



Physical forcing and nutrient conditions associated with patterns of Chl *a* and phytoplankton productivity in the southeastern Bering Sea during summer

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ABSTRACT

Measurements of nutrients, primary (¹⁴C) productivity and new (nitrate) productivity collected in the southeastern Bering Sea in July and August 2004 together with measurements from July 1981 are used to characterize the regional production system during summer and to analyze the major physical and nutrient factors controlling biological patterns. The patterns of surface productivity suggested by the two different summers were remarkably similar in the regions of data overlap and agree with recent compilations of summer conditions from remotely sensed data. Summer was characterized by low production in the middle and outer shelf associated with surface mixed layers that were stabilized by heat. Elevated productivity was restricted to regions associated with the surface expression of thermohaline fronts, as well as to tidally mixed regions adjacent to and between the Pribilof Islands. Based on Chl *a* and productivity measurements, the biological impact of the shelf-break front of the southeastern Bering Sea extends at least as far inshore as the Pribilof Islands. The existence of elevated summer productivity associated with a recently identified shelf-partition front between the Pribilof domain and the middle shelf domain east of St. Paul Island was confirmed, and its thermohaline nature resulting from cumulative intrusions of slope-derived water is described. Yearly estimates of new and primary productivity compiled for the various biophysical regimes range from $> 1800 \text{ mmol N m}^{-2} \text{ yr}^{-1}$ and $> 170 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the shelf-break front to less than $700 \text{ mmol N m}^{-2} \text{ yr}^{-1}$ and $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ in oceanic and coastal waters. We hypothesize that trace metals, rather than macronutrients or grazing, likely restrict the seaward extent of elevated production at the shelf-break front. Iron may be supplied to the front by isopycnal mixing from deeper shelf waters that were in contact with sediments. By extending elevated production throughout the summer, the thermohaline and tidal fronts enhance the coupling of primary production to epipelagic food webs for the large populations of fish, birds and mammals in the region. Changes in the intensity or location of these frontal systems may impact populations that forage in them from the nearby Pribilof Islands.

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1. Introduction

Phytoplankton productivity is elevated on continental shelves and the adjoining slope regions in most places in the ocean (Longhurst et al., 1995). At high latitudes, the nutrients accumulate during winter and support a spring bloom that redistributes the nutrients in shelf waters (Riley, 1942). Following this relatively brief period of production, vertical stability restricts the vertical re-supply of nutrients, and shelf productivity in summer is often low. Primary production that is so transitory in nature typically is not well coupled to pelagic food webs, and much of the organic

matter produced reaches the benthos. Coupling of surface production to the benthic food web is particularly apparent on high-latitude, ice-impacted shelves (Grebmeier et al., 2006; Schmid et al., 2006; Wassmann et al., 2006), although it may characterize ice-free shelves as well (Moll and Radach, 2003). Persistent elevated pelagic production is maintained at frontal regions by a variety of processes that facilitate a more or less continuous supply of nutrients to surface waters (Sournia, 1994). Ocean fronts form in response to several processes (Pingree et al., 1976; Holligan et al., 1984; Horne et al., 1989). Horizontal variability in vertical mixing by tides in shallow regions creates tidal or structure fronts. Thermohaline fronts form at the interface between water masses with different temperatures and salinities, such as those that occur at shelf breaks and often are associated with elevated summer production (Malone et al., 1983; Marra,

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1990; Ryan et al., 1999). Although the supply of macronutrients most often has been implicated in sustaining elevated production in such regions, the role of trace elements, such as iron, also has been shown to be important in the North Pacific Ocean (Boyd et al., 2004).

The ultimate trophic impact of nutrient supply to shelf food webs in subarctic seas is of particular importance because these regions produce the bulk of the world's fish supply (Houde and Rutherford, 1993). Even when compared to other productive shelf regions, the eastern Bering Sea (EBS) supports elevated biomass in virtually every trophic level of the marine food web (NRC, 1996). Like other high-latitude shelves, the southeastern region supports high phytoplankton production during spring in association with the receding ice edge (Stabeno et al., 2008a). In ice-free areas, the initial stabilization of the upper water is due to heating, and the spring bloom occurs later, typically during April–May (Sambrotto et al., 1986; Niebauer et al., 1990; Doyon et al., 2000; Eslinger and Iverson, 2001).

Within the huge shelf region (~600,000 km²) of the EBS, the Pribilof Islands, a group of small islands on the outer part of the southeastern shelf, are home to large populations of marine birds and pinnepeds. Although the Pribilof Islands provide breeding habitat for these populations, they also provide access to favorable feeding conditions and support large populations of birds throughout the summer that feed on small fish and zooplankton (Decker and Hunt, 1996; Hunt et al., 1996).

The relationships among hydrography, nutrients and production on the southeastern Bering shelf have been well described (e.g., Kachel et al., 2002). Tidal fronts around the Pribilofs have vertical mixing rates that are sufficient to maintain nutrient supply to surface waters in summer (Whitledge et al., 1986; Stabeno et al., 1999; Stockwell et al., 2001). Such fronts also support elevated zooplankton production (Coyle and Cooney, 1993), although no direct relationship between these fronts and upper trophic level stocks has been made. In some years, the growth rate of age-0 walleye pollock (*Theragra chalcogramma*) has been found to be greater outside of the tidal front around the Pribilof Islands (Brodeur et al., 2002; Ciannelli et al., 2002). Recently, a frontal region called the shelf-partition front (a structure front between the middle shelf domain and the Pribilof domain; Sullivan et al., 2008) has been described that supports elevated production outside of the tidal fronts around the Pribilof Islands (Flint et al., 2002).

Another potential site for intensified trophic exchange during the summer is the thermohaline front that is associated with elevated production along the shelf break in the EBS (Iverson et al., 1979). Springer et al. (1996) suggested that summer productivity at this front is a crucial factor for the large upper trophic level stocks in this region. The communication of the shelf-break front with deeper, slope-derived water along isopycnal surfaces increases its access to macronutrients (Coachman, 1986). Also, the proximity of the Pribilof Islands to the shelf break increases the likelihood that nutrient-rich water from the slope reaches this region as well (Stabeno and van Meurs, 1999; Stabeno et al., 2001; Mizobata et al., 2008). This access to slope-derived water may result in considerable summer production at the tidal fronts around the Pribilofs and even as far as the shelf-partition front. Similar tidal fronts found along the inshore regions of the EBS derive nutrients from the bottom layer of the middle shelf, where nutrient concentrations are considerable although less than at the slope (Kachel et al., 2002). In each of these frontal regions, the elevated phytoplankton production during summer stands out against the rest of the shelf that is otherwise characterized by density-stratified and nutrient-depleted surface waters after the initial, short-lived (<1 month) spring bloom.

This paper addresses the coupling between nutrient supply and phytoplankton production during summer around the Pribilof Islands and the adjacent shelf region to the southeast. The linkage between the dominant physical processes, such as the means by which nutrient-rich slope water and shelf bottom water reaches the surface, and epipelagic production is critical to the analysis of the contemporary upper trophic level ecology of the region. A more detailed understanding of the mechanisms that support extended summer production would improve the ability to anticipate the impact that variations in these mechanisms have on shelf biogeochemical fluxes and upper trophic levels, both of which appear to respond significantly to climate forcing (Hunt and Stabeno, 2002; Piepenburg, 2005). This paper focuses on the relationship between summer physical conditions and biological productivity on the large shelf region in the southeastern Bering Sea to help document the aspect of a system that may be susceptible to periodic climatic variations or longer-term warming.

2. Methods

To assess regional patterns of productivity, we measured primary (¹⁴C) production, as well as new (nitrate) and regenerated (ammonium) production. Nitrogen productivity provides a useful tool in this analysis because the new (nitrate) component links the supply of nutrients with the biological response, and also because the ratio of new to total nitrogen production (the *f*-ratio) provides a way to assess how well coupled surface production is to epipelagic trophic transfer (Dugdale and Goering, 1967; Laws et al., 2000). Nitrate fluxes to surface waters appear to be significant in the shelf-break front region (Hansell et al., 1989). We use data from two summers to characterize meso-scale (~100s of km) spatial patterns that may be consistent from year to year for the region and to infer the mechanisms that lead to these patterns. In addition to the biological rate measurements, we also have compiled extensive hydrographic and nutrient data for this analysis.

Unless otherwise specified, data come from two cruises; (1) R/V *Alpha Helix* cruise 288 (AH288), from July 26 to August 20, 2004 and (2) R/V *T.G. Thompson* cruise 159 (TGT159) from June 26 to July 21, 1981. We use only the July 1981 cruise data that overlap the seasonal coverage of the 2004 data. Some of the hydrographic and nutrient data for the 1981 cruise have been presented in previous publications (e.g., Whitledge et al., 1986), although here we include additional spatial coverage, as well as carbon and nitrogen productivity rates. Station locations from the two cruises are shown in Fig. 1. The spatial coverage of the two cruises overlaps in the regions immediately south and east of the Pribilof Islands, as well as in the middle shelf region off Cape Newenham. For this unusually broad continental shelf, it is useful to refer to hydrographic domains that differ in their vertical physical structure and mixing regime roughly with depth (Coachman, 1986). The domains will be referred to here as the inner shelf (~<50 m); the middle shelf (~50–100 m); the outer shelf (~100–150 m); and the slope and basin region (~>150 m). The boundaries between them are the inner front, the middle transition zone and the shelf-break front, respectively. The Pribilof Islands, which sit near the outer boundary of the middle shelf, have their own inner or structure front and inshore region where water shoals between the structure front and the island shore. Both cruises sampled all domains in adjacent parts of the EBS. At each station in Fig. 1, a CTD cast was made for temperature and salinity with an instrument calibrated by the manufacturer. Water was collected at various depths for the analysis of nutrient chemistry and biological variables. All nutrients were analyzed

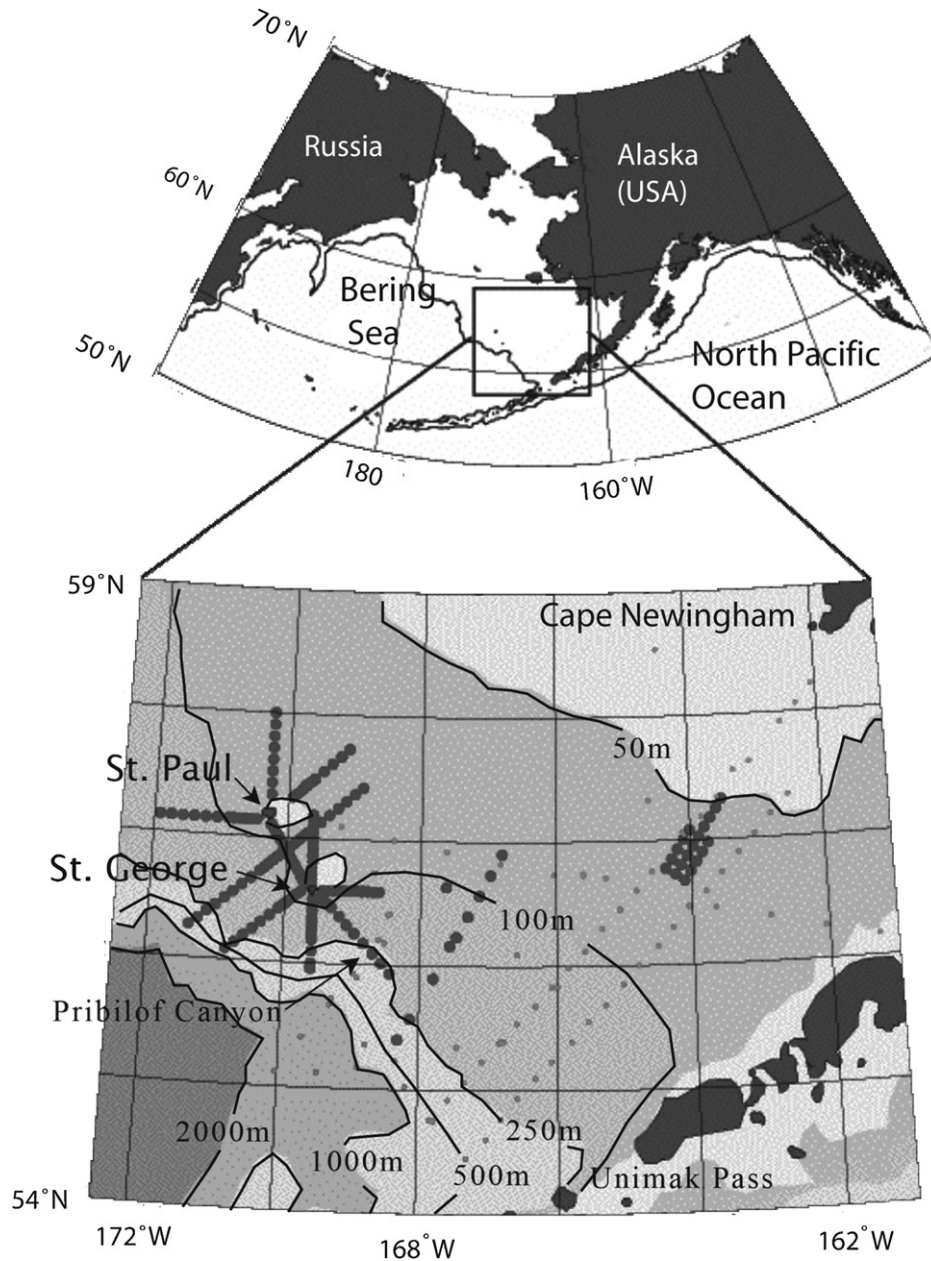


Fig. 1. Large-scale map of the North Pacific Ocean showing the location of the study region in the southeastern Bering Sea. The expanded view shows bathymetry of the study region, as well as the distribution of stations. Small dots are stations from the *Alpha Helix* cruise in 2004 (AH288) and large dots are stations from the *T.G. Thompson* cruise in 1981 (TGT198). Also identified on the expanded view are places referred to in the text including the Pribilof Islands (St. Paul and St. George), Pribilof Canyon, Unimak Pass and Cape Newenham.

using on-board autoanalyzer methods as described by Whitley et al. (1986) for TGT159 in 1981 and Mordy et al. (2005) for AH288 in 2004.

Measurements of phytoplankton productivity were done with incubation tracer methods for carbon and nitrogen uptake. Water for incubations was collected with Niskin bottles on the CTD rosette. During the AH288 cruise, 20-L samples for primary production measurements using ^{14}C -labeled bicarbonate were collected at the surface and in the chlorophyll maximum, if one was present, or just below the thermocline if a chlorophyll maximum was not present. The 20-L samples were subsampled into 250-mL polycarbonate bottles, and triplicates were incubated at eight light intensities, between 0 and $800\ \mu\text{M photons PAR m}^{-2}\ \text{s}^{-1}$, in an artificially lighted, on-board incubator for 1 h at

sea-surface temperature. A dark bottle correction was made and the filter only was counted to reflect particulate productivity. The relationship between photosynthesis and irradiance at each station was determined using non-linear least squares regressions (SYSTAT 10, Chicago, IL) to the equations of Jassby and Platt (1976) and Platt et al. (1980). Chl *a* determinations were made using the method of Evans et al. (1987). Daily production rates were calculated from Chl *a*-specific production as a function of irradiance using in situ measurements of PAR attenuation and Chl *a*, and hourly averaged surface irradiance (Zeeman, 1992). Separate photosynthesis—irradiance relationships were constructed in each layer sampled and these relationships were used to integrate production from the surface to a depth of no production, and from sunrise to sunset (Whitley et al., 1988;

Zeeman and Jensen, 1990a,b). During the earlier TGT159 cruise, primary production also was measured with the ^{14}C -tracer approach, but in this case incubations were done in seawater-cooled, on-deck incubators under ambient light that simulated the submarine light field (Iverson et al., 1979).

Stable nitrogen (^{15}N) isotope methods were used to measure new (nitrate) and regenerated (ammonium) productivity. For these measurements, 10-L samples were collected throughout the euphotic zone at 100%, 55%, 30%, 17%, 9%, 5% and 1% of surface light levels based on protocols reported previously (Sambrotto and Mace, 2000). Briefly, the incubations were done in on-board, surface seawater-cooled incubators under ambient light. Ambient nitrate and ammonium concentrations were measured before adding the tracer, so that a minimal perturbation ($<10\%$) of ambient concentrations could be added. Incubations were done in bottles made of PET (in 2004) or polycarbonate (in 1981) that were covered with neutral-density screens to simulate subsurface light levels. Most incubations in 2004 lasted 4–6 h around local noon, although in four cases (stns. 23, 49, 154 and 252) the incubations were done in the late afternoon. In 1981, some of the incubations were done for 24 h. At the end of the incubations, particulate material was collected on pre-combusted GF/F filters and dried on-board before being returned to the laboratory in a desiccator. Isotopic ratios and total nitrogen content of the samples from 2004 were measured using a Europa 20–20, continuous flow, mass spectrometer with an automated combustion system. The 1981 samples were analyzed with an emission spectrometer (Sambrotto et al., 1986). Uptake rates were calculated from the equations in Dugdale and Goering (1967). In the following text, we discuss both the mass flux of nitrogen ($r\text{NO}_3$ or $r\text{NH}_4$) in units of moles $\text{N vol}^{-1} \text{time}^{-1}$, as well as the specific nitrogen uptake rate ($v\text{N}$) in units of time^{-1} , when we wish to discuss the physiological rate independent from the biomass. The f -ratio ($r\text{NO}_3/(r\text{NO}_3+r\text{NH}_4)$) also is used to describe the relative amount of new to total nitrogen production. Trapezoidal

integration was done to estimate areal (m^{-2}) production from a depth profile. Daily nitrogen uptake rates were estimated by extrapolating the hourly new productivity rates to 10 h, and the hourly regenerated productivity rates to 12 h to account for the lower light dependence of ammonium uptake.

3. Results

3.1. Frontal structure, nutrient and Chl *a* patterns

The surface Chl *a* distribution based on a composite of the AH288 and TGT159 cruise data in 2004 and 1981 is shown in Fig. 2. Although there is considerable interannual variability on the shelf, ice coverage in 1981 and 2004 was similar, and the combined rendering accurately reflects several important features that also were apparent in the individual years. These include the large region of low surface salinity (<31.8) and relatively low Chl *a* ($<1 \text{ mg m}^{-3}$) along the 100-m isobath and over the middle shelf. This low Chl *a* and salinity region was recorded in both summers immediately east of St. George Island. In contrast, regions with higher surface salinity were associated with elevated Chl *a* levels. This was evident around St. Paul Island and in the region to its immediate east. It also was evident along the slope where elevated Chl *a* levels typified regions seaward of the 32.2 surface isohaline. The band of elevated Chl *a* associated with the shelf-break front was found at approximately the 250-m isobath and followed this depth contour into Pribilof Canyon.

A region of the middle shelf was sampled in both 1981 and 2004. Surface Chl *a* and salinity were slightly higher in 1981 ($0.5\text{--}2.5 \text{ mg m}^{-3}$ and ~ 31.83) than in 2004 ($0.5\text{--}1.0 \text{ mg m}^{-3}$ and ~ 31.77), although data from both cruises show that this is a relatively low biomass region in summer. Surface nitrate and silicic acid concentrations across this region in 1981 also conformed to this pattern. Except for a station very close to

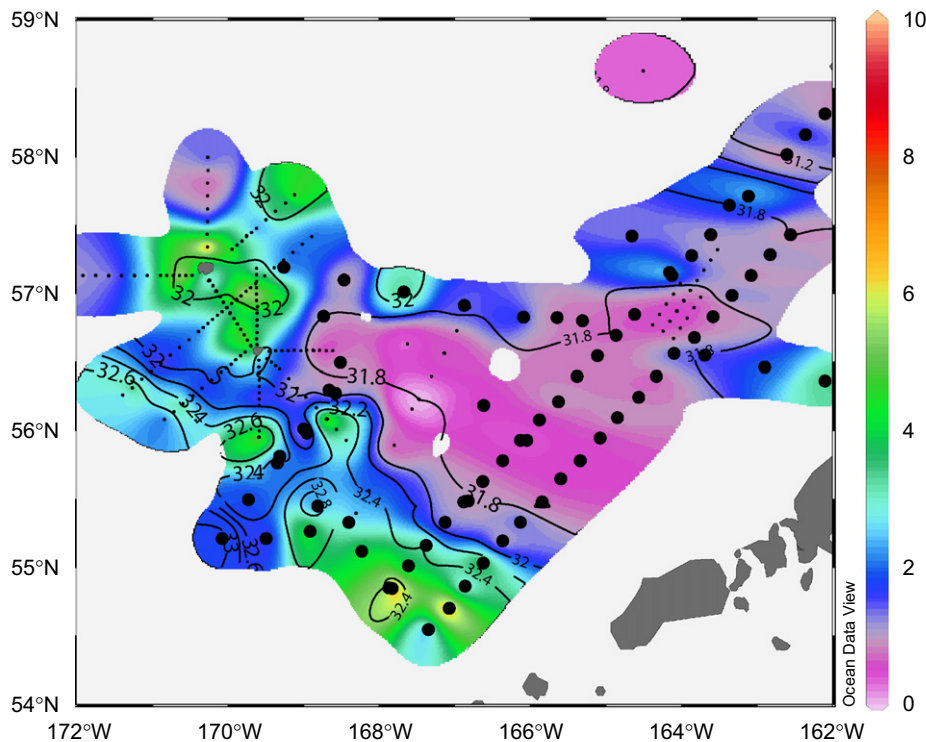


Fig. 2. Surface Chl *a* distribution based on the combined 2004 and 1981 data. Values in mg m^{-3} are shown on the vertical color bar. The labeled isopleths are surface salinity values. Large dots indicate stations from 1981, and small dots indicate stations from 2004.

Unimak Island, in 1981 surface nitrate and silicic acid levels here were less than 1 and $2\ \mu\text{M}$, respectively, and were separated from nutrient-rich, deeper waters by a vertical density change of $0.3\text{--}0.5\sigma_t$ units.

In the 1981 data, surface salinities less than 31.9 extended over the middle shelf along a line from just east of St. Paul Island eastward to the Alaska Peninsula (Fig. 3). Fig. 3 also shows higher-salinity water at depth in the western edge of the section (northeast of St. George Island). The temperature field in Fig. 3 reflects the strong vertical density stratification that typified the middle shelf region in mid-July 1981. Surface waters in this region in 2004 were warmer ($>12\ ^\circ\text{C}$), although this may be partially a result of this region being sampled 2–3 weeks later in 2004 than it was in 1981. The deeper water over the southeastern middle shelf was mainly above $4\ ^\circ\text{C}$ in 1981 and in 2004 exceeded $5\ ^\circ\text{C}$.

The relatively low-salinity water in the southern middle shelf region also was associated with elevated ammonium concentrations (Fig. 4, 55.5°N , 165.5°W). Although this tongue of elevated ammonium north of Unimak Pass was not associated with any significant increase in surface Chl *a* (Fig. 2), it had some of the lowest surface salinity values observed (<31.7 , not shown). This low-salinity implies the presence of low-nutrient, Alaska Coastal Current (ACC) waters as suggested by Whitley et al. (1986). The region around the Pribilof Islands in 2004 also exhibited elevated ammonium levels (Fig. 4) but, unlike the ACC-influenced region to the south, the elevated ammonium near the Pribilof Islands was associated with higher-salinity and Chl *a* levels (Figs. 2 and 3). The high surface salinity feature located about 150 km east of St. Paul Island also was associated with higher Chl *a* levels, as was a

detached parcel of high-salinity water at the surface about 50 km to the northeast.

The cross-shelf features in the Chl *a* and salinity data collected in 2004 around the Pribilofs (Fig. 5A) are similar in several respects to those from the more southerly section extending out from Cape Newenham in 1981 (Fig. 5B). Both show the elevated Chl *a* at, and seaward of, the shelf-break front associated with the salinity gradient that marks the interface between the slope and shelf water. Another similarity is the low Chl *a* associated with the low-salinity surface water of the outer and middle shelf domains. Vertical stratification marked by the lower-salinity surface waters broke down over the middle shelf in 1981 along the Cape Newenham section, with some weak restratification seaward of the inner front. In 2004, weak vertical salinity stratification persisted along the entire Pribilof section. There was also a significant difference in the horizontal extent of the outer and middle shelf regions in the two cross-shelf sections. The distance from the shelf-break front to the Pribilof domain was <150 km (Sullivan et al., 2008). We can infer that the distance to the Pribilof structure front was similar. In contrast, the distance to reach the inner front on the Cape Newenham line was ~ 450 km. The difference in bottom slope between the steeper topography near the Pribilof Islands and the more gradual slope along the Cape Newenham line illustrates how the broad width of the EBS shelf permits distinct individual shelf regimes to exist. Despite the large differences in the cross-shelf slope, the close association between elevated Chl *a* levels, and the shelf-break front and the structure or inner front is clear. The Pribilof domain was associated with greater Chl *a* levels than was the inner front of the Cape

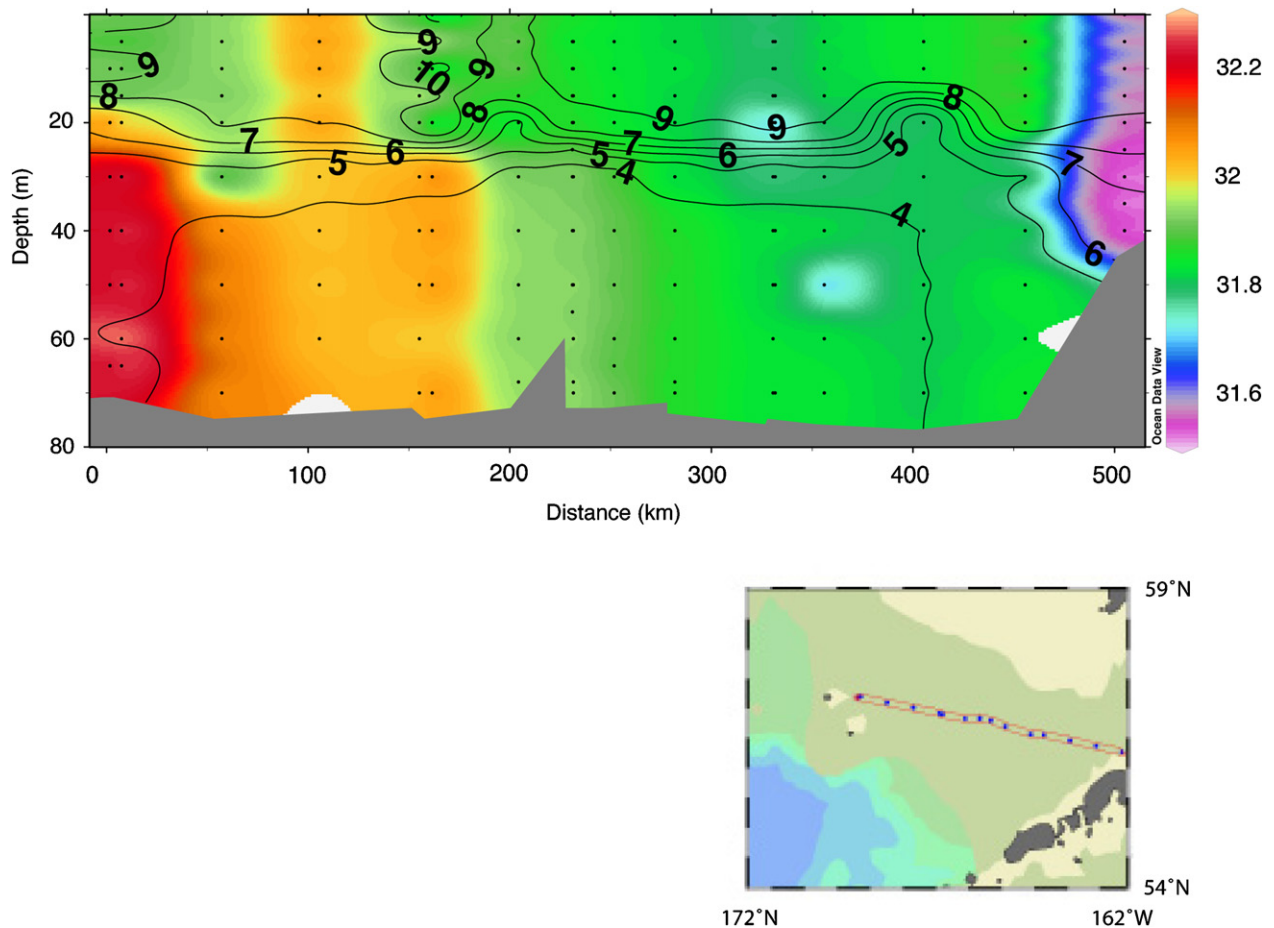


Fig. 3. Along-shelf (~ 75 m) section from the 1981 cruise. The section runs from just west of St. Paul Island on the west to the Alaskan Peninsula on the east as indicated by the inset map. The vertical color bar denotes salinity, and labeled isotherms denote temperature ($^\circ\text{C}$).

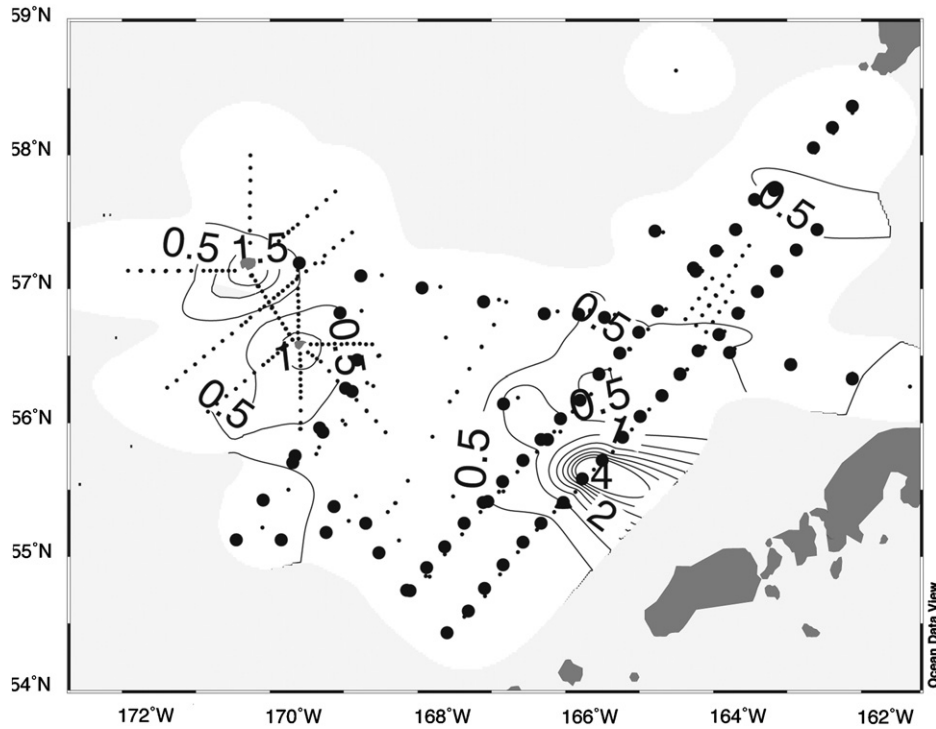


Fig. 4. Surface ammonium levels (μM) based on the combined 2004 and 1981 data. Large dots indicate stations from 1981 and small dots indicate stations from 2004.

Newenham line (Fig. 5A, B). The higher Chl *a* concentrations around the Pribilofs are a result of higher nutrient concentrations (Fig. 6A) and enhanced vertical mixing due to complex bathymetry (Stabeno et al., 2008b). Near Cape Newenham, there are lower, but still sufficient, concentrations of nutrients (Fig. 6B) to support elevated Chl *a* but less mixing.

3.2. Primary and nitrogen production

The distributions of total phytoplankton biomass relative to fronts in the southeastern Bering Sea as presented above provide a context for the interpretation of the summer productivity rates measured in 1981 and 2004 (Fig. 7A, B). Depth-integrated primary (^{14}C) productivity exceeded $1\text{ gC m}^{-2}\text{ d}^{-1}$ at six stations in the combined summer data set. These stations were in the shelf-break front, the shelf-partition front, or the region around the Pribilof Islands. There was a similar, although even greater, difference between the low, vertically integrated new (nitrate) production rates in the middle and outer shelf and those in the frontal regions. The three stations that had new production over $10\text{ mmol m}^{-2}\text{ d}^{-1}$ also were at the shelf-break front, the shelf-partition front and in the region between the Pribilof Islands. The rates of primary and new productivity in these regions during summer are comparable to the most eutrophic regions of the ocean and to the highest rates measured in the EBS shelf at the height of the spring bloom (Sambrotto et al., 1986). There was a similar increase in the nitrogen *f*-ratio in the frontal regions (Fig. 7C), although several stations with only moderate new productivity had a relatively large *f*-ratio.

The association between productivity rates and the regions of high surface salinity at the outcrop of the thermohaline frontal regions is apparent when the stations are grouped by location (Fig. 8). These profiles were constructed from the average of four groups of stations. These groups were based on their surface water properties, vertical structure and geographic location. The thermohaline front (thf) group comprised the stations at which the 25.5 isopycnal entered the euphotic zone ($\sim 30\text{ m}$) and

included the shelf-break and shelf-partition fronts. The outer shelf (os) and the middle shelf (ms) stations were grouped on the basis of depth. The middle shelf stations between the Pribilof Islands (ms-i) include stations that are similar in depth to the middle shelf stations, but have been segregated because of their potential proximity to slope-derived water. The low specific rates of nitrate uptake (νNO_3) that prevailed on the middle and outer shelves were associated with the lowest salinity surface waters. In the higher-salinity water associated with the shelf-break or shelf-partition front, rates of nitrate uptake were significantly higher. On the basis of specific nitrate uptake, the stations at thermohaline fronts and those in the region between the Pribilof Islands (ms-i in Fig. 8B) showed similar marked increases in the euphotic zone. The shallow regions immediately around both St. Paul and St. George Islands also supported elevated production (not shown). The likely cause of this productivity was the enhanced vertical mixing due to tides, similar to the process that occurs at the inner front region described by Kachel et al. (2002).

Table 1 summarizes the nutrient and productivity conditions recorded during summer in the combined 1981 and 2004 data based on the four groups defined above for Fig. 8. This summary indicates that the thermohaline front regions had the greatest average new productivity, specific nitrate uptake rates and *f*-ratios, while the strongly vertically stratified middle and outer shelf regions had the lowest surface nutrients and, consequently, the lowest new and primary productivity and nitrogen. The ms-i group had similar primary productivity, but lower new productivity and *f*-ratios, than the thermohaline frontal region. A *t*-test was done among all of the groups in Table 1 to assess the significance of the regional differences in the various parameters. The surface ($<20\text{ m}$) salinity values were significantly different among all regions ($p < 0.01$). For new production, differences were found at the $p \sim 0.1$ level for most combinations, except that there was no significant difference between the thermohaline front group and the region near the Pribilof Islands, nor was there a significant difference between the middle and outer shelf.

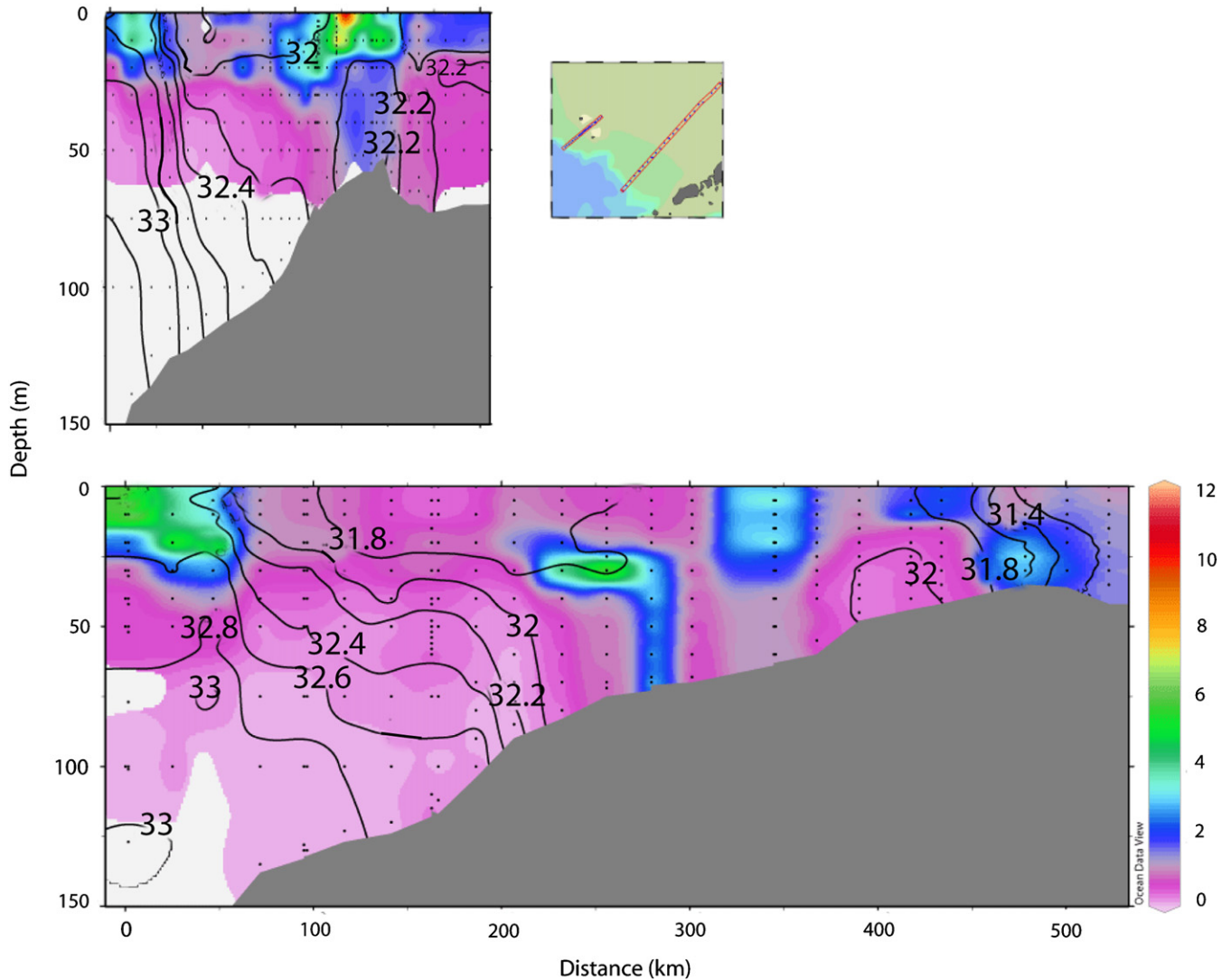


Fig. 5. Cross-shelf sections of Chl *a* corresponding to the vertical color bar on the right in units of mg m^{-3} . (A) Section between the Pribilof Islands in 2004 (AH288) and (B) section between Cape Newenham and the northwest side of Unimak Pass in 1981 (TGT179). The small inset map shows the section locations. Each section is overlain by labeled isohalines.

The statistical patterns for primary production were similar to that of new production.

4. Discussion

4.1. Nutrient–productivity interactions and estimates of yearly primary and nitrogen production

The presence of significant ammonium in surface water can inhibit nitrate uptake and depress the *f*-ratio (Wheeler and Kokkinakis, 1990). However, in the present southeastern Bering Sea data, ammonium level was not a good predictor of *f*-ratios and specific rates of nitrate uptake. Also, relatively large *f*-ratios were found in regions of low productivity. An example was the station west of St. Paul Island (Fig. 7C). This station was near the edge of a high Chl *a* region (Fig. 2) and may represent the initiation of elevated growth in which productivity rates were increasing as biomass accumulated. The uptake rates of carbon, nitrate-N and ammonium-N are known to have different light and concentration dependencies (Smith and Harrison, 1991), and this would contribute to some variation among their respective distributions.

As suggested for other coastal regions (Harrison et al., 1987), specific rates of nitrate uptake varied with nitrate concentrations. The middle and outer shelf regions had the lowest *f*-ratios, which likely are a result of the low nitrate levels and the well-developed bacterial growth and recycling in the summer months (Flint et al., 2003).

The rates of new productivity explained only a small portion of the variance in primary (^{14}C) productivity rates ($r^2 = 0.25$). The fit improved when total nitrogen uptake rates were used to predict primary productivity rates ($r^2 = 0.49$) and demonstrates the importance of regenerated nitrogen in maintaining productivity in summer. A detailed comparison between new and primary productivity is complicated, however, by the different methodology used for the ^{14}C -tracer incubations on the two cruises. The shorter ^{14}C incubations from the recent AH288 cruise exhibited a greater range in the C/N uptake ratio when compared to the new (nitrate) uptake rates than did the comparison between the ^{14}C rates and new production from the TGT159 cruise that were incubated from 12 to 24 h. The comparison of new to primary productivity for the shorter ^{14}C -tracer incubations suggests greater C/N uptake ratios in the region between the Pribilof Islands, the shelf-partition front, and the shelf-break front in the

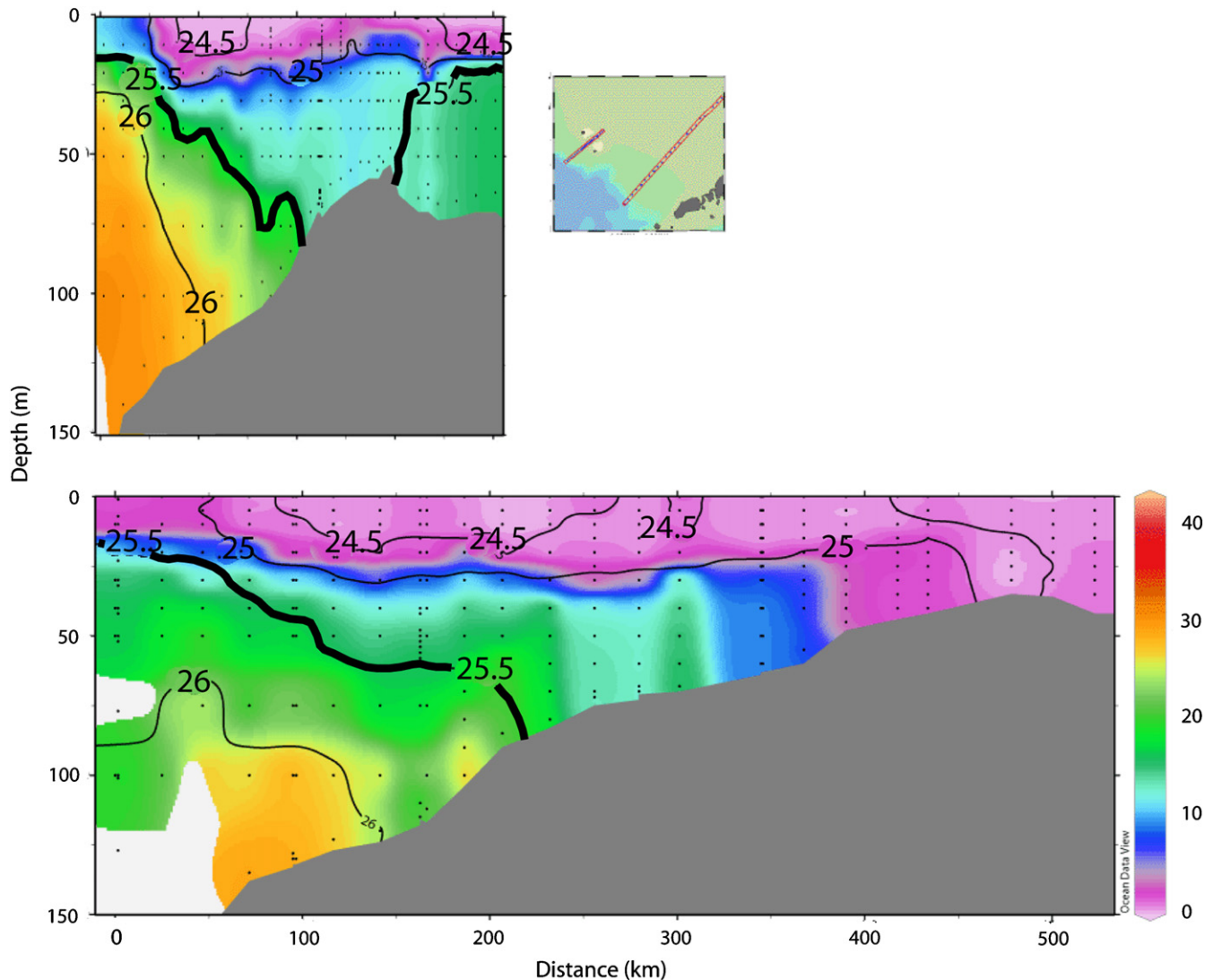


Fig. 6. Cross-shelf sections of dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_3 + \text{NO}_2 + \text{NH}_4$) corresponding to the vertical color bar on the right in units of mM. (A) Section between the Pribilof Islands in 2004 (AH288) and (B) section between Cape Newenham and the northwest side of Unimak Pass in 1981 (TGT179). The small inset map shows the section locations. Each section is overlain with isopleths of neutral density (σ_t). The 25.5 density surface is highlighted.

southeast. If new productivity is assumed to represent net productivity (after an appropriate conversion by the Redfield ratio of 6.6; Redfield et al., 1963), the greater primary productivity values in comparison to new productivity suggests a tendency for the shorter ^{14}C -tracer incubations to reflect gross rather than net primary productivity, a tendency noted in short incubations for primary production (Marra, 2002). Unlike the C/N uptake ratios from the AH288 cruise, the longer incubations from the TGT159 cruise did not show any obvious spatial pattern, but the average uptake ratio for these earlier data (21) also was greater than the Redfield ratio. The tendency for the short ^{14}C -tracer incubations to reflect a greater proportion of gross production also may reflect the supply of regenerated nutrients from either concurrent grazing or from earlier regeneration of ammonium in these regions. The ready supply of regenerated nutrients on shelves during summer also complicates the use of the nitrogen f -ratio to predict carbon export (Chen, 2003).

The recent 2004 productivity measurements from the AH288 cruise occurred in the summer season, a period that has been poorly sampled in the southeastern Bering Sea. Together with other available productivity data, they make possible estimates of

new and primary productivity over the entire growing season in the major biophysical regimes, and these are presented in Table 2. New production in the coastal domain is poorly constrained. The estimate in Table 2 is based on the assumption that all of the nitrate present at the end of winter ($\sim 11 \mu\text{M}$) was consumed together with a continued input of nitrate from the middle shelf that was derived from the heat flux estimates of Kachel et al. (2002) along with average horizontal nitrate gradients. This estimate (650 mmol m^{-2}) also includes a fall (September–October) bloom that increases primary productivity about 15% from summer values (Rho and Whitlege, 2007) and has been recorded in remotely sensed Chl a time series as well (Muller-Karger et al., 1990). Productivity values for the middle and (to a lesser extent) the outer shelf regions have a wide range and reflect in part, the dependence of seasonal production on the vagaries of wind mixing in these regions. Importantly, the present data document the elevated and prolonged productivity in the Pribilof Island region that has not been addressed in prior compilations.

The present productivity measurements also raise the estimates of new production in the thermohaline frontal regions. The mass balance of Hansell et al. (1993) for the shelf-break region

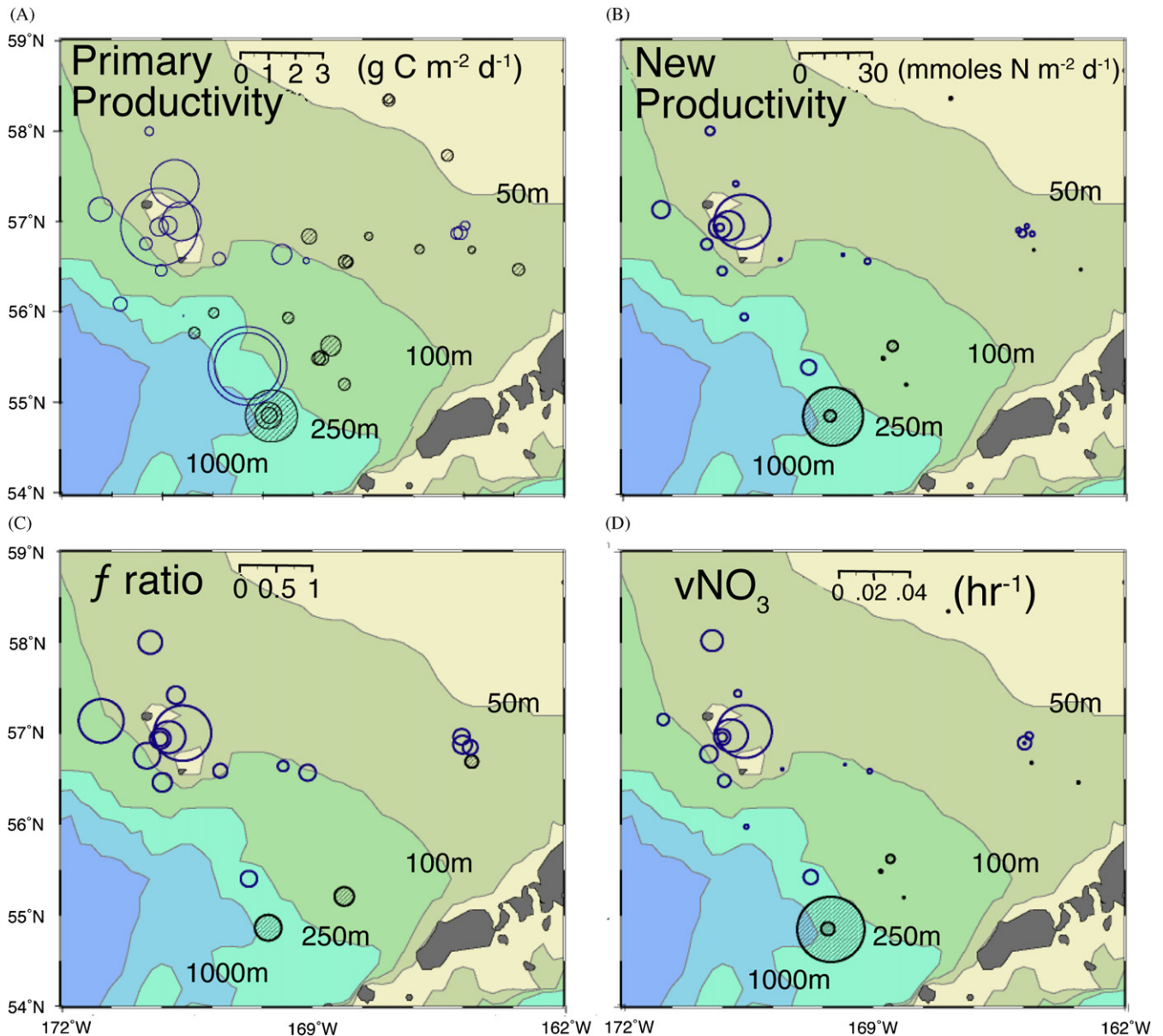


Fig. 7. Distribution and relative intensity of selected productivity parameters. In all graphs, the data from the two cruises have been combined and the open circles represent 2004 data (AH288) and the cross-hatched circles represent the 1981 data (TGT159). The diameter of the circle is proportional to the value of the variable and is scaled to the labeled horizontal bar in each panel. (A) Integrated primary productivity in $\text{g C m}^{-2} \text{d}^{-1}$. (B) Integrated new (nitrate) productivity in $\text{mmol NO}_3 \text{m}^{-2} \text{d}^{-1}$. (C) The nitrogen f -ratio (new production/[new+ammonium production]). (D) The specific rate (h^{-1}) of nitrate uptake.

neglected mixing during the summer, and this may account for much of the difference between this earlier estimate and the present one. The present estimate of primary productivity for the thermohaline front regions also is greater than that from the compilation of Rho and Whitlege (2007). Some of this discrepancy may be due to the paucity of summer data in the historical compilation. The compilation relied on relatively low values of primary productivity at the shelf-break front in June that were averaged with a few higher values measured in July for the summer estimate. The additional summer values from July to August measurements provided here raise the summer average significantly. However, there may be a period of relatively low productivity in June at the shelf-break front that separates the more productive May and July–August periods. There are relatively few productivity measurements in basin waters ad-

acent to the southeastern shelf. However, both the nitrate budget of Wong et al. (2002) and the available primary productivity measurements suggest that productivity here is significantly less than in the nearby shelf-break frontal region.

4.2. Major physical factors influencing summer phytoplankton patterns

The pattern of Chl *a* suggested by the merged data in Fig. 2 matches the summer patterns in remote sensing measurements (Aqua MODIS level 3 data, NASA/Goddard Space Flight Center, <http://oceancolor.gsfc.nasa.gov/cgi/level3.pl>). The 4-year composite (2003–2006, not shown) of ocean color for summer clearly shows the low Chl *a* region in the outer shelf ($0.2\text{--}0.5 \text{ mg m}^{-3}$), as well as the band of elevated Chl *a* along the shelf break.

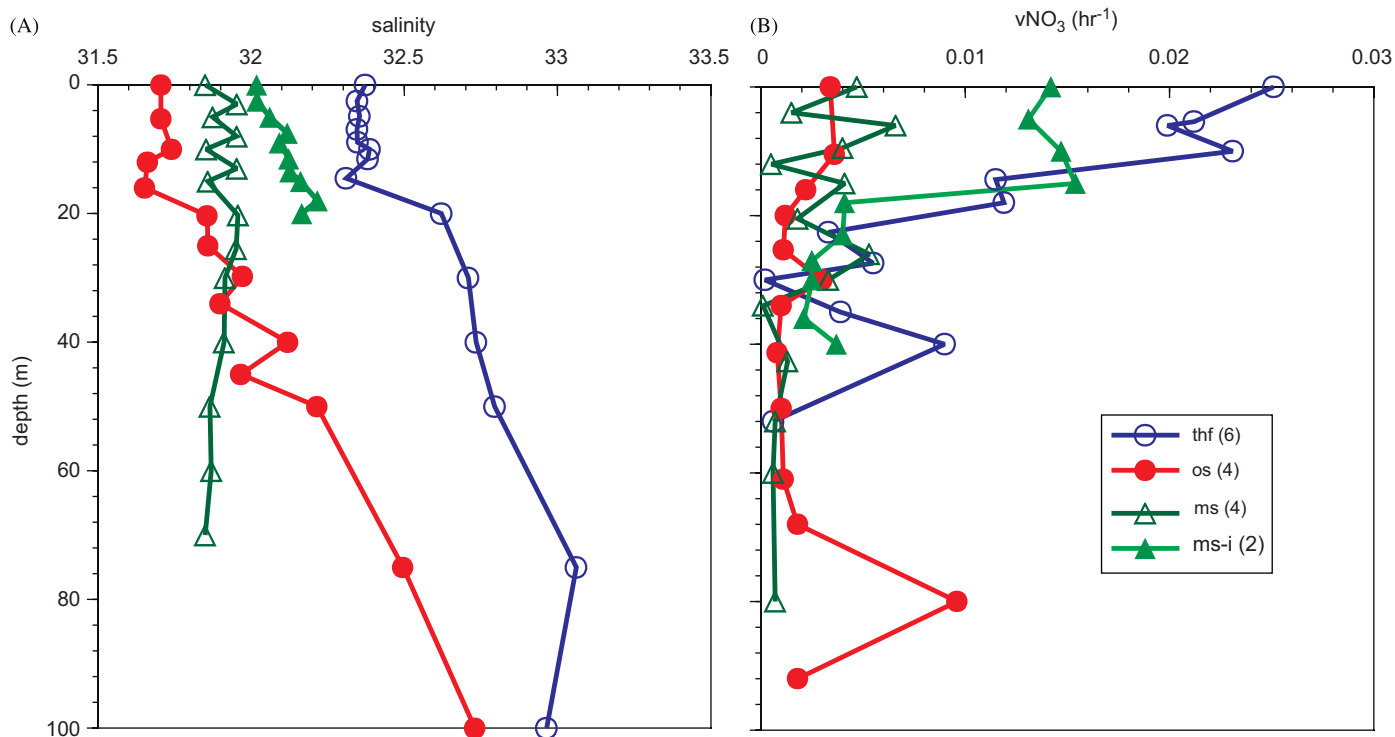


Fig. 8. Comparison of typical salinity (A) and specific nitrate uptake (B; h^{-1}) profiles in the major hydrographic regions discussed. The symbols in both panels correspond to the legend in the specific nitrate uptake panel. The legend also includes the number of profiles that were used to produce each average profile (in parentheses): thf—thermohaline front (open circles); os—outer shelf (solid circles); ms—middle shelf (open triangles); ms-i—middle shelf in vicinity of the Pribilof Islands (solid triangles).

Table 1
Average values for selected nutrients, Chl *a* and rate measurements in various shelf regimes

[NO ₃]	[NH ₄]	[Si(OH) ₄]	Chl <i>a</i>	¹⁴ C	ρNO_3	$v\text{NO}_3$	<i>f</i>
<i>Middle shelf</i>							
0.2±0.2 (12)	0.3±0.3 (12)	2.3±3.2 (11)	1.4±0.9 (14)	407±310 (13)	2.0±1.1 (9)	0.004±0.004 (9)	0.24±0.05 (6)
<i>Middle shelf near Pribilof Islands</i>							
1.1±0.8 (3)	0.4±0.1 (3)	3.7±2.4 (3)	6.7±2.1 (3)	1116±1009 (3)	8.5±4.7 (3)	0.011±0.007 (3)	0.32±0.13 (3)
<i>Outer shelf</i>							
0.1±0.2 (12)	0.4±0.4 (12)	4.4±2.8 (12)	1.1±0.7 (12)	404±154 (12)	3.0±2.2 (9)	0.004±0.003 (9)	0.30±0.16 (7)
<i>Thermohaline fronts</i>							
3.9±6.6 (5)	0.4±0.1 (5)	8.7±3.3 (5)	4.3±3.1 (14)	1075±805 (8)	12.6±10.8 (5)	0.017±0.016 (5)	0.46±.30 (3)

Nutrient values ([NO₃], [NH₄] and [Si(OH)₄]) are in μM ; Chl *a* values are in mg m^{-3} ; ¹⁴C productivity values are in $\text{mg C m}^{-2} \text{d}^{-1}$; ρNO_3 values are in $\text{mmol m}^{-2} \text{d}^{-1}$; $v\text{NO}_3$ values are in h^{-1} ; and the *f* ratio is dimensionless. The average is followed by the standard deviation and the number of observations (in parentheses).

The individual monthly composites of MODIS data (not shown) show some features not recorded in our ship sampling such as an intense bloom in the outer shelf in June 2004 that faded before our July sampling (Stabeno et al., 2008b). The July and August 2004 ocean-color composites also show a large patch of elevated Chl *a* off Cape Newenham that was inshore of our sampling region.

Surface (<30 m) salinities less than 32.0 were recorded along the 70-m isobath during summer in the mid-shelf region from the years 1998–2000 (Stabeno et al., 2002a). Stabeno et al. (2008a) speculate that this fresher water (<32.0) is a result of (1) inflow of ACC water through Unimak Pass during winter that then spreads across the southern shelf and (2) ice melt at the leading edge of the seasonal sea ice advance. This fresher water is the source of the lower salinity water that spreads into the Pribilof domain during summer (Stabeno et al., 2008b).

There is spatial association between Chl *a* and the shelf-break front. This likely derives from mixing of macronutrient rich slope

water with iron-rich shelf water. Horizontal mixing in this region is accomplished through the export of shelf water to the slope and basin by eddies, on-shelf flux of slope water due to instabilities (Stabeno and van Meurs, 1999) and bathymetric steering in canyons. The elevated Chl *a* depicted along the southeastern Bering Sea shelf edge was measured on the 1981 cruise and likely represents the yearly reestablishment of elevated Chl *a* described at the shelf-break front in this region (Iverson et al., 1979). The detailed underway mapping by Iverson et al. (1979) suggests that the elevated Chl *a* along the front is a narrow (<40 km), band-like feature. The 2004 sampling indicates that these conditions extend along the shelf break at least as far north as the Pribilof Islands. The 2004 sampling recorded a tongue of elevated Chl *a* extending into Pribilof Canyon that was not recorded in 1981. The many differences observed in these years underscore the multiple time and space scales that are important to the variability in this dynamic region.

Table 2Estimates of seasonal new (nitrate) and primary (^{14}C) production for the major biophysical regimes in the southeast Bering Sea

New prod. (mmol m^{-2})	Sources and notes	C prod. (g C m^{-2})	Sources and notes
Coastal domain 650 (52 g C m^{-2})	Seasonal nitrate decrease plus horizontal flux derived from Kachel et al (2002)	99	Rho and Whitledge (2007) ^a
Middle shelf 545–1100 ($43\text{--}88 \text{ g C m}^{-2}$)	Bloom values from (Sambrotto et al., 1986; Whitledge et al., 1986; Hansell et al., 1993), summer values this study	117–184 112	Bloom values from Probes data; summer values this study Rho and Whitledge (2007)
Middle shelf near Pribilof Islands 1400–1600 ($110\text{--}127 \text{ g C m}^{-2}$)	Higher bloom values from middle shelf; summer values this study	200–250	Higher bloom values from middle shelf, summer values this study
Outer shelf 820–970 ($65\text{--}77 \text{ g C m}^{-2}$)	Bloom-nitrate budget from Probes data; summer values this study	133–177	Bloom values from Probes data; summer values this study
Thermohaline front regions 1890 (150 g C m^{-2})	Summer values this study, extrapolated for 150 days	165	Summer values this study, extrapolated for 150 days
1000 (79 g C m^{-2})	Shelf-break only; Hansell et al. (1993)	90	Rho and Whitledge (2007)
Near-shelf basin region 690–730 ($55\text{--}58 \text{ g C m}^{-2}$)	Wong et al. (2002)	70–100	(Mordy et al., 2005; Whitledge et al., 1988) ^b

Estimates are for the 150-d period from April 15 to September 15, unless otherwise noted.

^a Compilation of several data sources; includes fall production to October 24.^b Based on stations north of Unimak Pass and in central basin.

The most important physical aspect for summer productivity in the middle and, to a lesser degree, outer shelf regions is the vertical density stability that restricts mixing and surface nutrient levels, and thus results in low-productivity levels (Stabeno et al., 2002a). Variations in wind mixing that can disrupt this stability are associated with large-scale atmospheric patterns that impact the regional productivity (Saitoh et al., 2002), and it is likely that regional productivity would be significantly influenced by changes in these patterns. Surface heating continues to contribute to stability throughout the summer, and data suggest heating continues into early September (Belkin and Cornillion, 2005; Stabeno et al., 2008a).

Near-surface (<30 m) salinities fresher than 32.0 were recorded along the 70-m isobath during summer in the mid-shelf region from the years 1998 to 2000 (Stabeno et al., 2002a) and suggest that this is a consistent yearly feature of the southeastern middle shelf. Relatively low-salinity surface water contributes to the vertical density stability of the southeastern Bering Sea's outer shelf in summer, but in most years it contributes only slightly to stability over the middle shelf (Stabeno et al., 2008a). Salinity over the middle shelf can be pre-conditioned by ice melt. Both 1981 and 2004 were low ice years in the eastern Bering. In 1981, the maximum ice extent was almost a degree north, and in 2004, almost two degrees north of the 50-yr mean maximum ice extent along 169°W (based on data from the NOAA National Ice Center). Moreover, the timing of ice retreat impacts surface salinity, because a late retreat would leave significant freshwater. However, since ~1990, sea ice over the southern shelf usually retreats before the transition to calmer atmospheric conditions of summer. Thus, the freshwater from ice melt typically is mixed vertically by winds (Stabeno et al., 2008a). This was true in 1981 and 2004.

Other freshwater sources are the several rivers that enter the region from the northeast and may contribute to salinities below 32.2 in the coastal regions in Fig. 2. Although some of this freshwater crosses the inner front, most of the flow is directed

alongshore to the northwest by the prevailing current system (Kachel et al., 2002).

Current measurements across Unimak Pass suggest that, although inflow into the Bering Sea there varies both seasonally and tidally, it averages $\sim 0.2 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ (Stabeno et al., 2002b). Minimum salinities at Unimak Pass (31.4 psu) occur in January, concurrent with maximum northward flow ($\sim 0.3 \times 10^6 \text{ m}^3 \text{ s}^{-1}$). Thus, water from Unimak Pass in the winter also acts to lower salinity on the southeastern Bering Sea shelf. During late spring and summer, flow through Unimak Pass is weak ($0.1 \times 10^6 \text{ m}^3 \text{ s}^{-1}$), and the salinity in the ACC is higher than in winter. So, it is unlikely that this late spring and summer transport contributes to freshening along the peninsula and 100-m isobath (Stabeno et al., 2008b).

In the region of the Pribilof Islands, intrusions of water from the outer shelf and slope are common (Stabeno and van Meurs, 1999; Stabeno et al., 2001), especially in the more dynamic winter season. Tidal rectification helps generate a clockwise circulation around the islands that further enhances mixing (Kowalik and Stabeno, 1999). This results in relatively high-salinity, high-nutrient, slope-derived water on all sides of the islands that maintains surface dissolved inorganic nitrogen (DIN) levels over $3 \mu\text{M}$ despite the large biomass of phytoplankton present (Figs. 5A and 6A).

While tidal mixing can account for the elevated production in the shoals immediately around the islands, it is less important in the deeper region to the east of St. Paul that also supported high Chl *a* levels (Fig. 2). Elevated production in this region likely was associated with the shelf-partition front characterized by Flint et al. (2002). This structure front was suggested as the boundary between water of the Pribilof domain (which could include tidally mixed, slope-derived water that had flowed onto the shelf) and lower salinity, middle shelf water. In fall 2003 and winter 2004, there was a northward flow of 100-m water east of St. George Island, as evidenced by satellite-tracked drifters (Stabeno et al., 2008b). Flow during late winter and spring was weaker, thus the

source of higher-salinity water was the ~ 100 -m isobath south of the islands. The observation of high-salinity (32.2) water east of the Pribilof Islands in 2004 supports this interpretation (Fig. 5A, as well as Stabeno et al., 2008b).

The contrast in the vertical water structure between the shelf-partition front and that in the nearby tidally mixed region also impacts the phytoplankton growth environment. For example, the shelf-partition front exhibits stronger stratification ($\Delta\sigma_t \sim 1.3$ vs. ~ 0.9 in the more tidally mixed regions), as well as higher subsurface nutrient levels. Therefore, the shelf-partition front may be able to supply a comparable flux of nutrients to a stable, shallow surface layer that maintains a more favorable light environment for phytoplankton growth than does the tidally mixed region. The combined data sets presented here, therefore, reflect the influence of at least two important water masses to local hydrography and nutrient distributions on this shelf: extensive intrusions of ACC and slope water from the south during winter, and incursions of slope-derived water around the Pribilof Islands from the west during summer. These observations help to fill what has been a relative dearth of information on the along-shelf biological patterns.

4.3. Evidence for mixing between deeper shelf waters and the shelf-break region

We found that among the expressions for water density, the neutral-density surface (γ_t) used in Fig. 9 was most compatible with the observed distributions of nutrients and presumably also best in defining the mixing and spreading surfaces for water properties (Jackett and McDougall, 1997). For example, the extension of the elevated ammonium concentrations on the middle shelf (i.e. > 2 mM) over the outer shelf and slope region closely follows the 25.5 neutral-density surface. The topography of this isopycnal surface also reflects the greater baroclinicity of the thermohaline front near the Pribilof Islands than in the region to the southeast. Importantly, the foot of this isopycnal surface at approximately 80 m on the shelf marks the seaward extent of the greatest bottom water ammonium concentrations, and deep ammonium concentrations decrease rapidly offshore from this point. This sudden decrease in ammonium concentrations is compatible with the detachment and isopycnal mixing of shelf bottom waters from both the inner and outer side of the shoreward foot of the front that has been demonstrated with

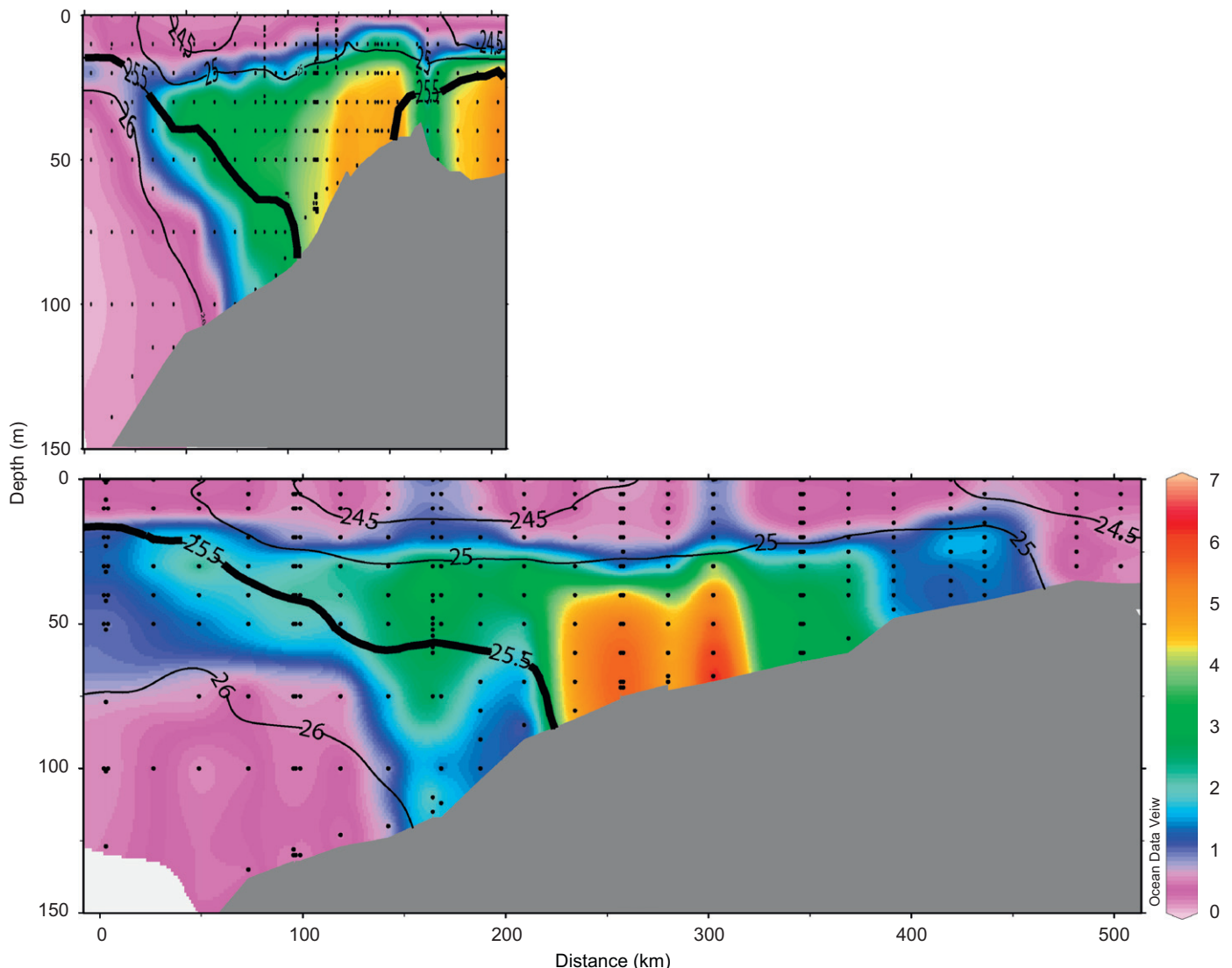


Fig. 9. Cross-shelf sections of ammonium (NH_4) corresponding to the vertical color bar on the right in units of mM. (A) Section between the Pribilof Islands in 2004 (AH288) and (B) section between the Pribilof Islands and Unimak Pass 1981 (TGT179). The small inset map shows the section locations. Each section is overlain with isopleths of neutral density (γ_t), and the 25.5 density surface is highlighted.

dye tracers experiments on other shelves (Houghton, 1997; Houghton and Visbeck, 1998). The bottom, onshore edge of this gradient is considered the middle front (Coachman, 1986) and results from the balance between the spreading of the more inshore, along-shelf flow caused by bottom friction and the vertical shear due to the horizontal density gradient (Chapman and Lentz, 1997). The steeper isopycnals at the Pribilof Islands (Fig. 5A), however, suggest more organized and energetic flow than along the southern line (Fig. 5B), and drifter tracks recorded in July and August 2004 also suggest this difference (Stabeno et al., 2008b). The evidence for mixing along the isopycnal surfaces that form the thermohaline fronts highlights the physical connection between deeper water and surface water along the isopycnal. The shallowing of these isopycnals at the shelf-break and shelf-partition fronts provides a path along which nutrients from the deeper on-shelf waters can reach the shelf-break front during summer. The regions where the 25.5 isopycnal surfaces enter the euphotic zone (~30 m along the shelf break) closely match the regions of elevated Chl *a* there (Fig. 2).

Fine-scale sampling across the New England shelf-break front revealed parcels of cold-pool water (~10 km in cross-shelf diameter) apparently pulled from the shelf into the frontal region (Vaillancourt et al., 2005). The meanders of the shelf-break front observed in the present data likely reflect the behavior of the Bering slope current (BSC). The troughs formed by these meanders facilitate upwelling at the shelf break (Ryan et al., 1999) and some meanders may result in detachment of parcels of shelf water. Okkonen et al. (2004) describe similar processes at the shelf break in the southeastern Bering Sea that remains a region of eddy formation throughout the summer. The complete three-dimensional topography of the 25.5 neutral-density surface (not shown) also suggests extensive interactions between the middle shelf bottom water and the more offshore regions. For example, an anticyclonic loop in the 25.5 density surface was apparent just west (downstream) of elevated ammonium levels that were deeper on the density surface in the 2004 data. A similar situation was recorded in 1981, in which elevated ammonium levels also were found adjacent to a less intense (on the basis of the coarse sampling grid) meander of the density surface. These observations suggest that the instabilities in the path of the BSC may enhance the mixing of water from the deeper outer shelf region to the shelf-break front and have a significant impact on shelf-break production.

4.4. Importance of regeneration in or near shelf sediments to productivity at the shelf-break front

The addition of the 2004 sampling near the Pribilof Islands to the existing nutrient and productivity data for the southeastern Bering Sea brings several previously suggested aspects of summer productivity patterns into better focus but also raises additional questions. One of the most important observations that requires further interpretation is the contrast in temporal extent between the relatively short-lived spring bloom that ends by June across most of the region, and the prolonged and elevated productivity at the surface expressions of the thermohaline fronts that persists at least through August. The persistence of elevated Chl *a* at the shelf break was captured in SeaWiFS images during 2004 that are presented in Stabeno et al. (2008b). Among several important questions related to the regions of the southeastern Bering Sea that support elevated summer production, two will be considered here: What are the underlying processes that support this elevated primary production; What are the implications of these relatively small but productive regions on the flow of resources to higher trophic levels?

The enhanced vertical supply of macronutrients along shelf-break fronts has been invoked as one of the primary factors sustaining elevated phytoplankton growth in shelf-break front environments (e.g., Ryan et al., 1999; Gibbs, 2000). However, the shelves discussed in those studies are in lower latitude regions, where both shelf and basin waters are depleted in macronutrients in summer. In contrast, macronutrients typically remain at high concentrations in the basin waters of the southeastern Bering Sea in summer, and nitrate concentrations were >10 μM in basin waters in the sampled years (Fig. 6A, B), confirming its high-nutrient, low-chlorophyll character. Also, although they are not as strongly stratified as the middle and outer shelf regions, the basin waters were stratified at 20–30 m, making it likely that light conditions for phytoplankton growth were not significantly worse in the basin. Thus, other factors must restrict the seaward extent of the production associated with the shelf-break front. One factor could be the greater consumption rates of phytoplankton in basin waters by oceanic grazers (Frost, 1991). In the Bering Sea, large oceanic copepods such as *Neocalanus* spp. and *Eucalanus* spp. are found primarily in slope and basin waters (Coyle et al., 2008), and thus grazing by macrozooplankton might account for the seaward limit of the shelf-break productivity. Additionally, microzooplankton in these waters may graze as much as 50% of the primary production (Strom and Fredrickson, 2008). However, modeling studies in the northeastern Bering Sea suggest only a small role for macrozooplankton grazing in limiting phytoplankton in frontal regions (Shuert and Walsh, 1993).

An alternate explanation for the restricted seaward extent of the elevated productivity associated with the shelf-break front is the lack of iron, an essential element that is suspected to play a significant role in several high nutrient but low Chl *a* regions, including the North Pacific (Boyd et al., 1996, 2004). There are no parallel measurements of iron in the present data. However, positive results were obtained from iron addition experiments in the oceanic region of the present study region during summer (LeBlanc et al., 2005; Peers et al., 2005). Part of the iron response in these and other iron addition experiments (e.g., Tsuda et al., 2003) is the stimulation of the growth of diatoms, and this observation is compatible with the relative abundance of diatoms along the shelf-break front in the southeastern Bering Sea.

There are several possible sources of iron for phytoplankton growth at the shelf-break front. While iron deposition from the atmosphere is relatively low in the Bering Sea (Fung et al., 2000), deep Pacific Ocean waters contain moderate amounts of iron (Johnson et al., 1997). The levels of iron in the waters of the eastern shelf, however, are greater still (Aguilar-Islas et al., 2007). Thus, deeper shelf water that has been in recent contact with the sediments may be a more important source of iron for phytoplankton growth at the shelf-break front than is the upwelling of slope and/or deeper basin waters. Unlike most well-oxygenated surface waters, reducing conditions in sediments can mobilize dissolved iron into deep waters, and there is a clear association between marginal seas that have extensive sediment interaction and elevated production (Tyrrell et al., 2005). The elevated ammonium levels in deep shelf waters in summer reflect, in part, the extensive reducing environment at or near shelf sediments, and iron often follows regeneration pathways similar to that of nitrogen (Johnson et al., 1997; de Baar and de Jong, 2001). The significant regeneration of organic matter in the sediments and overlying water of the middle and outer shelf regions of the southeastern Bering Sea has been well documented (Whitledge et al., 1986; Mordy et al., 2008). The vertical flux of organic matter from spring phytoplankton growth provides the reductant that results in lower oxygen levels and an extraordinary increase in ammonium concentrations in deeper shelf waters as summer progresses (Fig. 9).

Despite levels of dissolved iron in shelf bottom waters that may exceed 4 nM, iron concentrations in the surface waters of both shelf and oceanic regions of the southeastern Bering Sea are generally low during summer (Aguilar-Islas et al., 2007). Exceptions to this general pattern include the tidally mixed region between the Pribilof Islands and subsurface (~50 m) waters at the shelf break. Importantly, the elevated dissolved iron concentrations were accompanied by similar trends in dissolved manganese, reflecting a continental and/or sediment source. The subsurface maxima in iron concentrations at the shelf break recorded by Aguilar-Islas et al. (2007), therefore, may be associated with shelf-slope mixing processes, similar to those discussed in the prior section, that could facilitate the flux of iron to offshore regions. A similar shelf-slope transfer of iron was attributed to eddies generated at the shelf edge in the Gulf of Alaska (Johnson et al., 2005). The possible existence of elevated shelf-slope exchange of iron in the EBS suggests that more complex biogeochemical processes may be involved in generating elevated production at this shelf-break front than have been addressed previously.

In addition to the questions regarding the limiting factors for the seaward extent of shelf-break front productivity, it is clear that these regions are important in the upper trophic level ecology of the region (Springer et al., 1996; Decker et al., 1995). The relatively small spatial extent of the elevated productivity associated with these fronts together with the coarse hydrographic and biological sampling has hampered the analysis of this relationship. The 2004 sampling around the Pribilofs, for example, was the first extensive spatial survey of productivity in this region. It has largely confirmed the suspected elevated epipelagic production that has been inferred from bird feeding patterns in the region (Kinder et al., 1983; Schneider et al., 1987; Hunt et al., 1996). The persistent elevated productivity associated with the frontal regions may result in more efficient trophic transfer by allowing upper trophic level predators to focus on a restricted region. The fish harvest relative to the productivity of the region provides indirect evidence for this efficiency. For example, the groundfish catch (mainly walleye pollock) in the southeastern Bering (~ 1.5×10^{12} g yr⁻¹; Bailey et al., 1999, or about 4×10^{10} g N), the size of the shelf region (~ 3×10^{11} m²) and the levels of yearly production in Table 2 suggest that ~1.3% of the new production and ~3.5% of the carbon production is harvested in the southeastern Bering each year. These estimates may be conservative, considering that the pollock are not evenly distributed on the shelf. Even based on the conservative area used, this one species represents over 50% of the total carnivorous fish and squid production that would be expected from local primary production based on Iverson's (1990) compilation of several ocean regions. Perhaps in part because so much of the primary production is channeled into one major species, the EBS is highly efficient at converting nitrate into harvestable fish protein in its present ecological configuration.

If such trophic efficiency is dependent in part on the highly organized and persistent spatial patterns in epipelagic productivity, then there are several ways in which changes in primary production could propagate to higher trophic levels. In addition to the obvious impacts that changes in total regional productivity would have, upper trophic level impacts could be expected from any redistribution in existing patterns. For example, changes in the location of critical feeding regions such as the shelf-partition front may have important implications for the vertebrate populations that forage in this region. Drifters released in the Bering Slope Current and shelf near Unimak Pass were transported to the east of the Pribilofs in 2004, and this differed from most prior drifter tracks that were advected to the west of the islands (Stabeno et al., 2008b). If such circulation changes impact the

location of the shelf-partition front, they would alter the access to this front by populations that use such environments during forage trips from the nearby Pribilof Islands. Thus, several physically, and, potentially, climatically linked mechanisms may impact upper trophic levels through bottom up effects on primary production. Information on the Bering Sea environment should be sufficient to address such hypotheses from the expanded sampling that is planned in the next few years.

5. Summary and conclusions

A combined analysis of summer hydrographic and productivity data in the vicinity of the Pribilof Islands and adjacent southeastern Bering Sea indicates that:

- (1) Low production dominates the middle and outer domains during summer as surface stability increases due to heating and fresher, low-nutrient water ultimately derived from the ACC alter the environment.
- (2) Rates of new (nitrate) and primary (¹⁴C) productivity range from > 1800 mmol m⁻² yr⁻¹ and > 170 g C m⁻² yr⁻¹ in the shelf-break front to less than 700 mmol m⁻² yr⁻¹ and 100 g C m⁻² yr⁻¹ in the basin and coastal waters.
- (3) Elevated productivity during summer is restricted to two basic types of oceanographic fronts. Structure fronts (the front between the well-mixed coastal domain and the two-layer middle shelf) dominate the periphery of the EBS as well as the region immediately around the Pribilof Islands. Thermohaline fronts that form between shelf and slope waters characterize the shelf-break region from north of Unimak Pass to at least as far as the Pribilof Islands.
- (4) The existence of a recently identified shelf-partition front east of St. Paul Island was confirmed. It appears to be a thermohaline front caused by the intrusion of slope-derived water.
- (5) An isopycnal connection exists between deeper shelf waters and the shelf-break front region. Isopycnal mixing, together with dynamics associated with frontal meanders and eddy generation, likely promote significant exchange between the two regions.
- (6) Macronutrient supply to the shelf-break front is not sufficient to explain the spatial pattern of this productive region, and we suggest that dissolved iron mobilized from shelf sediments is an important factor in maintaining elevated summer productivity.

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