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Global change and the biogeochemistry of the North Sea: the possible role of phytoplankton and phytoplankton grazing

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Abstract Phytoplankton plays a dominant role in shelf biogeochemistry by producing the major part of organic matter. Part of the organic matter will reach the sediment where diagenetic processes like denitrification, apatite formation or burial will remove nutrients from the biogeochemical cycle. In this article current knowledge on the decadal plankton variability in the North Sea is summarized and possible implications of these changes for the biogeochemistry of the North Sea are discussed. Most of the observed interdecadal dynamics seem to be linked to large-scale oceanographic and atmospheric processes. Prominent changes in the North Sea ecosystem have taken place around 1979 and 1988. In general, the phytoplankton color (CPRS indicator of phytoplankton biomass) reached minimum values during the end of the 1970s and has increased especially since the mid 1980s. Changes with a similar timing have been identified in many time series from the North Sea through the entire ecosystem and are sometimes referred to as regime shifts. It is suggested that the impact of global change on the local biogeochemistry is largely driven by the phyto- and zooplankton dynamics during spring and early summer. At that time the extent of zooplankton–phytoplankton interaction either allows that a large part of the new production is settling to the sediment, or that a significant part of the new production including the fixed nutrients is kept within the pelagic system. The origin of the extent of the phytoplankton–zooplankton interaction in spring is probably set in the previous autumn and winter. In coastal areas, both large-scale atmospheric and oceanographic changes as well as anthropogenic factors influence the long-term dynamics. Due to eutrophication, local primary production nowadays still is up to five times higher than during pre-industrial conditions, despite a decreasing trend. Recently, introduced species have strengthened the filter feeder component of coastal ecosystems. Especially in shallow coastal seas like the Wadden Sea, this will enhance particle retention, shift organic matter degradation to the benthic compartment and enhance nutrient removal from the biogeochemical cycle by denitrification or apatite formation.

Introduction

Phytoplankton plays a major role in the carbon and nutrient budgets of coastal seas. For instance, in the North Sea the annual primary production is about three orders of magnitude larger than the terrestrial (riverine) organic matter input (Thomas et al. 2005). The site where this organic matter is degraded depends on the water depth (Suess 1980; Heip et al. 1995; Middelburg et al. 1997). This global trend also holds for the North Sea. At shallow sites like the Wadden Sea, about equal amounts are degraded in the water column and in the sediment (van Beusekom et al. 1999). In deeper parts of the coastal seas, the relative importance of the sediment decreases with depth and already at a water depth of about 30 m, 80% of the annual organic matter degradation takes place in the water column

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(e.g., German Bight: von Westernhagen et al. 1986). In the Skagerrak (northeastern North Sea, up to 705 m deep), most of the locally produced organic matter is remineralised in the water column (Aure and Dahle 1994).

Whether the primary produced organic matter is degraded in the water column or in the sediment has large repercussions on the nutrient budgets. Several biogeochemical processes that remove nutrients from the biogeochemical cycle like denitrification or apatite formation are confined to the sediment. Phosphorus may be transformed to apatite. This relatively stable authigenic phosphorus carbonate mineral is mainly formed in sediments. Ruttenberg and Berner (1993) and Slomp et al. (1996) suggested that apatite formation is an important phosphorus sink. Budget calculations show that also in the Wadden Sea apatite formation is a major sink (van Beusekom and de Jonge 1997). The phosphorus sink might, however, be of local importance and confined to the Wadden Sea: Hydes et al. (1999) estimate that the North Sea as a whole is not a sink of phosphate. Denitrification is a major nitrogen sink by transforming nitrate or nitrite to nitrogen gas. For example, denitrification in sediments of the North Atlantic Ocean continental shelf and adjacent estuaries is thought to exceed the fluvial nitrogen input (Galloway et al. 1996). Hydes et al. (1999) reach the same conclusion for the North Sea based on a nitrogen budget. Recently, it has been shown that the Anammox reaction may also play a large role in removing nitrogen from the marine biogeochemical cycle (Thamdrup and Dalsgaard 2002). Also the silica cycle may be influenced by the sediment, but here the role is less clear. On one hand, will the high Al concentrations in marine sediments slow down the dissolution process by incorporation of Al in the frustules (van Cappellen et al. 2002). On the other hand, may especially permeable sediments enhance the dissolution of silica frustules by keeping the silica concentrations in the pore water far below the saturation concentrations of biogenic opal (Ehrenhaus and Huettel 2004).

Whereas the general trend that the amount of organic matter (and nutrients) that reaches the sea floor decreases with increasing depth also holds for the North Sea, it is feasible that interannual variations exist.

Purpose of this article is to explore how (1) climate change and interdecadal weather dynamics may influence the relation between the amount of organic matter produced in the water column and the amount that reaches the sea floor and (2) how this may influence the biogeochemistry of the North Sea and the adjacent Wadden Sea. Based on possible relations between the amount of organic matter produced in the water column and the amount reaching the sediment hypotheses will be formulated for future research programmes.

Physical setting

The North Sea is a shallow basin that gradually deepens from approximately 30 m in the south to 200 m in the north. It encompasses a surface area of 575,000 km^2 (Kossinna 1921). Two of the most pronounced geographic features are the Dogger Bank in the central North Sea with depths of about 20 m and the Norwegian Trench along the Norwegian coast with a maximum depth of 705 m. The Dogger Bank plays an important role in the hydrographical structure of the North Sea. It separates the North Sea in two hydrographically different parts. The northern part is strongly influenced by water from the Atlantic Ocean. It is relatively deep (40–200 m) and during summer much of the area is stratified. The influence of Atlantic water in the northern North Sea reaches to the northern margin of the Dogger Bank. The southern part is shallow (20–40 m) and in most areas the water column is mixed by wind and tides throughout the year. Here Atlantic Water intrudes via the Dover Channel. In contrast to the northern part, the southern North Sea is under strong continental influence since it receives most of the continental run-off.

The different water masses in the North Sea can be distinguished by their salinity. "Atlantic Water" is characterized by salinities of about 35.5 (Hydes et al. 1999). The major part enters the North Sea in the north between the Shetland Islands and the Norwegian coast. In general, it intrudes the North Sea deeper in winter than in summer. Atlantic Water entering the North Sea via the Dover Channel can be identified by a tongue with salinities >34.75 (Fig. 1). Interannual differences exist in the amount of Atlantic water entering the North Sea (Turrell et al. 1996) influencing the ecology of the North Sea (Reid et al. 2003).

Apart from oceanic influences, the North Sea also experiences strong continental influences. Along the Scottish, British and Continental coasts low salinity water masses are formed by the admixture of fresh run-off with Atlantic water. Along the Scottish and British coast salinities usually are between 34 and 35 suggesting a rapid dilution of run-off. Along the Continental coast salinities reach as low as 29–30. Due to the predominant clockwise circulation and the inflow of Atlantic water through the Dover Channel, the continental run-off is confined to a narrow zone along the continental coast. Here, riverine nutrients may exert a strong influence on the coastal ecosystem. Another important water mass is the Baltic Sea outflow which enters the North Sea via the Kattegat and the Skagerrak in the northeast. It has salinities of 24–30 most of the year.

The three important dynamic factors in the North Sea are tidal currents, stratification and wind. The most important hydrodynamic force is the tidal motion (Otto
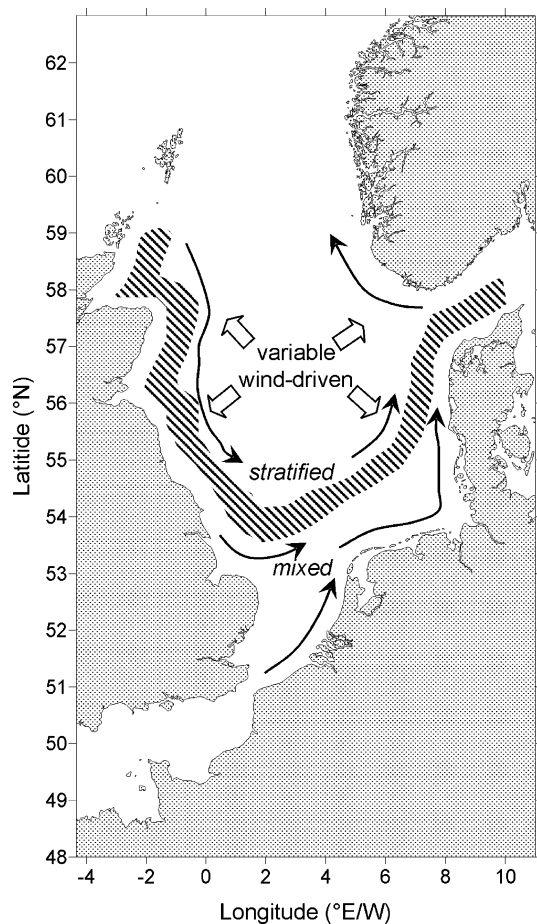
Fig. 1 Map of the North Sea. The location of fronts separating the seasonally stratified central North Sea from the permanently mixed coastal zone is indicated by the *hatched area*. The *arrows* indicate the main direction of flow

et al. 1990). It is among others responsible for the predominantly anti-clockwise residual currents that affect all North Sea coasts.

The German Bight takes in a special place in the southern and southeastern North Sea, due to the Elbe Rinne, the former bed of the river Elbe during glacial times—seasonal stratifications may occur. Along most of the northern Dutch and German North Sea stretches the Wadden Sea, a shallow coastal sea with extensive tidal flats covering about 50% of the area. The Wadden Sea region includes an area extending from Den Helder in the Netherlands to the Skallingen peninsula in Denmark, about 500 km of coastline. It is a strip of tidal flats, sandbanks and barrier islands. On average this strip is some 10 km wide, although in some areas it can reach a width of over 30 km. The Wadden Sea area covers approximately 13,000 km^2. Its environment is very dynamic. Wind, tidal forces and water turbulence cause the formation and erosion of the typical landscape elements of the area, the tidal flats, sandbanks, salt marshes and islands. The tidal range is

about 1.5 m in the westernmost and northernmost part and increases to about 3 m in the central part near the estuaries of the rivers Elbe and Weser. One of the main characteristics of the Wadden Sea is that it accumulates particles and organic matter from the open North Sea (Postma 1981). As a consequence, remineralisation is higher than primary production (van Beusekom et al. 1999).

Nutrient concentrations

The distribution of nutrients is studied best in winter when phytoplankton growth is at a minimum (van Bennekom and Wetsteijn 1990). One of the data sets covering the entire North Sea was collected during the ZISCH project (Brockmann et al. 1990). Figure 2 shows the distribution of nitrate + nitrite during the winter of 1987 (January 28–March 6). Phosphate and silicate show a more or less comparable distribution pattern. In general, lowest concentrations were found in the central North Sea (phosphate < 0.5 μM, nitrate + nitrite < 6 μM and silicate < 5 μM). The extreme low silicate levels in the Dogger Bank area (<1 μM) are caused by an early diatom bloom (Brockmann et al. 1990; Rick 1990). All concentrations increased towards the coasts as a consequence of an increased admixture of fresh, nutrient-rich water. Phosphate concentrations up to 3 μM and silicate and nitrate concentrations above 50 μM can be observed. Of course, these concentrations will be higher near the river mouths as the fresh water contribution increases (van Bennekom and Wetsteijn 1990; Weichart 1986). Typical river concentrations are ~300–400 μM nitrate, 100–200 μM silicate, and 2–3 μM phosphate. Total nitrogen ranges from 300 to 600 μM and total phosphorus ranges from 3–15 μM (van Beusekom et al. 2005). Whereas nitrate and silicate behave conservatively during estuarine mixing, phosphorus behaves non-conservatively having a clear mid-estuarine maximum (van Bennekom and Wetsteijn 1990; van Beusekom and Brockmann 1998; van Beusekom and de Jonge 1998; Weichart 1986). Since about 1985 the riverine nutrient loads generally decrease (van Beusekom et al. 2005).

In the Atlantic Ocean Water nutrient concentrations (phosphate ~ 0.75 μM, nitrate ~ 10 μM, silicate ~ 6 μM) are higher compared to the central North Sea. The Atlantic Ocean thus acts as an important source of nutrients for the North Sea.

During summer, the nutrient concentrations are generally very low (Brockmann et al. 1990). Woodward and Owens (1990) studied the nitrate and nitrite distribution during July 1987 using an extremely sensitive chemoluminescence detection method. Their results showed that nitrate and nitrite levels are extremely low (NO$_3^-$
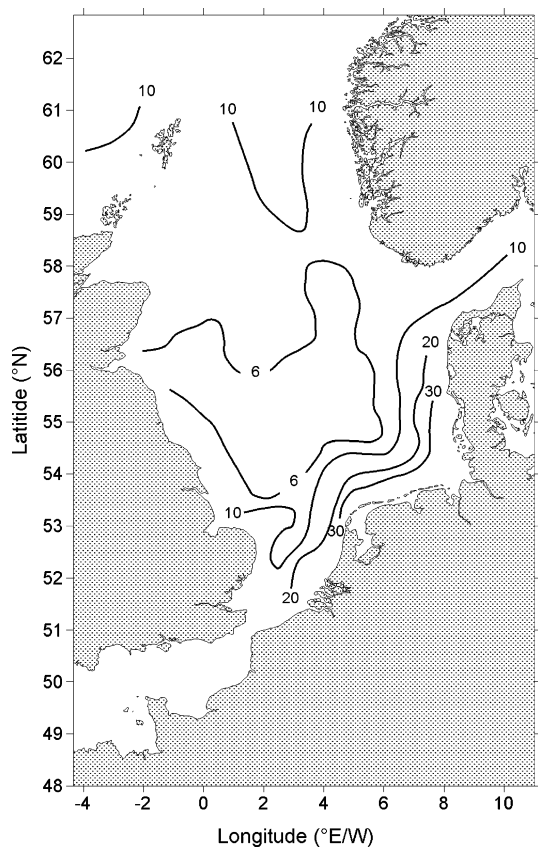
Fig. 2 Distribution of nitrate (μM) in the North Sea during winter. Redrawn after Brockmann et al. (1990)

10–100 nM and NO_2^- < 5–100 nM) over large parts of the North Sea. N/P levels were also very low (<0.1 compared to ±16 in winter) indicating that during summer the phytoplankton was potentially nitrogen limited. This is supported by in situ nutrient uptake studies by Riegman et al. (1990).

The plankton system of the North Sea

In the pelagial, two main dietary routes of energy transfer exist (Fig. 3). During nutrient-rich periods, the classical type food web dominates: microphytoplankton (diatom) production is directly transferred into secondary (herbivore) and higher trophic levels. Such short-chained systems allow a high yield of top predators like fish (Ryther 1969). In contrast, during calm, nutrient-poor periods pico- and nanophytoplankton (flagellates) prevail. Most of its production is channeled through heterotrophic flagellates and ciliates as primary grazers via mesozooplankton (copepods) to the higher trophic levels or reaches higher trophic levels via bacterial production (microbial loop, Azam et al. 1983, see Fig. 3). In these systems most of the primary energy dissipates within the food web (Fogg 1991). Thus,

on one hand, the heteroflagellate-ciliate-copepod link makes extra food sources accessible, by coupling bacterial production via heteroflagellates etc. with higher trophic levels. However, in comparison to the short food chain less energy will reach the highest trophic levels, because each additional step in the food web a large part of the available energy is lost. Thus, depending on the physical and chemical conditions for plankton growth the efficient, short food chain or the longer, less efficient food chain dominates pelagic production. In the following, we will address the temporal and spatial dynamics of the above mentioned different pathways in the North Sea.

Winter

Winter is the period of low biological activity. The entire North Sea is, with the exception of the haline stratified Skagerrak and Kattegat, vertically mixed and nutrient-rich. The phytoplankton is light-limited, whereas for zooplankton temperature and food are the limiting factors. Light availability is influenced by day length, cloudiness and the degree of water column mixing. In the open sea, a high degree of mixing causes the phytoplankton to spend more time in the deep, dark zones, thereby loosing more energy through metabolic processes than can be compensated for by production in the photic zone (Sverdrup 1953). In the coastal zone, the mixing depth is fixed by the water depth. Here, light availability is influenced by water turbidity (Colijn 1982; Cadée 1986a).

Thus, during cloudy, stormy winters, the phytoplankton standing stock will be very low and in consequence the survival of the zooplankton stocks and of their predators is reduced. During relatively calm, clear winters primary production is to a lesser extent light-limited, larger phytoplankton stocks are present and a larger zooplankton population may be able to survive. At times, predation on the zooplankton may be compensated for by (food-dependent) reproduction (Hay et al. 1990; Fransz and Gonzalez 1991).

Spring

During winter net phytoplankton growth is only possible under sporadic favorable weather conditions. With increasing day length, the chances for net phytoplankton growth also increase. When light availability exceeds a critical level, phytoplankton growth enters an exponential phase: the spring bloom (Sverdrup 1953; Gieskes and Kraay 1977). These blooms, which are dominated by diatoms, can occur as early as January–February in the shallow, low-turbidity waters like off the Dutch west coast,

Fig. 3 Schematic representation of the main dietary routes of energy- and nutrient transfer. Microphytoplankton (mainly diatoms) play a main role in short foodwebs connecting primary production with either large copepods or organic matter fluxes to the sediment. Pico- and nano phytoplankton is mainly part of the microbial foodweb, which are less efficient in terms of biomass yield and biomass transfer to the benthos
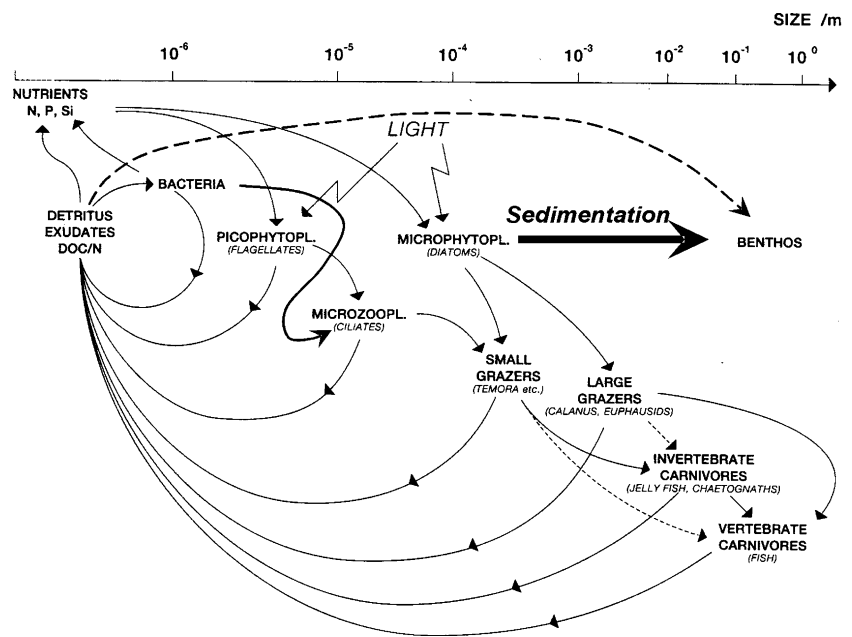
the Dogger Bank area or the Skagerrak (due to its haline stratification). In the turbid coastal water and in the deeper parts of the central and northern North Sea the spring bloom develops later. First peaks are observed during April (Gieskes and Kraay 1977; Horwood 1982; Joint and Pomroy 1993). In coastal areas light availability (water mixing, turbidity) has a strong impact on the timing of the spring bloom (Cadée 1986a).

The phytoplankton bloom can be delayed up to 3 to 6 weeks under unfavorable conditions (Glover et al. 1972; Dickson et al. 1988; Cadée 1986a). In the open North Sea early blooms are supposedly related to transient thermoclines which can be formed before the permanent summer stratification is established (Colebrook 1979). They have a higher probability to occur when large differences between winter and summer temperature exist. Of course, storms have a negative effect on the formation of these transient thermoclines. The timing of the bloom will influence its shape. In general, early blooms can be expected to develop slower (less light, colder) and therefore last longer.

The size and species composition of the spring bloom is determined by nutrient availability and nutrient ratios. Thus in the eutrophic coastal zone peak concentrations of 40 µg Chl *a*/l are common (Cadée 1986b) as compared to only 6 µg Chl *a*/l in the low-nutrient western central North Sea (Horwood 1982). A common characteristic of the coastal North Sea spring bloom is its two-stage appearance. It is determined by nutrient ratios. The first stage is dominated by diatoms and limited by silicate availability and the second stage is dominated by flagellates (along the continental coast, mainly *Phaeocystis* sp.). The potential size of this second bloom is determined by the amount of N

and P nutrients left after the diatom bloom (Gieskes and van Bennekom 1973).

The start of the spring phytoplankton bloom triggers the zooplankton population to feed and reproduce at temperature dependent rates. At low temperatures, the food concentration necessary to achieve maximum growth and reproduction is lower than at high temperatures (Vidal 1980; Runge 1984). The overwintering grazer population assimilates only a small portion of the algal biomass available during the spring bloom (Fransz and Gieskes 1984).

Nevertheless, the degree of phytoplankton–zooplankton interaction may have important consequences for the energy- and nutrient flow, especially in the offshore parts of the North Sea ecosystem. In the absence of grazing most of the phytoplankton population (and the sequestered nutrients) will sink out of the water column and will be channeled into the benthic food web (Davies and Payne 1984). During intense grazing, however, a considerable portion of the primary production will flow via the zooplankton into the pelagic system (Colebrook 1982a, b).

The stratified central and northern North Sea during summer

During spring, water temperature continuously rises due to the increasing solar radiation. In the deeper parts of the North Sea this results in the stratification of the water column. In the shallower parts of the North Sea stratification is prevented by tide-induced turbulence (Pingree et al. 1978). These contrasting hydrographic conditions have a

profound influence on the plankton development. The two closely entwined factors—nutrient availability and turbulence—segregate the plankton community during summer into the low turbulent, nutrient poor central and northern North Sea, and the nutrient-rich, turbulent coastal zones (Margalef 1978; Tett and Mills 1991).

Under stratified conditions, nutrients in the upper water column will soon be depleted and a phytoplankton community will evolve that is adapted to low nutrient, low turbulent conditions. Such communities usually consist of small (<20 μm) pico- and nanophytoplankton (Fogg 1991). In contrast to the larger microphytoplankton (>20 μm), their high surface to volume ratio guarantees that even under very low nutrient concentrations optimum growth is possible. Because of their small size loss due to sedimentation out of the photic zone is negligible (Margalef 1978).

A further consequence of being small (a high surface-to-volume ratio) is that a relative large part of the photosynthetically produced organic matter is lost to the environment by passive diffusion (Bjørnsen 1988). This pool of organic matter is being used by bacteria. Since these bacteria are preyed upon by microzooplankton (e.g., ciliates and heteroflagellates), this "microbial loop" forms an important alternative link of primary production to higher trophic levels. However, the number of steps involved makes it a rather inefficient link in terms of fish yield for instance. The pico- and nanophytoplankton is also preyed upon by microzooplankton. These predators have similar generation times as their prey and, therefore, the pico- and nanophytoplankton is tightly controlled by grazing (Fogg 1991).

Of course, the actual summer plankton distribution in the stratified North Sea never has a 100% "stratified" appearance. Both the microplankton-based and the pico- and nanoplankton-based systems can be found at the same locality. Indeed, the presence of the microbial loop and the presence of the "short" food chain has been demonstrated for the North Sea in several papers (Brussaard et al. 1996; Nielsen and Richardson 1989). The contribution of the "short" food chain, however, determines the amount of energy channeled to the highest trophic levels. Two factors seem to influence the microphytoplankton (diatom)–mesozooplankton (copepod) abundance:

(1) The extent of phyto–zooplankton interaction during the spring bloom (Colebrook 1982a, 1986)
(2) The amount of turbulence during the stratified season (nutrient injection into the euphotic zone, Riegman et al. 1990)

The effect of phytoplankton–zooplankton interaction on benthic–pelagic coupling can be visualized as follows. If only little zooplankton is present at the start of the spring phytoplankton bloom, this bloom will grow until nutrients are depleted and sink from the euphotic zone to the bottom. In this way, a large part of the primary production is channeled directly into the benthic system. If, however, a large zooplankton population is present before the spring bloom, the zooplankton population can graze a substantial part of the phytoplankton standing stock. Both the so-called "superfluous feeding" (Cushing and Vucetic 1963) and the fact that the fecal pellets of zooplankton can remain for a long time in the upper water column (Krause 1981; Martens and Krause 1990) are responsible for a shift of the remineralization of organic matter from the benthic to the pelagic system. In this manner, the zooplankton replaces nutrients at the disposal of phytoplankton and thus refertilises "its own meadow" (Margalef 1978).

The amount of turbulence during summer has an important influence on microphytoplankton growth and thus on the overall productivity. A high degree of turbulence, which in the deeper parts of the North Sea is entirely due to wind, will increase the nutrient flux from the deep into the nutrient depleted, euphotic surface layer. It also stimulates microphytoplankton growth by preventing it from sinking out of the euphotic zone and by enhancing nutrient uptake. On the other hand, extreme stratification (low wind speeds, high temperatures) will force the plankton system towards a low biomass, pico- and nanophytoplankton–microzooplankton system in which most of the primary energy dissipates without contributing to higher trophic production.

The well-mixed coastal zone during summer

In contrast to the open North Sea, the well-mixed coastal zone is subject to a continuous nutrient input. Main sources are rivers and remineralized organic matter. After the spring phytoplankton bloom, one to two additional diatom blooms occur. They are mostly followed up by non-diatom (flagellate) blooms (Cadée 1986; Radach et al. 1986). The occurrence of these summer blooms has a local character (Vosjan et al. 1992). The principal forcing factor in the coastal zone during summer is the nutrient status (van Bennekom et al. 1975; de Jonge 1990; Schaub and Gieskes 1991; Cadée and Hegeman 1993; Radach et al. 1990). Next to nutrient availability, nutrient ratios also have a profound influence on phytoplankton species composition (Officer and Ryther 1980; Riegman et al. 1992). Shifts in phytoplankton composition can be intensified by zooplankton selective grazing (Verity and Smayda 1989; Maestrini and Granéli 1991; Riegman 1991). Thus, the interaction between nutrient levels, nutrient ratios, phytoplankton species composition and zooplankton grazing determine the actual biomass and production levels during summer in the coastal zone.

If herbivores are present in large enough numbers they can control phytoplankton production (Fransz and Gieskes 1984; Loebl 2005). However, if part of the phytoplankton induces grazer avoidance strategies (colony formation, toxin production), the absence of grazing allows an unbridled growth for this part of the phytoplankton. If toxin production is involved in the grazer repellent tactics such blooms can have disastrous effects on the entire ecosystem (e.g., fish kills, anoxia; Rosenberg et al. 1988). What exactly triggers toxicity in algae is not yet clear. An alga which is well known for its massive blooms along the continental coasts is *Phaeocystis* sp. (Lancelot *et al.* 1987). These blooms are characterized by the formation of large colonies that cannot be preyed upon by zooplankton.

Whatever induces grazer avoidance and wherever this occurs, if such patches of algae originate in or are drifted into the eutrophic coastal zone large blooms can develop. If such blooms collapse, the benthic system has to cope with a sudden and large flux of fresh biomass. If the oxygen demand necessary to remineralize the organic matter exceeds the oxygen flux into the benthic system, hypoxic conditions will occur.

Autumn

Just like the annual debut, the end of the growing season is determined by light availability. In the open North Sea, the cooling of the surface layer together with autumn storms break down the thermocline. The accompanying nutrient injection can lead in some areas to an autumn bloom of diatoms and dinoflagellates (Colebrook 1979). Both the timing of the end of the growth season and the size of the zooplankton community at this point will have an important impact on the plankton development during the following year. Large initial overwintering zooplankton stocks will increase the chance that a considerable fraction of this population will survive the winter. This will allow a larger interaction with the spring phytoplankton bloom, and a larger zooplankton summer population is possible in the next year (Colebrook 1986). A late thermocline break down will also enhance the survival of the zooplankton (shorter winter). Wiltshire and Manley (2004) analyzed the response of the phytoplankton to the warming of the German Bight based on the Helgoland Road Time Series. They found a significant correlation between higher than average autumn temperatures and a delay of the following spring bloom that is probably related to an enhanced survival of grazers.

In the coastal zone, the end of the plankton season will depend on the solar radiation (day length, cloudiness) and turbidity (sediment resuspension by wind-wave action; de Jonge and van Beusekom 1995).

Observed long-term changes and their forcing factors

Two main factors influence the long-term plankton development in the North Sea: a climate/ocean driven and a nutrient driven change. Whereas the climate/ocean driven change is noticeable on a large geographic scale (Edwards et al. 2002), the nutrient driven change is confined to the coastal areas (van Beusekom et al. 2001). Much of our knowledge on the large scale, long-term changes in the phyto- and zooplankton of North Sea and adjacent Atlantic Ocean is based on data from the Continuous Plankton Recorder Survey. The CPR survey is a long-term marine monitoring programme which consists of a network of transects, towed monthly across the major geographical regions of the North Atlantic (Edwards et al. 2001). The CPR is a high-speed sampler sampling at a depth of about 10 m behind commercial ships. In the open North Sea and in the Atlantic Ocean, a comparable trend in phytoplankton
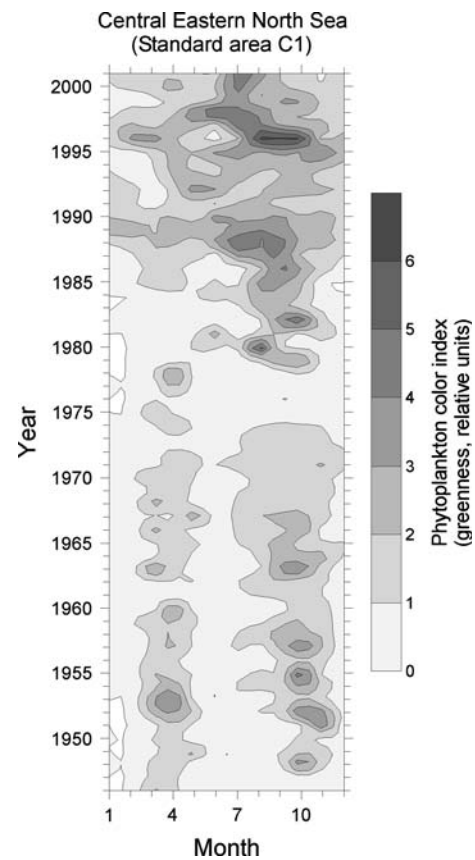
Fig. 4 Long-term dynamics of "phytoplankton color" in the eastern central North Sea (standard area C1). "Phytoplankton color" is an index based on the greenness of the gauze of continuous plankton recorders (CPR) due to phytoplankton retained by the gauze. The gauze used during the CPR Surveys has a mesh of about 270 μm. Therefore, the greenness is only a rough estimate of phytoplankton biomass as most phytoplankton may slip through the gauze. Data were taken from the SAHFOS website (http://www.sahfos.ac.uk/standard_areas.htm)

and zooplankton abundance was observed. From 1958 until about 1980, a continuous decrease in phyto- and zooplankton was observed (Colebrook 1982a). From about 1980 onward, the trend reversed (Colebrook et al. 1984). Especially since the middle of the 1980s, a high phytoplankton biomass (measured as green color on the mesh of the plankton recorder) was observed in the North Sea and adjacent east Atlantic (Edwards et al. 2002; Reid 2005; Fig. 4). During the past five decades, the seasonal shape also changed with clear spring and late-summer peaks until the early 1970s, a shortening of the seasonal cycle between the mid-1970s and the mid-1980s. Since the mid-1980s, the winter phytoplankton biomass is higher than before. Also the summer minimum was replaced by periods with relatively high values. Edwards et al. (2002) discussed the influence of extreme events on the phytoplankton biomass in the North Sea. Two events punctuated the above-described trends. During the late 1970s and early 1980s, the North Sea was characterized by reduced Atlantic inflow, reduced salinities and temperatures. Together with the Great Salinity Anomaly this produced a period of more boreal conditions. During the end of the 1980s, an increased inflow of warm and more saline water influenced the North Sea. This was coupled with positive NAO values and a strong westerly wind component. The changes in phyto- and zooplankton possibly exerted an impact on higher trophic levels. Aebischer et al. (1990) showed that changes in phytoplankton and zooplankton abundance were closely followed by changes in Kitty Hawk clutch size and young herring standing stock, for instance. Weijerman et al. (2005) collected a total of 78 data sets (28 environmental and 50 biological) from the North Sea and the Wadden Sea from the past four decades. They also identified two major shifts, centered around 1979 and 1988 and a third possible shift around 1998. The shifts were most clearly in the biological data sets, but appeared to have been triggered by environmental factors. Salinity and meteorological conditions were predominant in the 1979 shift and temperature and meteorological conditions were predominant in the 1988 shift. The fact that the changes were observed on different trophic levels supports that profound shifts in the entire ecosystem had taken place. Beaugrand (2004) also stresses that the cause of the above described regime shift is related to pronounced changes in the large-scale hydro-climatic forcing. Instead of discerning two periods of change (late 1970s and late 1980s), he suggests that one large regime shift took place around the mid 1980s related to a change in biogeographical boundaries along the European shelf and triggered by large-scale hydro-climatic forcing.

Along the continental coast the influence of changing climatic and hydrodynamic conditions on the phytoplankton is blurred by the local influence of increased nutrient input and nutrient ratios. Nowadays the annual primary production levels in the Dutch coastal zone are approximately 3–6 times higher (up to 441 g C m^{-2} a^{-1}, Peeters et al. 1991) compared to the open North Sea (75–100 g C m^{-2} a^{-1}, Joint and Pomroy 1993) and compared to the near shore productivity during 1960s (170 g C m^{-2} a^{-1}, Postma and Rommets 1970). Van Beusekom (2005) estimated a five-fold increase in primary production and remineralisation in the Wadden Sea and adjacent North Sea as compared to pristine riverine nutrient levels. For the Dutch coastal zone a direct relation between annual phosphate input and primary production (de Jonge 1990), between river Rhine discharge and summer Chl a levels (Schaub and Gieskes 1991) and between nitrogen discharge by the river Rhine and Chl a levels in the Marsdiep area (Cadée 1992) have been suggested. Van Beusekom and de Jonge (2002) and van Beusekom et al. (2005) suggest that nitrogen is the main nutrient determining the eutrophication status in the Wadden Sea. However, no conclusive evidence is available yet, that either pinpoints nitrogen or phosphorus as the ultimate limiting nutrient (Colijn and Cadée 2003; Philippart et al. 2000). This is not surprising, as temporal trends of both elements in European rivers are tightly coupled (van Beusekom et al. 2005). Despite the importance of nutrient levels in coastal areas, the regime shifts observed in the open North Sea have also been observed in the Wadden Sea (Weijerman et al. 2005; Philippart et al. 2007).

Interdecadal variability in the transfer of phytoplankton to the benthos: consequences for biogeochemical cycles

Large-scale climatic and oceanographic variability

Given the large interdecadal variability of the North Sea plankton, it is intriguing to wonder how this is reflected in the biogeochemistry of the North Sea. In the "Introduction", it was suggested that benthic processes have a large potential to influence the biogeochemical cycle of nutrients, for instance, by denitrification or by the formation of stable phosphorus minerals like apatite. Therefore, it is important to understand, which processes are responsible for the amount of organic matter transported from the pelagic to the benthic system. One of the explanations put forward to explain the differences in phytoplankton standing stock in the North Sea was a change in nutrient loads from the Atlantic Ocean to the North Sea. However, winter nutrient concentrations in the northern North Sea, where most of the Atlantic Water flows into the North Sea do not show a large interannual variability. Between 1984 and 2000 nitrate concentrations were about 9 μM

(Brockmann and Topcu 2002). During the Flex Experiment in 1976 during the "boreal dynamic period" sensu Beaugrand (2004) similar concentrations prevailed. This suggests that not the external loading but internal processes may be responsible for the observed differences between the low phytoplankton stocks around 1980 and the high biomass observed during the last decade. In the following, a possible explanation based on the work by Colebrook (1979, 1982a, b, 1985, 1986) will be put forward.

Most of the annual primary production occurs during the spring bloom (for a compilation of primary production data; see, van Beusekom and Diel-Christiansen 1994). This new produced organic matter is the basis for most of the following pelagic and benthic organic matter turn-over. A large portion of the newly produced organic matter can sink to the sediment (Davies and Payne 1984). As a first approximation, the relative amount of organic matter that reaches the bottom depends on the water depth (Suess 1980; Heip et al. 1995). Whereas at shallow depths about 50% of the total respiration takes place in the sediment (like in the Wadden Sea, van Beusekom et al. 1999) most of the organic matter is remineralised in the water column in deeper parts of the North Sea (von Westernhagen et al. 1986). It is, however, conceivable that large interannual differences exist. One possible mechanism proposed by Colebrook (1986) is the extent to which the spring bloom interacts with the zooplankton. The origin of this interaction may be found in the previous year. Both the timing of the end of the previous growth season and the size of the zooplankton community at this point will have an important impact on the plankton development during the following year. Large initial overwintering zooplankton stocks will increase the chance that a considerable fraction of this population will survive the winter. This will allow a larger interaction with the spring phytoplankton bloom, and a larger zooplankton summer population is possible in the next year (Colebrook 1986). For the phytoplankton this implies that more zooplankton is refertilizing the sea with its excretory products, thereby stimulating primary production. In this way a larger proportion of the organic matter produced during the spring bloom is recirculated in the pelagic phase instead of being transported to the benthos. It is interesting to note that Wiltshire and Manly (2004) also found a relation between autumn conditions and the following spring bloom in the German Bight (Helgoland Road time series).

Based on the above, three lines of research for the open North Sea are proposed that are all directed towards understanding the survival of zooplankton in the North Sea during winter and the interaction with the phytoplankton spring bloom: The research should comprise: (1) an experimental approach based on regular observations and accompanying experiment on phytoplankton–zooplankton interactions; (2) mooring studies to capture the short-term dynamics of weather conditions, hydrodynamic conditions, light conditions, and plankton dynamics; and (3) cruise-based studies of the (pre-) bloom dynamics in the North Sea. A similar experiment (FLEX) was carried out during the 1970s but under completely different climatic conditions (boreal dynamic vs. Atlantic dynamic; sensu Beaugrand 2004). A comparison of both data sets would shed light on the nature of the regime shifts observed in the North Sea. The latter experiments should include an extensive benthic component, not part of the original Flex study to investigate the relation between spring bloom dynamics, sedimentation processes and the benthic response, in particular processes like denitrification, anammox or apatite formation.

Invader-enhanced filter capacity in the coastal zone?

Many studies have addressed the implications of higher temperatures for the global biogeochemistry (Archer et al. 2004). Temperature has a large effect on biological processes in the North Sea with possible repercussions on coupling of benthic and pelagic processes. Edwards and Richardson (2004) pointed towards changes in the phenology of phytoplankton in the North Sea. They discussed the potential mismatch between trophic levels due to increased temperatures. Here, we address an additional aspect that potentially has a large impact on the bentho-pelagic coupling in coastal areas. Due to global maritime traffic many neophytes and neozoa (invaders) have appeared in the North Sea (Reise et al. 2002). Evidence exists that their recent success in the Wadden Sea is related to increased temperatures. The slipper limpet *Crepidula fornicata*—a filter-feeding snail—is limited by cold winters. Due to the recent absence of these cold winters the population has strongly increased (Thieltges et al. 2004). Since 1987, the pacific Oyster is cultivated in the Wadden Sea near Sylt and was first observed outside of the culture plots in 1991. Especially in warm summers (like 2001 and 2003) recruitment was successful and this filter feeder now is a dominant species in the intertidal Wadden Sea (Diederich et al. 2005). Since the 1980s the American Razor clam *Ensis americanus* has invaded the Wadden Sea and now is one of the dominant bivalves in the Wadden Sea. The above-mentioned neozoa are all filter feeders. They have a yet unknown impact on the suspended matter dynamics and on the biogeochemistry in coastal areas. The above case studies indicate that global warming will enhance the success of these introduced species. We therefore expect that especially in shallow coastal waters the neozoa will enhance the particle retention, strengthen the benthic organic matter remineralisation and support a

stronger removal of nutrients from the biogeochemical cycle, e.g. by denitrification.

Conclusions

Prominent changes in the entire North Sea ecosystem have taken place during and around 1979 and 1988. In general, "phytoplankton color" (an indicator of phytoplankton biomass derived from the CPR surveys, see Fig. 4) reached a relative minimum during the end of the 1970s and increased especially since the mid 1980s. Changes with a similar timing have been identified in many time series from the North Sea through the entire ecosystem and are sometimes referred to as regime shifts. It is suggested, that the impact on global change on the local biogeochemistry is largely driven by the phyto- and zooplankton dynamics during spring and early summer. At that time the extent of zooplankton–phytoplankton interaction either allows that a large part of the new production is settling to the sediment, or that a significant part of the new production including the fixed nutrients is kept within the pelagic system. The origin of the extent of the phytoplankton-zooplankton interaction in spring is probably set in the previous autumn and winter. It is suggested that the extent of phytoplankton–zooplankton during spring determines how much of the total primary production is channeled into the benthic system. This again determines the potential of removing nutrients from the biogeochemical cycle, e.g. by denitrification or anammox.

It is further hypnotized that recently introduced species have strengthened the filter feeder component of coastal ecosystems. Especially in shallow coastal seas like the Wadden Sea, this will enhance particle retention, shift organic matter degradation to the benthic compartment and remove more nutrients from the biogeochemical cycle.

References

Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels and weather. Nature 347:753–755

Archer D, Martin P, Buffett B, Brovkin V, Rahmstorf S, Ganopolski A (2004) The importance of ocean temperature to global biogeochemistry. Earth Planet Sci Lett 222:333–348

Aure J, Dahle E (1994) Oxygen, nutrients, carbon and water exchange in the Skagerrak Basin. Cont Shelf Res 14:965–917

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the Sea. Mar Ecol Prog Ser 10:257–263

Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245–262

Bjørnsen PK (1988) Phytoplankton exudation of organic matter: why do healthy cells do it? Limnol Oceanogr 33(1):151–154

Brockmann UH, Topcu D (2002) Nutrient atlas of the central and northern North Sea. Texte 26/02, Umweltbundesamt, Berlin, pp 1–64

Brockmann UH Laane RWPM, Postma H (1990) Cycling of nutrient elements in the North Sea. Neth J Sea Res 26(2–4):239–264

Brussaard CP, Gast GJ, van Duyl FC Riegman R (1996) Impact of phytoplankton bloom magnitude on a pelagic microbial food web. Mar Ecol Prog Ser 144:211–221

Cadée GC (1986a) Recurrent and changing seasonal patterns in phytoplankton of the westernmost inlet of the Dutch Wadden Sea from 1969 to 1985. Mar Biol 93:281–289

Cadée GC (1986b) Increased phytoplankton primary production in the Marsdiep area (Western Dutch Wadden Sea). Neth J Sea Res 20(2/3):285–290

Cadée GC (1992) Phytoplankton variability in the Marsdiep, The Netherlands. ICES Mar Sci Symp 195:213–222

Cadée GC, Hegeman J (1993) Persisting high levels of primary production at declining phosphate concentrations in the Dutch coastal area (Marsdiep). Neth J Sea Res 31(2):147–152

Colebrook JM (1979) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. Mar Biol 51:23–32

Colebrook JM (1982a) Continuous plankton records: phytoplankton, zooplankton and environment, North-East Atlantic and North Sea. 1948–1980. Oceanol Acta 5:473–480

Colebrook JM (1982b) Continuous plankton records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. J Plankton Res 4:435–463

Colebrook JM (1985) Continuous plankton records: overwintering and annual fluctuations in the abundance of zooplankton. Mar Biol 84:261–265

Colebrook JM (1986) Environmental influences on long-term variability in marine plankton. Hydrobiologia 142:309–325

Colebrook JM Robinson GA, Hunt HG, Roskell J, John AWG, Bottrell HH, Lindley XN, Collins NR, Halliday NC (1984) Short note: continuous plankton records: a possible reversal in the downward trend in the abundance of the plankton of the North Sea and the Northeast Atlantic. J Cons Int Explor Mer 41:304–306

Colijn F, (1982) Light absorption in the waters of the Ems-Dollard Estuary and its consequences for the growth of phytoplankton and microphytobenthos. Neth J Sea Res 15:196–216

Colijn F, Cadée GC (2003) Is phytoplankton growth in the Wadden Sea light or nitrogen limited? J Sea Res 49:83–93

Cushing DH, Vucetic T (1963) Studies on a calanus patch. III. The quantity of food eaten by *Calanus finmarchicus*. J Mar Biol Ass UK 43:349–371

Davies JM, Payne R (1984) Supply of organic matter in the northern North Sea during a spring phytoplankton bloom. Mar Biol 78:315–324

De Jonge VN (1990) Response of the Dutch Wadden Sea ecosystem to phosphorus discharges from the River Rhine. Hydrobiologia 195:49–62

De Jonge VN, van Beusekom JEE (1995) Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnol Oceanogr 40:766–778

Dickson RR, Kelly PM, Colebrook JM, Wooster WS, Cushing DH (1988) North winds and production in the eastern North Atlantic. J Plankton Res 10:151–169

Diederich S, Nehls G, van Beusekom JEE, Reise K (2005) Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea:

invasion accelerated by warm summers? Helgoland Mar Res 59:97–106

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884

Edwards M, Reid PC Planque B (2001) Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). ICES J Mar Sci 58:39–49

Edwards M, Beaugrand G, Reid PC, Rowden AA Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. Mar Ecol Prog Ser 239:1–10

Ehrenhaus S, Huettel M (2004) Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments. J Sea Res 52:179–197

Fogg GE (1991) The phytoplanktonic ways of life. New Phytol 118:191–232

Fransz HG, Gieskes WWC (1984) The unbalance of phytoplankton and copepods in the North Sea. Rapp P-v Réun Cons Int Explor Mer 183:218–225

Fransz HG, Gonzalez SR (1991) Daily egg production of *Temora longicornis* (Copepoda, Calanoida) during winter and early spring in the Marsdiep (Southern North Sea). Hydrobiol Bull 25(1):61–64

Galloway JN, Howarth RW, Michaels AF, Nixon SW, Prospero JM Dentener FJ (1996) Nitrogen and phosphorus budgets of the North Atlantic Ocean and its watershed. Biogeochemistry 35:3-25

Gieskes WWC, van Bennekom AJ (1973) Unreliability of the ^{14}C-method for estimating primary production in eutrophic Dutch coastal waters. Limnol Oceanogr 18:494–495

Gieskes WWC, Kraay GW (1977) Primary production and consumption of organic matter in the southern North Sea during the spring bloom of 1975. Neth J Sea Res 11(2):146–167

Glover RS, Robinson GA, Colebrook JM (1972) Plankton in the North Atlantic—an example of the problems of analysing variability in the environment. In: Ruivo M (ed) Marine pollution and sea life. FAO and Fishing News Books Ltd., London, pp 624

Hay SJ, Hislop JRG, Shanks AM (1990) North Sea scyphomedusae: summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25:113–130

Heip CHR, Goosen NK, Herman PMJ, Kromkamp J, Middelburg JJ, Soetaert K (1995) Production and consumption of biological particles in temperate tidal estuaries. Ocean Mar Biol Ann Rev 33:1–149

Horwood J (1982) Algal production in the west-central North Sea. J Plankton Res 4:103–124

Hydes DJ, Kelly-Gerreyn BA, Le Gall AC, Proctor R (1999) The balance of supply of nutrients and demands of biological production and denitrification in a temperate latitude shelf sea—a treatment of the southern North Sea as an extended estuary. Mar Chem 68(1–2):117–131

Joint I, Pomroy A (1993) Phytoplankton biomass and production in the southern North Sea. Mar Ecol Prog Ser 99:169-182

Kossinna E (1921) Die tiefen des weltmeeres. Veröff. Inst. Meeresk. Berlin, N.F. A9: p 7

Krause M (1981) Vertical distribution of faecal pellets during FLEX'76. Helgol Meeresunters 34:313–327

Lancelot C, Billén G, Sournia A, Weisse T, Colijn F, Veldhuis MJW, Davies A, Wassman P (1987) *Phaeocystis* blooms and nutrient enrichment in the continental coastal zones of the North Sea. Ambio 16:38–46

Loebl M (2005) Annual dynamics of pelagic carbon fluxes in a tidal lagoon. PhD Thesis, Univ. Bremen, 130 pp

Maestrini SY, Granéli E (1991) Environmental conditions and ecological mechanisms which led to the 1988 *Chrysochromulina polylepis* bloom: a hypothesis. Oceanologica Acta 14:397–412

Margalef R (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol Acta 1:493–509

Martens P, Krause M (1990) The fate of faecal pellets in the North Sea. Helgol Meeresunters 44:9–19

Middelburg JJ, Soetaert K, Herman PMJ (1997) Empirical relationships for use in global diagenetic models. Deep Sea Res I 44:327–344

Nielsen TG, Richardson K (1989) Food chain structure of the North Sea plankton communities: seasonal variations of the role of the microbial loop. Mar Biol 56:75–87

Officer CB, Ryther JG (1980) The possible importance of silicon in marine eutrophication. Mar Ecol Prog Ser 3:83–94

Otto L, Zimmerman JTF, Furnes GK, Mork M, Sætre R Becker G (1990) Review of the physical oceanography of the North Sea. Neth J Sea Res 26(2–4):161–238

Peeters KCH, Haas H, Peperzak L (1991) Eutrophiering, primaire productie en zuurstofhuishouding in de Noordzee. GWAO-91.083. Dutch Ministry of Transport, Public Works and Water Management, The Hague (in Dutch)

Philippart CJM, Cadée GC, van Raaphorst W, Riegman R (2000) Long-term phytoplankton-nutrient interactions in a shallow coastal sea: algal community structure, nutrient budgets, and denitrification potential. Limnol Oceanogr 45(1):131–144

Philippart, CJM, Beukema JJ, Cadée GC, Dekker R, Goedhart PW, van Iperen JM, Leopold MF, Herman PMJ (2007) Impact of nutrients on coastal communities. Ecosystems 7. doi:10.1007/s10021-006-9006-7

Pingree RD, Holligan PM Mardell GT (1978) The effect of vertical stability on the phytoplankton distribution on the northwest European shelf. Deep Sea Res 25:1011–1028

Postma H (1981) Exchange of materials between the North Sea and the Wadden Sea. Mar Geol 40:199–215

Postma H, Rommets J (1970) Primary production in the Wadden Sea. Neth J Sea Res 4:470–493

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

Radach G, Berg J, Hagmeier E (1990) Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at Helgoland and at LV ELBE 1 in the German Bight. Cont Shelf Res 10(4):305–328

Reid PC (2005) Atlantic wide regime shift? Globec Internation Newsletter, October 2005, 9–10

Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish Oceanogr 12:260–269

Reise K, Gollasch S, Wolff WJ (2002) Introduced marine species of the North Sea coast. In: Leppäkoski E, Gollasch S, Olenin S (Eds) Invasive aquatic species of Europe: distribution, impact and management. Kluwer, Dordrecht, pp 260–266

Rick HJ (1990) Ein Beitrag zur Abschätzung der Wechselbeziehung zwischen den planktischen Primärproduzenten des Nordseegebietes und den Schwermetallen Kupfer, Zink, Cadmium und Blei. Dissertation, RWTH Aachen

Riegman R (1991) Mechanisms behind eutrophication induced novel algal blooms. NIOZ Rapport 9, 49 pp

Riegman R, Colijn F, Malschaert JFP, Kloosterhuis HT, Cadée GC (1990) Assessment of growth rate limiting nutrients in the North Sea by the use of nutrient-uptake kinetics. Neth J Sea Res 26(1):53–60

Riegman R, Noordeloos AM, Cadée GC (1992) *Phaeocystis* blooms and eutrophication of the continental coastal zones of the North Sea. Mar Biol 112:479–484

Rosenberg R, Lindahl O, Blanck H (1988) Silent spring in the sea. Ambio 7(4):289–290

Runge JA (1984) Egg production of the marine planktonic copepod *Calanus pacificus* (Brodsky): laboratory observations. J Exp Mar Biol Ecol 74:53–66

Ruttenberg KC, Berner RA (1993) Authigenic apatite formation and burial in sediments from non-upwelling continental margins. Geochim Cosmochim Acta 57:991-1007

Ryther JH (1969) Photosynthesis and fish production in the sea. Science 166:72–76

Schaub BEM, Gieskes WWC (1991) Eutrophication of the North Sea: the relation between Rhine river discharge and chlorophyll-a concentration in Dutch coastal waters. In: Elliot M, Ducrotoy J-P (eds) Estuaries and coasts: spatial and temporal intercomparisons. International Symposium Series. Olsen & Olsen, Fredensborg

Slomp CP, Epping EHC, Helder W, van Raaphorst W (1996) A key role for iron-bound phosphorus in authigenic apatite formation in North Atlantic continental platform sediments. J Mar Res 54:1179-1205

Suess E (1980) Particulate organic carbon flux in the oceans-surface productivity and oxygen utilization. Nature 288:260–263

Sverdrup HU (1953) On the conditions for the vernal blooming of phytoplankton. J Cons Perm Int Explor Mer 18:287–295

Thamdrup B, Dalsgaard T (2002) Production of N_2 through anaerobic ammonium oxidation coupled to nitrate reduction in marine sediments. Appl Environ Microbiol 68(3):1312–1318

Tett P, Mills D (1991) The plankton of the North Sea-Pelagic ecosystems under stress? Ocean Shoreline Manage 16:233–257

Thieltges DW, Strasser M, van Beusekom JEE, Reise K (2004) Too cold to prosper—Winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. J Exp Mar Biol Ecol 311:375–391

Thomas H, Bozec Y, de Baar HJW, Elkalay K, Frankignoulle M, Schiettecatte -S, Kattner G, Borges AV (2005) The carbon budget of the North Sea. Biogeosciences 2(1):87–96

Turrell WR, Slesser G, Payne R, Adams RD, Gillibrand PA (1996) Hydrography of the East Shetland Basin in relation to decadal North Sea variability. ICES J Mar Sci 53:899–916

Van Bennekom AJ, Wetsteijn FJ (1990) The winter distribution of nutrients in the Southern Bight of the North Sea 1961–1978 and in the estuaries of the Scheldt and the Rhine/Meuse. Neth J Sea Res 25(1/2):75–87

Van Bennekom AJ, Gieskes WWC, Tijssen SB (1975) Eutrophication of Dutch coastal waters. Proc R Soc B 189:359–374

Van Beusekom JEE (2005) A historic perspective on Wadden Sea eutrophication. Helgoland Mar Res 59:45–54

Van Beusekom JEE, Diel-Christiansen S (1994) A synthesis of phyto- and zooplankton dynamics in the North Sea environment. WWF, Godalming, p 146

Van Beusekom JEE, Bot PVM, Goebel JHM, Lenhart H, Paetsch J, Peperzak L, Petenati T, Reise K (2005) Eutrophication. In: Essink K, Dettmann C, Farke H, Laursen K, Lüerßen G, Marencic H, Wiersinga W (eds) Wadden Sea Qualitiy Status Report 2004. Wadden Sea secretariat, Wilhelmshaven, 141–154

Van Beusekom JEE, Brockmann UH (1998) Transformation of phosphorus in the Elbe Estuary. Estuaries 21:518–526

Van Beusekom JEE, Brockmann UH, Hesse K-J, Hickel W, Poremba K, Tillmann U (1999) The importance of sediments in the transformation and turnover of nutrients and organic matter in the Wadden Sea and German Bight. German J Hydrogr 51:245–266

Van Beusekom JEE, de Jonge VN (1997) Transformation of phosphorus in the Wadden Sea: apatite formation. German J Hydrogr 49(2/3):297–305

Van Beusekom JEE, de Jonge VN (1998) Retention of phosphorus and nitrogen in the Ems estuary. Estuaries 21:527–539

Van Beusekom JEE, de Jonge VN (2002) Long-term changes in Wadden Sea nutrient cycles: importance of organic matter import from the North Sea. Hydrobiologia 475/476:185–194

van Beusekom JEE, Fock H, de Jong F, Diel-Christiansen S, Christiansen B (2001) Wadden Sea specific eutrophication criteria. Wadden Sea Ecosystem 14, Wilhelmshaven (Germany), 115 pp

Van Cappellen P, Dixit S, van Beusekom JEE (2002) Biogenic silica dissolution in the oceans: reconciling experimental and field-based dissolution rates. Global Biogeochem Cycles 16(4):1075. doi:10.1029/2001GB001431

Verity PG, Smayda TJ (1989) Nutritional value of *Phaeocystis pouchetii* (Prymnesiophyceae) and other phytoplankton for *Acartia* spp. (Copepoda: ingestion, egg production, and growth of nauplii. Mar Biol 100:161–171

Vidal J (1980) Physioecology of zooplankton: I. Effects of phyto-plankton concentration, temperature and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar Biol 56:111–134

Vosjan JH, Gunkel W, Tijssen SB, Pauptit E, Klings KW, Bruns K, Poremba, K Hagmeier E (1992) Distribution and activity of microorganisms in coastal waters off the Netherlands and Germany. Neth J Sea Res 29(4):333–341

von Westernhagen H, Hickel W, Bauerfeind E, Niermann U, Kröncke I (1986) Sources and effects of oxygen deficiencies in the south-eastern North Sea. Ophelia 26:457–473

Weichart G (1986) Nutrients in the German Bight, a trend analysis. Dt hydrogr Z 39:197–205

Weijerman M, Lindeboom H Zuur AF (2005) Regime shifts in marine ecosystems of the north Sea and Wadden Sea. Mar Ecol Prog Ser 298:21–39

Wiltshire KH BFJ Manly (2004) The warming trend at Helgoland Roads, North Sea: phytoplankton response. Helgoland Mar Res 58:269–273

Woodward EMS Owens NJP (1990) Nutrient depletion studies in off-shore North Sea areas. Neth J Sea Res 25(1/2):57–63