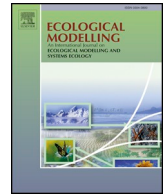




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Modeling of intra-annual abundance distributions: Constancy and variation in the phenology of marine phytoplankton species over five decades at Helgoland Roads (North Sea)

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ABSTRACT

Annually recurring environmental processes such as the cycle of temperature and light drive the phenology of marine plankton populations. Improved knowledge about the homogeneity and amplitude of the phenological response of phytoplankton to climate change is essential for an assessment of ecological consequences on the marine ecosystem. We analyzed phenological variability of 21 phytoplankton species monitored work-daily at Helgoland Roads from 1962–2015. We used a function of “Weibull”-type to estimate phenological dates of species-specific abundance peaks. The combination of derived dates and peak abundances formed the basis for the analyses of long-term changes in phenological time slots and associated environmental conditions.

Species-specific preferences in combination with seasonally varying environmental trends resulted in a complex pattern of phenological long-term response. Phenological trends showed both constant occurrence and shifts to an earlier or later occurrence. Co-occurring phytoplankton species were shown to exhibit different phenological trends even within identical time slots. Differences in species-specific trends in timing also reflected the seasonally varying shifts in water temperature ranges due to warming. In spring and summer, the main patterns of common variability in timing were associated with different abiotic and biotic drivers. The majority of species showed more narrow time slots related to the occurrence of higher peaks. Considering the variation of species occurrence in their “typical” time window provided insight in terms of assigning the effect of environmental drivers on inter-annual phenological variation. Phytoplankton species with similar long-term trends in timing (days) showed different trends in biomass, i.e. the phenological changes resulted from different ecological responses to environmental change. The local character of environmental trends at Helgoland underpins the limits for comparison of findings between different measuring sites or wider areas, such as the North Sea. The study emphasizes the benefit and necessity of a highly resolved phytoplankton record for a true understanding of long-term ecological changes in a highly dynamic marine environment such as the North Sea.

1. Introduction

Marine ecosystems in mid and high latitudes are characterized by distinct seasonality. Periodicity of light and temperature govern the recurrence of growth and timing (i.e. the phenology) in marine plankton. Spring phytoplankton blooms form the early annual energy base for higher trophic levels, e.g. zooplankton and fish (Smetacek and Passow, 1990; Cushing, 1990; Richardson, 2008; Calbet et al., 2014). Marine phytoplankton dynamics and timing are driven by light, temperature, water column mixing (stratification), hydrography, nutrient availability and consumption by zooplankton (Wiltshire et al., 2008; Winder and Sommer, 2012; Wiltshire et al., 2015). The relative

importance of the drivers of phytoplankton phenology on the regional scale is likely to be variable. Winder and Cloern (2010) emphasize the role of site characteristics in ecological responses to climate change and also the relative importance of the annual cycle versus other drivers of inter-annual variability. Sarker et al. (2018) have demonstrated the sensitivity of role of different drivers on species combinations on the long term occurrence of species. The seasonality of the regional climate constrains the seasonality of plankton (Sommer, 1994; Lohmann and Wiltshire, 2012; Wiltshire et al., 2015). Different trends in phenology can manifest for the spring and autumn period for the same species, (e.g. Edwards and Richardson, 2004; Conversi et al., 2009). In particular in turbid waters, like those of the southern North Sea, the

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seasonality of light availability related to turbulence, seems to be most relevant to the onset of the primary production (Gaedke et al., 2010; Wiltshire et al., 2015).

Long term shifts in plankton have been related to climate change in the marine ecosystem (Edwards and Richardson, 2004; Thackeray et al., 2008; Ji et al., 2010; Poloczanska et al., 2013; IPCC et al., 2014; Wiltshire et al., 2015). Warming of ocean and coastal seas is considered to be especially important for considerations on biogeographical shifts of species and phenology of marine planktonic organisms (Richardson, 2008; Beaugrand, 2009; Beaugrand et al., 2009; IPCC et al., 2014; Atkinson et al., 2015). Consequences of changes in phytoplankton phenology are often discussed in the context of temporal decoupling (“match-mismatch”) of primary producers and consumers (Cushing, 1990; Richardson, 2008; Atkinson et al., 2015). The asynchronous phenological responses between phytoplankton and zooplankton with regard to warming, for example, can lead to local changes in the plankton composition and feeding relationships (Wiltshire et al., 2010; Mackas et al., 2012). As outlined in several studies, the timing of, for example, the spring phytoplankton bloom, or “trophic mismatch” is not necessarily closely related to seasonal temperature variation (Wiltshire et al., 2008; Poloczanska et al., 2013; Atkinson et al., 2015). Several studies had shown changes in the temporal and spatial occurrence of individual zooplankton species (Edwards et al., 2010; Mackas et al., 2012), zooplankton communities (Beaugrand, 2009; Beaugrand et al., 2009), or populations of diatoms and dinoflagellates (Wiltshire et al., 2008, 2015) in the North Sea area. With regard to the analysis of individual phytoplankton species on the time scale of decades, the number of available investigations is however, limited (e.g. Gebühr et al., 2009; Schlüter et al., 2012; Atkinson et al., 2015).

Species-specific preferences can be reflected by variable phenological responses (e.g. Schlüter et al., 2012; Wiltshire et al., 2015), i.e. by non-uniform timing shifts to changes in environmental conditions. The goal of this study was to better assess the inter-annual and seasonal variation of timing occurrence for single phytoplankton species on a multi-decadal scale. For this we used the species and environmental data from the Helgoland Roads time series which represents one of the most comprehensive data sets available for marine observations (see Wiltshire et al., 2010). We chose a broad spectrum of species representative of intra-annual occurrence and reflecting fundamental differences due to, for example, varying preferences to light and water temperature (e.g. Gebühr et al., 2009; Mieruch et al., 2010; Scharfe, 2013; Wiltshire et al., 2015).

Most existing phenological indices (e.g. Ji et al., 2010; Brody et al., 2013) have been applied to aggregated variables such as total biomass or the abundances of phytoplankton groups such as diatoms and dinoflagellates (Edwards and Richardson, 2004; Wiltshire et al., 2008). However, for a broader understanding on marine phenology it is important to know more about the species-specific reactions and whether these behave in the same manner as total populations. When related to a summed population of organisms, the temporal structure in the

occurrence of individual species will be significantly more heterogeneous. Reflecting this variability, we focused on a peak-based model approach, instead of a cumulative population abundance approach, or compared to approaches with fixed exceedance values (e.g. Ji et al., 2010). We used a Weibull-type fitting approach described by Rolinski et al. (2007) for modeling of abundance peaks of single phytoplankton species. In order to describe the temporal course of phenological variation we applied LOESS smoothing (Cleveland and Delvin, 1988; Cleveland et al., 1988) to scatterplots of species-specific intra-annual abundance distributions. We proceeded as follows: First, we analyzed the species-specific differentiation of occurrence windows, including their different seasonal modes. Second, we focused on the identification of environmental parameters which are relevant to variation or constancy of species phenology. Third, we determined the variability in species-specific phenological timing against the backdrop of environmental long-term variability. We discuss the uncertainties of assessing long-term phenological shifts and the consequences of our results to considerations of shelf sea ecosystem reaction to climate fluctuations.

2. Methods

2.1. Data

In 1962, a pelagic monitoring program at the measuring site Helgoland Roads (54°11.3' N, 7°54.0' E) was started by the Biologische Anstalt Helgoland. This site, about 60 km of the German coast, represents a marine transition zone between coastal waters and the open sea. On working days surface water samples were taken with a bucket lowered from a research vessel. Secchi depth and water temperature were measured directly on station. Water samples were analysed in the laboratory for nutrients, salinity and phytoplankton. Phytoplankton subsamples were preserved using Lugol's solution at 0.1% concentrations in brown glass bottles and were counted daily using the Utermöhl method (Lund et al., 1958). The identification of the phytoplankton was usually carried out down to the species level (Wiltshire and Dürselen, 2004). Nutrient concentrations were measured using the standard colorimetric methods as described by Grashoff (1976). Salinity was measured using a salinometer (Autosal, Gamma Analysen Technik GmbH). In our study we considered the time series of the parameters water temperature, Secchi depth, salinity and the nutrients nitrate, phosphate and silicate (Table 1). The regular monitoring of the zooplankton was started in 1974. Since then, nets of two different sizes, a 150-µm Nansen net and a 500-µm CalCOFI net, have been used for sampling three times a week. For more detail of the sampling procedure and analytical methods used at Helgoland Roads, see Greve et al. (2004) and Boersma et al. (2015) for zooplankton, Wiltshire and Dürselen (2004) for phytoplankton and Raabe and Wiltshire (2009) for nutrients. We used the sum of five important herbivore grazers as an indicator for zooplankton impact (Table 1). The analysis of the phenological response of phytoplankton was carried out using a representative seasonal cross section

Table 1

List of observational time series at Helgoland Roads considered in the study. Sunshine duration was provided by the German Weather Service for the Helgoland area.

Diatoms	<i>Asterionellopsis glacialis</i> (Castracane) Round, <i>Cerataulina pelagica</i> (Cleve) Hendeby, <i>Chaetoceros</i> spp, <i>Detonula pumila</i> (Castracane) Schütt, <i>Ditylum brightwellii</i> (West) Grunow, <i>Eucampia zodiacus</i> Ehrenberg, <i>Guinardia delicatula</i> (Cleve) Hasle, <i>Guinardia flaccida</i> (Castracane) Peragallo, <i>Leptocylindrus minimus</i> Gran, <i>Odontella aurita</i> (Lyngbye) Agardh, <i>Odontella sinensis</i> (Greville) Grunow, <i>Pseudo-nitzschia</i> spp, <i>Rhizosolenia imbricata</i> Brightwell, <i>Rhizosolenia setigera</i> Brightwell, <i>Skeletonema costatum</i> (Greville) Cleve, <i>Thalassionema nitzschioides</i> (Grunow) Hustedt, <i>Thalassiosira</i> spp	1962-2015	cells L ⁻¹
Dinoflagellates	<i>Ceratium furca</i> (Ehrenberg) Claparède und Lachmann, <i>Ceratium fusus</i> (Ehrenberg) Dujardin, <i>Noctiluca scintillans</i> (Macartney) Kofoid und Swezy, <i>Prorocentrum micans</i> Ehrenberg	1962-2015	cells L ⁻¹
Zooplankton	as sum of: <i>Acartia</i> spp, <i>Pseudo-/Paracalanus</i> spp, <i>Calanus</i> spp, <i>Centropages</i> spp, <i>Temora longicornis</i>	1974-2015	N m ⁻³
Nutrients	Nitrate (NO ₃), Phosphate (PO ₄), Silicate (SiO ₂)	1962-2015 Silicate (1966-2015)	µmol L ⁻¹
Physical parameter	Water temperature, Sunshine duration, Salinity, Secchi depth	1962-2015 Secchi (1968-2015)	°C, hours day ⁻¹ , m

of the species observed. Specifically, eighteen phytoplankton species and three phytoplankton genera of the most dominant marine phytoplankton groups were selected (Table 1).

The species were selected according to the criteria for a complete and homogeneous monitoring within the time period 1962–2015. Data pre-processing was performed as follows: First, all daily time series were subjected linear interpolation to fill the gaps of missing data. Second, the interpolated time series were smoothed using a moving five-day average (see Mieruch et al., 2010). These time series formed the basis for all subsequent analyses.

2.2. Peak modeling – deriving phenological dates

Earlier analyses of long-term changes in individual phytoplankton species at Helgoland Roads stressed the importance of recording seasonally different developments and the non-homogeneous changes in abundance or biomass over time (e.g. Schlüter et al., 2012; Scharfe 2013). The high-resolution data set of Helgoland Roads allowed the application of a model-based approach to describe long-term phenological changes in more detail. In addition, a non-cumulative approach would also provide a detailed overview of the intra-annual shifts in relation to species-specific biomass. To take these different aspects into account, we applied a method proposed by Rolinski et al. (2007). This procedure entails the fitting a Weibull function to an annual (seasonal) phytoplankton abundance curve and then estimating phenological dates from the function parameters. Rolinski et al. (2007) applied the Weibull-type fitting approach to the spring biomass of total diatoms, i.e. their study was related on the phenological description of the uni-modal case of a highly aggregated parameter. Here, we focused on the identification of phenological dates of single phytoplankton species abundance which showed uni- and multi-modal peak distributions. In addition to timing, this approach also provided information on the size of the peaks (integral of the curve, see below), which was used in a second step for modeling and analysis of long-term phenological changes (see section 2.3).

Weibull functions are versatile in their adaptability to different distributions and thus, provide information on location and shape parameters. We followed the approach of Rolinski et al (2007) and used a six-parametric Weibull function of the form

$$w(x) = (p_4 + \exp(-(x/p_5)^{p_6})) \times (1 - p_1 \times \exp(-(x/p_2)^{p_3})) \quad (1)$$

where x is a time variable (days of year) and p_1, \dots, p_6 are parameters to be determined, the latter describing characteristics of increasing and decreasing branches of the curve and considering different base levels before and after a peak. After scaling the original abundance curve to the interval $[0, 1]$ (i.e. to the original peak maximum, y_{max}) the function parameters in Eq. (1) are determined by fitting a nonlinear regression of the function w to the scaled values. The goodness of fit was estimated by the coefficient of determination (R^2) between the original and the fitted curve w_{fit} . Based on w_{fit} the phenological dates (“cardinal dates”, Rolinski et al., 2007) were then determined. All calculations were performed using the CDW algorithm implemented in the R-package carditates (Rolinski et al., 2015) which extracted the phenological dates from fitted six-parametric Weibull curves (Eq. (1)).

The date of the maximum value of the w_{fit} of a single peak was taken as a description of the timing of the maximum abundance, hereinafter referred to t_{mid} (Fig. 1a). We determine the integral of w_{fit} (area below the curve) considering potentially different base levels before and after t_{mid} . As many of the peaks showed an asymmetry between the increasing and decreasing branches, the phenological dates describing the beginning and the end of a peak were calculated as follows: As shown in Fig. 1a, the date of the 10% quantile of the integral before t_{mid} was defined as the beginning of the peak (t_{beg}) and the date of the 90% quantile of the area after t_{mid} was defined as the end of the peak (t_{end}). The use of a moving five-day average of the original abundance (see above) improved the fitting of the rising and falling curve segments, i.e. the determination of t_{beg} and t_{end} . The peak width was defined as the interval t_{beg} to t_{end} .

Species-specific differences and inter-annual variability result in a high number of different intra-annual peak structures. The distance between individual peaks as well as the ratio of the height of the maximum peak to the next smaller peak showed a high variation (Fig. 1). This prevented the use of the same algorithm setting and a constant offset of the peak window for all years and species. Therefore, visual inspection of the data to ensure correct handling was imperative. Two unequal peaks within one year compared to two equal peaks required the variation of the tuning parameter $minpeak$ (range 0–1, used default: 0.3) which defined the minimum value of the maximum peak height which is regarded as another peak (Rolinski et al., 2015). The model fit shown for *Guinardia delicatula* (Fig. 1a), for instance, was based on a value of 0.1 and that of *Skeletonema costatum* (Fig. 1b) on a value of 0.3. Cases showing a non-zero base abundance level between two peaks closely adjacent in time caused further tuning effort due to the difficulty of their clear separation. In such cases we used the tuning parameter $mincut$ (range 0–1, used default: 0.15) which controls for the minimum relative height of a decline compared to the lower of the two neighbouring peaks at which these peaks are regarded as separate peaks (Rolinski et al., 2015). In the case of *Eucampia zodiacus* in the year 1996 (Fig. 1c) the use of the default to separate the peaks was sufficient.

The whole procedure was repeated for each year and each species (genus) separately. The number of years of presence as well as the average number of peaks differed in part between single phytoplankton species. Considering all fitted peaks of each species in the period of observation, the mean value of R^2 ranged between 0.86 (*Thalassionema nitzschioides*) and 0.96 (*Cerataulina pelagica*).

2.3. Analysis of phenological long-term changes

The phenological dates and peak sizes derived in the previous section produced a detailed picture of species-specific intra-annual abundance distributions on the long-term. Fig. 2 showed this as an example for the diatom *Guinardia flaccida*. The center of a circle refers to the value of t_{mid} and its diameter corresponds to the root-transformed abundance of the 90% area under the peak curve (i.e. the sum between t_{beg} and t_{end} , see above). The largest diameter referred to a maximum peak sum of 5.67×10^5 cells L^{-1} (year 1970). These time-weighted distributions can be considered as a scatterplot, with the scale for x on the horizontal axis (in years) and the scale for y on the vertical axis (in day of year). In order to determine the temporal course of phenological changes we applied LOESS smoothing to the scatterplot (Cleveland et al., 1988, 1992). Analyses were performed using the LOESS (acronym for local regression) algorithm implemented in the Stats package of R, version 3.3.3 (R Core Team, 2018). LOESS is a non-parametric regression technique that can be used to fit a curve through points in a scatterplot. In this context, non-parametric means that no assumptions need to be made about the underlying distribution (form) of the data (Jacoby, 2000). However, fitting a LOESS smoothed curve to data pairs in a scatterplot required the estimation of two parameters. The first parameter α (span) determines the degree of smoothing, i.e. the proportion of all data that is to be used in each local fit (size of neighborhood of x). Here, we used $\alpha = 0.25$ for all fits. This was proved to be a suitable compromise between smoothing and preserving of temporal structural information. The second parameter λ specifies the degree of the polynomial which the LOESS procedure fits to the data (Jacoby, 2000). We used $\lambda = 2$, i.e. the local regression fitting based on quadratic equations.

In the LOESS procedure, the points in a specific neighborhood determined by α (span) were weighted according to their distance to x (tricubic weighting, R Core Team, 2018). This weighting approach initially contained no information on the size of the peaks associated with individual points (grey circles in Fig. 2). In order to take into account the information on different sizes of the peaks, prior to LOESS smoothing the single peak timing dates (i.e. t_{mid}) were weighted by the associated root-transformed abundance sum belonging to the 90% integral (see above). The solid line in Fig. 2 represents the LOESS fit based

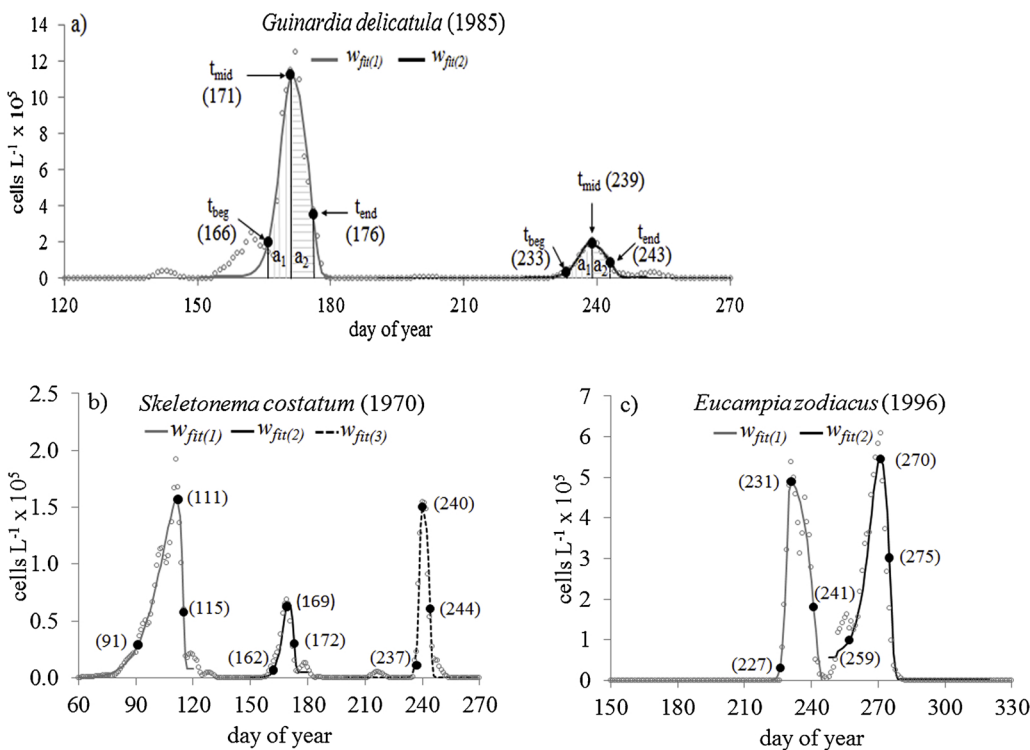


Fig. 1. Scheme of the modeling approach for the intra-annual abundance distribution of three phytoplankton species in different years. Observations (open circles) and fitted Weibull-type functions w_{fit} (lines) were re-scaled to the respective original peak maximum (y_{max}). For each fit shown R^2 is > 0.9 . Phenological dates (dots) were derived from w_{fit} (in brackets: day of year). The hatched areas (a_1 , a_2) each describe 90% of the area under the curve (only marked in the upper panel) before and after the maximum of w_{fit} (t_{mid}). The dates of the 10% quantiles are termed as t_{beg} and t_{end} .

on this approach, hereinafter referred to (time series of) mean t_{mid} . The dashed lines showed the related 95% confidence interval. During years without peaks (no open circle on the solid line, Fig. 2) no LOESS fit value is available. In such cases gaps were filled by linear interpolation, between neighboring LOESS fit values.

Where species showing one (seasonal) occurrence pattern (e.g. *G. flaccida*, Fig. 2), the LOESS procedure was performed only once for the period 1962–2015. Where species showed different seasonal occurrence patterns, the LOESS procedure was applied for each sub-period separately.

2.4. Timing conditions

Species-specific preferences in terms of the environmental conditions as described by eight environmental parameters (Table 1) were analysed by calculating the conditions associated with the time series of mean t_{mid} derived from the LOESS procedure (see previous section). The resulting time series (e.g. water temperature at mean t_{mid}) were then compared to the background conditions in the corresponding time window, in order to analyse the response in timing conditions and timing dates to long-term environmental changes.

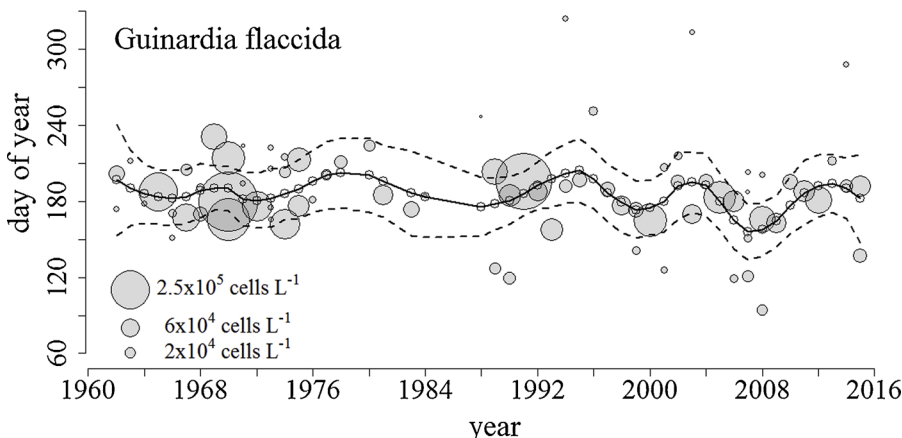


Fig. 2. LOESS curve (solid line) fitted with $\alpha = 0.25$ and $\lambda = 2$ to the annual distribution of t_{mid} (center of grey circles) of the species *Guinardia flaccida*. The LOESS smoothing of timing dates t_{mid} considered the peak sizes (diameter of grey circles) by additional weights. The dashed lines represented the 95% confidence interval. During years without peaks no fitted value is available (no open circle on the solid line). Gaps were filled by linear interpolation.

2.5. Comparison of periods

A comparison of the periods 1962–1988 and 1989–2015 was made to test for changes in timing and related environmental conditions. The Kruskal-Wallis-test was applied to test for significant differences in the medians. To test for equal coefficient of variation (CV), we used the Fligner-Killeen-test (Fligner and Killeen, 1976). The t -test was used to test for changes in the mean value. All statistical tests were performed using the software Past, version 3.16 (Hammer et al., 2001).

2.6. Analysis of common variation in timing

Principal Component Analysis (PCA, see von Storch and Zwiers, 1999) was applied to the time series of mean t_{mid} for analyses of the pattern of common variation in species-specific developments. These analyses were carried out separately for the first and second half of the year, with different numbers of time series included. The strength of relationships between the Principal Components (PCs) and background environmental conditions was analyzed using the Spearman correlation coefficient r_s . Analyses were performed using Past, version 3.16.

3. Results

3.1. Peak structure characteristics

The phytoplankton species considered here occurred in the annual

time period from February to October (Fig. 3a). The timing of the “spring species” (ranging from *O. aurita* to *C. pelagica*) was between March and May. The mean timing of most of the other diatom and dinoflagellate species was between late June and late August. The timing dates (i.e. t_{mid}) varied considerably between single species

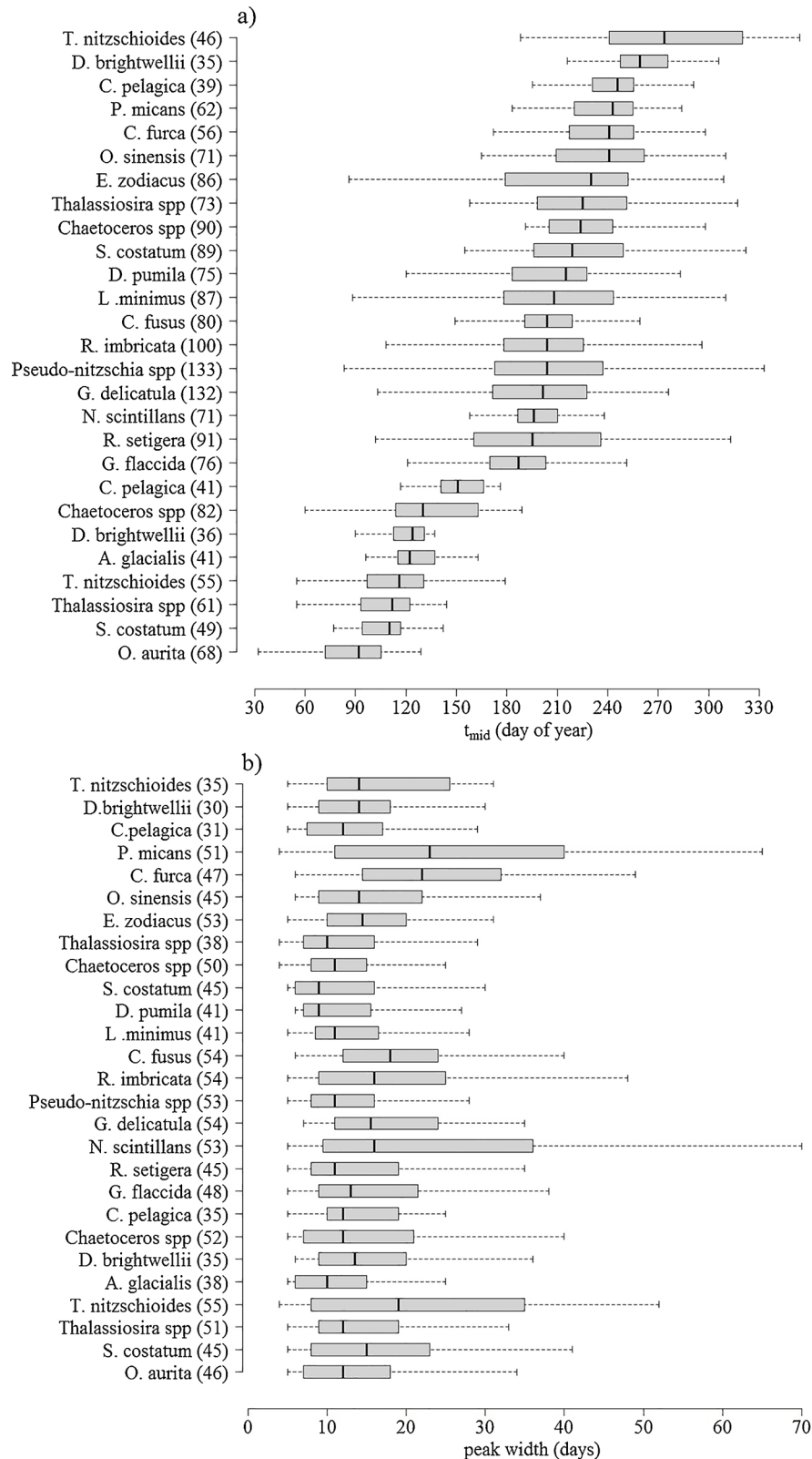


Fig. 3. Boxplots of t_{mid} (a) and peak width (b) for all species for the period 1962-2015. The numbers in parentheses indicate (a) the number of peaks taken into account and (b) the number of years of presence in the period 1962-2015. Double species names are given if different calculation periods in spring and summer have been used.

within similar time periods (Fig. 3a).

The calculated long-term occurrence of most diatoms had a mean peak width of around two weeks (Fig. 3b). The occurrence phases of the dinoflagellates were significantly longer at three to four weeks. No species-characteristic relationships were found between the intra-annual position of t_{mid} and the width of the peak. While some species showed no correlation between peak width and sum of abundances (e.g. *C. pelagica*, *C. fusus*), others showed a significant correlation (e.g. *N. scintillans*, *Chaetoceros* spp, $r_s = 0.58$ and 0.61 , both $p < 0.001$).

3.2. Intra – annual peak distribution of phytoplankton species

Intra-annual peak occurrence was found to be different for each species, reflecting the environment needs (niche) and the adaptive

ability of a species. On the basis of 16 example phytoplankton species, different changes of properties were visible over their long-term occurrence (Fig. 4). The forms of temporal occurrence showed a high variation. Species such as *O. aurita* in spring (Fig. 4a) or *N. scintillans* in early summer (Fig. 4h) consistently showed little variation with regard to their temporal occurrence. For species occurring in both halves of the year, the trends of both developments could be similar (*S. costatum*, *Thalassiosira* spp, Fig. 4b, c) or different (*Chaetoceros* spp, Fig. 4f). Shifts towards an earlier occurrence in spring (e.g. *T. nitzschioides*, *D. brightwellii*, Fig. 4d, e) and early summer (*R. imbricata*, Fig. 4k) as well as shifts towards a later occurrence in late summer (e.g. *E. zodiacus*, Fig. 4m) were found. In summer, *R. setigera* showed a 10-year phase of strongly reduced abundance (or absence) which was followed by an abrupt shift towards later occurrence (Fig. 4g). In contrast, the species

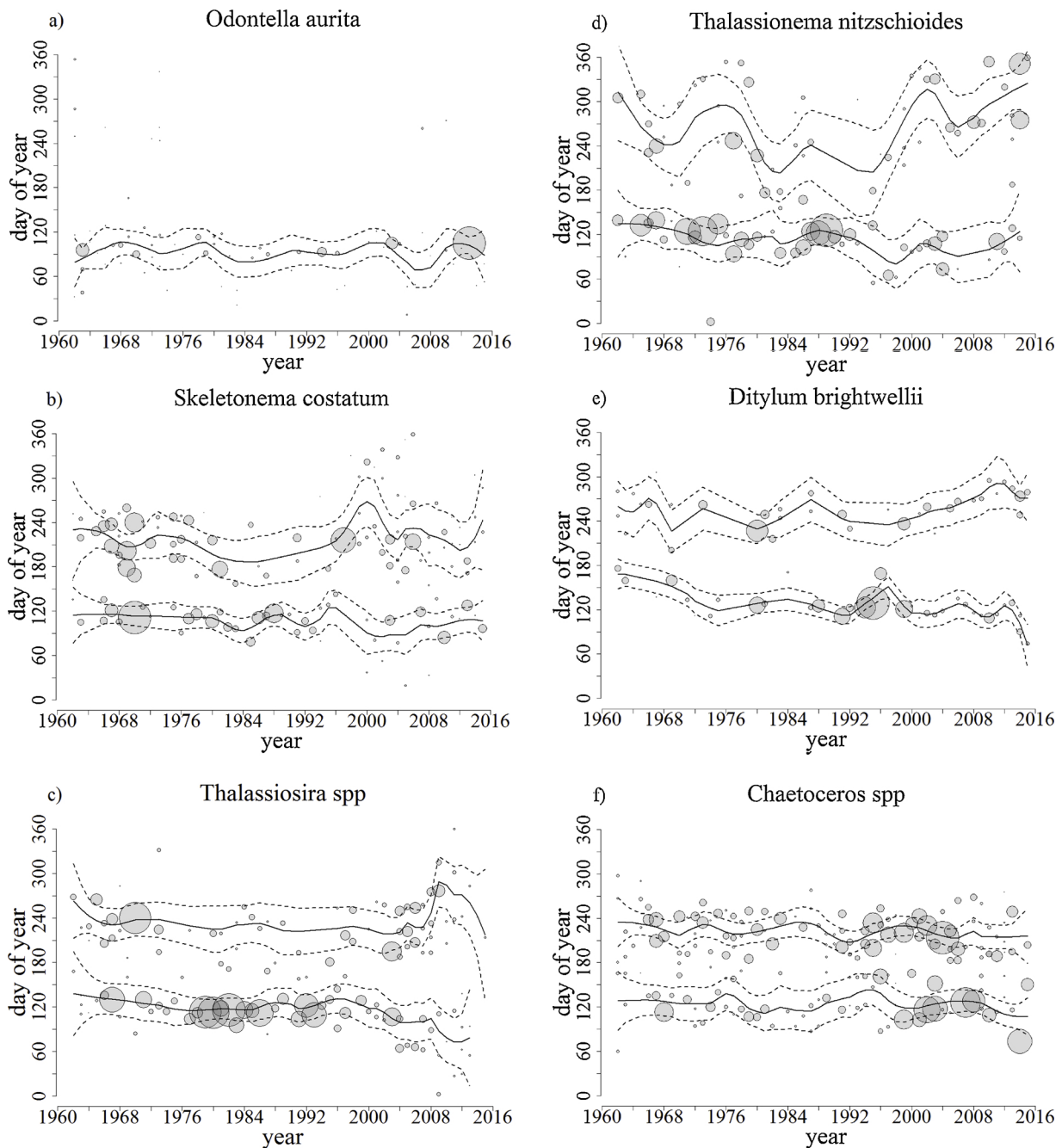


Fig. 4. Intra-annual distribution of abundance peaks (grey circles) of 16 different phytoplankton species during the period 1962–2015. Solid lines represent LOESS fits (mean t_{mid}) and dashed lines represent the 95% confidence interval. Variations in the diameter of the circles are scaled to the specific species cell numbers.

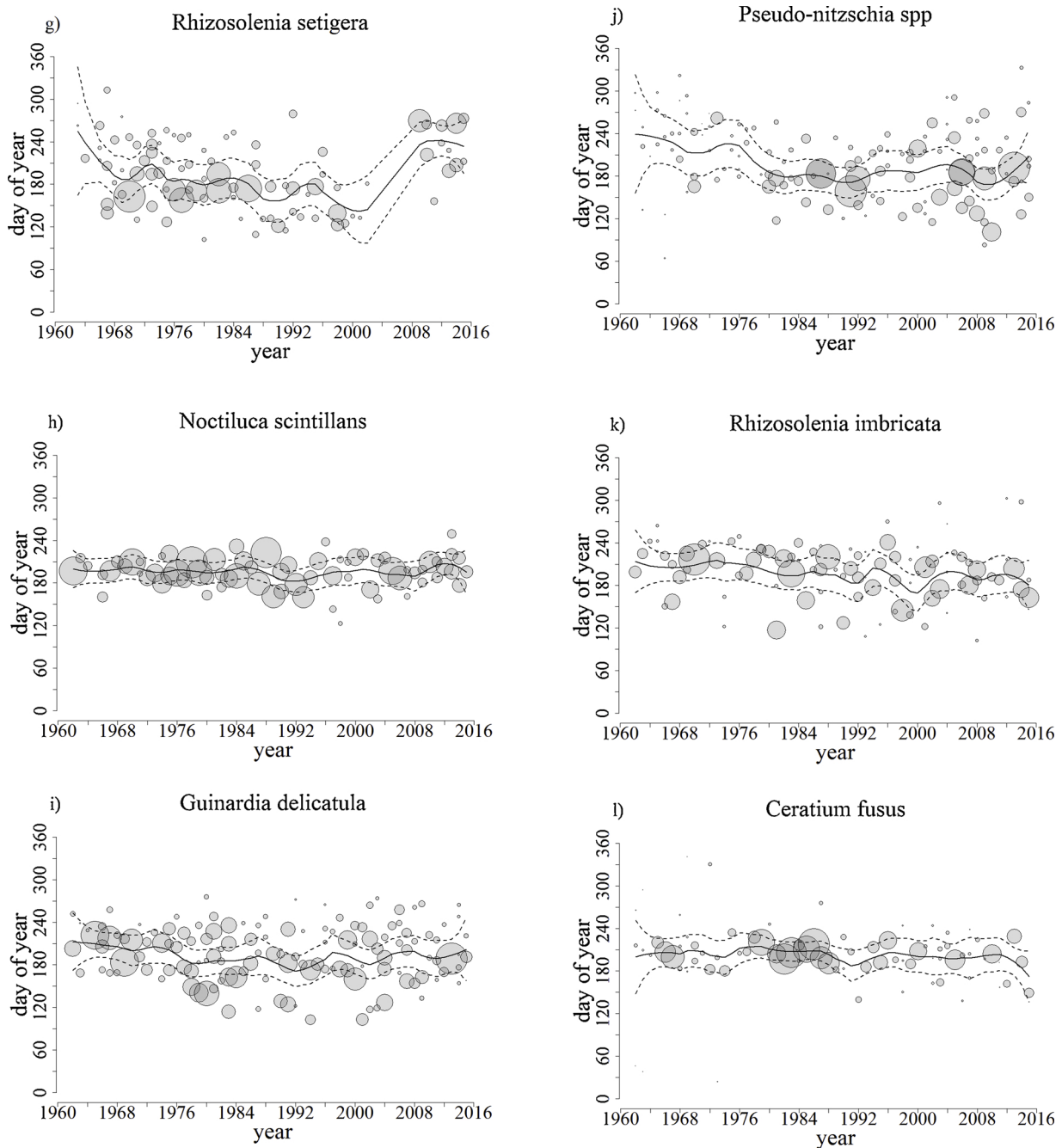


Fig. 4. (continued)

O. sinensis showed a temporary shift of the occurrence into spring (Fig. 4n). Species such as *G. delicatula* (Fig. 4i) showed a consistently broad occurrence throughout the year. This made it impossible to calculate a suitable separation into two different periods for a more meaningful mean estimate of t_{mid} . On the other hand, *Pseudo-nitzschia* spp showed an increase in the range of occurrence since the end of the 1990s (Fig. 4j). The inter-annual variation in t_{mid} (expressed as the CV) was lower for the dinoflagellates *N. scintillans* (Fig. 4h), *C. fusus* (Fig. 4l), *C. furca* (Fig. 4o), and *P. micans* (Fig. 4p) than for most diatoms.

Shifts in timing were often associated with different changes in abundance and occurred at different times (e.g. Fig. 4c, j, o). Phases with absence or reduced occurrence numbers differed between species. These were also seen to vary between the first and second half of the year in one species (e.g. Fig. 4c). There were also significant differences

in the regularity of the level of total annual abundance (biomass). Here the species *N. scintillans* (Fig. 4h), *G. delicatula* (Fig. 4i) and *R. imbricata* (Fig. 4k) showed the most uniform occurrence. The temporal changes of most other species (cf. Table 1) included in the study could be assigned to temporal change forms as shown in Fig. 4.

3.3. Shifts in timing

Fig. 5 summarized the range of temporal shifts of all phytoplankton species. Due to the discontinuous nature of several species-specific shifts over time we used the medians of mean t_{mid} (black lines in Fig. 4) of the two periods, 1962–1988 and 1989–2015, to analyse the extent of temporal shifts. Shifts amounted to 0 to -17 days for those species occurring between late march and early June (Fig. 5). In July, the strongest shifts towards earlier occurrence were found for *Pseudo-*

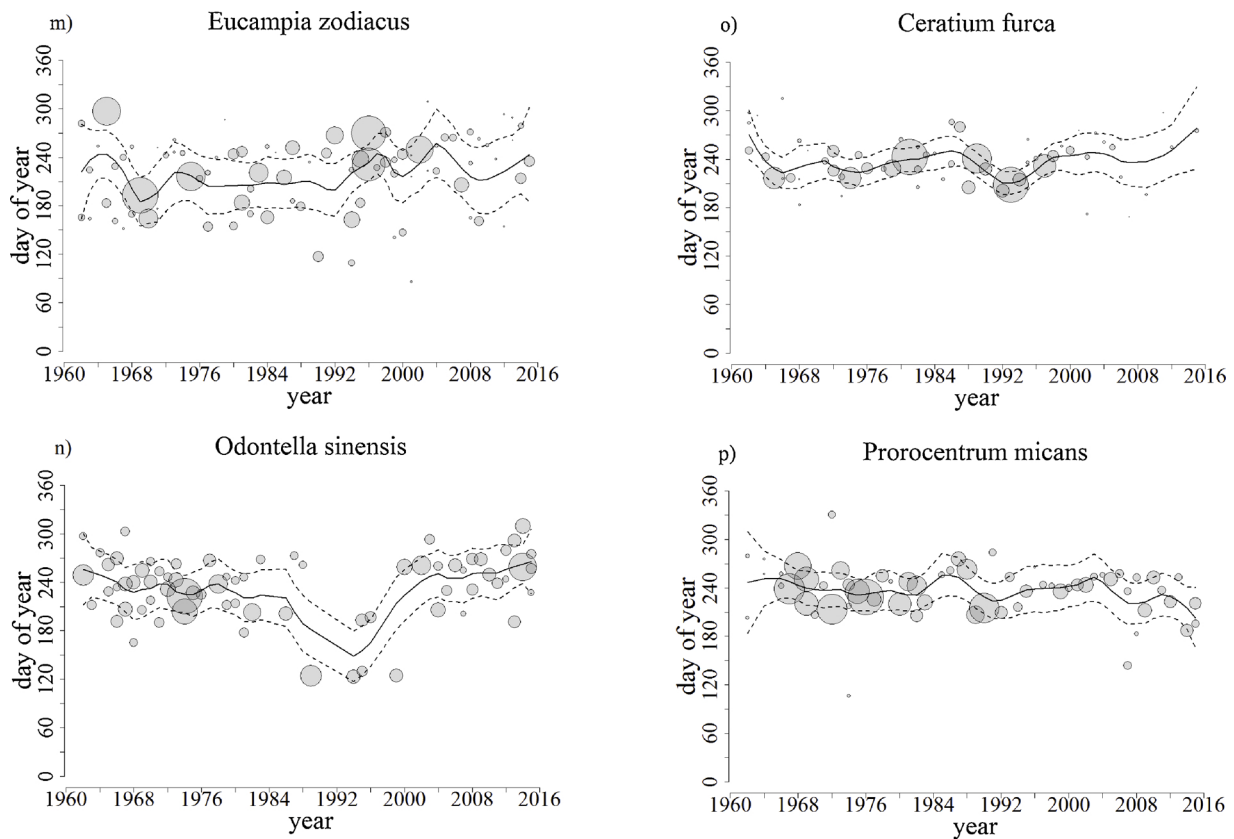


Fig. 4. (continued)

nitzschia spp and *L. minimus*. Neighboring species could show significant differences in the shifts. In late August and early September, for example, the dinoflagellate *P. micans* showed a shift towards earlier occurrence (-7 days) and the diatoms *D. brightwellii* and *T. nitzschioides* showed shifts towards a later occurrence (+10 and +24 days).

In order to put the phenological shifts in the context of changes in abundance (biomass), we also checked for changes in species-specific abundances between both periods. Species showing significant phenological trends exhibited different developments with regard to abundance (e.g. spring situation). Cases of later occurrence were not coupled with significant increases in abundances. The development of *Chaetoceros* spp in spring was the only example of a temporally constant occurrence with increasing abundances (Fig. 5).

We found that in spring several species showed significantly lower peaks at earlier occurrence (Table 2). This was in line with their corresponding trends in abundance and timing. In summer, species such as *Pseudo-nitzschia* spp and *R. imbricata* had significantly higher peaks at earlier occurrence, in accordance with existing trends in abundance.

Significantly higher peaks at earlier occurrence were also found for species without corresponding trends (e.g. *D. pumila*, Table 2). No species in the second half of the year showed significantly higher peaks at later occurrence not even if there are significant trends in timing, (e.g. *E. zodiacus*). For the majority of species the occurrence of higher peaks was coupled to a lower variability in t_{mid} (see CVs in Table 2), i.e. their occurrence was focused on a more narrow time window. Phytoplankton species thus showed a high range of changes in biomass with respect to temporal fluctuations.

3.4. Changes in environmental conditions at Helgoland Roads

We analyzed the changes in the marine environment at Helgoland Roads by comparing the mean annual course of two periods for eight different parameters. Water temperature at Helgoland Roads showed a

significant increase (Fig. 6a). Warming was evident throughout the year, but different parameter ranges showed different shifts. The temperature range of 6–8 °C (representing the starting conditions in spring), for example, showed a shift of about 14 days between both periods (Fig. 6a). The intra-annual period with temperatures > 16° is now greatly extended (before and after the annual maximum), while the timing of the annual maximum did not change on the long-term. Sunshine duration also showed an increase during the second period between March and April (Fig. 6a). Between April and July the warming trend was superimposed by a significant increase in Secchi depth (Fig. 6b). The increase in Secchi depth temporally coincided with the phase of highest light availability (sunshine duration, Fig. 6a). Salinity showed strongest increases between May and October (Fig. 6b). The time of decline in spring (April) remained largely the same over time.

Phosphate concentrations were highest in a period from about 1975 to 1988 and showed a declining trend thereafter (Fig. 6c). Intra-annual courses of nutrient concentrations are net values as these are of course modified by the nutrient uptake of e.g. the phytoplankton. The decrease in the phosphate concentrations was most pronounced in April and May. In contrast to nitrate, phosphate showed an earlier drop in concentrations in spring (~20 days, Fig. 6c). The long-term development of nitrate was characterized by a period of increased concentration from the early 1980s to the second half of the 1990s and that of silicate concentrations was characterized by high inter-annual variability and a period of higher concentration from about the end of the 1980s to the end of the 1990s. As with phosphate, but less pronounced, an earlier decrease of silicate concentration took place during spring in the second period (~10–15 days, Fig. 6d). The biggest differences (increases) between both periods were found in August and September (Fig. 6d). Intra-annual changes in nutrient concentrations were analyzed in more detail together with the changes in timing conditions of the different phytoplankton species (next section). Zooplankton abundance was highest in the 1980s and decreased significantly from the second half of

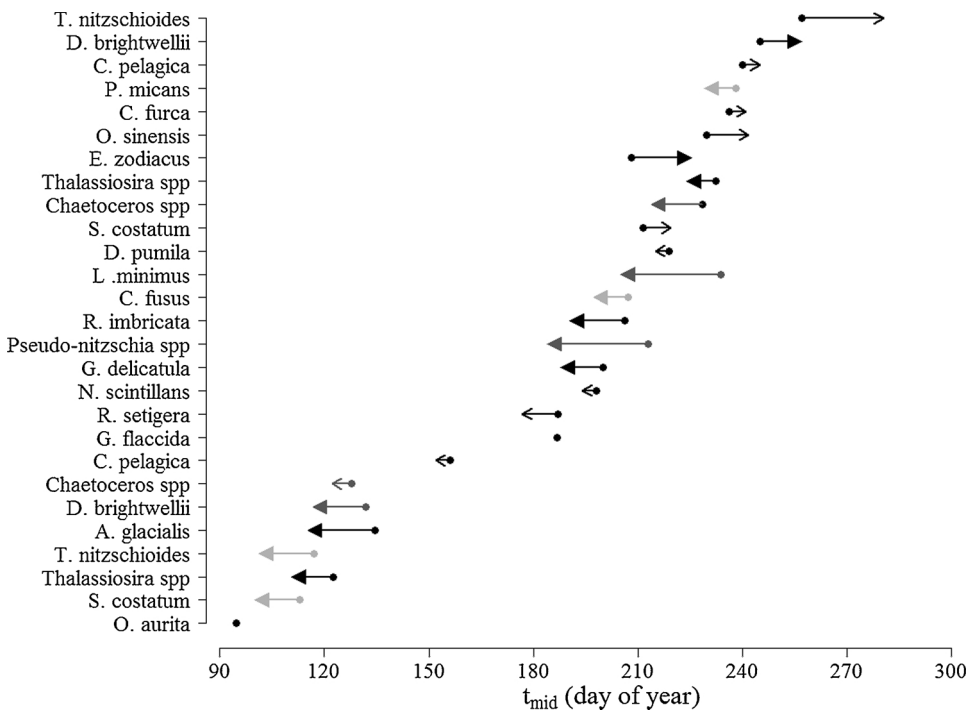


Fig. 5. Changes in phytoplankton species timing and abundance. Length of arrows (in days) describe shifts in the median of t_{mid} between the periods 1962–1988 (dot) and 1989–2015 (end of arrow). Full triangles denoted differences at a significance level of at least $p < 0.05$. Open triangles: no significant change. No arrow: difference in medians ≤ 3 days. Light grey (dark grey) arrows denoted species with significant decreases or increases in the annual or seasonal summed abundance (black: no significant change).

Table 2

Comparison of timing characteristics between small and large peaks of phytoplankton species. Groups were defined as the lower (small) and upper (large) quartile for the total number of single peak sum abundances of a species (cf. Fig. 4). The number of values in the quartiles is given by n. Crosses marked significant differences in the mean and the coefficient of variation (CV) of t_{mid} on a significance level of at least $p < 0.05$.

		lower quartile mean t_{mid} (days)	upper quartile mean t_{mid} (days)	sign. diff.	lower quartile CV t_{mid} [%]	upper quartile CV t_{mid} [%]	sign. diff.
<i>O. aurita</i>	n = 17	73	92	*	38.3	18.5	*
<i>S. costatum</i>	n = 12	82	109	*	46.3	13.2	–
<i>Thalassiosira</i> spp	n = 19	104	115	–	46.0	8.6	*
<i>T. nitzschoides</i>	n = 13	97	120	*	30.9	10.9	*
<i>A. glacialis</i>	n = 11	119	134	*	10.4	13.6	–
<i>D. brightwellii</i>	n = 10	126	130	–	14.9	15.1	–
<i>Chaetoceros</i> spp	n = 18	139	124	–	19.4	18.6	–
<i>C. pelagica</i>	n = 10	146	154	–	15.4	9.9	–
<i>G. flaccida</i>	n = 19	206	184	–	25.2	10.8	*
<i>R. setigera</i>	n = 23	209	184	–	25.1	22.4	–
<i>N. scintillans</i>	n = 18	193	194	–	16.7	9.1	*
<i>G. delicatula</i>	n = 33	214	184	*	20.9	17.3	–
<i>Pseudo-nitzschia</i> spp	n = 33	213	179	*	29.0	24.3	–
<i>R. imbricata</i>	n = 25	211	188	*	23.7	16.8	*
<i>C. fusus</i>	n = 20	191	208	–	43.4	5.7	*
<i>L. minimus</i>	n = 22	198	202	–	26.7	19.0	*
<i>D. pumila</i>	n = 19	219	195	*	15.0	18.4	–
<i>S. costatum</i>	n = 22	254	213	*	19.7	11.8	–
<i>Chaetoceros</i> spp	n = 25	228	220	–	13.0	8.2	*
<i>Thalassiosira</i> spp	n = 15	253	236	–	16.9	10.9	–
<i>E. zodiacus</i>	n = 21	226	225	–	25.0	16.1	–
<i>O. sinensis</i>	n = 18	246	226	–	12.3	20.3	–
<i>C. furca</i>	n = 15	243	226	–	19.2	6.6	*
<i>P. micans</i>	n = 15	236	236	–	18.9	8.2	–
<i>T. nitzschoides</i>	n = 12	276	281	–	15.9	19.3	–

the 2000s afterwards (Fig. 6d). Over the year, zooplankton abundances were always highest in summer (Fig. 6d).

3.5. Long-term changes in timing conditions

We used the environmental conditions associated with the trajectories of occurrence (conditions at mean t_{mid} , black lines in Fig. 4) to relate the temporal shifts to the seasonally varying environmental

conditions. Changes in species-specific timing conditions were related to a) the temporal shift of a species, b) the preferences of a species (specific parameter range), and c) the characteristics of temporal change of a parameter. Species-specific changes in timing conditions with regard to eight environmental parameters are shown in Fig. 7.

3.5.1. Water temperature

In spring and early summer, species showing a significant earlier

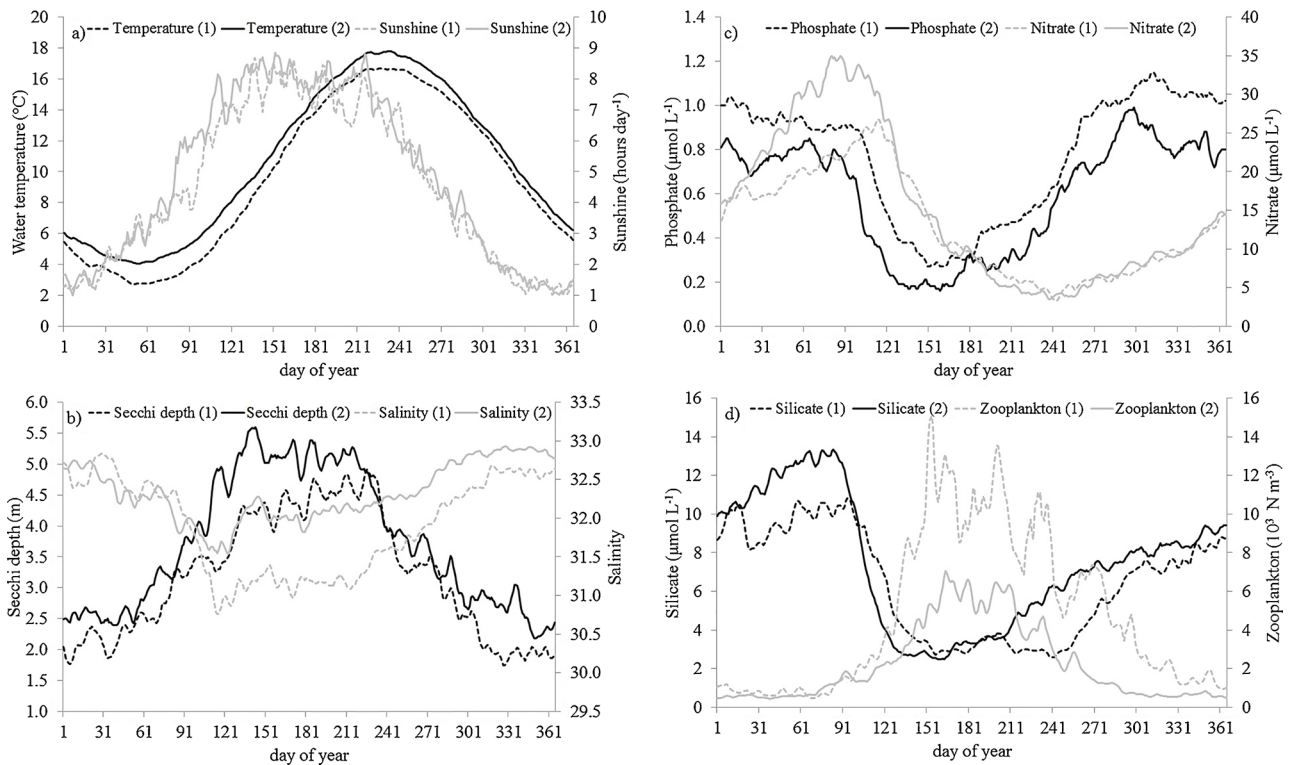


Fig. 6. Long-term mean annual courses of abiotic and biotic parameters for the periods 1962–1988 (1) and 1989–2015 (2). The length of the first period varied (Table 1).

occurrence do not show significant changes in associated water temperatures (black arrows in Fig. 7a), i.e. the shift in timing (in days) was of the same order of magnitude as the shift in the corresponding temperature range. Species with constant occurrence, on the other hand, usually reflect the increase in temperature in the respective time window (e.g. *Chaetoceros* spp in spring, Fig. 7a). Species such as *C. pelagica* and *G. flaccida*, showed no significant changes in associated temperatures, but also no significant shift in timing (see Fig. 5). This was probably due to lower temporal shifts in temperature ranges in that part of the year or the influence of other parameters. Before and after the annual maximum, warming led to a different manifestation of temporal shifts of temperature ranges (see Fig. 6a). Both *Chaetoceros* spp and *P. micans*, for example, had shown shifts towards earlier occurrence but in these cases we had observed also significant increases in timing temperatures, reflecting a shift towards the highest temperature range. The increase in timing temperatures of *E. zodiacus* reflected the finding that the timing shift (in days) towards later occurrence was lower than the temporal shifts in temperature ranges during that time of the year. In turn, in early autumn, *D. brightwellii* again showed a close relationship between a shift in timing and temporal displacement of the temperature range. These findings underlined the variability in which warming became apparent in the species-specific timing conditions.

3.5.2. Sunshine duration and Secchi depth

The shifts in spring were not associated with statistically significant changes in sunshine duration (see black squares and arrows, Fig. 7a). Rise in sunshine duration during spring occurred much more unevenly (compared to water temperature) and the temporal extent of shifts in specific parameter ranges was smaller than the observed shifts in timing (not shown). Species without shift in timing, however, reflected the significant changes in sunshine duration in April and May (see *C. pelagica*, Fig. 7b). The significant increase in light conditions at occurrence of the summer species *R. imbricata* and *Pseudo-nitzschia* spp was associated with an occurrence shift towards the phase of the annual maximum of sunshine duration (cf. Fig. 6a).

The increase in Secchi depth in spring was reflected differently in the timing conditions (Fig. 7b). Species that occurred significantly earlier in spring (black arrows) mostly showed smaller changes in the associated conditions than the species with the most constant occurrence (black arrows). This was related to the fact that the temporal displacements of the species and that of Secchi depth (and water temperature) were of a similar order of magnitude. However, there were differences in the relationship to both water temperature and Secchi depth. For example, *Thalassiosira* spp showed no change in associated temperatures over time and the temporal shift between the two periods (~10 days, Fig. 5) was of the same order of magnitude than that of the corresponding temperature range (~13 days, see Fig. 6a). With regard to Secchi depth, however, the shift in t_{mid} resulted in a change from 3.2 to 3.9 m between the two periods (arrow length in Fig. 7b). That meant that *Thalassiosira* spp did not “follow” the earlier occurrence of the same parameter range, but only reflected the higher Secchi depth in the second period at the earlier point in time. Comparable correlations were also found in other spring species (e.g. *T. nitzschoides*, *D. brightwellii*). This indicated, despite the rise in the Secchi depth, the water temperature as the main driver of phenological shifts in spring (see also next section). In the further course of the year, the various species reflected the underlying trends in different ways (Fig. 7b). The Secchi depth conditions of adjacent species were often uncorrelated (e.g. *C. fusus*, *L. minimus*). Significant increases in Secchi depth conditions of *L. minimus*, *Chaetoceros* spp and *P. micans* seemed to be a consequence of the temporal shift (earlier occurrence) towards a period with a stronger trend in Secchi depth (July).

3.5.3. Salinity, nutrients and zooplankton

The changes in salinity conditions for species occurring after April mainly reflected the underlying increasing trend in salinity (Fig. 7b). Significant increases observed with *Thalassiosira* spp and *D. brightwellii* occurrences, for example, in spring, also reflected shifts towards phases with higher average salinity (begin of April, Fig. 6b). Yearly patterns in nutrient concentrations were controlled by the uptake of

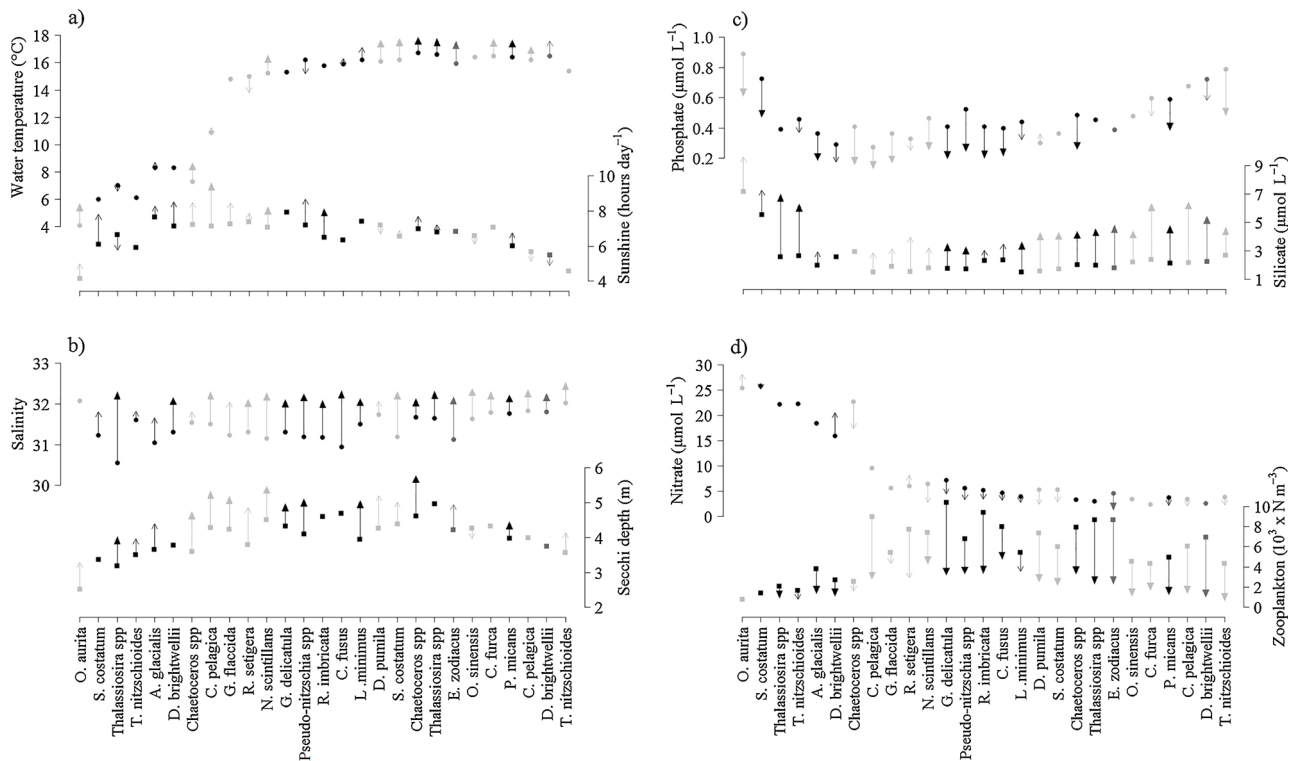


Fig. 7. Changes in the timing conditions of phytoplankton species. Arrows described changes in the median of eight environmental parameters associated with t_{mid} between the periods 1962–1988 (dot or square) and 1989–2015 (end of arrow). Arrows with full triangles denoted differences on a significance level of at least $p < 0.05$ (decrease: down arrow). Black (dark grey) arrows denote species showing a shift towards earlier (later) timing. Light grey: no change in timing. The arrows are omitted in the case of small differences.

phytoplankton. Changes in the nutrient patterns, however, cannot only be attributed to the species considered here, as these are a subset of the entire phytoplankton community. However, an earlier decrease in nutrient concentrations of phosphate and silicate (Fig. 6c, d) could be a consequence of the earlier occurrence of different types of phytoplankton. Shifts in concentrations were in the same order of magnitude as the phenological shifts identified for several spring species (cf. Fig. 5). As a result, some species (e.g. *Thalassiosira* spp, *T. nitzschoides*) showed no significant changes in phosphate concentrations associated with timing, despite the strong negative trends in mean phosphate concentrations during April and May. Such examples were also found for silicate (e.g. *A. glacialis*, *D. brightwellii*, Fig. 7c). Differences in the time of re-increase of phosphate and silicate concentrations between both periods (Fig. 6c, d) resulted in very different trends in the timing conditions during that period of the year (e.g. *Thalassiosira* spp, *E. zodiacus*, and *O. sinensis*, Fig. 7c). The course of the nitrate concentrations (grey lines in Fig. 6c) was delayed compared to that of the other nutrients. Regardless of the individual shift of the species, there were no statistically significant changes in the timing conditions regarding nitrate (Fig. 7c). The only exception was *E. zodiacus*, whose occurrence in the second period (Fig. 4m) coincided with the phase of the lowest nitrate concentration (cf. Fig. 6c). With the exception of the earliest occurring species, all species showed significant reduced zooplankton abundances at occurrence timing in the second period, i.e. there were no differences in species showing significant shifts in timing or constant occurrence (Fig. 7d).

3.6. Common variation in timing

The above results show that even co-occurring phytoplankton species may exhibit different phenological trends within identical time windows. Different species also had different phases of reduced or shifted presence superimposing the phenological long-term trends

(Fig. 4). We used principal component analysis (PCA) to identify the main factors of (common) inter-annual variability in the timing of the phytoplankton species. PCA was applied to the time series of mean t_{mid} (black lines in Fig. 4) for species occurring in spring and summer, respectively (cf. Fig. 4). In spring, the first PC reflected the trend towards earlier occurrence (Fig. 8a). Strongest relationships were found with regard to water temperature ($r_s = -0.51$, $p < 0.001$) and zooplankton abundance in spring ($r_s = 0.64$, $p < 0.001$). The pattern of component loadings reflected the temporal shifts and the different sensitivity against the predictors (Fig. 8c). In contrast, for the diatom *C. pelagica* (lowest loading) a negative relationship with zooplankton abundance was found. Higher abundances were associated with a shift of mean t_{mid} to an earlier date. Other PCs seemed to present non-significant components (Broken-Stick criterion).

The temporal course of the first PC during summer appears different (Fig. 8b). PC1 shows the highest correlation to nitrate concentration in summer ($r_s = -0.57$, $p < 0.001$). Higher nitrate concentrations were associated with earlier occurrences or displacements of mean t_{mid} (cf. Fig. 4). Diatom species without significant shifts in timing contributed most to the variability of this pattern (higher loadings in Fig. 8d). The second and the third PC of timing variability during summer had significantly lower explained variances (14 and 11.2%, not shown). PC2 showed weak correlations to zooplankton abundance ($r_s = -0.37$, $p < 0.05$) and silicate ($r_s = 0.40$, $p < 0.01$). Interestingly, PC3 showed a significant negative relationship with the mean water temperature in summer ($r_s = -0.49$, $p < 0.001$). The course of PC3 in summer strongly corresponded to that of PC1 in spring. Species-specific loadings of this third pattern were highly correlated ($r_s = -0.89$, $p < 0.0001$) with the corresponding species-specific shifts (days) in timing (Fig. 5). Thus, for the part of the phytoplankton community considered here, the part of timing variability induced by temperature changes is of secondary importance in summer and significantly lower than in spring.

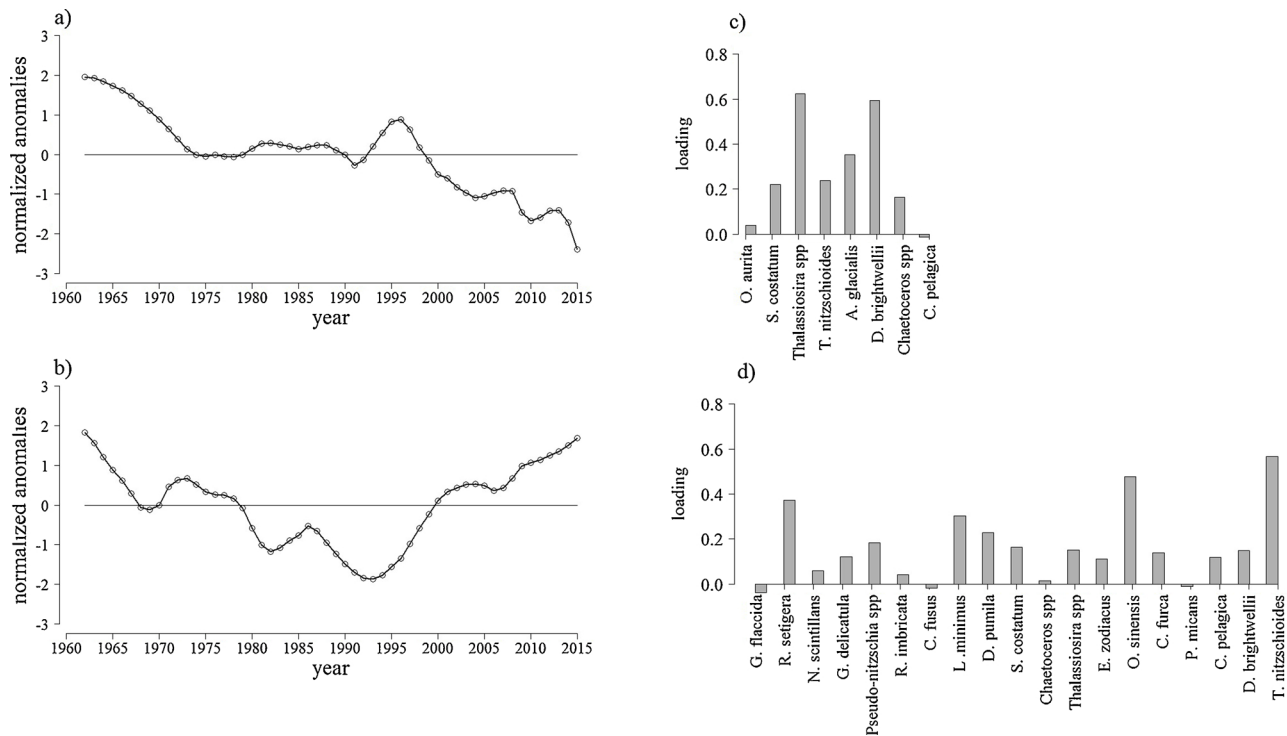


Fig. 8. Variation in species-specific timing. Panels to the left show the first principal components (PC1) for a PCA of the species-specific time series of mean t_{mid} in spring (top) and summer (bottom). Explained variances of PC1: 51.7% in spring, 49.3% in summer. Panels to the right show the respective loadings pattern.

4. Discussion

Especially in the context of climatic changes, phenological studies on phytoplankton species occurrence or growth are often used to evaluate phytoplankton growth conditions (e.g. Poloczanska et al., 2013). In order for such studies to be of real use in scenario analyses, appropriately long-term data sets are prerequisite (see Wiltshire et al., 2010). This study creates new insights of the phenological response of marine phytoplankton species in temperate shallow seas. We showed that different species are “slotted” into different, species-specific phenological time slots during annual succession. More than half of the species examined here show significant shifts between the selected comparison periods 1962–1988 and 1989–2015. Most changes relate to an earlier timing occurrence in the period April to July and are found in both diatom species and dinoflagellates, whereby several species also show remarkable constancy in timing over decades. Unchanged timing associated with water temperature clearly reflect the answer of a species into the variable displacement of temperature ranges. As a consequence, (seasonal) displacements due to the same parameter have shown different temporal dimensions. Our study clearly shows the influence of warming on phenological changes of specific diatom species in spring. With this study we clearly demonstrate that species-specific relationships cannot simply be derived or inferred from the reactions of the total numbers, e.g. diatoms to the different conditions (e.g. Wiltshire and Manly, 2004; Edwards and Richardson, 2004; Atkinson et al., 2015; Wiltshire et al., 2015). Such summed parameters may be dominated by the abundance (biomass) of single or merely a few species which may, for example, have no sensitivity or differing sensitivities to temperature changes. The most dominant genus in spring (*Chaetoceros* spp) shows a rather constant timing over time related to temperature.

Regarding species with a narrow occurrence range the temporal course of the borders of the intra-annual growth window can be considered approximately parallel to that of mean t_{mid} (e.g. *D. brightwellii*, Fig. 4). This describes a displacement of approximately constant width trajectories of occurrence rather than an expansion of the borders of the

growth window or period (see Wiltshire et al., 2015). Other species such as *Pseudo-nitzschia* spp showed an increasing intra-annual range of peak occurrence, coupled to a significant increase in abundance (cf. Fig. 4). Typically, common timing indices take into account only the inter-annual variation of the middle of season or the time of seasonal peak (see Ji et al., 2010), but not the inter-annual differences in the level of abundance achieved. For a better assessment of the shifts and their potential ecological consequences it is very useful to combine the information about the temporal extent of shifts and the associated developments in abundance or biomass. The Weibull-type fitting approach used in our study allows for a precise description of changes in phenological dates and related (peak) abundances. The multitude of annual abundance curve structures, however, prevents the use of the same algorithm setting, causing further tuning effort. Ultimately, a visual inspection of the annual peak structures is essential to ensure correct model adaptation. The use of LOESS curve fits for the description of annual occurrence timing (mean t_{mid}) provides a suitable method to describe phenological variation on the long-term scale. It turns out that the LOESS curve fit of a species is consistent, in terms of the (mean) temporal position and the trend, with other phenological indices such as the 50th percentile of cumulative abundance or the central tendency (e.g. Ji et al., 2010). The main difference arises from the reduced year-to-year variation caused by smoothing, i.e. the inclusion of part of neighboring points to estimate mean t_{mid} in a specific year. The value of $\alpha = 0.25$ used here increases the influence of the timing date of larger (than the surrounding) peaks on the neighboring dates and reduces it in case of the timing of smaller (than the surrounding) peaks. In addition, the use of additional weights in LOESS smoothing leads to a weighting of the temporal position of larger peaks. This procedure takes the following aspects into account. Nearly half of the species analyzed show a significantly higher variability in timing at small peak abundance sums (Table 2), i.e. the “typical” time corridor of main occurrence is often narrower in time. Furthermore, if we only consider the variation between the time points of main occurrence in successive years (i.e. without smoothing or as in an approach such as the central tendency, for example), fluctuations of > 2–3 months often

occur. This variability is often due to the fact that a peak is missing in the “typical” corridor and significantly smaller peaks (which otherwise do not matter) form the focus of the occurrence at different times. It does not seem plausible to assign such high temporal offsets to the variation of an environmental parameter range, whose inter-yearly variation is usually significantly lower. Using the smoothing approach we were thus able to investigate more precisely how each species was placed phenologically in the system and to relate this to environmental shifts.

We know from previous studies that because of the varying auto-ecological characteristics of phytoplankton species differences in the responses to long-term environmental changes are likely (e.g. Gebühr et al., 2009; Grüner et al., 2011; Freund et al., 2012; Schlüter et al., 2012). Schlüter et al (2012) analyzed the timing of three diatom species over the period 1962–2008. They showed that a low Secchi depth plays the most important role in earlier appearance of *O. aurita* in spring. This was however not confirmed by our study. Although lower peaks of *O. aurita* occurred significantly earlier (Table 2), no significant differences in Secchi depth conditions between earlier and later peaks were found (not shown). Using a cumulative approach, Wiltshire et al. (2015) showed that *O. aurita* achieved higher abundances during years with high Secchi depth conditions in spring. We only found a weak relationship between the Secchi depth in February and the total abundance (all peaks) of *O. aurita* in spring ($r_s = 0.39$, $p < 0.01$) and a slight negative shift in the timing of *O. aurita* on the long-term. *O. aurita* occurred most frequently in March in a period in which the Secchi depth remained constant and sunshine duration only recorded a slight (albeit significant) increase. Peak conditions between the dates t_{beg} and t_{end} (see Fig. 1) were found not to differ significantly in terms of sunshine duration (~ 5 h/day) and Secchi depth (~ 3 m), but in terms of water temperature (~ 4.3 to 5.3 °C). Sunshine duration in March was also significantly less variable than water temperature and Secchi depth. However, the CVs of t_{mid} conditions with regard to these three parameters do not differ and the conditions at t_{end} show a significantly lower variability with respect to water temperature and Secchi depth. This suggests that *O. aurita* occurs in a comparatively constant range of light and turbulence conditions, whose position is limited by the increase in water temperature and Secchi depth in April. It is beyond the scope of this paper to analyze the environmental conditions at individual peaks of all the phytoplankton species. This example, however, demonstrates the potential for further analysis of species subsets versus cumulative whole population approaches.

The comparison of phenological shifts for different sub-periods (cf. Fig. 5) also showed that changes do not occur evenly over time. The division, into comparative periods, as used here represents only one possible perspective. It weighted the phenological shifts of the individual species relative to specific environmental changes between both the comparison periods. Both of these aspects make it questionable whether it makes sense to specify a rate of phenological change as days per 1 °C increase (e.g. Atkinson et al., 2015). The superposition of anthropogenic influences, the inference with hydrodynamic conditions (Scharfe, 2013; Callies and Scharfe, 2015) and the local warming trend in the southern North Sea (Holt et al., 2012) cause a strong local impact on the pattern of phenological variation in the German Bight. Such pattern may therefore differ from other phenological changes for even the same species described for the greater North Sea. The dinoflagellate *C. fusus*, for example, has shifted significantly by about 10 days at Helgoland Roads (see Fig. 4). This magnitude is significantly lower than that reported by Edwards and Richardson (2004) for this species in the North Sea area in general. Such a difference is probably related to the environmental heterogeneity of locations (conditions) in the greater North Sea data set as used by Edwards and Richardson (2004). This illustrates, as emphasized by McQuatters-Gollop and Vermaat (2011), the complexity of down-scaling generalizations from the whole North Sea to a local area and vice-versa.

Phenological changes of the same species can also vary between

single sites. Atkinson et al. (2015) analyzed the phenological variation of different plankton groups observed at the Plymouth L4 monitoring site (English Channel). They described late August as the time of mean occurrence of the dinoflagellate *N. scintillans* and found a significant later occurrence (44 days over a time period of 20 years) coupled to an increase in water temperature. At Helgoland Roads, *N. scintillans* occurs in mid-July and no significant trend could be observed. This also demonstrates the differences in the succession and seasonal courses of controlling factors between Helgoland Roads and the Plymouth L4 station. One controlling aspect is likely to be the dynamics of the long-term changes in nutrient conditions (e.g. Shchekinova et al., 2017). Moreover, especially with concomitant changes in the food quality of zooplankton (e.g. Boersma et al., 2015) and their declining abundances are likely to play a role. Nitrate concentrations at Helgoland Roads are closely related to variation in the River Elbe discharge (Wiltshire et al., 2010; Callies and Scharfe, 2015; Vaynova et al., 2017), reflecting the position of Helgoland Roads as a marine transition zone between coastal waters and the open sea (Raabe and Wiltshire, 2009; Emeis et al., 2015).

In our study of a subset of the total phytoplankton community considered here, nitrate concentration and zooplankton abundance were found to contribute most to timing variability in summer (see Fig. 8b). From the beginning of the 1980s until the mid-1990s several species show an earlier timing occurrence, along with a significant increase in abundance (e.g. *L. minimus*), shifts of similar amplitude in just a few years (e.g. *O. sinensis*), or an accumulation of years of absence (e.g. *T. nitzschoides*). In summer, this induced variability in timing superimposes shifts resulting from warming. This causal differentiation is important for the understanding and classification of climatic fluctuations on the (future) development of the marine ecosystem. Even though changes in the nutrient patterns are not alone responsible for the selection of species considered, the similar magnitude in the time shifts (10–20 days) with an earlier decline in spring silicate and phosphate suggest a relationship to the phenological shifts of the phytoplankton species (see Wiltshire et al., 2015). Decreasing long-term trends in phosphate and silicate concentration were greater in April and May than in the adjoining months (see Shchekinova et al., 2017). This underpins the interesting fact that species showing phenological shifts in spring are not affiliated with changes in the phosphate concentrations.

Climate-induced changes in phenology are implicit with shifts in the size, structure and composition of the phytoplankton community overall and will influence the transfer of energy to higher trophic levels (Hays et al., 2005; Cheung et al., 2011; Winder and Sommer, 2012; Wiltshire et al., 2008, 2010, 2015). A closer look at the interference with time-shifted nutrient uptake processes remains an interesting question for the future, with regard to changes in the food quality of zooplankton and against the background of changing nutrient conditions in the German Bight (e.g. Boersma et al., 2015; Sarker, 2018). When zooplankton occurrence and shifts are combined with the phenological shifts which we have observed here for phytoplankton species it is clear that there is potential for “mismatch” (Cushing, 1990). As shown by Greve et al. (2004) for the Helgoland site, also different zooplankton species exhibit species-specific phenological responses. The non-homogenous response of both trophic levels in terms of phenology as a response to climate warming is well known (e.g. Edwards and Richardson, 2004; Richardson, 2008; Wiltshire et al., 2008; Poloczanska et al., 2013). However, in a comparison of very warm and cold years, Atkinson et al. (2015) pointed out that different strategies and compensation processes may reduce potential “mismatch” effects. This could also be reflected in the differences described here between species-specific changes in timing and more constant behavior at the level of the whole community.

The zooplankton abundance of various important copepods shows a strong decline in the southern North Sea (Boersma et al., 2015). In the subset of five zooplankton taxa used here (Table 1), the reduction is

particularly pronounced in the period from 2007. The changed timing occurrence along with a reduction in abundance in spring and summer of *Thalassiosira* spp (Fig. 4c), for example, shows a high temporal coincidence with this phase. The nature of this relationship has not become clear here, but underlines the necessity of considering species-specific relationships in the analysis of long-term ecological changes in the coupling of phytoplankton and zooplankton and for the evaluation of climatic impacts on phenological changes.

5. Conclusions

The model approach used here contributes to a broader understanding of the phenological response at species level in temperate shallow seas. We showed that different species are “slotted” into different, species-specific phenological time slots during annual succession. Thus, the effect of climatic and hydrological changes and especially warming on phytoplankton depends on the species and how it is enriched in a system. Our analysis shows that with the annual transition through seasonal environmental conditions, even co-occurring phytoplankton species may exhibit different phenological trends within overlapping time windows. There are different forms of changes in the timing of growth windows of phytoplankton species on the intra-annual and inter-annual scale, which reflect the strong warming at Helgoland Roads to varying degrees. The local character in seasonality and trends also of other drivers of phenological variability makes it difficult to compare the impact of phenological shifts on ecosystem processes at different sites. The complex phenological response illustrates the uncertainties regarding the assessment of the future development of the marine ecosystem under changing climatic conditions.

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