 m isobath line (Fig. 4d) also showed distinctly higher con-

centrations north of 61° N.

Across the shelf, there were three distinct regions of DIC concentrations during spring. Concentrations on the inner shelf were fairly constant with depth. Coastal Domain DIC concentrations rapidly decreased by \sim 50 µmol kg⁻¹ through the inner front to the Middle Domain. Middle Domain DIC concentrations were relatively low along all lines, but particularly in the upper 10 m along the SL line. Seaward of the middle front, DIC concentrations increased, and stratified into a two-layer system. DIC concentrations increased more rapidly below 40 m to \sim 2125 µmol kg⁻¹ at 100 m, and to \sim 2225 µmol kg⁻¹ at 250 m.

Summertime concentrations of DIC averaged over the upper 30 m (Fig. 5), were on average lower than springtime concentrations by ${\sim}90\,\mu\text{mol}\,\text{kg}^{-1}$ and decreased

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most in the middle and outer domains. Inshore, concentrations of DIC were moderate (~2050 μ mol kg⁻¹) and constant with depth. In contrast to spring, summer DIC concentrations horizontally stratified into a two layer system in the middle domain (Fig. 6a–d). In the middle domain, the upper layer (0m–25m) had a dramatically lower concentration (~1900 μ mol kg⁻¹) than the slightly westward bottom 40 m of water (~2200 μ mol kg⁻¹). This stratification was not present seaward of the middle front along the SL line, where DIC concentrations were constant with depth (~2050 μ mol kg⁻¹). Along the MN and NP lines, Outer Domain DIC concentrations increased with depth (~2050 μ mol kg⁻¹ at 0 m to 2250 μ mol kg⁻¹ at 250 m).

10 5 Discussion

5.1 Rates of net community production

As discusses earlier, we normalized DIC concentrations in spring and summer to a salinity of 35 in the estimate of NCP rates (Table 3). In the spring, nDIC concentrations ranged from 2230 µmol kg⁻¹ to 2330 µmol kg⁻¹, with an average nDIC con-¹⁵ centration of ~2300 µmol kg⁻¹. In summer, nDIC concentrations were lower, ranging from 2100 µmol kg⁻¹ to 2280 µmol kg⁻¹, with an average nDIC concentration of 2197 µmol kg⁻¹. Summertime drawdown was on average ~90 µmol kg⁻¹ (see Table 3), and was highest in the Middle and Outer Domains in the region of the "Green Belt". The corrective effects of normalization on DIC concentrations can be seen in Fig. 7a–

- d. Here, DIC and nDIC are plotted relative to salinity in both spring and summer. While the relationship between nDIC and salinity (Fig. 7c and d) was similar to the relationship between DIC and salinity (Fig. 7a and b), the summertime dispersion of nDIC was much more vertically distributed. In Fig. 7c and d, the horizontal dispersion of DIC concentrations once due to changing salinity has been removed by normalization, and any
- dilution effects on DIC concentrations have been eliminated. As a result, the effects of biological processes are more correctly indicated. In spring (Fig. 7c), nDIC concentra-

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tions were constrained within a small range of salinities. In summer (Fig. 7d), some nDIC concentrations were drawn down by primary production, causing an increase in dispersion closer to the *x*-axis. Water column and sedimentary remineralization raised concentrations of nDIC in bottom waters, increasing the range of summertime disper-⁵ sion in the opposite direction.

NCP is also apparent in Fig. 8a and b, where nDIC is plotted relative to inorganic nitrogen. In spring (Fig. 8a), average nDIC concentration was approximately 2300 µmol kg⁻¹, as indicated by the dotted line, and most nDIC concentrations were well constrained within a small range of inorganic nitrogen concentrations, indicated by the dotted circle. In Fig. 8b, the springtime average and clustering location is also shown relative to the summertime nDIC concentrations. Dispersion beneath the dotted line and dotted circle increased due to biological processes. As production affects both axes, the biological process vectors are skewed: primary production decreases both nDIC and inorganic nitrogen, and increases dispersion in the direction of the origin, where as the production of nDIC and inorganic nitrogen through water column and sedimentary oxidation of organic matter increases dispersion away from the origin.

Inorganic nitrogen concentrations in surface waters decreased to zero in summer at most locations and caused an accumulation of points at and near the *y*-axis. In areas where nitrate is not limiting, such as the HNLC middle and outer domains, nDIC

- ²⁰ concentrations are not clustered near the axes, but do accumulate below the spring average concentration. There is also an increased dispersion to the upper right, due to some oxidation of organic matter in bottom waters. This can be seen as an amplified DIC signal in the bottom waters (most obvious in Fig. 6a) beneath the areas of highest drawdown in the surface waters. The coupling of NCP at the surface to increases of DIC
- ²⁵ in bottom waters has also been observed in the Chukchi Sea (Bates et al., 2009; Bates and Mathis, 2009). Similarly, this remineralized DIC lowers the pH of these bottom waters suppressing the carbonate mineral saturation states (Mathis et al., 2010).

The relationships between nDIC and DO in spring and summer are shown in Fig. 9a and b. The relationship between nDIC and DO is tightly clustered in spring, shown by

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the dotted circle. The cumulative effects of biological processes cause the increase in dispersion seen in summer, compared to the springtime cluster (again indicated by the dotted circle). Production also affects both of these axes but the vectors are opposite to those for the inorganic nitrogen vs. nDIC: production produces dissolved oxygen while

⁵ decreasing nDIC, and thus draws points towards the *x*-axis and away from the *y*-axis, while nutrient regeneration increases nDIC and decreases DO, drawing points towards the *y*-axis but away from the *x*-axis.

NCP estimates integrated over the upper 30 m calculated from nDIC according to the Eq. (1) are shown in Fig. 10 and Table 3. The average time between station occupations was ~100 d leading to an average DIC drawdown of ~90 μ mol kg⁻¹, with

cupations was ~100 d leading to an average DIC drawdown of ~90 μmol kg⁻¹, with a subsequent average NCP of 334 μmol kg⁻¹. However, rates of NCP varied across the biogeochemical domains (see Table 4). NCP was lowest in the northern region of the Inner Domain (19.3±6.0 mmol C m⁻² d⁻¹), and highest in the northern region of the Middle Domain (37.4±8.2 mmol C m⁻² d⁻¹). Limited sampling prevented calculation of a value for the northern section of the Outer Domain, but NCP in the southern half of the Outer Domain was similar to the high NCP in the northern section of the Middle

Domain $(34.2 \pm 10.7 \text{ mmol C m}^{-2} \text{ d}^{-1}).$

NCP in the Coastal Domain is likely low because of the low initial stock of macronutrients relative to the remainder of the shelf. Although waters over the inner domain were often mixed to depth, the Coastal Domain is the shallowest of the three alongshelf zones. Despite mixing, the available stock of nutrients, particularly nitrate in this smaller domain could not sustain production, and macronutrients were completely depleted in both the northern and southern halves of this domain.

The high NCP of the Middle and Outer Domain is likely due to the confluence of shelf-derived iron and basin-derived nutrients at the shelf-break front that provides an ideal environment for primary production. Eddies spawned along the shelf break and proximity to the basin further supply nutrients well into the growing season, sustaining longer periods of primary production relative to the zones to the east and west.

High levels of NCP appear to be coupled to the summertime bottom water maxima

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in DIC concentrations. This may be due to the sedimentary and water column remineralization of organic matter exported to depth in large quantities, although a previous study indicated that this export should be minimal over the shelf, and ungrazed organic matter should be deposited over the slope (Walsh and McRoy, 1986).

- Other studies in the region show similar values of NCP (e.g., Rho and Whitledge, 2007; Springer et al., 1996; Springer and McRoy, 1993). Springer and McRoy (1993) and Rho and Whitledge (2007) used a combination of estimates from different times during the production season across several years to obtain average annual measurements across the season. Despite high error, average values from Rho and Whitledge
 were within 2.5 mmol C m⁻² d⁻¹ of the estimates presented here. Springer and McRoy estimated production rates for the Coastal Domain fell within 1.7 mmol C m⁻² d⁻¹ of our estimates. The average estimates taken from the "Green Belt" literature review by
- Springer et al. (1996) also fell within 2.5 mmol C m⁻² d⁻¹ of our NCP estimates calculated from DIC drawdown.

15 5.2 Estimates of early season NCP

The lack of DIC data on the Bering Sea shelf prior to the spring cruise makes it difficult to determine rates of primary production in the early part of the growing season. However, DIC concentrations were fairly uniform across most of the domains (Fig. 4a–d). nDIC distributions did show locations along the southern end of the shelf where
concentrations were slightly lower in some places (Fig. 7a), perhaps indicating early season NCP, but these waters were still nutrient-rich (Fig. 8a) and showed no signs of enhanced oxygen production (Fig. 9a). Sea-ice cover was also present at all sampled locations in spring, further reducing the possibility that any significant production had occurred do to limited solar irradiance. It is likely that any productivity that did occur prior to our initial occupation in spring was limited to the water column-ice interface and did not significantly influence our NCP estimates.

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5.3 Assumptions and caveats

We had to make several assumptions in order to use the seasonal carbon mass balance to estimate NCP. This method does not take into account contributions of DIC to the mixed layer through air-sea CO₂ gas exchange and vertical diffusion (Bates, 2006). Both of these processes do add DIC to the mixed layer, particularly as productivity widens the gradient between the surface ocean and the atmosphere and the mixed layer and deeper water masses.

Previous studies have indicated that the Bering Sea is a net sink for atmospheric CO₂ during ice-free periods (Takahashi et al., 2002, 2009). Bates et al. (2005) determined that in the Chukchi Sea, given a CO₂ flux rate from the atmosphere to the surface ocean of ~5–10 mmol CO₂ m⁻² d⁻¹ the added contribution of DIC to the mixed layer would be on the order of ~5–10 µmol kg⁻¹. Assuming a similar flux into the Bering Sea would add ~4–8 mmol m⁻² d⁻¹ to our NCP estimates, an approximately 10–20% underestimation of NCP. This contribution is likely smaller because the shelf was not

15 100% ice-free for the entire period between spring and summer, which would have limited air-sea exchange. DIC concentrations were also not drawn down as much over the Bering Sea shelf as over the Chukchi Sea shelf which would have reduced the air-sea disequilibrium and further reduced the flux of CO₂.

Vertical diffusion of CO2 across the interface between the mixed layer and bottom wa-

ters would have also contributed a minor amount (<1-2 μmol kg⁻¹) of CO₂ to the DIC pool in the upper 30 m. Following the approach of Bates et al. (2005), we estimated vertical diffusivity of CO₂ over the Bering Sea shelf as the product of the vertical diffusion coefficient *K*_v, the vertical gradient of inorganic carbon (*δ*DIC/*δz*) below the mixed layer (i.e., vertical gradient in DIC between 30–50 m), and the seawater density (Denman and Gargett, 1983). Even though *K*_v, is variable, ranging from 0.2–80 cm² s⁻¹ (Denman and Gargett, 1983), and average *K*_v, of 30 cm² s⁻¹ (Bates et al., 2005) increased the upper 30 m DIC pool by ~3.6 μmol kg⁻¹ over a 100 d period. Taking this flux into account would add ~0.7–1.25 mmol Cm² d⁻¹ to our NCP rates estimates. However,

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the intense stratification that sets up between spring and summer between the surface and bottom layers likely reduced this flux of DIC across the interface.

Underestimation of NCP may also occur due the remineralization of organic matter in the upper 30 m between spring and summer. While most of the particulate organic

- ⁵ carbon (POC) is exported in a highly productive Subarctic system (e.g., Mathis et al., 2007), the remineralization of highly labile dissolved organic carbon (DOC) between station occupations (Hansell et al., 1997) can add DIC back into surface layer, decreasing the seasonal drawdown signal. However, any significant contribution of DIC from remineralization directly within the mixed layer seems unlikely given the slow rates of unside the seasonal draw back in the seasonal draw back is a seasonal draw back in the seasonal draw back in the seasonal draw back is a seasonal draw back in the seasonal draw back is a seasonal draw back in the seasonal draw back is a seasonal draw back in the seasonal draw back in the seasonal draw back is a seasonal draw back in the seasonal
- of remineralization and the relatively short time between station occupations. It has also been shown in other highly productive polar seas (e.g., Mathis et al., 2006) that only a small fraction of NCP (~10%) is retained in the mixed layer and is available for remineralization.

6 Conclusions

In the spring and summer of 2008, spatio-temporal variability of inorganic carbon and NCP were measured for the southeastern Bering Sea shelf region. Hydrographic and biogeochemical characteristics divided this shelf into six distinct regimes. Bottom water temperature and density split the shelf into northern and southern regimes at approximately 60° N. Frontal systems approximately overlying the 50 m and 100 m isobaths
 also divided the shelf into three zones: the Coastal Domain (0 m–50 m water depth); the Middle Domain (50 m–100 m water depth) and the Outer Domain (100 m–180 m water depth).

Biogeochemical characteristics were unique in each zone and dictated the character of productivity in each domain. Macronutrient concentrations (i.e., nitrate) were ²⁵ higher nearer the basin, while micronutrient (i.e., iron) concentrations were higher nearer to the coast. As expected, the intersection of these inverse gradients at the Central Front produced the highest rates of NCP in the region (~47 mmol C m⁻² d⁻¹).





The limited availability of macronutrients in the Inner Domain limited NCP to $\sim 19.3\pm6.0 \text{ mmol C} \text{m}^{-2} \text{d}^{-1}$ in the northern zone and $\sim 22.5\pm6.5 \text{ mmol C} \text{m}^{-2} \text{d}^{-1}$ in the southern zone. Outer Domain NCP rates ($\sim 34.2\pm10.7 \text{ mmol C} \text{m}^{-2} \text{d}^{-1}$) was very similar to Middle Domain NCP rates ($\sim 37.4\pm10.7 \text{ mmol C} \text{m}^{-2} \text{d}^{-1}$ in the northern zone and $\sim 25.8\pm7.7 \text{ mmol C} \text{m}^{-2} \text{d}^{-1}$ in the southern zone).

Extrapolating calculated NCP rates to a 120 d growing season in the Bering Sea gave an annual average NCP of ~35 mmol C m⁻² yr⁻¹ for the shelf, similar to the values reported by Springer et al. (1996) (see Table 5). Because high levels of surface layer NCP appeared to coincide with high summertime bottom water concentrations of DIC in the Middle and Outer Domains, it is likely that much of this production is exported to depth and remineralized in these zones, increasing DIC concentrations in the bottom waters over the shelf during summer.

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By integrating NCP over the upper 30 m of the water column based on area-weighted averages in the six distinct zones (Table 5), we estimated a total production of organic ¹⁵ carbon over the entire shelf ($\sim 8.8 \times 10^{11} \text{ m}^2$) at $\sim 105 \pm 38.2 \text{ Tg C yr}^{-1}$ ($1 \text{ Tg} = 10^{12} \text{ g}$) which is comparable to estimates reported by Springer et al. (1996) of $\sim 102 \text{ Tg C yr}^{-1}$. Due to the paucity of consistent, comparable productivity data over the shelf it is impossible at this time to quantify whether the system is becoming more or less productive.

In an ecosystem undergoing dynamic change like the southeastern Bering Sea, warming temperatures and earlier retreat of sea ice could expose the surface layer to more wind mixing and subsequent reductions in stratification, thereby increasing productivity under certain climate scenarios. Hunt et al. (2002) correlates the earlier retreat of sea-ice with higher export to the benthos, thus strengthening the benthic ecosystem (i.e., crab fisheries) at a cost to the pelagic fisheries such as pollock. How-

ever, under other possible scenario, earlier retreat of sea ice could increase the availability of solar radiation which could warm and stratify the water earlier thus limiting production through decreased nutrient fluxes and give the Bering Sea shelf a more pelagic character.

The impacts of changes in the character of productivity in the Bering Sea would likely

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be felt downstream in the Chukchi Sea. Waters entering the Arctic Ocean through Bering Strait are modified as they cross the Bering Sea shelf (e.g., Rudels, 1995). Increased rates of Bering Sea shelf primary production could further increase nutrient depletion and limit productivity in the western Arctic Ocean. Enhanced export produc-

tion in the Bering Sea could also lower DIC concentrations in the surface waters and thereby increase the CO₂ sink in the Arctic Ocean.

We have shown here that NCP can be a valuable method for assessing primary production over large areas of the Bering Sea. As environmental conditions in the region continue to change, it will be important to monitor the rates of NCP and the fate of the organic matter. Under certain climate scenarios, the vast and highly valuable

¹⁰ of the organic matter. Under certain climate scenarios, the vast and highly valuat fisheries of the Bering Sea could be diminished or shifted northward.

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	Production, mmol C m ^{-2} d ^{-1}						
Investigator	Year	Method	Total	Green	Outer	Middle	Inner
			Sea	Belt	Snell	Shelf	Sheir
Graham and Edwards	1962	Stock of Fish supported	75				
Koblentz-Mishke et al.	1970	Radiocarbon	13				
		incubations	to				
			42				
Taguchi	1972	Radiocarbon	77				
Motoda and Minoda	1974	Radiocarbon incubations	42				
McRoy and Goering	1976	Radiocarbon incubations	67				
Saino et al.	1979	Radiocarbon	0				
		incubations	to				
			342				
Tsiban and Korsak	1987	Radiocarbon incubations	53				
Springer et al.	1996	Assimilation of data		51	33	31	17
Sorokin	1999	Radiocarbon incubations	117				
Walsh and Dieterle	1994	Model				37	
Rho and Whitledge 2007	1978–1981+ 1997–2000	Radiocarbon Incubations			33	34	28

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Table 2. Previous estimates of NCP in the southeastern Bering Sea, calculated using the drawdown in oxygen, nitrogen, and inorganic carbon. Estimates based on oxygen consumption were converted to carbon based production values in the original work. Estimates of nitrate production were converted to carbon-based production within the study or by using f-ratios of 0.4 for the Middle and Outer Domains and 0.3 for the Inner Domain.

				Production, mmol C m ^{-2} d ^{-1}					
Investigator	Year	Timing	Method	Total Bering Sea	Outer Shelf	Middle Shelf	Inner Shelf	Northern Shelf	Southern Shelf
Ivanenkov	1961	Annual	Oxygen Modification	217					
Azova	1964	Summer (Jul)	Oxygen Modification		667				
Sapozhnikov and Naletova	1992 1995	Summer (Jun)	Oxygen Modification	64					
Hansell et al.	1993	Summer (midsummer)	New Nitrate Production		3 to 40	17 to 29	less than 16	132	
Codispoti et al. 1982	1980	Spring Bloom	DIC/NCP			14 to 23			
Codispoti, 1986	1980	Spring Bloom	DIC/NCP			20			200
Codispoti, 1986	1981	Spring Bloom	DIC/NCP						100

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Table 3. Spring and summer DIC concentrations and NCP by station in 2008. Drawdown was on average $\sim 90 \,\mu\text{mol}\,\text{kg}^{-1}$, and was highest in the Middle and Outer Domain in the region of the greenbelt, where NCP was also highest.

Station	Spring	nDIC Average (30m)	Summer	nDIC Average (30 m)	Days Between	nDIC Deficit	NCP
		µmol kg		µmol kg	Occupations	µmol kg	mmol C m ⁻ d ⁻
NP Line							
NP13	1 Apr	2233	15 Jul	2169	106	64	18.6
NP10	2 Apr	2268	15 Jul	2166	104	102	30.4
NP4	3 Apr	2285	14 Jul	2198	103	88	26.2
NP1	3 Apr	2295	13 Jul	2214	103	81	24.3
MN Line							
MN3	4 Apr	2341	9 Jul	2302	97	38	12.1
MN5	5 Apr	2326	9 Jul	2272	96	53	17.1
MN8	6 Apr	2278	10 Jul	2218	94	61	19.8
MN12	7 Apr	2245	24 Jul	2131	109	114	32.2
MN14	8 Apr	2267	24 Jul	2122	108	144	41.2
MN15	8 Apr	2239	25 Jul	2113	109	126	35.5
MN18	9 Apr	2252	25 Jul	2106	109	146	41.3
SL Line							
SL12	11 Apr	2279	26 Jul	2198	107	81	37.2
SL10	12 Apr	2320	27 Jul	2186	107	134	38.5
SL8	13 Apr	2286	27 Jul	2198	106	88	25.5
SL6	13 Apr	2299	12 Jul	2220	91	79	26.7
SL4	4 Apr	2280	12 Jul	2221	99	59	18.4
SL2	4 Apr	2321	13 Jul	2276	100	45	13.9
70 M Line							
70M56	30 Apr	2298	27 Jul	2164	88	134	46.9
70M46	1 May	2290	28 Jul	2213	88	77	26.9
70M32	2 May	2308	28 Jul	2217	88	91	31.8
70M30	3 May	2308	28 Jul	2210	88	98	34.2
70M24	3 May	2291	29 Jul	2198	88	93	32.6
70M14	4 May	2274	29 Jul	2207	88	66	23.3
70M2	5 May	2234	30 Jul	2198	88	36	12.6
Average		2284±29		2197±48	99	87±33	27.8±9.7

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Table 4. NCP in mmol $C m^{-2} d^{-1}$ by domain in 2008. Error listed is one standard deviation from the mean.

Domain Specific Productivity, in mmol $C m^{-2} d^{-1}$					
	Outer Domain	Middle Domain	Coastal Domain		
Northern Domain	_	37	19		
Southern Domain	34	26	23		

Table 5. Annual productivity across the entire shelf weighted by NCP rates in each domain, as compared to the values reported by Springer et al., 1996. Inner Shelf, Surface Productivty Estimates (Tg $C yr^{-1}$) 4 6

	Area (m ²)	Rate (mmol C m ⁻² d ⁻¹)	NCP (TgCyr ⁻ ')	From Springer et al., 1996
North	2.7×10 ¹¹	19.3	24.1	
South	1.2×10 ¹¹	22.5	12.0	
Total	3.9×10^{11}	41.8	36.1	32.0
		Middle Shelf, Surface		
North	1.7×10 ¹¹	37.4	28.5	
South	1.9×10 ¹¹	25.8	21.0	
Total	3.6×10 ¹¹	63.1	49.5	47.0
		Outer Shelf, Surface		
South	1.3×10 ¹¹	34.2	19.5	23.0

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Fig. 1. Map of the Bering Sea showing the locations of the three domains, Outer Middle and Coastal. The dashed line at 60° N indicates the division between the northern and southern domains. The locations of the four sampled lines are also shown as well as generalized surface circulation.

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Fig. 2. Biogeochemical features of the Outer, Middle, and Coastal domains of the Bering Sea Shelf.

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Fig. 3. Spring DIC concentrations (μ mol kg⁻¹) averaged over the upper 30 m of the water column across the shelf.

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Fig. 4. Spring DIC concentrations (μ mol kg⁻¹) along the four lines. The domains and fronts as well as station numbers are shown across the top of each figure. **(A)** SL line. **(B)** MN line. **(C)** NP line. **(D)** 70 m line.

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Fig. 6. Summer DIC concentrations (μ mol kg⁻¹) along the four transect lines shown in Fig. 1. The domains and fronts as well as station numbers are shown across the top of each figure. **(A)** SL line. **(B)** MN line. **(C)** NP line. **(D)** 70 m line.

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Fig. 7. Spring and summer concentrations of DIC (μ mol kg⁻¹) relative to salinity. **(A)** Spring. Bering shelf water salinity ranged from 31.3 to 33, with concentrations of DIC from 1950 μ mol kg⁻¹ to 2170 μ mol kg⁻¹, while deep Bering Sea salinity ranged from salinity 33–35, with concentrations of DIC from 2140 μ mol kg⁻¹ to 2380 μ mol kg⁻¹. **(B)** Summer. DIC concentrations (μ mol kg⁻¹) relative to salinity. Arrows show the relative influence of freshwater input, on both salinity and DIC, whereas productivity decreased DIC and remineralization increased DIC relative to salinity. **(C)** Spring. Most nDIC concentrations fell within the range of salinities of 31 and 33. **(D)** Summer. nDIC concentrations relative to salinity decreased from spring. NCP draws springtime clustering down as DIC is consumed; remineralization distributes the clustering up, as DIC is produced. The effects of each process are shown by arrows.







Fig. 8. Spring and summer concentrations of nDIC (μ mol kg⁻¹) relative to nitrate+nitrite (μ mol kg⁻¹). **(A)** Spring. For nearly all concentrations of nitrate+nitrite, nDIC ranged from ~2225 μ mol kg⁻¹ to 2350 μ mol kg⁻¹. Average spring concentration (2300 μ mol kg⁻¹) is marked by the dotted line. Spring and summer concentrations of nDIC (μ mol kg⁻¹) relative to nitrate+nitrite (μ mol kg⁻¹). **(B)** Summer. nDIC concentrations decreased with respect to nitrate, ranging from ~2050 μ mol kg⁻¹ to 2350 μ mol kg⁻¹. The springtime average (2300 μ mol kg⁻¹) is also plotted here, showing that most summertime points fall below the springtime average due to primary production.

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Fig. 9. Spring and summer concentrations of nDIC (μ mol kg⁻¹) relative to spring and summer concentrations of DO (μ mol kg⁻¹) **(A)** Spring. Most points clustered within the highlighted area of DO concentrations between 300 and 400 μ mol kg⁻¹, and DIC concentrations between ~2200 and 2450 μ mol kg⁻¹. Spring and summer concentrations of nDIC (μ mol kg⁻¹) relative to spring and summer concentrations of DO (μ mol kg⁻¹) **(B)** Summer. DIC concentrations were much less clustered and mostly lower relative to DO concentrations in spring. For ease of comparison, the springtime cluster is also shown in this figure (highlighted area). The arrows show the effects of primary production between station occupations: NCP draws values down and to the right, as surface layer DIC is consumed and DO is produced; remineralization draws values up and to the left as DIC is produced and DO is consumed.

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