

1 **Late summer early fall phytoplankton biomass (chlorophyll *a*) in the eastern Bering Sea:**
2 **spatial and temporal variations and factors affecting chlorophyll *a* concentrations**

3
4
5
6 **Lisa B. Eisner^{a*}, Jeanette C. Gann^b, Carol Ladd^c, Kristin Cieciel^b, Calvin W. Mordy^{c,d}**

7
8
9
10
11 ^aNOAA-Fisheries, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA,
12 Lisa.Eisner@NOAA.gov, 001-206-526-4060

13 ^bNOAA-Fisheries, Alaska Fisheries Science Center, 17109 Point Lena Loop Road, Juneau, AK 99801,
14 USA, Jeanette.Gann@NOAA.gov; Kristin.Cieciel@NOAA.gov

15 ^cNOAA-Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA,
16 Carol.Ladd@NOAA.gov; Calvin.W.Mordy@NOAA.gov

17 ^dJoint Institute for the Study of the Atmosphere and Ocean, University of Washington, 3737 Brooklyn
18 Ave NE, Box 355672, Seattle, WA 98105-5672 USA

19
20
21
22 *Corresponding Author
23

24 **Abstract**

25 The spatial and temporal variability of late summer/early fall phytoplankton biomass estimated
26 from in situ chlorophyll *a* (Chl*a*) concentrations was investigated over a 10-year time period
27 from 2003-2012 in the eastern Bering Sea, encompassing both warm, (2003-2005) and cold
28 (2007-2012) temperature regimes. Warm temperature regimes were characterized by above
29 average water temperatures and low seasonal sea ice extent and cold by below average
30 temperatures and high seasonal sea ice extent. The highest phytoplankton Chl*a* was observed
31 near the Pribilof Islands and the southeastern shelf break where nutrient concentrations were
32 high due to onshore flow from Pribilof and Bering Canyons. The lowest Chl*a* was observed on
33 the northeastern middle and inner shelf, north of Nunivak and St. Matthew Islands and south of
34 St. Lawrence Island (~61- 63°N). Stations north of St Matthew Island (61°N) did not show
35 significant variations in Chl*a* between temperature regimes. To the south, total phytoplankton
36 Chl*a* was significantly higher in warm compared to cold years on the south-outer shelf and on
37 portions of the middle shelf. Large phytoplankton Chl*a* was higher in warm years over most of
38 the southern middle-shelf. For the entire southeastern Bering Sea shelf (~30-200 m bathymetry,
39 south of Nunivak Island), the highest Chl*a* was seen in 2005 and lowest in 2007 and 2008.

40 On the south-middle shelf, wind mixing and temperature below the pycnocline had strong
41 positive associations with Chl*a* (total and large-size fraction) integrated over the top 50 m,
42 explaining 85% of the variability in mean Chl*a*. This indicates that Chl*a* in summer and early fall
43 is positively affected by wind-induced upwelling of nutrients to the surface and possibly by other
44 bottom up effects such as temperature-mediated growth. Higher bottom temperature is related to
45 reductions in sea ice extent which may elicit ecosystem responses such as reduced biomass of
46 large crustacean zooplankton grazers, potentially due to the removal of ice algae, an important
47 food resource for zooplankton in early spring. This, in turn, could reduce or alter the grazing
48 pressure on phytoplankton later in the growing season. Overall, spatial and temporal variations in
49 phytoplankton Chl*a* are due to a combination of factors, from local inputs of nutrients related to
50 mixing or advection, up to large scale ecosystem effects.

51 **Keywords: phytoplankton, nutrients, cold pool, chlorophyll *a*, climate, eastern Bering Sea**

52 **1. Introduction**

53 Phytoplankton biomass variations (using chlorophyll *a* [Chl*a*] as a proxy) may reflect changes in
54 energy (primary production) available to zooplankton and higher trophic level consumers such as
55 marine birds and fish on the eastern Bering Sea shelf (Brown et al., 2011). Production that is not
56 grazed will sink and support benthic production, often producing benthic “hot spots”, particularly
57 in regions with high levels of primary production and large-size, quickly sinking phytoplankton
58 taxa (Grebmeier et al., 2006). Large phytoplankton taxa such as diatoms can also allow for a
59 shorter food web with more efficient energy transfer to higher trophic levels (e.g. diatoms to
60 large copepods such as *Neocalanus* spp. to seabirds, Springer et al., 1996). Phytoplankton
61 metrics (biomass, taxonomy and production) vary spatially across the eastern Bering Sea shelf
62 (Rho and Whitley, 2007; Brown et al., 2011; Liu et al., this issue) and temporally, both
63 seasonally (Lomas et al., 2012; Moran et al., 2012) and interannually (Brown and Arrigo, 2013).

64 Spatial variations in phytoplankton metrics may be associated with strong cross-shelf variations
65 in physics and nutrients during summer. This wide (> 500 km) coastal shelf is characterized by a
66 well-mixed inner shelf, a highly stable two-layer water column on the middle shelf, and a three-
67 layer system with a well-mixed surface and bottom layer on the outer shelf (Coachman, 1986).
68 Zooplankton communities (meso- and micro-zooplankton) also show strong cross-shelf gradients
69 (Eisner et al., 2014; Stoecker et al., 2014a, 2014b). Therefore, both bottom-up (e.g. stratification,
70 nutrient concentrations) and top-down factors (e.g. meso- and micro-zooplankton grazing) can
71 produce cross-shelf variations in phytoplankton Chl*a* and size structure. Likewise, variations in
72 phytoplankton production may influence zooplankton abundances. There are also large
73 ecosystem variations within the cross-shelf domains (inner, middle and outer shelf), so it is
74 useful to examine finer scale variation using the smaller spatial areas (regions) defined for the
75 Bering Sea Project (Bering Sea Ecosystem Study [BEST] and Bering Sea Integrated Ecosystem
76 Research Program [BSIERP], Ortiz et al., 2012; Wiese et al., 2012). These regions are based on
77 oceanographic, ecosystem, and fisheries characteristics and parse the eastern shelf into seven
78 regions south and six regions north of ~60 °N (Fig 1).

79 Interannual variations in phytoplankton metrics may be driven by physical forcing associated
80 with large-scale changes in sea ice extent and water temperature. Marked multiannual shifts in
81 sea ice have occurred during recent years in the eastern Bering Sea, with a series of warm years

82 with low sea ice extent (warm temperature regime, 2000-2005) followed by a series of cold years
83 with extensive sea ice (cold temperature regime, 2007-2013) (Stabeno et al., 2012b; Zador,
84 2014). However, it is debated whether warming will increase or decrease biological productivity
85 (Brown et al., 2011; Lomas et al., 2012; Brown and Arrigo, 2013; Liu et al., this issue), partially
86 due to uncertainty of how temperature regime changes will affect nutrient availability.
87 Phytoplankton biomass, production, size structure and taxonomic composition have been
88 evaluated for recent cold years (2008-2010); but few studies were conducted during recent (early
89 2000s) warm years (Strom and Frederickson, 2008; Liu et al., this issue), so data are limited for
90 temperature regime comparisons.

91 The timing of primary production is important to functioning of the Bering Sea ecosystem
92 (Sigler et al., this issue). Many prior studies on the eastern Bering Sea shelf have focused on
93 production and biomass during spring (when the bulk of the yearly production is thought to
94 occur) and early summer periods on the eastern Bering Sea shelf (McRoy et al., 1972; Sambrotto
95 and Goering, 1983; Sambrotto et al., 1984, 1986, 2008; Walsh and McRoy, 1986; Whitley et
96 al., 1986; Hansell et al., 1993; Springer et al., 1996; Kopylov et al., 2002; Rho and Whitley,
97 2007; Lomas et al., 2012). However, fewer studies have focused on understanding variations in
98 phytoplankton ecology during late summer and early fall, near the end of the growing season
99 (Springer and McRoy, 1993; Rho and Whitley, 2007; Strom and Frederickson, 2008; Sigler et
100 al., 2014; Liu et al., this issue) and none of those studies covered a large number of consecutive
101 years for the entire eastern Bering Sea shelf. Summer and early fall are critical periods for
102 growth of many larval and juvenile fish in the eastern Bering Sea (Duffy-Anderson et al., 2006;
103 Sigler et al., this issue), and this is an important time for lipid accumulation in age-0 Walleye
104 Pollock (*Gadus chalcogrammus*) and other forage fish prior to overwintering (Siddon et al.,
105 2013; Sigler et al., this issue).

106 The goal of this manuscript is to synthesize ten years of phytoplankton Chla data and associated
107 physical and chemical variables (hydrography, nutrients, and wind mixing) collected during late
108 summer/early fall across the entire eastern Bering Sea shelf. Variations in total and large-size
109 phytoplankton Chla will be described both spatially (north-south and cross-shelf) and
110 interannually over extended temperature regimes. We describe spatial variability over the entire
111 shelf, and for the southern middle shelf domain we investigate interannual variability and

112 environmental factors related to these variations (temperature, salinity, August stratification,
113 summer wind mixing and nutrients). We chose to focus on this domain (50-100 m bathymetry,
114 south of $\sim 60^{\circ}\text{N}$) since it has a long record of environmental variability (e.g., sea ice, temperature,
115 salinity) from mooring observations collected by the Pacific Marine Environmental Laboratory
116 (PMEL). During summer, the southern middle shelf domain has warm surface temperatures and
117 cool bottom temperatures separated by a sharp pycnocline (Coachman, 1986). A cold pool
118 (bottom temperatures $< 2^{\circ}\text{C}$) expands southward into the southern middle shelf only during
119 years with high southerly sea ice extent, so there is high variability between temperature regimes.
120 Large variations in zooplankton community composition have also been observed on the south-
121 middle shelf between temperature regimes (Eisner et al., 2014), resulting in changes in prey
122 availability for key forage fish in this area, such as age-0 Walleye Pollock and Pacific Cod
123 (*Gadus macrocephalus*) (Heintz et al., 2013). For our environmental factor analysis, we focus on
124 two sub-regions of the south-middle domain that encompass two long-term oceanographic
125 moorings, PMEL Mooring 2 (M2, Region 3) and Mooring 4 (M4, inshore of the Pribilof Islands,
126 Region 6) (Fig. 1). We also evaluate the timing and strength of the fall blooms from ocean color
127 *Chla* measurements for the entire southeastern middle shelf (Regions 1, 3, 5 and 6).

128

129 **2. Data and Methods**

130 *2.1 Temperature regime designation*

131 Years used in this analysis were designated as warm (2003-2005), average (2006) or cold (2007-
132 2012) based on depth-averaged temperature anomalies on the southeastern middle shelf (Stabeno
133 et al. 2012b, Zador, 2014). Water temperatures reflect southerly ice extent and timing of retreat,
134 with colder temperatures associated with increased southerly ice extent and later retreat
135 compared to years with warmer temperatures. Water temperature between temperature regimes
136 varied by an average of $\sim 3^{\circ}\text{C}$ for both surface and deep waters on the south-middle shelf in late
137 summer (Eisner et al., 2014).

138 *2.2 Phytoplankton *Chla* biomass and size structure, hydrography and nutrients*

139 From 2003-2012, Bering-Arctic Subarctic Integrated Survey (BASIS) hydrographic data were
140 collected at stations spaced ~60 km apart, over a survey grid which spanned the shelf (160-
141 172°W, 54.5-65 °N, Fig. 1). Sampling occurred from mid-August to early October, although
142 survey start and end times varied by up to three weeks among years (Table 1). Conductivity-
143 temperature-depth (CTD) measurements were collected with a Sea-bird (SBE) 911 or SBE 25
144 CTD equipped with a Wetlabs Wet-Star or ECO fluorometer. Water samples for nutrients and
145 total and size-fractionated Chl a were collected during the upcast with Niskin bottles attached to
146 the CTD. Nutrient samples were collected at 2 to 6 depths distributed above and below the
147 pycnocline. Samples were frozen at -80 °C on board ship and analyzed for dissolved phosphate,
148 silicic acid, nitrate, nitrite, and ammonium at a shore-based facility using colorometric methods
149 (JGOFS, 1994). Dissolved inorganic nitrogen (DIN) was estimated by summing nitrate, nitrite,
150 and ammonium.

151 It has been shown that freezing may be problematic to ammonium measurements (Grasshoff,
152 1976; ICES, 2004). To evaluate this potential error in our data set, we compared samples
153 collected in similar locations (within 60 km) and depths within a two-week period on two
154 different cruises on the eastern Bering Sea shelf in 2005 (Mordy et al., 2010). On one cruise
155 samples were stored frozen while on the second cruise samples were analyzed at sea. Analytical
156 methods were the same for both sample sets (modified indophenol blue method; Slawyk and
157 MacIsaac, 1972; Mantoura and Woodward, 1983). Ammonium sample concentrations in 2005
158 ranged from 0.1 to ~ 10.5 μ M (after removal of one outlier of 12.3 μ M), similar to our entire
159 data-set. This analysis indicated a strong linear relationship between frozen and unfrozen
160 ammonium samples ($N= 61$, $R^2 = 0.89$, $P < 0.001$), although values were slightly (17% on
161 average) higher for frozen samples (paired t-test, $P = 0.004$, 95% CI for differences = 0.14 to
162 0.73, mean = 0.44). Some of the difference between unfrozen and frozen samples was likely due
163 to variations in collection dates and locations. Based on this evaluation, we chose to include
164 ammonium values from frozen samples in our analysis.

165 Chl a samples were collected at similar depths as nutrients. Samples were filtered through
166 Whatman GF/F filters (nominal pore size 0.7 μ m) to estimate total Chl a , and through
167 polycarbonate filters (pore size 10 μ m) to estimate large-size fraction Chl a . Filters were stored
168 frozen (-80°C) and analyzed within 6 months with a Turner Designs (TD-700) bench top

169 fluorometer following standard methods (Parsons et al., 1984). In vivo fluorescence data,
170 calibrated with discrete Chla samples by fluorometer and year (mean $R^2 = 0.68$ (standard
171 deviation (sd) 0.13), mean N = 250 (sd 140)) were used to calculate integrated Chla over the top
172 50 m, or to the bottom for station depths less than 50 m. The integrated >10 μm (large) size-
173 fractionated Chla was similarly estimated by multiplying the total integrated Chla from
174 calibrated in vivo fluorescence data by the mean large-size fraction ratio (>10 μm Chla /total
175 Chla) from discrete samples. The integrated <10 μm (small) size-fractionated Chla was
176 estimated by subtraction of the large-size fraction from the total integrated Chla. We used in vivo
177 Chla data for our integrations since discrete Chla samples (total and size-fractionated) did not
178 provide sufficient vertical resolution (ranged 10-30 m between sample depths).

179 Station locations sampled 5 years or more were used for all graphical and statistical analysis
180 (Fig. 1) for a total of ~1000 sampling events for all years combined. This 5-year cutoff
181 eliminated stations sampled only a few times (near the edge of our grid or with uneven station
182 spacing). The following means were determined for each region and each year: integrated total
183 and large-size fraction Chla, and T, S and nutrients in surface and deep waters. For T and S, we
184 used mean values above and below the pycnocline, since these were most representative of
185 surface and deep water masses. The depth of the pycnocline (mixed layer depth) was defined as
186 the first depth where sigma-t was 0.10 kg m^{-3} higher than the 5 m value (Danielson et al., 2011).
187 Since nutrient data were sparser than for T and S, 5 m nutrient samples were considered
188 representative of the surface layer and 30-60 m samples representative of the deep layer.
189 Preliminary plots indicated that relative spatial patterns of Chla and nutrients were fairly
190 consistent among years; therefore, we used data from all years combined to visualize the average
191 late summer spatial distributions. ArcMap (ESRI, 2014) with Natural Neighbor contouring was
192 used to make horizontal contour maps of integrated Chla (total and large-size fraction), surface
193 and deep nitrate, ammonium, DIN, and silicic acid. Integrated Chla and surface and deep
194 temperatures were also plotted separately for warm years and cold years.

195 To statistically evaluate differences in Chla between temperature regimes for each region, we
196 used mixed models in SYSTAT (Systat Software Inc., 2009) with Residual or Restricted
197 Maximum Likelihood (REML), with station location and year nested within regime as random
198 effects. Analyses were conducted on mean natural log transformed integrated Chla (total, large

199 and small size fractions), surface and deep T and S, transformed (4th root transformation) surface
200 and untransformed deep DIN and silicic acid, for warm and cold years for each Bering Project
201 Region (1-14, excluding 8). Region 8 was excluded due to small sample size (infrequent
202 sampling). To visualize interannual variations in Chl a among regions, we computed standardized
203 anomalies (standardized to maximum anomaly value) for natural log transformed integrated Chl a
204 (total and large size-fraction) for each year and region.

205 *2.3 Stratification*

206 A stratification index using data from the PMEL M2 mooring located on the south-middle shelf
207 (56.9°N, 164.1°W) was determined following the methods described in Ladd and Stabeno
208 (2012). Potential energy relative to the mixed state ($J m^{-2}$) can be used as a stratification index
209 (SI):

$$SI = \int_{-h}^0 (\rho - \langle \rho \rangle) g z dz; \quad \langle \rho \rangle = \frac{1}{h} \int_{-h}^0 \rho dz$$

210 where ρ is density and h the depth of the water column (Simpson et al., 1977). The stratification
211 index is equal to 0 for a vertically mixed system and increases with increasing water column
212 stability. SI was integrated to $h = 70$ m (approximate bottom depth at M2).

213 For the average August stratification index at M2, we used the data from Ladd and Stabeno
214 (2012) updated with two additional years (2011 and 2012). Similar calculations were also
215 conducted using temperature and salinity measurements from BASIS surveys for 2002-2009 to
216 determine areas of higher and lower stratification. For this analysis, we used data from the top 70
217 m or bottom, whichever was shallower to estimate the mean ($J m^{-3}$) instead of the integrated (J
218 m^{-2}) water column stratification.

219 *2.4 Wind mixing*

220 Friction velocity cubed (u_*^3 ; $m^3 s^{-3}$) is proportional to the rate of mechanical energy applied at
221 the ocean surface for stirring (Bond and Adams, 2002) and was used as a proxy for wind mixing.
222 Data for summer months (June-August) were obtained from National Centers for Environmental
223 Prediction (NCEP) reanalysis data set (Kalnay et al., 1996) and were averaged over 2° latitude
224 by 5° longitude boxes (N. Bond, NOAA PMEL, pers. comm.) centered over each of the NOAA

225 PMEL moorings, M2 (56.9°N, 164.1°W) and M4 (57. 9°N, 168. 9°W; Stabeno et al., 2010). As
226 wind speeds at M2 and M4 are similar and winds in the southeastern Bering Sea show strong
227 coherence over large spatial areas (Stabeno et al., 2010), we assumed M2 and M4 winds
228 approximated wind fields over the Bering Project Regions 3 and 6, respectively. The number of
229 days that exceeded a threshold u_*^3 value of $0.05 \text{ m}^3 \text{ s}^{-3}$ (one standard deviation above mean daily
230 u_*^3 for June-August for 2000-2012) at M2 was used as an index of the frequency of summer wind
231 mixing events.

232 *2.5 Timing and strength of the fall bloom from ocean color observations*

233 Moderate Resolution Imaging Spectroradiometer (MODIS) ocean color data were used to
234 generate monthly (August, September, October) composites of mean Chla (mg m^{-3}) over the
235 south-middle shelf for Regions 1, 3, 5, and 6 (Fig. 1). High cloud cover precluded the use of 8-
236 day or bi-weekly composites. For the monthly composites, regions or months with less than 50%
237 data coverage were excluded from the analysis. The months of highest Chla within each region
238 (all years combined) provides a rough estimate of the timing of the fall surface phytoplankton
239 bloom on the south-middle shelf. Summation of the average Chla for August, September and
240 October (termed Aug-Oct MODIS) for Region 3 (area surrounding M2) was used as an index of
241 the magnitude of the fall bloom. In situ Chla data (5 m depth) from discrete samples collected on
242 BASIS surveys were included for comparison.

243 *2.6 Mechanisms influencing integrated Chla*

244 Environmental variables potentially related to variations in integrated total and large-size
245 fraction Chla in Regions 3 and 6 during late summer/early fall were evaluated visually, followed
246 by Generalized Linear Models (GLM) using backwards stepwise selection (Type 3 Sum of
247 Squares) in SYSTAT. The environmental variables tested included means for August u_*^3 (~2
248 weeks prior to sampling), August stratification index at M2, in situ surface T, deep T and deep S,
249 and surface and deep nutrients (nitrate, ammonium, and silicic acid), using depths defined above
250 (*Section 2.2*). Surface salinity and surface phosphate were not included in GLM analysis since
251 they were found to be highly correlated with other variables (deep T and surface ammonium,
252 respectively, Pearson correlation > 0.85). Stratification data were not available at M4 for many
253 of the years, so this variable was not included in the model for Region 6. Finally, to determine if

254 there was a relationship between Chla and relative size structure, we conducted linear
255 regressions between mean integrated total Chla and percent large phytoplankton (>10 µm Chla/
256 total Chla) for all regions.

257

258 **3. Results**

259 *3.1 Phytoplankton biomass and size structure, hydrography and nutrients for entire shelf*

260 *3.1.1 Spatial variation*

261 There was considerable spatial variability over the shelf for all years combined (2003-2012) for
262 integrated Chla (total and large-size fraction), surface and deep nitrate, DIN and silicic acid and
263 stratification over the top 70 m (Table 2, Figs. 2 and 3). The areas with the highest integrated
264 total Chla were the southern-most region of the inner shelf (Region 2), the southern middle shelf
265 north of the Alaska Peninsula (Region 1), near M4 (Region 6) and around the Pribilof Islands
266 (Region 5), over the south-outer shelf (Region 4), north of St. Lawrence Island (Region 12), and
267 at the single shelf break station (Region 16) (Fig 1, 2A). The areas with the lowest integrated
268 Chla were the north-inner and north-middle shelf (Regions 11, 10), Norton Sound (Region 14)
269 and the region surrounding M2 (Region 3). The high integrated Chla on the south-outer shelf
270 was primarily from small phytoplankton (large < 25% of total Chla), while the relatively high
271 biomass near the Pribilof Islands and M4, and on the south-inner shelf was from a mix of large
272 and small assemblages (large ~50-75% of total Chla) (Fig. 2A, B). In general higher
273 concentrations of large cells were seen in regions with higher total integrated Chla.

274 Spatial patterns in nitrate and DIN reflected the locations of the cross-shelf domains; nitrate and
275 DIN were mostly depleted throughout the water column in the well-mixed inner domain, and
276 nitrogen-replete deep water was overlain by depleted surface water in the 2-layer middle shelf
277 (Fig. 3A, C, E, G). The highest surface nitrate and DIN were found in the south-outer shelf and
278 offshore, and north of St. Lawrence Island, with the remainder of the shelf generally depleted (<
279 0.5 µM nitrate and < 1 µM DIN, Fig. 3A, C). The highest deep nitrate and DIN was seen over
280 the southern middle and outer shelf, with low values seen in the northern inner and middle shelf
281 (Fig. 3E, G). The deep DIN values were ~ 5 µM higher than nitrate levels in the south-middle

282 domain due to the presence of a deep ammonium pool (Fig. 3F); these high ammonium
283 concentrations are commonly observed at depth in this domain during summer (Kachel et al.,
284 2002; Mordy et al., 2008). Surface silicic acid concentrations over the entire shelf were generally
285 in the range of 3-7 μM , with the highest concentrations over the southern outer shelf and in
286 Norton Sound (Fig. 3D). Deep silicic acid was higher over most of the southern middle and outer
287 shelves and around St. Lawrence Island, and lower over much of the south-inner shelf (Fig. 3H),
288 similar to nitrate and DIN. The highest stratification was observed in the south-middle shelf in
289 Region 3 (Fig. 4), a region characterized by low Chla and small cells, and elevated ammonium in
290 the deep water.

291 3.1.2 Temporal Variation

292 Integrated total and large-size fraction Chla show similar spatial patterns across temperature
293 regimes, but values were higher in warm (2003-2005) than in cold (2007-2012) years for all
294 southern regions and most northern regions (Fig. 5A, B, E, F). Significant differences between
295 temperature regimes for integrated Chla (total, large-size and small-size fraction) were only seen
296 in middle and outer shelf regions at or south of 61°N (near St Matthew Island and south) (Table
297 3, Fig. 1). In warm years, there was higher total Chla for Regions 1, 4 and 9, and higher large-
298 size fraction Chla for Regions 1, 3, 4, 6 and 9. The small-size integrated Chla was also higher in
299 two of the regions that had higher total integrated Chla (Regions 4 and 9). Similarly, surface and
300 bottom temperature (Fig. 5C, D, G, H) and salinity (not shown) were significantly higher in
301 warm compared to cold years only in regions at or south of 61°N (Table 3). Significant
302 differences in salinity were only observed in the middle domain (Regions 3, 5, 6, and 9), while
303 difference in temperature were seen in all cross-shelf (inner, middle and outer) domains. There
304 were no significant differences for surface or deep DIN or silicic acid between warm and cold
305 regimes ($P > 0.10$).

306 Interannual variations in Chla were also observed. Total and large-size fraction integrated Chla
307 were high in 2005 (and secondarily in 2004) in most southern regions and near St. Matthew
308 Island (Region 9) and low in 2006 and 2007 (and to some extent 2008) in more disparate regions
309 (Table 2). There were significant linear relationships (ANOVA, $P < 0.05$) between mean
310 integrated Chla and percent large-size fraction for Regions 1, 3, 4 and 10 for 2003-2012 (Fig. 6).
311 The north-middle shelf (Region 10) had a smaller range of variability in percent large Chla than

312 regions farther south, suggesting phytoplankton size classes were more consistent across years in
313 the north compared to the southeastern Bering Sea shelf.

314 *3.2 Stratification, wind mixing and phytoplankton biomass on the southeast middle shelf*

315 *3.2.1 Stratification and wind mixing*

316 August stratification intensity, August u_*^3 (a proxy for wind mixing magnitude), and the number
317 of threshold wind mixing events ($> 0.05 \text{ m}^3 \text{ s}^{-3}$) for summer (June-August) did not vary
318 significantly between temperature regimes in Region 3 ($P = 0.12$, $P = 0.33$, and $P = 0.92$,
319 respectively, t-test, Table 4). The highest August stratification was seen in 2004 and 2007, and
320 the lowest number of wind mixing events was in summer 2007, indicating that conditions during
321 2007 were anomalously stable. Low integrated Chla (total and large-size fractions) were
322 observed in 2007 (Table 2). In contrast, August stratification in 2005 was average, while August
323 u_*^3 , number of summer wind mixing events and integrated total and large-size fraction Chla were
324 the highest in our time series.

325 *3.2.2 Mechanisms influencing phytoplankton biomass*

326 Linear regressions of single environmental variables in the southeast middle domain show a
327 positive relationship between August u_*^3 at moorings M2 and M4 and mean integrated total Chla
328 for Regions 3 and 6 ($R^2 = 0.77$ and 0.69 , respectively, $P < 0.05$ ANOVA, Fig. 7), with the
329 highest wind mixing indicated in 2005. Removal of 2005 data from the analysis yields $R^2 = 0.43$
330 and 0.23 ($P = 0.05$ and 0.11) for Regions 3 and 6, respectively. Positive relationships also were
331 seen for deep T and integrated total Chla, with a weaker relationship in Region 3 than in Region
332 6 ($R^2 = 0.50$ and 0.83 , respectively, $P < 0.05$ ANOVA, Fig. 7). Similar to wind mixing, removal
333 of 2005 from the analysis reduces the correlation, with $R^2 = 0.28$ and 0.76 ($P = 0.15$ and 0.002)
334 for Region 3 and 6, respectively. Stepwise multiple linear regressions show that the best model
335 for predicting integrated total Chla for Region 3 includes August u_*^3 , deep T and August
336 stratification (Table 5). Similarly, the best model for Region 6 included August u_*^3 and deep T.
337 August stratification was not included in the regression model for this region as no data were
338 available. These models explain 86-96% of the interannual variation in integrated total Chla,
339 with 85-86% explained by u_*^3 and deep T alone. Similar to total Chla, u_*^3 was positively related
340 to large-size fraction Chla for both Regions 3 and 6. However, deep T was only significant for

341 large-size fraction Chla in Region 3 (Table 5). Deep nutrients were important in both Regions 3
342 and 6, with a negative relationship for silicic acid in Region 3 and a positive relationship for
343 ammonium in Region 6. Similar to total Chla, these factors explained 83-96% of the variability
344 in large-size fraction Chla.

345 *3.3 Timing and strength of fall blooms from ocean color data*

346 Comparisons of monthly averages of Chla from MODIS ocean color measurements for the
347 south-middle regions combined (Regions 1, 3, 5 and 6) indicated that Chla concentrations were
348 lowest in August ($P < 0.05$, ANOVA), with similar Chla during September and October ($P >$
349 0.05) (Fig. 8A). Among these three months, the highest Chla was in September and October for
350 the majority of the south-middle shelf area (Regions 3 and 6), and in September near the Alaska
351 Peninsula (Region 1) and surrounding the Pribilof Islands (Region 5). Interannual variability in
352 MODIS data is somewhat consistent with in situ 5 m Chla data (higher values in 2005 and 2009
353 in both datasets), although the high in situ values for 2011 were not observed in the MODIS data
354 (Fig. 8B). Lower values were observed in 2007, 2008 and 2012 in both data sets.

355

356 **4. Discussion**

357 The over-arching goals of this study are to evaluate spatial and temporal variability in
358 phytoplankton Chla during late summer/early fall, associated environmental variables driving
359 this variability and potential ecosystem interactions. We discuss 1) the spatial variability of
360 phytoplankton biomass and associated physical and chemical oceanographic variables, 2) the
361 temporal variations (interannual and between temperature regimes) in phytoplankton Chla over
362 the entire eastern Bering Sea shelf and the environmental factors associated with these variations
363 (for the south-middle shelf, in particular), 3) implications for fisheries, and 4) estimations for fall
364 bloom timing on the south-middle shelf.

365 *4.1 Spatial variability*

366 Phytoplankton Chla showed considerable spatial variations during late summer/early fall likely
367 due to variations in nutrient availability from horizontal advection, e.g. along-shelf currents,
368 flows through canyons (Kinney et al., 2009; Stabeno et al., 2010, this issue) and/or vertical

369 upwelling/mixing of nutrient-rich waters (Sambrotto and Goering, 1983; Sambrotto et al., 1986;
370 Kachel et al., 2002). Preliminary maps (data not shown) indicate that the relative distribution
371 patterns were also fairly similar among years (e.g. Pribilof Islands and south-outer shelf had
372 relatively high Chla; north of 61°N had relatively low Chla).

373 *4.1.1 North–South variations*

374 The low Chla observed on the north-middle shelf between 61-63 °N (Fig. 2) was associated with
375 relatively low nitrate and ammonium below the pycnocline (implying that wind mixing events
376 would be less effective at mixing nutrients to the surface). Since this region had lower
377 stratification than the southern middle shelf (Stabeno et al., 2012a; Fig 3), less energy (lower
378 wind speeds) would be necessary to mix the water column. Thus, deep nutrients may be
379 decreased in this region due to summer wind mixing (prior to our survey time period) or from the
380 prevalence of sub-pycnocline primary production observed in the northern middle shelf (Stabeno
381 et al, 2012a; Mordy et al., 2012). This could lead to greater draw-down of deep nutrients in this
382 region than on the middle shelf farther south. In addition to wind mixing, the canyons that incise
383 the shelf-break can result in on-shelf flux of nutrients. Stabeno et al. (this issue) estimate that
384 over 50% of nutrients are replenished on the southern middle shelf each year with much of that
385 coming from the deep basin through the Bering Canyon (Fig. 1), which may explain the high
386 levels of deep nutrients near the shelf-break and intruding into the middle shelf in the south.
387 Slope water does not appear to greatly replenish the inner shelf (Granger et al., 2012).
388 Unfortunately, we did not collect data on the northern shelf at bathymetry > 70 m, so we cannot
389 evaluate variations on the northern outer shelf or shelf-break.

390 Phytoplankton Chla (both total and large-size fraction) did not vary significantly between
391 temperature regimes in regions north of 61°N, unlike several southern regions; this coincides
392 with lower variability in surface and deep T and S in the north compared to the south (Fig. 5;
393 Stabeno et al., 2012a). Likewise, variability in zooplankton community composition between
394 temperature regimes was lower in the northeastern compared to the southeastern Bering Sea
395 shelf during late summer/early fall (Eisner et al., 2014). The northern Bering Sea is always
396 seasonally ice covered (Stabeno et al., 2012a, with some exceptions influenced by polynyas)
397 with more consistent ice coverage, timing of ice retreat and timing of the spring bloom compared
398 to the southern Bering Sea (Sigler et al., 2014). Both ice algae and ice edge spring blooms occur

399 annually in this northern region unlike the southern shelf which only has ice associated
400 production in cold years. Thus, an early spring food source (phytoplankton or ice algae) for large
401 crustacean zooplankton may be available in both warm and cold years on the northern shelf,
402 although there are still variations among regions within the northern shelf. In general, we may
403 expect lower trophic pelagic organisms (ice algae, phytoplankton and zooplankton) to be less
404 affected by temperature regime changes in the northern compared to the southeastern Bering Sea.

405 Benthic biomass also varies between the north and south Bering Sea shelf with a predominance
406 of invertebrates in the north (McCormick-Ray et al., 2011). Benthic biomass is fueled by sinking
407 organic material, so areas of higher benthic biomass may coincide with areas with high
408 abundances of larger faster sinking phytoplankton or ice algae (e.g. large diatoms). Grebmeier et
409 al. (2006) described patterns of integrated *Chla* in the northern Bering Sea for April to
410 September 1976-2004, and found that concentrations were lower from 60 to 62 °N (Region 9),
411 Norton Sound (Region 14) and the north-inner shelf (Region 11), and higher north of St.
412 Lawrence Island (Regions 12 and 13). These patterns are generally similar to the current study,
413 although for the area south of St. Lawrence Island (Region 10), higher values were observed by
414 Grebmeier et al. (2006). A majority of the primary production in the northern Bering Sea reaches
415 the benthos likely due to short food chains and shallow bathymetry (Grebmeier et al., 2006), high
416 sub-pycnocline production (Mordy et al., 2012; Stabeno et al., 2012a), a high annual flux of ice
417 algal production, and temperature restriction of grazing pressure. This sinking production fuels
418 large benthic invertebrate communities (epifauna and infauna) in areas that coincide with water
419 column production hot spots (Grebmeier et al., 2006). For example, epifaunal biomass was
420 higher north of St. Lawrence Island, and northeast of St. Mathew Island, and lower from ~61 to
421 63 °N, east of ~172 °W; this corresponds with higher and lower integrated *Chla* seen in our
422 current study. Epifaunal biomass was also relatively high west of 172 °W, outside our study area,
423 in an area where high *Chla* was observed along the 70 m isobath (Stabeno et al., 2012a).

424 4.1.2 Cross-shelf and finer scale variations

425 Phytoplankton *Chla* and taxonomic composition varied offshore to onshore and at finer scales as
426 observed in prior studies (e.g. Goering and Iverson, 1981; Brown et al., 2011; Lomas et al.,
427 2012; Moran et al., 2012;). Similarly, primary production has been shown to decrease from
428 offshore to onshore on the southern shelf (e.g., Hansell et al., 1993; Springer et al., 1996; Lomas

429 et al., 2012). High *Chla* along the shelf break, as observed for our single shelf-break station (Fig.
430 1), is a well-established phenomenon due to high nutrient availability from mixing of oceanic
431 waters at this front (e.g. “green belt”, Springer et al., 1996). In the south-outer domain (Region 4)
432 the higher *Chla* was associated with higher surface nutrient concentrations (nitrate and silicic
433 acid, Fig. 2A, D) due to on-shelf flow through Bering Canyon (Stabeno et al., this issue).
434 Likewise, the higher percentage of small cells observed in this region were likely of oceanic
435 origin, transported by on-shelf flows. Due to the break-down of the frontal structure in fall,
436 cross-shelf fluxes are higher in fall than summer (Stabeno et al., this issue).

437 In the south-middle domain, finer scale variations in phytoplankton *Chla* and size structure were
438 observed among the four regions (Regions 1, 3, 5, 6). The somewhat higher *Chla* (total and
439 large-size fraction) near M4 (Region 6) compared to M2 (Region 3) may be due in part to the
440 relatively lower stratification at M4 (Fig. 4; Ladd and Stabeno, 2012), which may allow a greater
441 flux of nutrients to the surface during wind events. Nitrogen was usually the limiting nutrient on
442 the south-middle shelf, with the exception of 2007 when silicic acid was likely limiting to diatom
443 growth in Region 3 (Gann et al., this issue). The region north of the Alaska Peninsula (Region 1)
444 is influenced by the Alaska Coastal Current (ACC). The ACC flows through the eastern Aleutian
445 Passes and mixes with nutrient-rich slope waters before flowing on-shelf toward the east along
446 the Alaska Peninsula; this flow provides a relatively constant supply of nutrients (Stabeno et al.,
447 2002) which may fuel production there throughout the summer. Near the Pribilof Islands (Region
448 5), the high *Chla* and relatively high surface nitrate, ammonium and silicic acid is due to the
449 influx of nutrients along the 100-m isobath with intrusions from Pribilof Canyon, and the
450 westward transport and vertical mixing of middle-shelf water containing nutrient-rich (high
451 ammonium and nitrate) bottom water (Stabeno et al., 2008, this issue; Sullivan et al., 2008).
452 Prior studies have found the tidally mixed region adjacent to the Pribilof Islands to have high
453 primary production throughout the summer (Sambrotto et al., 2008) which contributes to the
454 high abundance of planktivorous and piscivorous seabirds (e.g., murre, kittiwakes, puffins,
455 auklets and others) and pinnipeds (e.g., northern fur seals) (Byrd et al., 2008; Call et al., 2008;
456 Hunt et al., 2008; Jahncke et al., 2008). Our study confirms that the Pribilof region has the
457 highest phytoplankton *Chla* on the shelf in both warm and cold years.

458 In the south-inner domain (Regions 2 and 7), the moderate large-fraction Chla may have been
459 fueled by nutrient inputs at the inner front (Kachel et al., 2002). Nutrient uptake was likely
460 immediate since ambient DIN concentrations were low ($< 1 \mu\text{M}$, Fig. 2C). Interestingly, surface
461 ammonium was observed in higher concentrations than nitrate (Fig. 2A, B). Recent taxonomic
462 analysis for 2012 indicated that many of the diatoms observed in this region were degraded and
463 lacking chloroplasts, with few long intact chains (data not shown), possibly due in part to large
464 senescent cells being mixed up from the bottom and suspended in the water column by tidal
465 mixing. However, some fraction of the phytoplankton biomass was actively growing; surface
466 primary production rates in the inner domain, estimated at a subset stations in the current study,
467 were moderate (Liu et al., this issue). Other studies have also found appreciable production in the
468 inner domain regions during summer (Rho and Whitley, 2007; Brown et al., 2011).

469 North of St. Lawrence Island (Regions 12 and 13), the high Chla in both warm and cold years is
470 due to high nutrients in the Anadyr Current which continuously fuel production near the surface
471 (Sambrotto et al., 1984; Springer and McRoy, 1993; Grebemeier et al. 2006). This water is
472 advected from the Gulf of Anadyr and flows northeastward through Anadyr Strait into Bering
473 Strait and the Chukchi Sea (e.g., Coachman et al. 1975; Walsh et al., 1989).

474 *4.2 Temporal variability*

475 Warm years generally had higher mean late summer/early fall Chla than cold years. Chla and
476 primary production are positively related on an annual basis for the eastern Bering Sea shelf ($R^2 =$
477 0.65 , Brown et al., 2011), so higher Chla is likely to be associated with higher productivity.
478 Recent analysis of satellite MODIS data for summer (defined as July-September in their study)
479 attributed higher primary production in warm years to presumed weaker stratification and
480 increased mixing of nutrients to the surface (Brown and Arrigo, 2013). However, there were no
481 significant differences in stratification in warm and cold years for the southeast middle shelf
482 based on M2 data for our survey years (2003-2012) or found by Ladd and Stabenro (2012) for
483 1995-2010. Other studies suggest that annual production may be lower (Lomas et al., 2012) or
484 similar (Liu et al., this issue) in warm compared to cold years. Modeled annual gross
485 phytoplankton production in the north was found to be higher in warm than cold years, due to the
486 persistence of sea ice in cold years in spring, but was similar between regimes for the south in
487 spring and for the entire shelf in summer (Liu et al., this issue). The high spatial and interannual

488 variability make it difficult to resolve this issue; it has been estimated that changes would have to
489 exceed a factor of two to be detected (Lomas et al., 2012).

490 Variations in nutrient concentrations at depth could impact biomass and production, since the
491 flux to the surface will vary for a given magnitude of wind mixing. Deep ammonium was found
492 to be positively related to large-size fraction Chl a near M4 (Region 6) using general linear
493 models (Table 5). Salinity below the pycnocline was ~ 0.5 units higher in warm years in this
494 region (Appendix). Cold, northerly winds result in westward (directed off-shelf) Ekman transport
495 and thus, cold summers with higher freshwater content (Danielson et al., 2011, 2012). Warm
496 years exhibit higher on-shelf fluxes of salty, nutrient-rich water (Stabeno et al., 2001). Salinity
497 and nutrients have been shown to be positively related in the eastern Bering Sea (Mordy et al.,
498 2005), suggesting that deep nutrient concentrations are higher in warm years. In our study we
499 could not detect differences between regimes for DIN collected between 30-60 m, possibly due
500 to the non-conservative nature of nutrients closer to the surface. Comparisons of near-bottom
501 nutrients may offer more insight but unfortunately, bottom nutrients were not consistently
502 sampled during all years of our surveys.

503 Wind mixing (two weeks prior to sample collection) and in situ bottom temperature were the
504 most important factors related to changes in Chl a . The positive association with wind mixing
505 following a two week lag time is expected, since time is required for the water column to
506 stabilize after a storm event (so that adequate light is available) and for phytoplankton to grow.
507 Increased primary production has been observed following wind mixing events for several
508 studies on the southeast Bering Sea shelf (e.g., Sambrotto et al., 1986; Mordy et al., 2012).

509 The positive relationship between bottom temperature and Chl a could be related to bottom-up
510 effects such as temperature effects on growth rates (Eppley, 1972), top-down effects such as a
511 reduction in grazing pressure on phytoplankton (Goering and Iverson, 1981), or a combination of
512 these factors. Both bottom and surface temperatures were higher in warm years, so temperature-
513 mediated growth could increase biomass throughout the water column in warm years. However,
514 the temperature response of normalized productivity (mg C mg Chl a ⁻¹ h⁻¹) for 2008 and 2009
515 indicated that above a threshold of ~5°C, productivity decreased (Lomas et al., 2012). In our
516 study, temperatures in the surface mixed layer were above this threshold for all regions in both

517 warm and cold years with the exception of the region near St. Matthew Island in 2012
518 (Appendix).

519 Bottom temperature during late summer/early fall may be indirectly related to grazing pressure
520 on phytoplankton. Bottom temperature largely reflects the location of the cold pool, which
521 extends farther south in cold years when ice coverage is farther south (Stabeno et al., 2012b).
522 The presence of sea ice in late winter and spring affects the availability (timing and magnitude)
523 of ice algae and phytoplankton prey for zooplankton and larval fish, and thus impacts the
524 ecosystem at many trophic levels. An early algal food source may enhance reproduction in
525 spring of large copepods such as *Calanus* spp. and other-ice associated taxa (Baier and Napp,
526 2003). Cooler temperatures can also reduce respiration costs throughout the year, and reduce the
527 presence of zooplankton grazers over the middle shelf (Coyle et al., 2008, 2011; Sigler et al.,
528 2014). These favorable conditions in cold years can lead to high zooplankton biomass throughout
529 the growing season. Accordingly, large crustacean zooplankton such as *Calanus* spp. and
530 euphausiids had higher abundances in cold compared to warm years during summer and early
531 fall for our current study years (2003-2010) (Coyle et al., 2011; Ressler et al., 2012; Eisner et al.,
532 2014). The higher *Chla* and greater percentage of large-size phytoplankton seen in late summer
533 in warm compared to cold years may be partially related to a reduction in large zooplankton
534 abundance and subsequent reduction in grazing pressure, on large phytoplankton, in particular
535 (Goering and Iverson, 1981). This hypothesis suggests that the lower trophic level community
536 structure and biomass observed late in the growing season (August–October) may be set, at least
537 partially, during spring. However, to confound this issue, new research has shown that
538 microzooplankton are the primary grazers of phytoplankton in summer (Stoecker et al., 2014a),
539 so the effects of grazing on phytoplankton biomass may be more complicated. It is unknown if
540 microzooplankton are in higher abundance or have increased grazing rates in warm compared to
541 cold years on the eastern Bering Sea shelf. Although microzooplankton grazing was found to be
542 lower in a single, highly stratified, warm year (2004) than in cold years (2008-2010) (Olson and
543 Strom, 2002; Strom and Frederickson, 2008; Stoecker et al., 2014a; Liu et al., this issue), there
544 are not sufficient data sets to determine conclusively if microzooplankton are in higher
545 abundance or if they have increased grazing rates in warm compared to cold years.

546

547 Over the shelf, the average percent large biomass ($> 10 \mu\text{m}$ Chla/total Chla) was 42% in warm
548 years and 30% in cold years (similar to cold year results for June-July 2008 and 2009 for $> 5 \mu\text{m}$
549 size fractions, Lomas et al., 2012). Phytoplankton biomass in summer 2008 was dominated by
550 flagellates (dinoflagellates and microflagellates) with diatoms in high concentrations at a few
551 locations (e.g., near the Pribilof Islands) (Moran et al., 2012). Therefore, the larger
552 phytoplankton in our study may be a combination of diatoms and dinoflagellates. The transfer of
553 energy up the food web may be more efficient with large phytoplankton (e.g., large
554 phytoplankton to large zooplankton to fish) than occurs with small phytoplankton taxa, which are
555 typically grazed by microzooplankton. Copepods cannot effectively graze on phytoplankton
556 particles below a threshold size. This size can vary with taxa and stage e.g., *Acartia tonsa*, a
557 small copepod, was limited by 2-4 μm size for all stages, with higher optimal particle sizes as
558 development progressed (Berggreen et al., 1988); whereas, calanoid copepods have a slightly
559 larger size threshold of $\sim 5 \mu\text{m}$ (Gauld, 1966; Boyd, 1976). Some of the larger fraction Chla
560 could also be due to retention of mixotrophic (Chla containing) microzooplankton on the filters,
561 as was observed on the shelf during June-July 2008-2010 (Stoecker et al., 2014b). Accordingly,
562 it is possible that the higher large-size fraction Chla seen in warm years is related to a
563 combination of higher abundances of mixotrophic microzooplankton and reduced abundances of
564 large zooplankton predators.

565 Variations in late summer/early fall Chla were seen both interannually and between temperature
566 regimes. Warm years generally had higher mean values than cold years, but significantly higher
567 Chla was only seen immediately north of the Alaska Peninsula, near St. Matthew Island and in
568 the south-outer shelf. Currents at the moorings on the middle shelf vary between warm and cold
569 conditions (Stabeno et al, this issue) but it is unclear whether differences in the currents are
570 responsible for the differences in Chla. The higher Chla in warm years was due to large and
571 small phytoplankton taxa in the south-outer shelf and near St. Mathew Island and due to large
572 taxa north of the Alaska Peninsula. Large-size phytoplankton Chla also was significantly higher
573 in the south middle shelf (Regions 3 and 6) in warm years, suggesting changes in phytoplankton
574 community composition, although the total Chla was similar for both temperature regimes. This
575 suggests that as the climate warms, phytoplankton biomass and community composition changes
576 may be observed only in specific regions, not over the entire shelf. Some of the lack of
577 significance is due to the high variability among years within a temperature regime.

578 Phytoplankton Chla also had strong interannual variations, largely associated with variations in
579 wind mixing and stratification. The high Chla observed in 2005 over the southern middle shelf
580 were in part related to the high August wind mixing that was observed up to 2 weeks prior to
581 sampling (Table 4). At M2 in the south-middle domain, the breakdown of stratification occurred
582 early (mid-October) in 2005 (Ladd and Stabeno, 2012), likely in part related to early wind
583 mixing events. The bottom temperatures in the south-middle domain were also high in 2005, so a
584 combination of high wind mixing and high bottom temperatures (the two most important factors
585 explaining variability in integrated total Chla) led to the anomalously high Chla. In contrast,
586 2007 was the year with the lowest total and large-fraction Chla and was a year with high
587 stratification, low summer (June-August) wind mixing and anomalously low surface silicic acid
588 (which may be an indicator of surface nutrient input during summer, Gann et al., this issue). The
589 lack of surface nutrients, at least in part due to high stratification and low wind mixing, may have
590 led to lower Chla in 2007, with >80% of the community found in the small size (< 10 µm)
591 fraction.

592 *4.3 Implications for fisheries*

593 Forage fish data (Parker-Stetter et al., this issue) were collected concurrently with zooplankton
594 (Eisner et al., 2014) and hydrographic data (current study) during late summer/early fall in the
595 eastern Bering Sea. Strong cross-shelf variations were observed for all three trophic levels:
596 phytoplankton Chla and size structure, zooplankton community structure and forage fish
597 distributions (age-0 Walleye Pollock, Capelin (*Mallotus villosus*) and age-0 Pacific Cod). Fish
598 distributions were most strongly related to water temperature and bottom depth, and secondarily
599 to zooplankton prey (age-0 pollock only); however, there were no direct relationships to Chla at
600 the time of sampling. This is not unexpected, since there are temporal lags between primary,
601 secondary and higher trophic level production. In situ water temperature, important for all three
602 trophic levels, may relate to direct effects on growth or temperature tolerances, or may be
603 indicative of other environmental factors associated with changes in temperature or larger scale
604 ecosystem variations (Eisner et al., 2014, Parker-Stetter et al., this issue).

605 Low age-0 pollock weights and lengths were associated with low Chla and primary production,
606 low surface silicic acid and small phytoplankton cells in August/September 2007 in the southeast
607 Bering Sea (Gann et al., this issue). We speculate that high stratification and low wind mixing

608 may have limited summer primary production, resulting in less trophic production reaching age-
609 0 pollock. The small size of these pollock likely led to poor overwinter survival since recruitment
610 to age-1 was low (Heintz et al., 2013). Thus, variations in summer phytoplankton production and
611 *Chla* can affect the ecosystem at distant trophic levels and may impact over-winter survival of
612 forage fish and subsequent recruitment into the fishery.

613 *4.4 Estimations of fall bloom timing*

614 The timing of our BASIS surveys in relation to fall storm events and stratification breakdown
615 (mixing to bottom) may confound some of our interpretation, since the timing of decreases in
616 stratification determines when nutrients are mixed to the surface to fuel the fall phytoplankton
617 bloom. At M2, stratification breakdown (complete water column mixing) occurred during mid to
618 late October in 2003-2005 (the three warm years), mid to late November in 2006-2008, late
619 September to early October in 2009, with timing unknown for 2010-2012 (Ladd and Stabeno,
620 2012); although the start of fall mixing is earlier than breakdown. The average timing of the fall
621 bloom at M2 was in late September based on mooring fluorometer data (Sigler et al., 2014); this
622 is typically later than our surveys occurred in Region 3, indicating that we primarily sampled
623 during late summer conditions (Table 1). MODIS data near M2 and M4 indicated that the highest
624 fall *Chla* occurred in September and October during 2002-2012, and SeaWiFS data over the
625 shelf indicated highs in October for 2000-2010 (Liu et al., this issue). Our shelf-wide surveys
626 ended by late September or early October, so we did not sample during the October bloom
627 period. We could not adequately evaluate the timing of the fall blooms at higher resolution scales
628 (8-day or bi-weekly), due to high cloud cover in this region, which reduced the number of pixels
629 available for averaging MODIS data (<50% of the area could be evaluated consistently).
630 Improved algorithms for ocean color measurements that account for variations in colored
631 dissolved organic matter (CDOM) in the Bering Sea might improve the accuracy of our *Chla*
632 estimations (Naik et al., 2013), although estimations will still be severely hindered by the lack of
633 cloud free days.

634

635 **5. Summary**

636 The large spatial and temporal variability in phytoplankton *Chla* over the eastern Bering Sea in
637 late summer/early fall is partially driven by spatial and temporal variations in nutrient inputs.
638 Regions with consistently high values are associated with onshore transport of nutrients through
639 bathymetric features such as canyons (e.g., near Pribilof Islands) or nutrient-rich currents (e.g.
640 north of St. Lawrence Island). *Chla* was positively associated with wind-mixing that occurred on
641 average 2 weeks prior. This lag allows time for surface water to re-stratify and phytoplankton to
642 undergo exponential growth. This process is important on the southeast middle shelf where
643 nutrient concentrations are depleted in the surface, but are high at depth. In contrast, wind mixing
644 during late summer/early fall will have little effect on *Chla* on the northern shelf where deep
645 nutrients are in low concentrations. Bottom temperature, associated with variations in sea ice and
646 the cold pool extent, also has a positive relationship to *Chla*. This may be related to larger
647 ecosystem changes (e.g., variations in zooplankton communities and grazing pressure) that are
648 set earlier in the growing season; however, the mechanisms are unknown. Bottom-up factors
649 such as direct temperature effects on growth or increases in nutrients in the bottom pool could be
650 relevant. Increases in *Chla* in the warm, low ice years were greatest in the southeastern Bering
651 Sea, with significant increases observed over the middle and outer shelf. These *Chla* increases
652 were due at least partially to increases in the large-size fraction phytoplankton (changes in
653 phytoplankton community structure), perhaps due to changes in grazing pressure. The south-
654 middle domain is highly impacted by reduction in sea ice, and zooplankton community structure
655 (Stabeno et al., 2012b; Eisner et al., 2014), so large variations in *Chla* there, are not unexpected.
656 In the south-outer domain, additional factors may be driving changes in *Chla* between
657 temperature regimes; this area has lower variability in water temperature and zooplankton
658 community structure, than seen in the middle shelf (Stabeno et al. 2012a; Eisner et al. 2014).
659 Reductions in southerly sea ice extent and subsequent increases in water temperature associated
660 with a warming climate may lead to increases in phytoplankton total and large-size fraction *Chla*
661 in the southeastern Bering Sea, but interannual variability in local wind mixing and stratification,
662 uncorrelated with temperature regime changes in the current study, will continue to be important
663 factors driving variations in biomass in stratified regions during summer.

664

665 **Acknowledgements**

666 We are grateful to the captains and crews of the NOAA ship *Oscar Dyson*, and charter vessels, *Sea*
667 *Storm*, *NW Explorer*, and *Epic Explorer*, and *Bristol Explorer* for their years of hard work and diligence
668 on our surveys. We appreciate the assistance in field sampling, data processing and analysis from NOAA
669 scientific staff and volunteers. In particular, we appreciate the help from J. Lanksbury, J. Pohl, and F. Van
670 Tulder for analysis of numerous chlorophyll samples. J. Lanksbury also assisted with database
671 management. We thank S. Danielson for assistance with QA and processing of CTD data. Kathy
672 Krogslund Lab (UW) and C. Mordy Lab (PMEL) provided processing of nutrient samples. We thank N.
673 Bond for NCEP re-analysis wind data and S. Salo for MODIS ocean color data retrieval (via NOAA
674 CoastWatch Program and NASA's Goddard Space Flight Center, OceanColor Web). We thank K.
675 Mier for guidance on statistical analyses. We greatly appreciate the helpful comments from M. Sigler on
676 an earlier version of this manuscript and edits and suggestions provided by the special edition editor, M.
677 Lomas, and four anonymous reviewers. Funding was provided by the North Pacific Research Board
678 (NPRB), Bering Sea Fisherman's Association, Arctic-Yukon-Kuskokwim-Sustainable-Salmon-Initiative,
679 Coastal Impacts Assistance Program (CIAP), Bureau of Ocean Energy Management (BOEM),
680 and NOAA National Marine Fisheries Service including the Fisheries and the Environment (FATE)
681 Program. This research is contribution 4164 to PMEL, contribution EcoFOCI-0822 to NOAA's
682 Ecosystems and Fisheries-Oceanography Coordinated Investigations, Bering Sea Project
683 publication number 160 and NPRB publication number 539. The findings and conclusions in the
684 paper are those of the author(s) and do not necessarily represent the views of the National Marine
685 Fisheries Service. Reference to trade names does not imply endorsement by the National Marine
686 Fisheries Service, NOAA.

687

688 **References**

- 689 Baier, C.T. Napp, J.M., 2003. Climate-induced variability in *Calanus marshallae* populations. J.
690 Plankton Res. 25, 771-782.
- 691
- 692 Berggreen, U., Hansen, B., Kiorboe, T., 1988. Food size spectra, ingestion and growth of the
693 copepod during development: implications for determination of copepod production.
694 Mar. Biol. 99, 341-352.
- 695
- 696 Bond, N.A., Adams, J.M., 2002. Atmospheric forcing of the southeast Bering Sea Shelf during
697 1995-99 in the context of a 40-year historical record. Deep-Sea Res. II 49, 5869-5887.
- 698
- 699 Boyd, C.M., 1976. Selection of particle sizes in filter-feeding copepods: A plea for reason.
700 Limnol. Oceanogr. 21, 175-180.
- 701
- 702 Brown, Z.W., Arrigo, K.R., 2013. Sea ice impacts on spring bloom dynamics and net primary
703 production in the eastern Bering Sea. J. Geophys. Res. 118, 1-20.
- 704
- 705 Brown, Z.W., van Dijken, G.L., Arrigo, K.R., 2011. A reassessment of primary production and
706 environmental change in the Bering Sea. J. Geophys. Res. 116, C08014.
- 707
- 708 Byrd, G.V., Schmutz, J.A., Renner, H.A., 2008. Contrasting population trends of piscivorous
709 seabirds in the Pribilof Islands: A 30-year perspective. Deep Sea Res. II 55(16-17), 1846-
710 1855.
- 711
- 712 Call, K. A., Ream, R.R., Johnson, D. Sterling, J.T., Towell, R.G., 2008. Foraging route tactics
713 and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the
714 Pribilof Islands. Deep Sea Res. II 55(16-17), 1883-1896.
- 715
- 716 Coachman, L.K., 1986. Circulation, water masses and fluxes on the southeastern Bering Sea
717 shelf. Cont. Shelf Res. 5, 23-108.
- 718
- 719 Coyle, K.O., Eisner, L.B., Mueter, F.J., Pinchuk, A.I., Janout, M.A., Ciciel, K.D., Farley, E.V.,
720 Andrews, A.G., 2011. Climate change in the southeastern Bering Sea: impacts on pollock
721 stocks and implications for the oscillating control hypothesis. Fish. Oceanogr. 20, 139-
722 156.
- 723
- 724 Coyle, K.O., Pinchuk, A.I., Eisner, L.B., Napp, J.M., 2008. Zooplankton species composition,
725 abundance and biomass on the eastern Bering Sea shelf during summer: the potential role
726 of water column stability and nutrients in structuring the zooplankton community. Deep
727 Sea Res. II 55, 1775-1791.
- 728
- 729 Danielson, S., Eisner, L., Weingartner, T., Aagaard, K., 2011. Thermal and haline variability
730 over the central Bering Sea shelf: Seasonal and interannual perspectives Cont. Shelf Res.
731 31, 539-554. doi:10.1016/j.csr.2010.12.010.
- 732

733 Danielson, S., Hedstrom, K., Aagaard, K., Weingartner, T., Curchitser, E., 2012. Wind-induced
734 reorganization of the Bering shelf circulation. *Geophys. Res. Lett.* 39, L08601.
735 10.1029/2012gl051231.
736

737 Duffy-Anderson, J., Busby, Mier, K. L., Deliyaniades, C. M., Stabeno, P. J., 2006. Spatial and
738 temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea
739 shelf 1996-2000. *Fish. Oceanogr.* 15(1), 80-94.
740

741 Eisner, L., Napp, J., Mier, K., Pinchuk, A., Andrews A., 2014. Climate-mediated changes in
742 zooplankton community structure for the eastern Bering Sea. *Deep Sea Res. II*
743 <http://dx.doi.org/10.1016/j.dsr2.2014.03.004>.
744

745 Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. *Fish Bull.* 70(4), 1063-
746 1085.
747

748 ESRI, 2014. ArcGIS Desktop: Release 10.2.2 Redlands, CA: Environmental Systems Research
749 Institute.
750

751 Gann, J.C., Eisner, L.B., Porter, S., Watson, J.T., Cieciel, K.D., Mordy, C.W., Yasumiishia,
752 E.M., Stabeno, P.J., Ladd, C., Heintz, R.A., Farley, E.V., this issue. Possible mechanism
753 linking ocean conditions to low body weight and poor recruitment of age-0 walleye
754 pollock (*Gadus chalcogrammus*) in the southeast Bering Sea during 2007. *Deep Sea Res.*
755 *II*.
756

757 Gauld, D.T., 1966. The swimming and feeding of planktonic copepods, In: H. Barnes (ed.) Some
758 contemporary studies in marine science. Allen and Unwin, London, p. 313-334.
759

760 Goering, J.J., Iverson, R.L., 1981. Phytoplankton distribution on the southeastern Bering Sea
761 shelf. In: D.W. Hood and J.A Calder (eds.) *The eastern Bering Sea shelf: oceanography*
762 *and resources*. Vol. 2, 933-946.
763

764 Granger, J, Prokopenko, M.G., Mordy, C.W., Sigman, D.M., 2013. The proportion of
765 remineralized nitrate on the ice-covered eastern Bering Sea shelf evidenced from the
766 oxygen isotope ratio of nitrate. *Global Biogeochem. Cycles*, 27(3), 962–971. doi:
767 10.1002/gbc.20075.
768

769 Grasshoff, K., 1976. *Methods of seawater analysis*. Verlag Chemie, Weinheim, New York.
770

771 Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem Dynamics of the
772 Pacific-Influenced Northern Bering and Chukchi Seas. *Progress in Oceanography*, 71:
773 331-361.
774

775 Hansell, D.A., Whitledge, T.E., Goering, J.J., 1993. Patterns of nitrate utilization and new
776 production over the Bering–Chukchi Shelf. *Cont. Shelf Res.*, 13(5-6): 601-627.
777

778 Heintz, R.A., Siddon, E.C., Farley E.V., Napp, J.M., 2013. Correlation between recruitment and
779 fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea
780 under varying climate conditions. *Deep Sea Res. II* 94,150-156.
781

782 Hunt, G.L., Stabeno, P.J., Strom, S., Napp, J.M., 2008. Patterns of spatial and temporal variation
783 in the marine ecosystem of the southeastern Bering Sea, with special reference to the
784 Pribilof Domain. *Deep Sea Res. II* 55, 1919–1944.
785

786 ICES, 2004. Chemical measurements in the Baltic Sea: Guidelines on quality assurance. In: E.
787 Lysiak-Pastuszak and M. Krysell (eds.) ICES Techniques in Marine Environmental
788 Sciences. No. 35. 149 pp.
789

790 Jahncke, J., Vlietstra, I.S., Decker, M.B., Hunt, G.L., 2008. Marine bird abundance around the
791 Pribilof Islands: A multiyear comparison. *Deep Sea Res. II* 55, 1809-1826.
792

793 JGOFS, 1994. Protocols for the joint global ocean flux study (JGOFS) core measurements. IOC,
794 Scientific Committee on Oceanic Research. Manuals and Guides. Vol. 29, Paris, France,
795 UNESCO Publishing, 170 p.
796

797 Kachel, N.B., Hunt Jr., G.L., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Whitley, T.E., 2002.
798 Characteristics and variability of the inner front of the southeastern Bering Sea. *Deep Sea*
799 *Res. II* 49 (26), 5889–5909.
800

801 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha,
802 S., White, G., Woollen, J., Zhu, Y., Leetmaa, A., Reynolds, B., Chelliah, M., Ebisuzaki,
803 W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Jenne, R., Joseph,
804 D., 1996. The NCEP/NCAR 40-Year Reanalysis Project. *Bull. Amer. Meteor. Soc.* 77,
805 437–472.
806

807 Kinney, J.C., Maslowski, W., Okkonen, S., 2009. On the processes controlling shelf-basin
808 exchange and outer shelf dynamics in the Bering Sea. *Deep-Sea Res. II* 56, 1351-1362,
809 doi:10.1016/j.dsr2.2008.10.023.
810

811 Kopylov, A.I., Flint, M.V., Drits, A.V., 2002. Primary production of phytoplankton in the eastern
812 part of the Bering Sea. *Oceanol.* 42, 215-225.
813

814 Ladd C., Stabeno, P.J., 2012. Stratification on the Eastern Bering Sea shelf revisited. *Deep Sea*
815 *Res. II* 65-70, 72-83.
816

817 Lomas, M.W., Moran, S.B., Casey, J.R., Bell, D.W., Tiahlo, M., Whitefield, J., Kelly, R.P.,
818 Mathis, J.T., Cokelet, E.D., 2012. Spatial and seasonal variability of primary production
819 on the eastern Bering Sea shelf. *Deep Sea Res. II* 65-70, 126-140.
820

821 Liu, C. L., Zhai L., Zeeman, S.I., Eisner, L.B., Gann, J., Mordy, C.W. Moran, S.B., Lomas,
822 M.W., this issue. Seasonal and geographic variations in modeled primary production and

823 phytoplankton losses from the mixed layer between warm years and cold years on the
824 eastern Bering Sea shelf. *Deep Sea Res. II*.

825

826 Mantoura, R.F.C., Woodward, E.M.S., 1983. Optimization of the indophenol blue method for the
827 automated determination of ammonia in estuarine waters. *Estuar. Coast. Shelf Sci.* 17,
828 219–224.

829

830 McCormick-Ray, J., Warwick, R.M., Ray, G.C. 2011. Benthic macrofaunal compositional
831 variations in the northern Bering Sea. *Mar Biol.* 158, 1365-1376.

832

833 McRoy, C.P. Goering, J. J., Shiels, W.E., 1972. Studies of primary production in the eastern
834 Bering Sea. In: Takenouti, A.Y. (Ed.), *Biological Oceanography of the Northern North*
835 *Pacific Ocean*. Idemitsu Shoten, Tokyo, p. 199-216.

836

837 Moran, S.B., Lomas, M.W., Kelly, R.P., Gradinger, R., Iken, K., Mathis, J.T., 2012. Seasonal
838 succession of net primary productivity, particulate organic carbon export, and autotrophic
839 community composition in the eastern Bering Sea. *Deep Sea Res. II* 65-70, 84-97.

840

841 Mordy, C.W., Cokelet, E.D., Ladd, C., Menzia, F.A., Proctor, P., Stabeno, P.J., Wisegarver, E.,
842 2012. Net community production on the middle shelf of the eastern Bering Sea. *Deep Sea*
843 *Res. II* 65-70, 110-125.

844

845 Mordy, C.W., Eisner, L.B., Proctor, P., Stabeno, P., Devol, A.H., Shull, D.H., Napp, J.M.,
846 Whitlege, T., 2010. Temporary uncoupling of the marine nitrogen cycle: Accumulation
847 of nitrite on the Bering Sea shelf. *Mar. Chem.* 121, 157166.

848

849 Mordy, C.W., Stabeno, P.J., Ladd, C., Zeeman, S., Wisegarver, D.P., Hunt, G.L., Jr., 2005.
850 Nutrients and primary production along the eastern Aleutian Island Archipelago. *Fish.*
851 *Oceanogr.* 14, 55-76.

852

853 Mordy, C.W., Stabeno, P.J., Righi, D., Menzia, F.A., 2008. Origins of the subsurface ammonium
854 maximum in the southeast Bering Sea. *Deep-Sea Res. II*, 55, 1738-1744.

855

856 Naik, P., D'Sa, E.J., Gomes, H.R., Goés, J.I., Mouw, C.B., 2013. Light absorption properties of
857 southeastern Bering Sea waters: Analysis, parameterization and implications for remote
858 sensing. *Remote Sensing of Environment* 134, 120–134.

859

860 Olson, M.B., Strom, S.L., 2002. Phytoplankton growth, micro-zooplankton herbivory and
861 community structure in the southeast Bering Sea: insight into the formation and temporal
862 persistence of an *Emiliana huxleri* bloom. *Deep-Sea Res. II* 49, 5969-5990.

863

864 Ortiz, I., Wiese, F., Greig, A., 2012. Marine regions boundary data for the Bering Sea shelf and
865 slope. UCAR/NCAR - Earth Observing Laboratory/Computing, Data, and Software
866 Facility. Dataset. doi:10.5065/D6DF6P6C.

867

868 Parker-Stetter, S., Urmy, S., Horne, J., Eisner, L., Farley, E., this issue. Factors affecting summer
869 distributions of Bering Sea forage fish species: assessing competing hypotheses. Deep-
870 Sea Res. II.
871

872 Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for
873 Seawater Analysis. Pergamon Press, Oxford, England, 173 pp.
874

875 Ressler, P.H., De Robertis, A., Warren, J.D., Smith, J.N., Kotwicki, S., 2012. Developing an
876 acoustic survey of euphausiids to understand trophic interactions in the Bering Sea
877 ecosystem, Deep Sea Res. II 65–70,184-195.
878

879 Rho, T., Whitley, T.E., 2007. Characteristics of seasonal and spatial variations of primary
880 production over the southeastern Bering Sea shelf. Cont. Shelf Res. 27, 2556-2569.
881

882 Sambrotto, R.N. Goering, J.J., 1983. Interannual variability of phytoplankton and zooplankton
883 production on the southeast Bering Sea shelf. In From Year to Year. W.S. Wooster (ed.)
884 Washington Sea Grant, Seattle, pp161-177.
885

886 Sambrotto, R.N., Goering, J.J., McRoy, C.P., 1984. Large yearly production of phytoplankton in
887 the western Bering Strait. Science 225,1147-1150.
888

889 Sambrotto, R.N., Mordy, C.W., Zeeman, S.I., Stabeno, P.J., Macklin, S.A., 2008. Physical
890 forcing and nutrient conditions associated with patterns of Chl *a* and phytoplankton
891 productivity in the southeastern Bering Sea during summer. Deep Sea Res. II 55, 1745–
892 1760.
893

894 Sambrotto R.N., Niebauer, H.J., Goering, J.J., Iverson, R.L., 1986. Relationships among vertical
895 mixing nitrate uptake and phytoplankton growth during the spring bloom in the southeast
896 Bering Sea middle shelf. Cont. Shelf Res. 5, 161–198.
897

898 Siddon, E.C., Heintz, R.A., Meuter F.J., 2013. Conceptual model of energy allocation in Walleye
899 Pollock (*Theragra chalcogramma*) from larvae to age-1 in the eastern Bering Sea. Deep
900 Sea Res. II 94,140-149.
901

902 Sigler, M.F., Heintz, R.A., Hunt, G.L., Lomas, M.W., Napp, J. M., Stabeno, P., this issue. A
903 mid-trophic view of subarctic productivity: lipid storage, location matters and historical
904 context. Deep-Sea Res. II.
905

906 Sigler, M.F., Stabeno, P., Eisner, L.B., Napp, J. M., Mueter, F.J., 2014. Spring and fall
907 phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea,
908 during 1995-2011. Deep-Sea Res. II, <http://dx.doi.org/10.1016/j.dsr2.2013.12.007>.
909

910 Simpson, J.H., Hughes, D.G., Morris, N.C.G., 1977. The relation of seasonal stratification to
911 tidal mixing on the continental shelf. Deep Sea Res. 24(Suppl.), 327–340.
912

913 Slawyk, G., MacIsaac, J.J., 1972, Comparison of two automated ammonium methods in a region
914 of coastal upwelling, *Deep Sea Res.* 19, 521-524.
915

916 Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering
917 Sea- III. Patterns of primary production.
918

919 Springer, A.M., McRoy, C.P., Flint M.V., 1996. The Bering Sea Green Belt: shelf-edge
920 processes and ecosystem production. *Fish. Oceanogr.* 5, 205- 223.
921

922 Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A., Schumacher, J.D., 2001. On the temporal
923 variability of the physical environment over the south-eastern Bering Sea. *Fish.*
924 *Oceanogr.* 10, 81-98.
925

926 Stabeno, P.J., Danielson, S., Kachel, D., Kachel, N.B., Mordy, C.W., this issue. Currents and
927 transport on the Eastern Bering Sea shelf. *Deep-Sea Res.* II.
928

929 Stabeno, P.J., Farley, E.V., Kachel, N., Moore, S., Mordy, C., Napp, J.M., Overland, J.E.,
930 Pinchuk, A.I., Sigler, M., 2012a. A comparison of the physics, of the northern and
931 southern shelves of the eastern Bering Sea and some implications to the ecosystem. *Deep*
932 *Sea Res.* II 65-70:14-30.
933

934 Stabeno, P.J., Kachel, N.B., Moore, S.E., Napp, J.M., Sigler, M., Yamaguchi, A., Zerbini, A.N.,
935 2012b. Comparison of warm and cold years on the southeastern Bering Sea shelf and
936 some implications for the ecosystem. *Deep Sea Res.* II 65-70:31-45.
937

938 Stabeno, P. J., Kachel, N., Mordy, C., Righi, D., Dalo, S., 2008. An examination of the physical
939 variability around the Pribilof Islands in 2004. *Deep Sea Res.* II 55(16-17), 1701-1716.
940

941 Stabeno, P.J., Napp, J., Mordy, C., Whitledge, T., 2010. Factors influencing physical structure
942 and lower trophic levels of the eastern Bering Sea shelf in 2005: sea ice, tides and winds.
943 *Prog. Oceanogr.* 85 (3-4), 180–196.
944

945 Stabeno, P.J., Reed, R.K., Napp, J.M., 2002. Transport through Unimak pass, Alaska. *Deep Sea*
946 *Res.* II 49, 5919-5930.
947

948 Stoecker, D.A. Weigel, A., Goes, J.I., 2014a. Microzooplankton grazing in the eastern Bering
949 Sea in summer, *Deep Sea Res.* II, <http://dx.doi.org/10.1016/j.dsr2.2013.09.017>.
950

951 Stoecker, D.K., Weigel, A.C., Stockwell, D.A., Lomas, M.W., 2014b. Microzooplankton:
952 Abundance, biomass and contribution to chlorophyll in the eastern Bering Sea in
953 summer. *Deep Sea Res.* II, <http://dx.doi.org/10.1016/j.dsr2.2013.09.007>.
954

955 Strom, S.L., Fredrickson, K.A., 2008. Intense stratification leads to phytoplankton nutrient
956 limitation and reduced microzooplankton grazing in the southeastern Bering Sea. *Deep*
957 *Sea Res.* II 55(16-17), 1761-1774.
958

959 Sullivan, M.E., Kachel, N.B., Mordy, C.W., Stabeno, P.J., 2008. The Pribilof Islands:
960 Temperature, salinity and nitrate during summer 2004. *Deep Sea Res. II* 55(16-17), 1729-
961 1737.

962

963 Systat Software, Inc., 2009. For Windows, Version 13, San Jose, CA.

964

965

966 Walsh, J.J., McRoy, C.P., Coachman, L.K., Goering, J.J., Nihoul, J.J., Whitley, T.E.,
967 Blackburn, T.H., Parker, P.L., Wirick, C.D., Shuert, P.G., Grebmeier, J.M., Springer,
968 A.M., Tripp, R.D., Hansell, D.A., Djenidi, S., Deleersnijder, E., Henriksen, K., Lund,
969 B.A., Andersen, P., Mullerkarger, F.E., Dean, K., 1989. Carbon and nitrogen cycling
970 within the Bering Chukchi Seas - source regions for organic-matter effecting AOU
971 demands of the Arctic Ocean. *Prog. Oceanogr.* 22, 277-359.

972

973 Whitley, T.E., Reeburgh, W.S., Walsh, J.J., 1986. Seasonal inorganic nitrogen distributions
974 and dynamics in the southeastern Bering Sea Cont. Shelf Res. 5, 109-132.

975

976 Wiese, F.K., Wiseman, W.J., van Pelt, T.I., 2012. Bering Sea linkages. *Deep Sea Res. II* 65-70,
977 2-5.

978

979 Zador, S., 2014. Ecosystem Considerations 2014, Stock Assessment and Fishery Evaluation
980 Report, North Pacific Fisheries Management Council, 605 W 4th Ave, Suite 306,
981 Anchorage, AK 99501.

982

983 Table 1. BASIS survey dates for entire shelf and Region 3.

year	Entire shelf		Region 3	
	start	end	start	end
2003	21-Aug	8-Oct	2-Sep	23-Sep
2004	14-Aug	30-Sep	16-Aug	4-Sep
2005	14-Aug	6-Oct	15-Aug	13-Sep
2006	18-Aug	20-Sep	20-Aug	3-Sep
2007	15-Aug	8-Oct	16-Aug	13-Sep
2008	11-Sep	27-Sep	12-Sep	26-Sep
2009	30-Aug	27-Sep	4-Sep	27-Sep
2010	18-Aug	4-Oct	19-Aug	16-Sep
2011	21-Aug	19-Sep	24-Aug	19-Sep
2012	19-Aug	12-Oct	24-Aug	13-Sep

984

985 Table 2. Means of (A) integrated total Chla, (B) integrated Chla > 10 μm (mg m⁻²), and (C)
 986 number of stations sampled by region and year. Standardized anomaly calculated on natural log
 987 transformed data and standardized to maximum. Color coding indicates if anomaly is negative
 988 (red, -1 to -0.3), small (yellow, -0.3 to 0.3) or positive (green, 0.4 to 1). Means for each region
 989 for all years combined are shown in the last column in panels A and B. *Intended for color*
 990 *reproduction on the Web and in print.*

991 (A)

Domain	Region		2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Mean
Inner	South	2	55	65	86	56	42	26	40	65	57	55	55
	Mid-north	7	59	60	63	44	15	41	40	48	50	40	46
	North	11	34	52	45	19	23		36	46	58	36	39
Middle	AK Penn	1	75	86	136	48	38	34	58	51	62	50	64
	South	3	67	67	112	47	26	32	55	42	71	62	58
	Pribilofs	5		217	178	39	52		53		243	79	123
	Mid-north	6	115	79	118	42	48	29	69	39	76	77	69
	St Matthew	9	77	86	85	32	43		56	29	60	42	57
	North	10		50	55	17	23		17	37	66	15	35
Outer	South	4	85	75	121	65	61	29	64	46	55	77	68
	> 63°N	12	32	60		1	29		88	58	81	32	48
	S Bering Strait	13	73	32	18	35	39		54	41	69	96	51
	Norton Sound	14	9	31	14	9	36		25	43	53	26	27
Offshore	southeast	16	92	113	137	80				315	174		152

992
993
994

(B)

Domain	Region		2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Mean
Inner	South	2	31	23	51	21	10	8	13	39	33	15	24
	Mid-north	7	49	33	40	13	5	7	14	30	32	15	24
	North	11	19	26	34	8	10		13	19	30	18	20
Middle	AK Penn	1	31	39	82	8	9	3	16	14	19	25	25
	South	3	32	32	70	11	4	4	16	13	16	15	21
	Pribilofs	5		60	131	24	20		10		129	44	60
	Mid-north	6	41	50	85	18	12	12	24	10	30	41	32
	St Matthew	9	36	40	40	9	17		13	9	25	25	24
	North	10		20	29	4	5		5	11	26	4	13
Outer	South	4	16	16	55	10	8	4	10	3	5	38	17
	>63°N	12		38		0	16		102	5	13	1	25
	S Bering Strait	13	1	12	10	21	16		29	10	34	61	21
	Norton Sound	14	5	10	7	4	11		6	24	31	10	12
Off shelf	southeast	16	38	30	67	17				208	135		82

995
996
997

(C)

Domain	Region		2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Total
Inner	South	2	14	16	16	13	12	7	7	14	10	12	65
	Mid-north	7	4	9	9	9	9	3	3	8	4	8	121
	North	11	8	16	15	12	14		14	15	15	13	199
Middle	AK Penn	1	8	7	8	6	6	3	4	8	7	8	72
	South	3	15	23	21	24	23	13	13	22	21	24	17
	Pribilofs	5		2	2	3	3		1		3	3	95
	Mid-north	6	6	10	5	13	13	4	7	12	12	13	66
	St Matthew	9	4	6	7	5	7		5	7	6	3	50
	North	10		10	10	10	9		10	9	9	1	68
Outer	South	4	3	7	9	6	10	1	7	10	10	9	122
	>63°N	12	2	2	2	2	2		2	1	2	1	14
	S Bering Strait	13	5	7	4	7	8		8	9	9	9	66
	Norton Sound	14	4	4	1	4	2		5	6	6	6	38
Off shelf	southeast	16	1	1	1	1				1	1		6
	Total		74	120	108	115	118	31	86	122	115	110	999

998

999 Table 3. Statistical differences between regimes (warm and cold years) for integrated Chla (total,
 1000 large (> 10 µm), and small (< 10 µm) size fractions, natural log transformed), and temperature
 1001 and salinity above (surface) and below (deep) the pycnocline by region. Results show Type III
 1002 Tests for Fixed Effects for Regime using Hierarchical Mixed Model with REML estimation in
 1003 SYSTAT. The * indicates significantly ($P < 0.05$) higher values in warm years.

Domain	Region		Int Chla total	Int Chla large	Int Chla small	T surface	T deep	S surface	S deep
			P-value	P-value	P-value	P-value	P-value	P-value	P-value
Inner	South	2	0.099	0.142	0.507	0.001 *	0.000 *	0.836	0.456
	Mid-north	7	0.153	0.061	0.976	0.022 *	0.006 *	0.124	0.183
	North	11	0.622	0.275	0.995	0.638	0.054	0.708	0.588
Middle	AK Penn	1	0.015 *	0.022 *	0.314	0.003 *	0.002 *	0.111	0.075
	South	3	0.149	0.014 *	0.712	0.004 *	0.001 *	0.000 *	0.029 *
	Pribilofs	5	0.267	0.485	0.530	0.070	0.003 *	0.002 *	0.060
	Mid-north	6	0.094	0.020 *	0.104	0.013 *	0.000 *	0.000 *	0.001 *
	St Matthew	9	0.010 *	0.018 *	0.015 *	0.286	0.001 *	0.003 *	0.048 *
	North	10	0.246	0.137	0.171	0.248	0.149	0.293	0.284
Outer	South	4	0.013 *	0.037 *	0.030 *	0.074	0.001 *	0.907	0.512
> 63°N	St Lawrence	12	0.354	0.979	0.443	1.000	0.561	0.675	0.782
	S Bering St	13	0.284	0.139	0.148	0.204	0.085	0.249	0.063
	Norton S	14	0.106	0.274	0.939	0.060	0.055	1.000	0.137

1004

1005

1006 Table 4. August stratification index ($J m^{-2}$) and u_*^3 ($m^{-3} s^{-3}$, an indicator of wind mixing), and
 1007 number of summer (June-August) wind mixing events ($u_*^3 > 0.05 m^3 s^{-3}$) at M2 on the southeast
 1008 middle shelf for 2003-2012. Bold indicates warm years; all other years were cold with the
 1009 exception of 2006, which was average.

Year	Stratification Index	u_*^3	# Wind Mixing Events
2003	5234	0.015	7
2004	6099	0.026	9
2005	5432	0.045	10
2006	4625	0.019	9
2007	6036	0.018	3
2008	4271	0.008	6
2009	4436	0.025	10
2010	4927	0.019	9
2011	5036	0.020	14
2012	4124	0.021	5
Ave 1995-2012	4655		
SD 1995-2012	848		

1010

1011

1012 Table 5. Best fit environmental variables explaining interannual variation in integrated total and
 1013 > 10 μm Chl*a* using GLM stepwise regressions for Region 3 (near M2) and Region 6 (near M4).

Region 3 (M2)	P-value and direction	Region 6 (M4)	P-value and direction
Integrated Chl <i>a</i> total			
T deep	0.001 (+)	T deep	0.002 (+)
Aug u_*^3	0.001 (+)	Aug u_*^3	0.088 (+)
Aug stratification	0.004 (-)	NA	NA
Adjusted multiple r^2	0.96		0.86
Integrated Chl <i>a</i> >10 μm			
T deep	0.001 (+)	Aug u_*^3	0.003 (+)
Aug u_*^3	0.001 (+)	Ammonium deep	0.059 (+)
Silicic acid deep	0.015 (-)		
Adjusted multiple r^2	0.96		0.83

1014

1015

1016

1017 **Figure captions**

1018 Figure 1. Stations within each Bering Sea Project Region (Ortiz et al., 2012) sampled a minimum
1019 of 5 years between 2003 and 2012. We sampled three inner shelf regions (Regions 2, 7, 11), six
1020 middle shelf regions (Regions 1, 3, 5, 6, 9, 10), one outer shelf region (Region 4) and three
1021 regions north and east of St. Lawrence Island (Regions 12, 13 and 14).

1022 Figure 2. Contours of (A) integrated total Chla and (B) integrated $> 10 \mu\text{m}$ Chla averaged over
1023 2003-2012. Data integrated over the top 50 m. *Intended for color reproduction on the Web and*
1024 *in print.*

1025 Figure 3. Contours of (A) surface nitrate (NO_3), (B) surface ammonium (NH_4), (C) surface
1026 dissolved inorganic nitrogen (DIN), (D) surface silicic acid (Si), (E) deep NO_3 , (F) deep NH_4 ,
1027 (G) deep DIN, and (H) deep Si averaged over 2003-2012. Nutrients were collected at depths of 5
1028 m (surface) and 30-60 m (deep). *Intended for color reproduction on the Web and in print.*

1029 Figure 4. Contours of mean water column stratification index averaged over 2003-2009. Stars
1030 indicate locations of PMEL moorings, M2 and M4. *Intended for color reproduction on the Web*
1031 *and in print.*

1032 Figure 5. Contours of data averaged over warm (2003-2005) years (top panel) and cold (2007-
1033 2012) years (bottom panel) for (A, E) integrated total Chla, (B, F) integrated $> 10 \mu\text{m}$ Chla, (C,
1034 G) surface (above pycnocline) temperature, and (D, H) deep (below pycnocline) temperature.
1035 *Intended for color reproduction on the Web and in print.*

1036 Figure 6. Linear regressions of mean integrated total Chla and percent large-fraction Chla (mean
1037 $> 10 \mu\text{m}$ Chla /total Chla) from discrete samples averaged over the top 50 m for 2003-2012 for
1038 Regions 1 and 3 (south-middle), 4 (south-outer) and 10 (north-middle).

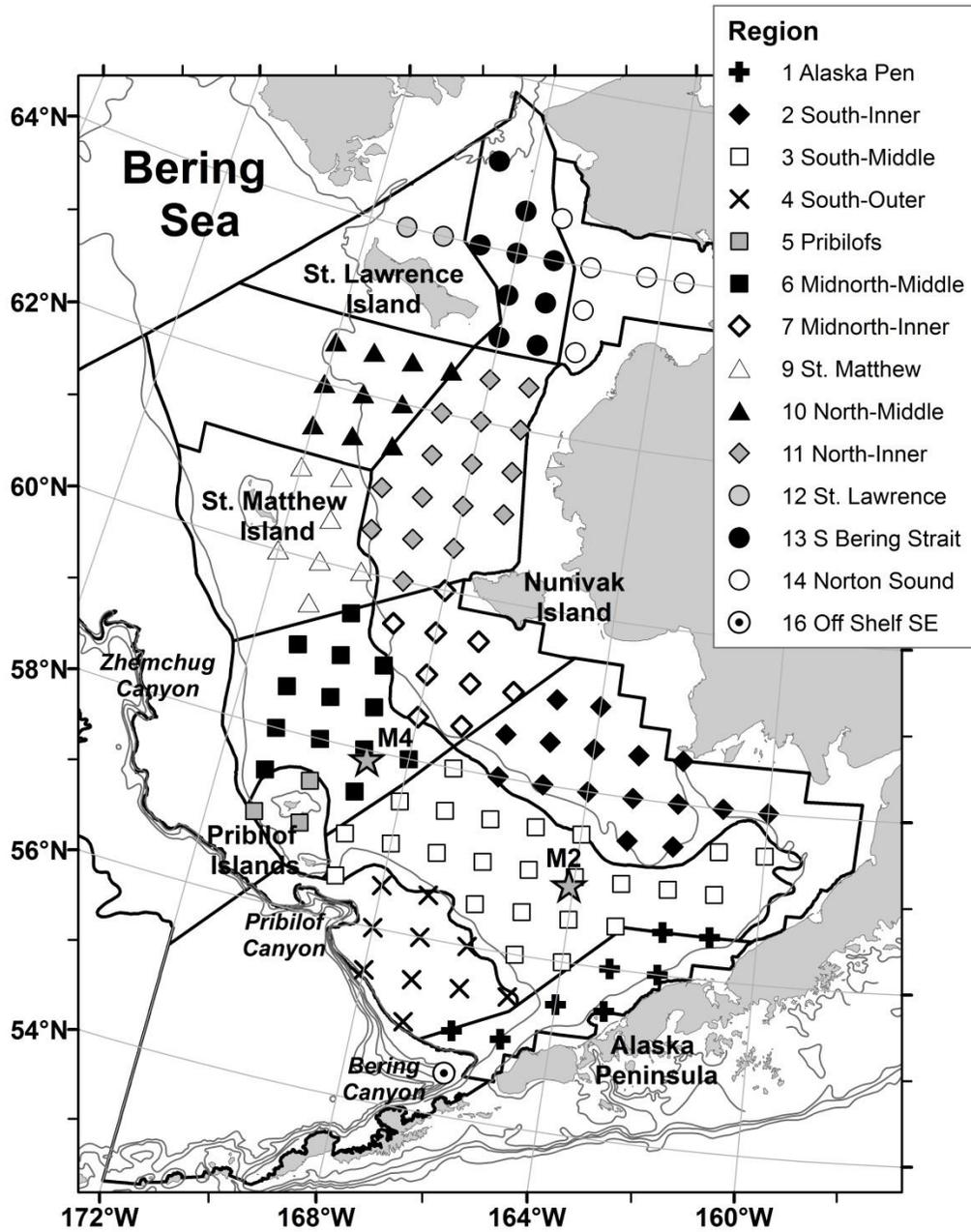
1039 Figure 7. Linear regressions between integrated total Chla and (A, B) u_*^3 , a proxy of August
1040 wind mixing, (C, D) temperature below the pycnocline, and (E) August stratification for 2003-
1041 2012 for Regions 3 and 6.

1042 Figure 8. (A) Mean Chla (mg m^{-3}) from MODIS for 2002-2012 by Region (1, 3, 5, and 6) for
1043 August, September and October. * indicates October significantly lower than September in

1044 Region 5, and August significantly lower than later months for Regions 3 and 6 ($P < 0.05$,
1045 ANOVA with Tukey tests). Errors bars show ± 1 standard error. (B) Chl a from MODIS for
1046 August, September, and October for Region 3 by year. Aug-Oct MODIS is the sum of Chl a from
1047 MODIS for all three months for each year. BASIS surface Chl a (~5 m) shown for comparison.

1048

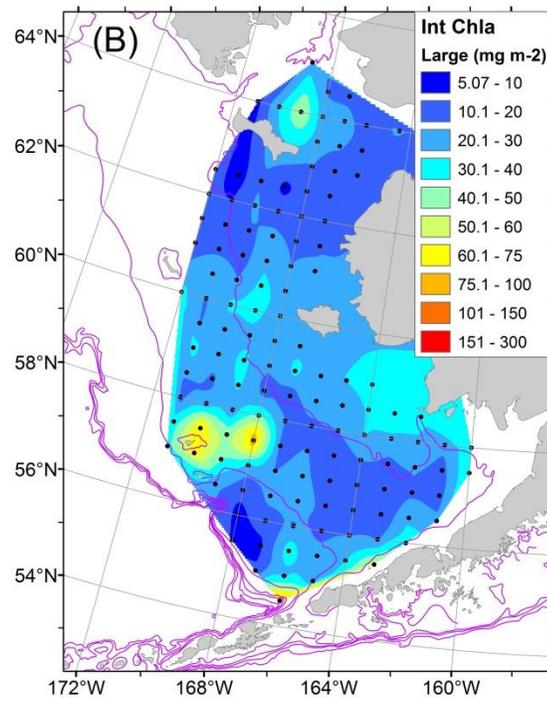
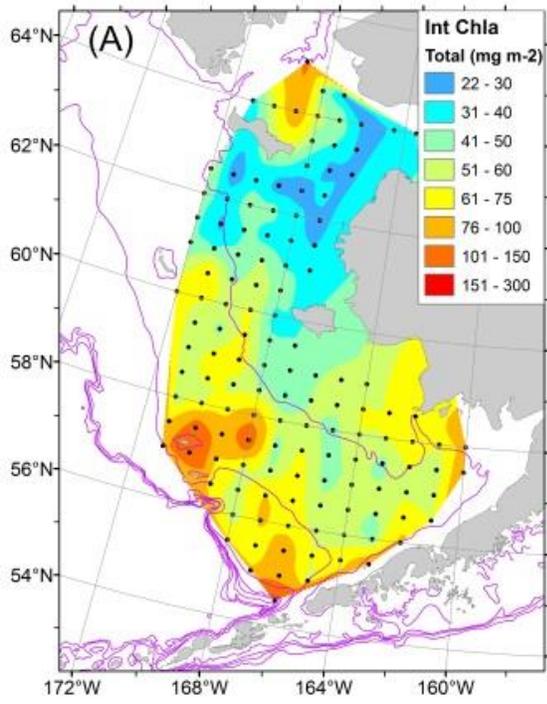
1049



1050

1051 Figure 1.

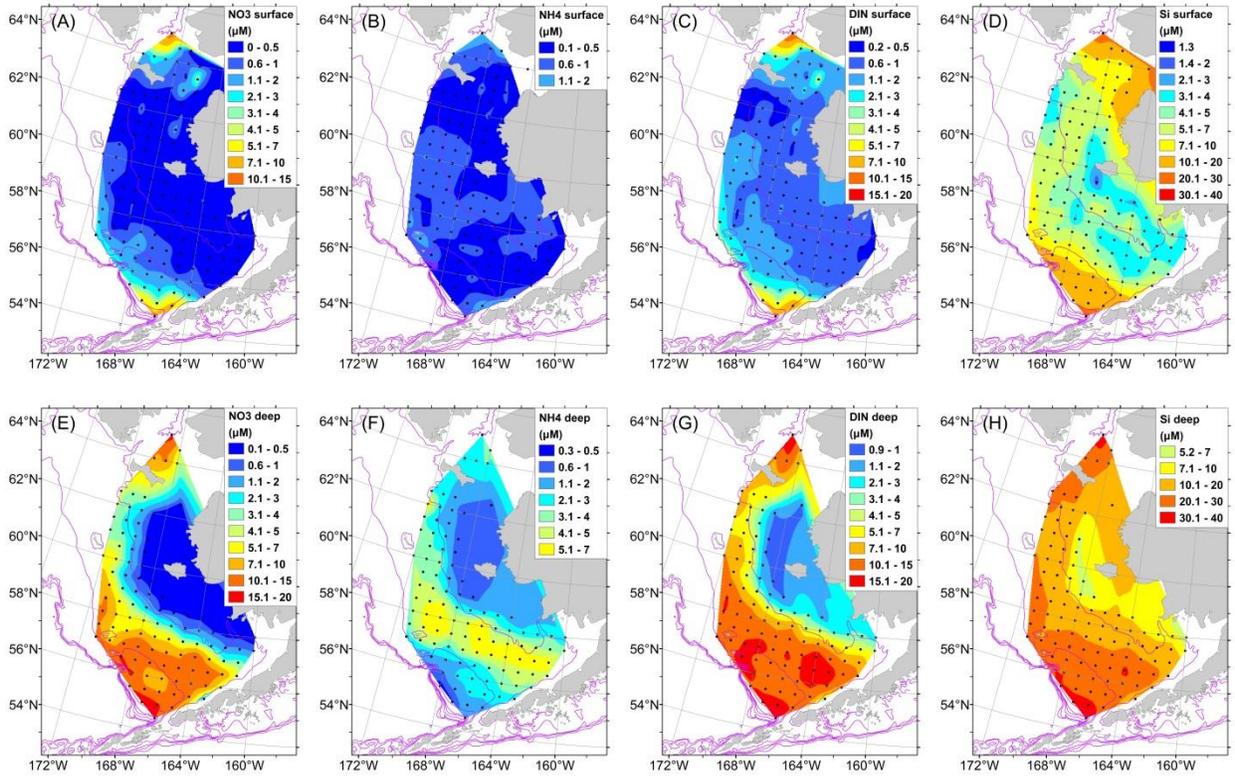
1052



1053

1054

1055 Figure 2.

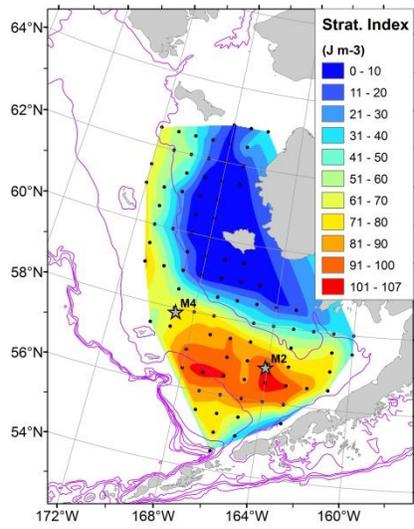


1056

1057

1058 Figure 3.

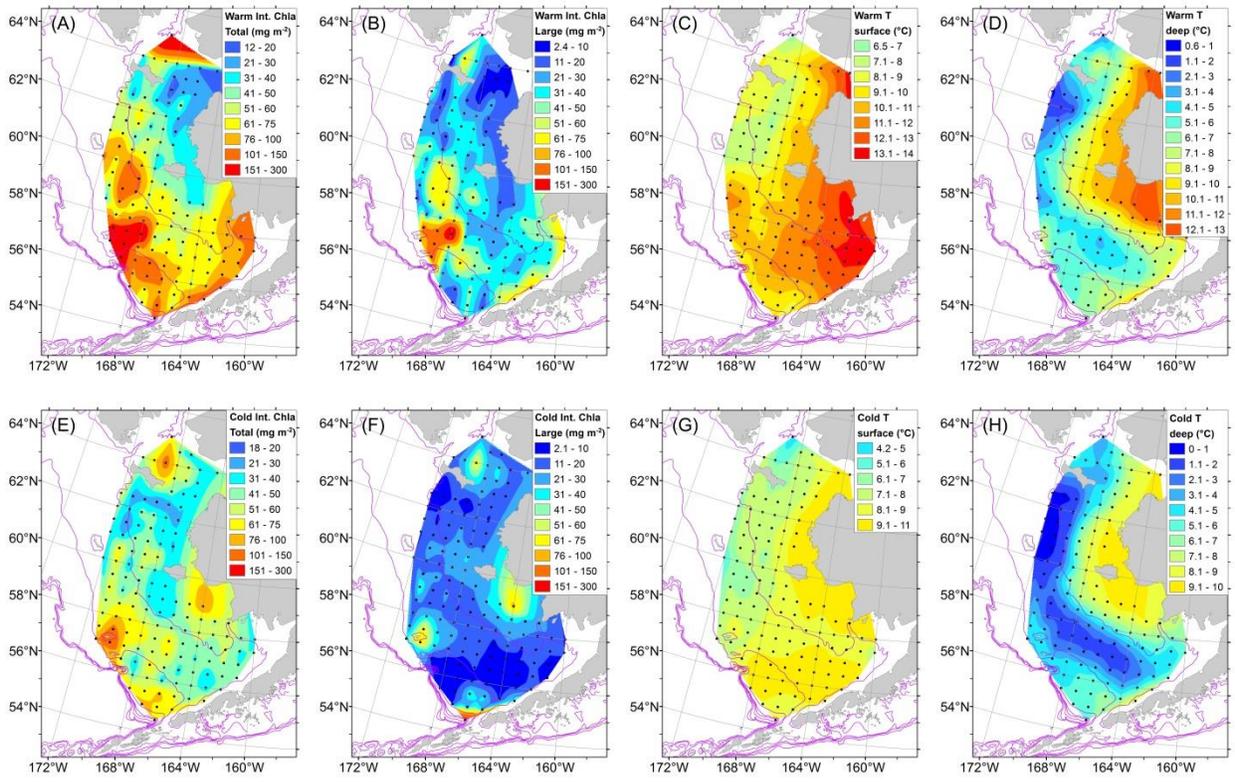
1059



1060

1061 Figure 4.

1062

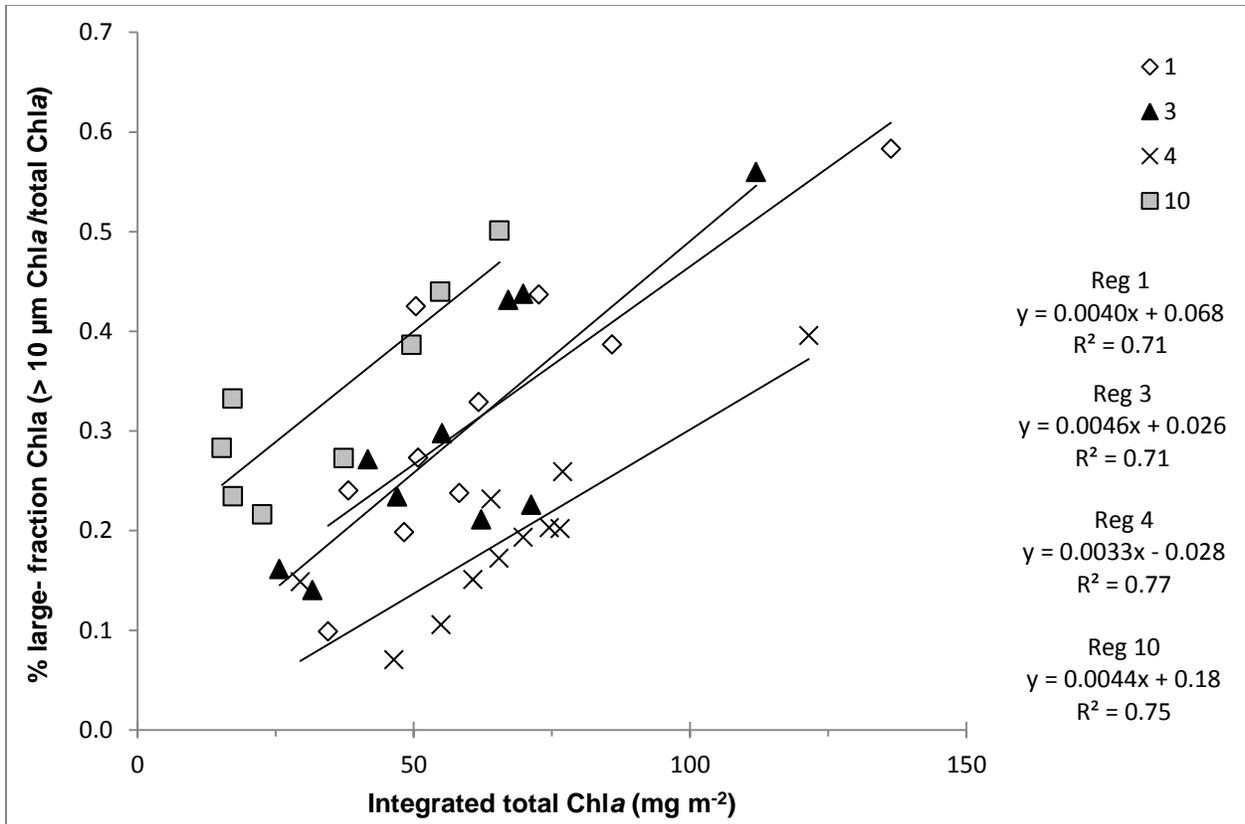


1063

1064

1065 Figure 5.

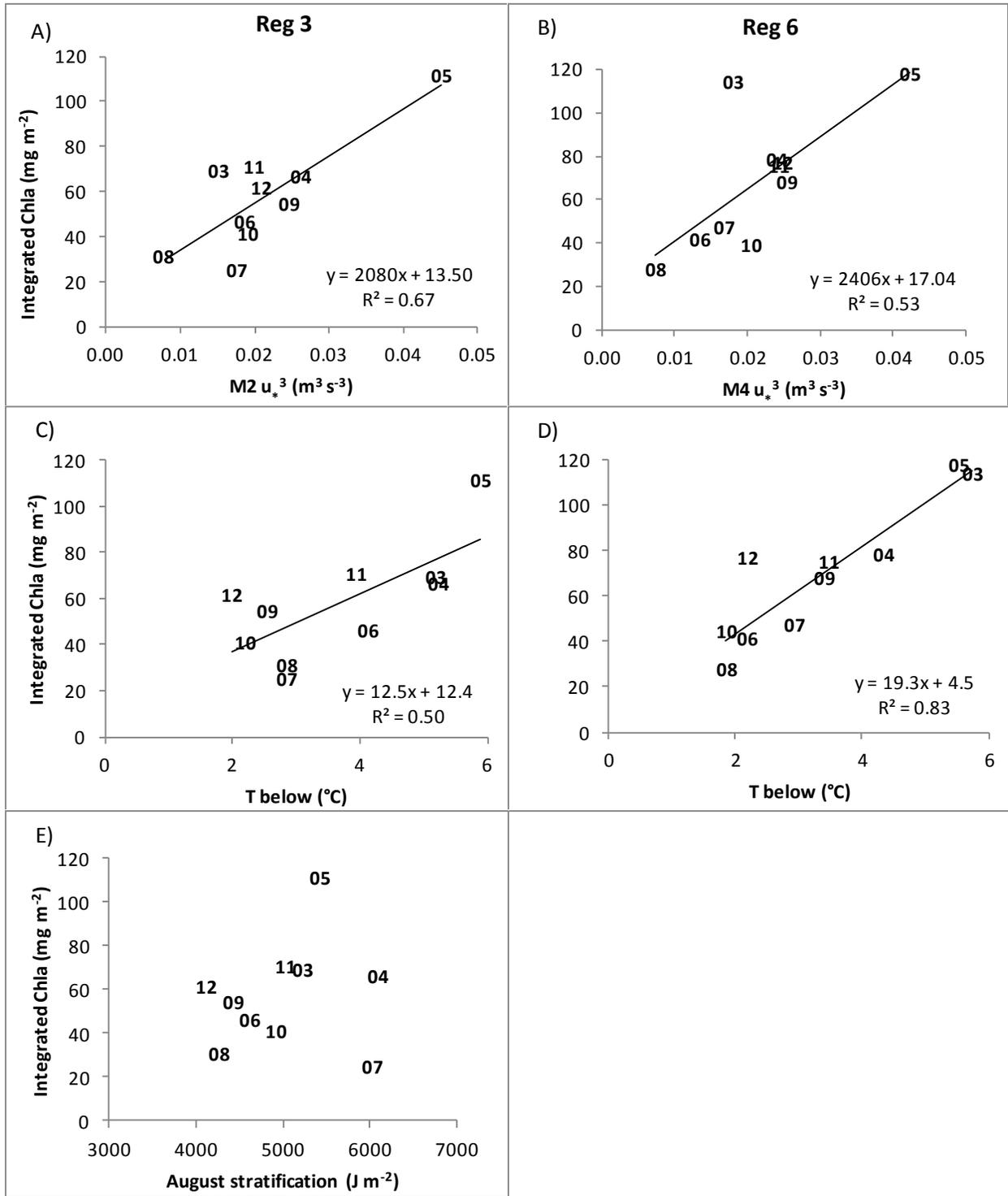
1066



1067

1068 Figure 6.

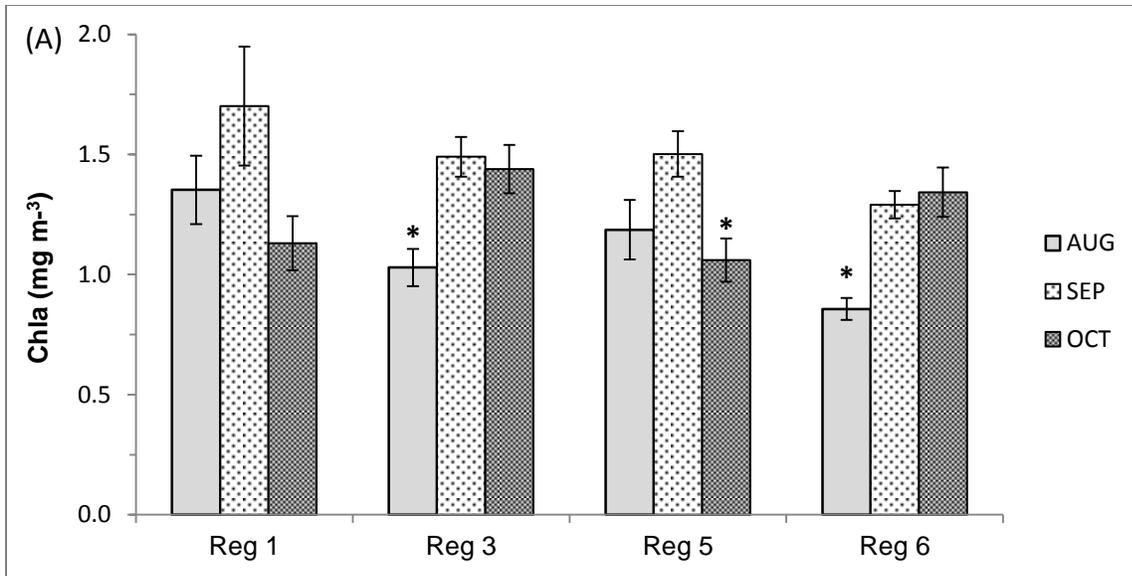
1069



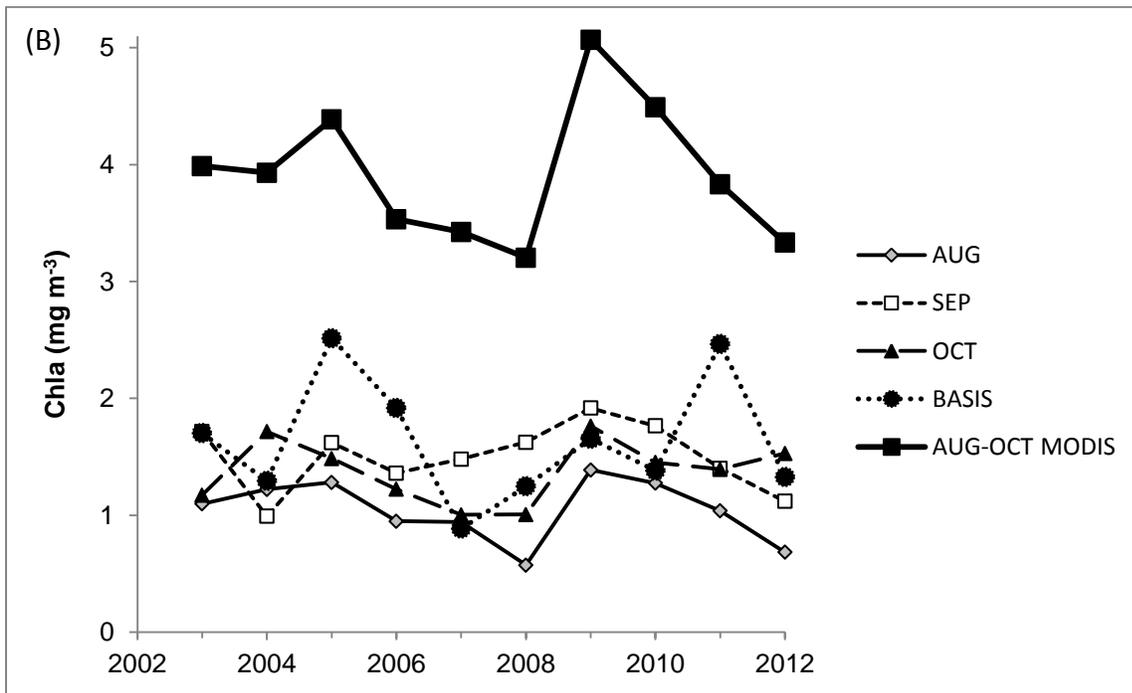
1070

1071 Figure 7.

1072



1073
1074



1075

1076 Figure 8.

1077

1078 Appendix. Mean values by region and year for surface and deep temperature (T, °C), salinity (S)
 1079 and nutrients (phosphate, silicic acid, nitrate, ammonium, µM). T and S are means above
 1080 (surface) and below (deep) the pycnocline. Nutrients are from ~ 5 m (surface) and 30-60 m
 1081 (deep). Only stations sampled 5 years or more (Fig. 1) were used in the analysis.

1082 T (surface)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	11.11	10.53	11.68	10.07	10.34	9.61	9.11	8.94	9.00	9.37	10.05
2	11.42	12.48	12.65	9.43	10.11	8.86	9.83	8.39	8.77	7.96	10.22
3	11.66	12.17	11.20	9.85	10.85	8.85	7.81	8.49	8.55	8.58	9.87
4	10.41	10.49	10.04	10.04	10.52	9.41	8.02	9.59	8.91	8.85	9.59
5		10.57	9.74	8.91	8.02		6.93		8.91	6.53	8.51
6	9.74	11.29	8.11	9.45	7.47	7.41	7.47	7.86	7.82	6.08	8.22
7	9.88	11.06	8.88	8.24	9.41	7.64	8.16	7.78	7.21	7.25	8.70
9	7.38	8.89	6.68	7.48	6.80		7.50	7.11	7.36	3.84	7.15
10		9.42	7.11	8.07	7.76		7.59	7.63	6.27	5.06	7.67
11	7.85	9.98	7.14	7.88	8.37		8.25	8.47	7.65	7.17	8.13
12	8.67	9.07		8.43	8.93		6.68	5.44	5.09	6.06	7.52
13	7.31	10.28	7.91	7.22	8.80		6.92	7.54	5.91	5.04	7.34
14	10.52	11.98	10.28	10.41	10.37		9.67	9.04	8.33	7.49	9.52
16	9.66	8.23	8.83	8.30				8.24	8.80		8.68
Grand Avg	10.15	10.95	9.59	8.99	9.23	8.64	8.05	8.28	7.88	7.44	8.93

1083

1084 T (deep)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	7.76	7.84	7.81	7.88	5.35	6.80	7.02	5.97	6.92	5.41	6.87
2	9.33	9.52	9.17	7.87	6.30	6.45	7.28	7.11	6.95	6.54	7.86
3	5.19	5.23	5.90	4.13	2.86	2.86	2.55	2.20	3.94	1.99	3.69
4	6.83	6.10	6.32	5.98	5.43	4.92	5.56	5.00	5.28	5.26	5.60
5		7.58	7.46	5.54	4.16		4.22		4.97	3.64	5.25
6	5.74	4.34	5.54	2.19	2.93	1.86	3.40	1.86	3.47	2.19	3.11
7	9.87	9.91	8.45	7.56	7.87	6.14	7.58	7.31	7.16	6.47	7.93
9	6.02	3.76	3.98	1.49	0.81		0.71	0.72	1.86	1.05	2.21
10		3.25	1.33	1.41	1.03		1.26	1.44	0.89	4.06	1.57
11	7.68	9.00	6.97	6.70	7.12		6.41	6.12	6.83	6.34	7.01
12	4.42	7.01		4.66	6.37		3.86	5.36	3.95	5.53	5.10
13	5.79	6.91	7.43	4.74	6.08		3.70	5.52	5.10	3.22	5.21
14	10.17	11.41	10.16	8.12	10.26		7.98	8.63	7.52	6.81	8.69
16	6.74	5.50	6.10	6.02				5.27	5.20		5.81
Grand Avg	7.24	6.92	6.49	5.05	4.73	4.31	4.48	4.51	4.91	4.30	5.31

1085

1086

1087 S (surface)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	31.57	31.67	31.81	31.74	31.79	31.75	31.81	31.68	32.02	31.84	31.76
2	30.92	30.89	30.58	30.55	31.09	30.76	30.56	31.08	30.59	31.05	30.82
3	31.63	31.70	31.74	31.43	31.37	31.49	31.44	31.32	31.45	31.41	31.49
4	31.86	31.88	31.96	31.92	31.94	31.63	31.95	31.81	32.09	32.08	31.95
5		31.94	31.96	31.98	31.68		31.80		31.71	31.68	31.81
6	31.93	31.86	31.98	31.49	31.52	31.43	31.43	31.16	31.33	31.37	31.50
7	31.25	31.21	31.12	30.85	30.95	31.12	31.18	31.22	31.05	31.03	31.08
9	31.45	31.56	31.78	30.99	31.06		31.19	30.74	30.98	31.23	31.21
10		31.12	31.27	30.88	31.16		30.95	31.11	31.06	30.58	31.07
11	30.54	30.31	31.02	30.56	30.63		30.77	30.58	30.78	30.66	30.66
12	31.41	32.08		31.90	31.62		31.47	31.63	32.00	31.72	31.74
13	30.55	30.82	31.21	31.31	31.45		30.56	31.24	31.54	31.45	31.17
14	26.38	28.75	29.86	25.62	28.74		27.58	28.11	28.22	28.40	27.84
16	32.35	32.61	32.77	32.42				32.55	32.54		32.54
Grand Avg	31.02	31.20	31.38	31.00	31.21	31.31	30.94	31.04	31.16	31.20	31.14

1088

1089 S (deep)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	31.94	32.02	32.08	32.01	32.18	31.89	32.05	31.99	32.21	32.16	32.06
2	31.25	31.05	31.17	30.96	31.30	31.18	31.07	31.26	30.90	31.30	31.15
3	31.88	31.96	32.08	31.88	31.81	31.91	31.77	31.73	31.94	31.81	31.88
4	32.61	32.48	32.49	32.53	32.59	32.43	32.66	32.51	32.64	32.61	32.57
5		32.07	32.09	32.07	31.91		32.24		32.08	32.09	32.06
6	32.06	31.97	32.07	31.83	31.64	31.74	31.61	31.53	31.63	31.72	31.75
7	31.25	31.20	31.20	30.88	30.99	31.21	31.28	31.29	31.06	31.12	31.13
9	31.57	31.57	32.04	31.38	31.52		31.54	31.15	31.24	31.49	31.50
10		31.13	31.60	31.37	31.75		31.45	31.77	31.39	31.56	31.49
11	30.65	30.68	31.04	30.66	30.77		30.91	30.77	30.91	30.93	30.82
12	31.72	32.12		31.99	31.80		31.90	31.68	32.22	31.80	31.92
13	31.49	31.24	31.21	31.62	31.68		31.68	31.56	31.75	32.00	31.62
14	27.95	29.80	29.92	29.69	29.15		29.98	29.80	29.51	29.71	29.51
16	32.74	33.09	33.22	32.74				32.91	33.02		32.95
Grand Avg	31.40	31.46	31.66	31.46	31.53	31.67	31.47	31.46	31.53	31.58	31.51

1090

1091

1092 Phosphate (surface)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	0.56	0.88	0.48	0.55	0.57	0.57	0.70	0.53	0.57	0.34	0.56
2	0.54	0.58	0.44	0.31	0.50	0.54	0.45	0.54	0.40	0.47	0.48
3	0.23	0.34	0.43	0.31	0.38	0.41	0.50	0.37	0.57	0.32	0.38
4	0.60	0.65	0.72	0.42	0.39	0.32	0.74	0.46	0.64	0.55	0.57
5		0.43	0.52	0.59	0.56		0.47		0.45	0.73	0.54
6	0.32	0.31	0.66	0.39	0.64	0.50	0.46	0.50	0.58	0.69	0.51
7	0.55	0.46	0.51	0.37	0.47	0.58	0.62	0.69	0.09	0.67	0.50
9	0.60	0.45	0.79	0.59	0.52		0.39	0.70	0.72	0.92	0.62
10		0.56	0.63	0.61	0.66		0.48	0.72	0.82	0.67	0.63
11	0.82	0.77	0.78	0.65	0.68		0.54	0.77	0.45	0.62	0.67
12	0.48	0.22		0.34	0.41		0.38	0.78	1.13	0.16	0.50
13	0.61	0.63	0.80	0.54	0.57		0.54	0.84	1.13	0.64	0.71
14	0.64	0.57	0.96	0.53	0.99		0.60	0.73	0.78	0.55	0.68
16	0.94	1.49	1.39	1.14				0.74	0.66		1.06
Grand Avg	0.51	0.54	0.60	0.46	0.54	0.48	0.53	0.60	0.62	0.53	0.55

1093

1094 Phosphate (deep)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	1.51	1.23	1.40	1.34	1.64	1.24	1.14	1.06	1.18	1.21	1.29
2	1.23	0.91	1.09	0.58	0.83	0.81	0.93	0.83	0.78	0.61	0.84
3	1.54	1.54	1.49	1.39	1.67	1.36	1.46	1.33	1.45	1.38	1.45
4	1.37	1.25	1.46	1.19	1.57	1.47	1.32	1.30	1.18	1.19	1.29
5		1.28	1.25	1.21	1.30		1.16		1.44	1.40	1.30
6		1.49	1.39	1.40	1.33	1.23	1.24	1.26	1.40	1.38	1.36
7		0.65	0.70	0.78		0.85	0.55	0.83	0.18	0.87	0.74
9	1.16	1.09	1.58	1.22	1.66		1.26	1.30	1.36	1.36	1.32
10		1.15	1.31	1.11			1.19	1.43	1.57		1.30
11	1.07	0.81	0.93	0.86			0.92	1.06	0.85	0.83	0.92
12		0.90			0.94		1.00		1.82		1.17
13	2.13			1.06	1.32		1.34	1.92	1.56	1.46	1.48
14											
16	1.47	1.86	1.81	1.51				0.91			1.51
Grand Avg	1.43	1.22	1.34	1.23	1.43	1.19	1.21	1.18	1.29	1.18	1.25

1095

1096

1097 Silicic acid (surface)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	9.93	15.44	7.91	12.83	6.42	12.99	9.41	8.16	12.14	3.68	9.58
2	3.53	6.56	1.48	2.60	1.78	7.44	2.98	6.71	3.76	6.27	4.22
3	2.71	6.32	5.69	3.71	1.61	5.33	5.95	3.70	9.94	3.58	4.82
4	14.62	17.79	13.90	10.84	10.89	10.84	10.00	7.97	17.14	13.98	12.89
5		5.83	13.23	6.22	9.43		6.52		2.80	9.40	7.42
6	3.38	5.48	5.57	2.81	8.25	6.39	5.06	5.05	5.52	6.04	5.37
7	2.31	3.31	3.01	2.10	1.86	7.17	5.13	7.48	1.00	9.03	4.16
9	5.62	5.45	8.50	2.75	5.06		4.56	5.49	5.12	11.58	5.75
10		3.89	2.82	2.50	3.33		3.92	5.96	10.93	11.37	4.61
11	8.89	5.74	4.86	4.73	3.22		6.72	7.15	5.36	7.61	5.93
12	1.07	3.54		1.90	7.52		4.42	11.27	23.40	1.03	7.24
13	8.17	7.45	4.35	5.66	9.02		7.41	11.84	21.07	10.77	10.20
14	17.92	14.51	6.84	11.21	11.70		14.71	16.67	17.58	14.07	14.79
16	8.00	40.84	36.53	33.32				9.93	13.20		23.64
Grand Avg	6.25	7.52	5.89	5.01	4.99	7.04	6.51	7.11	9.95	7.46	6.79

1098

1099 Silicic acid (deep)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	29.09	18.96	25.92	32.50	29.93	20.22	17.14	18.20	23.66	20.08	23.45
2	16.77	12.41	10.98	7.37	7.79	11.89	11.65	14.33	9.69	8.05	11.33
3	23.47	24.50	21.88	22.36	23.80	20.71	18.57	17.04	27.88	20.53	22.24
4	25.03	24.46	28.79	27.07	26.24	30.82	22.95	22.32	24.62	25.53	25.40
5		19.97	26.86	17.63	19.50		19.05		25.10	24.97	21.83
6		21.29	15.84	17.08	13.21	15.95	15.09	17.36	19.52	20.50	17.87
7		7.10	5.95	5.19		12.92	4.68	10.42	1.90	11.85	8.30
9	17.17	13.94	23.10	8.58	21.80		12.27	20.50	20.03	22.32	17.62
10		17.41	15.80	11.06			15.48	27.30	27.73		19.33
11	16.78	9.81	10.30	7.48			10.14	10.31	9.98	10.53	10.24
12		16.17			15.51		8.40		39.30		19.84
13	37.71			13.07	24.70		24.97	33.25	33.08	20.43	26.25
14											
16	25.25	49.18	44.58	39.74				14.21			34.59
Grand Avg	23.73	18.62	20.09	18.11	21.04	18.03	15.79	17.92	22.57	18.33	19.22

1100

1101

1102 Nitrate (surface)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	1.72	4.15	2.09	1.30	3.30	0.77	3.28	1.35	1.73	0.66	1.99
2	0.04	0.11	0.09	0.01	0.56	0.14	0.06	0.19	0.14	0.08	0.14
3	0.06	0.28	0.73	0.13	0.75	0.14	0.79	0.11	1.98	0.16	0.52
4	1.68	3.20	3.24	0.78	0.95	0.05	4.21	0.57	3.25	2.91	2.29
5		0.08	0.87	0.90	1.75		1.16		0.17	4.20	1.24
6	0.22	0.05	1.19	0.02	1.86	0.14	0.34	0.12	0.50	0.87	0.55
7	0.06	0.08	0.30	0.03	0.45	0.01	0.09	0.28	0.18	0.24	0.20
9	0.17	0.24	2.48	0.29	0.68		0.08	0.12	0.17	1.22	0.59
10		0.22	0.10	0.01	0.07		0.13	0.07	0.84	0.29	0.18
11	0.11	0.21	0.60	0.10	0.17		0.71	0.08	0.09	0.11	0.25
12	0.25	0.16		0.02	0.62		1.38	3.86	9.05	0.00	2.06
13	0.20	0.20	0.11	0.53	0.53		2.30	3.02	5.01	2.72	1.89
14	0.35	0.12	0.08	9.12	0.34		0.14	0.11	0.43	0.07	1.10
16	4.34	15.02	14.00	9.89				3.32	5.40		8.66
Grand Avg	0.42	0.71	1.07	0.65	0.84	0.18	1.04	0.51	1.54	0.81	0.83

1103

1104 Nitrate (deep)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	14.09	7.18	10.27	10.87	14.83	4.88	7.51	5.36	8.91	7.91	9.27
2	2.03	0.78	1.42	0.35	0.90	0.49	1.76	1.08	0.90	0.23	0.87
3	8.45	8.73	9.12	10.86	11.81	7.27	9.08	5.99	9.61	8.41	8.86
4	11.98	10.31	14.70	9.83	15.75	12.36	12.49	9.75	11.18	9.85	11.38
5		6.48	6.47	7.66	7.85		7.65		8.70	12.35	8.18
6		4.07	4.71	9.63	5.21	3.41	4.71	4.81	6.71	5.27	5.83
7		0.30	0.86	1.19		0.32	0.10	0.58	0.10	0.95	0.62
9	1.17	0.98	6.45	3.64	7.55		3.95	3.52	5.08	4.62	4.01
10		1.06	2.83	1.82			1.86	3.11	7.92		3.14
11	0.25	0.39	1.81	0.67			0.36	1.25	0.63	0.47	0.77
12		4.15			3.92		7.00		15.80		7.72
13	18.42			4.96	6.15		6.73	13.77	11.81	10.95	9.69
14											
16	11.45	22.02	21.37	16.13				4.56			15.11
Grand Avg	8.63	4.79	7.32	7.53	8.91	4.78	5.43	4.33	7.47	6.06	6.32

1105

1106

1107 Ammonium (surface)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	0.20	1.02	0.23	0.76	0.74	0.80	1.01	0.79	0.77	0.50	0.64
2	0.11	0.50	0.35	0.38	0.85	0.98	0.16	0.52	1.42	0.58	0.55
3	0.13	0.25	0.52	0.32	0.63	0.50	0.75	0.37	0.82	0.18	0.43
4	0.04	0.48	0.31	0.20	0.58	1.07	0.68	0.44	0.56	0.11	0.41
5		0.20	1.10	1.18	1.09		0.47		0.26	0.90	0.81
6	0.34	0.26	2.06	0.22	1.30	0.63	0.37	0.77	0.47	0.82	0.69
7	0.17	0.30	0.89	0.22	0.96	0.53	0.36	1.34	0.08	0.22	0.57
9	1.45	0.26	1.89	0.71	0.78		0.13	0.34	0.24	1.49	0.75
10		0.08	0.42	0.08	0.27		0.23	0.33	0.26	0.31	0.23
11	0.45	0.09	1.42	0.56	0.70		0.14	0.25	0.25	0.32	0.46
12	0.00	1.75		0.30	1.17		0.35	0.79	1.65	0.09	0.85
13	0.19	0.19	0.35	0.19	0.41		0.17	0.61	1.76	0.53	0.54
14	0.08	0.04	1.06	0.31	3.23		0.60	0.59	1.18	0.26	0.77
16	0.81	0.95	0.42	0.27				1.76	0.45		0.78
Grand Avg	0.26	0.33	0.76	0.36	0.83	0.68	0.37	0.54	0.74	0.42	0.53

1108

1109 Ammonium (deep)

Region	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>	<u>2009</u>	<u>2010</u>	<u>2011</u>	<u>2012</u>	<u>Grand Avg</u>
1	1.27	2.63	4.69	3.97	1.72	4.38	2.97	2.99	2.67	3.66	3.06
2	4.41	2.89	5.79	2.81	2.19	3.57	4.67	2.55	3.37	1.76	3.15
3	4.59	4.15	5.67	3.98	5.51	4.00	3.64	4.52	4.58	3.27	4.29
4	1.54	1.25	0.79	2.86	1.76	3.10	1.40	2.41	1.00	1.64	1.65
5		3.17	4.92	4.35	4.43		0.88		4.98	2.41	3.95
6		5.75	6.43	4.16	5.65	5.06	3.57	3.85	4.26	4.49	4.64
7		1.38	2.18	2.07		2.44	0.44	2.16	0.20	0.25	1.50
9	3.02	3.23	6.47	4.05	4.48		2.40	1.94	1.35	3.74	3.36
10		1.46	4.07	4.23			2.02	2.78	2.28		2.70
11	0.81	0.89	3.06	1.57			0.85	1.31	0.69	0.67	1.17
12		0.84			1.94		0.64		4.33		1.94
13	4.27			2.35	3.25		3.38	2.27	3.36	2.53	3.03
14											
16	2.90	0.22	0.50	1.36				3.02			1.60
Grand Avg	3.02	2.96	4.49	3.61	3.90	3.92	2.64	2.83	3.02	2.73	3.24

1110

1111