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# SPATIAL AND TEMPORAL TRENDS IN ORDER RICHNESS OF MARINE PHYTOPLANKTON AS A TRACER FOR THE EXCHANGE ZONE BETWEEN COASTAL AND OPEN WATERS

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ABSTRACT

Quantifying exchange of particulate matter between coastal and open waters is an important and often unresolved issue. Here, we apply phytoplankton order richness as an innovative marine tracer to identify the geographical position of a coastal exchange zone in the SE North Sea, including its variability in time and space. Previous observations on dynamics of suspended particulate matter accumulation resulted in a hypothesized boundary between coastal waters (including the Wadden Sea) and open North Sea waters, the so-called "line-of-no-return". Our study along two transects (Terschelling, Noordwijk) in the Dutch coastal zone showed seasonality patterns in phytoplankton order richness, both for diatoms and flagellates. The coastal Wadden Sea was found to be clearly different from the open North Sea, implying that seasonality in Wadden Sea phytoplankton is at least partly driven by local environmental conditions. Seasonality in flagellates was found to be more uniform than seasonality in diatoms. Stations in the coastal North Sea to a distance of 10 km (Terschelling) to 20 km (Noordwijk) from the shore appeared to be at the inside of the "line-of-no-return". Our findings indicate that this approach is a useful aid in exploring mixing of particulate matter between coastal and open waters and to study the responses of phytoplankton communities to environmental drivers.

## 1.1   INTRODUCTION

Coastal areas are among the most productive marine ecosystems (among others: Field et al., 1998). Functioning of these coastal systems is determined by the interplay of global drivers with local hydrodynamic and morphological conditions (Cloern and Jassby, 2008). The interactions between land, rivers, coastal zones and open waters are complex with transitions being gradual or more abrupt, and reliable proxies for the detection of such gradients in time and space are not easy to find. Exchange of particulate matter between coastal and open waters has been studied for several decades, especially for the highly productive estuarine areas such as the Wadden Sea (Postma, 1961, 1982, 1984; Visser et al., 1991; van Beusekom and de Jonge, 2002). This coastal zone is separated from the North Sea by a chain of barrier islands and bordering the Dutch, German and Danish coastline. The Wadden Sea is one of the largest estuarine coastal systems worldwide; it fulfils an important nursery function for commercial and non-commercial fish species and provides an important feeding area for migrating coastal birds (for overview see Zijlstra, 1972; Wolff, 1983). The productivity of the Wadden Sea is mainly the result of pelagic and benthic primary production by microalgae, which is partly fueled by the import of nutrients and accumulating organic matter from the North Sea (Verwey, 1954; Postma, 1984; van Beusekom et al., 1999). The strong impact of increased nutrient loads from rivers into the area in the 1970s-1980s (e.g. de Jonge et al., 1993; van Raaphorst and de Jonge, 2004; Philippart et al., 2007) on primary and secondary production in the western Wadden Sea (Beukema and Cadée, 1986; Beukema et al., 1998) illustrates the importance of variation in local conditions on productivity and ecosystem functioning. However, to what extent the exchange and input of organic matter from the North Sea is spatially and temporally contributing to these local conditions and productivity of this shallow coastal sea remains an open issue.

Nutrient budgets of the western Wadden Sea suggest a relatively limited contribution of imported organic nitrogen and phosphorus from the North Sea compared to the import by rivers (van Raaphorst and van der Veer, 1990; Philippart et al., 2000). Van Beusekom et al. (2012) state that local nutrient dynamics are mainly driven by organic matter import from the North Sea (e.g. van Beusekom and de Jonge, 2002) and, as a consequence, the Wadden Sea should be considered to be predominantly heterotrophic, i.e. consuming more organic matter through respiration than produced through local photosynthesis (Verwey, 1954; Postma, 1984; van Beusekom et al., 1999, e.g. ). These different views might be related to the time frame of the various studies, e.g. before, during or after the peak in eutrophication in the 1980s (van Raaphorst and de Jonge, 2004). This at least warrants a re-examination of the importance of exchange and import from the North Sea and to what extent spatial and temporal variation does occur. Identifying the importance of input of the North Sea requires identifying of the mixing and the area of exchange between the Wadden Sea and the North Sea by an inert tracer with sufficient variation between endmembers and robust in time and space. Suspended particulate matter (SPM) is more or less inert, but exhibits a strong spatial and temporal variability both in amount and size composition in the North Sea (Postma, 1981; van Raaphorst et al., 1998) and especially inside the Wadden Sea (e.g. Postma, 1961). Despite these disadvantages, cross-shore gradients in suspended particulate matter showed indeed on average a minimum outside the Wadden islands, at approximately 50 to 100 km from the shore (Postma, 1981; Visser et al., 1991). A compilation of scarce field measurements and satellite information on SPM concentrations revealed a narrow turbidity minimum zone of a few kilometres width just outside the barrier islands of the Wadden Sea extending from the Netherlands to Denmark (van Raaphorst et al., 1998), which was considered to represent the boundary between coastal Wadden Sea and open North Sea waters. This has led to the confirmation of the so-called "line-of-no-return" in front of the Wadden Sea postulated by Postma (1984). The boundary is enhanced due to the residual transport in north-easterly directions that decreases the exchange between the water masses and increases the accumulation of suspended matter in the coastal zone (de Jonge and de Jong, 2002). However, it is unknown how well defined this boundary

is and, if present, if this boundary shows spatiotemporal variation, e.g. as a result of variation in temperature, wind or rainfall (Postma, 1984). For identification and an analysis of spatial and temporal variability in exchange of SPM, a precise tracer with high temporal resolution is required. Salinity potentially is such an inert tracer, and differences in salinity between open North Sea and the estuarine Wadden Sea are large enough. However, salinity in the area of interest is not only influenced by fresh water input directly into the Wadden Sea via Lake IJssel, the most prominent fresh water input, but also by a narrow band of coastal water with river Rhine input from the south (Zimmerman and Rommets, 1974; Postma, 1982; Philippart, 1988; de Jonge, 1990; de Vries et al., 1998) as well as smaller canals and rivers. Due to these different sources and the fact that the most prominent fresh water sources is separated from the area by a dike and fresh water inflow is controlled via sluices, the salinity in the area is not following the classical estuarine pattern with a gradual salinity gradient. This means that the hydrodynamic situation prevents the use of salinity as a mixing tracer in this area. Also nutrient concentrations are not suited as tracer due to their high turnover rate, and are therefore not inert over longer time scales (Pinckney et al., 2001). Phytoplankton seems be an alternative candidate. Comparison of chlorophyll a time series has revealed different patterns of phytoplankton biomass variability, and also species composition in oceans and coastal waters (Cloern and Jassby, 2010; Winder and Cloern, 2010). Phytoplankton species composition might be a more sensitive tracer than biomass as each water mass with its own seasonal fluctuations in environmental conditions and biological forcing will contain its own unique plankton community due to specific physiological preferences and tolerances (Hutchinson, 1961; Cloern and Dufford, 2005; Carstensen et al., 2015). Deviations from the "classical seasonal pattern", in the North Sea of a spring bloom dominated by diatoms followed by a summer bloom of dinoflagellates (Alvarez-Fernandez et al., 2012; Carstensen et al., 2015), might then be indicative for potential boundaries between water masses exchanging SPM in the coastal zone. If indices based on phytoplankton species richness are used as a tracer we face a major problem, as species identification of all algae within a sample is often incomplete (Zingone et al., 2015), A solution is a reduction of the taxonomic resolution to family or genus level to make the dataset more homogeneous and more robust to variations in species' identification (Heino and Soininen, 2007; Ptacnik et al., 2008; Carneiro et al., 2013; Olli et al., 2013). This implies, however, that algae that were not indentified up to this level are subsequently excluded from further analyses. In order to keep the samples as complete as possible, we decided to use phytoplankton order richness that was calculated as the number of orders of which phytoplankton species or species groups were found in a sample. We assumed that this index still contains the information on seasonality on phytoplankton community structure, whilst the possible bias as a result of reducing the actual sample size is relatively low. Applying the phytoplankton order richness as a tracer to identify the area of exchange between Wadden Sea and North Sea, including its spatial and temporal variability, requires long-term data sets that are consistently collected and analysed without any methodological changes in time. Within the framework of the Dutch national marine monitoring program (`www.waterbase.nl`), phytoplankton species composition was determined along two transects from the Dutch coast (including the Wadden Sea) to the central North Sea and consistently analysed since 2000. For each sample, the order richness of diatoms and flagellates was calculated as the number of orders of which phytoplankton species of these functional groups were present. Diatoms and flagellates were selected because they are two of the species richest groups of the phytoplankton (Guiry, 2012) and therefore expected to be most sensitive to variations in environmental conditions. We used the order richness data set to examine (I) if there is a seasonality in the order richness of phytoplankton, and, if so, (II) if there are differences in seasonality from the coast (Wadden Sea) to the central North Sea, (III) if there are specific spatial patterns in this seasonality which covary with spatial variation in environmental conditions such as the "line of no return", and (IV) if seasonal patterns in order richness can be attributed to specific phytoplankton groups related to environmental conditions.

## 1.2 MATERIALS AND METHODS

### 1.2.1 *Study area*

The stations used in this study were part of the Dutch national marine monitoring program (`www.waterbase.nl`) and located at two transects perpendicular to the Dutch coast with one ("Terschelling") off the Wadden Sea island Terschelling and the other ("Noordwijk") just north of the outflows of the rivers Rhine and Meuse (Fig. 1.1). In addition, information on phytoplankton species composition from two stations within the Wadden Sea ("Danziggat" (TDG), "Marsdiep Noord" (TMD)) was added. The numbering of the stations at these transects reflects their distance (km) to the coastline, e.g. sampling station "T100" is located 100 km from the shoreline of the island of Terschelling.
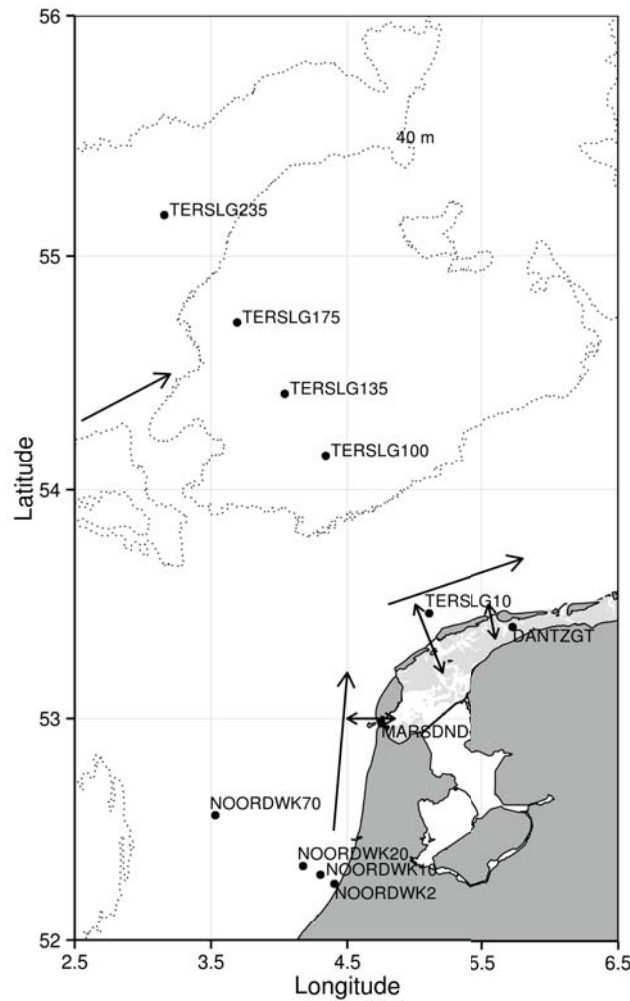


Figure 1.1: Map of study area with phytoplankton sampling stations (red points) and residual currents (van Raaphorst et al., 1998, black arrows; ), see Table 1.1 for description of stations.

The Terschelling transect covers a range of environmental conditions (Fig. 1.1 & Tab. 1.1) from shallow permanently mixed waters in the coastal zone ("T10") via the relatively shallow Oyster Grounds and a deeper channel (around 50 m) with mostly muddy ground and summer stratification ("T100", "T135") to the Dogger Bank that is a really shallow (18 m) sand bank in the middle of the central North Sea ("T235"). Except for the "T10", which is closest to the coast, thermal stratification occurs on all stations during summer (Baretta-Bekker et al., 2009).

The Noordwijk transect ranges from the coastal zone to 70 km offshore ("N70"). Except for the shallowest station ("N2") all stations are in permanently mixed waters (Fig. 1.1). At this transect, thermal and haline stratification occur intermittently for short periods (Baretta-Bekker et al., 2009).

Table 1.1: Names, codes (1: this paper; 2: original data base RWS) and geographical position (latitude in °N; longitude in °E) of sampling stations of phytoplankton with their distance to shore (in km), depth (in m), average salinity (in PSU) and indication if summer stratification occurs or not as obtained from Otto et al. (1990).

| Transect | Station Code 1 | Station Code 2 | Latitude | Longitude | Distance | Depth | Salinity | Stratification |
|---|---|---|---|---|---|---|---|---|
| Terschelling | TDG | DANTZGT | 53.401140 | 5.726982 | 0 | 5 | 28.89 | No |
| | TMD | MARSDND | 52.982540 | 4.749931 | 0 | 16 | 28.43 | No |
| | T10 | TERSLG10 | 53.461111 | 5.100833 | 10 | 24 | 32.68 | No |
| | T100 | TERSLG100 | 54.149444 | 4.341944 | 100 | 49 | 34.57 | Yes |
| | T135 | TERSLG135 | 54.415556 | 4.041111 | 135 | 35 | 34.64 | Yes |
| | T175 | TERSLG175 | 54.719167 | 3.691667 | 175 | 35 | 34.74 | Yes |
| | T235 | TERSLG235 | 55.172222 | 3.157500 | 235 | 18 | 34.8 | Yes |
| Noordwijk | N2 | NOORDWK2 | 52.261389 | 4.406111 | 2 | 13 | 29.14 | No |
| | N10 | NOORDWK10 | 52.302222 | 4.302500 | 10 | 18 | 30.65 | Transition |
| | N20 | NOORDWK20 | 52.341667 | 4.175000 | 20 | 20 | 32 | Transition |
| | N70 | NOORDWK70 | 52.569444 | 3.531389 | 70 | 28 | 34.92 | Transition |

### 1.2.2 *Sampling*

The data used in this study are part of the Dutch monitoring program that is executed by the Dutch Ministry of Transport and Public Works. Methods of sampling and counting of the samples were described in detail by Prins et al. (2012). The data was accessed through the national database (DONAR, `www.waterbase.nl`) and cell counts were separated into taxonomical groups (in this case Order). Taxonomical classification for each (group of) species was obtained from Koeman et al. (2005) and the database WoRMS (World Register of Marine Species; `www.marinespecies.org`).

### 1.2.3 *Statistical analysis*

Data exploration was applied following the protocol described in Zuur et al. (2010). Time series were plotted for each location and inspected for outliers and zero inflation. Spatial and temporal trends and variability in phytoplankton order richness was analyzed by testing a set of different models. Since the order richness is a count, a Poisson distribution with a log-link was used. This means that the basic model is of the form:

$$Order\ richness_{it} \sim Poisson(\mu_{it})$$
$$E(Order\ richness_{it}) = \mu_{it}$$
$$\mu_{it} = exp(\eta_{it})$$

*Order richness*$_{it}$ is defined here as the number of taxonomical orders for which phytoplankton of a taxonomical group (i.e. diatoms or flagellates) was found at location i at time t. The predictor function μit is a function of the covariate terms representing a long-term trend, seasonality and location. Due to the non-linearity of seasonal patterns, generalized additive models (GAM) were applied (Wood, 2006; Zuur et al., 2013, 2014). The basic model was of the following form:

$$\eta_{it} = \alpha + f(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$$

The notation $f(DayInSeason_t)$ is a smoothing function of the seasonal pattern. In model M1 we use one long-term smoother for the all the locations (i.e. the $Year_i$ term) and also one seasonal smoother for all locations. The categorical covariate $Location_i$ allows for a different mean value per location. This basic model was subsequently adjusted to test the different hypotheses (see "Model selection" and Tab. 1.2).

The time series were highly irregular spaced in time, and sampling days differed per location, so the auto-correlation function could not be used. Therefore, a variogram was used via the gstat package (Pebesma, 2004) in R to assess temporal and spatial residual correlation. Variograms of Pearson residuals from each location did not show temporal correlation. However, when all residuals were combined, temporal correlation up to 6 days (indicating spatial correlation) were found and therefore a spatially correlated residual term was added and fitted to all models using integrated nested Laplace approximation via R (INLA Rue et al., 2009, 2015). As in other Bayesian approaches, INLA estimates the posterior distribution of all random effects and parameters that are included into the model. It can handle different distributions as well as complex temporal and spatial correlations. The tools available for smoothing techniques in the current version of INLA are limited, especially for interaction terms between smoothers and categorical variables. However, the INLA package allows specification of a smoother in terms of its basis functions. Most smoothers can be written as $\mathbf{X} \times \mathbf{b} + \mathbf{Z} \times \mathbf{u}$, where the $\mathbf{u}$'s as normally distributed random intercepts, see Zuur et al. (2014) for a detailed explanation. This notation is accepted by INLA. Here we used 35 knots (Ruppert et al., 2003) and O'Sullivan splines as the most widely used smoother functions and being implemented into the mgcv package (Wand and Ormerod, 2008). For models with interactions between the smoother and the categorical variable location or group, the matrices $\mathbf{X}$ and $\mathbf{Z}$ are defined as block diagonal matrices.

### 1.2.4  *Model selection*

Outcomes of fits of different models were compared to examine if seasonal patterns in the phytoplankton order richness of diatoms and flagellates at stations along the two transects perpendicular to the coastline could be best explained:

(I) by local variation dominating the geographical variation in phytoplankton order richness (null hypothesis), or

(II) by one common seasonality pattern for all stations within a transect (Hypothesis 1), or

(III) by a gradual shift in seasonality from the central North Sea to the coast (Hypotheses 2), or

(IV) by groups of seasonal patterns related to specific spatial processes such as summer stratification or the "line of no return" (Hypotheses 3-4), or

(V) by groups of seasonal patterns related to specific physical properties such as water depth and distance to the shore (Hypotheses 5-6, only possible for the Terschelling transect), or

(VI) by local seasonal variation dominating variation at large spatial scales (Hypothesis 7; Tab. 1.2).

Models fitted with the INLA package were compared by the DIC (Deviance Information Criterion). DIC is the Bayesian equivalent to the Akaike's information criterion (AIC), a tool to measure the goodness-of-fit of an estimated statistical model and model complexity. If competing models are ranked according to their DIC, the one having the lowest DIC is the best. Differences ($\Delta DIC = DIC_i - DIC_{min}$) between the DIC of a particular model ($DIC_i$) and

Table 1.2: Hypotheses and statistical models for patterns in seasonality in phytoplankton order richness ($\eta_{it}$) along a transect.

| # | Hypothesis | Statistical model | Description | Model |
|---|---|---|---|---|
| H0 | There is no trend, just noise (local variation dominates geographic variation in phytoplankton order richness) | $\eta_{it} = \alpha + Location_i + \epsilon_{it}$ | | |
| H1 | All the time series have one (similar) underlying seasonal trend | $\eta_{it} = \alpha + f(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$ | The notation $f(DayInSeason_t)$ is as smoothing function of the seasonal pattern. In this model we use one seasonal smoother for all locations and year ($factor(Year_t)$) as a categorical variable. The categorical covariate $Location_i$ allows for a different mean value per location | Model# 1 |
| H2 | Seasonality changes over the transect which is related to salinity | $\eta_{it} = \alpha + f_j(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$ | $j = 1,2$; where $j$ refers to the Salinity zone with avg. Salinity below 30 PSU refers to brackish, above to marine | Model# 2 |
| H3 | All the time series havethree underlying seasonal trends which are related to stratification | $\eta_{it} = \alpha + f_k(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$ | $k = 1,\dots,3$; where $k$ refers to stratification zones (mixed, transit and stratified) | Model# 3 |
| H4 | All the time series have two underlying seasonal trends which are related to the line of no return two underlying seasonal trends which are related to the line of no return | $\eta_{it} = \alpha + f_l(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$ | $l = 1,2$; where $l$ refers to zone inside or outside line of no return nb: no predefined clustering, so 5 submodels possible | Model# 2, Model# 3, Model# 4c-e |
| 4c | Terschelling: separation between "T100" and "T135" Noordwijk: separation between "N10" and "N20" | | | |
| 4d | Terschelling: separation between "T135" and "T175" Noordwijk: separation between "N20" and "N70" | | | |
| 4e | Terschelling: separation between "T175" and "T235" Noordwijk: Not possible | | | |
| H5 | All the time series have two underlying seasonal trends which are related to the depth of the station | $\eta_{it} = \alpha + f_m(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$ | $m = 1,\dots,3$; where $m$ refers to the depth of the station (only Terschelling transect) | Model# 5 |
| H6 | All the time series have two underlying seasonal trends which are related to a combination of depth of the station and it's distance to the shore | $\eta_{it} = \alpha + f_n(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$ | $n = 1,\dots,4$; where $n$ refers to a combination of depth and distance to the shore (only Terschelling transect) | Model# 6 |
| H7 | All the time series alongthe transect have a different seasonal trend | $\eta_{it} = \alpha + f_o(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$ | $o = 1,\dots,$ max station number; where $o$ refers to the station code | Model# 7 |

the that of the best model ($DIC_{min}$) of more than 10 might definitely rule out the particular model i with the higher DIC, and differences between 2 and 10 imply substantially less good fit of the particular model compared to the best model. If the difference in DIC is less than 2, then the fit of the particular model is considered to be comparably good as that of the best model (Burnham and Anderson, 2002). In case one of these two models is simpler than the other, this one should be considered being the best. However, if models with DIC differences of less than 2 are comparably complex, then there is no best model. The likelihood of a particular model i to be the best one was calculated following Burnham and Anderson (2002) by applying the following formula:

$Likelihood = exp\left(\frac{(DIC_{min} - DIC_i)}{2}\right)$

where $DIC_{min}$ is the lowest found DIC of the different models tested and $DIC_i$ is the DIC of the model i for which the likelihood is calculated.

## 1.3 RESULTS

### 1.3.1 *Phytoplankton order richness*

A total of 26 different orders of diatoms were found within the study area and study period, of which six were only found occasionally (Achnanthales, Aulacoseriales, Corethales, Licmophorales, Striatellales and Thalassiophysales, App. Fig. **??**). Several orders (among others Anaulales, Centrales and Thalassiosirales) were more abundant close to the shore than further offshore. For diatoms, the highest number of orders (20) was found at the "Marsdiep Noord" station orders on 17th October 2005, and the lowest (0) at the stations "T100" and "T235" on 2nd May 2007. For diatoms, the order richness showed a seasonal pattern that differed spatially (Fig. 1.2). The Wadden Sea stations ("TMD" and "TDG") had the highest order richness in summer/autumn. At the Terschelling transect, the station 10 km off the coast showed the highest order richness of diatoms in winter and the stations at 100, 135 and 175 km off the coast showed a less clear seasonal pattern (Fig. 1.2, right). The diatoms at the station at 235 km off the coast ("T235") had relatively low order richness in summer, but not as low as at the "T10" station (Fig. 1.2, right). The Noordwijk transect showed low order richness in diatoms at all stations during summer (Fig. 1.2).

For flagellates, a total number of 31 different orders were found of which 13 occurred only occasionally (Chlorodendrales, Coccidiniales, Coccosphaerales, Euglenida, Floenciellales, Isochrysidales, Mischococcales, Nephroselmidales, Pyrocystales, Synurales, Synacosphaerales, Thannatomonadida and Volvocales, App. Fig. **??**). Several orders of flagellates had a higher presence closer to the shore (Noctilucales and Sphaeropleales), whilst others showed a clear offshore preference (Dinophysiales, Gonyaulacales and Prorocentrales). Flagellates order richness showed less variation than that of diatoms with a maximum value of 16 orders at "T235" (21st February 2006, 22nd June 2004 and 2nd May 2007). The minimum order richness in flagellates (0) was found at stations "N10" and "N2" on various dates. For flagellates, the seasonal pattern appeared to be less variable than for diatoms and more or less similar between the stations with a relatively high order richness found in summer compared to winter (Fig. 1.2).

### 1.3.2 *Spatial and temporal trends*

*Terschelling transect*

For diatoms, spatial and temporal trends in order richness was best explained by Model # 6 with a grouping of stations into four areas according to the combination of water depth and the distance to the shore (Tab. 1.3). The difference in DIC compared to the next best model (# 2) was more than 40, indicating that other explanations (Models) were not competing with Model # 6. The results of this model indicated a seasonal pattern with generally high order richness in summer in the Wadden Sea (Area 1) compared to the three areas in the North Sea (Fig. 1.3).

Table 1.3: DIC and likelihood of the different models at the Terschelling transect for diatoms and flagellates ΔDIC refers to the difference of the DIC from this model to the one with the lowest DIC.

| | Diatom | | | Flagellates | | |
|-------|---------|--------|------------|---------|--------|------------|
| Model | DIC | ΔDIC | likelihood | DIC | ΔDIC | likelihood |
| 1 | 5462.04 | 274.75 | 0 | 4622.72 | 0 | 1 |
| 2 | 5227.82 | 40.53 | 0 | 4637.92 | 15.2 | 0 |
| 3 | 5301.13 | 113.84 | 0 | 4786.88 | 164.16 | 0 |
| 4c | 5392.32 | 205.03 | 0 | 4734.75 | 112.03 | 0 |
| 4d | 5420.46 | 233.17 | 0 | 4771.45 | 148.73 | 0 |
| 4e | 5485.49 | 298.2 | 0 | 4783.38 | 160.66 | 0 |
| 5 | 5267.23 | 79.94 | 0 | 4655.45 | 32.73 | 0 |
| 6 | 5187.29 | 0 | 1 | 5187.29 | 564.57 | 0 |
| 7 | 5372.51 | 185.22 | 0 | 5372.51 | 749.79 | 0 |

Table 1.4: DIC and likelihood of the different models at the Noordwijk transect for diatoms and flagellates ΔDIC refers to the difference of the DIC from this model to the one with the lowest DIC.

| | Diatom | | | Flagellates | | |
|-------|---------|-------|------------|---------|--------|------------|
| Model | DIC | ΔDIC | likelihood | DIC | ΔDIC | likelihood |
| 1 | 3609.79 | 35.54 | 0 | 3089.59 | 21.46 | 0 |
| 2/3 | 3590.21 | 15.97 | 0 | 3068.12 | 0 | 1 |
| 4c | 3578.66 | 4.42 | 0.11 | 3069.67 | 1.54 | 0.46 |
| 4d | 3574.24 | 0 | 1 | 3072.14 | 4.01 | 0.13 |
| 7 | 3584.15 | 9.91 | 0.01 | 3584.15 | 516.03 | 0 |

In the North Sea, lowest summer values were found at "T10" (Area 2). The other stations at this transect showed a pattern with a peak in the middle of the summer and two phases with lower order richness and the furthest offshore station, which was more pronounced in Area 3 ("T100", "T135" and "T175") than in Area 4 ("T235") (Fig. 1.3). For this model, the diatom order richness in Area 1 (Wadden Sea) was significantly higher compared to the other areas in the North Sea and appeared to decrease within the North Sea from inshore to offshore areas (Tab. 1.5). The annual estimates for seasonality showed no significant difference between the year 2001 and the other years, implying the seasonal variation in order richness of diatoms was more or less similarly strong for all years (Tab. 1.5, Fig. 1.7A).

Table 1.5: Posterior estimates (mean and 95% credibility interval) of model parameters of Model #6 for diatoms, Area 1 refers to the Wadden Sea stations ("TMD", "TDG"), Area 2 refers to "T10", Area 3 to "T100", "T135" and "T175" and Area 4 to "T235". The parameters values of the year 2001 and Area 1 ("Wadden Sea") are zero by definition.

| Parameter | mean | $Q_{0.025}$ | $Q_{0.975}$ |
|---|---|---|---|
| Intercept | 2.5557 | -2.2538 | 7.1897 |
| 2002 | -0.0794 | -0.2615 | 0.1231 |
| 2003 | -0.0773 | -0.3818 | 0.2826 |
| 2004 | -0.0504 | -0.4711 | 0.4856 |
| 2005 | -0.067 | -0.6041 | 0.6432 |
| 2006 | -0.1053 | -0.7526 | 0.7854 |
| 2007 | -0.1462 | -0.9554 | 0.8639 |
| 2008 | -0.1334 | -1.1553 | 0.9411 |
| 2009 | -0.2434 | -1.4424 | 0.9171 |
| Area 2 | -0.2846 | -0.3509 | -0.219 |
| Area 3 | -0.298 | -0.3446 | -0.2515 |
| Area 4 | -0.3517 | -0.4195 | -0.2845 |
| Smoother Area 1 | 0.0133 | -0.0319 | 0.0586 |
| Smoother Area 2 | 0.0079 | -0.0549 | 0.0706 |
| Smoother Area 3 | 0.0189 | -0.028 | 0.0652 |
| Smoother Area 4 | -0.0402 | -0.1046 | 0.0235 |

For flagellates, Model # 1 with only one seasonal trend with a peak in summer and lower values in winter for all stations had the lowest DIC (Tab. 1.3; Fig. 1.4). The DIC of the next best model was considerably higher (>10), so Model # 1 was selected as the best model. The posterior estimates of model parameters of this model indicted, however, that the flagellate order richness at Area 1 ("TDG") was significantly lower than that at all other stations (Tab. 1.6). Annual signals showed no significant differences between years, implying that all years experienced more or less the same strength in seasonality in order richness of flagellates (Tab. 1.6, Fig. 1.7B).

*Noordwijk transect*

For diatoms, the model with the lowest DIC was Model # 4d (Tab. 1.4), i.e. one of the models where the grouping of the stations was tested according to a possible presence of a "line-of-no-return". The difference in DIC between this model and other second best model (Model # 4c) was larger than 2, so Model # 4d was considered to be the best model. This model implied that the pattern in seasonality shifted between station "N20" and "N70", with the relatively low diatom order richness in summer at the outermost station of the Noordwijk transect (Area 2; "N70") being more pronounced than those in Area 1, comprising the other three stations closer to the shore (Fig. 1.5) and having an overall lower order richness (Tab. 1.7). Compared to the

Table 1.6:  Table 6. Posterior estimates (mean and 95% credibility interval) of model parameters of Model #1 for flagellates, Area 1 refers to "TMD", Area 2 to "TDG", Area 3 to "T10", Area 4 to "T100", Area 5 to "T135", Area 6 to "T175" and Area 7 to "T235". The parameters values of the year 2001 and Area 1 (station "TMD") are zero by definition.

| Parameter | mean | $Q_{0.025}$ | $Q_{0.975}$ |
|---|---|---|---|
| Intercept | 1.7436 | 0.2919 | 1.1564 |
| 2002 | -0.1248 | 0.1511 | -0.4379 |
| 2003 | -0.1283 | 0.2045 | -0.5704 |
| 2004 | -0.1993 | 0.2498 | -0.774 |
| 2005 | -0.3584 | 0.2933 | -1.0664 |
| 2006 | -0.1973 | 0.3134 | -0.9535 |
| 2007 | -0.2503 | 0.3416 | -1.0708 |
| 2008 | -0.2779 | 0.3794 | -1.2217 |
| 2009 | -0.1264 | 0.4136 | -1.1442 |
| Area 2 | 0.2381 | 0.0433 | 0.1533 |
| Area 3 | 0.3456 | 0.0449 | 0.2575 |
| Area 4 | 0.4708 | 0.0438 | 0.3848 |
| Area 5 | 0.4479 | 0.044 | 0.3615 |
| Area 6 | 0.4198 | 0.0446 | 0.3324 |
| Area 7 | 0.4226 | 0.0444 | 0.3355 |
| Smoother | 0.0724 | 0.0205 | 0.0313 |

year 2001, the overall order richness in diatoms was significantly lower in the years 2005 and 2009 (Tab. 1.7, Fig. 1.7C).

Table 1.7:  Posterior estimates (mean and 95% credibility interval) of model parameters of Model #4d for diatoms, Area 1 refers to "N2", "N10" and "N20", Area 2 to "N70". The parameters values of the year 2001 and Area 1 ("N2", "N10","N20") are zero by definition.

| Parameter | mean | $Q_{0.025}$ | $Q_{0.975}$ |
|---|---|---|---|
| Intercept | 2.4292 | 2.288 | 2.5727 |
| 2002 | -0.1205 | -0.2875 | 0.0565 |
| 2003 | -0.0844 | -0.2851 | 0.0921 |
| 2004 | -0.1293 | -0.324 | 0.0678 |
| 2005 | -0.2548 | -0.4516 | -0.0525 |
| 2006 | -0.1544 | -0.3553 | 0.0415 |
| 2007 | -0.1803 | -0.3679 | 0.0352 |
| 2008 | -0.162 | -0.3561 | 0.0485 |
| 2009 | -0.2433 | -0.4526 | -0.046 |
| Area 2 | -0.058 | -0.1163 | -0.0003 |
| Smoother Area 1 | 0.01 | -0.0215 | 0.0415 |
| Smoother Area 2 | -0.037 | -0.0845 | 0.0103 |

With regard to flagellates, the combined Model # 2/ Model # 3 had the lowest DIC, however the difference in DIC to the next best model was less than 2 (Model # 4c). As both model have the same complexity they should be treated as equally good in their prediction of the seasonal pattern (Tab. 1.4). Model # 2/3 implied that the pattern in seasonality shifts between station "N2" (Area 1, where there is no stratification) and Area 2 ("N10", N20" and "N70") that is considered as a transition zone between waters that are continuously mixed and that experience summer stratification (Tab. 1.8) with a peak in late summer order richness being higher in the outermost stations (Fig. 1.6A). The most inshore station "N2" had overall higher

order richness in flagellates (Tab. 1.8). Model # 4c implied that the pattern in seasonality shifts between Area 1 ("N2" and "N10") and Area 2 ("N20" and "N70"; Tab. 1.8) with a peak in late summer order richness being higher in the outermost stations (Fig. 1.6B). The most inshore station "N2" had overall higher order richness in flagellates (Tab. 1.8). In both models seasonal signals did not significantly differ between years and showed the same overall pattern (Tab. 1.8, Fig. 1.7D; only graph from best model shown).

Table 1.8: Posterior estimates (mean and 95% credibility interval) of model parameters of Model #2 /3 and Model #4c for flagellates, Area 1 refers to "N2" in Model #2 /3 and "N2" & "N10" in Model #4c and Area 2 to "N10", "N20" and "N70" in Model #2 /3 and "N20" and "N70" in Model #4c. The parameters values of the year 2001 and Area 1 ("N2" or "N2"and "N10") are zero by definition.

| Parameter | Model #2 /3 | | | Model #4c | | |
|---|---|---|---|---|---|---|
| | mean | Q0.025 | Q0.975 | mean | Q0.025 | Q0.975 |
| Intercept | 1.8072 | 0.6227 | 0.3746 | 1.9805 | 1.3662 | 2.7155 |
| 2002 | -0.0816 | 0.134 | -0.3704 | -0.1082 | -0.4253 | 0.185 |
| 2003 | 0.0359 | 0.1955 | -0.4123 | -0.0984 | -0.5471 | 0.2991 |
| 2004 | -0.1279 | 0.26 | -0.7776 | -0.1827 | -0.7728 | 0.2782 |
| 2005 | -0.0929 | 0.3232 | -0.9231 | -0.3483 | -1.0812 | 0.1531 |
| 2006 | 0.0461 | 0.3664 | -0.872 | -0.186 | -0.9726 | 0.4055 |
| 2007 | -0.0187 | 0.4195 | -1.0202 | -0.2267 | -1.0769 | 0.4587 |
| 2008 | -0.063 | 0.4726 | -1.224 | -0.2583 | -1.2352 | 0.4804 |
| 2009 | -0.0112 | 0.5261 | -1.3292 | -0.0974 | -1.1536 | 0.7611 |
| Area 2 | -0.1502 | 0.041 | -0.2313 | 0.2016 | 0.152 | 0.2511 |
| Smoother Area 1 | 0.06 | 0.0435 | -0.0258 | 0.0612 | 0.0135 | 0.1082 |
| Smoother Area 2 | 0.0858 | 0.0256 | 0.0343 | 0.0782 | 0.0261 | 0.1298 |
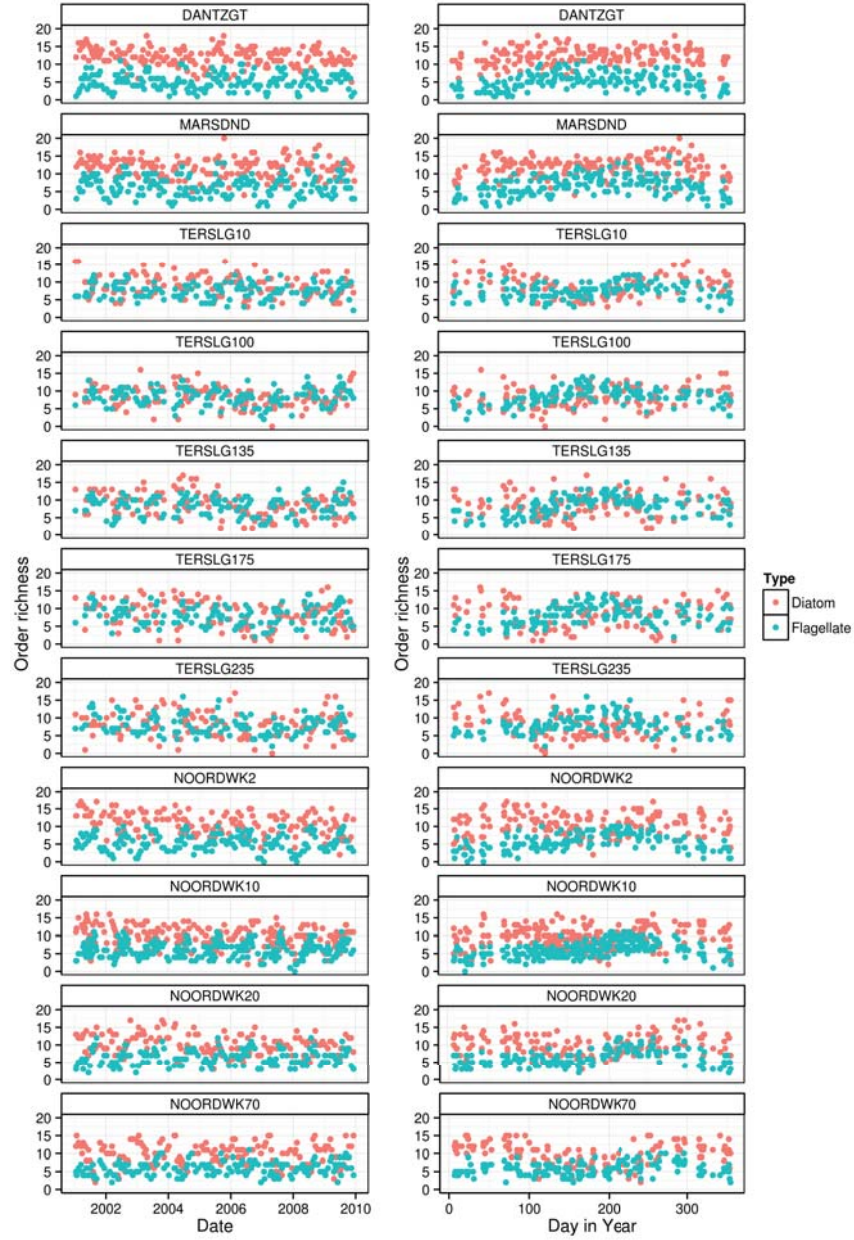
Figure 1.2: Order richness ($\eta_{it}$) based on the number of taxonomical orders of diatoms and flagellates in a sample for stations in the Wadden Sea and North Sea for the period 2001-2009 (left panels) and during the season (right panels).
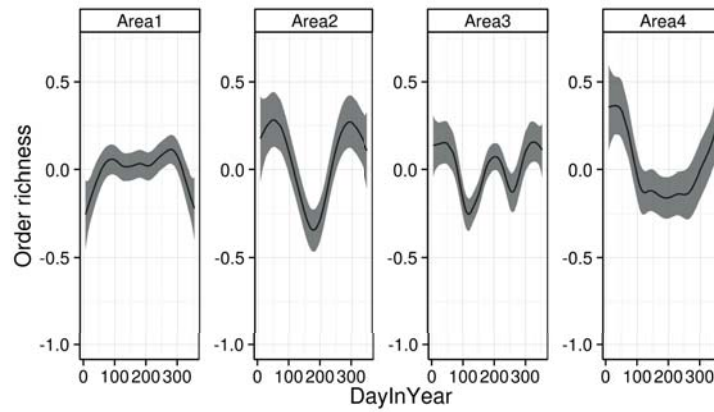
Figure 1.3: Seasonal smoother for order richness in diatoms at the Terschelling transect for four different areas as described by Model #6, i.e. Area 1 ("TMD", "TDG"), Area 2 ("T10"), Area 3 ("T100", "T135", "T175") and Area 4 ("T235").
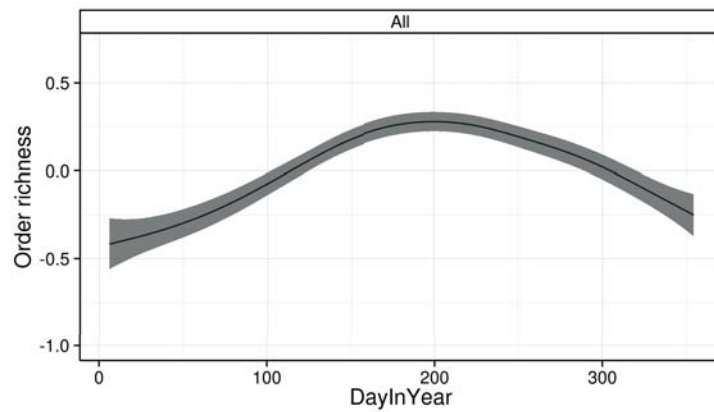


Figure 1.4: Seasonal smoother for order richness in flagellates at the Terschelling transect as described by Model # 1, i.e. one common smoother for seasonality at all stations in the Wadden Sea and North Sea.
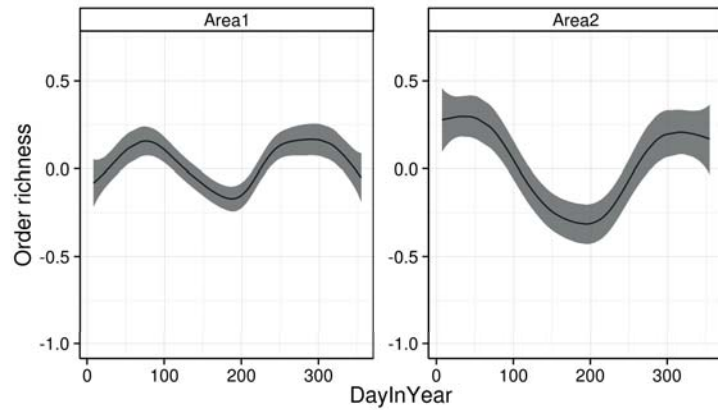
Figure 1.5: Seasonal smoother for order richness in diatoms at the Noordwijk transect for two different areas as described by Model 4d, i.e. Area 1 ("N2", "N10", "N20") that is assumed to be inside the "line-of-no-return" and Area 2 ("N70") that is assumed to be outside the exchange area.
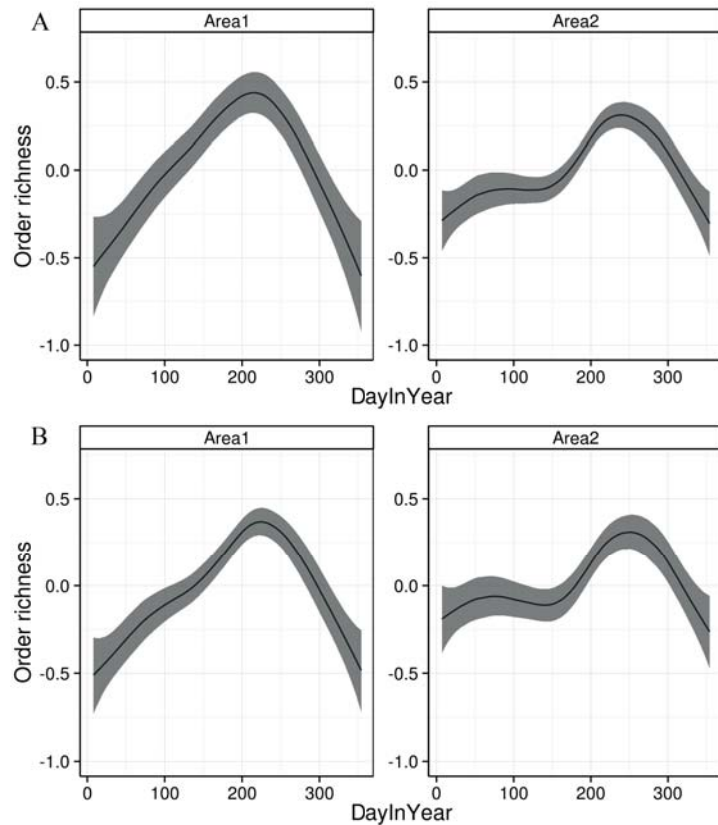


Figure 1.6: Seasonal smoother for order richness in flagellates at the Noordwijk transect for two different areas as described by A) Model 2/3, i.e. Area 1 ("N2") that is permanently mixed and Area 2 ("N10", "N20", "N70") that occasionally experiences thermal and haline stratification and B) Model 4c, i.e. Area 1 ("N2" and "N10") and Area 2 ("N20", and "N70").
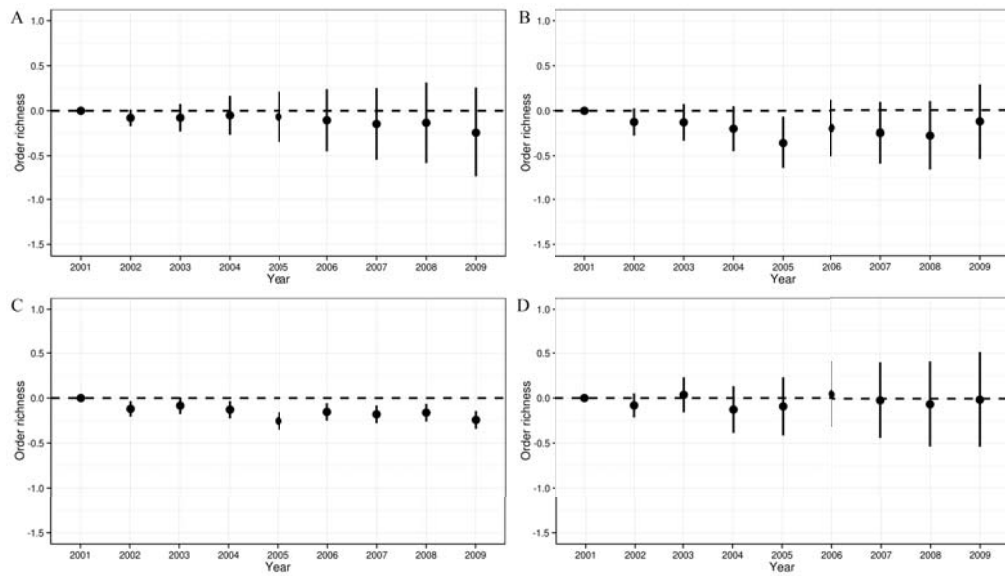
Figure 1.7: The year effect of the various models, i.e. Model #6 for diatom order richness along the Terschelling transect (A), Model #1 for flagellate order richness along the Terschelling transect (B), Model #4d for diatom order richness along the Noordwijk transect (C) and Model #2 / Model #3 for flagellate order richness along Noordwijk transect (D).

## 1.4   DISCUSSION

The seasonality patterns in phytoplankton order richness along transects perpendicular to the shore, both for diatoms and flagellates suggests that it might be a promising tracer for identifying mixing of particulate organic matter between coastal and open waters. Several other studies indicate that the number of species is related to the general functioning of an ecosystem (Naeem et al., 1994) such as nutrient cycling, production and resource use efficiency (Loreau et al., 2001; Naeem, 2009; Finkel et al., 2010). However, not only richness on a species level can be used to assess such ecological relationships (Gaston et al., 1993). The higher taxon approach was first used for terrestrial ecosystem (Balmford et al., 1996, and literature therein) and is now also transferred to aquatic ecosystems (Passy and Legendre, 2006; Heino and Soininen, 2007; Gallego et al., 2012; Carneiro et al., 2013; Mueller et al., 2013; Machado et al., 2015). Several studies dealing with the higher taxon approach in freshwater algae (e.g. Heino and Soininen, 2007; Carneiro et al., 2013) and marine phytoplankton (e.g. Ptacnik et al., 2008; Olli et al., 2013, 2014) showed that higher taxa can be used to assess eutrophication state and resource use. Also our findings with regard to exchange of particulate matter based upon seasonality patterns in order richness underlines the strength of the higher taxon approach. For the two transects (Terschelling, Noordwijk) and the two phytoplankton groups (diatoms, flagellates), there was no common model that could explain the observed seasonality in phytoplankton order richness. For the group of Terschelling stations (in total six stations, including two stations in the Wadden Sea), seasonality in order richness varied according to depth and distance to shore for diatoms and was uniform along this transect for flagellates. At the four Noordwijk transect stations, there appeared to be two groups in seasonality with the outermost station ("N70") being separated from the rest for the diatoms, and the seasonality at innermost non-stratified station ("N2") being different from the rest for the order richness in flagellates. This implies that the seasonality pattern in diatom order richness at Noordwijk was not explained by ambient environmental conditions with respect to depth, distance to shore, salinity and stratification, and may therefore be the result of a "line-of-no-return" between 20 and 70km from the shore. For the Terschelling transect, there are no stations at comparable distances from the shore and there appears to be a change in seasonality of diatoms somewhere between 10km and 100 km. This implies that a "line-of-no-return" might also exists in this part (10 – 100 km) of the Terschelling transect. Our findings on a possible "line-of-no-return" between 20 and 70 km from the shore at Noordwijk and between 10 and 100 km at Terschelling is in line with previous observations of a minimum in suspended particulate matter (SPM) concentrations at 50 to 100 km from the shore (Postma, 1981; Visser et al., 1991). The sampling grid of this data set was, however, not fine enough to narrow down the exact position of the "line-of-no-return". Within coastal waters, the phytoplankton spring bloom is generally dominated by large, fast-growing diatoms, followed by a number of summer and autumn blooms comprised of diatoms and flagellates (Tett et al., 1986; Mallin et al., 1991; Carstensen et al., 2015). Diatoms often dominate phytoplankton blooms in the coastal zone because they are so highly adaptable to different environmental conditions such as varying light and other physical stress (Armbrust, 2009; Carstensen et al., 2015). As phytoplankton blooms are mostly dominated by a single species (e.g. the flagellate *Phaeocystis globosa*), highest observed order richness is expected outside blooms but still within the growing season. Different patterns in seasonality in the order richness (as, for example, found for diatoms along the Terschelling transect) might, therefore, reflect different timing in (low diversity) blooms. Different strength in seasonality (as, for example, found for diatoms along the Noordwijk transect) might reflect different strength of coinciding blooms at these stations. In addition, however, higher overall densities increase the probability of finding more species in a sample of a given volume (Gotelli and Colwell, 2001). In Dutch coastal waters, dinoflagellates tend to have a higher biomass in summer-stratified (lower turbulence) offshore stations, thus attaining highest biomass on stations further from the coast where thermal and/or haline stratification occurs (Baretta-Bekker et al., 2009). However, biodiversity is expected to be low during blooms (Baretta-Bekker et al., 2009), with the lowest order richness of flagellates

in summer months. Our results contradict these expectations, as we find the highest order richness in flagellates at both transects in summer. We also found an increase in seasonality along the Noordwijk transect, being subject to short periods of intermittent thermal and haline stratification. This signal of stratification was not observed for flagellate order richness along the Terschelling transect where thermal stratification occurs on almost all (with exception of "T10") stations during summer. During periods of haline stratification, phytoplankton samples taken from the water surface at "N2" might have contained (more) freshwater flagellates closer to shore. This is in agreement with the gradual decline of the presence of the freshwater order "Sphaeropleales" between "N2" and "N20" at the Noordwijk transect (see Appendix Fig. **??**). From these observations, it appears that seasonality in order richness in flagellates is more driven by an overall seasonality in phytoplankton communities, driven by nutrient cycling and inflow of freshwater algae, then by thermal stratification during summer. Our findings suggest that patterns in seasonality in order richness of diatoms and flagellates reflect different water masses and drivers of phytoplankton dynamics along the coastline of the Netherlands. The Wadden Sea was found to be clearly different from the North Sea, implying that seasonality in Wadden Sea phytoplankton is at least partly driven by local environmental conditions and /or that the exchange between the Wadden Sea and the North Sea is limited, in particular during summer. The stations "N2", "N10", "N20" and "T10" appear to be at the inside of the "line-of-no-return". Similarity in seasonality in diatom order richness at "T100", "T135" and "T175" compared to the more shallow stations in the close surroundings suggests that depth is a strong driver for phytoplankton dynamics and that this signal is not diffused as the result of mixing along the transect. Our findings with regard to clear grouping of stations based on seasonality and long-term variation in order richness of diatoms and flagellates underline the potential of using information at higher taxonomic levels to detect spatial and temporal patterns in mixing. In order to take full advantage of this technique, a grid on order richness with a higher resolution in time and space is required.

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