

Spring and Fall Phytoplankton Blooms in the Eastern Bering Sea During 1995–2011

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Introduction

The timing and magnitude of phytoplankton blooms in subarctic ecosystems often strongly influence the amount of energy transferred through subsequent trophic pathways. In the southeastern Bering Sea, spring bloom timing has been linked to production of large crustacean zooplankton and walleye pollock (*Gadus chalcogrammus*); if ice is present after mid-March, an early ice-associated bloom occurs there; otherwise a spring bloom usually occurs in May. Although spring bloom timing is well-characterized in the southeastern part of the shelf, less is known about the spring bloom elsewhere in the eastern Bering Sea, as well as the characteristics of the fall bloom.

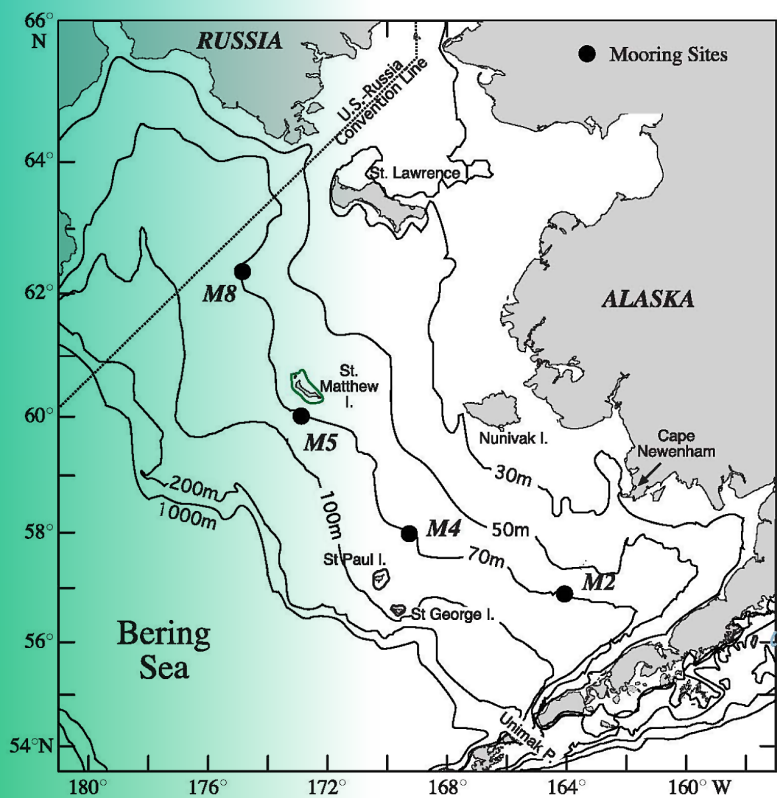


Figure 1. Study area and mooring locations.

The eastern Bering Sea is dominated by a broad continental shelf (~500 km wide), a large part of which is ice-covered during winter, with the maximum extent varying more than 100 km among years. In ice-covered areas, the seasonal cycle of primary production begins with ice algae (primarily large diatoms), which begin to grow in the spring when light level becomes adequate. Ice algae are adapted to lower light levels than pelagic phytoplankton and grow within the ice and at the ice-water interface depending on the amount of overlying snow cover. Ice algae begin to grow in mid-February in the Bering Sea and may provide an early concentrated food source for zooplankton.

Phytoplankton in the Bering Sea exhibit net growth in the spring once the water becomes stratified and the mixed layer is shallower than the critical depth. Prior to this, phytoplankton are considered to be light-limited, but have adequate nutrients due to the advection of nutrient-rich slope water onto the shelf during the previous winter, which is mixed throughout the water column; nutrient recycling on the shelf also is important. The phytoplankton spring bloom typically ends when the surface nutrient supply is exhausted and phytoplankton growth becomes nutrient limited (typically below 1 μM nitrate). Grazing pressure from mesozooplankton and microzooplankton also increases as the spring progresses, which can reduce the net accumulation of phytoplankton standing stocks.

In the summer, phytoplankton concentration in the surface mixed layer is typically low due to nutrient limitation and continued grazing pressure. Episodic wind events can break down stratification and mix nutrients and viable phytoplankton cells to the surface during this period. During fall, increased frequency and intensity of storms and overall cooling of the water column reduces stratification and deepens the mixed layer so that nutrients are mixed to the surface to fuel fall phytoplankton blooms. The fall bloom ends when phytoplankton become light-limited, due to decreased day length and deepening of the mixed layer.

In this article we focus on the middle domain of the eastern Bering Sea shelf where four oceanographic moorings have been located. The measurements on the moorings include temperature and chlorophyll *a* fluorescence. In summer, the middle domain is strongly stratified into two layers, with a wind-mixed upper layer and a tidally-mixed lower layer. The middle domain typically extends from the 50-m isobath to the 100-m isobath and is bounded by oceanic fronts or transition zones. In winter, the middle domain is usually well mixed and cold, with a large part (> 50%) ice-covered. These four oceanographic moorings provide the longest daily record of in situ oceanographic measurements in the eastern Bering Sea. This article describes the first examination of the chlorophyll *a* fluorescence data, excepting previous analyses of the spring bloom at the southern-most mooring. In this article our objectives are to characterize spring and fall blooms over the eastern Bering Sea middle shelf; relate their timing and strength to physical characteristics including spring ice retreat and fall overturn; and discuss some implications of these results for one of the large crustacean zooplankton taxa characteristic of that domain (*Calanus* spp.).

Data and methods

Four oceanographic moorings have been deployed along the 70-m depth contour of the eastern Bering Sea shelf, with two southern locations sampled almost continually since 1995 (M2) and 1999 (M4) and two northern locations since 2004 (M8) and 2005 (M5) (Fig. 1). Data collected by instruments on the moorings included temperature (miniature temperature recorders, SeaBird SBE-37 and SBE-39) and chlorophyll *a* fluorescence (WET Labs DLSB ECO Fluorometer). A transition to fluorometer sensors with wipers that sharply reduced fouling occurred during 2001–04.

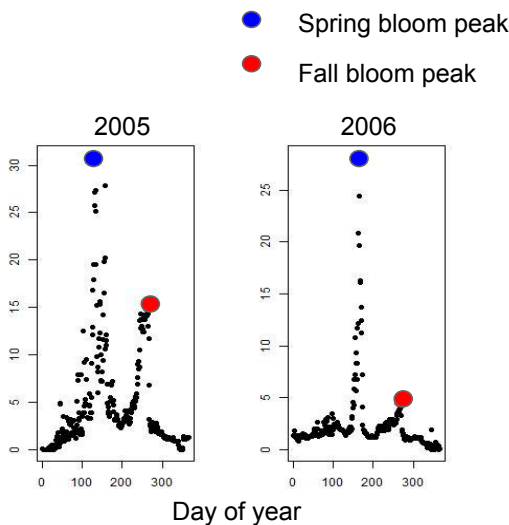


Figure 2. Example annual records of chlorophyll *a* values with spring (blue circle) and fall (red circle) blooms marked.

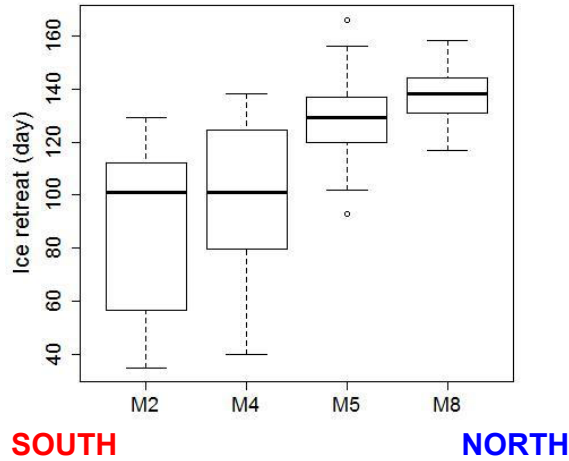


Figure 3. A boxplot of ice retreat (day) by mooring. The box extends from the first quartile to the third quartile, the heavy line dividing the box is the median and the whiskers are the smallest and largest values. The number of years with ice present were 12 (M2), 15 (M4), 17 (M5) and 17 (M8).

Data were collected at least hourly. For consistency, our analyses focus on data recorded at 11 m (or the shallowest instrument at M5 (15 m) and M8 (20 m) during autumn, winter, and early spring).

Two sources of sea-ice data were used. The first source was the National Ice Center (NIC), with data available from 1972 to 2005; the second source was the Advanced Microwave Scanning Radiometer EOS (AMSR), with data available from 2002 to 2012. These two data sets provide data over the entire period (1972–2012) for which high-quality data on sea-ice extent and areal concentration are available. To examine how the ice cover varies along the 70-m isobath, a 100-km by 100-km box was defined around each of our biophysical moorings (M2, M4, M5, and M8) maintained by NOAA. AMSR and NIC data overlap during the 4-year period 2002–05, during which time they have very similar values. To span the period 1972–2012, we used both NIC and AMSR data, using the average value in the overlap years to derive the annual cycle of percent ice cover for each mooring location.

Winds were estimated using daily data from the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) Reanalysis; wind velocity was interpolated to the locations of the four moorings. The daily winds from the reanalysis are reliable in this region based on a comparison to independent buoy measurements from 1995 to 2000.

Data analysis

Ice cover for each mooring and year was examined to determine if ice was present at any time that winter or spring and if present, when the ice retreated for the last time. Ice retreat was considered to have occurred when ice cover fell below 15% for the last time during that spring. The temperature records for each mooring and year were examined to determine 1) when the ocean began warming following ice retreat; and 2) when fall overturn occurred. When ice was present the temperature was approximately -1.7°C . Warming was considered to have started when the near surface temperature rose above -1°C for the last time that spring. Fall overturn was considered to have occurred once temperature fell 2°C below the summer maximum.

Chlorophyll *a* values for each mooring and year were examined to determine the time and magnitude of the maximum value in spring and fall. These records were plotted and the times and magnitudes of the spring and fall blooms were assigned (Fig. 2). Each year, the spring bloom was assigned to the maximum value before day 180 (ca. June 27) and the fall bloom was assigned to the maximum value after day 210 (ca. July 27). In some years the data record was discontinuous and the maximum value could not be determined.

Results

Ice was present for about two out of three years at M2 (12 of 17), nearly all years at M4 (15 of 17), and all years at M5 and M8 (17 of 17). When ice was present, retreat was significantly (ANOVA, $p < 0.001$, $df = 3, 57$) earlier in the south (mean M2: day 88; M4: 99; M5: 130; M8: 138) (Fig. 3). In some years when ice was present, retreat occurred before mid-March (M2 during 1998, 2000, 2002, 2006 and M4 during 2000 and 2002). Ice was absent at M2 during 1996, 2001, and 2003–05 and at M4 during 2001 and 2005. Ice presence reduced ocean temperature below -1°C in all cases but one (ice was present at M2 in 2002, but for only 11 days, and minimum temperature was -0.1°C).

During years when ice was absent (or was present, but retreated before mid-March), the spring bloom maximum occurred in late May to early June (average day 148, $SE = 3.5$, $n = 11$) (Fig. 4). This pattern occurred for M2 and M4 but not M5 or M8 where ice always was present after mid-March (Fig. 5). There was no statistically significant difference in timing of the spring bloom maximum in years when ice was absent (average day 141) and when ice was present, but retreated before mid-March (average day 153) (two-way t -test, $df = 9$, $p = 0.10$). During years when ice was absent or retreated before mid-March, spring bloom maximum averaged 19 mg Chl l^{-1} (log-transformed, $SE = 1.2$, $n = 11$). There was no statistically significant difference in spring bloom maximum in years when ice was absent (average 25 mg Chl l^{-1}) and when ice retreated before mid-March (average 15 mg Chl l^{-1}) (log-transformed, two-way t -test, $df = 9$, $p = 0.14$).

In contrast to the late May to early June timing of the spring bloom in years when ice was absent or retreated early, if ice was present after mid-March (day 75), an ice-associated bloom occurred between early April and mid-June, and the bloom timing was related to ice retreat timing, regardless of mooring. Later blooms occurred when ice retreat was later (linear regression, y -intercept=53, slope=0.66, $df = 1, 24$, $p < 0.001$) (Fig. 6). This relationship implies that bloom day is 119 when ice retreat occurs on day 100, 152 when ice retreat occurs on day 150, and 172 when ice retreat occurs on day 180. There was no statistically significant difference in spring bloom magnitude when ice was present, but retreated before mid-March or ice was absent (average 19 mg Chl l^{-1}) and when ice was present after mid-March (average 17 mg Chl l^{-1}) (log-transformed, two-way t -test, $df = 35$, $p = 0.70$); the overall average spring bloom magnitude was 17 mg Chl l^{-1} (log-transformed, $SE = 1.2$, $n = 37$).

Fall overturn timing was similar among moorings on average (M2 mean was day 259; M4: 261; M5: 259; M8: 268 (ANOVA, $df = 3, 34$, $p = 0.49$)), but was more variable at M2 and M4. Fall bloom timing was similar among moorings (M2 mean: day 276; M4: 277; M5: 258; M8: 281) (ANOVA, $p = 0.32$, $df = 3, 29$). Fall bloom magnitude also was similar among moorings (ANOVA, log-transform, $p = 0.93$, $df = 3, 30$). On average, the fall bloom occurred on day 274 (late September) ($SE = 4.2$, $n = 33$) with an average chlorophyll value of 8 mg Chl l^{-1} ($SE = 1.2$, $n = 34$).

The magnitudes of the spring and fall blooms were correlated (Pearson's $r = 0.46$, $df = 28$, $p = 0.011$, log-transformed values) (Fig. 7). The interval of time between the spring and fall blooms ranged from about 4–6 months, with longer intervals occurring for earlier spring blooms (linear regression, intercept=294, slope=-1.16, $df = 1, 27$, $p < 0.001$) (Fig. 8).

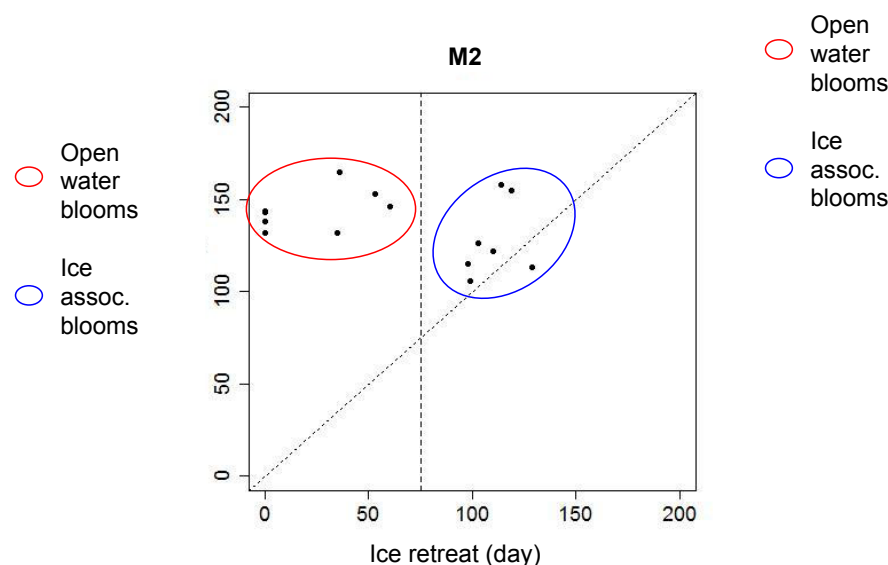


Figure 4. Scatterplot of spring bloom maximum (day) versus ice retreat (day) for mooring M2. If ice was absent that year, then the ice retreat date is zero. The diagonal dashed line is the 1:1 line to compare timings of spring bloom and ice retreat. The vertical dashed line is March 15. The red oval encloses open water blooms and the blue oval encloses ice-associated blooms.

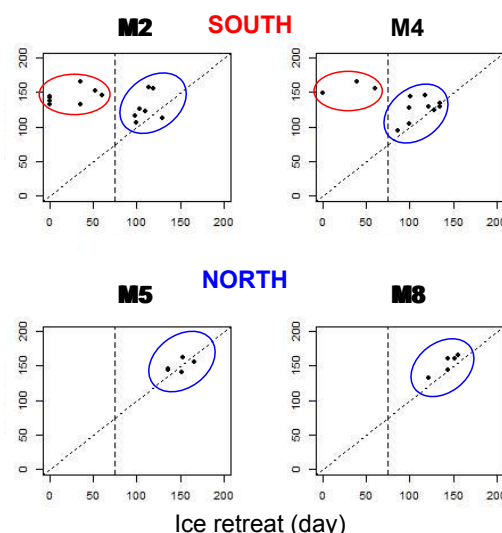


Figure 5. Scatterplot of spring bloom maximum (day) versus ice retreat (day) by mooring. If ice was absent that year, then the ice retreat date is zero. The diagonal dashed line is the 1:1 line to compare timings of spring bloom and ice retreat. The vertical dashed line is March 15. The red oval encloses open water blooms and the blue oval encloses ice-associated blooms.

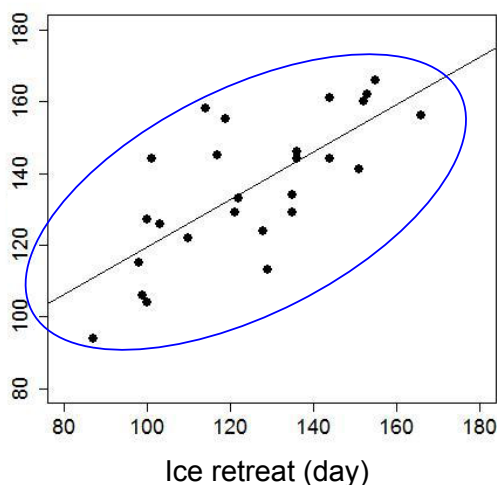


Figure 6. Scatterplot of the observed (number) and fitted (line, based on simple linear regression, y -intercept=53, slope=0.66, $df=1, 24$, $p<0.01$) values of spring bloom maximum (day) versus ice retreat (day) for all moorings when ice was present after March 15. The number indicates mooring number.

Discussion

Spring

We found that in the eastern Bering Sea, if ice was present after mid-March, spring bloom timing was related to ice retreat timing; if ice was absent or retreats before mid-March, a spring bloom usually occurred in May or early June. In general, ice-associated phytoplankton blooms are observed near the retreating ice edge on shipboard surveys and in ocean color data, due to melting ice increasing the stability of the water column. While the spring bloom usually moves northward as the eastern Bering Sea becomes ice free, sometimes ice melts in the north before disappearing farther south and a spring bloom occurs in the northern ice-free area before it occurs in the south if light levels are sufficient (e.g., 2010). Percent ice cover also influences whether or not ice-associated blooms occur by modulating both light and stratification. The relationship between the timing of the spring bloom and ice retreat when ice retreat occurred after mid-March was statistically significant for the eastern Bering Sea (pooled data from the north and south; Fig. 6).

We summarize these findings on spring bloom timing and ice retreat timing as follows (Fig. 9). If ice retreats after mid-March, an ice-associated bloom occurs; this pattern applies throughout the eastern Bering Sea. If the ice retreats early (before mid-March), there is no ice-associated bloom because sunlight is insufficient to initiate an ice-associated bloom. To date, early ice retreat occurs only in the southeastern Bering Sea and not in the northern Bering Sea; this pattern of persistent ice in the northern Bering Sea is expected to continue into the foreseeable future. An open-water bloom occurs if ice retreats before March 15 or ice is absent; this pattern applies only in the southeastern Bering Sea.

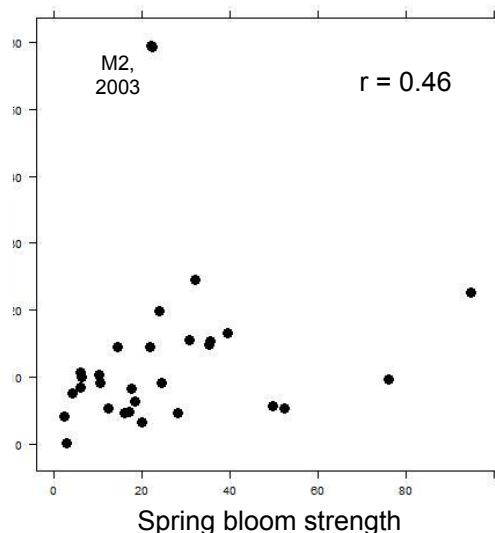


Figure 7. Scatterplot of maximum spring bloom magnitude and maximum fall bloom magnitude. The number indicates mooring number.

Fall

A fall bloom commonly occurred in both the northern and southeastern Bering Sea, on average in late September. Winds at M2, M4, M5, and M8 are significantly correlated, which will tend to synchronize fall blooms, as was observed. However, bloom timing was not significantly related to either storm or fall overturn timing. The lack of a significant effect was unexpected; however a timing effect for the fall bloom may be difficult to detect because timing is affected by several interacting factors including wind strength, stratification, fall cooling, and light level. For example, fall overturn requires strong winds, but once cooling begins in late September and early October, less wind energy is necessary to overturn the ocean. A fall bloom also depends on sufficient light, introduction of nutrients from below the pycnocline, short periods of stabilization that allow phytoplankton to remain in the sunlit waters and grow, and may be influenced by zooplankton grazing.

Our mooring data and previous middle-shelf observations indicated that the magnitudes of fall blooms were weaker than spring blooms on average. It may be that nutrient supply rates are limiting (e.g., storm mixing) and/or the accumulation of chlorophyll *a* is limited by grazing. For instance, if the lower layer has 20 μM of nitrate and the surface mixed layer is 20 m deep and depleted of nitrate, which are typical conditions during summer, then deepening the mixed layer by 5 m will result in only 4 μM of nitrate, compared to 18 μM available for consumption in the top 20 m of water column in spring. In addition, variations in chlorophyll *a* reflect the result of multiple processes including phytoplankton growth, grazing, sinking, and advection. Chlorophyll *a* will not increase until cell growth exceeds losses by grazing and other factors. While grazing impact has been measured for spring, grazing impact has not been measured for fall, so comparing grazing pressure on spring and fall blooms is not possible. Finally, phytoplankton physiological status and species composition can impact bloom intensity.

Biological implications

Spring bloom timing predictably varied between early April and mid-June depending on ice presence/absence and ice retreat timing. Thus the secondary community (zooplankton species) that benefits will depend on how close timing of their spring energy-intensive needs, such as reproduction and awakening from winter diapauses, matches the timing of the spring bloom. Species that require an early pulse of energy will benefit from years when ice is present but retreats in late March (conditions that tend to result in early April phytoplankton bloom). In contrast, species with a phenology timed for a late energy pulse will benefit from years with no ice (conditions that tend to result in a late May to early June bloom).

These observations also imply that climate, through its connection to the production, transport, and dissipation of sea ice, has the potential to affect the success of zooplankton populations and the strength of coupling between primary production and higher trophic levels. For example, the large crustacean zooplankton taxa *Calanus* spp. may benefit in years when ice is present after March 15 but retreats relatively early (Fig. 10). Spring *Calanus* spp. concentrations in the southeastern Bering Sea were higher in cold years with late ice retreat than in warm years with early ice retreat. Here we simplify *Calanus* spp. life history into four major steps from winter/late spring through the following winter: spawning, metamorphosis, accumulation of depot lipids, and overwintering. The timing of spawning by *Calanus* spp. in the eastern Bering Sea is protracted (from February to May), and the longer that conditions are suitable, the more total eggs each female will produce. Both early and late spawning by *Calanus* spp. females may benefit in cold years with late ice retreat, as reproduction timing then coincides with either the ice algae or the spring bloom. Individuals likely metamorphose from naupliar to copepodite stages during the early spring bloom. It has been hypothesized that metamorphosis is a recruitment bottleneck and that an early spring bloom benefits copepodite recruitment. The spring bloom occurs during April in years when ice is present, but retreats relatively early, which may promote strong recruitment of copepodites. In addition, a cold winter with ice present likely reduces metabolism and lipid utilization by *Calanus* spp. and thus may promote winter survival. Daily respiration rates are 47% higher for average winter bottom temperatures of warm (2°C) versus cold (-1.8°C) years in the southeastern Bering Sea. Overall, three conditions favor *Calanus* spp. production in cold years: the availability of ice algae or an early spring bloom to support egg production, the match of copepodites with the spring bloom for early spawners, and reduced metabolic rates during winter.

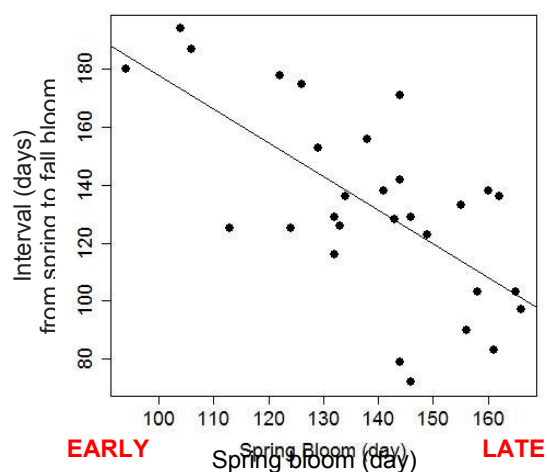


Figure 8. Scatterplot of observed (number) and fitted (line, based on linear regression, intercept=204, slope=-1.16, df=1, 27, $0 < 0.001$) values for all moorings. The y-axis is the interval between the spring and fall bloom maximum (days). The x-axis is the spring bloom maximum (day). The number indicates mooring number.

Spring/fall comparisons

Spring and fall bloom magnitudes were related, implying that a common factor influences spring and fall primary production (e.g., overwinter replenishment of nutrients). The fall bloom may be linked to the spring bloom by the fraction of spring bloom organic matter that sinks to the benthos, is remineralized, and ultimately is reintroduced to the euphotic zone during convection in the fall. In addition, this relationship likely amplifies secondary production during good years (both spring and fall blooms tend to be strong) and vice versa during bad years (both spring and fall blooms tend to be weak). An analysis of nutrient information, comparing spring–fall differences by year, would help us to understand the mechanism for this relationship.

The fall bloom occurred in late September on average, and the timing was less variable than for the spring bloom (varies over ~ 60-day compared to ~ 120-day period) regardless of location, so the spring–fall interval largely depends on spring bloom timing. In the northern Bering Sea, where ice is present every year and on average retreats in late May (Fig. 3), the interval typically lasted 4 months (Fig. 8). The interval also typically lasted 4 months in the southeastern Bering Sea in years when ice was absent or retreated before March 15. In contrast, the interval lasted up to 6 months in the southeastern Bering Sea in years when ice was present after March 15, but retreated soon thereafter.

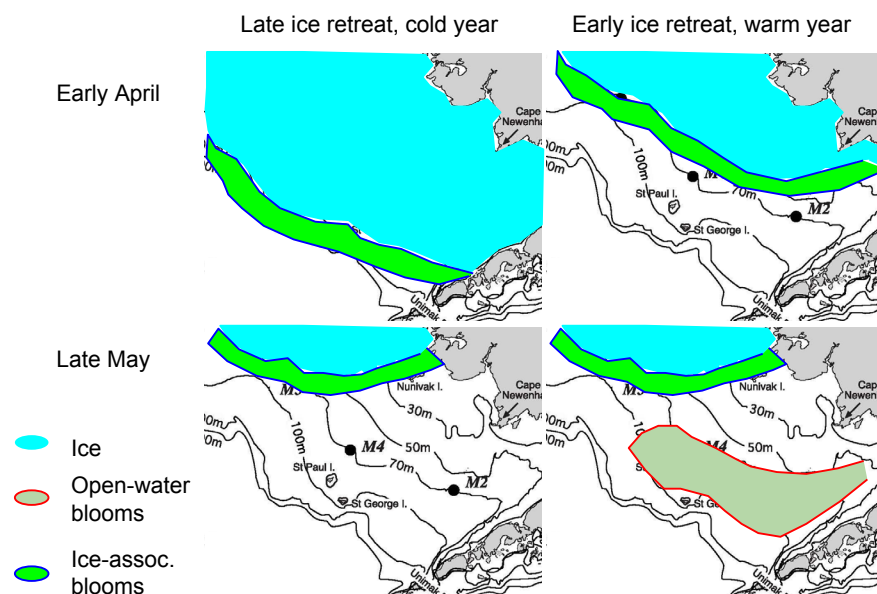


Figure 9. If ice retreats after mid-March, an ice-associated bloom occurs; this pattern applies throughout the eastern Bering Sea. If the ice retreats early (before mid-March), there is no ice-associated bloom because sunlight is insufficient to initiate an ice-associated bloom. An open-water bloom occurs if ice retreats before March 15 or ice is absent; this pattern applies only in the southeastern Bering Sea. This open-water bloom occurs in late May.

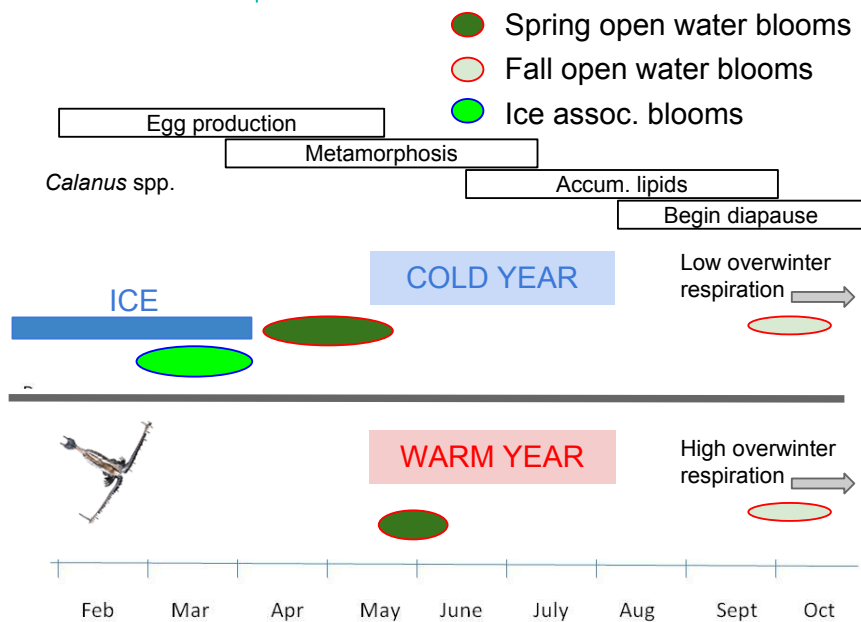


Figure 10. Timing of *Calanus* spp. reproduction relative to the presence of ice and ice algae, and the spring and fall blooms. The *Calanus* spp. life history is simplified and the timings are approximate. The blue rectangle is the period of ice cover. The dark green oval is the period for the spring bloom and the light green oval is the period for the fall bloom. Ice algae blooms occur during ice cover and ice retreat (bright green oval) and begin as early as mid-February.

Summary

The timing and magnitude of phytoplankton blooms in subarctic ecosystems often strongly influence the amount of energy that is transferred through subsequent trophic pathways. In the eastern Bering Sea, spring bloom timing has been linked to ice retreat timing and production of zooplankton and fish. A large part of the eastern Bering Sea shelf (~ 500 km wide) is ice-covered during winter and spring. Four oceanographic moorings have been deployed along the 70-m depth contour of the eastern Bering Sea shelf with the southern location occupied annually since 1995, the two northern locations since 2004, and the remaining location since 2001. Chlorophyll *a* fluorescence data from the four moorings provide 37 realizations of a spring bloom and 33 realizations of a fall bloom. We found that in the eastern Bering Sea, if ice was present after mid-March, spring bloom timing was related to ice retreat timing ($p < 0.001$, $df = 1$, 24); if ice was absent or retreated before mid-March, a spring bloom usually occurred in May or early June (average day 148, $SE = 3.5$, $n = 11$). A fall bloom also commonly occurred, usually in late September (average day 274, $SE = 4.2$, $n = 33$), and its timing was not significantly related to the timing of storms ($p = 0.88$, $df = 1$, 27) or fall water column overturn ($p = 0.49$, $df = 1$, 27). The magnitudes of the spring and fall blooms were correlated ($p = 0.011$, $df = 28$). The interval between the spring and fall blooms varied between 4 to 6 months depending on year and location. We present a hypothesis to explain how the large crustacean zooplankton taxa *Calanus* spp. likely respond to variation in the interval between blooms (spring to fall and fall to spring).

Conclusions

- In the eastern Bering Sea, if ice is present after mid-March, spring bloom timing is related to ice retreat timing; if ice is absent or retreats before mid-March, a spring bloom usually occurs in May or early June.
- Spring and fall bloom magnitudes are related, implying that a common factor influences spring and fall primary production.
- We hypothesize that large crustacean zooplankton such as *Calanus* spp. benefit from cold, icy winters in the southeastern Bering Sea because ice algae or ice-associated phytoplankton blooms provide an early spring food source, and respiration rates are lower during cold winters.

Additional Reading

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