Temperature, growth season length and phytoplankton abundance in the Gulf of Maine 46

Running head: Temperature impact on phytoplankton abundance

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3660 words in main text

Abstract

I show that the relation between annual average phytoplankton concentration (as mg Chl-a·m^{-3}) and *in situ* sea surface temperature, SST, is positive (Chl-a ≈ 0.5 × SST, $r = 0.8$, $p < 0.001$) at an average temperature of 11°C (range 10°C – 12°C) in the Gulf of Maine. However, within seasonal observations 2005-2009 were predominant negatively associated. For the first, annual average relationship, the extension of the growth season with increasing temperature may be an important factor. I show that an increase by 1°C start the growth season 8 days earlier and lengthen the season with 13 days (temp > 10°C). Tentative calculations suggest that the increased length matches the increase in annual phytoplankton concentration. For the second, negative relationship, I suggest that warmer water during late summer increases stratification and limits nutrient supply to the upper productive layer.

KEY WORDS Phytoplankton, Chl-a, temperature, growth season, coastal region, Gulf of Maine

Introduction

There are concerns that global warming will cause a decrease in the abundance of phytoplankton in the warmer regions (> 12°C) of the Northeast Atlantic, (Richardson and Schoeman 2004 Figure 2, phytoplankton as cell counts) as well as in the 74% of the ice-free oceans that have surface sea temperatures, SST, > 15°C (Behrenfeld et al. 2006). Thus, there may be less food to support higher trophic level production e.g., fisheries (Ottersen et al. 2010; Stegert et al. 2010; Cheung et al. 2011). A major reason for the smaller phytoplankton production in tropical and subtropical oceans is suggested to be increasing stratification that limits nutrient supply (Boyce et al. 2010). Changing taxonomic composition may also limit phytoplankton production, and increased zooplankton grazing may limit phytoplankton standing biomass, but not necessarily phytoplankton production (Kalff 2000; Li 2002; Sommer and Lewandowska 2011). Grazing by zooplankton is for example responsible for the “clear water” phase following the first phytoplankton bloom in temperate lakes (Sommer et al. 1986). A third factor that may decrease phytoplankton at high temperatures (≥ 20°C) is onset of temperature limitation of phytoplankton growth rate (Cloern and Dufford 2005). However, temperature increases may change community composition towards species with higher temperature optima. Factors that potentially may increase the annual production of phytoplankton are an increased growth rate and lengthening of the growth season for phytoplankton (Stegert et al. 2010). Thus, there appears to be a balance between factors that decrease, and factors that increase phytoplankton production.

Mathematical modelling may give a mechanistic description of the ecosystem, e.g., Doney et al. (2009) or Song et al. (2011). However, there are different views on the effects of important mechanisms in the system, e.g., Banse (2013) and Behrenfeld and Boss (2014) on the importance of zooplankton grazing, and Siegel et al. (2002) and Chiswell (2011) on stratification.

Here I examine the relationship between temperature and phytoplankton concentration in regions within the western Gulf of Maine, a coastal region where the annual average temperature is just below the transition temperature of 12°C identified by Richardson and Schoeman (2004 Figure 2B) for a change from a positive to a negative response to increasing water temperature. Our *first* hypothesis is that there will be a positive relationship between annual average values of phytoplankton concentration and temperature in these regions because the annual average temperatures are in the range 10 ^{o}C to 12 ^{o}C, c.f., Richardson and Schoeman (2004). *Secondly*, I hypothesizes that although annual average relationships may be positive, within year relationships will be negative because phytoplankton deplete the waters for nutrients with increased efficiency as the temperature increases. *Lastly*, I hypothesize that the growth season for phytoplankton will be extended with increasing temperature since the time window for temperatures greater than, say 10^{o}C, will be longer.

I first present our results for habitat identification. Then I calculate annual averages for temperature and chl-a for all habitat types. Thirdly, I examine seasonal data, and lastly I present the results for the relationship between average sea surface temperatures, SST, and phytoplankton growth season.

Materials

The Gulf of Maine experiences a tidal range that exceeds 3 m, leading to complex and vigorous circulation patterns (Brooks 2009). The study sites are located in the western Gulf of Maine and stretches from the Merrimac River in the south to Kennebec River in the north, Figure 1. The area stretches out about 75 km offshore (coordinates for the farthest offshore station is 42^{o}85’,-69^{o}86’). The stations can be divided into two series, one along a transect going from the near shore and out to deep waters of Wilkinson Basin (the WB stations) and one along a coastal transect close to the shore (the CT stations). Station depths along the WB transect ranged from 20 m nearshore to 270 m offshore, and the CT station depths ranged from 20 m to 100 m. A particular station, CT4, was located about 2000 m west of the mouth of the Kennebec river. The river has a flow volume in the range 1000 to 6000 m^{3}.s^{-1} and the station is well within the influence zone of that river as indicated by salinity profiles around the mouth (Salisbury et al. 2008).

Figure 1 in here (map)

During the period January 2005 to February 2009, samples of physical, chemical and biological variables were taken at 29 stations in the western Gulf of Maine. The time series for physical, chemical and biological variables, including phytoplankton species groups are shown in Figure 2 for the ocean habitat, WB7. I show WB7 because successional patterns are easiest to identify visually at this station.

Figure 2 in here (time series for ocean habitat)

The physical variables were sea surface temperature, T, ^{o}C, light, L, as daily Photosynthetic active radiation, PAR, µE $m^{-2}s^{-1}$, wind, W; as U3 $m^{3}s^{-3}$. The chemical variables were salinity (as Practical Salinity Units), nitrogen as the sum of nitrite NO_2^- and nitrate NO_3^-, designated NO_{23} (mg m^{-3}), and orthophosphorus PO_4 (mg m^{-3}). Ammonium NH_4 was not available. Phytoplankton concentration were indexed as chl-a (mg m^{-3}), Chl-a, and as the fractions of diatoms, flagellates and cyanobacteria derived from HPLC pigment concentrations and CHEMTAX (Mackey et al. 1996). The fractions were multiplied by chl-a to get an expression of the biomass of each species group. All samples were surface samples, taken down to 1 or 2 meters, depending upon data available. There were 21 species of zooplankton, the most abundant being *Calanus finmarchicus* and *Oithona similis* (ind. m^{-3}, unfortunately, neither mass nor length measurements were taken for the zooplankton). Zooplankton samples were taken from 0 to 20 m depth to include effects of vertical migratory behavior. As a proxy for zooplankton abundance I used the sum of concentrations of all individuals. The sampling frequency at each station was normally monthly and occationally bimonthly during the summer half year from about April to September and less frequently during the winter half year. During some winter months no samples were taken. A total of 282 samples were taken that included all variables. All data available from GoMOOS (2010), now NERACOOS (2013). Details of sampling and sample preparation is given in Moore (2008). In addition, hourly temperature measurements were taken at 1 m depth from

Western Maine shelf 2002 - 2010, Buoy 1, BO1, (GoMOOS 2010). This station was the station most representative for our study region. Thus, I use i) the complete data set 2005-2009 to group the habitats, ii) the 2005-2009 SST and Chl-a series to identify the series intra- and interannual relations, and iii) the 2002-2010 SST series to define growth periods.

Method

Data preparation for principal component analysis. To identify habitat types in the Gulf of Maine all time series were normalized to unit standard deviation to get each variable on the same scale. This eliminates any effects of measuring units, and strengthens emphasis on time series variations.

Grouping observations. To identify habitats that would include more stations and give higher sampling frequency for the habitats I used PCA (Camo A/S ©), followed by a hierarchical clustering analysis (SigmaStat 13 ©) of the two first principal components for the full dataset of 29 observation stations. By applying the PCA I identified clusters of stations that are similar in the values of their variables (morphological, pysico-chemical and biological) and I avoid effects of coo-linearity. Cut off for the clusters identified were about 2/3 of the distance separation scale. Grouping of habitats in two Australian estuaries were done with a similar method by Valesini et al.(2010).

Growth season. Growth season periods were here identified as periods where water temperature is in the range 10°C and 20°C, although algal growth may occur both below and above these temperatures. Cloern and Dufford (2005, Fig 6) reports 10th and 90th percentile temperatures for species occurrences in their study of San Francisco Bay as 12°C and 20°C respectively. Karentz and Smayda (1984) report phytoplankton optimum growth values for dominant species in Narragansett Bay between 10°C and 25°C. In our data 12°C is exceeded in 47 % of the observations and 20°C is exceeded in 2% of the observations.

Identification of the growth season period using SST. The data were used in their original version, but also as smoothed as described below to aid interpretations and (for temperature) to identify growth season periods. However, as in Head and Pepin (2010 p. 1643) the temporal resolution for chl-a was too crude to allow calculation of growth period lengths. Brody et al. (2013, pp. 2,5) find differences in the timing of bloom initiation obtained by three different methods using 8 day data. Therefore, to find the lengths of the periods I used hourly temperature at 1 m depth from Western Maine shelf 2002- 2010, Buoy 1, BO1, (GoMOOS 2010). Average annual temperatures were calculated over all temperature measurements (range 8000 to 18.000 samples per year for nine years). To identify dates when the temperature rose above 10°C and sunk below 10°C, I used the 2D smoothing algorithm from SigmaPlot12.5 © with a running average of 20% of the series length and 2nd order polynomial smoothing. This gave a relatively smooth bell shaped curve with clear crossings of the 10°C temperature line during spring and fall. The smoothed curve never exceeded the 20°C line, Figure 3.

Figure 3 in here (temperature profile)

Results

The results are presented in four sections. The full data set is used to identify habitats in the Gulf of Maine. During the rest of the analysis I focus on the relationship between chl-a and temperature as SST.

Habitat identification

The two first components of the PCA explained 34% and 20 % of the variance respectively. Nutrients, temperature, depth and Chl-concentration were the four dominating structuring variables. I identified 5 habitat types A to E that had a sufficient number of samples (> 20). For example, habitat A seems to be characterized by shallow waters so that WB1, WB2 and WB5 belongs to it (25 - 62 m depths), whereas station WB3 and WB4 are on larger depths (106-144 m depth), but all variables included in the PCA have some impact. Table 1 shows characteristic values for the variables. The map in Figure 1 also shows habitat identifications. Stations not assigned to habitat type had too few observations to be included.

Table 1 in here

Annual averages

Chl-a and temperature, T, is positively associated when I calculate the annual averages (3 – 4 years) at the habitat types A, B, C, E (The exceptional river mouth habitat, D, excluded);

Eq. (1) $$Chl - a = -3.735 + 0.475 \times T,\ r = 0.745, p < 0.001, n = 15$$

The annual average data is shown as the filled circles in Figure 4a. The β – coefficient for the relations between annual average chl-a and temperature is plotted as the encircled dot in Figure 3b and compared to the relation between "phytoplankton concentration (ind.m^{-2}) – SST correlation" and mean SST (^{o}C) as expressed by the regression line, RS, in Richardson and Schoeman (2004 Fig 2B). The other points in this graph show the β – coefficients for seasonal data at each habitat type to be discussed below.

Figure 4 in here (2 ×2) panel

Seasonal data relationships

I also calculated the least squares regresson, LSR, for the seasonal chl-a and temperature data at each habitat type. The result is shown as open legends in Figure 3a. There is near zero, or an inverse relationship between chl-a and temperature for all habitat types except for habitat D close to the mouth of Kennebec River. The β – coefficients are depicted in Figure 3b and shows that the seasonal data, with one exception, show largely negative, or no, relationships (A = - 0.142; B = - 0.164, C = 0.066; D = 0.534 and E= - 0.323). The regressions for A, B, C and E were non - significant, p > 0.05.

Growth season as a function of temperature, SST

Since one reason for the increase in chl-a with annual average temperature may be associated with an extended growth season at higher temperatures, I calculated annual average temperature versus i) maximum temperature, ii) beginning of growth season, iii) end of growth season, and iv) growth season length, i.e., days with temp > 10°C, Fig 4c. Average temperature and maximum temperature (smoothed data) were positively correlated, R = 0.786, p = 0.012; maximum temperature for smoothed data were 19.2 °C, and observed maximum was 22°C. Statistics for growth season length is:

Eq. (2) $$Days > 10\ ^{o}C = 34.72 + 12.86 \times T_{annual}, \mathrm{R} = 0.837, \mathrm{p} = 0.005, \mathrm{n} = 9$$

Statistics for the beginning of growth season are R = 0.720, p = 0.03. The end of the growth season increased with average annual temperature, but not significantly (R = 0.59, p = 0.1).

Discussion

For the Gulf of Maine I found a β – coefficient for the equation that relate mean annual chl-a concentration to mean annual temperature that was positive for waters with annual average temperatures in the range 10°C to 12°C. Compared to the RS regression for the northeast Atlantic, a β – coefficient of 0.475 would correspond to waters with an average temperature of 6°C (Figure 4 b). However, the ecologies may differ between the northeast Atlantic and the northwest Atlantic as well as between pelagic waters and enclosures, like the Gulf of Maine. The seasonal variables gave rise to non-significant negative, or near zero, β – coefficients, except at habitat D close to the mouth of Kennebec river.

To examine if the contrast between seasonally negative and annual positive slopes could be due to i) differences in sampling frequency, ii) different dates for sampling of the first and the last samples, or iii) sampling at different dates, habitat data were split into sampling stations. I made new regressions based on stations with equal number of samples and approximately equal dates for the first and last samples. The slope for the annual data were positive significantly when the combination of stations and number of years sampled at each stations gave n > 7. Slopes for seasonal data were either negative or near zero, except for habitat D.

Graphs that combine intra- annual and inter-annual time scale for ecological systems may show the pattern of a tilted mast; the inter-annual regressions show negative associations sloping down to the right, whereas the inter-annual regressions slope upwards to the right, Fig 4a. The intra- and inter - annual β- coefficients relate to different mechanisms.

At the *seasonal* scale phytoplankton density is lowest during warm periods, that is during late summer. With temperatures that increase from ≈ 12°C and up, stratification increases, phytoplankton will respond with relatively large increases in growth rates, thus they may deplete the waters faster for nutrients. An additional effect is enhanced grazing by zooplankton in warmer waters, (Sommer and Lewandowska 2011).

Several explanations are offered to explain both positive and negative relationships between chl-a and temperature at annual scales (Richardson and Schoeman 2004; Boyce et al. 2010). In estuarine-like environments, the combination of freshwater nutrient sources entering above the stratification depth (Seip 1991) and water turbulence that allow cold, saline and nutrient rich water to be mixed into stratified waters may increase phytoplankton growth rate. Brooks (2009) show that the spongiform coastal morphology of the central Maine basin (east of Wilkinson basin) allows enhanced exchange between offshore waters, estuaries and internecine bays. Enhanced stratification caused by increase in SST may suppress the nutrient exchange that occurs through vertical mixing. *Th*e graph of *salinity* versus nutrient concentrations may act as a diagnostic tool for nutrient source to the water, Figure 4d. With a high positive correlation between nutrients and salinity, the probable source for the nutrients is upwelling because nutrient rich saline waters enter the upper layers. With a negative slope the main source may be nutrient washed out from land. For example, Kitheka et al. (1996 , Fig 7) found R = – 0.98 for a study of nutrient transport in a tropical bay. In our study, site D, at the river mouth, had R = - 0.03, n.s., whereas the other sites had R - values in the range 0.59 to 0.67, $p < 0.001$, highest at the ocean water station, C. Salinity may play a large role in stratifying waters, (Collins et al. 2009 , fig 7a; Song et al. 2010; Zingone et al. 2010), but simply using salinity as a diagnostic tool, our results suggest that both upwelling and wash - out contribute to enhanced nutrient supplies to the nearshore regions in the Gulf of Maine.

A factor that would increase the annual average phytoplankton concentration with increasing temperature is an extended growth season. I were not able to identify increase in growth season from the normal monthly to bi- monthly sampling, but hourly sampling of temperatures at one representative station showed that the first and the last day with temperatures > 10^{o}C move respectively backward (significantly) and forward (n.s.) in time as the annual average temperature increases. One may visualize the temperature curve as a fixed bell shaped form that is lifted or lowered across a time line. The water temperature versus time graph shown in Figure 3 suggests that if the growth season were defined by somewhat different temperature limits, the results would be similar. An overall lengthening of the growth season in the Northern hemisphere with about 7 days from 1960 to 1995 was found by Bacastow and Dewey (1996)

If temperature is an important factor for phytoplankton growth, this would also help explain the negative correlation between spring and fall phytoplankton peaks ($R = -0.446$, $p < 0.001$) found by Song et al. (2010) for the Nova Scotia shelf – Gulf of Maine region. Sommer and Lewandowska (2011) found for mesocosms filled with water from Kiel Fjord that spring phytoplankton peak occurred 1 day earlier per 1^{o}C warming (temperature range 2.4^{o}C to 8.4^{o}C). Marshall and Peters (1989) give an equation showing that bloom date occur earlier with increasing mean annual air temperature for lakes, and Kahru et al. (2011) indicate that an earlier start of the phytoplankton bloom maximum is related to earlier disappearance of ice in the Arctic. Stegert et al. (2010 p. 273) assumed for their model study of the North Atlantic (Including the Gulf of Maine) that 1^{o}C increase in temperature compared to 13^{o}C would increase chlorophyll concentration with 10%. Our results, Eq. (1), suggest that the corresponding increase in the western Gulf of Maine would be 3.7 % per ^{o}C. An increase in temperature of 1^{o}C would lengthen the growth season with 8 %. (Equation in Figure 4c). Assuming triangular shapes for chl-a versus growth season length, the theoretical increase in chl-a would be 4% per ^{o}C, close to the observed 3.7 % per ^{o}C.

In the waters of the Gulf of Maine the average SST is below 13^{o}C at all stations, and I found an overall negative relationship between seasonal chl-a and temperature for these waters. At the site at the mouth of the Kennebec River, site D, the water temperature was the highest among all stations, 12^{o}C, but here temperature and chl-a showed a high positive correlation ($R = 0.534$, $p < 0.01$), Figure 4b. This supports the expectation that sites that are in the impact zone of strong river discharge may be exceptions to other near shore areas.

It appears that temperature changes would change stratification, growth season length, nutrient supply and probably also species composition and the timing of peak species abundance (Sommer and Lewandowska 2011) in the Gulf of Maine. However, I do not know if these changes will destroy the sequential match between zooplankton and its food sources (Ottersen et al. 2010), as it may be doing in the Northwest Atlantic (Head et al. 2011) or in the Arctic (Kahru et al. 2011).

A mechanistic model would require several calculations, almost certainly in the format of an ecosystem simulation model. However, mechanistic models require results from statistical models, both to be calibrated and to be tested. The study present a statistical model and should be useful for testing the results of complex mechanistic models. I am presently examining leading and lagging relationships between ecosystem variables in the Gulf of Maine to examine if causal relations (that would require the cause to lead the effect) can be identified in the system.

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Bacastow, R. B. and R. K. Dewey (1996). "Effectiveness of CO2 sequestration in the post-industrual ocean." Energy Conversion and Management **37**(6-8): 1079-1086.

Banse, K. (2013). "Reflections About Chance in My Career, and on the Top-Down Regulated World." Annual Review of Marine Science, Vol 5 **5**: 1-19.

Behrenfeld, M., R. T. O´Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier and E. S. Boss (2006). "Climate-driven trends in contemporary ocean productivity." Nature **444**: 752-755.

Behrenfeld, M. J. and E. S. Boss (2014). "Resurrecting the ecological underpinnings of ocean plankton blooms." Annu. Rev. Mar. Sci. **6**: 167-194.

Boyce, D. G., M. R. Lewis and B. Worm (2010). "Global phytoplankton decline over the past century." Nature **466**(29): 591-596.

Brody, S. R., M. S. Lozier and J. P. Dunne (2013). "A comparison of methods to determine phytoplankton bloom initiation." Journal of Geophysical Research-Oceans **118**(5): 2345-2357.

Brooks, D. A. (2009). "Circulation and dispersion in a cancellate coast: The rivers, bays and estuaries of central Maine." Estuarine Coastal and Shelf Science **83**(3): 313-325.

Cheung, W. W. L., J. Dunne, J. L. Sarmiento and D. Pauly (2011). "Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic." Ices Journal of Marine Science **68**(6): 1008-1018.

Chiswell, S. M. (2011). "Annual cycles and spring blooms in phytoplankton: don't abandon Sverdrup completely." Marine Ecology Progress Series **443**: 39-50.

Cloern, J. E. and R. Dufford (2005). "Phytoplankton community ecology: principles applied in San Francisco Bay." Marine Ecology-Progress Series **285**: 11-28.

Collins, A. K., S. E. Allen and R. Pawlowicz (2009). "The role of wind in determining the timing of the spring bloom in the Strait of Georgia." Canadian Journal of Fisheries and Aquatic Sciences **66**(9): 1597-1616.

Doney, S. C., I. Lima, J. K. Moore, K. Lindsay, M. J. Behrenfeld, T. K. Westberry, N. Mahowald, D. M. Glover and T. Takahashi (2009). "Skill metrics for confronting global upper ocean ecosystem-biogeochemistry models against field and remote sensing data." Journal of Marine Systems **76**(1–2): 95-112.

GoMOOS (2010). Gulf of Maine Ocean Observing System. Portland, Maine ME 04101, GoMOOS.

Head, E. J. H., W. Melle, P. Pepin, E. Bagøien and C. Broms (2011). "A comparative study of the ecology of *Calanus finmarchicus* in shelf, slope and deep ocean areas of the Labrador and Norwegian seas." Prog. Oceanogr. **accepted**.

Head, E. J. H. and P. Pepin (2010). "Spatial and inter-decadal variability in plankton abundance and composition in the Northwest Atlantic (1958-2006)." Journal of Plankton research **32**(12): 1633-1648.

Kahru, M., V. Brotas, M. Manzano-Sarabia and B. G. Mitchell (2011). "Are phytoplankton blooms occurring earlier in the Arctic?" Global Change Biology **17**(4): 1733-1739.

Kalff, J. (2000). Ecology. Upper Saddle River, Prentice Hall.

Karentz, D. and T. J. Smayda (1984). "Temperature and seasonal occurence patterns of 30 dominant phytoplankton species in Narragansett Bay over a 22-year period (1959-1980)." Marine Ecology-Progress Series **18**: 277-293.

Kitheka, J. U., B. O. Ohowa, B. M. Mwashote, W. S. Shimbira, J. M. Mwaluma and J. M. Kazungu (1996). "Water circulation dynamics, water column nutrients and plankton productivity in a well-flushed tropical bay in Kenya." Journal of Sea Research **35**(4): 257-268.

Li, W. K. W. (2002). "Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean." Nature **419**(6903): 154-157.

Mackey, M. D., D. J. Mackey, H. W. Higgins and S. W. Wright (1996). "CHEMTAX - a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton." Marine Ecology-Progress Series **144**: 265-283.

Marshall, C. T. and R. H. Peters (1989). "General patterns in the seasonal development of chlorophyll a for temperate lakes." Limnology and Oceanography **34**: 856-867.

Moore, T., S. (2008). Dynamics of phytoplankton community compsition in the western Gulf of Maine Doctor of philosophy, University of New Hampshire.

NERACOOS. (2013). "Northeastern regional assocciation of coastal and ocean observing systems." Retrieved December 12, 2013, 2013.

Ottersen, G., S. Kim, G. Huse, J. J. Polovina and N. C. Stenseth (2010). "Major pathways by which climate may force marine fish populations." Journal of Marine Systems **79**(3-4): 343-360.

Richardson, A. J. and D. S. Schoeman (2004). "Climate impact on plankton ecosystems in the Northeast Atlantic." Science **305**(5690): 1609-1612.

Salisbury, J., M. Green, C. Hunt and J. Campbell (2008). "Coastal acidification by rivers: a threat to shellfish." EOS transaction, AM Geop. Union **89**(50): 513.

Seip, K. L. (1991). "The ecosystem of a mesotrophic lake-II. Interactions among nutrient load, river flow, and epilimnion depth." Aquatic Sciences **53**(263-272).

Siegel, D. A., S. C. Doney and J. A. Yoder (2002). "The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis." Science **296**(5568): 730-733.

Sommer, U., Z. M. Gliwicz, W. Lampert and A. Duncan (1986). "The PEG-model of seasonal succession of planktonic events in fresh waters." Arch. Hydrobiol. **106**: 433-471.

Sommer, U. and A. Lewandowska (2011). "Climate change and the phytoplankton spring bloom: warming and overwintering zooplankton have similar effects on phytoplankton." Global Change Biology **17**(1): 154-162.

Song, H. J., R. B. Ji, C. Stock, K. Kearney and Z. L. Wang (2011). "Interannual variability in phytoplankton blooms and plankton productivity over the Nova Scotian Shelf and in the Gulf of Maine." Marine Ecology Progress Series **426**: 105-U133.

Song, H. J., R. B. Ji, C. Stock and Z. L. Wang (2010). "Phenology of phytoplankton blooms in the Nova Scotian Shelf-Gulf of Maine region: remote sensing and modeling analysis." Journal of Plankton research **32**(11): 1485-1499.

Stegert, C., R. B. Ji and C. S. Davis (2010). "Influence of projected ocean warming on population growth potential in two North Atlantic copepod species." Progress in Oceanography **87**(1-4): 264-276.

Valesini, F. J., M. Hourston, M. D. Wildsmith, N. J. Coen and I. C. Potter (2010). "New quantitative approaches for classifying and predicting local-scale habitats in estuaries." Estuarine Coastal and Shelf Science **86**(4): 645-664.

Zingone, A., L. Dubroca, D. Iudicone, F. Marigotta, F. Corata, d. A. M. Ribera, V. Saggiomo and D. Sarno (2010). "Coastal phytoplankton do not rest in winter." Estuaries and coasts **33**: 342-361.

Figure 1

Gulf of Maine with coastal transect and Wilkinson basin transect. Darker shades show increasing depths. Letters in bold identify sites that are similar in terms of 13 equally weighted morphological, chemical and biological characteristics. Station CT2 had too few samples to be included in the analysis, see text.

Figure 2

Observations of physio-chemical and biological data from the ocean habitat C (WB7) during the period October 2005 to February 2007 in the Gulf of Maine. Shaded area is 2006. All data were normalized to unit standard deviation, but shifted 2 units relative to each other for clarity. Curves show smoothed data in a) and b). a) Physical variables: WT = surface water temperature, PAR = Light, U2 = wind; b) Chemical variables: PSU = salinity; SiO = silica, PO4 = orthophosphate, NO23 = sum of nitrite and nitrate; c) Biological variables: Chl-a = phytoplankton as Chl-a, Log Zoopl = The logarithm of zooplankton counts d) Phytoplankton species groups: Dia = diatoms, Fla = Flagellates, Cya = Blue-greens.

Figure 3

Example of observed and smoothed hourly average water temperature measurements during the year 2002, Bouy 1 at 1 m: Intersections with $T = 10^{o}C$. There is no intersection with the smoothed curve at $20\ ^{o}C$.

Figure 4

a) Phytoplankton (as Chl-a) versus temperature at sites A, B, C and E (open symbols, one point at (3.4,12.2) for E not shown; none of the slopes were significant and regression lines are therefore not identified. Filled symbols, annual average phytoplankton (Chl-a) versus annual average temperature at sites A, B, C and E. Slope for annual average is significant, $p < 0.001$.

b) The inverse relation between “phytoplankton concentration- SST correlations” and mean SST (^{o}C). Line “RS” is regression line from Richardson and Schoeman (2004) showing the inverse relation they find between correlation and mean SST (^{o}C) in each of their regions. Read from their graph it is: β – coefficient = 0.92 – 0.072 × Mean SST(^{o}C). Letters represent sites in the Gulf of Maine. Encircled dot shows the results for annual average values.

c) Days with temperature > 10^{o}C as a function of annual average temperature (filled symbols, $R = 0.84$, $p = 0.005$) and day when smoothed temperature > 10^{o}C (open symbols, $R = 0.72$, $p = 0.03$) at Bouy 1, Gulf of Maine. Small numbers are last digit in year 200x.

d) Nutrient concentration, NO_{23} as a function of salinity at site A which is typical for all sites except site D. The positive association starts at salinity values > 25 PSU.

Table 1

Table 1 Characteristics of habitats

Numbers and their standard deviations in parentheses. The biomass of phytoplankton was calculated as chl-a times the fraction of each functional group in the samples. A to E are cluster of observations identified as habitats in the study.

Sites	A	B	C	D	E
Characteristics	Shallow water	Deep water	Ocean water	River mouth	Coastal water
Depth, m	48 (15)	123 (20)	259 (2)	28 (3)	67 (4)
Stations	WB1-2,WB5, CT3	WB3-4	WB7	CT4	CT1
#samples	115	62	24	23	29
Distance from land. km	16 (15)	22 (6)	63	4.5	13
Temp. °C	11.29 (5.67)	11.16 (5.74)	10.61 (5.26)	12.06 (5.43)	11.23 (5.96)
Light, L, μE m^{-2}s^{-1}	34.19 (13.68)	33.15 (12.93)	35.42 (12.42)	35.74 (13.19)	34.29 (14.41)
Wind, W, U^3. m^{3}s^{-3}	338 (296)	360 (297)	366 (311)	259 (259)	345 (305)
Salinity, S,	31.14 (1.19)	31.46 (0.88)	32.12 (0.70)	29.53 (1.10)	31.25 (0.96)
NO$_{23}$, (mgm^{-3})	2.79 (3.60)	3.29 (4.05)	3.34 (4.14)	3.61 (3.53)	3.01 (3.34)
PO$_4$, (mgm^{-3})	0.37 (0.29)	0.39 (0.32)	0.33 (0.27)	0.41 (0.29)	0.36 (0.27)
Chl-a, C, mgm^{-3}	1.44 (1.14	1.16 (0.82)	0.87 (0.63)	2.59 (1.82)	1.64 (2.31)
Zooplankton, Z (ind.m^{-3})	832.42 (1611)	972.06 (2248)	605.22 (1740)	797.29 (1718)	855.38 (1447)

Figures

Figure 1 Map

▲

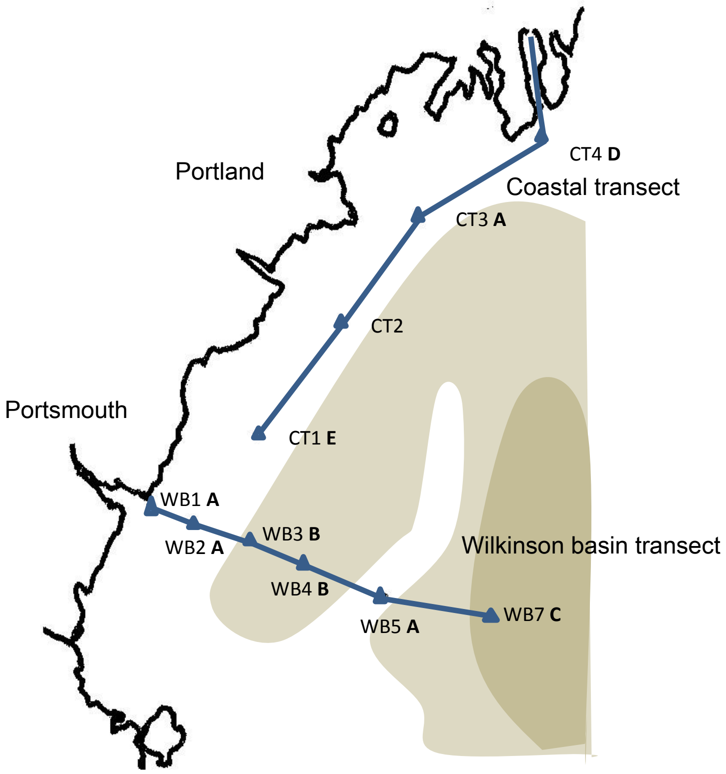


Figure 2

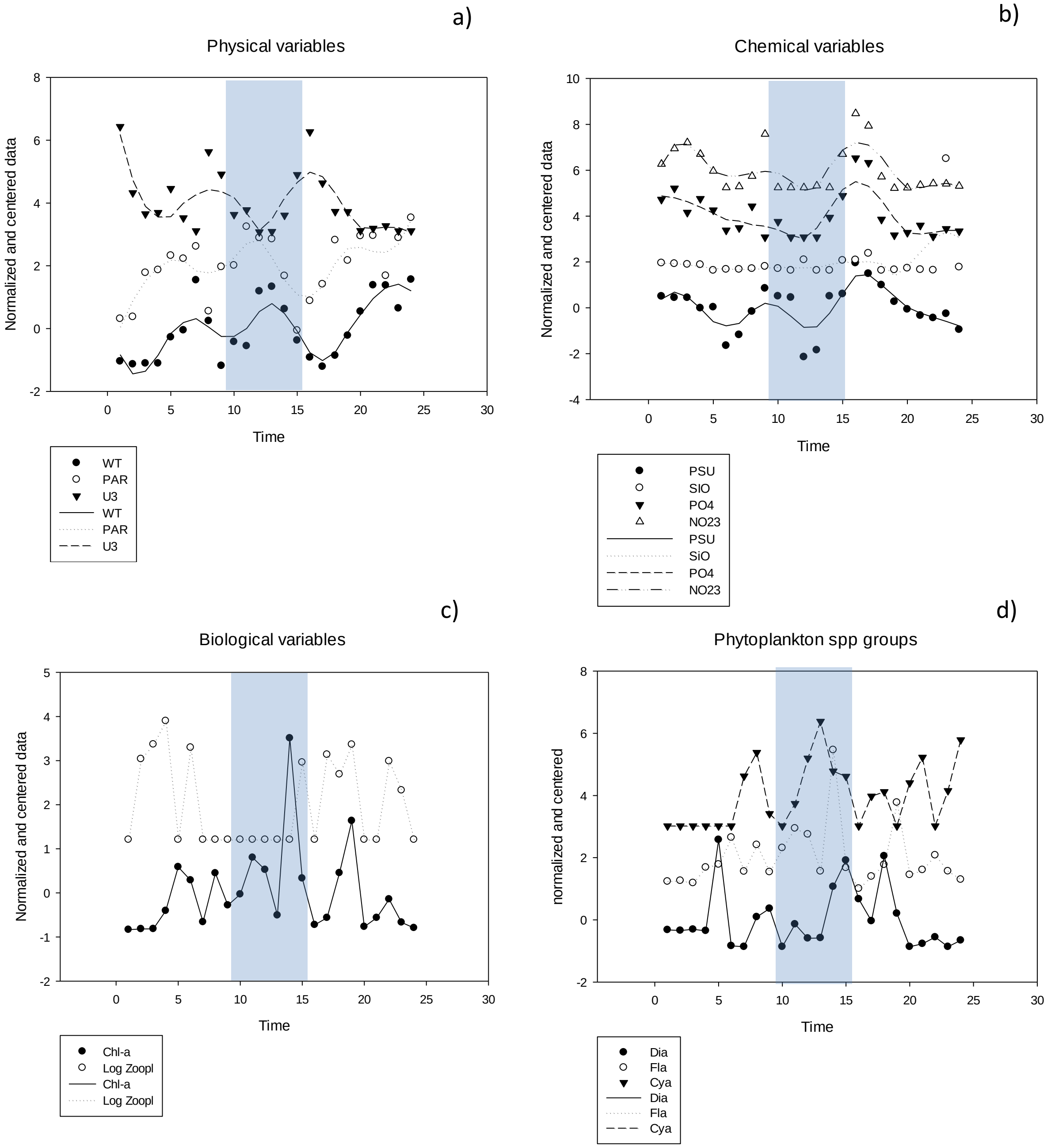

a)
Physical variables
Normalized and centered data
Time
WT
PAR
U3
WT
PAR
U3
b)
Chemical variables
Normalized and centered data
Time
PSU
SIO
PO4
NO23
PSU
SiO
PO4
NO23
c)
Biological variables
Normalized and centered data
Time
Chl-a
Log Zoopl
Chl-a
Log Zoopl
d)
Phytoplankton spp groups
normalized and centered
Time
Dia
Fla
Cya
Dia
Fla
Cya

Figure 3

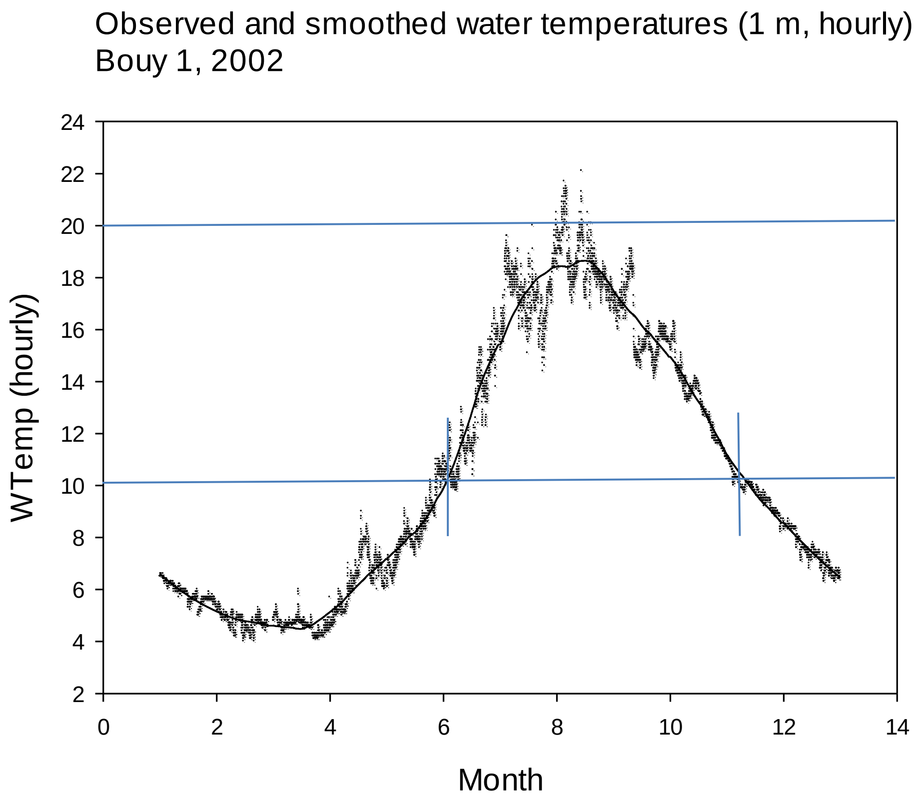
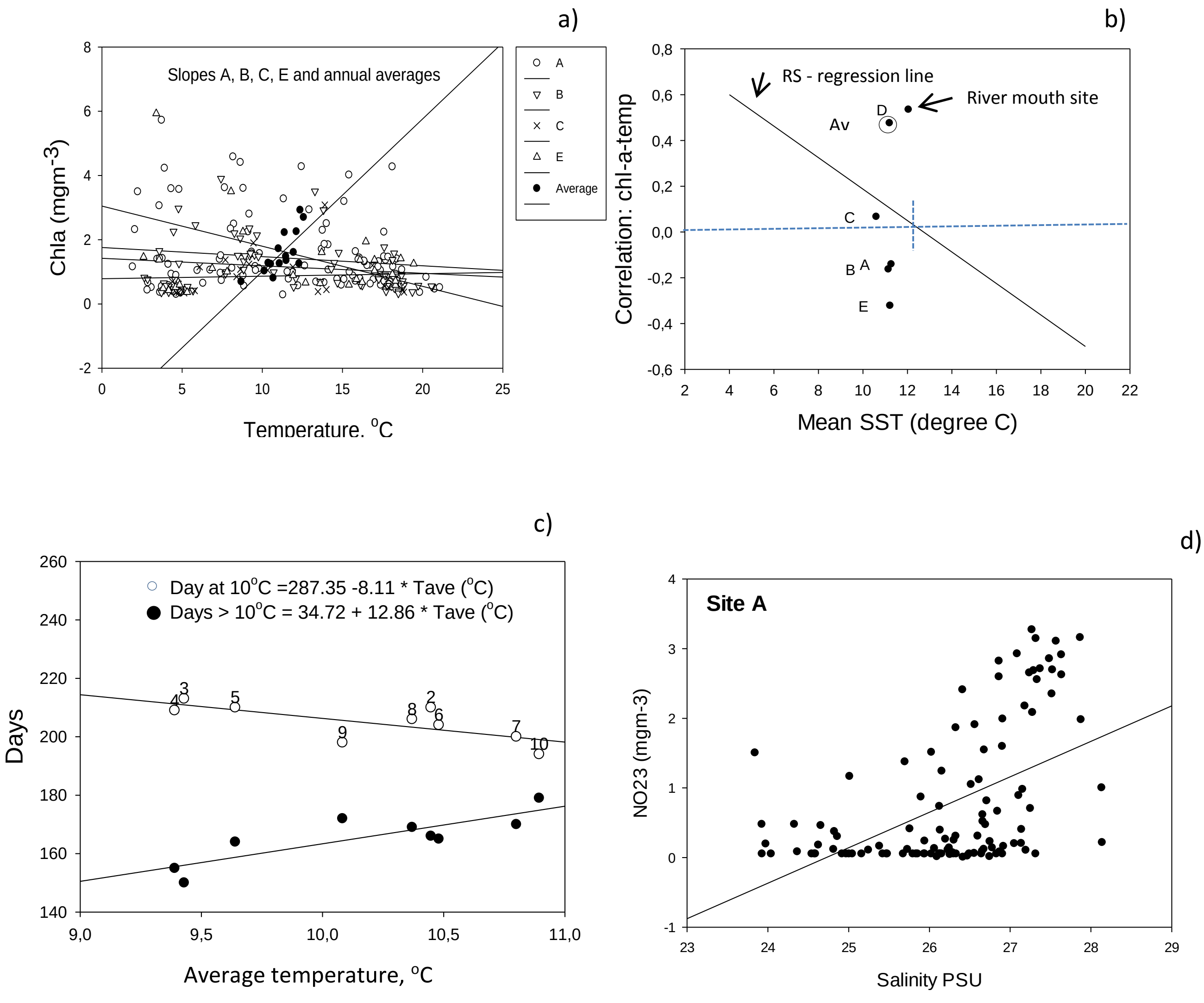

Observed and smoothed water temperatures (1 m, hourly)
Bouy 1, 2002
WTemp (hourly)
24
22
20
18
16
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
Month

Figure 4


a)
Slopes A, B, C, E and annual averages
Chla (mgm-3)
Temperature, °C
A
B
C
E
Average
b)
RS - regression line
River mouth site
D
Av
C
B
A
E
Correlation: chl-a-temp
Mean SST (degree C)
c)
Day at 10°C =287.35 -8.11 * Tave (°C)
Days > 10°C = 34.72 + 12.86 * Tave (°C)
Days
Average temperature, °C
d)
Site A
NO23 (mgm-3)
Salinity PSU

Additional material – not to be included

Figure A1. Sampling frequencies