Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland Roads

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Abstract

Analyzing one of the most extensive long-term data series in the North Sea, the Helgoland Roads time series, we investigated the changes in the factors that potentially drive phytoplankton bloom dynamics in the German Bight. We compared the changes in these factors with the changes in the spring bloom phenology. We combined zooplankton, nutrient, weather, and phytoplankton data to analyze whether there has been a shift in trophic interactions in the North Sea affecting the spring bloom timing. The potential influence of temperature, with a mean increase of 1.5°C, was investigated. We showed that the German Bight around Helgoland is a highly dynamic system and has undergone considerable change in the last 30 yr. Nutrient levels, temperature, underwater light climate and wind speed have all changed. However, the spring bloom dynamics have hardly changed at all. We showed that the spring bloom tends to come later in warmer years but that this is not directly correlated with the overall warming trend. The known regime shift of the late 1980s is clearly visible in our data in terms of average phytoplankton winter densities and average cell size, but even so the start of the spring bloom has not changed.

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The world's oceans have been warming at alarming rates (IPCC 2001*a*,*b*, 2007), with a global average temperature increase of about 0.6°C in the past 100 yr (IPCC 2001*b*). The temperature increase in the German Bight of the North Sea has been much more dramatic. Wiltshire and Manly (2004) have shown that the average temperature in the North Sea at Helgoland has risen by 1.13°C over the last 40 yr, which is in line with the warming trends measured in the English Channel (Hawkins et al. 2003), the North Sea (Edwards et al. 2002), and the North Atlantic (Edwards et al. 2001), and falls into the general pattern of higher latitudes showing a more pronounced warming (IPCC 2001*b*).

Despite detailed information on temperature changes, we have relatively little information on how these warming

trends of the last years have affected the food webs of aquatic systems (Cushing 1995; Walther et al. 2002). In contrast, the fingerprints of global warming on terrestrial animals and plants are fairly well documented (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). A poleward extension of species ranges and earlier/later onset of spring events and autumn events, respectively, have been shown for terrestrial systems. Examples include the flowering of trees, leaf loss, bird migration, and breeding (Hüppop and Hüppop 2003; Ahas and Aasa 2006). In aquatic environments, there is some evidence for the persistence of warm-water species in their summer residence and changes in the latitudinal distribution of zooplankton and phytoplankton (Straile 2002; Walther et al. 2002; Edwards et al. 2006). Knowledge of how climate warming affects phytoplankton phenology and interactions in marine environments is rarer, and only a few cases have been documented for the North Sea (Edwards and Richardson 2004; Wiltshire and Manly 2004). This is unfortunate, because the phytoplankton, in its important position at the base of aquatic food chains, determines the primary energy flow through the system. We do know from the literature that the trigger mechanisms governing phytoplankton events and seasonality probably have changed substantially in response to climate change in the shallow North Sea (Radach 1998).

Analogous to earlier blooming in terrestrial plants, a warming of aquatic systems could be expected to cause an earlier timing of the spring phytoplankton bloom. This has indeed been shown for lakes: a warming trend has moved the spring diatom bloom forward by up to one month (Weyhenmeyer et al. 1999; Weyhenmeyer 2001) because of earlier ice-off and/or stratification increasing the availability of light (Blenckner et al. 2007).

Surprisingly, Wiltshire and Manly (2004) have shown that earlier spring blooms caused by warming are not necessarily the norm for temperate coastal marine systems, because they observed a delay in the spring bloom timing over the years at Helgoland Roads. In the shallow waters of the German Bight there are typically two blooms in the first six months of the year: one bloom in early spring (weeks 6–14), the first production after the winter period, characterized by low production (Townsend et al. 1994); and a pronounced late spring or presummer bloom, mostly after week 12. As postulated by Wiltshire and Manly (2004), the observed delay of the early bloom may be related to a longer persistence of zooplankton grazers in autumn and early winter (Beare et al. 2002), which may depress the crucial biomass-building phase leading up to a phytoplankton bloom, thus delaying it.

The traditional way to describe phytoplankton bloom dynamics in marine environments is from a bottom-up perspective. The bloom starts when nutrient/light conditions are sufficient for positive growth in the bloom-forming species and terminates through the onset of nutrient (mostly silicate) limitation (Smetacek 1999), after which large amounts of organic material sediment out. In contrast, the PEG model of seasonal succession in freshwater planktonic communities (Sommer et al. 1986) describes the breakdown of the spring diatom bloom in

terms of increased grazing pressure by zooplankters. Hence, also keeping in mind that one of the main expected and observed results of global warming processes is a mismatch between the timing of predators and their prey (Cushing 1974), it is essential to consider both the bottom-up effects (e.g., light, nutrients) and the top-down mechanisms (e.g., consuming zooplankters) (Fig. 1). Moreover, fluctuations in temperature will affect organisms both directly and indirectly. Direct effects will be mediated via physiology and metabolic and reproductive processes. Indirect effects on organisms include predator-prey interactions, population dynamics, and competition. Indirect temperature effects on microalgae via the occurrence or activity of zooplankton may be more distinct than direct temperature effects on phytoplankton (Irigoien et al. 2005). Thus, investigating phytoplankton isolated from their trophic position may not yield the information needed to explain and predict changes in the phytoplankton community as a result of the changes in temperature. Accordingly, Townsend et al. (1994) postulated that the mechanisms governing spring bloom timing are more complex and possibly involve higher trophic levels.

In this paper we set out to test the hypothesis by Wiltshire and Manly (2004) that the mechanisms governing spring bloom timing are not merely driven by bottom-up temperature effects but involve more complex interactions at higher trophic levels. Hence, we combine North Sea phytoplankton, zooplankton, salinity, water transparency, and dissolved nutrient data (Helgoland Roads time series from 1975 to 2005), looking at both primary and secondary trophic levels. We investigated the changes in the factors that potentially drive phytoplankton bloom dynamics, and compared the changes in these factors with the changes in the spring bloom phenology, addressing the following questions: (1) Have possible bloom-triggering mechanisms for the phytoplankton blooms at Helgoland Roads changed in the first quarter of the year over the past decades? (2) Have the zooplankton abundances changed over the past decades, and, if so, is this related to warming? (3) Can changes in nutrient availability and zooplankton densities be related to phytoplankton bloom dynamics?

Methods

Since 1873, the surface water temperature of the North Sea at Helgoland Roads (54°11′03″N, 7°54′00″E) has been recorded, providing an excellent basis for analyzing long-term temperature trends (Wiltshire and Manly 2004). In addition, in 1962 the Biologische Anstalt Helgoland initiated a long-term monitoring program at Helgoland Roads. Apart from temperature recordings, this involves monitoring nutrients (SiO_4, NO_2, NO_3, NH_4, and PO_4), salinity, light penetration (measured as Secchi depth), and phytoplankton species composition on a work-daily basis (for methods, *see* Hickel et al. 1993). Phytoplankton is counted to species level, whereby 370 species are recognized (Hickel et al. 1993; Wiltshire and Dürselen 2004; Wiltshire and Manly 2004). From 1975 onwards, zooplankton sampling was added to the time series at Helgoland Roads (Greve et al. 2004). This involves sampling three times a
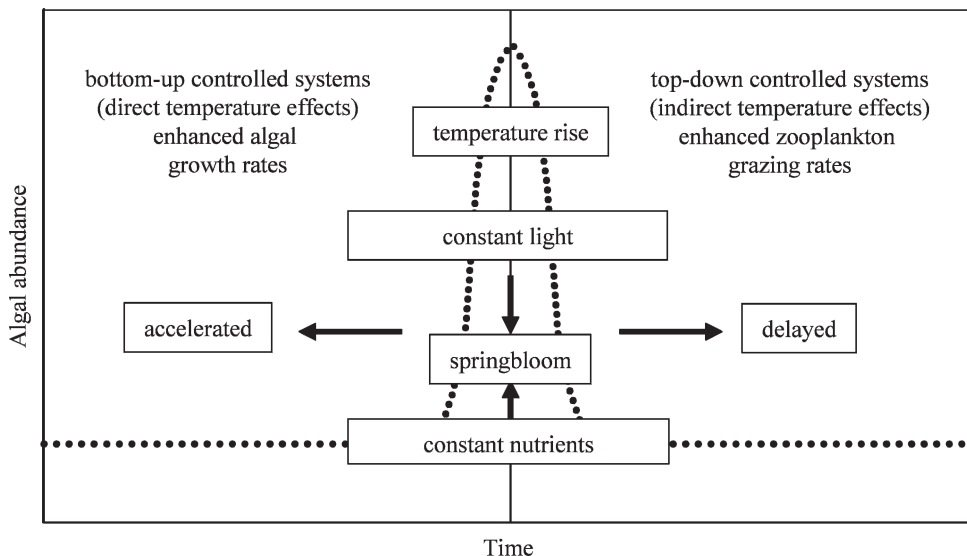
Fig. 1.   Conceptual sketch of how differential effects of a temperature rise may affect the timing of phytoplankton blooms. Under the assumption that light and nutrient availability did not change, phytoplankton growth may either be accelerated by direct physiological effects or delayed by indirect effects such as enhanced grazing activity of herbivores.

week, at the same time as the phytoplankton and nutrient samples of the daily time series. Analyses of the zooplankton data are also carried out to species level (Greve et al. 2004). Wiltshire and Manly (2004) reported on data (1873–2001) from the same site. The data set we use here is, however, different for two reasons. First, because we included zooplankton data, which were regularly sampled only from 1975, we had to omit the data from before 1975 from the analysis. Second, we included the years until 2005, for which we now have the complete data set.

The spring and presummer phytoplankton community at Helgoland Roads consists of over 90% diatoms. Because cell counts of these are also the most reliable data (as opposed to calculated biomass values) in the time series (Wiltshire and Dürselen 2004, for quality control) we took the sum of the total cell numbers on a daily basis to evaluate the blooms in the first quarter of the year. Describing bloom dynamics is not straightforward, especially in high-frequency (e.g., daily) data. Indeed, several different methods have been described (e.g., Rolinski et al. 2007), all of which have their merits, depending on the shape of the blooms and sampling frequency. Because this is not a methodological paper, we concentrated on two bloom descriptors here: the mean diatom day (MDD, as defined in Wiltshire and Manly 2004), and a low-pass method for determining the start of the bloom, described below. At Helgoland Roads the first "spring bloom" occurs in January–February (d 20–50), and towards the end of March (d 70–90) the late, second spring bloom starts. Thus, by investigating different intervals we found that the optimal time frame for analyzing the spring bloom timing was the first quarter (first 90 d of the year).

The MDD does not try to describe a bloom precisely, but is a measure of the complete algal distribution over the period preceding the long-term average in the onset of the late, second spring bloom, thus including algae, which form small blooms in January–February.

The MDD is given as

$$MDD = \sum f_i d_i \Big/ \sum f_i \tag{1}$$

where f_i is the diatom count on day d_i of the quarter, and the sum is over the available samples in the quarter. This method is very robust with respect to small-scale fluctuations in daily counts and is independent of exact bloom shapes. In the previous analysis of the MDD by Wiltshire and Manly (2004), when regression models (including a multiple linear regression evaluation with a linear trend term and seasonal effects) with autocorrelated errors were fitted to the data, it was found that quadratic, cubic, and quartic elements were not significant, but that there was a highly significant ($p < 0.001$) linear trend with time.

The second method introduced in this paper addresses the start of the exponential algal bloom, which usually starts in late spring. To identify its start is much more difficult, because it is clearly dependent on the individual daily counts. Thus, we needed to smooth the data considerably before being able to define the start of the bloom. This was carried out according to

$$\bar{x}_t = s^{-1} \cdot \sum_{\substack{|t-t'| \\ <\Delta t}} x_{t'} \cdot (1 + |t - t'|)^{-1} \tag{2}$$

$$s = \sum_{\substack{|t-t'| \\ <\Delta t}} (1 + |t - t'|)^{-1} \tag{3}$$

where x is the observed value in a time series (e.g., diatom abundance), and s a normalization factor equal to the sum of time-lag–dependent weighting coefficients. t denotes the day number and Δt the maximum distance of the moving

average, here 14 d, resulting in a moving window of 4 weeks. This averaging algorithm acts as a low-pass filter, reducing the short-term fluctuations inherent in the values because of hydrographic variability at the sampling location.

In order to confine our analysis to the phenologically important spring phase, wherein we hypothesize a control of diatoms by grazing copepods, we processed only observations made during the 3 months before the onset of the later spring bloom towards the end of the quarter. The bloom start was determined according to a simple rule: the first continuous increase in diatom biomass surpassing one order of magnitude defines the late spring bloom. From the annual statistics of averaged exponential rates during this phase, we derive a critical value for the relative growth rate of 0.03 d^{-1}, which is the long-term mean lowered by the standard deviation. The day within the continuous growth period when the relative growth rate reaches this value for the first time is identified as the first exponential bloom day (FEBD). Taking different values of the critical growth rate in the range of $0.02–0.05$ d^{-1} has only minor effects on the FEBD for most years.

Interestingly, there is a highly significant negative correlation between FEBD and MDD ($r^2 = 0.58$; $p < 0.001$), even though they are based on different assumptions. Clearly, the MDD is in part driven by the diatom abundance towards the end of the quarter, but it also takes the small blooms in January–February into consideration, whereas the FEBD method is driven by the second spring bloom.

There are several instances in which virtually no phytoplankton were present in the first 3 months of the year. Typically, such a situation will yield an MDD of 45, which obviously is nonsensical. Therefore, from abundance analyses we selected those years in which the peak density in the first 3 months of the year remained below 15 cells mL^{-1} (in contrast to the highest count in this period of over 600 cells mL^{-1}). Using discriminant analysis with two groups (bloom or no bloom), we separated these groups on the basis of the above-mentioned external conditions.

For the investigation of potential causes of the change in the timing of the phytoplankton spring bloom, we used a stepwise forward multiple regression analysis. We compared the MDD with copepod densities (the main herbivorous grazer during the first 3 months of the year; Greve et al. 2004), temperature, salinity, Secchi depth, total dissolved inorganic nitrogen (DIN), phosphate, sunshine hours, and wind for the first quarter of the year.

The phytoplankton bloom is driven by variables before bloom start only. Thus, it was necessary to consider independent variables only before the bloom; this was done on a per-year basis. For each MDD, we first calculated the mean of the measurements made prior to the MDD under investigation for all years, leading to 30 mean values. Second, we subtracted the grand mean of the 30 yr from the mean of the year under investigation. Lastly, we normalized the deviation of the year under investigation from the grand mean by dividing it by the standard deviation of the grand mean. This procedure was repeated for all years, resulting in 30 sets of anomalies of nutrient concentrations, copepod densities, and abiotic parameters. This data set was used for the multiple linear regression analysis. We applied an analogous treatment for analyzing prebloom correlations using 90-d averages before the FEBD.

Results

Changes in external factors—Many of the factors under consideration that potentially influence bloom phenology and dynamics showed considerable variation over time (Fig. 2). Temperature (here given as the annual mean temperature) increased significantly in the investigation period, resulting in an annual increase of around $0.043°C$ yr^{-1}, yielding an increase of the average temperature over the observational period of $1.33°C$. At the same time, the salinity of the water did not show a significant trend over the years, but considerable variation between years. Water transparency, measured as Secchi disc visibility, increased by almost 1 m in the period 1975–2005. Yearly averages of dissolved phosphates showed a significant decline from the mid-1970s. For spring phytoplankton bloom dynamics, copepod densities of the first 3 months of the year are most relevant. We observed no significant changes over the years in the winter densities of herbivorous copepods, but, as was the case with salinity, considerable variation between years. Copepod phenology, determined as the week in which we observed 10% of the total yearly cumulative density (5% or 25% could also have been used), showed a significant move forward in the study period, indicating that copepod populations started to increase earlier in the season. The change in all these factors made it seem extremely likely that the start of the spring phytoplankton bloom could have changed during these years also. However, we first compare those years without a bloom with those that have a significant spring bloom.

Bloom vs. no-bloom situations—Of the 31 yr under consideration, 8 yr had phytoplankton densities with a maximum value below 15 cells mL^{-1} in the first quarter (Jan–Mar). Discriminant analysis with a stepwise forward selection of dependent variables and bloom vs. no-bloom as grouping variables yielded a significant total model (Wilks $\lambda = 0.72$, $F_{2,28} = 5.54$, $p < 0.01$). The mean temperature of the autumn before the spring was the first variable to enter ($p = 0.006$), followed by the average winter temperature, which was significant at $p = 0.09$ (Fig. 3). Based on an a priori probability of a bloom occurring or not occurring, set at 50%, this meant that we could classify 84% of the years correctly. Autumn temperature entered the discriminate functions with a large (30.153 for no bloom; 32.404 for bloom) positive coefficient, whereas the coefficients for winter temperature were much smaller (0.173 and -0.485, respectively). Combined with an intercept of -152.598 for the no-bloom function and -173.079 for the bloom function, this implies that the most important factor correlating with the likelihood of bloom occurrence is the temperature in the preceding autumn.

Warm autumns increase the probability of a bloom in the following spring; higher temperatures in winter decrease this probability, albeit with a much lower impact.
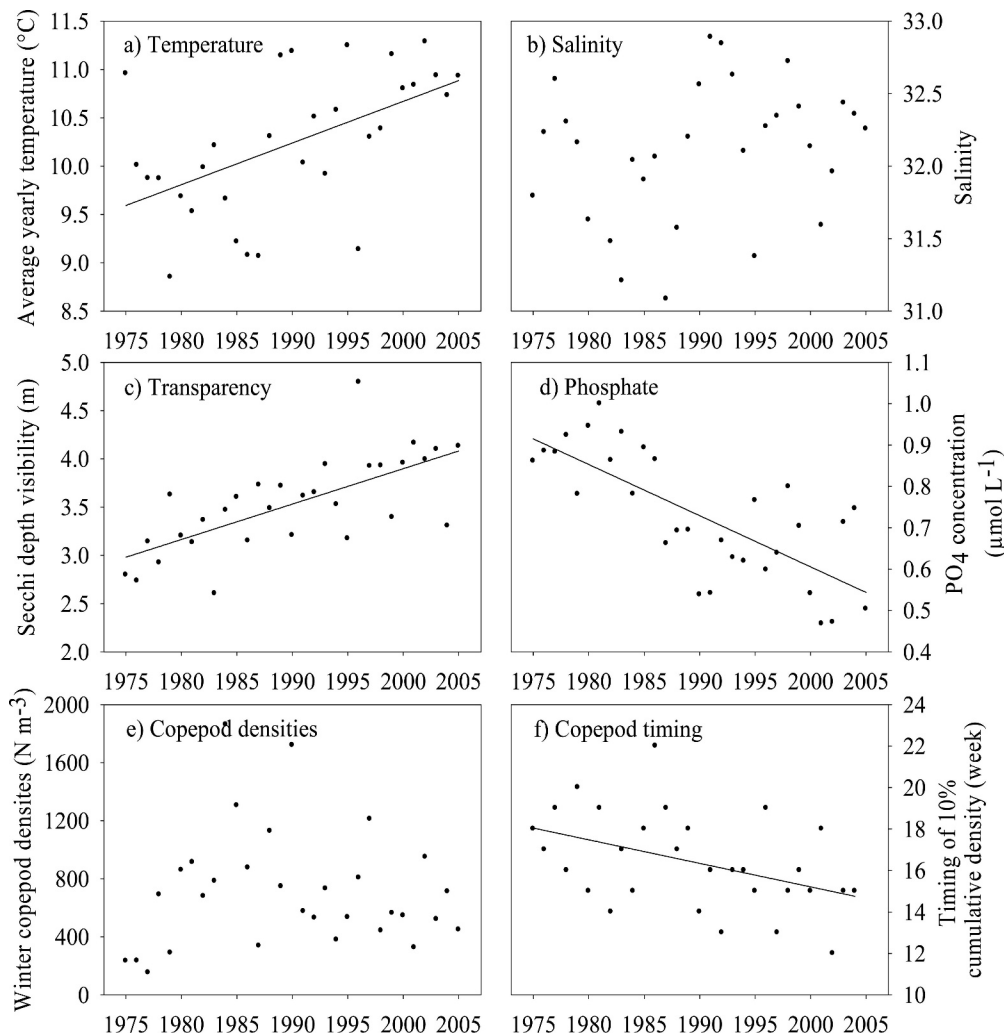
Fig. 2.   Time series of different variables in the Helgoland data series, indicating the large change that has occurred in the system. (a) Average yearly temperatures; (b) salinity; (c) transparency as Secchi depth; (d) phosphate concentration in μmol L^{-1}; (e) copepod densities; and (f) copepod timing (as 10% total cumulative density). Regression lines indicate significant relationships (temperature: temp $= -75.5 + 0.043 \times$ year, $r^2 = 0.29$, $p < 0.002$; transparency: Secchi $= -69.5 + 0.037 \times$ year, $r^2 = 0.48$, $p < 0.001$; phosphate: PO$_4 = 25.36 - 0.012 \times$ year, $r^2 = 0.55$, $p < 0.001$; copepod timing: week $= 242.13 - 0.114 \times$ year, $r^2 = 0.19$, $p < 0.02$).

Changes in spring bloom dynamics—Both the MDD and the bloom start (FEBD) showed considerable temporal variation (Fig. 4). The pattern depicted in Fig. 4 is different from the one depicted in Wiltshire and Manly (2004) for two reasons: first, the 5 yr added to the data set show a decrease in MDD in the years 2000–2005; and second, the main change in the MDD in the previous analysis was found around 1977, which because of the inclusion of the zooplankton data is at the edge of the data here, and hence it is not possible to see the same trend. Neither the MDD nor the FEBD showed a significant change in the years 1975–2005 with time. This was surprising, because the changes in the potential bloom triggering mechanisms showed considerable variation and directional change over the same time period.

The stepwise forward multiple regression analyses over the whole time period revealed that only the winter temperature (either as an anomaly of the average temperatures of that same period in other years, or as average temperature over the whole 90-d period) entered the regression. Winter temperature explained 17% of the variation in MDD ($p < 0.03$) and 17% of the variation in FEBD ($p < 0.03$), with higher winter temperatures leading to an increase in FEBD and a decrease in MDD. Anomalies (or absolute values) of salinity, DIN, phosphate, sunshine hours, wind, and mean copepod densities in winter or the previous autumn did not enter the model. After correcting for the winter temperature, Secchi transparency showed a significant positive partial correlation coefficient with the residuals of the regression for MDD ($p < 0.02$), indicating that higher transparency is linked to lower values for MDD. This is not an autocorrelation caused by higher algal densities making the water less clear. In fact, transparency and total algal
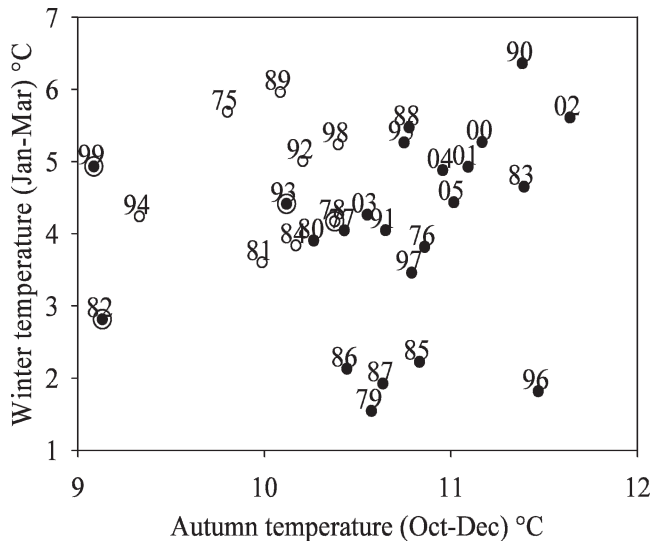
Fig. 3. Average autumn temperature (°C) against average winter temperature (°C) shows that these values are uncorrelated ($r^2 = 0.036$; $p > 0.70$). Open dots are years without an apparent spring bloom in the first 90 d of the year (see text), illustrating the results of the discriminant analysis that a no-bloom situation is most likely found in years with colder autumns followed by warmer winters. Double circles indicate those years that were incorrectly assigned by the discriminant functions.

density did not show a significant correlation for the first 90 d of the year.

Edwards et al. (2002) and Weijerman et al. (2005) analyzed 28 abiotic and 50 biological time series in the North Sea and Wadden Sea and identified a major shift ("regime shift") around 1988. This can also be seen in Fig. 5, which shows that from this year on the winter densities of algae increased substantially. To investigate whether this regime shift caused different relationships between the bloom descriptors and the explaining variables, we analyzed not only the data over the whole time
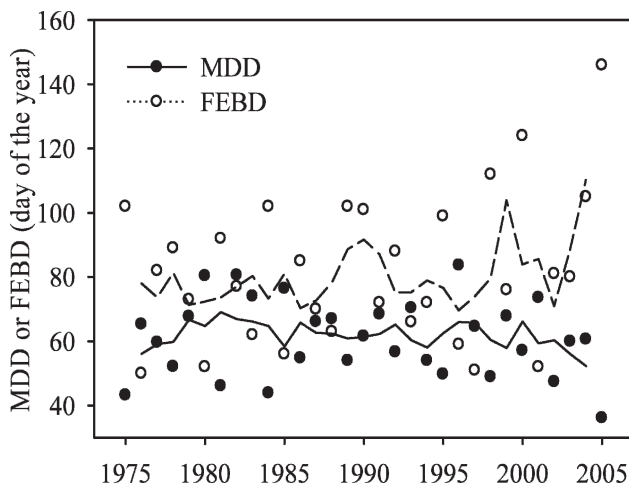

Fig. 4. Bloom descriptors in the years 1975–2005, mean diatom day (MDD), and first exponential bloom day (FEBD). For explanations of calculation see text. Lines indicate 3-point running averages of values.
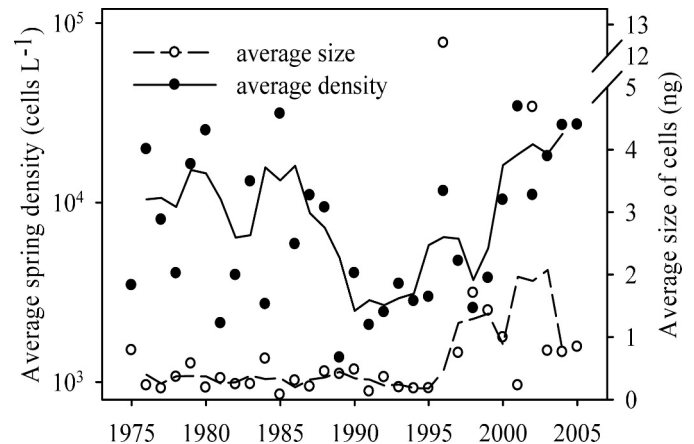

Fig. 5. Average algal density, with three-point running average, and average carbon content per algal cell in the period 1975–2005. The three-point running average of average mass is without the extremely high 1996 point. Average mass of algal cells increased in the first 3 months of the year.

period, but also the data set before and after this shift, with similar methodology to that described above. Even though clearly the components in the system changed considerably during this time, the regression analyses did not show clear differences.

Our results show that under the assumption that significant results in a regression analysis could indicate causality, the main driving force behind the variation in early spring bloom dynamics is the temperature, and no other variables entered the regression analysis. Neither copepod densities in winter nor those in the preceding autumn showed a significant correlation with the phenology of the spring bloom.

Discussion

The timing of spring blooms is naturally variable (Bigelow et al. 1940) and often very difficult to determine exactly, because mostly data are not resolved highly enough (i.e., under a week) to allow more than a subjective analysis. This is compounded by the fact that phytoplankton blooms are also difficult to describe mathematically from in situ data (*see also* Rolinski et al. 2007). However, the factors governing the onset of blooms are well recognized (Townsend et al. 1994). In deeper pelagic systems, it is the onset of stratification and increased light in spring that is usually the bloom trigger (Pingree et al. 1976; Sommer et al. 1986; Smetacek and Passow 1990). In well-mixed coastal waters such as Helgoland Roads with a maximum depth of 10 m, however, stratification rarely plays a role. The amount of incident light, rather than nutrients, will be the limiting factor in the early winter months at Helgoland Roads.

When considering only abiotic effects on blooms, it may be assumed that the onset of primary production is less dependent on temperature than on light (Sommer et al. 1986; Eilertsen et al. 1995; Eilertsen and Wyatt 2000). Consequently, a rise in temperature should not directly affect the beginning of the seasonal production. In reality,

the development of a bloom depends on the interplay of multiple factors, including light and nutrient availability as well as grazing pressure and species assemblages of both the grazing and the grazed communities (Irigoien et al. 2005). The grazing processes are obviously partly temperature-influenced, and the timing of phytoplankton blooms is consequently likely to be indirectly altered by warming. Evidence for indirect temperature-influenced onset of spring blooms exists for freshwater systems (Weyhenmeyer et al. 1999; Weyhenmeyer 2001) as well as Polar Regions (Smetacek and Nicol 2005). In ice regions, spring blooms are attributed to presence/absence of ice cover, which prevents light penetration of the water column. In temperate marine systems, ice cover usually is not a factor controlling phytoplankton growth. It can, however, be assumed that warming will play an underlying role, because the phytoplankton growth rates, which are usually accelerated by higher temperatures (Harrison and Platt 1980), should shift spring blooms towards earlier dates. Edwards and Richardson (2004) observed a fairly constant timing of spring blooms in the central North Sea based on the Continuous Plankton Recorder (CPR) data set, which has a different sampling emphasis (huge spatial range vs. low temporal resolution) that is in line with the findings presented in this study.

Wiltshire and Manly (2004) described an annual increase of temperature at the Helgoland Roads of $0.0283°C$ per year. The current study, working with a more up-to-date (1975–2005) data set of the same location, shows that the actual increase in the last 30 yr analyzed has been much higher, at $0.043°C$ yr^{-1} (the value for the last 45 yr is $0.033°C$ yr^{-1}). Not only the temperature but also other variables measured at Helgoland Roads have shown considerable variation and directional change. Increased light penetration and significant decreases in nutrient loading (illustrated as dissolved PO_4 concentrations) probably reflect a hydrographic shift to more marine conditions at Helgoland correlated to increased southwesterly wind events. In fact, recent work by Stockmann et al. (pers. comm.), who reanalyzed current patterns of the North Sea using the Hindcast of Dynamic Processes of the Ocean and Coastal Areas of Europe Project (HIPOCAS) data set, has shown this shift to a less coastally dominated system. The reduction in nutrient loading of the main rivers, Rhine, Weser, and Elbe, contributing nutrients to the German Bight, will also contribute to decreased nutrients at Helgoland.

Changing copepod phenology at Helgoland Roads is clearly linked to changes in temperature ($r^2 = 0.27$; $p < 0.003$). Given this and all the other changes (directional and year-to-year variability) in environmental conditions, we also expected to see a change in spring bloom timing. This, however, was not the case. Neither of our two descriptors of spring bloom dynamics showed a significant change over time. In fact, the timing of the spring bloom was surprisingly constant given the changes that have occurred in the last 30 yr at Helgoland Roads. This finding may seem in contrast to the previous findings of Wiltshire and Manly (2004). This is, however, not the case. First of all, the main change in the MDD reported in that study was between 1976 and 1977, which is only just inside the current data set. Moreover, the data set used by Wiltshire and

Manly (2004) stopped in 2001. In the years since 2001 there has been a decreasing trend in MDD, which has caused the previous overall pattern to become nonsignificant. The observed stability in spring bloom timing is also in line with the work of Edwards and Richardson (2004), who observed a fairly constant timing of spring blooms in the central North Sea based on the CPR data.

The results of the discriminant analysis show that the occurrence of a substantial early spring bloom (i.e., in the months Jan–Mar) depends mainly on the temperature in the preceding autumn. A high autumn temperature will lead to a bloom in the following spring, even though autumn temperature and autumn phytoplankton densities show no significant correlation. Actual winter temperatures have the opposite effect, but with much less strength. Interestingly, copepod densities did not significantly influence the likelihood of a bloom, so it remains unclear what the mechanisms are behind this observation. Possibly a higher temperature in autumn results in a higher copepod survival rate. This needs further clarification, in particular with regard to shifts in species composition, which are our next investigative topic.

The multiple regression analysis with all the environmental variables and the MDD and FEBD presented a significant effect for winter temperature only. Higher temperatures caused an increase in FEBD and a decrease in MDD. The increase in FEBD at higher temperatures means that the second spring bloom starts later (March–April) at higher temperatures. Concurrently, a decrease in the value of the MDD is indicative of a bloom that does not start in the first quarter. Thus, the finding of Wiltshire and Manly (2004) that a higher temperature causes a delayed bloom still holds, even though our results here show that actual winter temperature now plays the dominant role instead of the preceding autumn temperature.

Rapid and/or repeated environmental changes can act as a reset on ecosystems and open niches for previously inconspicuous species, allowing them to become dominant and form blooms in the new situation (Bakun and Broad 2003). Sudden events like extreme freshwater runoff, which change salinity and improved nutrient conditions in coastal waters, upwelling events, or severe storms, which might mix formerly stratified water bodies, could favor single species. These then could become dominant and form blooms.

Examples of trophic events are a sudden decrease in grazing pressure or the input of competing species into a system (Irigoien et al. 2005). Top-down control on phytoplankton growth in marine systems is an accepted phenomenon (Graneli and Turner 2002; Irigoien et al. 2005; Sommer and Sommer 2006). It is generally understood that in warmer waters (above $3–5°C$) blooms can be terminated by grazing pressure of the standing stock and the first cohort of zooplankton of the year (Townsend et al. 1994; Greve et al. 2004). In contrast, the idea of herbivores being able to influence the start of a bloom is a relatively new one. Wiltshire and Manly (2004) proposed this as a mechanistic explanation as to why increased temperatures delay the spring bloom, and suggested that higher temperatures should cause an increased winter survival of herbivorous copepods and an increase in grazing rates of

those animals present. In this study, we tested this hypothesis by relating copepod densities with bloom phenology descriptors and with temperature. Contrary to our expectation, we observed no significant effect of copepod densities on either the MDD or the FEBD, no significant change in winter copepod densities with time, and no significant relationship of winter copepod densities with temperature, from 1975 onwards. Thus, we have to conclude that the mechanistic explanation of the delayed bloom at higher temperatures does not lie in increased copepod densities. It could well be, however, that those copepods that are present graze at higher rates. Because this is directly related to temperature, this is impossible to investigate using our current data set, because it would imply artificially adding some sort of a temperature term to the copepod densities to mimic grazing or additional experimental work using mesocosms (e.g., Aberle et al. 2006; Sommer et al. 2007) to shed more light on this phenomenon.

The German Bight around Helgoland is a highly dynamic system and has undergone considerable change in the last 30 yr. Given this, it is interesting to note how resilient the system is when considering phytoplankton spring bloom dynamics. Even though nutrient levels, temperature, underwater light climate, and wind speeds (data not shown, but we know that winds are over 1 Beaufort, on average, stronger since 1975) have all changed, the spring bloom dynamics have hardly changed at all. We showed that spring blooms come later in warmer years, but because this is not an all-exclusive correlation, this has not translated into significantly later blooms over our study period. Even after the known regime shift of the late 1980s, also clearly visible in our data (as average phytoplankton winter densities and average cell size), the start of the spring bloom did not change. From our first analyses of species diversity, we know that there have been changes in species composition over these years, with a significant increase in the numbers of very large diatoms (e.g., *Coscinodiscus wailesii*), which are hard for copepods to eat. Thus, even though phytoplankton bloom dynamics have hardly changed over the time period examined, we expect increasing blooms of inedible diatoms as a result of higher grazing rates, and hence it remains to be seen for how much longer the system will remain relatively unchanged.

References

ABERLE, N., K. LENGFELLNER, AND U. SOMMER. 2006. Spring bloom succession, grazing impact and herbivore selectivity of ciliate communities in response to winter warming. Oecologia **150:** 668–681.

AHAS, R., AND A. AASA. 2006. The effects of climate change on the phenology of selected Estonian plant, bird and fish populations. Int. J. Biometeorol. **51:** 17–26.

BAKUN, A., AND K. BROAD. 2003. Environmental 'loopholes' and fish population dynamics: Comparative pattern recognition with focus on El Nino effects in the Pacific. Fish. Oceanogr. **12:** 458–473.

BEARE, D. J., S. BATTEN, M. EDWARDS, AND D. G. REID. 2002. Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. J. Sea Res. **48:** 29–49.

BIGELOW, H. B., L. C. LILLICK, AND M. SEARS. 1940. Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. Part 1. Numerical distribution. Trans. Am. Philos. Soc. **21:** 149–191.

BLENCKNER, T., AND OTHERS. 2007. Large-scale climatic signatures in lakes across Europe: A meta-analysis. Global Change Biol. **13:** 1314–1326.

CUSHING, D. H. 1974. The natural regulation of fish populations p. 399–412. *In* F. R. Harden Jones [ed.], Sea fisheries research. Paul Elek.

———. 1995. The long-term relationship between zooplankton and fish. ICES J. Mar. Sci. **52:** 611–626.

EDWARDS, M., G. BEAUGRAND, P. C. REID, A. A. ROWDEN, AND M. B. JONES. 2002. Ocean climate anomalies and the ecology of the North Sea. Mar. Ecol. Prog. Ser. **239:** 1–10.

———, D. G. JOHNS, S. C. LETERME, E. SVENDSEN, AND A. J. RICHARDSON. 2006. Regional climate change and harmful algal blooms in the Northeast Atlantic. Limnol. Oceanogr. **51:** 820–829.

———, P. REID, AND B. PLANQUE. 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). ICES J. Mar. Sci. **58:** 39–49.

———, AND A. J. RICHARDSON. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature **7002:** 881–883.

EILERTSEN, H. C., S. SANDBERG, AND H. TOELLEFSEN. 1995. Photoperiodic control of diatom spore growth: A theory to explain the onset of phytoplankton blooms. Mar. Ecol. Prog. Ser. **116:** 303–307.

———, AND T. WYATT. 2000. Phytoplankton models and life history strategies. S. Afr. J. Mar. Sci. **22:** 323–338.

GRANELI, E., AND J. T. TURNER. 2002. Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: A mesocosm study. Mar. Ecol. Prog. Ser. **239:** 57–68.

GREVE, W., F. REINERS, J. NAST, AND S. HOFFMANN. 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: Lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgol. Mar. Res. **58:** 274–288.

HARRISON, W. G., AND T. PLATT. 1980. Variations in assimilation number of coastal marine phytoplankton: Effects of environmental co-variates. J. Plankton Res. **2:** 249–260.

HAWKINS, S. J., A. J. SOUTHWARD, AND M. J. GENNER. 2003. Detection of environmental change in a marine ecosystem—evidence from the western English Channel. Sci. Total Environ. **310:** 245–256.

HICKEL, W., P. MANGELSDORF, AND J. BERG. 1993. The human impact in the German Bight: Eutrophication during three decades (1962–1991). Helgol. Wiss. Meeresunters. **47:** 243–263.

HÜPPOP, O., AND K. HÜPPOP. 2003. North Atlantic Oscillation and timing of spring migration in birds. Proc. R. Soc. Lond. B Biol. Sci. **270:** 122–240.

IPCC. 2001a. Intergovernmental Panel on Climate Change third assessment report; Climate change 2001: Impacts, adaptation, and vulnerability. J. J. McCarthy, O. F. Canziani, N. A. Leary, D. J. Dokken and K. S. White [Eds.], Cambridge Univ. Press.

———. 2001b. Intergovernmental Panel on Climate Change third assessment report; Climate change 2001: The scientific basis. J. T. Houghton, Y. Ding, D. J. Griggs, M. Nogouer, P. J. van der Linden, X. Dai, K. Maskell and C. A. Johnson [Eds.], Cambridge Univ. Press.

———. 2007. Intergovernmental Panel on Climate Change: Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the

Intergovernmental Panel on Climate Change. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller [Eds.], Cambridge University Press.

IRIGOIEN, X., K. J. FLYNN, AND R. P. HARRIS. 2005. Phytoplankton blooms: A 'loophole' in microzooplankton grazing impact? J. Plankton Res. **27:** 313–321.

PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421:** 37–42.

PINGREE, R. D., P. M. HOLLIGAN, G. T. MARDELL, AND R. N. HEAD. 1976. The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. J. Mar. Biol. Assoc. U. K. **56:** 845–873.

RADACH, G. 1998. Quantification of long-term changes in the German Bight using an ecological development index. ICES J. Mar. Sci. **55:** 587–599.

ROLINSKI, S., H. HORN, T. PETZOLDT, AND L. PAUL. 2007. Identifying cardinal dates in phytoplankton time series to enable the analysis of long-term trends. Oecologia **153:** 997.

ROOT, T. L., J. T. PRICE, K. R. HALL, S. H. SCHNEIDER, C. ROSENZWEIG, AND J. A. POUNDS. 2003. Fingerprints of global warming on wild animals and plants. Nature **421:** 57–60.

SMETACEK, V. 1999. Diatoms and the ocean carbon cycle. Protist **150:** 25–32.

———, AND S. NICOL. 2005. Polar ocean ecosystems in a changing world. Nature **437:** 362–368.

———, AND U. PASSOW. 1990. Spring bloom initiation and Sverdrup's critical-depth model. Limnol. Oceanogr. **35:** 118–234.

SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG model of seasonal succession of planktonic events in freshwaters. Arch. Hydrobiol. **106:** 433–471.

———, AND F. SOMMER. 2006. Cladocerans versus copepods: The cause of contrasting top-down controls on freshwater and marine phytoplankton. Oecologia **147:** 183–194.

———, AND OTHERS. 2007. An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. Oecologia **150:** 655–667.

STRAILE, D. 2002. North Atlantic Oscillation synchronizes food-web interactions in central European lakes. Proc. R. Soc. Lond. B Biol. Sci. **269:** 391–395.

TOWNSEND, D. W., L. M. CAMMEN, P. M. HOLLIGAN, D. E. CAMPBELL, AND N. R. PETTIGREW. 1994. Causes and consequences of variability in the timing of spring phytoplankton blooms. Deep-Sea Res. Part I Oceanogr. Res. Pap. **41:** 747–765.

WALTHER, G. R., AND OTHERS. 2002. Ecological responses to recent climate change. Nature **416:** 389–395.

WEIJERMAN, M., H. LINDEBOOM, AND A. F. ZUUR. 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. Mar. Ecol. Prog. Ser. **298:** 21–39.

WEYHENMEYER, G. A. 2001. Warmer winters: Are planktonic algal populations in Sweden's largest lakes affected? Ambio **30:** 565–571.

———, T. BLECKNER, AND K. PETTERSSON. 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. Limnol. Oceanogr. **44:** 1788–1792.

WILTSHIRE, K. H., AND C.-D. DÜRSELEN. 2004. Revision and quality analyses of the Helgoland Reede long-term phytoplankton data archive. Helgol. Mar. Res. **58:** 252.

———, AND B. F. J. MANLY. 2004. The warming trend at Helgoland Roads, North Sea: Phytoplankton response. Helgol. Mar. Res. **58:** 269–273.