Chapter 8

Synthesis

In this thesis the variability of phytoplankton has been characterized across different temporal scales in different areas of the North Sea. Also the mechanisms driving this phytoplankton variability have been analyzed and identified with different types of data sets and different methods. In this way experience has been gained in how large data sets from novel monitoring methods can be analyzed to create added value from their enhanced temporal and spatial resolution. This knowledge supports the development of a new monitoring strategy for the North Sea, including novel monitoring methods, such as moorings and satellite remote sensing.

8.1 PHYTOPLANKTON VARIABILITY AND ITS DRIVERS

*Total phytoplankton biomass*

Highest chlorophyll concentrations are generally observed in coastal waters, where nutrient availability is relatively high due to river inputs. Comparing chlorophyll fluorescence between four mooring stations in the North Sea showed highest fluorescence at the two coastal stations influenced by the rivers Rhine and Thames (chapter 7 in this thesis). Based on riverine nutrient input one would expect to see a negative correlation between seasonally averaged phytoplankton biomass and salinity. However, de Vries et al. (1998) found that in Dutch coastal waters chlorophyll levels remained fairly constant at salinities below 32 and only decreased at higher salinities, even though nutrient concentrations decreased linearly with salinity. This indicates that phytoplankton biomass near-shore may be limited by something else than nutrients. High turbidity in near-shore waters may limit phytoplankton growth through light limitation (e.g. Colijn and Cadée, 2003, Loebl et al., 2009). Also estuarine circulation may keep phytoplankton confined in subsurface patches during parts of the tidal cycle, where it might be missed by surface measurements (Joordens et al., 2001).
Our analysis of mooring data at the seasonal time scale identified the availability of nutrients and light as most important drivers of seasonal variability (chapter 7 of this thesis). This corresponds to textbook knowledge and earlier studies (Llope et al., 2009; Stenseth et al., 2006). Since almost all environmental variables co-vary at the seasonal time scale it is hard to identify from correlation analysis which variable is really the driver of the seasonal variability. With mechanistic numerical models such as the Generic Ecological Model (GEM) spatial and seasonal variability of phytoplankton concentrations are simulated based on theoretical and empirical knowledge on the relation between growth rates and the availability of light and nutrients. We could reproduce observed seasonal and spatial variability of chlorophyll well with GEM for a wide range of locations (chapter 2 in this thesis). This confirms that seasonal and spatial patterns of phytoplankton variability can be explained by the availability of nutrients and light.

Contrary to the seasonal time scale, nutrients do not appear to play an important role in the interannual variability of total phytoplankton biomass in the North Sea. In the chlorophyll data of the Continuous Plankton Recorder, with a monthly sampling frequency, inter-annual variability in coastal waters was not significantly correlated with nutrient availability (McQuatters-Gollop and Vermaat, 2011). However, significant correlations were found with hydroclimatic variables such as sea surface temperature, Atlantic inflow and the North Atlantic Oscillation Index (NAO).

Our analysis of mooring data at short time scales from hours to weeks showed that fluctuations in chlorophyll fluorescence were mainly driven by transport and mixing by tides and wind (chapter 7 in this thesis). Day-to-day fluctuations did not show positive correlations with nutrient concentrations or solar irradiance at any of the four mooring stations we analyzed. Hour-to-hour variability within the day showed large diurnal fluctuations in chlorophyll fluorescence which were at least partly caused by physiological processes to protect phytoplankton from excess light (e.g., non-photochemical quenching). This day-night cycle in chlorophyll fluorescence was particularly strong in clear waters, such as the Oystergrounds area.

Furthermore, our analyses of the mooring data indicates that vertical mixing and sinking are dominant drivers of short-term phytoplankton fluctuations (chapters 6 and 7). If sinking of phytoplankton cells is important we expect to see lower chlorophyll concentrations near the surface than in deeper water layers, even if the water column is not stratified. This was indeed observed by Boon et al. (2003) at locations in permanently mixed deep waters in the southern North Sea. In areas that are seasonally stratified, such as the Oystergrounds, or intermittently stratified, such as the Rhine plume, vertical gradients in phytoplankton concentrations are even more pronounced. This is illustrated in Figure 8.1, which shows time series at the surface and vertical profiles of chlorophyll...
fluorescence and water temperature in 2007 at the Oystergrounds. The vertical profiles of temperature show the onset of stratification in April, with the pycnocline getting deeper throughout the year. Fluorescence is rarely homogeneous over depth; sometimes it is highest in the surface layer and sometimes in the lower layer.

Figure 8.1: Chlorophyll concentrations at station Oystergrounds in 2007: A) Time series of water temperature and nighttime chlorophyll fluorescence at 1 m below the surface measured at the mooring. Vertical profiles of B) chlorophyll fluorescence and C) water temperature measured from research vessels by Rijkswaterstaat. The fluorescence profiles in B) were obtained during daytime, except for one single nighttime profile in mid May. The fluorescence profiles are shaded at depths where local PAR was higher than 100 μmol.m⁻².s⁻¹, since these conditions are suspected to underestimate the actual chlorophyll concentration due to non-photochemical quenching.

Species composition
In this thesis the only phytoplankton species that we analyzed in detail is *Phaeocystis* globosa. This is the most important nuisance phytoplankton species in Dutch coastal waters. It is considered an indicator species for eutrophication, since its abundance has increased in the period that nutrient availability increased (Cadée and Hegeman, 2002). The relation between *Phaeocystis* abundance and nutrient availability was confirmed in our comparison of *Phaeocystis* abundance between 26 monitoring stations with different nutrient availability. This showed relatively high *Phaeocystis* abundance in nutrient-rich near-shore waters and lower abundance in off-shore waters (chapter 4 in this thesis.)
Not only the spatial distribution of *Phaeocystis* but also the inter-annual variability of *Phaeocystis* abundance can be explained by nutrient availability in some areas. In Belgian coastal waters and along the English south coast, *Phaeocystis* abundance has been monitored at weekly intervals during spring for many years. In these areas a positive correlation has been found between inter-annual variability of peak *Phaeocystis* abundance in spring versus nitrate concentrations (Breton et al., 2006) and river runoff (chapter 5 in this thesis) in the preceding months. A similar analysis on the *Phaeocystis* data in Dutch coastal waters did not show a significant relationship between inter-annual variability in peak *Phaeocystis* abundance and nutrient inputs from rivers (chapter 4 in this thesis). One possible explanation for this lack of correlation could be the low sampling frequency of once or twice per month in Dutch coastal waters. The peak abundance can be easily missed with such infrequent sampling. Another explanation could be the relatively high temporal variability of phytoplankton abundance due to transport and mixing processes in the Rhine plume. This strong variability is illustrated by the analysis of mooring data 10 km offshore from Noordwijk in chapters 4 and 7. A third explanation for inter-annual variability might be the intrinsic variability in species composition of phytoplankton communities. It is difficult to predict the abundances of one specific species in a phytoplankton community that may consist of a hundred different species (e.g., Beninca et al. 2008; Dakos et al. 2009).

In 2001 mass mussel mortality occurred in the Eastern Scheldt, an area with extensive commercial mussel farming, presumably due to a *Phaeocystis* bloom. For 2001 high quality satellite images of MERIS were not available yet. SeaWIFS images were also not available during the 2001 harmful algal bloom events due to cloud cover (Hesselmans et al., 2004). To test the feasibility of harmful algal bloom prediction with the GEM model for the southern North Sea, we reconstructed the short term temporal evolution and spatial distribution of the spring bloom of 2003 with different data sources. We cross-validated the GEM model with MERIS satellite remote sensing images of chlorophyll, in situ data of chlorophyll and *Phaeocystis* from the BIOMON programme and almost daily sampling from a nearby sluice. The general phytoplankton spring bloom period (measured as chlorophyll concentrations) was similar in the model and satellite remote sensing images, throughout the Eastern Scheldt and surrounding coastal waters. Daily data of *Phaeocystis* abundance at one station showed a short peak during a few days, about two weeks after the start of the general phytoplankton spring bloom. In the GEM model the *Phaeocystis* bloom started simultaneously with the general phytoplankton spring bloom (chapter 3 of this thesis). This study illustrates how data from different sources can be combined to improve early-warnings of harmful algal blooms. However, for a reliable assessment of the feasibility of such an early warning system, the cross validation should be repeated
for more years and with more frequent \textit{Phaeocystis} data in the Eastern Scheldt. Such \textit{Phaeocystis} time series with high temporal resolution are unfortunately lacking so far.

Day-to-day variability in foam intensity, due to \textit{Phaeocystis} blooms, was strongly correlated with wind speed and direction. Foam events at Noordwijk beach have been monitored with an hourly sampling frequency with ARGUS video cameras (Figure 8.2). Foam frequency and intensity was highest at days with strong landward winds and absent on days with seaward wind. Foam was hardly ever observed outside the \textit{Phaeocystis} bloom season. The time series of video images of Noordwijk beach is the first time series of foam events at high (hourly) temporal resolution. It allowed quantification of the relation between foam events, wind conditions and \textit{Phaeocystis} abundance. Foam events only occur a few days per year and often last less than a day, so they cannot be sampled reliably based on lower frequency sampling (chapter 4 in this thesis). The high frequency time series of sea foam may also provide information of sufficient resolution on inter-annual variability of \textit{Phaeocystis} blooms. Years with relatively high \textit{Phaeocystis} abundance (1999, 2001, 2003 and 2007) had more frequent and intense foam events than years with relatively low \textit{Phaeocystis} abundance (2000, 2002 and 2006). The year 2001 also shows high peak \textit{Phaeocystis} abundance in Belgian and south English coastal waters (Breton et al., 2006; chapter 5 in this thesis).

![Figure 8.2: Example of an ARGUS video image of Noordwijk beach showing sea foam.](image)
8.2 IMPLICATIONS FOR MONITORING STRATEGY

**Temporal resolution**

Our analyses have shown that data series of high temporal resolution are key to understanding phytoplankton variability. The present sampling interval of phytoplankton monitoring in Dutch coastal waters (BIOMON monitoring program) of once or twice per month is probably sufficient to estimate long-term monthly means over many years of measurement (green line in Figure 8.3). However, this sampling frequency is clearly insufficient to reliably assess the actual phytoplankton abundance in specific years (black line in Figure 8.3). Therefore, we cannot use these data to explain why the phytoplankton abundance in specific years deviates from the long-term mean. Moreover, we cannot use these data to explain and predict the intensity, duration and timing of phytoplankton blooms in specific years (chapters 3 and 4 in this thesis). A sampling interval of approximately 5 days is required to capture the actual phytoplankton abundance in specific years (blue solid line in Figure 8.3). More precisely, according to the autocorrelation structure of the Smartbuoy data, the predictive value of a chlorophyll measurement reduces below a R² of 0.5 within 5 days ahead at all 4 stations that we investigated in the North Sea (chapter 7). In other words, chlorophyll measurements remain a reasonable estimate of the actual chlorophyll concentrations for the next 5 days, but thereafter the chlorophyll concentrations have definitely changed. A shorter sampling interval is even better to investigate how the tides and weather affect phytoplankton variability and gain understanding of the underlying mechanisms (chapters 6 and 7).

![Chlorophyll time series at the Smartbuoy mooring at Noordwijk 10 km in 2001: daily averages (black line), the daily averages subsampled every 5 days (blue solid line) and subsampled every 30 days (blue dashed line). For comparison the monthly mean for 1997 – 2006 is shown of chlorophyll-a data from the BIOMON monitoring program (green line).](image-url)
With the help of advanced statistical models that take into account how environmental drivers affect the phytoplankton fluctuations, chlorophyll concentrations can be predicted reliably for more than 5 days ahead, but after several weeks also the model predictions start to diverge from the measurements. Hence, like the weather forecast, we can indicate a time horizon for the predictability of marine phytoplankton dynamics. According to our analysis, the time horizon for reliable model prediction of the chlorophyll concentration in the North Sea ranged from 2 to 4 weeks depending on the site (chapter 7).

The value of time series for ecosystem assessments not only depends on their sampling interval but also on the length of the time series. Long-term trends and shifts in phytoplankton abundance and community composition in response to, e.g., climate change and changes in nutrient inputs have been extensively investigated (e.g., Bot and Colijn, 1996; Laane et al., 1996; de Vries et al., 1998; Beaugrand, 2004; Philippart et al., 2010). The detection of significant trends and shifts generally requires time series of several decades. As such, the mooring data sets we have used for our analyses were still too short to detect long-term changes. However, continued high-resolution monitoring is likely to become very valuable for future assessments of long-term ecosystem change. One important question with respect to the phytoplankton monitoring strategy is: “What is the relation between sampling frequency and the power of the resulting time series to detect significant changes in phytoplankton abundance?” This would be an interesting subject for further research. The natural variability of phytoplankton abundance per site and the choice of statistical measure are important issues in such research. Large natural variability of phytoplankton concentrations reduces the power to detect significant changes.

**Spatial resolution**

The North Sea harbors a variety of different environments such as macro-tidal waters in the south, regions of freshwater influence near river outlets and along the continental coasts, the shallow Wadden Sea, and the seasonally stratified waters in the central North Sea. Our analysis at four mooring stations showed major regional differences in phytoplankton response to environmental conditions (chapter 7). Satellite remote sensing images also show clear regional differences in seasonal patterns and levels of chlorophyll throughout the North Sea. Therefore, measurements at a single location cannot be assumed to be representative for the whole North Sea. Yet, the timing and duration of the phytoplankton spring bloom was similar at different stations near the Eastern Scheldt (chapter 3) and at two stations 8 kilometer apart along the Noordwijk transect (chapter 4). So, measurements at one location can be assumed to be representative of some area around it. At this moment, we do not yet have a good quantitative understanding of the spatial scales of phytoplankton variability in the North Sea, and to what extent
the spatial autocorrelation function decays with distance from a measurement point. This autocorrelation function may differ per time scale and site, just like the dominant processes driving temporal variability.

Since phytoplankton concentrations show strong spatial variability, both horizontally and vertically, measurements should ideally capture both. Unfortunately, there are no monitoring methods available that can provide this. Satellite remote sensing and ships of opportunity can capture horizontal phytoplankton variability at a reasonable temporal resolution. To capture vertical variability at a high temporal resolution, fixed monitoring stations are required.

Important aspects for the choice of monitoring locations are:

1. **Relevance**: The monitoring location should be in an area where there is an interest in phytoplankton dynamics. This may be because of, e.g., special natural, economic or recreational values or severe eutrophication or climate impacts.

2. **Accessibility**: The monitoring location should be practical in terms of accessibility and easy maintenance. Experiences with moorings in the North Sea show that fouling and technical failure due to rough weather leads to many data gaps in time series, especially during the growing season of phytoplankton. Monitoring stations along the shore, like the one in the Marsdiep, from the pier of the NIOZ research station can provide time series with less data gaps. Also monitoring from ferries allows for regular maintenance of the sensors to reduce data gaps.

3. **Continuity**: Since sufficient length of time series is crucial for trend detection, continuation of existing time series is essential.

4. **Limited variability**: Detection of significant trends and cause-effect relations between environmental variables and phytoplankton responses is facilitated if natural variability is limited. When effects of changes in river inputs are the object of study the choice of location needs to optimize between expected impact and detectability of this impact. So the location should be strongly affected by river inputs, yet far enough downstream to reduce excessive salinity fluctuations. Although the effect of salinity (as an indicator for transport and mixing processes) could be clearly identified in cross correlations at a Smartbuoy station in the river Rhine plume, the predictability of short-term phytoplankton fluctuations based on salinity data was only limited. Therefore, we expect that it will not be feasible to correct measured phytoplankton fluctuations for salinity fluctuations during data analysis.
Sampling methodology for total phytoplankton

Each of the available sampling methods for phytoplankton has its strengths and weaknesses. High spatial coverage can be provided by satellite remote sensing data, but only for chlorophyll and a few other photosynthetic pigments (e.g., phycocyanin; Simis et al., 2005). High temporal resolution can be obtained by moorings or automated sampling from piers, but only for a limited number of locations. A combination of relatively high spatial and temporal resolution can be provided by automated measurements from ferries. Coverage back in time and ground truth for automated measurements can be provided by continuation of existing time series of chlorophyll measurements in water samples. The pieces of the puzzle from different monitoring platforms can be combined by smart interpolation with statistical models or mechanistic models such as GEM. This approach has been applied in chapter 3 of this thesis, and seems promising. Yet, so far coupling of automated moorings with satellite remote sensing is still in its infancy, and further development of such coupled spatio-temporal monitoring programs will be a major challenge for the next decades.

Our experience with the analysis of automated monitoring data has revealed two practical issues that are relevant for the implementation of high-resolution monitoring strategies:

- **Non-photochemical quenching:** Fluorescence measurements showed strong diurnal fluctuations, which were strongly correlated with the intensity of solar irradiance. Due to this non-photochemical quenching, reliable information about phytoplankton abundance during the day was lacking. CEFAS uses 100 $\mu$mol.m$^{-2}$s$^{-1}$ as a threshold for irradiance (PAR) during the quality assurance of fluorescence data. Above this threshold fluorescence data are flagged as unreliable. In the mooring time series of the Oystergrounds we found strong decreases of fluorescence already for PAR exceeding 50 $\mu$mol.m$^{-2}$s$^{-1}$. In practice, the PAR-threshold above which non-photochemical quenching effects occur depend on the species and is affected by the exposure time of phytoplankton to high light intensity, which in turn depends on vertical mixing intensity (Brunet et al., 2008). Non-photochemical quenching is especially problematic for vertical profiles of fluorescence, which are usually taken during daytime. Figure 8.1B shows vertical profiles of fluorescence measured at station Oystergrounds in 2007. Data near the surface (sometimes down to 15 m) are unreliable due to non-photochemical quenching, which is indicated by shading in the figure. The only vertical profile measured during the night (in mid May) shows much higher fluorescence than the profiles measured during the day, even though the time series in Figure 8.1A does not indicate a conspicuous peak in chlorophyll concentration at that time.
- **Fouling**: The sensors of automated moorings can provide an attractive habitat for benthic algae and bacteria. Therefore, the sensors were cleaned or replaced during monthly services. Furthermore, the mooring data of the Smartbuoys that we used in this thesis have been screened for fouling effects by the quality assessment procedure at CEFAS. In this procedure data that were possibly affected by fouling were detected by visual inspection of the time series. In our analysis we did not use data that were suspected of fouling effects. However, this resulted in many data gaps, particularly in summer. Therefore, there were relatively many data from those times of the year when phytoplankton is not growing fast and relatively few data after the peak of the phytoplankton spring bloom (chapters 6 and 7).

**Sampling methodology for species composition**

Moorings, ferryboxes and satellites can provide information on total phytoplankton biomass with high temporal and spatial resolution. Automated methods for measurements on species composition are not readily available yet. Since species differ in their response to environmental conditions, changes in eutrophication and climate are likely to affect species composition. For example, if the intensity of turbulent mixing decreases, due to global climate change, diatom abundance is likely to decrease but picoplankton abundance may increase (Huisman et al., 2004). These changes in species composition may affect higher trophic levels in the food web, the efficiency of carbon cycling, and the frequency and intensity of harmful algal blooms. Harmful algal blooms are often caused by specific toxic species, which cannot be detected as a peak in total phytoplankton abundance. For these reasons, it is often desirable to monitor not only total phytoplankton biomass but also changes in species composition.

Fluorometers can roughly distinguish between the major taxonomic groups (e.g., diatoms versus cyanobacteria) based on the fluorescence signal at different wavelengths. In this way the abundance of the different phytoplankton groups can be quantified (Jacob et al., 2005). Flow cytometers with high-resolution cameras are being developed for use on fixed stations or on ferries (Thyssen et al., 2009). A fine example is the Imaging FlowCytobot that collects images of phytoplankton particles at a daily basis since 2006 near Martha’s Vineyard on the Atlantic coast of the USA (Figure 8.4; Sosik and Olson, 2007). Algorithms are also being developed for satellite remote sensing to identify specific phytoplankton groups, such as cyanobacteria (Simis et al., 2005; 2007), or to distinguish blooms of the dinoflagellate *Karenia* and the haptophyte *Phaeocystis* (Kurekin et al., 2014). Once time series of different phytoplankton species or taxonomic groups become available, drivers of changes in species composition can be analyzed with similar methods as used in this thesis. Such data would also facilitate the calibration and validation of mechanistic models, such as GEM, that include variation in species composition.
Data processing and analysis

Raw data do not directly provide insight in ecosystem functioning, trends and compliance with regulations by themselves. The data need to be processed first. This means that the data should be stored, quality checked and made accessible for further analysis. Furthermore, the statistical analyses should be done, documented in a transparent way and the results should be accessible to people with an interest in ecosystem functioning, such as water managers and researchers. This all sounds very obvious, but in practice often not all of these steps are taken and the measured data do not provide the insight that they were collected for. The European Commission is now pressing open and transparent data management in Europe through several initiatives (e.g. SeaDataNet, EMODNET, INSPIRE).

Figure 8.4: Example of phytoplankton images collected by the FlowCytobot at 25 February 2014 at Martha’s Vineyard Coastal Observatory (USA) from: http://ifcb-data.whoi.edu/mvco

The research in this thesis has demonstrated that the analysis of phytoplankton data is often not straightforward. Much time is needed to find approaches to cope with problems like measurement artifacts, data gaps, autocorrelation and collinearity between variables. Automated sampling methods, like remote sensing, moorings and ferryboxes yield large amounts of data. Therefore, data processing methods should also be automated, and automatically run on databases with monitoring data. This helps to give efficient feedback on the results of measurement methods and to show their benefits to all stakeholders.