

Long-term Field Observations on Seasonality in Chlorophyll-*a* Concentrations in a Shallow Coastal Marine Ecosystem, the Wadden Sea

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Abstract Analyses of long-term field observations (1974–2007) on chlorophyll-*a* concentrations in the western Wadden Sea showed no long-term trends in the timing of the wax and wane of phytoplankton spring blooms. There is weak evidence, however, that the height of the autumn bloom has decreased since the early 1990s. This fading of the autumn bloom may have had consequences for the carbon transfer to higher trophic levels, currently hampering primary consumer species that mostly rely on food supply during late summer. Current and other findings suggest a shortening of the growing season due to the fading of the autumn bloom in the Wadden Sea and a lengthening of the growing season due to an advancement of the spring bloom in the North Sea. These regionally different changes in seasonality may have contributed to the coinciding decrease in bivalve filtering capacity in the western Wadden Sea and the large-scale offshore shift of juvenile plaice from the Wadden Sea to the adjacent North Sea.

Keywords Long-term dynamics · Phytoplankton · Chlorophyll-*a* · Phenology · Coastal marine ecosystems

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Introduction

In temperate marine waters that get stratified during summer, time series of phytoplankton biomass show recurring spring bloom events to begin anytime from late winter to early spring (Townsend et al. 1994). Each bloom is characterized by a period of rapid algae growth followed by a crash in population numbers, after which there is a period where phytoplankton numbers remain minimal. Hereafter, phytoplankton may bloom again in late summer before numbers get low for a longer period during the cold and dark winter. Shallow non-stratified coastal waters, such as estuaries, lagoons, and bays, however, are very diverse systems, and the relative importance and interplay of the various factors that can potentially affect bloom initiation and development show much more variation. For example, such waters may be characterized by series of pulses of growth during spring and summer (e.g., Colebrook and Robinson 1965; Riley 1967; Cadée 1986a). Typical patterns of phytoplankton variability over years include episodic blooms, cyclical blooms, seasonal shifts, long-term trends, stochastic blooms, and novel appearances (Smayda 1998).

The underlying mechanisms that control the timing of onset and duration of the spring bloom can be very different between areas and between years (Townsend et al. 1994; Cloern 1996; Smayda 1998), depending on the interplay of multiple factors, such as day length, light conditions, nutrient availability, and grazing (Iriogen et al. 2005). Although observed interannual variation in timing of onset and duration of blooms is more often attributed to external forcing such as weather conditions and nutrient concentrations than internal dynamics (e.g., Smayda 1998), modeling exercises suggest that such year-to-year variations can be also be fully explained by multispecies interactions (Dakos et al. 2009).

The timing of onset and duration of blooms is particularly important with respect to food web dynamics in these shallow marine systems. Consumption of the bloom by planktonic heterotrophs and filter-feeding bivalves is expected to be much reduced when the bloom occurs in relatively cold waters, e.g., when phytoplankton blooms relatively early in the year (Prins et al. 1994; Townsend et al. 1994). For invertebrates with a complex lifecycle, optimizing the time of spawning is necessary to match reproduction with the most optimal environmental conditions for the first vulnerable life stages (i.e., the settlement-timing hypothesis by Todd and Doyle 1981). In temperate waters, many larvae of marine macrozoobenthos species are planktotrophic, i.e., their food stores are not sufficient to survive the pelagic phase without ingesting exogenous food (Thorson 1950). Although there is still much debate on whether growth and development of invertebrate larvae are food-limited under natural conditions (e.g., Strathmann 1996), there may be a causal relationship between the timing of the planktonic food supply and subsequent bivalve recruitment success (Philippart et al. 2003).

The present paper deals with the long-term dynamics in seasonality of phytoplankton in the western Wadden Sea. Data analysis is based on a long-term dataset originating from one station near the Marsdiep tidal inlet

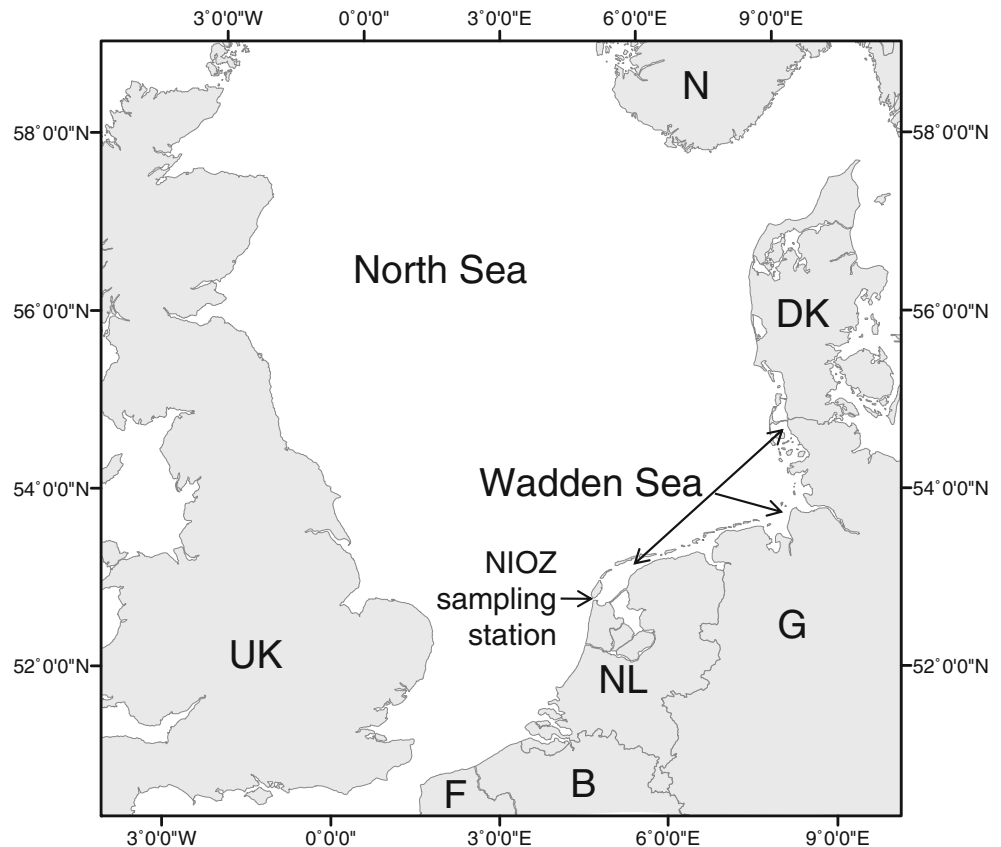
over a study period of 34 years (1974–2007). Previous analyses of parts of this dataset revealed that the phytoplankton community changed drastically both around 1978 and again around 1988 and that it was relatively stable in-between and hereafter (Philippart et al. 2000). The major changes in phytoplankton community structure coincided with changes in absolute and relative nutrient concentrations (Philippart et al. 2000) and were followed by changes in community structures of macrozoobenthos and estuarine birds (Beukema et al. 2002; Philippart et al. 2007). In this paper, we focus on the between-year variation in the timing of the wax and wane of phytoplankton blooms as derived from chlorophyll-*a* measurements.

Materials and Methods

Long-Term Field Observations

From 1974 onwards, bucket water samples have been collected at high tide from the NIOZ sampling jetty (53°00'06" N 4°47'21" E), located in the Marsdiep tidal inlet between the North Sea and the Wadden Sea (Fig. 1). Phytoplankton sampling frequency was 40–60 times per year, varying from once or twice a month in winter up to

Fig. 1 Location of the sampling station in the western part of the Wadden Sea, a shallow coastal sea at the southeastern border of the North Sea (*N* Norway, *DK* Denmark, *G* Germany, *NL* The Netherlands, *B* Belgium, *F* France, *UK* United Kingdom)



twice a week during phytoplankton spring blooms (e.g., Cadée and Hegeman 2002).

Chlorophyll-*a* concentrations were assessed from additional 0.5 to 1 l water samples, filtered over MgCO₃-coated filters (Cadée and Hegeman 2002). The concentrations in previous publications were calculated from the difference in spectrophotometric measurements of extinctions at 666 nm before and after acidification of the samples to correct for the extinction by chlorophyll degradation products (phaeopigments) in coastal waters at this wavelength (Lorenzen 1967). Serious doubts on the applicability of acidification to correct for the extinction by phaeopigments (Stich and Brinker 2005) motivated us to use the original data of non-acidified values (total chlorophyll-*a*) in the present paper. On average, this back-calculation resulted in higher chlorophyll-*a* concentrations ($n=1,344$, $r^2=0.98$, $\text{CHL}_{\text{non-acidified}}=1.174 \text{ CHL}_{\text{acidified}}$).

Data Analyses

Changes in seasonality of blooms were examined by means of two approaches, viz. a first approach in which the data of each year were analyzed separately for the timing of the spring bloom by means of determination of maximum and minimum daily changes in chlorophyll-*a* concentrations and a second approach at which the full dataset was examined which allowed for multiple blooms and possible auto-correlation structures.

For the first approach, we applied a generalized additive model (GAM) with a Gamma distribution and log-link function on data of each year, provided there were sufficient observations (>25) in that year. Hence, the following model is applied:

$$\text{Chlorophyll}_s \sim \text{Gamma}(\mu_s, \nu)$$

$$E(\text{Chlorophyll}_s) = \mu_s \quad \text{and} \quad \text{var}(\text{Chlorophyll}_s) = \frac{\mu_s^2}{\nu}$$

$$\mu_s = e^{\alpha+f(\text{Day})}$$

where Chlorophyll_{*s*} is the observed chlorophyll-*a* at time *s* in a particular year. This model estimated daily chlorophyll-*a* concentrations by interpolating observed chlorophyll-*a* concentrations in that year (Fig. 2a).

The onset of the spring bloom was defined as the date at which the maximum daily increase in the interpolated chlorophyll-*a* concentrations occurred, for the timing of the breakdown of this bloom we used the date for which the minimum value of the maximum daily increase in chlorophyll-*a* concentrations was found (Fig. 2b). To determine a more biologically realistic determination of the onset of the bloom, it would have been better to calculate specific net growth rates instead of daily increases. If we had used these growth rates, however, we could not have

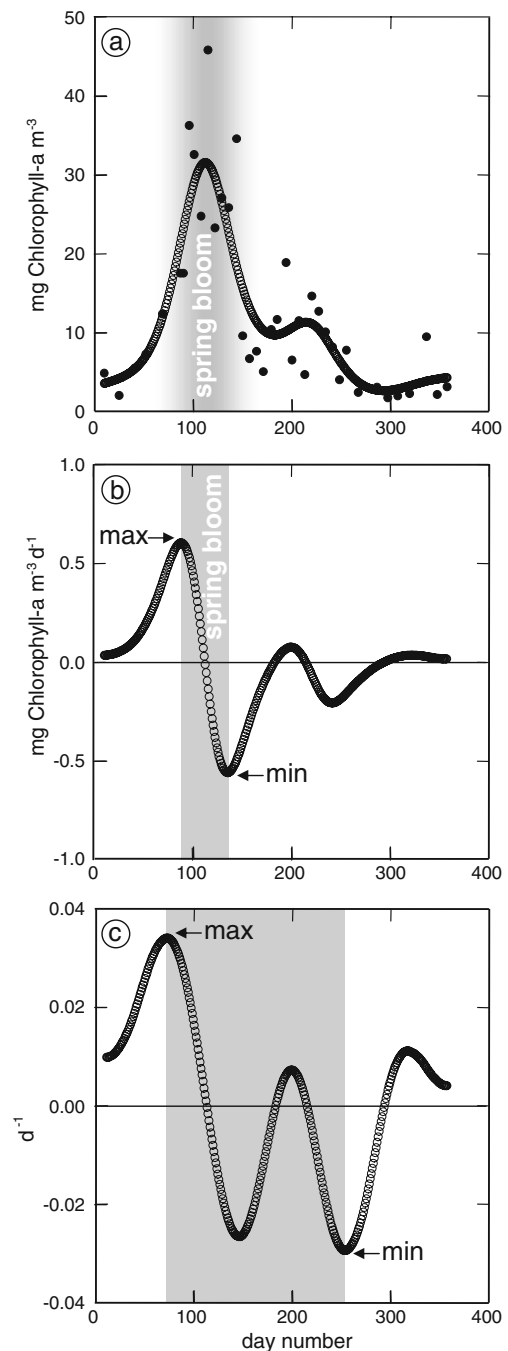


Fig. 2 Example of determination of timing of annual start and breakdown of phytoplankton bloom as derived from long-term observations on chlorophyll-*a* concentrations, viz. **a** interpolation of observations on chlorophyll-*a* concentrations (mg m^{-3}) by means of a model, **b** identification of maximum and minimum values of daily change in chlorophyll-*a* concentrations ($\text{mg m}^{-3} \text{ day}^{-1}$), and **c** identification of maximum and minimum values of specific growth rates (day^{-1}). The field observations on which these estimations are based upon were made in 1988

determined the end of the spring bloom as the minimum value of this parameter (Fig 2c). Results based upon daily changes should, therefore, be considered as consistent but rough approximations of the timing of the spring bloom.

The day on which the maximum and minimum daily changes were observed were extracted for each year, and these were further analyzed for the presence of a long-term trend using a Gaussian GAM with Year as a smoother. Hence, the following model was applied:

$$M_s \sim N(\mu_s, \sigma^2)$$

$$E(M_s) = \mu_s \quad \text{and} \quad \text{var}(M_s) = \sigma^2$$

$$\mu_s = \alpha + f(\text{Year})$$

where M_s is the maximum in year s (or the minimum). Both time series did not exhibit any strong autocorrelation as determined by an autocorrelation function, which justifies the application of GAM without an autocorrelation structure.

For the second approach, we applied a generalized additive mixed model (GAMM) with a Gamma distribution and log-link function (Wood 2006; Zuur et al. 2009) which was used to model the chlorophyll-*a* data for the full dataset. The log-link ensures that fitted values are always positive and the Gamma distribution uses the following mean and variance

$$E(\text{Chlorophyll}_s) = \mu_s \quad \text{and} \quad \text{var}(\text{Chlorophyll}_s) = \frac{\mu_s^2}{\nu}$$

The dispersion is determined by ν^{-1} ; a small value of ν (relative to μ^2) implies that the spread in the data is large. We used two different GAMM models; the first model contains a 2-dimensional smoother, and the second model consists of a smoother for day of the year and a smoother for year. Thin

plate regression splines were used for the smoother. Hence, these models are given by:

Model 1 : $\mu_s = e^{\alpha+f(\text{Day},\text{Year})}$
 Model 2 : $\mu_s = e^{\alpha+f_1(\text{Day})+f_2(\text{Year})}$

The term μ_s is the expected chlorophyll-*a* concentration at time s . The covariate Day is coded as the day of the year that sampling took place and has values between 1 (in 2004) and 364 (in 1993 and 1996). Year has values from 1974 to 2007. The term α is an intercept. Model 2 contains two smoothers; the long-term trend f_2 , and the seasonal effect is modeled with f_1 . This model assumes that the seasonal effect is the same in each year. Model 1, on the other hand, allows for a change of the seasonal effect over the years.

To allow for autocorrelation between sequential observations, a residual correlation structure was added to the model. For regular spaced data, the autoregressive correlation of order 1 (AR-1) is a sensible choice (Pinheiro and Bates 2000; Zuur et al. 2009) and is given by:

$$\text{cor}(\varepsilon_s, \varepsilon_{s-k}) = \rho^k$$

where ε_s is the residual at time s , k is the time lag (in days), ρ is an unknown parameter that has to be estimated. This approach allows for temporal correlation between 2 days that gets smaller for increasing time lags. However, our data are irregularly spaced in time; therefore, the AR-1 correlation had to be replaced by something more appropriate. Pinheiro and Bates (2000) discussed various correlation

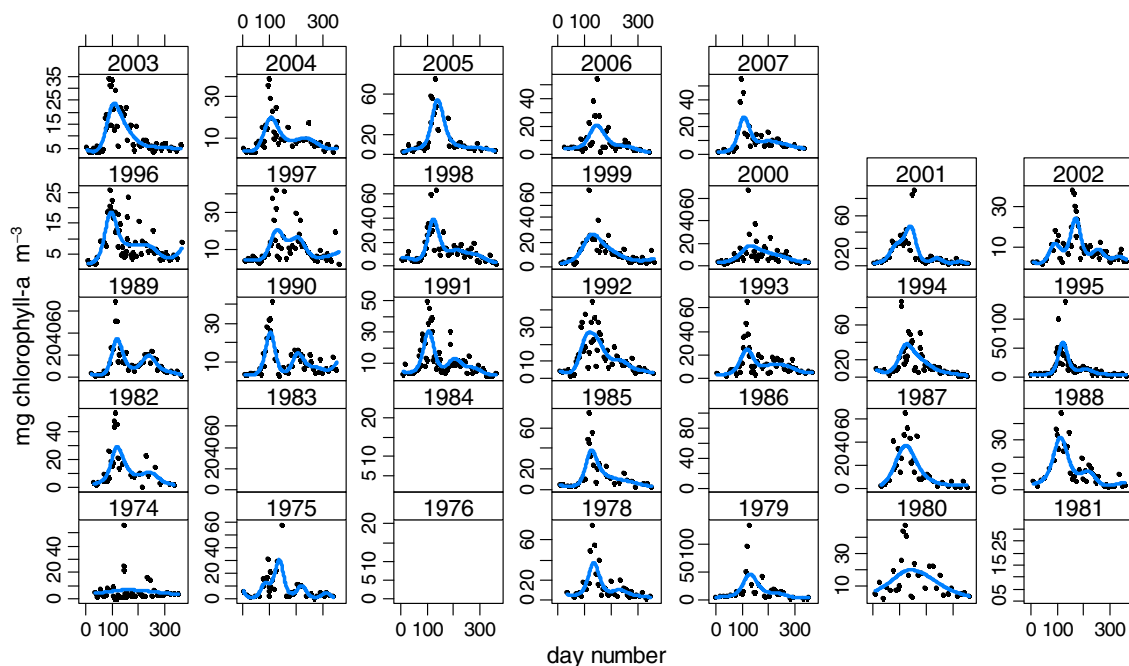


Fig. 3 Interpolation of annual observations on chlorophyll-*a* concentrations as measured in the Marsdiep tidal inlet at high tide between 1974 and 2007. Black dots indicate field observations and blue line

the interpolation. No data were available for 1977, and the model could not fit the observations for 1976, 1981, 1983, 1984, and 1986 because not enough data were available for these years

structures designed for (irregular-spaced) spatial data, which can easily be adopted for irregular-spaced time series (see Zuur et al. (2009) for various examples). We used the continuous autoregressive correlation, and the exponential, Gaussian, linear, and rational quadratic correlation structures (see Schabenberger and Pierce 2002 for their exact definitions). The correlation structures require estimation of two parameters: the range and the nugget. The range specifies the time frame (in days) in which temporal dependence can occur, and the nugget is the correlation between observations separated less than 1 day.

The models were compared using the Akaike's information criterion (AIC), a tool to measure the goodness-of-fit of an estimated statistical model and model complexity: if competing models are ranked according to their AIC, the one having the lowest AIC is the best. Calculations were carried out in the *mgcv* (Wood 2006) package from the software R (R Development Core Team 2008).

Results

For the first approach, years with insufficient information (1976, 1981, 1983, 1984, and 1986) and no (1977) data on chlorophyll-*a* concentrations had to be excluded from interpolation of field observations for each year separately by means of the GAM with a Gamma distribution and log-link function. The remaining dataset comprised 1,309 observations on chlorophyll-*a* concentrations in 30 years, with an average number of 43.63 ± 11.17 observations per year (Fig. 3). Fitted values for those 30 years show year-to-year variation in height of the blooms as indexed by chlorophyll-*a* concentrations (Figs. 3 and 4) and of the timing of the spring bloom as described by daily change in chlorophyll-*a* concentrations (Fig. 5).

The GAM in which the time series of maximum and minimum daily changes are modeled as a function of year gave nonsignificant smoother for the start of the spring bloom (Table 1; Fig. 6). The GAM of the timing of the end of the spring bloom gave a smoother with a *p* value of 0.033. According to Wood (2006), however, *p* values of a smoother in the order of 0.01 to 0.05 should be interpreted with care. Furthermore, the year 1974 was influential, and the nonlinear pattern of the smoother was mainly determined by the 1974 value (Fig. 6). We, therefore, conclude that no significant temporal changes in the timing of the wax and wane of the spring bloom in the Marsdiep tidal inlet occurred between 1974 and 2007.

The full dataset available for analysis by means of GAMM with a Gamma distribution and log link function, i.e., the second approach, consisted of 1,370 observations in 33 years, with an average number of 41.52 ± 12.72 observations per year. The two models without a correlation

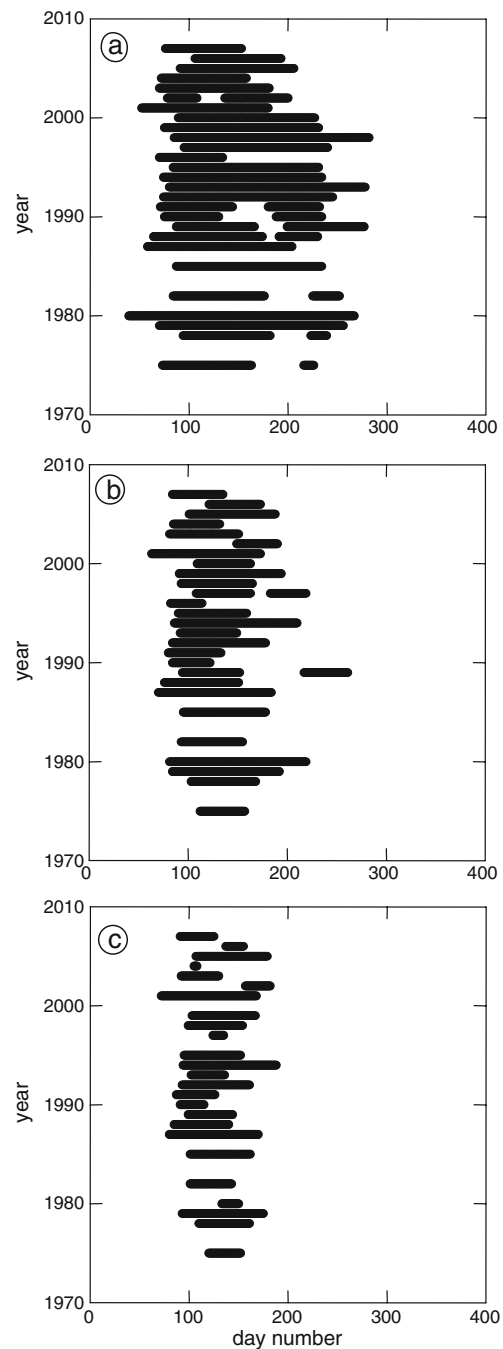


Fig. 4 Days of the year at which chlorophyll-*a* concentrations were **a** higher than 10 mg m^{-3} , **b** higher than 15 mg m^{-3} , and **c** higher than 20 mg m^{-3} as obtained by GAM with a Gamma distribution and log-link function using the annual datasets of field observations in the Marsdiep tidal inlet between 1974 and 2007

structure have the highest value for AIC (Table 2), indicating that these models give the worst fit compared to models that do take correlation structures into account. This result implies that autocorrelation between sequential observations does exist.

For all models that do include correlation structures, models with one 2-dimensional smoother have lower values

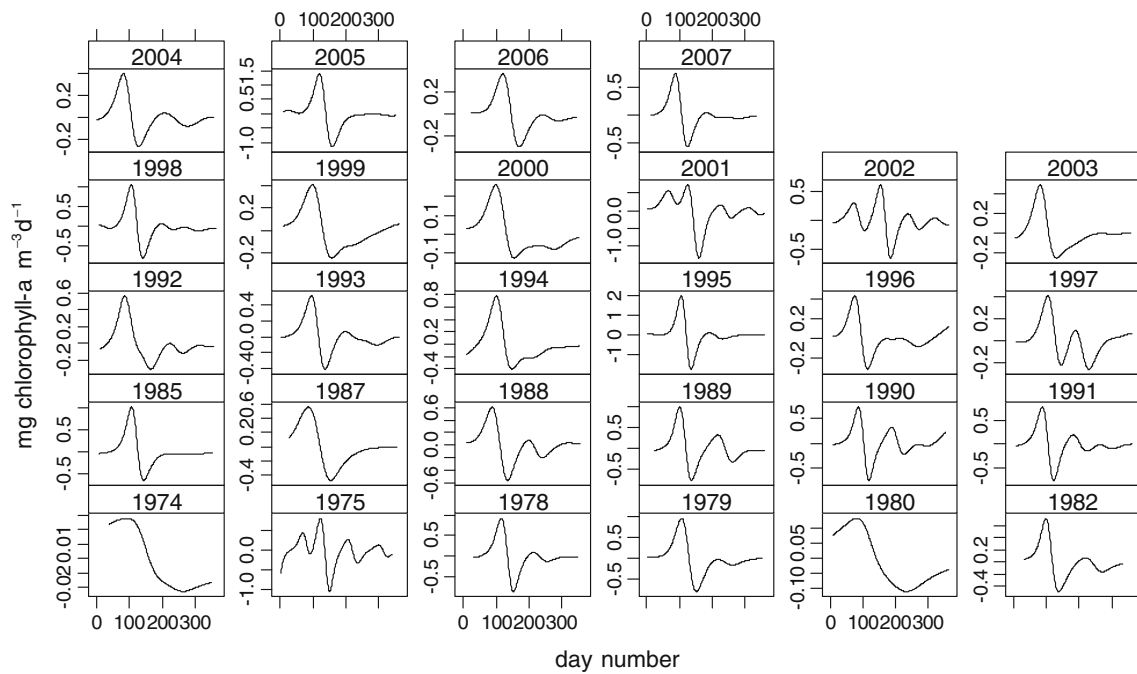


Fig. 5 Daily changes in chlorophyll-*a* concentrations as derived from interpolation of observations in the Marsdiep tidal inlet at high tide between 1974 and 2007 for each year separately. No interpolations

could be made for the years 1976, 1977, 1981, 1983, 1984, and 1986 due to insufficient field data

for AIC than those with two 1-dimensional smoothers (Table 2). This result implies that the seasonal effect was not the same in each year but has changed between 1974 and 2007.

The model with a 2-dimensional smoother and a rational quadratic correlation structure (Schabenberger and Pierce 2002) has the lowest AIC and is selected as the best model (Tables 2 and 3). For this model, the correlation structure (the estimated range is 9.70 and the nugget is 0.47) indicate that observational data are no longer correlated if 10 or more than 10 days apart. A model validation of this model did not show any patterns in the residuals (data not shown).

The results of the GAMM model fitted to the long-term field observations on chlorophyll-*a* concentrations show a fading of the autumn bloom from the 1970s towards the 2000s (Fig. 7). During the 1970s and 1980s, fitted chlorophyll-*a* concentrations were relatively high between

April and June and between mid-July and mid-August (Fig. 8). The relatively low values during midsummer did no longer occur since the early 1990s. Since the mid-1990s, chlorophyll-*a* concentrations higher than 10 mg m⁻³ do no longer occur during August (Fig. 8a). These findings suggest that fading of the autumn bloom occurred around the early 1990s.

Discussion

The limits of the dataset should be taken into account when interpreting the results of the analyses. First, the datasets of some years have fewer values than others. Second, even with a frequency up to 60 measurements a year, the precise timing of the onset of a bloom is very difficult to determine because wax and wane of phytoplankton may take place at a much shorter time scales, viz. days instead of weeks (e.g., Cadée 1986b). The resulting resolution in the dynamics implies that our findings should only be considered as an indication of actual phytoplankton dynamics (Rolinski et al. 2007).

For the western Wadden Sea, the timing of wax and wane of the phytoplankton spring bloom varied strongly but did not show mean long-term advancements or delays, while the autumn bloom appeared to have weakened between 1974 and 2007 (this paper). Our findings on timing of the wax of the spring bloom are in agreement

Table 1 Generalized additive model analysis of the day numbers at which maximum and minimum daily change occurred, indicating the respective wax and wane of the spring bloom, as derived from interpolation of long-term field observations of chlorophyll-*a* concentrations in the Marsdiep tidal inlet between 1974 and 2007

Timing of spring bloom	Estimated <i>df</i>	<i>F</i>	<i>p</i> Value
Wax	1.661	1.173	0.346
Wane	2.254	1.921	0.033

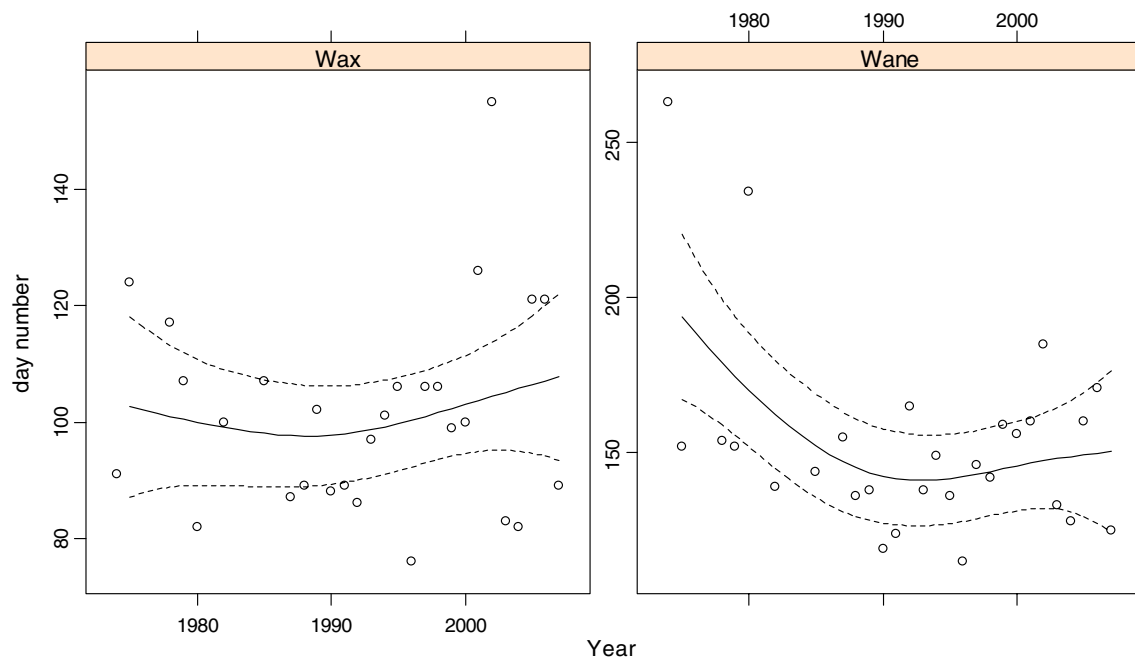


Fig. 6 Annual timing of wax and wane of spring phytoplankton bloom in the Marsdiep tidal inlet at high tide between 1974 and 2007, as derived from maximum and minimum values of daily changes in

chlorophyll-*a* concentrations. A LOESS smoother with a span width of 0.5 was added to aid visual interpretation

with observations for the eastern (Wiltshire et al. 2008) and central North Sea (Edwards and Richardson 2004) where the timing of the onset of the bloom was fairly constant during the last decades. There is a suggestion, however, of an advancement of the start and peak of the phytoplankton spring bloom by 1 month along the Dutch coastline in the southeastern North Sea (Gieskes et al. 2007; Baretta-Bekker et al. 2009) since the late 1990s.

The fading of the autumn bloom is in agreement with observations in the northern Wadden Sea where chlorophyll-*a* concentrations in summer (May–Sept) had

decreased since the mid-1990s (Loebl et al. 2008, van Beusekom et al. 2009). This decrease was explained by a combination of an enhanced grazing pressure by benthic filter feeder activity and mesozooplankton due to an increase in water temperatures and a decrease of the riverine nitrogen supply (van Beusekom et al. 2009). In the southwestern part of the Wadden Sea, however, the summed filtering capacity of the major benthic grazers declined during the last decades (Philippart et al. 2007). Unfortunately, we do not have long-term field observations on grazing pressure by zooplankton in this area. Assuming that

Table 2 Estimated AICs for various generalized additive models, with one and two dimensions and a number of correlation structures, of long-term field observations of chlorophyll-*a* concentrations in the Marsdiep tidal inlet between 1974 and 2007

Model Code	No. of dimensions	Smoothers	Correlation structure	AIC
M1	2	$f(\text{Day}, \text{Year})$	No correlation	2,679.164
M2	1	$f_1(\text{Day})+f_2(\text{Year})$	No correlation	2,705.32
M3	2	$f(\text{Day}, \text{Year})$	Autoregressive correlation	2,561.595
M4	1	$f_1(\text{Day})+f_2(\text{Year})$	Autoregressive correlation	2,652.674
M5	2	$f(\text{Day}, \text{Year})$	Exponential correlation	2,483.745
M6	1	$f_1(\text{Day})+f_2(\text{Year})$	Exponential correlation	2,528.89
M7	2	$f(\text{Day}, \text{Year})$	Gaussian correlation	No convergence
M8	1	$f_1(\text{Day})+f_2(\text{Year})$	Gaussian correlation	2,708.841
M9	2	$f(\text{Day}, \text{Year})$	Linear correlation	2,682.103
M10	1	$f_1(\text{Day})+f_2(\text{Year})$	Linear correlation	2,710.160
M11	2	$f(\text{Day}, \text{Year})$	Rational quadratic correlation	2,475.328
M12	1	$f_1(\text{Day})+f_2(\text{Year})$	Rational quadratic correlation	2,514.791

Table 3 Generalized additive mixed model analysis ($n=1,370$, $r^2=0.37$) with a rational quadratic correlation structure of long-term field observations of chlorophyll-*a* concentrations in the Marsdiep tidal inlet between 1974 and 2007

Variable	Coefficient	SE	<i>t</i>	<i>p</i> Value	GAMM			
					Source	Estimated <i>df</i>	<i>F</i>	<i>p</i> Value
Intercept (α)	2.33483	0.02695	86.64	<0.0001	s(Day, Year)	18.82	25.01	<0.0001

zooplankton grazing did not increase since the late 1990s, the fading of the autumn bloom could be reflecting the decline of the summer productivity of the phytoplankton as a result of the decrease in riverine nutrient inputs into the western Wadden Sea.

These findings point to regional differences in long-term trends in seasonality, viz. a shortening of the growing season due to the fading of the autumn bloom in the Wadden Sea and a lengthening of the growing season due to an advancement of the spring bloom in the open North Sea. If changes in chlorophyll-*a* concentrations reflect changes in primary productivity, the disappearance of the relatively high chlorophyll-*a* concentrations in late summer in the Wadden Sea may have resulted in decreased growth rates in primary consumers and have been restrictive to species that depended on food supply during this season (e.g., to build up reserves to reproduce or to survive low food conditions in winter). These changes in seasonality in the phytoplankton blooms may have contributed to the coincident shift in bivalve species composition, the decrease in bivalve filtering capacity since the late 1980s (Philippart et al. 2007), and the large-scale offshore shift of juvenile plaice from the Wadden Sea to the adjacent North Sea (Pastoors et al. 2000, Grift et al. 2004).

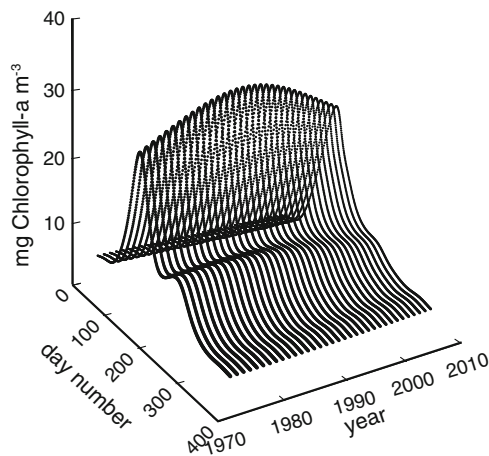


Fig. 7 Fitted values on long-term field observations on chlorophyll-*a* concentrations, as measured in the Marsdiep tidal inlet at high tide between 1974 and 2007, obtained by GAMM with a 2-dimensional smoother. The vertical axis shows the fitted values (mg chlorophyll-*a* m⁻³) and the other two axes the day number (with values between 1 and 364) and the year (from 1974 to 2007)

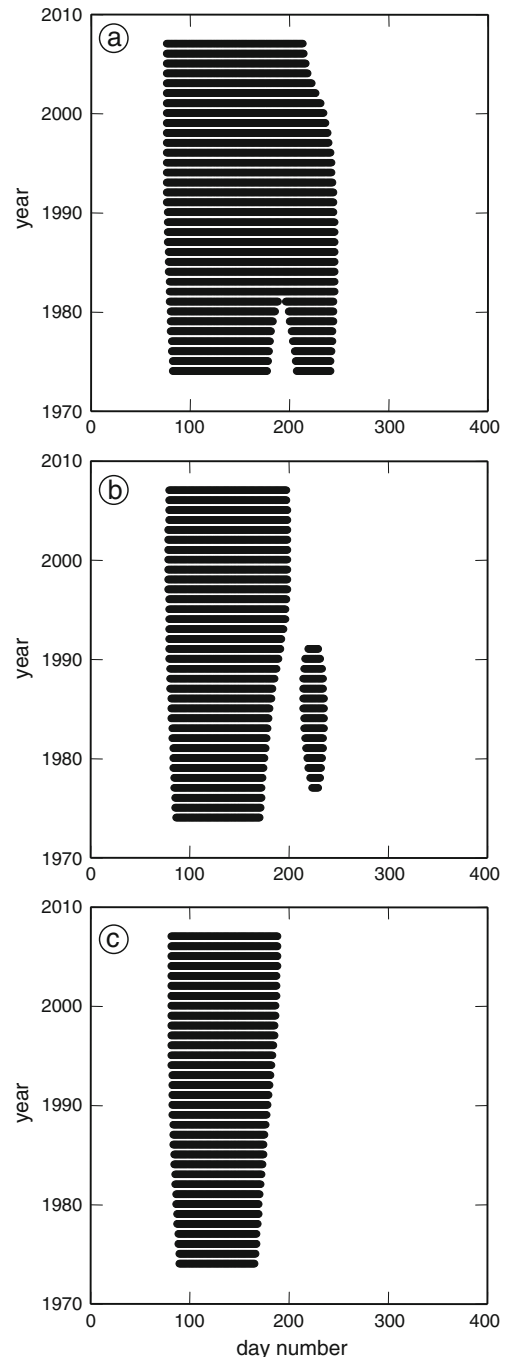


Fig. 8 Days of the year at which chlorophyll-*a* concentrations were **a** higher than 10 mg m⁻³, **b** higher than 11 mg m⁻³, and **c** higher than 12 mg m⁻³ as obtained by GAMM with a 2-dimensional smoother using the full dataset of field observations in the Marsdiep tidal inlet between 1974 and 2007

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