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(SUDDEN) CHANGES IN THE BIOTA OF THE NORTH SEA: OCEANIC INFLUENCES UNDERESTIMATED?

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SUMMARY

Several long-term datasets on phytoplankton, zooplankton, macrofauna, fishes and birds have been collected in the Wadden Sea and North Sea. Up till now, these datasets have mainly been used to demonstrate the effects of increasing eutrophication on the ecosystem. However, if the various datasets are combined it is striking that certain changes are very sudden and not gradual, as one would expect if a gradual increasing nutrient load was the cause. In the western Wadden Sea the algal biomass doubled between 1976 and 1978, followed by the macrobenthos in 1980, and in 1978 the breeding success of eider ducks went up several orders of magnitude. Apparently, large changes in the Wadden Sea ecosystem took place at the end of the seventies. An analysis of data collected in the North Sea indicates that large changes also occurred in this ecosystem in the same period. Dogfish disappeared from fish catches in 1978. In the same year the zooplankton composition changed, and the observed downward trend in zooplankton and herring biomass reversed. This all points to short-term large-scale changes.

It is suggested that a varying amount or composition of Atlantic water entering the North Sea may trigger these changes. In 1977/78 the great salinity anomaly entered the North Sea. However, large-scale weather patterns also changed in the same period. There are a few indications that the changes are linked with changes in the nitrogen cycle, and that the system switched from a 'benthic system' to a 'pelagic system'.

Other large-scale changes in the ecosystem may have occurred at the end of the previous century, in the thirties, and very recently all indicating the possibility that large-scale changes occur frequently. If this is true, certain observed trends in the ecosystem of the North Sea, which up till now have been attributed to eutrophication, pollution or fisheries, may have a completely different cause.

What does this mean for the future, and our exploitation of the sea? Preliminary hypotheses on the causes of sudden changes are presented and implications are discussed.

INTRODUCTION

Marine ecosystems are not in steady state, but exhibit continuous changes in production and species composition of different trophic levels. Presently, several long-term datasets on phytoplankton (CADÉE & HEGEMAN, 1991; 1993), macrobenthos (BEUKEMA, 1991), and eider ducks (SWENNEN, 1991) are available which indicate such changes in the Wadden Sea. Similar datasets exist for the German Bight region (HICKEL *et al.*, 1993; UHLIG & SAHLING, 1990; GERLACH, 1990). All these datasets indicate a biomass increase between the 70's and 80's. The observed changes have been attributed to different causes such as anthropogenic eutrophication, severe winters, or extreme river discharges.

Datasets on phytoplankton and zooplankton biomass have also been published for the North Sea (COLEBROOK, 1986; FRANSZ *et al.*, 1991). These datasets indicated a decreasing trend until around 1980, followed by an increase. AEBISCHER *et al.* (1990) suggested a correlation with trends observed in the westerly weather pattern.

However, in the process of determining the trends in these datasets there has been a tendency to apply linear fittings or long-term smooth curves, and so far sudden changes in the entire ecosystem have not been recognized as such.

In this paper we will bring together several datasets and point out a phenomenon which apparently happened in the late 70's. A possible explanation will be offered, and new hypotheses on the functioning of the marine ecosystem in shallow areas in the temporate zone will be formulated.

LONG-TERM DATASETS

THE WADDEN SEA

The long-term datasets from the Netherlands Institute for Sea Research have been collected in the western Wadden Sea (Fig. 1). In Fig. 2, the data on average chlorophyll-a concentrations in the Marsdiep area (CADÉE & HEGEMAN (1991), on macrofauna biomass in the Balgzand area (BEUKEMA, 1991), and on the number of eider duck fledglings on the island of Vlieland (SWENNEN, 1991) since 1970 (1962 for the eiders) are given. By comparing these independently collected datasets, a sudden change between 1977 and 1981 is observed. In 1977 only seven eider chicks fledged, whereas in 1978 more than 1000 successful fledglings were reported. This number stayed well above the long-term average for the following ten years. SWENNEN (1991) attributed the breeding success to an abundancy of food in the period after 1977. The data on the macrobenthos indicate a sudden increase of biomass between 1979 and 1981, whereas the phytoplankton data indicate a doubling of chlorophyll-a between 1976 and 1978. Unfortunately no data for 1977 are available. Although the timing seems to be different, the datasets clearly indicate that a sudden change, took place in the late 70s, and that a major part of the ecosystem, from algae to birds, was affected. What caused this change?

THE NORTH SEA

Several long-term datasets on biological variables have been published for the North Sea. In Fig. 3 some of these datasets have been brought together: phytoplankton and zooplankton data collected in the open North Sea with the continuous plankton recorder (COLEBROOK, 1986), and flagellate abundancies in the German Bight (HICKEL *et al.*, 1992).

When observing these datasets with the emphasis on the late 70's to the early 80's, we notice the following. The phytoplankton data show a continuous decrease with a distinct minimum in the late 70's, the zooplankton data show a steep drop in 1978 followed by an increase in 1982, the flagellates increase in 1979. Other data indicate that the number of dogfish caught in the northern, middle and southern part of the North Sea decreased dramatically in 1978 (see Fig. 8). Whereas the number of herring showed similar trends as observed for zooplankton (AEBISCHER *et al.*, 1990; DAAN *et al.*, 1990). Major changes were also observed in fish and Guillemot distribution in the North Sea (CAMPHUYSEN, 1990) and the velvet swimming crab disappeared from Dutch coastal waters in early 1978. Similar to the Wadden Sea data all datasets indicate a change in the late 70's-early 80's. Is this a coincidence, or are the changes the result of a similar event or mechanism?

POSSIBLE TRIGGERS

Climatic phenomena have been mentioned as a possible explanation for the observed biomass changes. COLEBROOK (1985) pictured a long-term trend in the intensity of westerly weather, while AEBISCHER *et al.* (1990) showed that the observed trend in the weather coincided with long-term changes in the biomass of phytoplankton, zooplankton and herring, and even in the breeding aspects of kittiwakes. Although a correlation seemed clear, the causal relationship remained unknown. CADÉE & HEGEMAN (1993) and HICKEL *et al.* (1992) suggested a relationship between river discharges and the observed phytoplankton blooms. However, although the river runoff was relatively high in 1979 and 1981, possibly adding to the extremely high phytoplankton values found by these authors in 1979 and 1981, this would not explain a major change in 1977/78. And other high runoffs did not always result in extreme phytoplankton biomasses (HICKEL *et al.*, 1992). BEUKEMA (1992) suggests the severe winter of 1979 on the European continent as a trigger for the macrofaunal increase, but other severe winters did not always lead to the same pattern. And although severe winters may change the macrofauna composition and age distribution it is difficult to see how it would explain a general biomass increase.

In several papers on the western Wadden Sea, anthropogenic eutrophication has been mentioned as a major cause for the increase of phytoplankton and macrofauna (CADÉE & HEGEMAN, 1993; BEUKEMA, 1991). RIEGMAN *et al.* (1992) compared the change in chlorophyll with the nutrient input from Lake IJssel and with the total molar N/P ratio in the Marsdiep area, and concluded that reduction of the lake surface area by dike construction had influenced the phosphate load to the Wadden Sea leading to higher phytoplankton biomasses. VAN RAAPHORST & VAN DER VEER (1990) calculated a substantial change in the phosphate budget of the western Wadden Sea between 1976 and 1979. However, this change was not only caused by eutrophication through freshwater discharge, which already started in the early seventies, but also the input of phosphorus associated with suspended matter from the North Sea increased in the late 70's.

Surprisingly, there is another event which coincided with the 1977/78 phenomena. Figure 4 shows the route followed by the great salinity anomaly, from its formation north of Iceland in 1961 to its return to the east coast of Greenland in 1981 (MANN & LAZIER, 1991). And this anomaly entered the North Sea in 1977/78. Coincidence, or a possible explanation? Could a small shift in salinity have changed the system? Not likely, the salinity difference caused by the anomaly was only in the order of 1‰ or less. And in the Wadden Sea area much larger differences are quite natural due to the variable freshwater input from Lake IJssel and the river Rhine (range 22-32‰). However, MAN & LAZIER (1991) describe major changes in the fishstocks both on the western and eastern side of the Atlantic at the moment that the anomaly arrives. Especially the number of cod, haddock and whiting showed a distinct decline. Is there a relationship between water composition and fish biomasses?

An analysis of wind data for the western Wadden Sea showed a striking phenomenon at the end of 1977. In November, a major storm with maximum wind velocities >140 $km.hr^{-1}$ hit the Wadden Sea area. November 1977 was by far the windiest November month recorded between 1975 and 1990. This very windy month was followed by a long period with hardly any storms at all. The year 1978 was one of the four years (1970, 1971, 1978 and 1984) in the 1970-1990 period during which no winds with a force >6 Beaufort were recorded between March and October along the Dutch coast. Can an extremity in the wind regime explain the changes observed?

On the other hand, Fig. 5, showing the mean high water level at Nes on the Wadden Sea (OOST & DIJKEMA, 1993), indicates that the mean levels in the 80's were about 20 cm higher than the levels in the 70's with a sudden increase between 1980 and 1981. Once again a change in physical conditions in the same period that some of the changes in the biological datasets were observed. Does it all lead to one explanation for the observed changes or is it a number of coinciding events?

A NEW HYPOTHESIS

From the above it seems clear that sudden events and changes do occur in the marine ecosystem and that these can affect the biomass and /or reproduction of all trophic levels. How does it work? Our hypothesis is that it has something to do with the factors that limit marine production and/or the biomass of algae, zooplankton, macrofauna and probably all predators, and that shifts in the availability of the limiting factors can lead to changes in the foodweb which in turn can lead to changes in the biomasses or in feeding behaviour. What is the major limiting factor for algal biomass and production in the North Sea and the Wadden Sea? In winter light is the limiting factor for algal growth. During the spring bloom, silicate becomes the limiting factor for diatoms while phosphate appears to be the first limiting factor for green algae, followed by nitrogen (VELDHUIS *et al.*,1988). There are clear indications that during most of the summer nitrogen is the major limiting factor in the central North Sea (RIEGMAN *et al.*,1990), although there have been suggestions that lack of iron may limit algal growth. After the algal bloom in autumn, light once again is the limiting factor. Now the question is which of these factors ultimately determines the biomasses of the biota. For the hypotheses, we have to assume that to explain the phenomena observed, the possibility must exist that the factor is influenced on a large scale by processes in the ocean, rendering the nutrients better candidates rather than light. Since nitrogen is an important limiting factor in summer, and because we observed a change in the organic nitrogen in 1978 coinciding with other phenomena, we will first focus on this element.

Nitrogen plays an essential role in different processes in the marine ecosystem (Fig. 6). It is of prime importance to all living organisms, since they use either organic or inorganic nitrogen compounds for protein and nucleic acid synthesis. Organic nitrogen is mineralized by bacteria to ammonia, which in turn can be used for building cell material or as energy source for autotrophic bacteria which convert it into nitrate. This nitrate can be transfered into cell material by algae and bacteria, which use iron- and molybdenum-containing enzymes to reduce the nitrate, or it can be used in the denitrification process by anaerobic bacteria. In this case the nitrogen is mainly converted to gaseous nitrogen and lost from the biological system. Cyanobacteria are capable of fixing gaseous nitrogen. The possitively charged ammonium ion readily adsorbs onto organic matter and clay minerals, which facilitates transport along with suspended matter. Nitrate as terminal electron acceptor in the absence of oxygen can determine redox conditions in sediments and the depth at which Fe-oxides start becoming reduced and subsequently mobilized. All this makes nitrogen well suited to play a crucial role in shallow marine ecosystems. In the nitrogen pathways in the marine environment there are crucial switches which may change the foodweb and the bioavailability of nitrogen. This is illustrated for the open North Sea and the shallow Wadden Sea in Fig.7.

Firstly, the amount and fate of the nitrogen transported to the sediment or retained in the water column. If the primary production is mainly consumed in the water phase, we have a 'pelagic system', in which most of the mineralized nitrogen remains available for the biota, leading to high biomasses of pelagic organisms. If a (large) part of the primary production settles on the sediment, we have a 'benthic system'. Now part of the nitrogen is transported to the sediment where it may be used by benthic organisms to build cell material, or where it may be removed from the biological system through denitrification or burial. In this case, we may have relatively high biomasses of benthic organisms, whereas the total biomass could drop as a result of nitrogen removal. In such a system the release of nitrogen compounds from the sediment becomes a major factor in determining the amount of nitrogen available to build biomass.

Secondly, ammonia may be used to build cell material, or autotrophs may oxydize it to nitrate to obtain energy. In the latter case, the nitrogen is only bioavailable if organisms are able to synthesize the reducing enzymes, which contain iron and molybdenum. Thus, iron may become a major limiting factor in this case. The close coupling between the geochemical cycles of iron, phosphate and nitrate makes the picture even more complex. It is known that phosphate is released from the sediment in summer when the oxygen penetration decreases (EINSELE, 1936; LINDEBOOM & MERKS, 1983; SUNDBY *et al.*, 1986; VAN RAAPHORST & KLOOSTERHUIS, 1994 (in prep.)). The mechanism behind this release is the reduction and subsequent mobilization of Fe-oxides when both oxygen and nitrate are exhausted as electron acceptors for organic matter oxidation. Increase of nitrate may thus suppress the release of phosphate from sediments.

All this leads to the following:

THE HYPOTHESES

1. In 1978 the ecosystem in the North Sea switched from a 'benthic system' to a 'pelagic system'.
2. This switch changed the nutrient cycles, both biologically and geochemically .
3. Depending on the depth and the location of the area the results of the switch can be different.
4. A changing composition of the inflowing ocean water was the major cause of the switch.
5. Once the system has switched to a certain configuration there are strong feedback mechanisms which will keep it in that particular configuration as long as possible.
6. Apart from sudden changes, the system can also change more gradually.
7. The phenomena have occurred more often.

SUPPORTING THE HYPOTHESES

1. *A switch in the system?*

Between 1977 and 1978 the number of dogfish caught in the North Sea decreased with approximately 90% (Fig. 8)! And the data clearly show that this happened throughout the entire North Sea. There may be several causes. It is possible that the fishing techniques changed such that the sharks were not caught anymore, or the sharks may have left the entire North Sea, or there was a change in the system causing a lower catchability of sharks. There is no evidence that fishing techniques, fishing distribution and effort, or the demand for sharks changed such that it could explain the observed decrease. However, apparently these shark species can, depending on the availability of food, change their way of living from a benthic lifestyle to a more pelagic lifestyle. Therefore, an explanation could be that in 1978 the sharks changed to a pelagic lifestyle which made them less catchable for beam trawl fisheries. JOSEFSON *et al.* (1993) describe a benthos community structure anomaly in the late 70's and early 80's as a result of a major food pulse. In 1978 major changes were observed in the Dutch Wadden Sea. The eider ducks increased their breeding success as result of an increase in benthic food items of a small size, the food source for the eider ducklings (SWENNEN, 1991). And in the same period the algal biomasses increased (CADÉE & HEGEMAN, 1993). In 1979, a major increase in algal biomass was observed in the German Bight (HICKEL *et al.*, 1993).

All these events hint at a change in food availability in the North Sea ecosystem at the end of the 70's. A switch from a 'benthic foodweb' to a more 'pelagic foodweb' would be an explanation for the phenomena observed. See also Fig. 7.

2. *Changing nutrient cycles?*
Figure 9 shows the long-term discharge and ratio figures for the Wadden Sea collected by the Dutch ministry of transport and public works. There has been a clear increase in both the phosphate and nitrogen input into the Wadden Sea in the 70's and early 80's. But can the gradual increase explain a sudden change in the biota? In Fig. 9 we see a striking phenomenon: the total N/P ratio in the Marsdiep area suddenly drops at the end of 1977. This drop cannot be explained by external nutrient loadings but seems almost entirely caused by a sudden decrease of organic nitrogen in these waters. The mean organic nitrogen concentration was around 1 $mg.dm^{-3}$ up till the end of 1977, at which time a steep decline was observed. From early 1978 the mean concentration varied around 0.4 $mg.dm^{-3}$. So a major change in the organic nitrogen concentration in the water phase was observed in the western Wadden Sea at the same moment of the supposed foodweb change. In the German Bight, HICKEL *et al.* (1992) show an increase in the nitrate concentration in the water. The initial increase originated from the North Sea water, and was not triggered by river discharges (HICKEL, pers. comm.). Both phenomena hint at a change in the nitrogen cycle at the end of the 70's.

3. *Differences between areas?*
In the central North Sea the benthic fauna and the sharks decrease in 1978, whereas in the shallow Wadden Sea the biomasses increase. In our hypothesis, this can all be the result of the same process. If we assume that the North Sea system switched from benthic to pelagic (Fig. 7), this would mean that less food (and nutrients) is transported towards the sediment, and that relatively more algal biomass stays in the water column. In that case the benthic system of the central North Sea would receive less food, but at the same time the transport of pelagic organic material into the coastal zone (POSTMA, 1981), including the Wadden Sea, would increase, leading to higher biomasses in that area.

4. *The trigger in the ocean?*
TAYLOR *et al.* (1992) have indicated a correlation between latitudal displacements of the Gulf Stream and the abundance of plankton in the North-East Atlantic, suggesting that changes in the hydrography of the western Atlantic may influence the biology of the eastern part. The observed changes in the late 70's coincide with the moment that the great salinity anomaly arrives in the North Sea (MANN & LAZIER, 1991). For other possible triggers to be the major cause they are either too common (storms), too limited in space (anthropogenic eutrophication), or the timing is not right (severe winters). Therefore, at this moment the entering of the anomaly seems to be a likely cause. But the salinity difference with the surrounding waters was less than 0.5 ‰, and it is unlikely that this difference explains a major change in the ecosystem. However, it is very possible that not only the salinity was different from 'normal' but that the entire chemical composition diverged from more saline ocean water. Although we have not been able to find supporting data so far, we postulate that the macro and micro nutrient ratios in the incoming ocean water was different. This may be caused by a different biology and geochemistry in this water during its travel through the ocean (e.g. less mixing with the bottom layers). It seems possible that the nutrients directly involved in the nitrogen cycle (nitrogen, iron and molybdenum), or the nutrients more indirectly involved (phosphate) were present in ratios different from the normal situation. This may have caused a switch in the nutrient pathways with a lower transport towards the sediment (see Fig. 7). On

the other hand, once the system has switched storms and other physical phenomena may have a distinct effect on the biological and chemical cycles. For example, the effect of a storm on a "benthic system" would be more pronounced than the effect on a "pelagic system". An alternative hypothesis could be that the internal dynamics of the ecosystem itself is sufficient to cause large-scale changes or to make the system susceptible to relatively small forcing by physical triggers. That this is theoretically possible was shown by a model run of W. Silvert at the COST 647 workshop on Modelling Benthos (Yerseke, 1991). However, many more datasets are needed before any definite conclusions can be drawn.

5. *A strong feedback mechanism?*

If we look at the datasets for the western Wadden Sea (Fig. 2) or the number of sharks caught (Fig. 8) it is clear that after the change the new numbers seem relatively stable. In the five years before 1978 there were never more than 10 eider ducklings which fledged, whereas between 1978 and 1987 the numbers were always close to 1000. CADÉE & HEGEMAN (1993) observed an increase in *Phaeocystis* blooms in 1978, which in 1993 was still observable. These are indications that once a change has taken place it can stabilize itself. For the western Wadden Sea this may work as follows: RIEGMAN *et al.* (1992) have shown that flagellates, especially *Phaeocystis*, become dominant algae when nitrogen is the limiting factor, and that colonies become the dominant *Phaeocystis* form when nitrate is the nitrogen source under such circumstances. Maybe the nitrogen source changed to nitrate in 1978. If we assume that colonies sink faster than single cells (Stokes law) it is likely that the sedimentation increased after 1978, loading the sediment with nutrients. After the sedimentation of the algae, phosphate is rapidly released followed by a delayed release of nitrogen, possibly triggering the next *Phaeocystis* bloom. In this way the presence of nitrate leading to *Phaeocystis* colonies, which have a higher sedimentation rate, leading to a delayed nitrogen availability might be feedback systems which have kept the blooms going for many years. This process may even be enhanced in the Wadden Sea with its increased anthropogenic nutrient load (RIEGMAN *et al.*, 1992). However, when comparing the changes in algal biomass in the western Wadden Sea with the changes in the German Bight (HICKEL *et al.*, 1992) we observe a striking difference. In both areas the algal biomass increased in the late 70's. But in the German Bight the change seems to have lasted much shorter. In this area *Phaeocystis* was much less dominant than in the western Wadden Sea (HICKEL *et al.*, 1992). But there could also be a relationship with the observed anaerobiosis in the German Bight between 1981 and 1983 (GERLACH, 1990). If the sediment becomes anoxic it releases fast amounts of phosphate and iron(II). This was demonstrated for the German Bight by SLOMP & VAN RAAPHORST (1993) for the summer of 1991. Iron(II) is oxidized to iron(III) oxides in the oxic part of the water column. These fresh oxides can scavenge phosphate very efficiently (MORTIMER, 1941/1942) finally resulting in a lack of both iron and phosphate for primary producers after anaerobiosis. This forms a possible feedback mechanism to overcome anoxia in marine sediments and could explain the drop in algal biomass in the German Bight in the early 80's.

6. *More gradual changes?*

AEBISCHER *et al.* (1990) have shown that changes in phytoplankton and zooplankton in the North Sea coincided with changes in herring stocks and kittiwake clutches. Their figures indicate a gradual decrease in the numbers untill 1978, when an increase began. A correlation with changes in weather pattern was demonstrated. However, the question of the actual cause-effect relationship was not answered. We propose that the same mechanism described for the sudden changes may be responsible for the more gradual changes. In this case it may be the weather pattern which influences the availability and ratio of the limiting nutrients in ocean or North Sea or both. However, presently we have no data to support this hypothesis.

7. *The phenomena occurred more often?*
Last but not least, more sudden changes may be observed in long-term datasets. The eider ducks had a low number of fledglings between the mid-60's and 1978, but the early 60's were very successful years. The phytoplankton data of the German Bight also indicate a significant increase in the second half of the 60's. And is it purely coincidence that in 1965 the average length of 4-year old female plaice increased from around 30 to about 34 cm (BODDEKE & HAGEL, 1991). Eutrophication and/or the development of beamtrawl fisheries have been held responsible for the changes. But again the abrupt change did not follow the gradual development of the anthropogenic influences. Maybe it was a switch from a pelagic to a benthic system?

In the early 30's a major change in the abundance of commercially important fish stocks was observed in the English Channel. This phenomenon, known as the Russell cycle was atributed to a change in ocean currents influencing the amounts of phosphate (MAN & LAZIER, 1991).

A dramatic decrease in the fish stocks has been observed at the end of the previous century (Fig. 10; HEMPEL, 1978). In those days, the fisheries collapsed and ICES was established to promote research into the possible causes of this event. Maybe again a major ocean induced change? However, the fact that these types of sudden changes happened already long before anthropogenic eutrophication took place, or before the fisheries techniques had caught up with nature are clear indications that we should look more for possible natural causes.

IN CONCLUSION

In studying the different datasets, it becomes clear that apart from gradual developments in shallow marine ecosystems sudden, large scale, changes can occur.

In the late 70's the North Sea system changed overnight, possibly caused by the entrance of ocean water with a different chemical composition by changes in weather pattern, and/or by internal changes. However, on a more local scale anthropogenic actions like fisheries, eutrophication and pollution may also have attributed to the changes observed. For future management of the North Sea and Wadden Sea it is of crucial importance that we increase our knowledge about the natural variation of the ecosystem. Only if we are capable of discriminating between the effects caused by man or by nature, a lasting management strategy can be developed. We will have to accept that the effects of managerial measures will not always be clear, and that the exploitation patterns of the marine ecosystem need to be adaptable to large scale natural changes.

We are eagerly looking forward to other datasets as well as to the scientific and political discussion arising from the formulated hypotheses.

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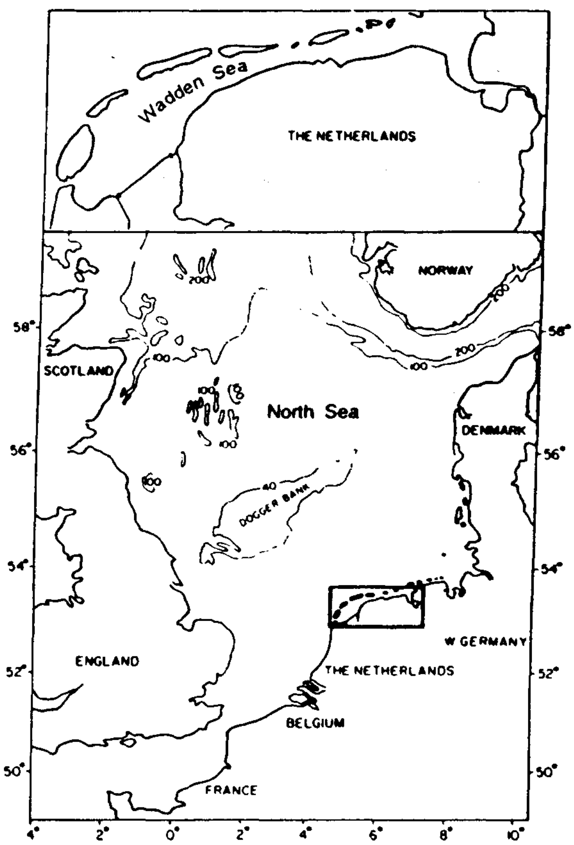

Fig. 1. Map of the sampling locations.

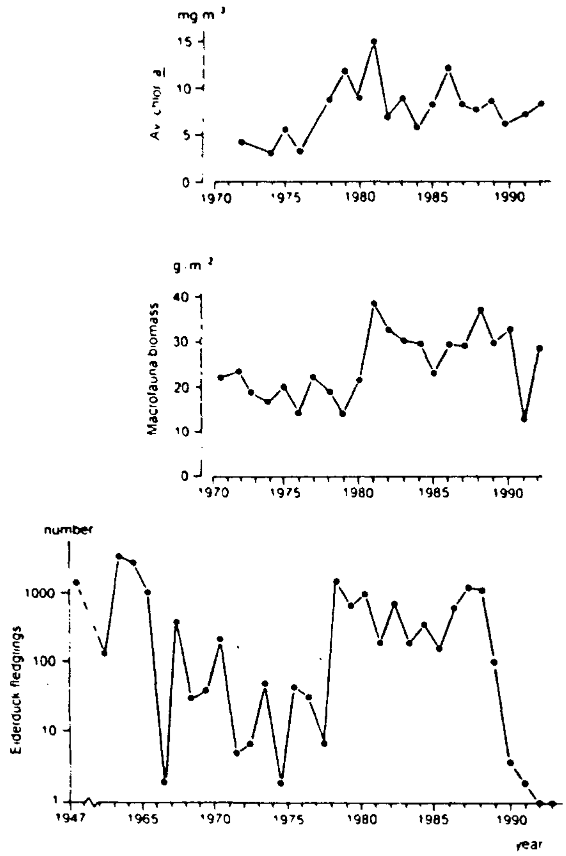

Fig. 2. Average chlorophyll-a content (after CADÉE & HEGEMAN, 1993), macrofauna biomass (after BEUKEMA, 1992) and Eiderduck fledglings (after SWENNEN, 1991) in the western Wadden Sea.

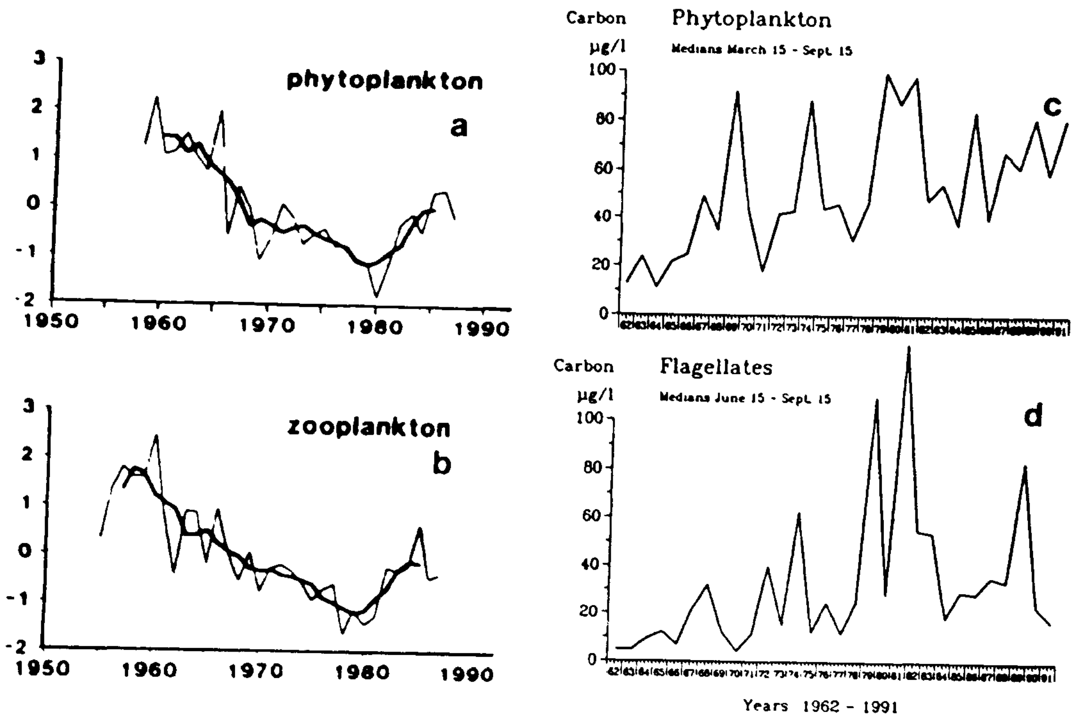

Fig. 3. Long-term datasets from the North Sea(a, b; AEBISCHER *et al.*, 1990) and German Bight (c, d; HICKEL *et al.*, 1992) (for details see text).

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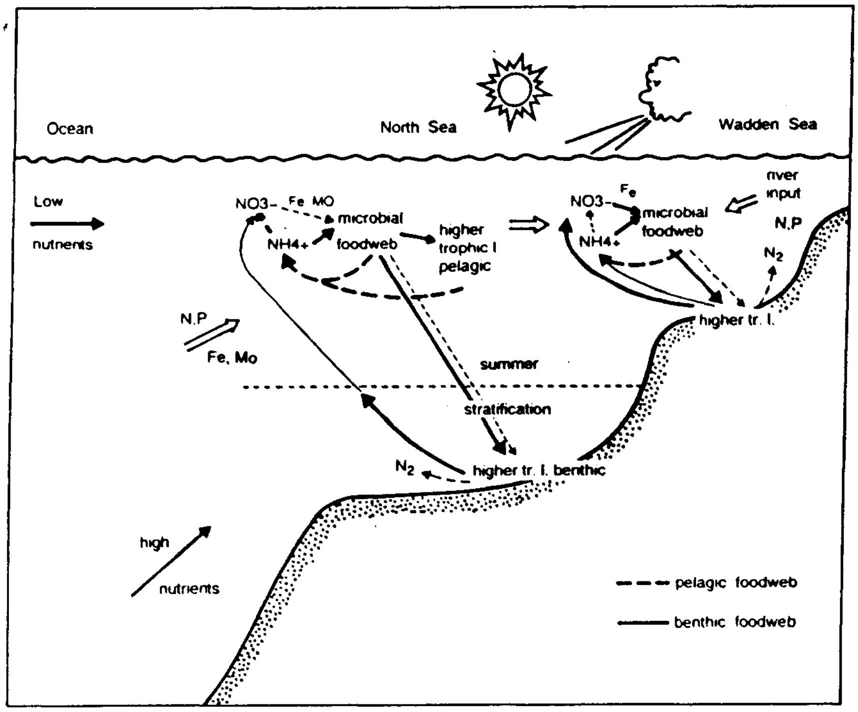

Fig. 7. The nitrogen cycle in a marine ecosystem switching from a 'benthic' to a 'pelagic' foodweb (for details see text).

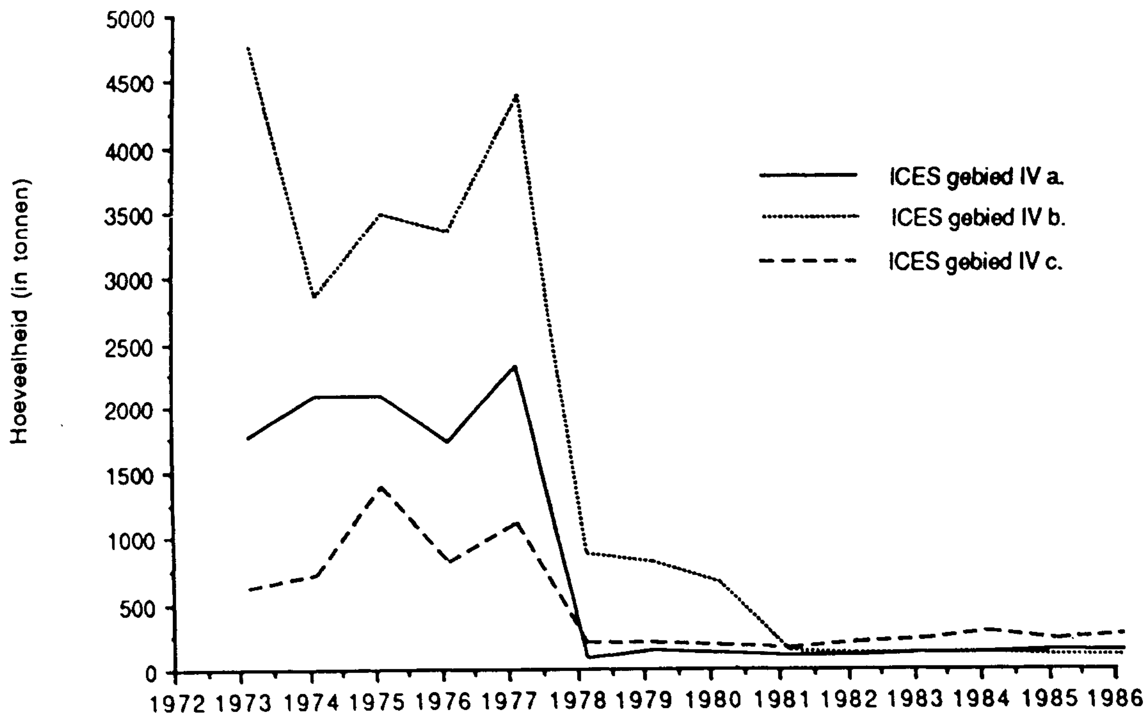

Fig. 8. Total number (in tonnes) of "dogfish" caught in different areas of the North Sea (DE BRUYNE, 1990).

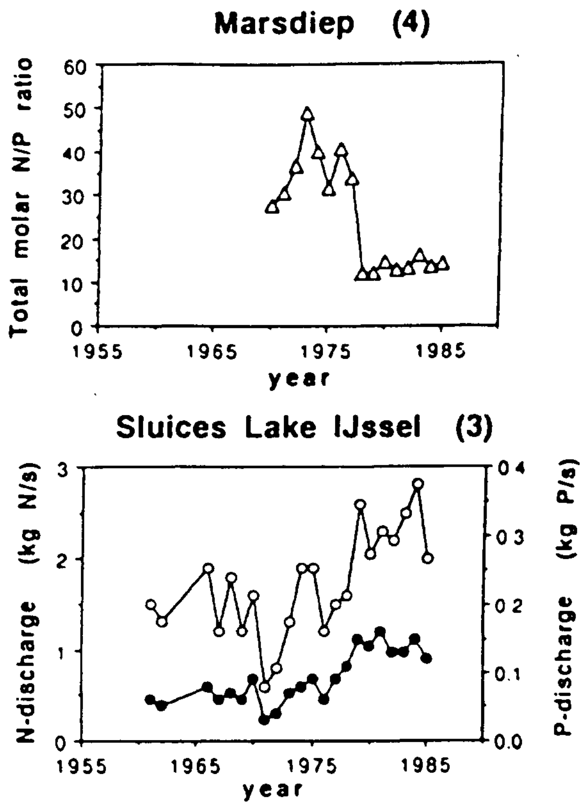

Fig. 9. Nitrogen and phosphorus discharges from Lake IJssel (3) and total-N/total-P ratio (4) in the Marsdiep area (RIEGMAN *et al.*, 1992).

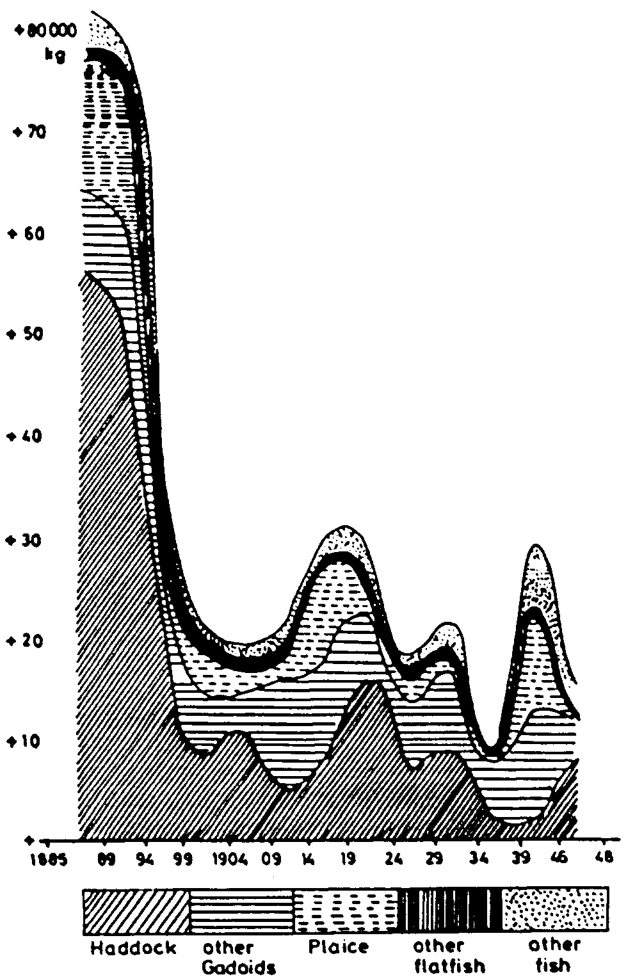

Fig. 10. Catch/10-d trip (corrected effort) of a standardized German trawler in the southern North Sea (HEMPEL, 1978).

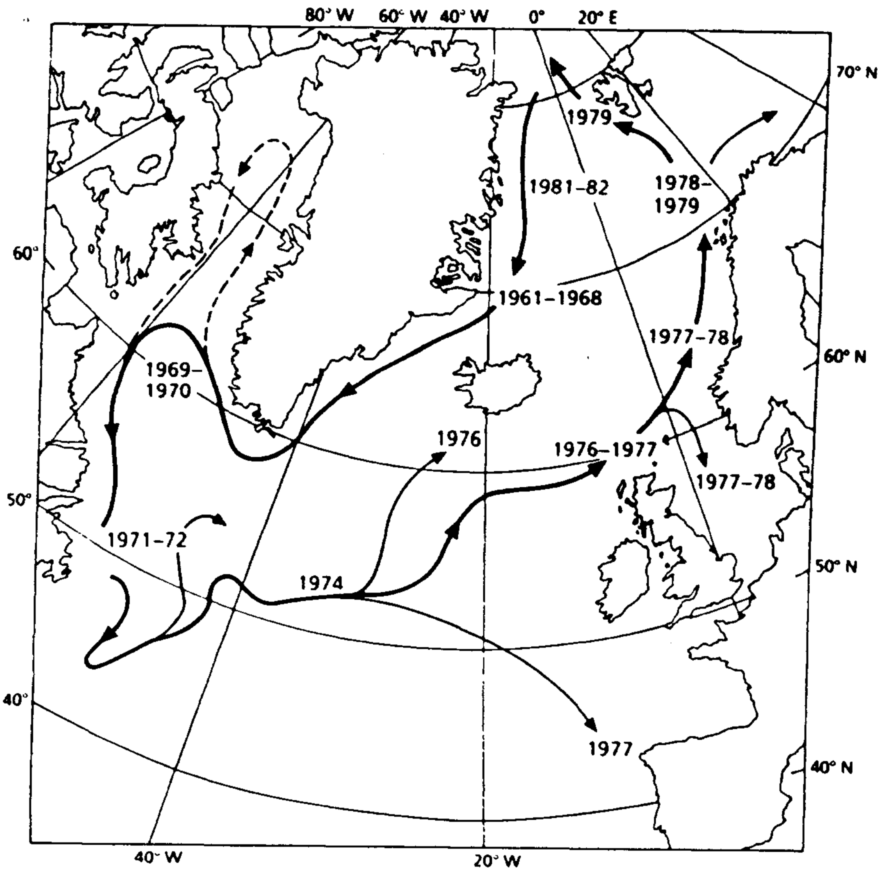

Fig. 4. Route followed by the great salinity anomaly, from its formation north of Iceland in 1961/1962 to its return to the east coast of Greenland in 1981 (MANN & LAZIER, 1991).

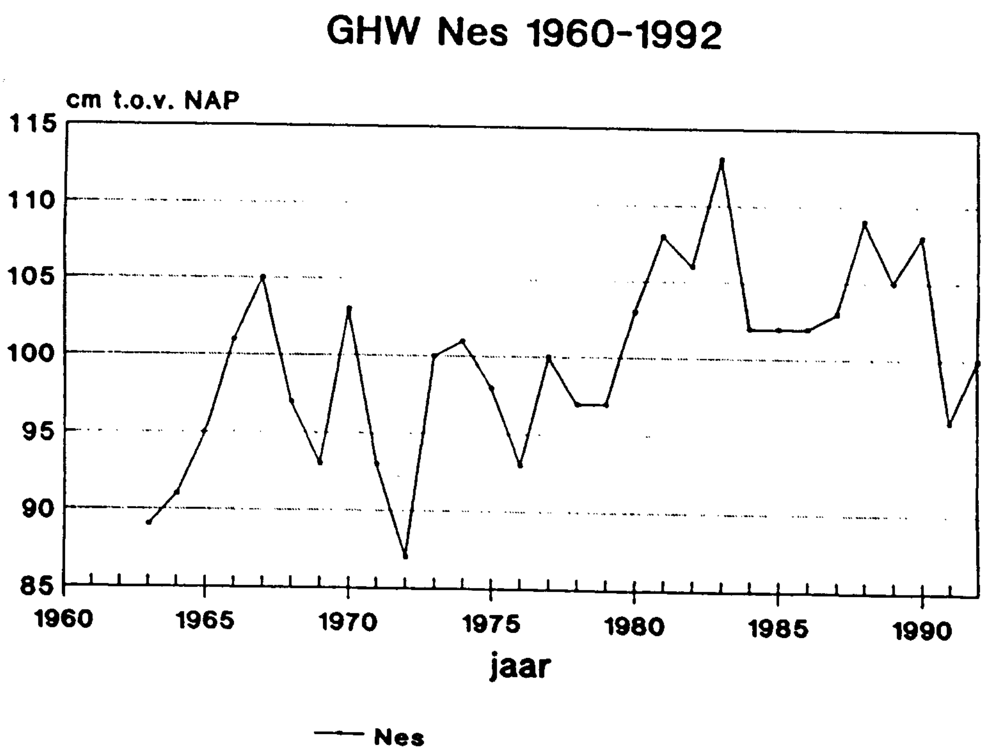

Fig. 5. Mean high water level at Ameland (western Wadden Sea) (OOST & DIJKEMA, 1993).

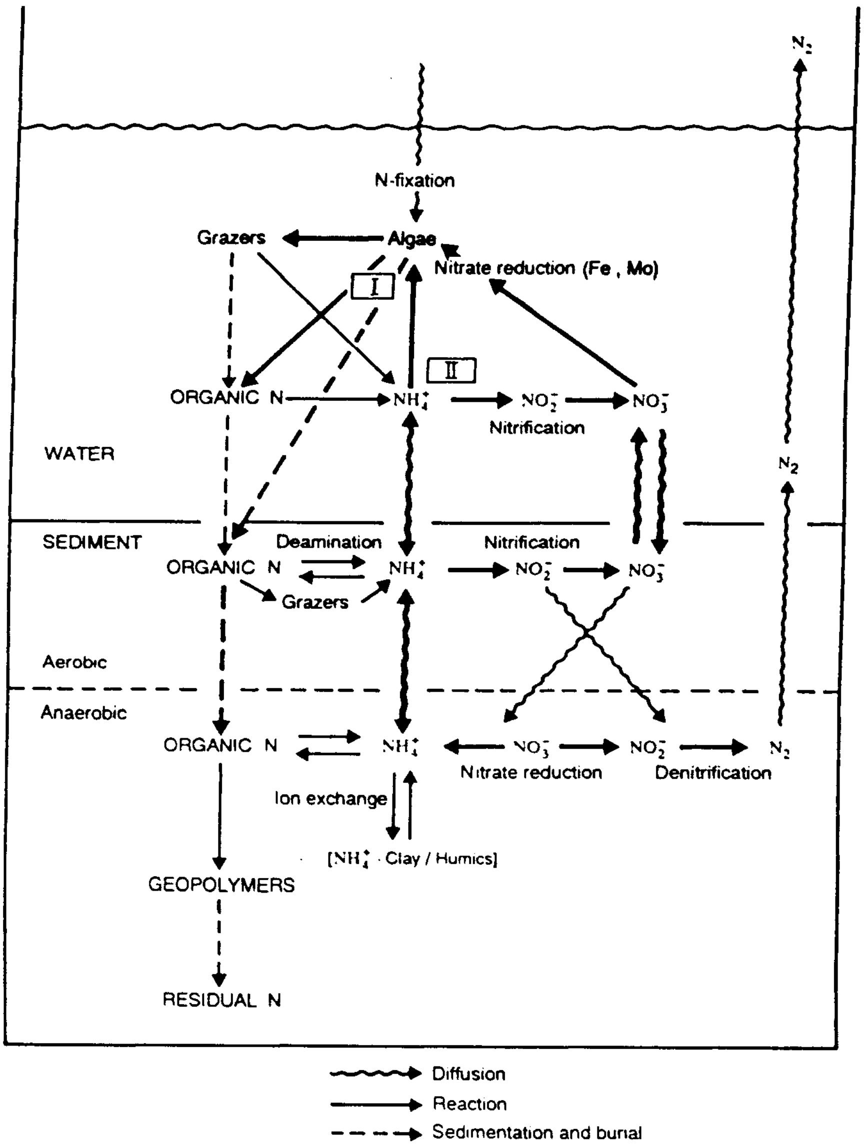

Fig. 6. The nitrogen pathways in the marine environment. Major switches are: I. The nitrogen stays in the water layer or is transported towards the sediment. II. Ammonia is used to build cell material, or autotrophs oxydize it to nitrate.