The effects of (reducing) eutrophication on the seasonality of nutrients and phytoplankton in the Dutch coastal area.

Abstract
The coastal area of the Netherlands is largely influenced by fresh water input from several large rivers that run through heavily populated areas in Western Europe. Due to agricultural land use, these rivers contain high concentrations of nutrients. The question is if and how (changes in??) these extra nutrients affect phytoplankton growth. The seasonality of phytoplankton is affected by nutrient dynamics and visa versa. Changes in nutrient balances have had large effects on the dynamics of phytoplankton growth and large changes in the ecosystem have been observed. Nutrient reduction efforts have shown some positive results, but the effects are still ongoing. Further reduction and close monitoring are therefore important measure in reaching pre-1980 ecosystem functioning and stability.
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1. Introduction

Phytoplankton production is the cornerstone of marine food webs. Production is particularly high in areas where the input of fresh water increases the nutrient load of the water column. In the case of the North Sea, these freshwaters carry agricultural run-off with high amounts of nutrients. These nutrients are usually found only in low concentrations in the open ocean and thereby the riverine input increases the nutrient concentrations in coastal waters. In combination with returning light and rising temperatures during spring, the increased nutrient concentration creates a favourable environment for extensive phytoplankton production (McQuatters-Gollop et al., 2009). The largest phytoplankton (in most cases diatoms) can grow in early spring due to high amounts of nutrients, light, temperature and low grazing pressure (Maddock et al. 1981). Then, a certain nutrient essential to this species becomes limited. For example in diatoms, silicate is usually the limiting nutrient, growth is stunted and the abundance rapidly declines (Beinfang et al. 1981). Other phytoplankton species that where first outcompeted by the more efficiently growing diatoms (or like some smaller phytoplankton experience heavy grazing), do not have this limitation (Riegman et al. 1993). Because they now lose their competition, they in turn can form blooms until their limiting nutrient is depleted. This succession can potentially happen multiple times per season due to recycling of nutrients. At the end of the season sunlight becomes the limiting factor (Rabalais et al. 2009).

Nutrient recycling is an important factor in sustaining phytoplankton growth throughout the season. There are multiple ways for nutrients to be recycled. Phytoplankton can get eaten and some nutrients are not used by the predator and are excreted into the water column (Dolan 1997). However, these are usually in the form of organic compounds or other molecular forms that cannot be used by phytoplankton directly. The same happens when phytoplankton cells die due to nutrient limitation or other factors. Phytoplankton mostly uses nutrients in the inorganic form (although some can use organic compounds) (Bronk et al. 2007). Remineralisation (the breakdown of organic matter into...
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Inorganic nutrients) is performed by bacteria (mostly) in the water column or at the bottom. When sunlight becomes limiting, nutrients build up because riverine input and recycled nutrients are no longer used at high rates (Falkowski et al. 1988). Some phytoplankton is still present, but growth rates are not higher than the grazing- and mortality rate. This is important because the phytoplankton that best survives the winter has the highest chance of dominating the bloom during next year’s spring (Maddock et al., 1981).

The Dutch coastal area is a drainage basin for a number of large rivers that have their origin and flow through a large number of European countries (figure 1). These rivers run through heavily agricultured areas in France, Belgium (the Meuse), Switzerland, Germany (the Rhine) and the Netherlands. Most of the fresh water drains into the sea near the southern parts of the Netherlands (the Meuse and the Rhine) and via lake IJssel in the Wadden Sea. Although usually counted as a German river, a relatively small amount of freshwater drains into the eastern Wadden Sea via the Ems river. A total of ~93-100 km$^3$ yr$^{-1}$ nutrient enriched fresh water drains via these rivers (the Rhine, Meuse and Ems) into the Dutch coastal areas (Radach and Pätsch 2007).

This essay will look into the seasonal dynamics and relationships of nutrients and phytoplankton in general and more specifically in the North Sea. In particular the question will be addressed if eutrophication reduction measures have lead to reduced phytoplankton blooming in Dutch coastal waters, e.g. how effective these measures have been proven to be. Eutrophication and later nutrient reduction will be discussed in more detail. Most of the articles are discussed in the body of the essay and a general conclusion will be provided in the end.

2. General relations between nutrient- and phytoplankton dynamics

Macronutrients in seawater are of importance for phytoplankton growth and can have large effects on phytoplankton biomass and species composition. The three most important nutrients are nitrogen, phosphorus and, in the case of diatoms, silicate. While open oceans are typically low in nutrients, in coastal areas riverine input largely increases the concentrations of available nutrients (Rabalais et al. 2009). This can lead to large phytoplankton production in these areas.

Pelagic nutrient concentrations are heavily influenced by phytoplankton production, and vice versa. Spring phytoplankton blooms deplete the available nutrients and thereby can cause their own collapse. This means that the nutrient concentrations follow a seasonal trend. However, there are different
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trends for different nutrients, depending on factors as phytoplankton utilisation, strength of atmospheric input, re-mineralisation and bacterial decomposition.

When nutrient concentrations are adequate and sunlight is sufficient, phytoplankton blooms can form massive blooms. These blooms however consume large amounts of nutrients. Phytoplankton uptake ratios typically follow the “Redfield ratio” (C:N:Si:P -> 106:16:15:1) (Redfield 1934, Brzezinski, 1985). The incorporated nutrients in the cells of most phytoplankton species are approximating this ratio. By using this ratio it is possible to determine the limiting factor for growth. When a deviation for this ratio occurs in the water column, one of the nutrients is determining how much phytoplankton production can take place. For example if the concentration of N is 40µM and the concentration of P is 2µM, then the maximum amount of phytoplankton production is determined by P. A distinction must be made between nutrient limitation and nutrient depletion. Nutrient limitation means that one nutrient is the limiting factor for growth while the production still can be high. Nutrient depletion on the other hand means, that growth is stunted and most likely the bloom will end. Typically, nutrient limitation is characterized by the half saturation constant. The half saturation constant is defined as half the maximum uptake rate of nutrients by a particular phytoplankton species (Eppeley et al. 1969). When the half saturation constant is reached, growth is severely stunted. This in turn can explain why some species of phytoplankton can thrive after the initial spring bloom. When one dominant species cannot keep growing anymore, species with a lower half saturation constant can become the new dominant species.

Some species of phytoplankton can however store excess nutrients in their cells to survive longer under nutrient limited conditions (Frost et al. 2005). This storage of nutrients means that the internal ratio of nutrients deviates from the Redfield ratio. This can have effects on the grazer population as they do not have such effective means of storing nutrients. This can lead to selectivity in grazing and/or exclusion of excess nutrients which in turn can affect phytoplankton growth, bloom composition and further transfer into the foodweb. (Meunier et al. 2015)

Multiple factors can have an effect on phytoplankton growth. Seawater temperature, nutrient availability, mixed water depth, water turbidity and predation all determine which phytoplankton species is the most successful and therefore can dominate the community.

3. Zooplankton effects on phytoplankton growth

Due to their higher surface:volume ratio, smaller phytoplankton species are better competitors for nutrients than larger phytoplankton species. They also have lower sinking rates than larger species and can therefore remain in the euphotic zone longer during calm weather conditions. Yet in coastal areas spring blooms are dominated by the larger phytoplankton species. Riegman et al. (1993) proposed and...
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tested whether this is caused by size differential grazing pressure by zooplankton.
Depending on size, there are two types of heterotrophic zooplankton in the coastal waters of the Netherlands; microzooplankton and mesozooplankton. Most common in these groups are the protozoan Ciliates within the group of microzooplankton and the Copepods (*Crustacea*) within the group of mesozooplankton. Ciliates can exhibit high growth rates (almost as high as phytoplankton (Montagnes, 1996)) due to asexual reproduction and can therefore rapidly follow the increase in phytoplankton biomass. Copepods however reproduce sexually and have a spawning time of up to a few weeks (Halsband & Hirche, 2001). Therefore, copepods are less likely to have a suppressive factor on early spring blooms, while ciliates can immediately start grazing on available phytoplankton. Ciliates are unable to consume the larger phytoplankton species. So while the smaller phytoplankton species are in a relative advantage on growth characteristics alone, they are heavily suppressed by the rapid expansion of the ciliate population. This frees the larger phytoplankton species from their competitive disadvantage and they are the species that bloom. The larger species are however repressed during the summer months as more and more mesozooplankton is present in the water column. While grazing by copepods affects larger phytoplankton, another effect can be observed. Copepods also consume ciliates, releasing smaller phytoplankton from predation. As stated, smaller phytoplankton is more effective in utilizing nutrients, thus nutrient depletion occurs earlier. This is strengthened by the fact that ciliates release nutrients faster than copepods (Sommer *et al*. 2005). Copepods release their nutrient rich waste products in the form of faecal pellets that sink to the bottom, where it remains until it is re-mineralised. Ciliates excrete their waste directly into the water.
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4. Re-mineralisation

When phytoplankton cells die or are eaten and digested, the remaining products are mostly in the form of organic compounds. While a small portion of the cells sink to the bottom (in the North Sea about 1% (Thomas et al. 2004)), most of the nutrients remain in the water column in the form of dissolved and particulate organic matter (DOM and POM respectively). Apart from a fraction of the nitrogen stored in DOM, these nutrients are not available for phytoplankton in their organic form (Bronk et al 2007). Therefore remineralisation of nutrients is vital for prolonged blooms.

Remineralisation is performed by bacteria in the water column and on the seafloor (figure 2). DOM is converted and released in the water column itself and the remineralised nutrients can be used directly by phytoplankton. While some POM is remineralised in the water column, most POM sinks to the bottom and is consumed by the microorganisms there. This so called detritus is partially covered and digested, with the potential of releasing the nutrients in their inorganic form. In most areas of the North Sea re-mineralisation and transportation towards the euphotic zone of nutrients in summer is very limited due to the pycnocline, whereas in other areas with tidal flats and sandbanks it can have a large effect on available nutrients. Tidal action and storms can release these nutrients from the sediment and thus can enhance the phytoplanktonic production in coastal areas. (Brockmann et al. 1990)
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Figure 3: "Nutrient data for the Marsdiep; (A) phosphate data, monthly average for two years combined and compared with data for 1950 from Postma (1954), (B) nitrate and (C) N-compounds as in a, compared with data for 1970 in Helder (1974), (D) Si data compared with data for 1970 from Van Bennekom et al. (1974). (Courtesy of Cadee and Heggeman 2002)

Large parts of the human population live along river areas, increasing the nutrient run-off from agricultural land use. This can have large effects on the nutrient input of rivers into the coastal systems. Abnormally high concentrations of nutrients unbalance the pelagic ecosystem in these areas. An unusually strong phytoplankton growth can cause anoxia due to bacterial decomposition, which in turn can be detrimental to other marine life (Druon et al. 2004). In the Marsdiep for example N and P rose from a ~20 and ~0.75 µmol dm$^{-3}$ to ~75 µmol dm$^{-3}$ in a few years (figure 3) (Cadee and Heggeman 2002). In recent decades this has led to more control in the amount of nutrients that are transported to the coastal areas by rivers.

In the beginning of the 1980s it was decided that a reduction of 50% of N and P runoff should be achieved until the 1990s (Parcom 1988). Although these goals were not fully met, it had an effect on phytoplankton production which will be explained in further sections. Changes in the total nutrient load were observed, as well as changes in the N:P ratio. This lead to large changes in phytoplankton species composition which in turn affected the phytoplankton biomass and ecosystem changes known as regime shifts (more on these regime shifts are explained in section 7). Regime shift are defined as large scale changes in the ecosystem that are followed by a period of (altered) stability and can be caused by a lot of factors, one of which is changes in nutrient conditions. Regime shifts can have large consequences throughout the food web (Alheit 2007).
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Multiple studies (e.g. Tungaraza et al. 2002, Rousseau et al. 2002) show a clear and relatively similar seasonal trend for silicate and nitrate load in the coastal areas. Highest concentrations of these nutrients are observed during winter and early spring, before the onset of the spring phytoplankton bloom. The concentrations then gradually decline to the lowest concentrations at the end of spring. This decrease coincides with peaks in chlorophyll a, suggesting that phytoplankton production is responsible for nutrient depletion. The concentrations in the open North Sea remain low in summer and autumn and gradually built up again during winter (remineralisation) and early spring (riverine input) (Figure 4).

For phosphate different studies show different results. Some studies suggest limited to no seasonal trends (Tungaraza et al. 2002). However, some find similar trends during spring/summer as with

5. Nutrient dynamics in the Netherlands

Figure 4: “Seasonal patterns in water nutrients: (a) ammonia (NH4), (b) total nitrogen (TN), (c) total phosphorus (TP), (d) silica (Si), (e) nitrate (NO3), (f) nitrite (NO2), (g) TN:TP ratio and (h) nitrogen:silica ratio. Each line represents the seasonal trend for a specific period: straight line is 1988–1997 and dashed line is 1997–2007. Horizontal dashed red line represents: (g) Redfield ratio and (h) N:Si ratio limitation limits for diatoms.” (Courtesy of Alvarez-Fernandez et al. 2012)
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Silicate and nitrate (high in early spring, low in summer (Rousseau et al. 2002). From the end of the summer the phosphate load starts to increase again. By mid-autumn the concentration of phosphate reaches similar concentration to winter values. This trend is not observed for nitrate or silicate.

Main sources of nutrient input are atmospheric input, riverine input, and regeneration (Falkowski 1994, Prins et al. 2012). While for nitrate the atmospheric input is considerably high, for phosphate this is negligible. Riverine input can also be ruled out, as nitrate to phosphate ratio in the rivers in the study area is relatively high, meaning higher input of nitrate than phosphate (Zee & Chou, 2005). This suggests that the regeneration of phosphate is responsible for the observed increase. Other studies have shown indeed that phosphate regeneration is higher than that of nitrate or silicate (e.g. Vidal et al., 1999).

Figure 5: "Molar ratios of (a–d) DIN : DIP and (e–h) DSi : DIP along the offshore transect (near shore to offshore northwest of the Dutch island Terschelling), during research cruises in (a, e) March 2013, (b, f) April 2013, (c, g) May 2012 and (d, h) August 2011. The Redfield ratio of 16 : 1 for DIN : DIP and 15 : 1 for DSi : DIP is indicated by the black contour line. Shading indicates depths below the euphotic zone (i.e., light levels<1% of surface light intensity). Arrows on x-axis indicate the four stations (7 km, 100 km, 250 km and 450 km) of the nutrient bioassay experiments." (Courtesy of Burson et al. 2016)

In the North Sea coastal area phytoplankton growth is usually limited by P (Turner et al. 2003a, b). However, riverine input of nutrients continues throughout spring. Input of both N and P are relatively high compared to Si. So while P can remain the limiting nutrient for quite some time, the Si concentration continues to decrease until Si becomes the limiting factor for production. A strong gradient can be observed when comparing coastal regions with open seas (figure 5). Due to more effective reduction of P eutrophication (explained in more detail in next section), coastal areas tend to
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be limited by P and Si. On the open sea however, N:P ratios drop below 16 and are N limited. In late summer, the nearest coastal band is N limited (Bursen et al. 2016). Si limitation occurs near shore throughout the season apart from very early in the season. However, in late summer Si:P rises above 15:1 again and Si limitation is no longer a factor offshore, as P limitation becomes much more relevant (figure 5h). Si however can only be limiting for diatoms and not for flagellate blooms as these do not utilize Si. Therefore, it can happen that a diatom dominated bloom is succeeded by a Phaeocytis spp. bloom.

Wetsteyn et al. (1990) found no nutrient depletion for both N and P in the Oosterschelde area. A minimum of P was found during in May that was below the half saturation constant of Phaeocystis spp. but bloom formation was most likely not affected. Si however seemed to be severely depleted by the end of the spring bloom until the end of summer. This would imply that silicate is the main limiting nutrient for diatoms.

6. Phytoplankton dynamics in the Netherlands

Although it is often debated that broad-scale seasonal patterns in phytoplankton are an established phenomenon (Cebrián and Valeliela, 1999), the phytoplankton in the closely studied Dutch coastal waters shows quite obvious seasonality. A long term study performed over 16 years in the Dutch Wadden Sea showed some interannual variability in timing, but very distinct seasonal patterns when considering biomass and cell numbers (Cadee, 1986). However, it must be noted that these trends do not occur on the species level. Especially the diatom spring bloom can have very different species dominating between years depending on nutrient concentrations and water temperature (Phillipart et al., 2000; Prins et al. 2012).

The phytoplankton spring peak can be observed sometimes from the middle of March to the end of May. The timing of this spring bloom seems not to be correlated to water temperature or irradiance. Rather there seems to be a relation with high winter turbidity, which causes a delay in the spring peak. (Cadee and Heggeman, 2002).

Following this spring diatom peak are large cell numbers of the flagellate Phaeocystis spp.. This flagellate peak usually has higher cell numbers than the diatom peak. This peak follows roughly two weeks after the diatom maximum. Some other, smaller diatom peaks are observed throughout summer, mostly closely followed by the Phaeocystis spp. peaks (Cadée, 1986).

One reason why Phaeocystis spp. can become so dominant is by escaping predation altogether. While in their solitary form they can be consumed (Weisse & ScheffelMöser 1990), they form large colonies that protect themselves with a gel matrix. Hansen & van Boekel (1991) found that copepod grazing on phytoplankton during the Phaeocystis spp. spring bloom in the Marsdiep removed less than 1% of the
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Phytoplankton standing stock per day. Combined with their smaller size, the absence of predation is one of the reasons why the *Phaeocysis spp.* peaks usually have higher cell numbers than the preceding diatom peaks.

7. Eutrophication in the Dutch North Sea

In the late 1970s the mean annual chlorophyll concentration in the Marsdiep area almost doubled in a few years (Cadee and Hegeman 2002, Phillipart et al. 2000). This could be potentially detrimental to the system due to enhanced bacterial activity. The degeneration of phytoplankton by bacteria uses oxygen and high phytoplankton biomass could therefore cause anoxic conditions (Billen et al. 2005). This could be a large problem in the Netherlands as these areas are important as nurseries for many species of fish.

*Figure 6:* “Covariance biplot (1st and 2nd axis) based on Principal Component Analysis of the species composition of the phytoplankton community during the nutrient-controlled periods of the growing season (July–August) between 1974 and 1994. Relative phytoplankton species abundances are represented by grey vectors and years by numbered dots. Indications of different growing circumstances for phytoplankton during the study period as derived from the trophic state and the ambient nutrient ratios. The indications of annual trophic state and TN:TP ratio are restricted to the period for which the nutrient budgets could be estimated (1975–1993); the remaining years (1974 and 1994) are indicated with asterisks” (Courtesy of Phillipart et al. 2000)
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Typically the Dutch coast is P controlled, however under N controlled conditions larger phytoplankton species are favoured due to their higher storage capacity for nitrogen and the absence of grazing. This in turn can be detrimental for higher trophic levels, because it reduces the availability of phytoplankton for grazers, ultimately affecting zooplanktivorous species through bottom-up control. The effects are most pronounced during the summer, when growth is most limited by nutrient availability and when zooplankton grazing is highest.

In the western Wadden Sea two large changes in phytoplankton community composition were observed during the period 1976-1994, also known as regime shifts ((Philippart et al, 2000, Alvarez-Fernandez et al, 2012) The regime shifts coincided with changes in total nutrient load and changes in N:P ratios. The first shift occurred in 1977-1978 when a doubling in phytoplankton biomass (cholophyll concentrations rose from 4.6 mg m$^{-3}$ to 9 mg m$^{-3}$ was observed. During the period following this shift a decrease of N:P ratios lead (from 40:1 to 15:1) to an N controlled environment during the growth season, although concentrations of N were higher than the half-saturation constant during the summer period. This suggests that other nutrients (such as Si) might have been the actual limiting factor. Furthermore, the shift to a more N controlled environment favoured larger diatom species. The second shift between 1987-1988 did not lead to a decrease in biomass, but was characterised by another shift in phytoplankton community structure (figure 6). This shift coincided with an increase of N:P ratios to a P controlled system. Phaeocystis spp. followed similar shifts. A sudden increase in bloom length as well as the total cell numbers was observed during the period between the two regime shifts. After the second regime shift Phaeocystis spp. blooms were declining again (Cadée & Hegeman, 2002). This would imply that Phaeocystis spp. are better suited under N-controlled environments as opposed to P-controlled.
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A decline in nutrient concentrations after 1990 was further observed (figure 7). Total nutrient load of both N and P declined with about 30% and 50% respectively. No decline in silicate concentrations was observed however. Interestingly enough this is most likely due to the decrease of both N and P in the rivers. Before, fresh water diatom blooms used up a large portion of the silicate in the rivers before it reached the North Sea. By reducing the amount of N and P in the run off, these blooms did not happen and the amount of silicate that reached the sea actually increased. This however appeared to have little effect on phytoplankton growth. No changes in total phytoplankton biomass were observed and both diatom and flagellate biomass seemed to have increased over the years 1990-2010. Observed increases were larger in coastal areas when compared to offshore sites. Significant increases in bloom frequencies and maximum cell concentrations were observed for both *Phaeocystis* spp. and multiple diatom species, especially the main blooming diatom species *Chaetoceros socialis*. (Prins et al. 2012).

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*Figure 7: Change in average nutrient concentration during the growth season over the years 1990-2010 in the Dutch North Sea. (Courtesy of Prins et al. 2012)*
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8. Eutrophication in other North Sea regions

Since the Paris commission recommendations in 1988 extensive monitoring and assessment of different sub regions of the North Sea on eutrophication are performed. Because different areas in the North Sea have different problems with eutrophication, the North Sea was divided into multiple areas (figure 8). Largest problems were observed along the coasts of Belgium, the Netherlands and Germany and the UK. Although elevated winter nutrient concentrations were found along the Danish coast, these were lower than other regions. The lowest were found along the coast of Norway, because agricultural run off is less (EEA 2001). Off shore areas generally have less problems with eutrophication due to lower input of riverine water (Lenart et al. 2010).

Extensive reduction plans of agricultural nutrient reductions (Nitrate Directive) and guidelines for water treatment (Water Framework Directive) by the EU have reduces the amount of nutrients that have been deposited in the North Sea. Nevertheless goals have not been fully met, and these directives might not fully reach the intenedt goal yet. Therefor the problem areas are still vulnerable to eutrophication. (Grimvall et al. 2017(3))
9. General conclusions and discussion

The coastal waters of the Netherlands are a very dynamic system. The tidal influence is large and river input plays an important role. Although some inter-annual variation in seasonality of phytoplankton occurs due to slightly different conditions, the trends are relatively stable. However when conditions such as nutrient load and N:P ratios change this can have large effects. These are not always noticeable in biomass alone, but nonetheless can have effects on the ecosystem.

Different species of phytoplankton react differently to the changing conditions. A dominant species can become outcompeted by another under altered conditions. Not always can these new dominant species be effectively grazed by higher trophic levels. Furthermore, their nutrient uptake rates are not always similar, which could alter the duration of the bloom.

Although trends for individual phytoplankton might be harder to predict, phytoplankton dynamics is more easily modelled when classifying phytoplankton into functional groups. Functional groups are multiple species of phytoplankton who more or less behave similar at similar conditions (Mutshinda et al. 2016). So while changes over time at the species level due to changes in the environment are less (or not at all) drastic, when changes in functional groups occur, it becomes much more obvious that the system is under stress.

Due to high and expanding population density around the rivers in the Netherlands, the ecosystem in the coastal waters has undergone a lot of changes during the last decades. Although some measures have been taken to reduce the anthropogenic impact, the effects of these is still under debate. Not only because it is yet unknown what the effects of reduction of nutrients in the coastal areas will be on phytoplankton, it is also unknown how large the anthropogenic effects are. Up until 50 years ago hardly any monitoring of phytoplankton was performed, so it is difficult to estimate what effect the natural cycles have on the ecosystem. Furthermore, Dutch coastal waters have historically been heavily exploited and altered. Even 100 years ago these were an entirely different system. Large building projects (like the Zuiderzee- and Delta works), overharvesting by fisheries, cockle fisheries, mussel cultures, and dredging all have had or still have effects on the ecosystem. The role of these factors in the present ecosystem are still under debate.

Although the Parcom guidelines have had an effect on reducing nutrient loads in the North Sea, the phytoplankton community reacted differently than what was expected. Less nutrients did not mean less production, and although run off was reduced, in the case of silicate the North sea concentrations actually rose. Therefore it is vital that reduction efforts continue but close monitoring is important. Because of the fact that not all nutrients decline at the same rate, more changes in N:P:Si ratios can be expected, with more changes in the phytoplankton community.
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Not only will the changes due to the attempted reduction of nutrient input from rivers affect nutrient dynamics and phytoplankton growth, but climate change is suspected to have effects as well. More winter storms could increase the turbidity of the water, therefore causing delay of the onset of the spring blooms, which could cause a mismatch in mesozooplankton coupling. More precipitation could lead to an increase in agricultural run-off, thereby effectively increasing eutrophication of the system and further off-set the nutrient balance (Cadee and Hegeman 2002).

The system of today will not be the same as it will be in 50 years. How different it will be is yet unknown. It is therefore important to continue monitoring and increase the research effort to better understand how all the different parameters fit together into the entire ecosystem model.

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