Changes in sinking of plankton–like particle: comparison between observations and numerical model

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Abstract

Sinking and resuspension are the most important processes determining the distribution of benthic–pelagic diatoms in the water column and influencing their variability. From the benthic–pelagic time series 1991–2008 we analyzed weekly concentrations of the diatom Paralia sulcata in the German Bight. The analysis was carried out for lower wind ranges (< 10 m s⁻¹) at two different seasons characterized by distinct sea surface conditions. Our results showed that the relationship between wind and diatom concentrations was much influenced by seasonal conditions: the decrease of abundances at higher winds was more pronounced in summer. Additional sampling procedure of species at two different water depths (bottom and surface layers) in the years 2007–2009 showed that in summer the surface abundance of species decreased substantially with increasing wind. In contrast, in winter the decrease of the surface concentration of species was less pronounced. To explain observed seasonal variations numerical simulations of plankton–like particles were performed using a two–dimensional turbulence model. Numerical simulations were carried using parameters corresponding to averaged winter and summer temperature and salinity at the study site. We showed that the reduction of cell counts was possibly linked to the changes in sinking of diatoms due to the altered buoyancy of algal cells. Our numerical results identified reduction of sinking speed of particles for the parameters corresponding to winter conditions.
Introduction

Together with tides, wind is one of the most important environmental drivers of turbulence and mixing processes in coastal seas (Young, 1999; De Jonge and van Beusekom, 1995; Demers et al., 1987; Song et al., 2011). Especially in shallow waters the wind energy causes vertical mixing, often through to the sea floor (Weisse and von Storch, 2009). As a consequence, life on the shelf is highly dependent on wind induced mixing processes (Demers et al., 1987). In particular, stormy conditions and wind mixing are responsible for the stirring and uplifting of sediments as well as organisms such as benthic diatoms into the water column (Therriault et al., 1978; Levasseur et al., 1983; Nichols and Briggs, 1985; McQuoid and Norberg, 2003a, b; Iriarte and Purdie, 2004). Moreover, in the shallow areas wind obviously also affects water clarity and underwater light climate, and as such the short-term variability of wind speeds can impact the timing of algal blooms via variations in turbidity, tidal fronts and surface mixed layer depth as exemplified for the spring bloom of diatoms in the southern North Sea by Tian et al. (2011).

Many algal species occur both in the water column as well as on the sediment of shallow seas, because they sediment out of the water column during quiet periods, and are resuspended during periods of turbulence. Some species, such as, for example, the diatom Paralia sulcata (Ehrenberg) Cleve 1873, form microphytobenthal mats, and leave these mats in periods of higher turbulence (Gebühr et al., 2009).

The relation between wind and the concentrations of bentho-pelagic algae in the water column was addressed previously for estuaries (De Jonge and van Beusekom, 1995; Demers et al., 1987). In the study of microphytobenthos in the Ems estuary (De Jonge and van Beusekom, 1995), the fraction of the benthic organisms moving from the top of sediment into the water column was linearly dependent on the effective wind speeds. In contrast, the analysis by Demers et al. (1987) on resuspension of organic particles in the littoral zone of the St. Lawrence estuary showed that a critical wind velocity was needed to cause a significant increase of particulate organic matter in the water column, and hence a non-linear response to wind was observed.

Previous observational studies (Roelofs, 1984; Hobson and McQuoid, 1997) showed positive correlations between increased wind and number of the benthic organisms that enter the water column from sediments. Moreover, the onset of high wind conditions in autumn is linked to the re-appearance of bentho-pelagic diatoms in the water column (Abrantes, 1988; McQuoid and Hobson, 1998; Gebühr et al., 2009), but an abrupt decrease of surface concentrations of diatoms such as P. sulcata sometimes was observed during storms (Gebühr, 2011). Thus, the dependence of the diatom concentrations on wind conditions remains not well understood.

In the studies of sedimentations under different temperature conditions (Krögel and Flemming, 1998) it was shown that sedimentation processes rely on the water kinematic viscosity adjustment and higher settling velocity of suspended particulate matter was observed in summer. Another study on sinking rates
Bienfang and Szyper [1982] showed that diatom cell buoyancy changes according to variations in sea surface temperature and salinity. This also implies that depending on the seasonal water conditions, wind may have a different impact on the sedimentation behavior of benthic–pelagic algae, which potentially could explain the somewhat varying results obtained from the literature [Roelofs 1984; Hobson and McQuoid 1997; Gebühr 2011]. The sinking behavior of a diatom cell [Lannergren 1979] could depend on variable sea surface conditions, specifically, it could be affected by seasonal changes of cell buoyancy and fluid density. This could occur due to seasonal variations in salinity and temperature.

Here, we investigated the influence of seasonal sea surface conditions, wind magnitude and densities of the benthic–pelagic diatom *P. sulcata* (Ehrenberg) Cleve in the water column at Helgoland in the North Sea. Our study is focused on lower weekly wind ranges (< 10 m s\(^{-1}\)) and observations during stormy weather conditions were not considered here. We used simultaneous long–term wind data and diatom cell counts from the same observational site. To evaluate the effect of seasonal variations of sea surface salinity and temperature on the sinking behavior of diatoms under turbulent conditions we performed a set of numerical simulations. We used a two–dimensional turbulence model with the mean temperature and salinity values from the observational data at Helgoland. The results were compared with the measurements of cell counts of *P. sulcata* obtained for the whole water column and for two distinct sea depth levels at different sea conditions.

**Materials and Methods**

**Description of study site**

For the estimates of plankton densities we used the Helgoland Roads (HR) algal data [Radach et al., 1986; Franke et al., 2004; Wiltshire and Dürsel, 2004]. Helgoland is located in the German Bight about 65 km off the German coast (Fig. 1) in the confluence of the estuaries of the rivers Weser and Elbe. Thus, the area is influenced by the circulation of the low saline coastal waters and the open waters of the southeastern North Sea [Bauerfeind et al., 1990; Ionita et al., 2008]. At HR the water is well–mixed due to tidal activity [Hickel, 1998] and shallow depths (between 3 and 10 m) [De Kluijver, 1991; Wiltshire et al., 2010]. The hydrographic situation at Helgoland is highly variable due to close proximity of the coastal waters and also due to variable wind conditions [Dippner, 1993; 1998; Siegesming and Schrum, 2001; Tian et al., 2011].

**Description of the *P. sulcata* dataset**

*P. sulcata* is representative (in terms of abundances and regularity in the data set) of the benthic–pelagic diatom community at HR [Wiltshire and Dürsel, 2004; Gebühr et al., 2009]. This species is a centric diatom that is regularly found in the sediment and in the water column in the North Sea [Drebels, 1974; Hoppenrath et al., 2009; Kraberg et al., 2010]. In general, it is more common in the
benthos than in the pelagic zone (Sancetta, 1989). In other areas of the world *P. sulcata* is usually found in zones with upwelling (Abrantes, 1988).

For *P. sulcata* continuous yearly records are available since 1962. In the study on *P. sulcata* response to various environmental factors by Gebühr et al. (2009) it was shown that the species is better adjusted to colder temperatures and lower light availability. Starting from 1998 the species has been found on a regular basis throughout the summer (Fig. 2) (Wiltshire and Manly, 2004; Gebühr et al, 2009).

In the long-term sampling, surface water samples were taken on every working day (Monday–Friday) except for holidays. The details of phytoplankton water sampling procedure and identification were described in Wiltshire and Düreslen (2004) and in Gebühr et al. (2009). Microalgae were identified to the species level. We used weekly means of the abundance data to avoid variability and to fill the gaps of missing data. Due to seasonal variability of weather and different environmental factors that influence diatom growth as well as the variability of HR daily diatom counts, we sorted data into winter (Dec–Feb) and summer (Jun–Aug) sets. Indeed, winter conditions at Helgoland are characterized by higher nutrient concentrations. In contrast, in summer, warmer water temperatures and higher light levels as well as limiting nutrients characterize the environment.

The abundances of *P. sulcata* typically correlated with periods of water turbulence (Kraberg et al., 2010). The species was often found in the plankton after storms due to strong vertical mixing of the water column (McQuoid and Hobson, 1998).

The weekly means and standard deviations of the species abundances were estimated and sorted according to the weekly wind speed evaluated in the week preceding to the algae measurements. The abundance data were grouped into two wind ranges (0 ≤ $W_{\text{mean}} < 5$ m s$^{-1}$, 5 ≤ $W_{\text{mean}} < 10$ m s$^{-1}$). Thus, we accounted for the changes in algae concentrations that could be affected by wind conditions in the previous week. Data were grouped separately for summer and winter observations.

Additionally to long-term sampling a weekly water sampling (in total 104 samples) was conducted at the same sampling site at HR (see Fig. 1) to investigate the occurrence of *P. sulcata* at 1 m above the sediment and at surface level during the period 16.10.2007 – 29.10.2009 (Gebühr, 2011). The samples were taken simultaneously from the bottom and surface depth levels (the depth at the sample site is within the range 6 – 10 m). The bottom and surface densities of *P. sulcata* were sorted according to seasons (winter and summer) and wind ranges.

*Description of wind data*

We used 10 m atmospheric wind measurements of the German Meteorological Service for Helgoland. The wind measurements from Helgoland site were used in the past as a proxy for studies of regional ecosystem processes (Tian et al., 2011) and energy productions of offshore wind turbines (Lindenberg et al.)
The mean daily winds were obtained as arithmetic means over at least 21 hours of hourly wind measurements. To evaluate the wind activity in recent decades (1991–2008) the weekly means of the daily wind measurements were analyzed. This allows avoiding spurious fluctuations on a daily scale. Here we concentrated on weekly winds below 10 m s\(^{-1}\). Unfortunately, we were forced to use a shorter time series than is available for phytoplankton because the wind station at Helgoland was moved in 1989 (Lindenberg et al., 2012), and a fairly large discrepancy exists between data before and after this move. Although the exact measuring procedure was altered several times in the period since 1989 these changes did not affect wind data consistency (Lindenberg et al., 2012).

Model

To describe diatoms vertical mixing we used a two-dimensional turbulence model for finite-sized, non-neutrally buoyant particles (Fung and Vassilicos, 2003; Fung and Perkins, 2008). For a heavy and spherical particles with a radius smaller than the Kolmogorov length scale only the drag and buoyancy forces are important. Based on the above assumptions the equation of motion is written as follows:

\[
\frac{dv}{dt} = \frac{1}{\tau_p} [u(x_p, t) - v(t)] + g,
\]

where \(v(t) = dx_p/dt\) is two-dimensional turbulence velocity field, \(\tau_p\) is relaxation time defined from the expression:

\[
\tau_p = \frac{2 \rho_p a^2}{9 \rho_f \nu},
\]

where \(\rho_p\) and \(\rho_f\) are algal cell and water densities respectively, \(a\) is radius of the diatom and \(\nu\) is the water kinematic viscosity. This velocity field is chosen as in Fung and Vassilicos, 2003 (see Appendix). The model of turbulent flow was used previously to investigate settling of heavy particles and the mechanism of prolonged suspension of particles in a turbulent fluid (Pasquero et al., 2003).

The density parameters of sea water depending on salinity and temperature were evaluated from the equation of state for sea water (Millero and Poisson, 1981). We used mean winter and summer salinity and temperature values obtained from the long-term times series at HR: \(T_{\text{win}} = 5.27^\circ\text{C}, S_{\text{win}} = 32.42\) PSU and \(T_{\text{sum}} = 16.32^\circ\text{C}, S_{\text{sum}} = 32.19\) PSU). The values for the summer and winter kinematic viscosities are \(\nu_{\text{sum}} = 1.1092 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}\) and \(\nu_{\text{win}} = 1.519 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}\) correspondingly. The mean radius of the diatom frustule is 10 \(\mu\)m and the average density of algal cell \(\rho_p = 1300 \text{ kg m}^{-3}\). We considered particles initialized in a square domain with a homogeneous, isotropic and statistically stationary random velocity field with periodic boundary conditions. The total number of 200 particles was simulated in a 2D box with open boundaries for time period \(t = 20\pi / \min(\omega_n)\), where \(\min(\omega_n)\) is the minimal wave frequency. Two sets of numerical tests were performed using summer and winter parameters.
1. Results

**Long-term sampling of P. sulcata**

The abundance of *P. sulcata* in the water column typically remains below \(7 \times 10^3\) cells L\(^{-1}\) (the maximum abundance \(10^4\) cells L\(^{-1}\) was observed in 2001) (Fig. 2a). For the study period the mean winter densities of *P. sulcata* (1548 cells L\(^{-1}\) ± 1340 cells L\(^{-1}\)) by far exceeded summer densities (171 cells L\(^{-1}\) ± 485 cells L\(^{-1}\)). The high winds were associated with the reduction of cell counts for both seasons (Fig. 3).

**Distributions of surface and bottom concentrations of P. sulcata**

The 1 m bottom cell counts generally exceeded the surface densities and ranged from 1500 cells L\(^{-1}\) to almost 3500 cells L\(^{-1}\) in winter and were typically below 1500 cells L\(^{-1}\) in the summer period. The surface cell densities did not exceed 2000 cells L\(^{-1}\) in winter and in summer were generally below 500 cells L\(^{-1}\) (Fig. 4).

According to analysis of diatom abundances at different depth calmer wind conditions were associated with higher cell counts at the surface. In contrast, an increase of wind led to the settling of part of algae to the sea bottom (Fig. 4): while only a slight decrease of cell counts occurred for winds < 5 m s\(^{-1}\) in winter (Fig. 4a), in summer the surface concentrations decreased substantially (Fig. 4b) which resulted in almost 100% reduction of the surface cell counts (Fig. 4b).

**Simulation results**

The results of simulation for summer and winter parameters are shown in terms of two-dimensional vertical distribution of positions of 200 particles (Fig. 5 a and c) and the percentage of particles found at given depths (Fig. 5 b).
Figure 2: (a) Abundance for *P. sulcata* from the HR data set for period 1991 – 2008. (b) Mean abundance of *P. sulcata* for the years 1991 – 1997 (circles) and 1998 – 2009 (triangles). Data were calculated based on the time series of weekly means of diatom abundances.

Figure 3: Mean and standard deviations of abundances [cells L⁻¹] of *P. sulcata* for winter (a) and summer (b) for two wind ranges: (1) [0, 5] m s⁻¹, (2) [5, 10] m s⁻¹. Data were regrouped using time series of weekly means of wind and diatom abundances for period 1991 – 2008. The abundances were sorted according to wind ranges observed in the week preceding the sampling of algae.
and d). The initial positions of particles are chosen randomly in both cases. An average fall distance of the particles during time $t = 369.01$ s in summer $\Delta Y_{\text{sum}} = 9.14$ m was greater than in winter $\Delta Y_{\text{win}} = 6.72$ m. From these estimates the average sinking speed was calculated: $v_{\text{sum}} = 0.025$ m s$^{-1}$ for summer and $v_{\text{win}} = 0.018$ m s$^{-1}$ for winter. These values were substantially lower than the terminal velocities for the diatom–like particle of the same size: (i) for winter $v_{\text{win}} = 0.039$ m s$^{-1}$ and (ii) for summer $v_{\text{sum}} = 0.054$ m s$^{-1}$ due to turbulent flow that slows in this case the vertical transport of particles.

2. Discussion

Experiments with artificial turbulence [Ruiz et al., 2004] showed that intense mixing events impose environmental stress for phytoplankton cells. Therefore, not only turbulent mixing can homogenize the distribution of phytoplankton cells, but it can intensify the settling of cells in vitro [Ruiz et al., 2004]. As in the natural condition, it was suggested that due to turbulent mixing more particles could be transported into trapping zone and further transferred to sediment [Oliver and Ganf, 2000]. Our results suggested that although an overall increase of cell concentrations in the water column was correlated with a higher wind intensity the algae vertical concentrations changed nonlinearly with the increase of wind. These changes were affected also by the seasonal water surface conditions as both field observations and model simulations here indicated. The phenomenon of a stress–avoiding behavior of diatoms [Ruiz et al., 2004] remains to be observed in natural conditions.

An increase of the bottom concentrations of diatoms at higher wind conditions could not be explained from the model described here. Most likely interaction of diatom cells with resuspended particulate matter could intensify diatoms
Figure 5: Simulation results from the model Eq. (1). (a) Vertical profile of the distribution of particles at the initial time (empty circles) and at final time \( t = 20\pi/\min(\omega_n) \) (filled circles) with parameters corresponding to winter values (a) and summer (c) values. (b) Percentage of particles found at a given distance for winter (b) and summer (d). The X in (a) and (c) is the width of domain in meters.
sinking at higher winds. More complicated feedback between sediment material and water movement could change the character of the suspended sediment with attached chains of *P. sulcata* diatoms.

It was shown (Chang et al., 2006) that storm and rough weather conditions in the southern North Sea and Wadden Sea could cause resuspension of heavy particles due to their break-up while sedimentation processes are typically observed more often during calm conditions. However, due to the lack of such observations for diatoms we do not discuss here the effects of break-up and clustering of particles on settling and resuspension processes (Nichols and Briggs, 1985).

Our theoretical estimates predicted higher sinking speed of diatom–like particles with increasing temperature due to lower sea water density and viscosity. Similar experimental studies of the sinking of diatoms *Ditylum brightwelli* (Bi-enfang and Szyper, 1982) showed an evidence of the decrease of the sinking rate with increasing temperature. These experiments pointed to the existence of direct physiological response of diatoms to changes of temperature and salinity. In the model we did not account for the physiological responses. Detailed monitoring of vertical transport of *P. sulcata* under different temperature, salinity and wind conditions could provide more insight into the existing mechanism of regulation of cell buoyancy under different physico–chemical and sea turbulence conditions.

**Conclusions**

Our analysis of long–term pelagic time series and weekly wind data for different seasonal conditions showed that stronger wind magnitude was associated with the reduction of diatom abundances in surface water. The decrease of abundances was less pronounced in winter. The reduction of cell counts was possibly linked to the changes in sinking of diatoms due to turbulent wave activity and changing buoyancy of algal cells. These observations were confirmed by separate analysis of the surface and bottom samplings of *P. sulcata* that revealed more intense settling behavior of diatoms in summer than in winter at higher wind magnitudes. The numerical results showed similar behavior: the simulations performed with plankton–like particles inside two–dimensional turbulent field identified on average higher sinking speed for summer than for winter parameters.

**Appendices**

The velocity field in Eq. (1) is chosen according to the kinematic simulation model (Fung and Vassilicos, 2003) with a flow that models small–scale turbulence with a Kolmogorov $-5/3$ energy spectrum. This flow was used previously to investigate settling of heavy particles and mechanism of prolonged suspension of particles in a turbulent fluid (Pasquero et al., 2003). The two–dimensional
an incompressible turbulent velocity field is modeled as a sum of random incompressible Fourier modes:

\[ u(x, t) = \sum_{n=1}^{N_k} [A_n \cos(k_n \cdot x + \omega_n t) + B_n \sin(k_n \cdot x + \omega_n t)], \]

\[ A_n = A_n (\cos \phi_n, -\sin \phi_n), B_n = B_n (-\cos \phi_n, \sin \phi_n), k_n = k_n (\sin \phi_n, \cos \phi_n), \]

and \( N_k \) is the number of modes. The amplitudes \( A_n \) and \( B_n \) satisfy the condition: \( A_n^2 + B_n^2 = E(k_n) \Delta k_n \). The condition of incompressibility \( A_n \cdot k_n = B_n \cdot k_n = 0 \) of velocity field holds for all \( n \). The angles \( \phi_n \) are chosen randomly and uncorrelated with each other. Here Eulerian energy spectrum \( E(k) \) is defined according to the expression: \( E(k) = E_0 L(kL)^{-5/3} \). \( L \) is the largest eddy scale of the turbulence. The wave numbers \( k_n = k_1 (L/\eta(N_k - 1))^{n-1} \) are chosen according to geometric progression with \( k_1 = 2\pi/L \) and \( k_{N_k} = 2\pi/\eta \). The frequencies \( \omega_n \) are determined from the expressions \( \omega_n = \lambda \sqrt{k_n^2 E(k_n)} \), where \( \omega_n \) is proportional to the eddy turnover time of wave mode \( n \). Here \( \lambda \) is a dimensionless constant.

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References

F. Abrantes Diatom assemblages as upwelling indicators in surface sediments off Portugal. Mar. Geol., 85 (1988), pp. 15–39. doi:10.1016/0025-3227(88)90082-5

E. Bauerfeind, W. Hickel, U. Niermann, H. V. Westernhagen Phytoplankton biomass and potential nutrient limitation of phytoplankton development in the southeastern North Sea in spring 1985 and 1986. Netherl. J. Sea Res., 25 (1990), pp. 131–142. doi:10.1016/0077-7579(90)90014-8

P. K. Bienfang, J. P. Szyper Effects of temperature and salinity on sinking rates of the centric diatom *Ditylum brightwelli*. Biol. Oceanogr., 1 (1982), pp. 211–223.

T. S. Chang, O. Joerdel, B. W. Flemming, A. Bartholomä The role of particle aggregation/disaggregation in muddy sediment dynamics and seasonal sediment turnover in a back–barrier tidal basin, East Frisian Wadden Sea, southern North Sea. Mar. Geol., 235 (2006), pp. 49–61. doi:10.1016/j.margeo.2006.10.004
R. M. Crawford Taxonomy and frustular structure of the marine centric diatom Paralia sulcata. J. Phycol. 15 (1979), pp. 200–210.

M. C. Davey The relationship between size, density and sinking velocity through the life cycle of Melosira granulata (Bacillaruiophyta). Diatom Res. 1(1) (1986): pp. 1–18.

G. Drebes Marine Phytoplankton, eine Auswahl der Helgoländer Planktonalgen (Diatomeen, Peridineen). Georg Thieme Verlag, Stuttgart, (1974).

S. Demers, J–C. Therriault, E. Bourget, A. Bah Resuspension in the shallow sublittoral zone of a macrotidal estuarine environment: Wind influence. Limnol. Oceanogr., 32 (1987), pp. 327–339.

V. N. De Jonge, J. E. E. van Beusekom Wind– and tide–induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnol. Oceanogr., 40(4) (1995), pp. 766–778.

M. J. De Kluijver Sublittoral hard substrate communities off Helgoland. Helgoländer Meeresunters, 45 (1991), pp. 317–344.

J. W. Dippner A frontal–resolving model for the German Bight. Cont. Shelf Res., 13 (1993), pp. 49–66.

J. W. Dippner Vorticity analysis of transient shallow water eddy fields at the river plume front of the River Elbe in the German Bight. J. Mar. Syst., 14 (1998), pp. 117–133.

H.–D. Franke, F. Bucholz, K. H. Wiltshire Ecological long–term research at Helgoland (German Bight, North Sea): retrospect and prospect– an introduction. Helgol. Mar. Res., 58(4) (2004), pp. 223–229. doi:10.1007/s10152-004-0197-z

J. C. H. Fung, J. C. Vassilicos Inertial particle segregation by turbulence. Phys. Rev. E, 68 (2003), 046309. doi:10.1103/PhysRevE.68.046309

J. C. H. Fung, R. J. Perkins Dispersion modeling by kinematic simulation: cloud dispersion model. Fluid Dyn. Res., 40 (2008), pp. 273–309. doi:10.1016/j.fluiddyn.2007.06.005

C. Gebühr, K. H. Wiltshire, N. Aberle, J. E. E. van Beusekom, G. Gerdts Influence of nutrients, temperature, light and salinity on the occurrence of Paralia sulcata at Helgoland Roads, North Sea. Aquat. Biol., 7 (2009), pp. 185–197. doi:10.3354/ab00191

C. Gebühr Investigations on the ecology of the marine centric diatom Paralia sulcata at Helgoland Roads, North Sea. PhD dissertation, Jacobs University, Bremen, (2011).

W. Hickel Temporal variability of micro– and nanoplancton in the German Bight in relation to hydrographic structure and nutrient changes. ICES J. Mar. Sci., 55 (1998), pp. 600–609.
L. A. Hobson, M. R. McQuoid Temporal variations among planktonic diatom assemblages in a turbulent environment of the southern Strait of Georgia, British Columbia, Canada., Mar. Ecol. Prog. Ser., 150 (1997), pp. 263–274.

M. Hoppenrath, M. Elbrächter, G. Drebes Marine phytoplankton Selected microphytoplankton species from the North Sea around Helgoland and Sylt. Schweizerbart Science Publishers, Stuttgart, (2009).

A. Iriarte, D. Purdie Factors controlling the timing of major spring bloom events in an UK south coast estuary. Est. Coast. Shelf Sci., 61 (2004), pp. 679–690. doi:10.1016/j.ecss.2004.08.002

M. Ionita, G. Lohmann, N. Rimbu, K. Wiltshire The influence of large–scale atmospheric circulation on the variability of salinity at Helgoland Roads station. Tellus A, 60(5) (2008), pp. 1103–1108. doi: 10.1111/j.1600-0870.2008.00352.x

A. Kraberg, M. Baumann, C. D. Dürselen Coastal Phytoplankton: Photo Guide for Northern European Seas, Verlag Dr. Friedrich Pfeil München, (2010).

F. Krögel, B. W. Flemming Evidence for temperature–adjusted sediment distributions in the back–barrier tidal flats of the East Frisian Wadden Sea (Southern North Sea). In: C. R. Alexandr, R. A. Davis, V. A. Henry, (eds.), Tidalities: Processes and Products. SEPM, special publications, 60 (1998), pp. 31–41.

C. Lännergren Buoyancy of natural populations of marine phytoplankton. Mar. Biol., 54 (1979), pp. 1–10.

M. Levasseur, J–C. Therriault, L. Legendre Tidal currents, wind and the morphology of phytoplankton spatial structures. J. Mar. Res., 41 (1983), pp. 655–672.

J. Lindenberg, H–T. Mengelkamp, G. Rosenhagen Representativity of near surface wind measurements from coastal stations at the German Bight. Meteorol. Z., 21 (2012), pp. 99–106.

M. R. McQuoid, L. A. Hobson Assessment of palaeoenvironmental conditions on Southern Vancouver Island, British Columbia, Canada, using the marine Tychoplankter Paralia sulcata. Diatom Res., 13 (1998), pp. 311–321. doi:10.1080/0269249X.1998.9705453

M. R. McQuoid, K. Nordberg The diatom Paralia sulcata as an environmental indicator species in coastal sediments. Estuar. Coast. Shelf Sci., 56 (2003), pp. 339–354. doi:10.1016/S0272-7714(02)00187-7

M. R. McQuoid, K. Nordberg Environmental influence on the diatom and silicoflagellate assemblages in Koljö–Fjord (Sweden) over the last two centuries. Estuaries, 26 (2003), pp. 927–937.
F. J. Millero, A. Poisson International one–atmosphere equation of state of seawater. Deep–Sea Res., 28 (1981), pp. 625–629.

M. N. Nichols, R. B. Briggs Estuaries. In: Davis, A. (ed.), Coastal Sedimentary Environments. Springer–Verlag (1985), pp. 77–186.

R. L. Oliver, G. G. Ganf Freshwater blooms. In: B. A. Whitton, M. Potts, (eds.), The Ecology of cyanobacteria, Their diversity in Time and Space. Springer (2000), pp. 149–194.

J. Padisák, E. Soróczki-Pintér, Z. Rezner Sinking properties of some phytoplankton shapes and the relation resistance to morphological diversity of plankton - an experimental study. Hydrobiologia, 500 (2003), pp. 243–257. doi:10.1023/A:1024613001147

C. Pasquero, A. Provenziale, E. A. Spiegel Suspension and fall of heavy particles in random two–dimensional flow. Phys. Rev. Lett., 91(5) (2003), 054502. doi:10.1103/PhysRevLett.91.054502

G. Radach, J. Berg, E. Hagneier Annual cycles and phenomena on the other time scales in temperature, salinity, nutrients and phytoplankton at Helgoland Reede, 1962 – 1984. ICES, C. M. 1986/C (1986), 8.

A. K. Roelofs Distributional patterns and variation of valve diameter of Paralia Sulcata in surface sediments of Southern British Columbia inlets. Est. Coast. Shelf Sci., 18 (1984), pp. 165–176. doi:10.1016/0272-7714(84)90104-5

J. Ruiz, D. Macias, F. Peters Turbulence increase the averaged settling velocity of phytoplankton cells. Proc. Natl. Acad. Sci., 101 (2004), pp. 17720–17724. doi:10.1073/pnas.0401539101

C. Sancetta Spatial and temporal trends of diatom flux in British Columbian fjords. J. Plankton Res., 11 (1989), pp. 503–520.

F. Siegismund, C. Schrum Decadal changes in the wind forcing over the North Sea. Clim. Res., 18 (2001), pp. 39–45. doi: 10.3354/cr018039

H. Song, A. J. Miller, B. D. Cornuelle, E. Di Lorenzo Changes in upwelling and its water sources in the California Current System driven by different wind forcing. Dyn. Atmos. Oceans, 52 (2011), pp. 170–191. doi: 10.1016/j.dynatmoce.2011.03.001

J–C. Therriault, D. J. Lawrence, T. Platt Spatial variability of phytoplankton turnover in relation to physical processes in a coastal environment. Limnol. Oceanogr., 23 (1978), pp. 909–911.

T. Tian, J. Su, G. Flöser, K. Wiltshire, K. Wirtz Factor controlling the onset of spring blooms in the German Bight 2002 – 2005: Light, wind and stratification. Cont. Shelf Res., 31(10) (2011), pp. 1140–1148. doi: 10.1016/j.csr.2011.04.008
D. Titman, P. Kilham Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing processes. Limnol. Oceanogr. 21 (3), pp. 409–417.

R. Weisse, H. von Storch Marine Climate and Climate Change: Storms, Wind Waves and Storm Surges. Springer (2009).

K. H. Wiltshire, B. F. J. Manly The warming trend at Helgoland Roads, North Sea: phytoplankton response. Helgol. Mar. Res., 58 (2004), pp. 269–273. doi: 10.1007/s10152-004-0196-0

K. H. Wiltshire, A. Kraberg, I. Bartsch, M. Boersma, H–D. Franke, J. Freund, C. Gebühr, G. Gerdts, K. Stockmann, A. Wichels Helgoland Roads, North Sea: 45 years of change. Estuar. Coasts, 33 (2010), pp. 295–310.

K. H. Wiltshire, C. D. Dürselen Revision and quality analyses of the Helgoland Reede long-term phytoplankton data archive. Helgol. Mar. Res., 58 (2004), pp. 252–268. doi: 10.1007/s10152-004-0192-4

I. R. Young Wind generated waves, Elsevier Ocean Engineering Book Series, Oxford (1999).