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Century-scale changes in phytoplankton phenology in the Gulf of Maine

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The phenology of major seasonal events is an important indicator of climate. We analyzed multiple datasets of in situ chlorophyll measurements from the Gulf of Maine dating back to the early 20th century in order to detect climate-scale changes in phenology. The seasonal cycle was consistently characterized by a two-bloom pattern, with spring and autumn blooms. The timing of both spring and autumn blooms has shifted later in the year at rates ranging from ~1 to 9 days per decade since 1960, depending on the phenology metric, and trends only emerged at time scales of >40 years. Bloom phenology had only weak correlations with major climate indices. There were stronger associations between bloom timing and physical and chemical variables. Autumn bloom initiation correlated strongly with surface temperature and salinity, and spring bloom with nutrients. A later spring bloom also correlated with an increased cohort of *Calanus finmarchicus*, suggesting broader ecosystem implications of phytoplankton phenology.

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ABSTRACT

The phenology of major seasonal events is an important indicator of climate. We analyzed multiple datasets of in situ chlorophyll measurements from the Gulf of Maine dating back to the early 20th century in order to detect climate-scale changes in phenology. The seasonal cycle was consistently characterized by a two-bloom pattern, with spring and autumn blooms. The timing of both spring and autumn blooms has shifted later in the year at rates ranging from ~1 to 9 days per decade since 1960, depending on the phenology metric, and trends only emerged at time scales of > 40 years. Bloom phenology had only weak correlations with major climate indices. There were stronger associations between bloom timing and physical and chemical variables. Autumn bloom initiation correlated strongly with surface temperature and salinity, and spring bloom with nutrients. A later spring bloom also correlated with an increased cohort of *Calanus finmarchicus*, suggesting broader ecosystem implications of phytoplankton phenology.

INTRODUCTION

One of the earliest studied and most striking oceanographic phenomena is the spring phytoplankton bloom. A prominent feature of satellite images, the bloom initiates as “flowerings of diatoms, resulting in local swarms so dense as to be the most spectacular event in the yearly planktonic cycle” (Bigelow, 1924). Efforts to predict the timing of the spring bloom in the Gulf of Maine helped to coalesce the interdisciplinary and quantitative approaches that underlie modern oceanography (Riley, 1949). Despite over 100 years of study and a corpus of theory, predicting the dynamics of phytoplankton blooms remains an important but elusive goal (Sverdrup, 1953; Taylor and Ferrari, 2011; Mahadevan et al., 2012; Behrenfeld and Boss, 2014; Zarubin et al., 2017).

Phytoplankton blooms are indeed spectacular events, and their timing is particularly important to marine ecosystems in strongly seasonal climates. Because they constitute the primary source of carbon fixation for the pelagic food web, animals across trophic levels have life history strategies tuned to the seasonal cycle of production. Productive systems depend on seasonal timing matches between trophic levels because mismatches in timing can mean that a grazer or predator misses its feeding window (i.e. match-mismatch hypothesis, (Cushing, 1969; Edwards and Richardson, 2004)). The Gulf of Maine is a quintessential example of this phenomenon. The zooplankton community is largely copepods of the genus *Calanus* (Bigelow, 1924), which time their emergence from diapause to exploit the spring phytoplankton bloom. The pulse of *Calanus* production is then succeeded by fish (Golet et al., 2015), mammal (Pershing et al., 2009), and other migrations.

There is growing attention to changing phenology as both an indicator and a consequence of climate change. Understanding phenology in a climate context requires time series that span many decades. Such datasets in the pelagic ocean are limited. In the Gulf of Maine, there have been noted phenological shifts in recent times, particularly regarding physical properties such as temperature (Thomas et al., 2017), stratification, and hydrology (Smith et al., 2012), related to climate change. To understand the associated phenological changes in the pelagic ecosystem in a climate context, we need biological time series that span many decades—in seasonal oceans a minimum of 40 years (Henson et al., 2010). To examine changes in phytoplankton phenology in the Gulf of Maine at the climate scale, we aggregated multiple datasets of in situ chlorophyll measurements over the past century. We used this data to address the following

47 questions: (1) Has the timing of phytoplankton blooms changed over the past century? (2) What are the
48 drivers of these changes? And (3) What are the ecological consequences of these changes?

49 DATA AND METHODS

50 Phytoplankton Dataset

51 We aggregated datasets of in situ phytoplankton measurements from multiple public sources. We used
52 chlorophyll as an estimate of phytoplankton biomass and used previously published datasets. Chlorophyll
53 time series in the interior Gulf of Maine vary together based on empirical orthogonal function analysis,
54 separately from the coastal Gulf of Maine (Thomas *et al.*, 2003). This analysis thus focused on the inner
55 Gulf of Maine, including all samples deeper than the 100 m isobath (106,257 samples, Fig 1). For some
56 data, measurements were in standard units (mg chl m^{-3}). For others, a conversion was necessary. For
57 phytoplankton colour index (PCI) measured by the continuous plankton recorder (CPR) and for Forel-Ule
58 (FU) scale, we used established relationships (Raitos *et al.*, 2005; Wernand *et al.*, 2013, respectively).
59 The data were all from calibrated, quality-controlled, public databases: Aggregated database of (Boyce
60 *et al.*, 2012) (1934-2010, mg chl m^{-3} and FU), Continuous Plankton Recorder (1961-2013, PCI), Gulf
61 of Maine North Atlantic Time Series (1998-2015, mg chl m^{-3} and FU (Balch *et al.*, 2016), including
62 measurements from (Bigelow, 1924b)), and the World Ocean Database (Boyer *et al.*, 2013) (1934-2010,
63 mg chl m^{-3} and FU). We averaged these data into a monthly time series, removing duplicates, spanning
64 the time period 1912-2015.

65 We tested the accuracy and limitations of a temporal cubic spline interpolation for missing data.
66 We validated the interpolation by removing each data point, interpolating, comparing the interpolated
67 value to the measured value, and comparing the phenology metric (described below) calculated from
68 the interpolation to that calculated from the measured value. For an interpolation that only included
69 points not surrounded by missing data, the interpolated values compared well to measured values
70 ($r = 0.37, p \ll 0.0001$ over all points, and $r > 0.99, p \ll 0.0001$ for phenology metrics). When the
71 interpolation was tested for points surrounded by missing data, there was no significant correlation
72 between interpolated and measured values, so we did not interpolate beyond one point.

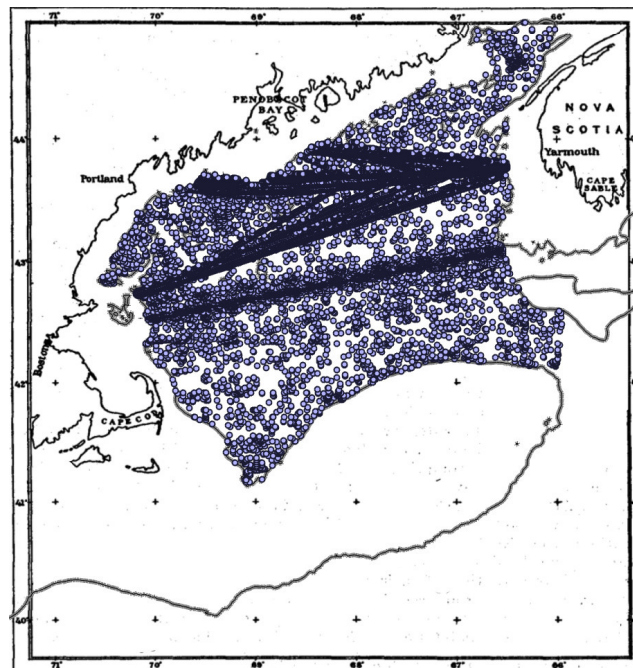


Figure 1. Sample locations for the compiled phytoplankton dataset in the inner Gulf of Maine. Background map adapted from (Bigelow, 1924). Grey line is updated 100 m isobath.

73 Oceanographic datasets

74 We assembled oceanographic time series to compare to chlorophyll phenology. We used previously pub-
75 lished data for water column physics (Fisheries and Oceans Canada, climate database, [http://www.bio.gc.ca/
76 science/data-donnees/base/run-courir-en.php](http://www.bio.gc.ca/science/data-donnees/base/run-courir-en.php), (Gregory, 2004)) and nutrients (Rebuck and Townsend,
77 2014). We used measurements that fell within the spatial domain matching the chlorophyll dataset and
78 averaged to monthly values. Physical data included temperature (T) and salinity (S) averaged over the
79 upper 50 m. We also included a stratification index (Δ), estimated as the difference of mean density (σ_T)
80 between the surface (0 - 50 m) and deep (50 m - bottom) layers (Drinkwater and Gilbert, 2004). Chemical
81 data included surface NO_3+NO_2 , $\text{Si}(\text{OH})_4$, and PO_4 measurements, using only those measurements that
82 passed all quality control criteria (Rebuck and Townsend, 2014). We also used annual climate indices:
83 the Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), Gulf Stream Index
84 (GSI), the Arctic Ocean Oscillation (AOO), and the Arctic Oscillation (AO) (cf NOAA Climate Prediction
85 Center).

86 Upper-trophic dataset

87 We used copepod count data from the CPR. The dominant seasonal copepod in the central Gulf of Maine
88 is *Calanus finmarchicus* (Runge et al., 2014), which has a seasonal peak in surface waters following
89 the spring bloom. Adults emerge from diapause and exploit the spring bloom for egg production. This
90 cohort reaches adulthood in the late spring and summer. We calculated a mean log anomaly for late-stage
91 (copepodite 5-6) *C. finmarchicus* for May-July, as an index of how well this species fares following the
92 spring bloom. We did not compute an analogous autumn time series because *C. finmarchicus* has entered
93 diapause at depth by that time, and the CPR makes surface measurements.

94 Analysis

95 We used a clustering analysis to examine the shape(s) of the bloom cycle across years. This helped to
96 confirm that our phenology metrics were applicable, and also to detect changes in the bloom pattern
97 across time. We clustered years based on the shape of the seasonal cycle of chlorophyll following the
98 methodology of (Foukal and Thomas, 2014): briefly, we used k-means multivariate clustering, with
99 the squared Euclidean distance as the similarity metric and randomly selected starting centroids. Other
100 similarity metrics yielded qualitatively similar results. To account for the randomness in the algorithm,
101 we computed an ensemble of 100 runs, sorted clusters by frequency, and analyzed the modal clusters for
102 each year.

103 We produced time series of phenology metrics for spring and autumn blooms. There are many metrics
104 for quantifying the timing of phytoplankton blooms, with most metrics targeting the timing of either bloom
105 initiation or bloom peak (Ji et al., 2010; Brody et al., 2013). Bloom shape can vary from year to year
106 and by location, so no single metric has emerged as the preferred choice. Because of the coarse temporal
107 resolution (1 month), some phenology metrics were not appropriate for this dataset. We computed five
108 phenology metrics for the spring and autumn blooms:

- 109 1. μ_m - Timing of maximum. Because the dataset is binned monthly, this is a coarse time series; values
110 are midpoints of months.
- 111 2. μ_c - Center of mass. This metric computes the center of mass within the February-May time period
112 (spring index) and of the August-November time period (autumn index), and provides a smooth
113 metric.
- 114 3. μ_g - Midpoint of Gaussian fit. This metric fits a Gaussian curve to half of the year (for spring and
115 autumn indices) and uses the fitted mean (μ) parameter as the bloom peak timing, providing a
116 smooth metric.
- 117 4. τ_d - Timing of maximum increase. This is a coarse (monthly) index of the timing of bloom initiation.
- 118 5. τ_t - Threshold timing. This metric computes the timing at which the total value crosses a threshold
119 that is some percentage of the year's total (i.e. the cumulative sum method). We computed this
120 metric for multiple thresholds for both spring and autumn indices.

121 We used the phenology metrics in time series analysis. We examined the time series for statistically
122 significant trends. We then looked for long-term associations with physical drivers and with upper

123 trophic levels to determine the potential causes and consequences of changing phenology. Analysis was
 124 performed using Pearson correlation and coherence analysis. The coarse spatio-temporal resolution of
 125 the dataset means that there is additional variance around time series and associated relationships, and
 126 correlation coefficients reflect that. We took steps to avoid over-reliance on single p-value determinations
 127 and dichotomous thinking (McShane and Gal, 2017). While we did use $p < 0.05$ as one benchmark,
 128 we disregarded those correlations driven by an outlier. Furthermore, only correlations that held up for
 129 multiple phenology metrics or with very strong relationships were considered robust. For the analysis
 130 with the climate indices and the *C. finmarchicus* time series, the time series were sufficiently long and
 131 gap-free to conduct a coherence analysis. We used the minimum variance distortionless response approach
 132 (Benesty et al., 2005). We also tested the climate indices at lags of 0-3 years, and for the *C. finmarchicus*
 133 time series, because of the ontogenetic lag and east-to-west hydrographic flow, we compared it to the
 134 phenology time series calculated for just the eastern Gulf of Maine (east of $> 68^\circ\text{W}$).

135 RESULTS

136 Clustering

137 Excluding singletons, there were three main bloom types that emerged consistently over the ensemble of
 138 cluster calculations (Fig 2). The most common was the conventional bloom, with a pronounced spring
 139 bloom peaking in April, a smaller autumn bloom peaking in October, and a seasonal minimum in January.
 140 This bloom type dominated in most of the 1980s and 1990s. The second most common was a two-bloom
 141 pattern where the spring and autumn blooms were of closer magnitude to each other, again peaking in
 142 April and October. The third bloom type had a pronounced but delayed spring bloom, peaking in May,
 143 a diminished autumn bloom, and a higher winter minimum. The second and third bloom patterns appeared
 144 sporadically over the later part of the time series. All of these bloom types had a predominantly two-peak
 145 shape, conducive to the phenology metrics used.

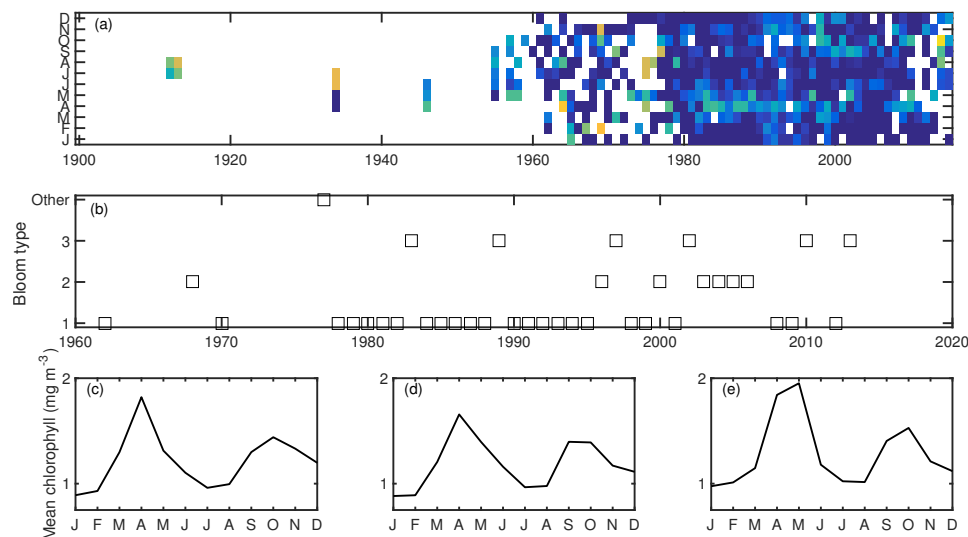


Figure 2. Aggregated chlorophyll dataset (a), showing monthly binned chlorophyll ($\log \text{mg m}^{-3}$), including a 1-unit spline interpolation. Years clustered by bloom type, as computed in the k-means clustering algorithm. (b) Bloom type for each year for which there is sufficient data, showing the most common three bloom types. Seasonal shapes for bloom types 1-3 (c)-(e) respectively, calculated as the climatology over all years within each cluster.

146 Trends

147 For all phenology metrics, spring and autumn, the trend over the time series was positive—i.e. shifting
 148 later in the year. The strongest trend was for μ_g , shifting later with mean rates of 8.9 ($p = 0.001$) and 4.3
 149 ($p = 0.02$) days per decade (spring and autumn, respectively). Other metrics with noteworthy trends were
 150 spring μ_m (4.4 days per decade, $p = 0.1$), spring μ_c (1.5 days per decade, $p = 0.1$), autumn μ_c (1.2 days

151 per decade, $p = 0.07$), and spring τ_t (4.1 days per decade, $p = 0.09$). Taking the average of metrics, trends
 152 were significant for both spring ($p = 0.03$) and autumn ($p = 0.01$), with rates of 3.7 and 3.8 days per
 153 decade, respectively. Over the past sixty-year period, where there is enough data to consistently capture
 154 the phenology metrics, these shifts equate to a roughly 10-50 day shift in timing. There is substantial
 155 inter-annual variance around these trends (Fig 3a). To test the robustness of these trends to sampling
 156 biases, we subdivided the Gulf of Maine into east, west, and coastal sections, divided at 68.5°W and tested
 157 the same phenology metrics for trends. Of the 30 significance tests, 10 were significant at the 0.05 level,
 158 5 were significant at the 0.01 level, and all significant trends were positive for both spring and autumn
 159 metrics. We also tested for trends over smaller sliding windows and found that time series of at least 40
 160 years were necessary for significant trends to emerge. Oceanographic variables had statistically significant
 161 trends as well, including increases in temperature and stratification and decreases in nitrate+nitrite and
 162 phosphate through much of the year (Fig 3b).

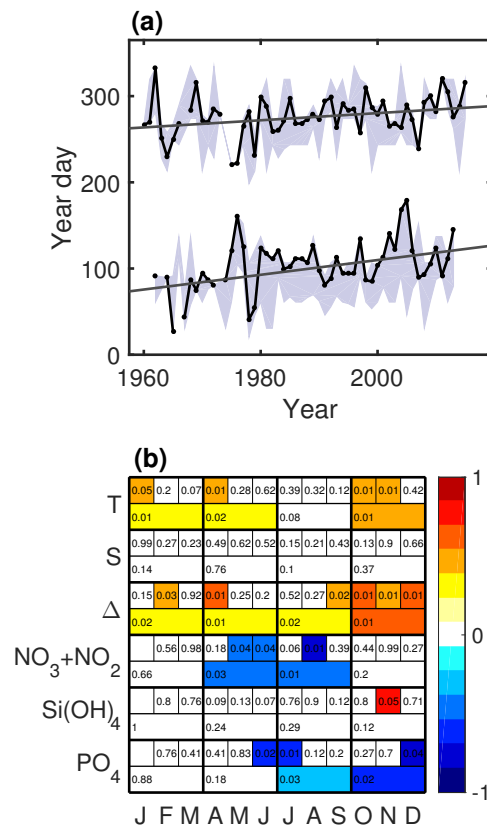


Figure 3. (A) Time series of spring and autumn μ_g and least squares line showing statistically significant increase since 1960. Shaded area shows the range of all phenology metrics. (b) Significant secular trends for the measured physical and chemical variables during different months and seasons. Color scale is the strength of the trend as measured by a correlation coefficient (r). Numbers are p values rounded up to the nearest hundredth. Trends with $p < 0.05$ are colored.

163 Associations

164 Correlations between phenology metrics and climate indices were generally weak, with only a few
 165 correlations at $p < 0.05$. Spring and autumn τ_t correlated positively with the AMO, and autumn τ_t
 166 correlated negatively with the NAO ($r^2 = 0.17, 0.16, 0.17$, respectively). These AMO correlations were
 167 also significant at lags of up to three years, with correlations peaking for spring τ_t at a three year lag
 168 ($r^2 = 0.19$), and for autumn τ_t at a two year lag ($r^2 = 0.24$). Coherence analysis (not shown) also showed
 169 weak associations, with r^2 typically below 0.2. The notable exceptions were spring phenology metrics
 170 and the AO, at ~ 3 year periods, and various metrics and the NAO, at both short and long periods, where
 171 r^2 increases to 0.3-0.4.

172 Correlations between phenology metrics and ocean physics and chemistry showed a moderate signal
 173 with some consistent patterns (Table 1). For spring metrics, the strongest signal was a correlation between
 174 stratification and earlier bloom timing. Additionally, high February nutrients correlated with a later bloom,
 175 and high June nutrients correlated with an earlier bloom. For autumn metrics there was a consistent
 176 pattern across all months of high temperature and salinity correlating with earlier bloom initiation. There
 177 was a very strong correlation between October silicate and earlier bloom timing, but these correlations
 178 consisted of only four data points.

Table 1. Correlation coefficients between the phenology metrics and the monthly temperature (T), salinity (S), and stratification (Δ) values, and the seasonal anomalies of nitrate+nitrite (N), silicate (Si), and phosphate (P). Each column represents the month or season over which the physical variable or nutrient anomaly was averaged. Numbers in parentheses indicate correlation coefficients (r, p). Only correlations with $p < 0.05$ shown.

SPRING METRICS					
J	F	M	A	M	J
Physical variables					
	$\Delta, \tau_t(-0.93, < 0.01)$				$T, \mu_g(-0.41, 0.03)$
Chemical variables					
	$N, \mu_m(0.61, 0.05)$				$N, \mu_g(-0.53, 0.04)$
	$N, \mu_c(0.66, 0.03)$				$Si, \mu_g(-0.55, 0.03)$
AUTUMN METRICS					
J	A	S	O	N	D
Physical variables					
$T, \tau_d(-0.61, 0.02)$	$T, \tau_d(-0.68, < 0.01)$	$T, \tau_d(-0.49, < 0.01)$	$T, \tau_d(-0.40, < 0.01)$	$T, \tau_d(-0.50, < 0.01)$	$S, \tau_t(-0.84, 0.03)$
$T, \tau_t(-0.55, 0.01)$	$S, \tau_d(-0.66, < 0.01)$	$S, \tau_d(-0.71, 0.03)$	$S, \tau_d(-0.64, 0.05)$	$S, \tau_d(-0.70, 0.01)$	$S, \tau_d(-0.64, 0.01)$
$\Delta, \tau_d(-0.48, < 0.01)$					$S, \mu_g(-0.45, 0.02)$
$\Delta, \tau_t(-0.55, 0.03)$					
Chemical variables					
	$N, \mu_g(-0.51, 0.04)$		$Si, \mu_g(-0.98, 0.04)$		
			$Si, \mu_m(-0.96, 0.02)$		
			$Si, \tau_d(-1.00, < 0.01)$		

179 Upper-trophic analysis

180 The *C. finmarchicus* index correlated significantly with μ_g ($r^2 = 0.17, p = 0.01$). The western Gulf of
 181 Maine *C. finmarchicus* population is supplied by coastal waters, so we compared the phenology metrics
 182 to the *C. finmarchicus* in the eastern Gulf of Maine ($> -68^\circ$) and found stronger and more consistent
 183 correlations: μ_m ($r^2 = 0.17, p = 0.01$), μ_c ($r^2 = 0.24, p = 0.003$), μ_g ($r^2 = 0.26, p = 0.001$). Coherence
 184 analysis (Fig 4) showed that these correlations were largely driven by the long-term secular trend. There
 185 was a dip in coherence for periods of approximately 10-40 years. There was also an increase in coherence
 186 for periods of < 10 years to $r^2 \approx 0.2$, depending on the metric.

187 DISCUSSION

188 This extended time series of in situ chlorophyll measurements in the Gulf of Maine gives a climate-scale
 189 perspective on changing phenology that is not available in the comparatively recent satellite records.
 190 Climate-scale changes in the timings of blooms are clear, as are associations between bloom phenology
 191 and changing physical conditions as well as changing *C. finmarchicus* abundance. The most surprising
 192 result is that spring bloom timing, primarily using measures of the bloom center, have gotten later at a rate
 193 of $\sim 1 - 9$ days per decade. This shift is apparent when comparing the recent seasonal cycle to that of a
 194 few decades ago (Fig 5). Typically, as the climate warms, summer lengthens, shifting spring events earlier
 195 and autumn events later. The shift toward later autumn blooms is consistent with this expectation, but the
 196 shift toward later spring blooms is unexpected in this context. Climate indices have been cited to explain
 197 recent temperature and ecosystem changes in the Gulf of Maine (Pershing *et al.*, 2015). However, our
 198 analysis did not reveal any compelling relationship with the NAO, AMO, GSI, AOO, or AO—the climate
 199 oscillations known to be important in the Gulf of Maine—either via direct correlation, lagged correlation,
 200 or coherence analysis.

201 Relationships between bloom phenology and water properties were somewhat more promising. A later
 202 spring bloom was associated with lower stratification, higher nutrients near the beginning of the bloom,
 203 and lower nutrients near the end of the bloom. Causality is difficult to assign regarding nutrients. Because
 204 an earlier spring bloom correlates with decreased February nutrients, and a later spring bloom with

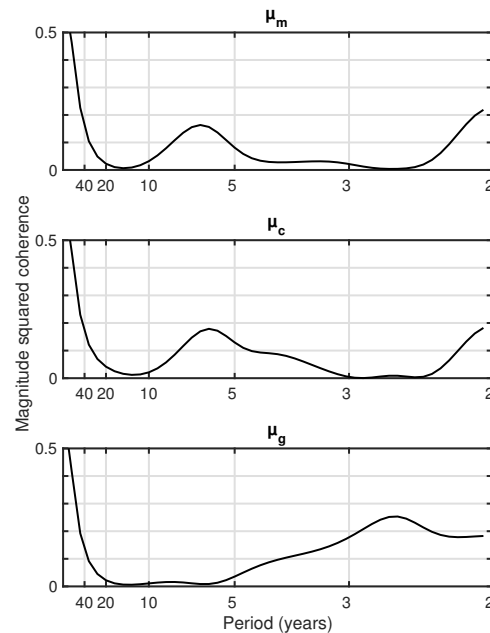


Figure 4. Coherence analysis of three spring phenology metric time series against the time series of late-stage *C. finmarchicus* abundance.

205 decreased June nutrients, it is likely that the bloom is driving the nutrient dynamics through drawdown
 206 (or lack thereof), rather than the reverse. The autumn bloom was more tightly associated with changes
 207 in physics. Low temperature and salinity are both associated with increased transport of Arctic-origin
 208 water via the Labrador Current, which altered autumn bloom patterns during the 1990s (*MERCINA*, 2012).
 209 The pattern seen here suggests similar physical forcing might have a more consistent long-term effect
 210 specifically on the timing of autumn bloom initiation.

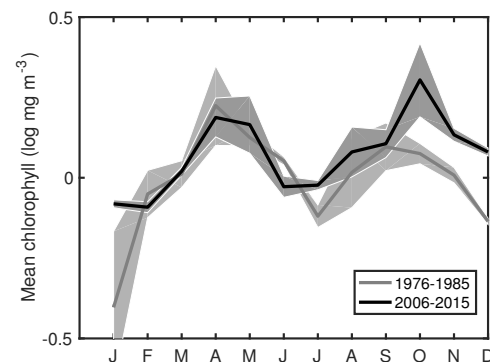


Figure 5. Comparison of mean seasonal cycle of chlorophyll between the most recent decade and an earlier period. Shaded area shows the variance.

211 It is worth noting the secular trends in conditions, as well as correlations, focus on high-frequency
 212 variability and can overlook climate-scale changes. Spring conditions have shifted towards higher
 213 stratification and lower nutrients. The timing shift of the spring bloom is consistent with short-term shifts
 214 in the three Gulf of Maine zones described by (*Ji et al.*, 2007); they hypothesize that higher stratification
 215 causes earlier blooms upstream on the Scotian Shelf, leading to depleted nutrients and later blooms by the
 216 time the water mass reaches the central Gulf of Maine. This hypothesis is consistent with our long-term
 217 observations and may provide a better explanation for the shift toward later spring blooms.

218 The positive association between spring bloom timing and late spring *C. finmarchicus* abundance
 219 is notable. If later timing of the center of the bloom is an indication of an extended bloom, then
 220 *C. finmarchicus* emerging from diapause could have a longer window for reproduction, and the first

221 generation cohort would be more abundant than in a typical year. This offers one possible explanation
222 for why the species has persisted in the western Gulf of Maine despite rapid warming and temperatures
223 that should be detrimental to the population (Runge *et al.*, 2014), but would require a consistent upstream
224 supply of late-stage individuals. This shift also runs counter to the expectation of a phenology “mismatch”
225 as conditions change (Edwards and Richardson, 2004).

226 While this chlorophyll data set gives us new insights into climate-scale phenology changes, there are
227 some caveats to bear in mind. First, chlorophyll is a proxy for phytoplankton. When the oceanography
228 changes, adaptation or replacement of species can occur, and chlorophyll measurements might not capture
229 this. As a means for detecting the major phenological events (i.e. blooms), chlorophyll is probably
230 effective, but this caveat should be kept in mind. Second, the dataset includes measurements that use
231 different methodologies. Measuring chlorophyll “*is endlessly complicated by diverse methods of collection*
232 *and analysis, each with its own virtues but only imperfectly comparable with other methods*” (Riley, 1949).
233 Again, the fact that we use relative changes to compute phenology metrics should hedge this caveat, but it
234 should be considered as the data are used in the future.

235 CONCLUSION

236 The shift of both spring and autumn bloom timing toward later dates is surprising. The high range in rate
237 estimates is indicative of the difficulty of quantifying bloom phenology, so the emphasis should be on the
238 consistent directionality across metrics rather than any specific rate. Finally, while the analysis here is
239 suggestive of possible drivers of the shift in bloom timing, a mechanistic explanation for bloom initiation
240 has been an elusive goal in oceanography. As (Evans and Parslow, 1985) wrote: “*Although it seems*
241 *intuitively reasonable that a sudden effect should have a sudden cause, ecological systems need not behave*
242 *intuitively. ...[S]pring blooms can occur without any sudden changes in driving variables.*” The Gulf of
243 Maine, with its unprecedented rapid changes (Pershing *et al.*, 2015) is often seen as a potential bellwether
244 for other marine systems. The apparent climate-scale shift toward later spring blooms underscores the
245 point that ecosystems do not always change as expected.

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251 Plankton Recorder, the World Ocean Database, the Gulf of Maine Nutrient Database, the Gulf of Maine
252 North Atlantic Time Series, and the Bedford Institute of Oceanography Hydrographic Database. The data
253 used here are listed in the references.

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