Integrated assessment of the carbon budget in the southeastern Bering Sea

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ARTICLE INFO

Keywords:
Bering Sea
Carbon budget
Biogeochemistry
Bering Ecosystem Study

ABSTRACT

During the primary field program for the Bering Ecosystem Study (2008–2010), independent seasonal estimates of net primary production (NPP), net community production (NCP), vertical export production \( (\text{C}_{\text{exp}}) \), and benthic carbon consumption \( (\text{BCC}) \) were used to construct a shelf-wide carbon budget for the southeastern Bering Sea. Here, we quantify the annual production, utilization, and transport of NPP for the southeastern shelf region of the Bering Sea (spatially partitioned into Outer, Middle, and Coastal Domains). We observed that approximately 25% and 30% of NPP on the shelf is exported horizontally from the Middle and Outer Domains, respectively. This horizontal transport was the dominant mode of carbon export in the Outer Domain, exceeding \( \text{C}_{\text{exp}} \) by more than 30 g C m \(^{-2}\) yr \(^{-1}\) \( (99 \text{ g C m}^{-2}\text{yr}^{-1}) \) compared to 67 g C m \(^{-2}\) yr \(^{-1}\) \( (10 \text{ g C m}^{-2}\text{yr}^{-1}) \), respectively. In the Middle Domain, \( \text{C}_{\text{exp}} \) was more prominent than lateral transport \( (65 \text{ g C m}^{-2}\text{yr}^{-1}) \) and vertically exported carbon was more efficiently recycled in this Domain than in the Outer Domain \( (53 \% \text{ and } 32 \% \text{ of } \text{C}_{\text{exp}} \text{ respectively}) \). In the Coastal Domain, lateral transport was a source of carbon to the bottom layer, with estimated input of carbon exceeding NPP by as much as 54 g C m \(^{-2}\) yr \(^{-1}\). While the source of this additional carbon is unknown, one possible source is transport from the Middle Domain during wind events that induce coastal convergence. Overall, the combined carbon reservoir attributed to burial and transport in the Middle and Outer Domains is similar to a previous budget for this region \( (47 \%) \) \( (\text{Walsh and McRoy, 1986}) \), although some qualitative differences are apparent. The data presented here indicate a more pelagic character in the Outer Domain relative to the Middle Domain, and that the Middle and Coastal Domain carbon budgets are balanced only when combined.

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1. Introduction

The southeastern Bering Sea is one of the most productive shelf areas of the global ocean, with daily rates of net primary production \( \text{(NPP)} \) during ice edge blooms exceeding \( \sim 10 \text{ g C m}^{-2}\text{d}^{-1} \) under optimal growth conditions \( (\text{Niebauer et al., 1995; Lomas et al., 2012}) \). The fate of this production has significant consequences for the attendant food web, and the energy provided by primary production sustains both pelagic and benthic commercial fisheries. However, varying physical and climatic conditions can favor energy accumulation in either the pelagic or the benthic compartments, with significant consequences for commercial populations \( (\text{Hunt et al., 2002, 2011}; \text{Hunt and Stabeno, 2002}) \). Remineralization of detrital

Please cite this article as: Cross, J.N., et al., Integrated assessment of the carbon budget in the southeastern Bering Sea. Deep-Sea Res. II (2014), http://dx.doi.org/10.1016/j.dsr2.2014.03.003
production in the subsurface water column and underlying sediments results in the seasonal accumulation of carbon dioxide (CO₂) in bottom waters, sharply reducing seawater pH during the highly productive spring-summer period (Mathis et al., 2011a, b). This process increases the vulnerability to ocean acidification processes via the uptake of anthropogenic CO₂, and has been observed to result in undersaturation of important calcium carbonate (CaCO₃) minerals critical for shell-building organisms in both the Bering and Chukchi Seas (Bates et al., 2009; Mathis et al., 2011a, b; Cross et al., 2013).

Although it is clear that the balance of production and export is critical to understanding the functioning of the Bering Sea ecosystem, some portions of the carbon cycle remain poorly understood. For example, a paucity of data from near-coastal regions has resulted in limited and often conflicting patterns in temporal variability and the balance of primary production and export (e.g., Lomas et al., 2012; Moran et al., 2012). Other aspects of the carbon cycle have only recently gained attention, such as micro-zooplankton herbivory and surface bacterial remineralization loops (Moran et al., 2012; Olson and Strom, 2002; Stiecker et al., in press-a,b). Recent physical and biogeochemical data has also provided some evidence that organic carbon losses due to lateral transport may be more complex than previously assumed (Danielson et al., 2012a, 2012b; Baumann et al., 2013a, 2013b).

In the last five years, oceanographic expeditions as part of the multidisciplinary Bering Sea Project provided an opportunity to evaluate independent estimates of the various rate and budget components of the Bering Sea shelf carbon cycle as a whole, and thereby examine some of these unresolved carbon sinks. In this study, we provide a synthesis of net primary production (NPP), net community production (NCP), vertical export production (Cₑₓᵖ), and benthic carbon consumption (BCC) estimates to construct a budget for determining the fate of organic carbon production through heterotrophic utilization and transport across the southeastern Bering Sea shelf.

2. Methods

2.1 Sample collection

Physical, chemical, and biological measurements for the water column and sediments were collected as part of the Bering Sea Project during the following cruises: USCGC Healy during spring (April/May) of 2008 and 2009, and summer (July) of 2008; R/V Knorr in summer (June/July) of 2009; and R/V Thomas G. Thompson during late spring (May/June) and early summer (June/July) of 2010. Hydrographic (CTD) stations were occupied along two east-west transect lines (i.e., NP and CN lines) and one north–south transect along the 70 m isobath (i.e., 70 M) as well as in several regions of opportunity (Fig. 1). Biological and sediment studies were conducted at a subset of these stations. At the beginning of each spring cruise, sea ice cover was near 100% at all stations except for the southern stations of the 70 M line, which were sea-ice free when sampled during spring in all years. During spring of 2010, the timing of the occupation of some stations, as well as the spatial extent of sampling, was limited by the ice breaking capability of R/V Thompson. Some inshore stations were sampled later than usual during spring to allow for some sea ice melt. During summer observations, the entire Bering Sea shelf was sea-ice free for all years.

In order to facilitate a common spatial reference for the participants in the Bering Sea Project, the study region was divided into 16 standardized domains based on hydrographic structure, circulation patterns, and macrofaunal population distribution (Ortiz et al., 2012, Harvey and Sigler, 2013). Data included in this study were collected in Region 4, which we denote as the Southern Outer Domain; Regions 3 and 6, which we denote as the southern central domain; and Regions 2 and 7, which we denote as the Southern Coastal Domain (Fig. 1). Our domains comprise both the southern and the central portions of the eastern shelf according to the project definitions. However, a proviso to the definition of spatial domains is that the boundary between the southern and central shelves described by Ortiz et al. (2012) was included to distinguish the spatial area covered by historical groundfish surveys and has no hydrographic or biogeochemical context. In the absence of a strong boundary between the southern and central shelves, we combined these two areas in our synthesis effort. This study thus assumes that the northern boundary between the southeastern and northeastern portions of the shelves is a cross-shelf jet occurring in the vicinity of Nunivak Island (Danielson et al., 2011; Ortiz et al., 2012). Near the shelf break, biological regimes in the vicinity of the Pribilof Islands also led to the distinction of an elliptical domain (e.g., Cianelli et al., 2004; Hunt et al., 2008). Because of the unique processes occurring here, we have not included data collected in the Pribilof Domain (Region 5).

2.2 Sample analysis

2.2.1 Water column rate measurements

2.2.1.1 Net primary production (NPP). Samples for ¹⁴C incubations were collected roughly every other day from depths approximately ~1.5%, ~5%, ~9%, ~17%, ~33%, ~55%, and ~100% light levels of surface incident photosynthetically active radiation (PAR) (Lomas et al., 2012). Light depths were determined by analysis of PAR profiles on the CTD downcast generated using an calibrated Biospherical Instruments PAR sensor. Net primary production (NPP) rates were calculated from the autotrophic incorporation of NaH¹⁴CO₃⁻ into particulate organic matter over a 24-h period using the ratio of added radiocarbon to total inorganic carbon present (Parsons et al., 1984; Lomas et al., 2012). Daily volumetric rates of NPP were integrated to the deepest sample depth (i.e., ~1.5% light level) and corrected for passive incorporation of NaH¹⁴CO₃⁻ using a dark control and the total added activity for the profile measured at the start of the incubation.

Please cite this article as: Cross, J.N., et al., Integrated assessment of the carbon budget in the southeastern Bering Sea. Deep-Sea Res. II (2014), http://dx.doi.org/10.1016/j.dsr2.2014.03.003
2.2.1.2. Net community production (NCP). NCP was measured using the seasonal drawdown of the photosynthetic reactors dissolved inorganic carbon (DIC; NCPDIC) and total inorganic nitrogen (nitrate + nitrite + ammonium or TIN; NCPNIN) over the mixed layer depth (average=30 m). Samples for DIC were taken at every hydrographic station along the MN and NP lines and every other station along the 70 M line and analyzed according to the protocol of Mathis et al. (2010) and Cross et al. (2012) using the VINDTA 3C system (MARIANDA Inc.). These samples were calibrated using certified reference material provided by A.G. Dickson (Scripps Institute of Oceanography) and normalized to a deep water reference salinity of 35. NCP estimates were corrected for precipitation of carbonate minerals (e.g., Lee, 2001; Mathis et al., 2010).

Samples for nutrient analysis were syringe filtered using 0.45 μm cellulose acetate membranes, collected in 30-ml acid washed, high-density polyethylene bottles after three rinses, and analyzed shipboard within 1–2 h of collection. Nutrient analysis closely followed the WOCE-JGFS standardization and analysis procedures specified by Gordon et al. (1994), including reagent preparation, calibration of lab ware, preparation of primary and secondary standards, and corrections for blanks and refractive index.

NCPDIC values were taken from Mathis et al. (2010) and Cross et al. (2012) comprising measurements for both 2008 and 2009. Insufficient DIC observations in spring 2010 prevented the calculation of NCP for this year using inorganic carbon data. NCPNIN calculations comprised data from all three years, and were performed as in Mordy et al. (2012), except that Mordy et al. only examined the middle shelf in 2008 and 2009, whereas we report NCPNIN for all three years in each domain here. Data were converted from net nitrogen consumption to net carbon production via the Redfield Ratio (106C:16 N). While some older work has documented non-Redfield water column ratios of DIC:DIN, these perturbations were assumed to result from persistent denitrification processes, and did not necessarily imply non-Redfield phytoplankton uptake ratios (e.g., Codispoti et al., 1986). More recently, others have documented anomalous water column N:P ratios, resulting from increased phosphate demand during periods of rapid growth (Horak et al., 2013). Although unusually high phosphate content in particulate phytoplankton does not necessarily imply that C:N ratios should not conform to Redfield stoichiometry, some others have documented that low nitrate and high phosphate content relative to carbon content commonly co-occur in particulate phytoplankton (e.g., Martiny et al., 2013a, b). Here, we conform to the standard Redfield ratio, as utilized by Mordy et al. (2012).

2.2.1.3. POC export (Cexp). Vertical POC export (Cexp) flux was calculated using sediment trap mass, sediment trap 234Th, and water column 234Th/238U disequilibrium, as described in Moran et al. (2012) and Baumann et al. (2013b). Surface tethered, free-floating sediment trap arrays were deployed in ice-free waters along the outer shelf and shelf break during spring and summer (n=spring and summer; 3 and 3 for 2008; 5 and 4 for 2009; 5 and 4 for 2010) (Baumann et al., 2013b). Briefly, sediment traps (4 per depth at depths of 25, 40, 50, 60, and 100 m) were filled with 0.4 μm pre-filtered, non-poisoned brine (5= 85%v) to isolate swimmers from settling material and deployed for ~1 d. Upon recovery and after settling, traps were siphoned to the seawater brine interface indicated by the discontinuity between layers. Traps were filtered onto a pre-combusted GF/F, sub-sampled (10 mm arc punch) for POC, and analyzed for 234Th at sea.

Total (dissolved + particulate) 234Th water column profiles were collected during each cruise throughout the shelf. 234Th profiles were high resolution (~10 m) throughout the photic zone. Water column 234Th samples were collected from CTD-rosette casts using the small volume (SV; 4 L) technique, in which 234Th is extracted via co-precipitation with manganese oxide (MnO2) (Benitez-Nelson et al., 2001; Buesseler et al., 2001). 234Th contained on sediment trap and water column filter samples was quantified by the measurement of beta emissions of 234mPa (E=2.19 MeV; t1/2=1.2 min) on a low-background beta detector (RISØ National Laboratory, Roskilde, Denmark; average detector efficiency: 44 ± 3%). 238U activities were calculated from salinity according to the relationship 238U (dpm L−1)=salinity (%e) × 0.0708 (Chen et al., 1986). The 10 mm arc punch POP sub-samples were dried, fumed with HCl, dried and analyzed for POP on a Carlo Erba–440 Elemental Analyzer (Exeter Analytical, Inc., North Chelmsford, MA, USA) (Pike and Moran, 1997).

2.2.2. Sedimentary respiration rates and benthic carbon consumption (BCC)

Rates of sedimentary respiration were determined on intact sediment cores collected using an Ocean Instruments MC-800 eight-tube multicore. Up to three cores per station were incubated at near in situ temperatures for the determination of oxygen consumption rates. These were subcored using 8-cm diameter polycarbonate tubes. The cores were stored in the dark uncapped, for approximately 24 h, after which they were sealed with silicone stoppers equipped with magnetic stirrers and connected reservoirs containing bottom water from the same stations. Overlying water was sampled from each core over a period of 2–5 days and dissolved oxygen concentrations were determined using a fiber optic oxygen microsensor (PreSens Microx TX3), calibrated before and after each reading. Oxygen fluxes were corrected using an empirical formula (y=1.125x+3.365, where y is the corrected flux and x is the uncorrected flux) for the slow diffusion of oxygen from the silicone stoppers used during incubations (Davenport et al., 2012). These fluxes were converted to benthic carbon consumption (BCC) via the revised Redfield ratio of carbon to oxygen (106C:150 O2; Anderson, 1995).

2.3. Carbon mass balance

While NPP and some carbon utilization and transport pathways were assessed through the Bering Sea Project as described above (NPP; NCP; Cexp; BCC), these parameters do not directly account for every aspect of the carbon cycle. However, these measurements do enable the calculation of the major carbon pathways and reservoirs; in particular, lateral carbon transport, heterotrophic respiration, and carbon accumulation in upper trophic level biomass. A generalized schematic of these sources and sinks are given in Fig. 2, separated into pelagic and benthic compartments.

Fig. 2. Schematic showing the various budgetary components of the southeastern Bering Sea shelf carbon cycle. The pelagic compartment is shown in green and the benthic compartment is shown in blue. Arrows indicate sinks for the only organic carbon source parameterized in this budget, net primary production (NPP).
2.3.1. Surface layer heterotrophic respiration

There are two components to primary production: new production, which is composed of that portion of NPP that can be attributed to external nutrient inputs (typically nitrate); and regenerated production, which is driven predominantly by the re-assimilation of nutrients generated by the heterotrophic consumption of organic matter (typically ammonia and nitrite; Dugdale and Goering, 1967; Platt et al., 1977; Williams, 1993). By contrast, NCP measures the balance of NPP and heterotrophic ($R_h$) respiration processes across a given time period, such that $NCP = NPP - R_h$ (Williams, 1993). Often, NCP measurements assume that macronutrient limitation facilitates the rapid re-assimilation of any regenerated nutrients, such that NCP is conceptually equivalent to new production (e.g., Bates, 2006). Based on this assumption, the difference between NPP and NCP should be equal to regenerated production, with $R_h$ occurring as a rapid intermediary step. During the early part of the production season, prior to the onset of nutrient limitation, we assume that there is some lag in this process, and that only late-season regenerated production is perfectly efficient. Over the entire production season, we assume that the difference between NPP and NCP can be partitioned evenly between regenerated production and heterotrophic respiration.

Outside of these theoretical definitions, measurement errors can also impact the magnitude of $T$; for example, sea-air CO$_2$ gas exchange and vertical diffusion have been shown to perturb $NCP_{DIC}$ estimates by as much as 13% (Cross et al., 2012). This offset decreases $NCP_{DIC}$ values, such that reported numbers can typically be considered conservative estimates. Here, a conservative estimate of $NCP_{DIC}$ resulting from these offsets will also result in a conservative estimate of lateral transport ($T$).

2.3.2. Surface layer lateral transport

The offset between independent measurements of NCP by the drawdown of two separate photosynthetic reactants allowed for the calculation of carbon removal by lateral transport under the assumption of Redfield C and N production. Previous studies (e.g., Mathis et al., 2010; Cross et al., 2012; Mordy et al., 2012) have shown that $NCP_{TN}$ is generally greater than $NCP_{TN}$. Errors in $NCP_{DIC}$ due to diffusion, gas exchange, and natural offsets produced by variations in the phytoplankton C:N ratio (Sambrotto et al., personal communication) are not large enough to account for this imbalance. Instead, we propose that $NCP_{DIC}$ and $NCP_{TN}$ are not equal due to the lateral movement of water with differing DIC:TIN ratios during the production season.

Because $TIN$ is a limiting factor in primary production on the Bering Sea shelf and is typically depleted to near-zero levels by summer despite any spatial variation in spring $TIN$ stocks, lateral transport does not strongly affect $NCP_{TN}$ calculations. In short, all $TIN$ is utilized everywhere over the shelf, so the contribution of lateral transport to $NCP_{TN}$ estimates is difficult to observe. In contrast, non-limiting photosynthetic reactants like DIC are not uniformly depleted to a standard level, and lateral transport can alter $NCP_{DIC}$ calculations. Further, the effect of lateral transport is magnified relative to $TIN$: Redfield production causes DIC to vary nearly ten times more strongly than nitrogen, and resulting contributions of lateral transport to $NCP_{DIC}$ are much more obvious. The amount of carbon exported by lateral transport ($T$) from the upper 30 m can therefore be estimated by the difference in NCP measured by seasonal DIC drawdown and $TIN$ drawdown, such that $NCP_{DIC} - NCP_{TN} = T$.

In the Outer Domain, a paucity of $NCP_{TN}$ data prevented the direct calculation of a transport term. However, Baumann et al. (2013a) estimate that ~30% of total $^{234}$Th production in the water column is exported off-shelf from the Outer and Middle Domains. In the absence of discrete measurements, as an upper estimate we apply this 30% lateral mass transport loss factor to the Outer Domain.

2.3.3. Surface layer retained biomass

Direct measurement of export production allowed for the calculation of carbon retention at the surface layer by subtracting carbon losses from the initial NPP value, such that $NPP - R_B - T - C_{exp} = surface layer retained biomass (Bio)$. Previous studies have shown that dissolved organic carbon (DOC) and lower trophic level particulate organic carbon (POC) do not accumulate in the surface layer (e.g., Cross et al., 2012; Baumann et al., 2013b). Therefore, any NPP unaccounted for by measured or assumed loss processes at the surface layer is likely not retained as part of the autotrophic carbon community, but rather is consumed and assimilated by higher trophic communities not included within the measured dissolved or particulate fractions.

2.3.4. Bottom layer carbon partitioning

We address the fate of exported carbon in bottom waters in two ways. First, we account for losses to benthic carbon consumption as directly measured by BCC. Second, we provide an upper estimate of carbon burial through a regional measurement of the thorioc focusing factor ($FF$) as reported by Baumann et al. (2013a). The focusing factor describes the ratio of the inventory of $^{234}$Th buried in the sediments relative to the water column deficit of $^{234}$Th. While this is not a direct estimate of the carbon retention in the sediment, $^{234}$Th is a particle reactive tracer, and can thus provide an upper-bound proxy for particulate carbon. By applying the percent focusing factor of $^{234}$Th in the sediments to $C_{exp}$, we can provide a first-order, upper estimate of carbon burial ($B$). (Focusing factor estimates were not available for the Coastal Domain, which prevented the calculation of carbon burial in this region.) Additional losses of $C_{exp}$ occur through heterotrophic consumption in the water column and bottom layer lateral transport. Some carbon will also be retained as accumulated biomass in higher trophic levels. However, we were not able to isolate these carbon reservoirs for bottom waters based on the available data.

3. Results

3.1. Net primary production

Twenty five seasonal estimates of NPP based on $^{14}$C incubations integrated over the photic zone were available for the southeastern Bering Sea Shelf, although the timing and spatial orientation of these estimates varied widely. In particular, only one NPP profile was available for the Southern Outer Domain (Spring 2008). The Southern Middle Domain exhibited the best coverage, with 20 profiles spanning both seasons of all three years. The southern inner shelf was not sampled during 2008, while a spring profile is available for 2009 and both spring and summer profiles are available for 2010. In both spring and summer, NPP was much higher in the Middle Domain ($118 \pm 259$ mmol C m$^{-2}$ d$^{-1}$ and $97 \pm 153$ mmol C m$^{-2}$ d$^{-1}$, respectively) than in the Coastal Domain ($7.5 \pm 12$ mmol C m$^{-2}$ d$^{-1}$ and $13.3 \pm 8.2$ mmol C m$^{-2}$ d$^{-1}$). Spring NPP was slightly higher than summer NPP for the Middle Domain on average, while NPP for the Coastal Domain was 75% higher than in spring.

3.2. Net community production

Because NCP requires two seasonal occupations to calculate a single rate of drawdown of dissolved gases or nutrients, only one seasonal estimate is available as a directly measured value for each
year. However, most of the time period occurring between the seasonal occupations fell under the spring category. These NCP estimates are more a reflection of the seasonal drawdown of DIC and TIN integrated over the period of the spring bloom than the drawdown occurring over summer, and we denote these rates as typical of spring (Table 1).

Coverage of NCPDIC over the shelf spanned all three domains. During spring of 2008 and 2009, DIC concentrations were nearly uniform throughout the water column and along each hydrographic section, indicating homogenized conditions typical of winter and preceding the spring bloom. DIC concentrations were drawn down as much as 176 μmol kg\(^{-1}\) by summer (Mathis et al., 2010; Cross et al., 2012), but varied spatially within each domain. At one station in the Southern Middle Domain, DIC concentrations in the upper 30 m were observed to increase between spring and summer. Some interannual variability was also observed. Coastal Domain NCPDIC was higher in 2008 relative to 2009, while 2009 NCPDIC was higher for the Middle and Outer Domains.

The greatest resolution for any single parameter in any single domain is provided by NCPTIN. Approximately 33 seasonal profiles were available for the Southern Coastal Domain and nearly 200 for the Southern Middle Domain, although no seasonal estimates of NCPTIN were available for the Southern Outer Domain. Additionally, this parameter represents the best temporal resolution of any other parameter in the dataset, with both spring and summer seasons sampled during all three years of the study.

Strong nutrient drawdown was observed between spring and summer station occupations, with substantial drawdown of bulk nutrient content integrated over the upper 30 m occurring by early to mid-May (e.g., year day 130; Fig. 3). The Middle Domain exhibited a much higher initial nutrient content (∼200–500 mmol DIN m\(^{-2}\)) than the Coastal Domain (∼50–250 mmol DIN m\(^{-2}\)). Additionally, low DIN concentrations were present in the water column through the summer season in the Middle Domain, while integrated values of DIN were substantially drawn down to <50 mmol DIN m\(^{-2}\) in the Coastal Domain. This spatial variation is typical of production in the Bering Sea. Limited macronutrient content (Sambrotto and Goering, 1983; Sambrotto et al., 1986; Whitledge et al., 1986; Springer and McRoy, 1993) but high micronutrient content (Aguilar-Islas et al., 2007; Hurst et al., 2010) of the Coastal Domain enables high rates of productivity in spring, but also facilitates faster and more complete drawdown of macronutrients. Prolonged productive periods are not typical of this domain relative to other areas of the shelf (Sambrotto et al., 1986; Whitledge et al., 1986; Springer and McRoy, 1993; Bond and Overland, 2005; Rho et al., 2005; Aguilar-Islas et al., 2007; Mathis et al., 2010). NCPTIN was higher through the Southern Middle Domain than in the Southern Coastal Domain by a factor of two (20 ± 9 mmol C m\(^{-2}\) d\(^{-1}\) and 10 ± 3 mmol C m\(^{-2}\) d\(^{-1}\), respectively; Table 1).

### 3.3. POC export

In total, 96 seasonal estimates of \(C_{\text{exp}}\) were made during the three years of this study. The \(C_{\text{exp}}\) rates given in Table 1 are an average of all three methods used to calculate this parameter, although some variability between the methods was observed. In general, sediment trap POC fluxes from open water deployments showed an increase in \(C_{\text{exp}}\) between spring and summer, while POC export estimated from \(234\text{Th}\) deficits generally decreased between the two seasons. Note that the sediment trap measurements of POC export were made only at the shelf-slope edge whereas POC export fluxes were determined from water column measurements of the \(234\text{Th}\) deficit (Baumann et al., 2013a) taken over the entire shelf. In areas where both sediment trap data and \(234\text{Th}\) profiles were taken at the same geographic locations, these different techniques agree to within a factor of 1.5–2 for POC export fluxes (Baumann et al., 2013b). In general, we observed that \(C_{\text{exp}}\) decreased by 15–25% between spring and summer (Table 1). The magnitude of this decrease increased towards the coast, indicating a stronger or more rapid seasonal cycle in the Coastal Domain than in the Middle and Outer Domains. Rates of \(C_{\text{exp}}\) were similar between the Outer and Middle Domains (22 ± 12 mmol C m\(^{-2}\) d\(^{-1}\) and 25 ± 11 mmol C m\(^{-2}\) d\(^{-1}\), respectively), while \(C_{\text{exp}}\) was higher in the Coastal Domain (32 ± 8 mmol C m\(^{-2}\) d\(^{-1}\)), reflecting an increasing gradient towards the coast.

### 3.4. Benthic carbon consumption

Spring and summer estimates of benthic carbon consumption (BCC) were available for the Outer, Middle and Coastal Domains, comprising 26 total estimates. Most data were available for the central and Outer Domains, while only four samples were available for the Coastal Domain. In general, we observed that BCC increased towards the coast, although this gradient was much stronger during spring than during summer. Respiration rates were very similar across the entire shelf in the later production season, varying by 30% compared to the 75% variation observed in spring. A shelf-wide average shows that benthic respiration decreases between spring and summer, although there was some cross-shelf gradient in this parameter. Rates of BCC decreased strongly from spring to summer in the Coastal Domain (~45%; Table 1), while these increased in the Outer Domain by an equivalent margin (~51%; Table 1). Benthic respiration was very similar between spring and summer for the Middle Domain (7.9 ± 4 mmol C m\(^{-2}\) d\(^{-1}\) and 8.0 ± 4 mmol C m\(^{-2}\) d\(^{-1}\)). However, the high respiration rate observed in the Coastal Domain in spring increased the average spring respiration rate over the shelf, contributing to a bias in the shelf-wide average towards the pattern of production observed in the Coastal Domain. Relative to other parameters, however, an 18% change occurring between the two seasons was minimal.

### Table 1

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abbrev.</th>
<th>Southern Outer Domain</th>
<th>Southern Middle Domain</th>
<th>Southern Coastal Domain</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Spring</td>
<td>Summer</td>
<td>Spring</td>
</tr>
<tr>
<td>Net primary production</td>
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<td>117.8 ± 259.3</td>
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<td>Net community production from DIC</td>
<td>NCPDIC</td>
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<td>38.6 ± 33.5</td>
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<tr>
<td>Net community production from TIN</td>
<td>NCPTIN</td>
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<td>–</td>
<td>20.2 ± 8.5</td>
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<tr>
<td>Export production</td>
<td>Cexp</td>
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<td>22.4 ± 12.3</td>
<td>24.4 ± 11.3</td>
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<tr>
<td>Focusing factor</td>
<td>FF</td>
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<td>0.2 ± 0.2</td>
<td>0.3 ± 0.1</td>
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<tr>
<td>Benthic carbon consumption</td>
<td>BCC</td>
<td>4.1 ± 0.8</td>
<td>6.2 ± 2.5</td>
<td>7.9 ± 3.8</td>
</tr>
</tbody>
</table>

Please cite this article as: Cross, J.N., et al., Integrated assessment of the carbon budget in the southeastern Bering Sea. Deep-Sea Res. II (2014), http://dx.doi.org/10.1016/j.dsr2.2014.03.003
ized patterns of carbon modifications, numerous other studies have provided evidence for general-
problematic at best. Despite obvious spatial and temporal limits, attempts to de-
spatially extensive regional domains, and infrequent samplings. An
ability is dif-
Bering Sea shelf (e.g., Lomas et al., 2012). Spatiotemporal varia-
processes that occur over short time and space scales on the
efforts of biogeochemical data sets due to the heterogeneity of
previous work has discussed the challenges facing synthesis
necessary to assess the budget on the annual scale. However,
resulting from natural biogeochemical processes, it is therefore
contradicting the average seasonal patterns for
section, with the remainder of
rates of
prevalence well-established light and strati-
seasonal thermocline and resulting convection that induce nutri-
ent replenishment. Our observational data shows that NPP fol-
lowed this pattern in the Middle Domain, but not in the Coastal
limited data prevented an observation of temporal patterns in Outer Domain NPP (see Table 1). Based on the
consistency of the pattern of production in the literature, we
chose to extrapolate Outer Domain data according to the Middle
Domain pattern. Coastal Domain data was allowed to vary as
observed in spring and summer, with fall production extrapolated
as an average of the two. Patterns for NCPDC and NCPTN were not
available across multiple seasons, and we thus assumed that they
would follow the pattern for NPP.

According to the literature and our data (see Table 1), \( C_{exp} \) increases with NPP at the onset of production, and then decreases
linearly through the summer and fall seasons. Our observations
show that the Coastal Domain adhered to this pattern, but that
\( C_{exp} \) in the Middle Domain was constant between spring and
summer, and Outer Domain \( C_{exp} \) increased over this season. In
either cases, fall rates of \( C_{exp} \) were assumed to decrease relative to
summer, as has been observed in other areas (Buesseler, 1998).
Due to a complete paucity of winter data, we assumed that
previously well-established light and stratification constraints on
primary production during this season resulted in negligible
primary production (e.g., Sigler et al., this issue; Moran et al.,
2012; Niebauer et al., 1990; Springer et al., 1996; Ladd and Stabeno,
2012), and therefore precluded subsequent carbon modification.
Where possible, the maximum amount of data were incorpo-
rated into this model to allow for naturally observed patterns, and
seasonal variability that may differ between regions. For example,
rates of NPP in active blooms were integrated over a 30-day period
to minimize the effect of these extremely high rates over the entire
season, with the remainder of NPP integrated over the remaining
61.25 days. Our data also indicate that benthic respiration varies
very little on a seasonal scale, exhibiting a nearly constant back-
ground activity. During our spring surveys, most of the primary
production had not reached the benthos although some respira-
tion was evident (see Table 1; Section 3.4). We therefore incorpo-
rated this winter baseline rate of BCC into our model. Observations
contradicting the average seasonal patterns for NPP and \( C_{exp} \)
were also incorporated into the model, as previously described.
Without temporally continuous observations available for each
parameter in a variety of locations within each domain, the
illustration given in Fig. 3A is beyond the reach of the data
collected. At present, we are unable to assess any variation in rate

Fig. 3. The normalized rate of carbon modification occurring in each of the four seasons, relative to peak NPP, which occurs in spring, according to the generalized seasonal cycle determined through the literature record and our available measurements, as indicated in Table 1(A) and describing the possible annual extrapolation of seasonal measurements (B), which does not include any rate variations within a particular season.

4. Discussion

4.1. An annual model for the SE Bering Sea carbon cycle

Assuming that the SE Bering Sea carbon budget is imbalanced
on the seasonal scale, it will be difficult to assess long-term (e.g.,
decadal) imbalances due to losses of carbon to lateral transport
using a seasonal resolution. To eliminate seasonal imbalances resulting
from natural biogeochemical processes, it is therefore
necessary to assess the budget on the annual scale. However,
previous work has discussed the challenges facing synthesis
efforts of biogeochemical data sets due to the heterogeneity of
processes that occur over short time and space scales on the
Bering Sea shelf (e.g., Lomas et al., 2012). Spatiotemporal vari-
bility is difficult to resolve given widespread station locations,
spatially extensive regional domains, and infrequent samplings. An
attempt to define an annual cycle of carbon production and
utilization over the shelf using observational data is therefore
problematic at best. Despite obvious spatial and temporal limitations,
numerous other studies have provided evidence for general-
ized patterns of carbon modification over the shelf (see Table 1).
For example, the literature record shows evidence from multiple
perspectives that NPP peaks in spring, decreases in summer, and
increases in fall (e.g., Sambrotto et al., 1986; Springer et al., 1996;
Rho and Whitledge, 2007; Lomas et al., 2012; Moran et al., 2012;
Mordy et al., 2012), although with regional variability.

Applying these emergent patterns to the observational data
collected here provides an opportunity not only to fill in the gaps
in our observational data and permit an analysis of this group as a
whole, but also to consider the Bering Sea from an annual
perspective, and to test the validity of these annual patterns. Here,
we approximate an annual carbon cycle by extrapolating
seasonal measurements using previously observed or hypothe-
sized patterns as a guide, and derive the resulting carbon mass
balance. A detailed description of this approach and its application
to this dataset is described in Supplemental Section 1, and an
illustration of this extrapolation and a brief description are
given below.

To extrapolate our seasonal data, we assumed that the year was
comprised of four 91.25-day seasons. Data were partitioned into
these seasons according to the timing of cruises and the physical
and biogeochemical cycles described in Table 2. In Fig. 3A, we
provide an illustration of the best generalized seasonal variation of
our observed parameters presently allowed, normalized to the
relative peak value for NPP. Data gaps were filled based on
observed patterns, where possible, and otherwise using patterns
observed in the literature.

As already mentioned, the literature record indicates that in
general, primary production peaks in spring, decreases in summer,
and increases again during fall storms, the breakdown of the
seasonal thermocline and resulting convection that induce nutri-
ent replenishment. According to the literature and our data (see Table 1),
\( C_{exp} \) increases with NPP at the onset of production, and then decreases
linearly through the summer and fall seasons. Our observations
show that the Coastal Domain adhered to this pattern, but that
\( C_{exp} \) in the Middle Domain was constant between spring and
summer, and Outer Domain \( C_{exp} \) increased over this season. In
either cases, fall rates of \( C_{exp} \) were assumed to decrease relative to
summer, as has been observed in other areas (Buesseler, 1998).
Due to a complete paucity of winter data, we assumed that
previously well-established light and stratification constraints on
primary production during this season resulted in negligible
primary production (e.g., Sigler et al., this issue; Moran et al.,
2012; Niebauer et al., 1990; Springer et al., 1996; Ladd and Stabeno,
2012), and therefore precluded subsequent carbon modification.

Please cite this article as: Cross, J.N., et al., Integrated assessment of the carbon budget in the southeastern Bering Sea. Deep-Sea Res. II (2014), http://dx.doi.org/10.1016/j.dsr2.2014.03.003
across a season. Accordingly, our model of this seasonal cycle is
given in Fig. 3B, representing a first-order approximation of the
annual cycle of production as allowed by the data.

4.2. Annual mass balance

The annual mass balance of carbon production and utilization is
given in Table 3 and visually represented in Fig. 4. NPP, our only
listed carbon source, is given in black, while the various pelagic
(green) and benthic (blue) sinks are indicated by the second series
of bars. The benthic $R_B + T + Bio$ bulk term is indicated in white.
The error given in each estimate in Table 3 is derived from the
individual measurement error (Table 1). Standard compounding
error was assumed for calculated variables, such that total stan-
dard error was equal to the square root of the sum of the squares
of error terms for the variables included in the calculation.

In general, the carbon budgets for the Outer and Middle Domains
were largely balanced even without distinguishing $R_B + T + Bio$ in the
benthic compartment, although some differences were apparent in
the internal partitioning of NPP between carbon sinks. In the Middle
Domain, a greater proportion of NPP was exported vertically and
remineralized more efficiently in the sedimentary compartment than
in the Outer Domain. While surface layer lateral transport was
similar between these two regions, lateral transport was larger than
vertical transport as a sink for carbon in the Outer Domain than in the
Middle Domain. In the Coastal Domain, very low estimates of NPP
were exceeded by NCP, $C_{exp}$ and $BCC$, indicating a large organic
carbon deficit in this region.

4.3. The Outer and Middle Domains lose carbon

The lateral mass transport terms given in Table 3 correspond
well to other recent calculations, indicating that the estimates
presented here are reasonable. Baumann et al. (2013a) provided an
estimate of off-shell export of POC of 19 mmol C m$^{-2}$ d$^{-1}$. An
upper boundary to this estimate was also calculated by Baumann
et al. (2013b) of 24 ± 35 mmol C m$^{-2}$ d$^{-1}$. Extrapolating these
estimates according to the same pattern of seasonal change we

### Table 2: Seasonality in the eastern Bering Sea

<table>
<thead>
<tr>
<th>Month</th>
<th>Physical description</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>Ice cover; appearance of N/S transition in middle domain due to solar insolation; weaker currents$^{1,2}$</td>
<td>EBS Groundfish Survey</td>
<td>EBS Groundfish Survey</td>
<td>KN195 (6/14–7/13); EBS Groundfish Survey</td>
<td>TN250 (6/16–7/14); EBS Groundfish Survey</td>
</tr>
<tr>
<td>July</td>
<td>Wind direction switches to northeastward; variable wind strength; weaker currents; euphotic zone, elevated chlorophyll fluorescence, and oxygen supersaturation deeper than pycnocline; loss of nutrients in bottom layer; majority small phytoplankton; NPP declines$^{1,2}$</td>
<td>EBS Groundfish Survey</td>
<td>HLY0803 (7/1–7/31); EBS Groundfish Survey</td>
<td>KN195 (6/14–7/13); EBS Groundfish Survey</td>
<td>TN250 (6/16–7/14); EBS Groundfish Survey</td>
</tr>
<tr>
<td>Aug.</td>
<td>Maximum annual stratification index [St (m$^2$); M2]; variable wind strength; secondary fresher (glacial melt)$^{2,3}$</td>
<td>BASIS Survey (8/15–10/8)</td>
<td>BASIS Survey (8/15–10/8; 8/31–9/23)</td>
<td>BASIS Survey (9/11–9/27)</td>
<td>BASIS Survey (8/18–9/25)</td>
</tr>
<tr>
<td>Sept.</td>
<td>Maximum annual heat content; small fall bloom, incl. coccolithophores; wind direction E/SE; winds weak; deep mixing, remineralization, denitrification/anammox significant biogeochemical modifiers$^{1,2,3}$</td>
<td>TN211 (9/25–10/11); BASIS Survey</td>
<td>ME0823 (8/24–9/17); BASIS Survey</td>
<td>MF071 (9/11–9/27)</td>
<td>MF0904b (9/22–10/13)</td>
</tr>
<tr>
<td>Oct.</td>
<td>Stratification begins to erode; winds strengthen; flushing of central shelf begins$^{1,2,3}$</td>
<td>TN211 (9/25–10/11); BASIS Survey</td>
<td>BASIS Survey (8/15–10/8)</td>
<td>MF0904b (9/22–10/13)</td>
<td>MF0904b (9/22–10/13)</td>
</tr>
<tr>
<td>Nov.</td>
<td>Ice formation begins; winds strong$^{1,2,3}$</td>
<td>BASIS Survey (9/25–10/11); BASIS Survey</td>
<td>BASIS Survey (8/15–10/8)</td>
<td>MF0904b (9/22–10/13)</td>
<td>MF0904b (9/22–10/13)</td>
</tr>
<tr>
<td>Dec.</td>
<td>Ice covers northern shelf; winds strong; wind direction W/SW$^{4,5,6}$</td>
<td>BASIS Survey (9/25–10/11); BASIS Survey</td>
<td>BASIS Survey (8/15–10/8)</td>
<td>MF0904b (9/22–10/13)</td>
<td>MF0904b (9/22–10/13)</td>
</tr>
<tr>
<td>Jan.</td>
<td>Well-mixed water column (M4); winds strong; ice covers northern shelf; input of nutrient content to central shelf from Anadyr Water begins$^{3,5,6}$</td>
<td>BASIS Survey (9/25–10/11); BASIS Survey</td>
<td>BASIS Survey (8/15–10/8)</td>
<td>MF0904b (9/22–10/13)</td>
<td>MF0904b (9/22–10/13)</td>
</tr>
<tr>
<td>Feb.</td>
<td>Winds strong; ice covers northern shelf$^{6,7}$</td>
<td>BASIS Survey (9/25–10/11); BASIS Survey</td>
<td>BASIS Survey (8/15–10/8)</td>
<td>MF0904b (9/22–10/13)</td>
<td>MF0904b (9/22–10/13)</td>
</tr>
<tr>
<td>Mar.</td>
<td>Typical maximum ice extent; Winds strong; wind direction S/SW; under-ice bloom$^{2,5,8}$</td>
<td>BASIS Survey (9/25–10/11); BASIS Survey</td>
<td>BASIS Survey (8/15–10/8)</td>
<td>MF0904b (9/22–10/13)</td>
<td>MF0904b (9/22–10/13)</td>
</tr>
<tr>
<td>Apr.</td>
<td>Ice retreat begins; ice-edge bloom; winds begin to weaken; depth-averaged temperature minimum$^{1,3}$</td>
<td>HLY0701 (4/11–5/11); MF0106 (4/18–5/6)</td>
<td>HLY0702 (5/16–6/18)</td>
<td>HLY0901 (3/10–3/31)</td>
<td>HLY0902 (4/1–5/11)</td>
</tr>
<tr>
<td>May</td>
<td>Rapid ice ablation; light availability increases; stratification sets up firmly; primary fresher (snow melt); weaker currents; widespread spring bloom; majority large phytoplankton; maximum rate NPP$^{1,2,3}$</td>
<td>HLY0801 (3/12–3/26)</td>
<td>HLY0802 (3/27–5/5)</td>
<td>HLY0902 (4/1–5/11)</td>
<td>TN249 (5/9–6/14)</td>
</tr>
</tbody>
</table>

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* Brabets et al. (2000).
* Danielson et al. (2012b).
* Dornblaser and Strieg! (2007).
* Iida et al. (2012).
* Ladd and Stabeno (2012).
* Lomas et al. (2012).
* Moran et al. (2012).
* Mordy et al. (2012).
* Sigler et al. (this issue).
* Stabeno et al. (2001).
* Stabeno et al. (2007).
* Stabeno et al. (2012a).
* Stabeno et al. (2012b).
attributed to \( C_{\text{exp}} \), here, this gives a range of annual transport between 50 and 66 g C m\(^{-2}\) yr\(^{-1}\). Our calculated \( T \) value for the Middle Domain is somewhat lower than these mass estimates. Given that \( T \) could not be calculated for the Outer Domain, we scaled \( T \) in this region as 30\% of NPP, as was estimated by Baumann et al. (2013a). The discrete rate measurement range from Baumann et al. (2013b) is somewhat lower than what we projected in Table 3 for the Outer Domain. However, this range accounts only for westward lateral transport, while the estimate based on Baumann (2013a) we show in Table 3 accounts for lateral transport in any horizontal direction out of the domain.

Lateral mass transport as \% NPP is similar in the Outer and Middle Domains (Fig. 5A and B). However, relative to other sinks for NPP, the significance of lateral mass transport is stronger in the Outer Domain than in the Middle Domain. In the Outer Domain, \( T \) occurs on approximately the same scale as \( R_R \) (Fig. 5A). Both of these terms are larger than \( C_{\text{exp}} \), indicating that organic carbon consumption in the surface layer and lateral mass transport are much more significant than vertical export and bottom water consumption of organic matter. In the Middle Domain, \( C_{\text{exp}} \) is the largest sink for NPP, indicating that vertical mass transport is more significant than lateral mass transport (Fig. 5B).

The relative importance of transport carbon losses in the Outer Domain may also be exhibited in bottom waters. Nearly identical focusing factors (FF) result in similar percentages of \( C_{\text{exp}} \) lost to

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### Table 3

Annual carbon budget for the Bering shelf (2008–2010). The annual carbon budget mass balance for the three domains of the Bering Sea shelf based on the seasonal estimates from Table 2, in g C m\(^{-2}\) yr\(^{-1}\). The abbreviation and measurement or calculation method for each parameter, as well as the water column layer over which it is valid, are also indicated. For measured parameters, the number of profiles contributing to the estimate is listed. For calculated parameters, the relative percent of NPP is also shown. The lateral transport term for the southern Outer Domain was calculated according to Baumann et al. (2013a). At bottom, remainder terms indicating percent loss of NPP to burial in the sediments or lateral mass transport were directly calculated by adding calculated burial and transport terms, and indirectly by accounting for all heterotrophic carbon requirements. The literature value for these estimates was calculated indirectly and taken from Walsh and McRoy (1986).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abbr.</th>
<th>Formula</th>
<th>Layer</th>
<th>Southern Outer Domain</th>
<th>Southern Middle Domain</th>
<th>Southern Coastal Domain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net primary production</td>
<td>NPP</td>
<td>Measured</td>
<td>Upper 30 m</td>
<td>331 ± 42</td>
<td>172 ± 72</td>
<td>26 ± 15</td>
</tr>
<tr>
<td>Net community production from DIC</td>
<td>NCPPDIC</td>
<td>Measured</td>
<td>Upper 30 m</td>
<td>11 ± 42</td>
<td>95 ± 83</td>
<td>39 ± 36</td>
</tr>
<tr>
<td>Net community production from TN</td>
<td>NCPTN</td>
<td>Measured</td>
<td>Upper 30 m</td>
<td>0.2 ± 0.3</td>
<td>0.26 ± 0.10</td>
<td>0.27 ± 0.11</td>
</tr>
<tr>
<td>Export production</td>
<td>( C_{\text{exp}} )</td>
<td>Measured</td>
<td>Sediment</td>
<td>67 ± 20</td>
<td>65 ± 18</td>
<td>80 ± 17</td>
</tr>
<tr>
<td>Baumann focusing factor</td>
<td>FF</td>
<td>Measured</td>
<td>Sediment</td>
<td>21 ± 6</td>
<td>35 ± 17</td>
<td>58 ± 11</td>
</tr>
<tr>
<td>Benthic carbon consumption</td>
<td>BCC</td>
<td>Measured</td>
<td>Sediment</td>
<td>110 ± 21</td>
<td>33% NPP</td>
<td>29% NPP</td>
</tr>
<tr>
<td>Heterotrophic respiration</td>
<td>( R_R )</td>
<td>0.5NPP–NCPPDIC</td>
<td>Upper 30 m</td>
<td>99 ± 6</td>
<td>30% NPP</td>
<td>46 ± 85</td>
</tr>
<tr>
<td>Lateral transport</td>
<td>( T )</td>
<td>NCPDIC–NCPPDIC</td>
<td>Upper 30 m</td>
<td>55 ± 29</td>
<td>17% NPP</td>
<td>12 ± 12</td>
</tr>
<tr>
<td>Carbon stored as biomass</td>
<td>( B )</td>
<td>( NPP–R_R–T–C_{\text{exp}} )</td>
<td>Upper 30 m</td>
<td>19 ± 0</td>
<td>6% NPP</td>
<td>17 ± 0</td>
</tr>
<tr>
<td>Carbon burial</td>
<td>( R )</td>
<td>( C_{\text{exp}}–BCC–B )</td>
<td>Below 40 m</td>
<td>27 ± 21</td>
<td>8% NPP</td>
<td>13 ± 25</td>
</tr>
<tr>
<td>Walsh remainder (indirect)</td>
<td></td>
<td>Literature</td>
<td>Full water column</td>
<td>49%</td>
<td>17% (0%)</td>
<td>–</td>
</tr>
<tr>
<td>BEST remainder (direct)</td>
<td></td>
<td>( B+T )</td>
<td>Full water column</td>
<td>35%</td>
<td>36%</td>
<td>–</td>
</tr>
<tr>
<td>BEST remainder (indirect)</td>
<td></td>
<td>( NPP–R_R–Bio–BCC )</td>
<td>Full water column</td>
<td>44%</td>
<td>44%</td>
<td>–</td>
</tr>
</tbody>
</table>

---

Fig. 4. Carbon production, utilization and transport by g C m\(^{-2}\) yr\(^{-1}\) by each of the measured and calculated processes listed in Table 3. Production terms are indicated in black and gray, surface water sinks are indicated in green, bottom water carbon sinks are indicated in blue, and the total value of the indistinguishable bottom layer carbon sinks (\( R_R \), where \( R_R=R_{\text{exp}}+T+Bio \) below 40 m) is indicated in white. This visualization highlights the increasing disconnect between NPP and carbon losses towards the Outer Domain, and the dominance of known carbon sinks (BCC, \( T \)) in excess of NPP in the Coastal Domain.

Fig. 5. Partitioning of the pelagic (A and B) sinks of NPP and benthic sinks of \( C_{\text{exp}} \) (C and D). Percent loss of carbon exported to 40 m in the Outer Domain (A and C) and the Middle Domain (B and D). Standard compounding error was assumed in the propagation of error terms from Table 3, except in cases where the values were estimated based on previous literature, indicated by lit est. In the benthic compartment, the \( R \) term is conceptually comprised of the bulk carbon modification by water column heterotrophy, carbon stored as biomass, and lateral transport. Partitioning between these sources was not possible with this dataset.
burial (B) in each domain. Because BCC is so much stronger in the Middle Domain, a much smaller portion of \( C_{\text{exp}} \) is left over after utilization in this region (Fig. 5C and D). As noted earlier, this bottom water remainder (hereafter referred to as R) should conceptually be split between \( R_{\text{B}}, B_{\text{o}}, \) and T. The smaller R for the Middle Domain may result from an insignificant contribution of benthic \( T \). Long residence times exhibited by bottom waters in the Middle Domain (Coachman, 1986; Danielsen et al., 2012b; Stabeno et al., 2012b) likely decrease the relative importance of \( T \) for the R term. The water column in the Outer Domain is much deeper than that for the Middle Domain, and residence times of bottom water for the Outer Domain are much shorter (Coachman, 1986). Based on this evidence, it is possible that a larger portion of \( R \) in this domain will be comprised of carbon lost to lateral mass transport occurring in the bottom layer of this region, and that the relative magnitude of this sink for NPP may account for the larger \( R \) in this domain.

4.4. The Coastal Domain gains carbon from the Middle Domain

Measured carbon utilization is greater than carbon production in the Coastal Domain. It is unlikely that this offset results from errors in \( C_{\text{exp}} \). While it is possible that \( C_{\text{exp}} \) values may be influenced by sediment resuspension, there is a 1.5–2 agreement between sediment trap particulate matter, implying that sediment resuspension may not be a significant concern (Moran et al., 2012; Baumann et al., 2013b). While a twofold difference cannot explain the entire deficit, this error may account for much of it. However, the concurrent observation of \( N_{\text{CPC}} \) and BCC values are also greater than NPP, indicating that multiple sinks are greater than the estimated observed sources. Two possible solutions remain to balance the carbon budget: poor annual extrapolation of production data, or lateral mass transport of carbon into the system unresolved by \( N_{\text{CPC}} \) and \( N_{\text{CPC}} \). Lomas et al. (2012) observed that the annual spring bloom may be somewhat delayed relative to the rest of the shelf, with peak production occurring later. We even observed this pattern on average in our seasonal data (see Table 1). According to our extrapolation for data with both seasons, this merely switches the spring and summer seasons in this productivity pattern, as estimates of fall production are the average of spring and summer values. For errors in extrapolation to cover the Coastal Domain carbon deficit, our fall extrapolations are also too low, indicating then that spring production increases linearly through summer and fall. However, some measurements included in our annual extrapolation of NPP were based on a single spring station occupation, which would have underestimated annual productivity that peaks in summer. Without the single-season occupation data, NPP in this region would still be lower than \( N_{\text{CPC}}, C_{\text{exp}}, \) and BCC, indicating that that compounding errors in our fall NPP extrapolation would be the source for this offset. However, nutrient limitation in later seasons is well established in the Bering Sea, and it is unlikely that fall production—even that stimulated by nutrient replenishment from persistent storms—would overwhelm peak productivity levels in nutrient-replete seasons.

While we cannot rule out that the large difference between NPP and \( C_{\text{exp}} \) is an artifact of the compounding of error during our calculations, there is some potential that this offset is caused by a supply of externally produced organic carbon to the Coastal Domain. As we have suggested with regards to \( N_{\text{CPC}} \), input of preconditioned waters may be altering BCC and \( C_{\text{exp}} \) by delivering organic matter produced in other areas. In the Coastal Domain, lateral mass transport may be a source of carbon to this region, rather than a sink. To balance the offset between NPP, surface carbon utilization, lateral mass transport, and \( C_{\text{exp}} \), a minimum of 66 g C m\(^{-2}\) yr\(^{-1}\), or 7.92 Tg yr\(^{-1}\) is required for input into the Southern Coastal Domain.

The most logical source of lateral mass transport of organic matter into the Coastal Domain are the Yukon and Kuskokwim Rivers, which contribute 234 km\(^3\) of freshwater to the Coastal Domain annually (Mathis et al., 2011a). Previous work has indicated that the organic matter delivered to the shelf with these river waters can dramatically influence the carbon cycle of the Coastal Domain (Mathis et al., 2011a; Cross et al., 2012). River data from the US Geological Survey (USGS) indicates the combined organic matter discharge from these rivers is approximately ~1.27 Tg C yr\(^{-1}\). Even under the extremely improbable assumption that all of this organic matter is delivered to the Southern Coastal Domain, organic matter from rivers cannot provide an adequate supplement to support the observed benthic activity. Assuming an average total organic carbon (TOC) concentration of 65 μmol kg\(^{-1}\) in the waters entering the Bering Sea from the north Pacific and using a volume transport from Unimak Pass into the Coastal Domain of 0.042 Sv (Kinney et al., 2009), we see that this source of carbon contributes another ~1.1 Tg C yr\(^{-1}\), a reservoir too small to cover the imbalance between \( C_{\text{exp}} \) and NPP. An additional supply of organic matter to the Southern Coastal Domain may be the Southern Middle Domain. Our estimate of T for the Middle Domain indicates that ~8.74 Tg C yr\(^{-1}\) is exported laterally. This mass could easily support the benthic carbon demand occurring in the Coastal Domain. If the Middle Domain is the source of this excess organic matter, this would imply a significant focusing of dispersed production in this area similar to that observed over the northern shelf (Cooper et al., 2012). Recent work suggests that during years exhibiting cold winters such as 2008–2010, enhanced northward flow occurring over the shelf results from an increased density gradient over the shelf due to greater volumes of ice production and brine rejection (Danielsen et al., 2012b). Under these conditions, northerly winds cause coastal convergence and upwelling near the shelf break. If the effects of the cross-shelf density gradient and upwelling reach all the way to the coast, this convergence could deposit Middle Domain productivity in the Coastal Domain under northerly wind conditions and account for the missing carbon supply, and indicates that the Middle and Coastal domains are balanced within 0.8 Tg C yr\(^{-1}\) when taken together.

4.5. Comparison with the previous Bering Sea carbon budget

Rates of primary production on the Bering Sea shelf have been estimated since the early 1960s (Ivanov, 1961; Azova, 1964), and several comprehensive reviews of the literature have been conducted each decade since the 1990s (e.g., Springer et al., 1996; Hunt et al., 2002; Mathis et al., 2010; Lomas et al., 2012). Because of the importance of the regional fisheries these measurements are often discussed at an ecosystem level, with a particular emphasis on the energy provided to upper trophic levels and pelagic fish populations. The Processes and Resources of the Bering Sea (PROBES) Program developed a complete carbon budget based on the relative consumption of NPP by upper trophic levels. After accounting for heterotrophic energy requirements, Walsh and McRoy (1986) estimated that approximately 49% and 17% of annual NPP remained for transport and burial in the Outer and Middle Domains, respectively.

With the available data, it is possible to discretely calculate both a transport and a burial term for comparison. However, like the method of Walsh and McRoy (1986), this combined burial/transport remainder term can also be indirectly calculated by subtracting all heterotrophic carbon utilization terms (\( R_{\text{B}}, B_{\text{o}}, B_{\text{CC}} \)) from NPP. For the BEST dataset, these indirect remainder terms are
higher than those calculated directly (Table 3). The difference between these two methods results from limited bottom water data, which prevents the partitioning of carbon between \( R_{\text{BH}} \), \( T \), and \( \text{Bio} \) below 40 m. In the direct calculation of the remainder term, any potential transport in bottom waters is ignored, and therefore the term is likely underestimated; in the indirect calculation of the remainder term, bottom water \( R_{\text{BH}} \) and stored biomass is ignored, resulting in an overestimation of the burial and transport term.

Of these two estimation methods, we suggest that the direct calculation is likely more accurate. Directly calculating the remainder term relies on fewer assumptions, and ignores only one carbon pool (bottom water \( T \)) while the indirect method ignores two (bottom water \( R_{\text{BH}} \) and \( \text{Bio} \)). Considering that the transport velocities in bottom water are very small (Danielson et al., 2012a; Stabeno et al., 2012a,b), loss of carbon by lateral transport in bottom waters is likely also very small (e.g., Bacon et al., 1994), which substantially reduces the error generated by ignoring this term. In comparison, the carbon pools ignored by the indirect calculation of this remainder term are likely much larger. Water column respiration is nontrivial in bottom waters over the shelf (Mathis et al., 2010), calculation of this remainder term relies on fewer assumptions, and ignores only one carbon pool (bottom water \( T \)), while as the biomass stored by a sedimentary community which respires over the entire year, are likely larger in scale than bottom water transport.

Both our directly and indirectly calculated remainder terms are on the same order as those calculated by Walsh and McRoy (1986). Given the uncertainties inherent in these extrapolations and the wider spatial area covered here relative to PROBES, this is likely to be the best possible comparison. However, there are also qualitative differences between our data and that reported by Walsh and McRoy in the partitioning of carbon implied by these remainder terms. Our directly calculated remainder term is slightly smaller for the Outer Domain (Table 3). The data presented here indicate a larger portion of productivity and less vertical export than Walsh and McRoy (1986) but also less storage of carbon as biomass. This implies that we observed a carbon sink not apparent in the Walsh and McRoy budget. A portion of this sink is accounted for by our addition of a carbon reservoir for heterotrophic respiration, and the strong surface remineralization loop we demonstrated here. Thus, while our remainder estimates may be lower than those calculated by Walsh and McRoy (1986), they also depict a more strongly pelagic system. This is illustrated in Fig. 5, where the relative magnitude of NPP compared to any benthic utilization or any pelagic utilization is very high. The extreme inherent variability in the Bering Sea makes it extremely difficult to document small long-term changes (Lomas et al., 2012). However, it is possible that the system has undergone a shift to a more strongly pelagic state in recent decades.

In the Middle Domain, Walsh and McRoy (1986) argued that despite a small, indirectly calculated \( B + T \) remainder, the carbon budget was likely balanced over this area. It was suggested that the remaining carbon was cycled through the bottom water and benthic system on the annual scale, and that the Middle Domain was a dominantly benthic carbon system. In fact, Fig. 5 indicates that carbon utilization and transport below 40 m is nearly twice as large for this domain than for the Outer Domain (\( C_{\text{exp}} = 38\% \text{ NPP} \) and 20% NPP in the Middle and Outer Domains, respectively). Following vertical export of NPP, BCC by \( S = C_{\text{exp}} \) is also much greater in the Middle Domain than in the Outer Domain (58% and 35%, respectively; Fig. 5). However, surface layer utilization still dominates the modification of NPP in the Middle Domain (\( R_{\text{BH}} + T + \text{Bio} = 62\% \text{ NPP} \)), indicating that while the Middle Domain may have a stronger connection between surface production and benthic heterotrophy than the Outer Domain, it is still a predominantly pelagic system. We also demonstrate a qualitative loss of NPP to lateral mass transport and carbon burial.

Walsh and McRoy (1986) did not publish a carbon budget for the Coastal Domain, and the subsequent Inner Shelf Transfer and Recycling Program (ISHTAR) focused more on the northern Bering Sea Shelf. Other previous work has indicated that the Coastal Domain of the northern shelf (\( > 60^\circ \text{N} \)) can be net heterotrophic on the seasonal scale (Cross et al., 2012), although the same study, and others, indicated that the Southern Coastal Domain surface layer is net autotrophic on an annual scale (e.g., Mathis et al., 2010; Lomas et al., 2012). This carbon budget indicates that the Southern Coastal Domain may be net heterotrophic on the annual scale when integrating over the full water column. We also suggest that the Coastal Domain may be a focusing center for carbon lost to transport from the Middle Domain.

### 4.6. Additional questions

While this work represents a first order estimate of the carbon budget in the SE Bering Sea, further questions also remain with respect to specific carbon biogeochemical processes. Given the demonstrated importance of lateral carbon transport and the dominance of heterotrophic processes at the coast, a better characterization of both of these terms is essential to improving our understanding of the biological and biogeochemical cycles. Given limited NCP data, our present model indicates that heterotrophic respiration in the surface layer maintains a constant ratio to NPP across the spring and summer seasons, although some variability has recently been inferred (Moran et al., 2012). Present efforts are focused on resolving the spatiotemporal variability of f-ratios and the role of regenerated production that may indicate a better parameterization for heterotrophic respiration in future models (Mordy, unpublished data; Prokopenko, unpublished data).

In the benthic compartment, our parameterization of benthic remineralization only accounts for aerobic pathways in the sediments. Other concurrent studies indicate that net denitrification over the entire Bering Sea shelf consumes 5.2–6.2 Tg C yr\(^{-1}\) (Horak et al., 2013). Our studies cover ~15% of the area of the Bering Sea shelf estimated by Horak et al. (2013), indicating that anaerobic respiration should account for 0.8–0.9 Tg C yr\(^{-1}\) over the southern Middle and Outer Domains. The combined \( R \) integrated over these domains is ~3 Tg C yr\(^{-1}\). Correspondingly, the anaerobic signal estimated by Horak et al. (2013) accounts for 25–30% of the combined Middle and Outer Domain \( R \) given in Table 3. Additional studies concerning the partitioning of \( R \) between anaerobic and aerobic sedimentary respiration, transport, and carbon stored as biomass could refine our understanding of bottom layer carbon cycling, especially in the Outer Domain where \( R \) accounts for nearly 40% of \( C_{\text{exp}} \) (Fig. 5).

While the carbon imbalance in the Coastal Domain prevented the partitioning of carbon pools in this region, a better understanding of respiration processes could be particularly important. Focused deposition of laterally transported carbon may support the benthic community of the coastal domain relative to the pelagic community. However, the resulting net heterotrophy in this region due to bacterial remineralization processes could also induce a strong vulnerability to ocean acidification. While we have sufficient data in this region to make some statements about the potential importance of laterally transported carbon to the Coastal Domain, it is clear that all carbon processes in this region require further study. Some of the conflicting temporal patterns in organic carbon production and the unbalanced budget may be resolved simply by better spatial and temporal resolution of data in this region.

Data gaps did not result in substantial carbon budgetary imbalances in the Outer Domain, but limited spatial coverage of NPP may have skewed our results. Although rates in the middle domain for both spring and summer were observed to be higher in
the Middle Domain, our annual extrapolation resulted in higher rates of NPP for the Outer Domain based on the single summer profile available for this region (Table 1). If a more highly resolved NPP value for the region were lower, this could adjust our surface layer carbon partitioning. Specifically, RE and BIO would decrease, and Cexp and T would represent a larger proportion of NPP than indicated in Fig. 5. Qualitatively, this would enhance our assessment that the Outer Domain loses carbon to lateral transport on the annual scale.

Across all domains, a better understanding of fall and winter processes would provide a better basis for assembling a true annual carbon budget. Here, we have neglected water column autotrophy and heterotrophy in the winter season, although winter production (e.g., Miksis-Olds et al., 2013) and respiration (e.g., Cross et al., in review) have been observed in the Bering Sea. It has also been hypothesized that under-ice blooms during late winter and early spring may play a critical role in determining ecosystem dynamics in the following late spring and summer (Hunt and Stabeno, 2002; Sigler et al., this issue). Understanding the contribution of winter processes should be a focus of any future process studies and synthesis efforts in the Bering Sea.

5. Conclusions

During the multi-disciplinary, multi-year field program executed by the Bering Sea Project, independent sampling for net primary production (NPP), two types of net community production (NCP), export production (Cexp), and benthic carbon consumption (BCC) allowed us to improve upon the annual carbon budgets of the Outer and Middle Domains of the southeastern Bering Sea Shelf constructed over thirty years ago. From these discrete measurements, estimates of heterotrophic respiration (RE), carbon stored as biomass (BIO), carbon burial in the sediments (B), and lateral mass transport (T) were calculated to develop a carbon mass balance.

Specifically, we observed that more carbon is lost laterally in the Outer Domain than is exported vertically. A more efficient coupling between pelagic production and benthic utilization in the Middle Domain indicated a more balanced carbon budget. Unlike the Middle and Outer Domains, a new insight is that lateral mass transport was a source of carbon to the Coastal Domain. While the source of the organic carbon necessary to balance benthic utilization with organic carbon supply requires further study, focused deposition of Middle Domain NPP lost to transport could account for this imbalance. Relative to previous carbon budgets that indirectly calculated a percentage of NPP lost to transport and burial, this dataset made it possible to directly calculate this sink. This direct method showed a similar, if somewhat smaller percentage of NPP lost to transport and burial in the Outer Domain (35% NPP, Table 3), and contradicted the previous assumption that the carbon budget was balanced in the Middle Domain by showing a 36% loss of NPP to transport and burial. However, taken in conjunction with the Coastal Domain, the combined carbon budget for both regions is fully balanced to within 1 Tg C yr\(^{-1}\).

As environmental conditions continue to change, it will be important to monitor spatial variations in carbon cycle and to continue to pursue a better understanding of the Bering Sea carbon budget, particularly with regards to the Coastal Domain. Some of the differences between this budget and the Walsh budget may have arisen due to the strong variability characteristic of the Bering Sea ecosystem. While striving for complete spatial resolution on short temporal scales is likely untenable, periodic synthesis efforts like the construction of carbon budgets may help to address some broad longer-term variability. For example, under future warming scenarios, TOC inputs from rivers will likely increase due to increased melting of permafrost and enhanced soil drainage (Striegl et al., 2005) which could strengthen the supply of organic matter to the benthos and increase net heterotrophic processes for the Coastal Domain. Construction of carbon budgets could also help to assess expected changes in pelagic/benthic partitioning in the coming decades.

Acknowledgments

The authors thank the officers and crew of USCGC Healy, R/V Knorr, and R/V Thomas G. Thompson, as well as Scott Hiller of SIO, Steve Roberts of UCAR, and the hydrographic team from the National Oceanic and Atmospheric Administration for their work in tirelessly supporting our science during multiple cruises. We also thank Ray Sambrotto for the provision of unpublished data for reference during this work. Lastly, we thank the Science Advisory Board, the data management team, and our colleagues in the Bering Sea Project, supported by the National Science Foundation and the North Pacific Research Board. The synthesis presented in this paper was supported by the National Science Foundation Grants ARC-1107997 to JTM, ARC-0732359 and ARC-1106910 to MWL, ARC-0732680 to SMB, PLR-1107250 to CWM, and Grant NPB-BS6 to SMB from the North Pacific Research Board. Partial funding for this project was also provided by the Joint Institute for the Study of the Atmosphere and Ocean (JISO) under NOAA Cooperative Agreement NA100AR4320148. This work is contribution EcoFOCI-0808 to NOAA’s Ecosystems and Fisheries-Oceanography Coordinated Investigations, contribution 2180 to JISO, contribution 3914 to NOAA’s Pacific Marine Environmental Laboratory, publication 124 of the BEST-BSIERP Bering Sea Project and publication 464 of the North Pacific Research Board.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2014.03.003.

References


Baumann, M.S., Moran, S.B., Kelly, R.P., Lomas, M.W., Bell, D.W., 2013b. Seasonal synthesis efforts like the construction of carbon budgets may help...


