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# Effecten van antropogene activiteiten op de produktiviteit van het ecosysteem in de westelijke Waddenzee

Beleidsgericht  
ecologisch onderzoek  
van de  
Noordzee/Waddenzee

**BEON**

**NIOZ**

# Effecten van antropogene aktiviteiten op de produktiviteit van het ecosysteem in de westelijke Waddenzee

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(Voor de vervaardiging van dit rapport is samengewerkt met:  
IBN-DLO, NIOO-CEMO, RWS-RIKZ)

Juli 1995

BEON rapport nr. 95-9

BEON project NIOZ 93 E 02

ISSN 0924-6576

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## 1. SAMENVATTING

De Waddenzee vormt een belangrijk opgroeigebied voor jonge vis en schaaldieren en als rust- en voedselgebied voor trekvogels. Gedurende de laatste decades is de Waddenzee meer en meer onder invloed gekomen van antropogene activiteiten, zoals eutrofiëring en commerciële visserij op vooral garnalen, kokkels en mosselen. In dit rapport wordt een eerste poging gedaan om de effecten van eutrofiëring en visserij in de Waddenzee op de produktiviteit van het gebied te kwantificeren. Deze studie richt zich op het westelijk deel van de Nederlandse Waddenzee. Het gebied staat onder invloed van zoetwater toevoer vanuit het IJsselmeer en van kustwater door middel van uitwisseling door de zeegaten.

De eerste bijdrage beschrijft de ontwikkeling van de nutriëntbelasting van de Waddenzee vanaf de 60-er jaren tot heden. De jaarvrachten van totaal-N en totaal-P zijn in de Rijn bij de Nederlands-Duitse grens de laatste jaren afgenomen (na een periode van eutrofiëring, die eind 70-er en begin 80-er jaren zijn hoogtepunt bereikte) tot waarden vergelijkbaar met die in de 60-er en 70-er jaren. De afname van de vrachten in de Rijn wordt niet weerspiegeld in de concentraties aan nutriënten in de kustzone van de Noordzee. De vrachten aan totaal-N en totaal-P in de lozingen van zoetwater vanuit het IJsselmeer in de Waddenzee, vertonen eenzelfde beeld als de patronen in de Rijn bij de Nederlands-Duitse grens, met een afname gedurende de laatste jaren tot vrachten die overeenkomen met de periode vòòr de 70-er jaren. De concentraties van totaal-N en totaal-P in de westelijke Waddenzee volgen de toename van de spui in de 70-er jaren. In tegenstelling tot de trend in de vrachten van de spui, laten de concentraties in de westelijke Waddenzee van zowel totaal-N als totaal-P echter al een afname zien voor het begin van de 80-er jaren, om daarna te stabiliseren op waarden die overeenkomen met concentraties in de 60-er en 70-er jaren.

De tweede bijdrage behandelt de veranderingen in pelagische primaire produktie in de westelijke Waddenzee vanaf eind 60-er jaren tot op heden. De jaarlijkse pelagische primaire produktie bedroeg ongeveer 150-200 gC.m<sup>-2</sup> in de 60-er en begin 70-er jaren. Een verdubbeling trad op in het begin van de 80-er jaren, en de produktie is tot op heden op dit hoge niveau gebleven. Hoewel in 1990 een relative lage produktie gemeten werd, zijn de waarden in 1991 en 1992 even hoog als in de 80-er jaren. Een verlaging gedurende de laatste jaren lijkt dus niet te zijn opgetreden. De afname van de concentratie van in het bijzonder totaal-P in de westelijke Waddenzee, heeft de produktiviteit van het gebied dus niet verlaagd, hoewel in de huidige situatie P een beperkende factor geworden lijkt te zijn gedurende een relatief korte periode tijdens de voorjaarsbloei.

De twee andere bijdragen behandelen veranderingen in de secundaire produktiviteit op en in de getijdeplaten. Lange-termijn series van het macrozoobenthos in de bodem in het voorjaar laten een trend in biomassa en produktie zien vanaf de 70-er jaren tot op heden. In het begin van de 70-er jaren werden biomassa's van ongeveer 30 g as-vrij drooggewicht (AVDW) per m<sup>2</sup> aangetroffen. In het begin van de 80-er jaren trad er een toename op tot ongeveer 20-35 g AVDW per m<sup>2</sup>. Tot op heden laten de biomassa en produktiviteit van het macrozoobenthos geen trendmatige achteruitgangen zien. Gedurende de jaren 1974-1993 zijn er waarnemingen verricht aan de vestiging en groei van onvolwassen platvis (schol en bot) en van garnaal op de getijdeplaten. Deze gegevens zijn gerelateerd met de trends in eutrofiëring. Er werd geen relatie gevonden tussen eutrofiëring en de grootte van de vestiging of op de groei van platvis en garnaal. De fluctuaties in aantallen lijken door andere factoren bepaald te worden dan door de voedselomstandigheden op de getijdeplaten. Op dit moment zijn er geen aanwijzingen voor een negatief effect van de afgenomen concentraties aan nutriënten in de westelijke Waddenzee op de biomassa en produktiviteit van het macrozoobenthos en de belangrijkste epibentische predatoren op de getijdeplaten. Commerciële visserij op vooral mosselzaad, de andere antropogene aktiviteit in het gebied, lijkt onder bepaalde omstandigheden wel een negatief effect te kunnen hebben op de vogelstand in de Waddenzee. In 1990 en 1991 waren er extreem geringe hoeveelheden mossels aanwezig in de Waddenzee als gevolg van een laag voortplantingssucces in de drie voorafgaande jaren (1988, 1989, 1990) in combinatie met een intensieve visserij op mosselzaad. In deze drie jaren was er

eveneens een geringe voortplanting van kokkels, een andere belangrijke voedselbron voor vogels, terwijl ook hierop de visserij door bleef gaan. Zowel de eidereend als de scholekster raakten hierdoor in een situatie waarin voedselgebrek voor deze soorten optrad. Een aanzienlijke hoeveelheid eidereenden verliet de Waddenzee of kwam om. Ook de sterfte van scholeksters was verhoogd in de winter 1990/1991.

## 2. CONCLUSIES EN BELEIDSRELEVANTIE

Antropogene activiteiten blijken invloed te kunnen hebben op het functioneren van het ecosysteem van de westelijke Waddenzee. De gevonden effecten zijn grotendeels gebaseerd op de resultaten van lange termijn series.

Monitoring programma's zijn van onschatbaar belang bij onderzoek naar en kwantificering van de effecten van antropogene activiteiten en het verdient aanbeveling op deze programma's ook in de toekomst te blijven voortzetten.

## 3. SUMMARY

The Wadden Sea plays an important role as a nursery area for fish and crustacean species and as a resting and refuelling area for migrant birds. During the last decades the area has become more and more influenced by anthropogenic activities, such as eutrophication and commercial fisheries. In this report a first attempt is made to study the impact of eutrophication and commercial fisheries on the productivity of the western Wadden Sea. The area of study is the western Dutch part of the Wadden Sea, an area under the influence of fresh water run-offs from the mainland and of intense water exchange with the adjacent coastal zone of the North Sea.

In the first contribution, the trends in nutrient loadings of the western Wadden Sea from 1960-1992 are reviewed. Annual nutrient loads of total-P and total-N in the main river Rhine at the Dutch-German border have decreased after a period of increasing eutrophication upto the late 1970s and early 1980s to values comparable to those in the 1960s and early 1970s again. Partly due to inputs in the Dutch part of the drainage basin of the Rhine, total nutrient loads from the river Rhine to the coastal zone of the North Sea decreased substantially less during the last decade. The recent decrease in nutrient loads from the river Rhine, however, is not reflected in the total-N and total-P concentrations in the Dutch coastal waters close to the Wadden Sea. The main source of fresh water input in the area are the discharges of Lake IJssel, which is fed by a branch of the river Rhine. The annual total-N and total-P loads in the discharges into the Wadden Sea follow a similar trend as in river Rhine, with a decrease during recent years to values as low as before the 1970s. The concentrations of total-N and total-P in the western Dutch Wadden Sea followed the steep increase in loads from Lake IJssel in the 1970s, but showed a different trend hereafter. In contrast to the trends in the discharges of Lake IJssel and in the concentrations in the adjacent coastal zone of the North Sea, concentrations of total-N and total-P in the western Wadden Sea dropped since the early 1980-ties and have stabilized at relatively low levels since then. At present concentrations are comparable to those in the 1960s and 1970s.

In a subsequent contribution the long-term trend in pelagic primary production near the Marsdiep inlet in the western part of the Wadden Sea is discussed and related to the observed trends in nutrient concentrations in the area. Annual primary production amounted to about 150-200 gC.m<sup>-2</sup> in the 1960-ties and early 1970-ties. A doubling took place in the early 1980-ties and values have remained high since. Primary production in 1990 was relatively low, but the values for 1991 and 1992 were as high as those in the mid-1980s. A recent lowering is absent. The decline in especially total-P did not yet reduce the productivity in the area, although in the present situation P might have become a limiting factor for primary production during a short period of the phytoplankton spring bloom.

The two other contributions deal with the secondary production of the intertidal flats. Long-term observations of the macrozoobenthic biomass and productivity show biomass values of about 20 g ash-free dry weight (AFDW) per m<sup>2</sup> in the beginning of the 1970s, with an increase in the beginning of the 1980s to values of about 30-35 g AFDW per m<sup>2</sup>. No consistent decline was observed in recent years. Time-series over the period 1974-1993 on settlement and growth of juvenile flatfish (plaice and flounder) and shrimps showed no effect of eutrophication. Year-class strength of both groups appeared to be determined by other factors than the food conditions in the area. At present, there is no indication of a negative impact of decreasing nutrient concentrations in the area on biomass or productivity of the macrozoobenthos and the major juvenile epibenthic predators at the tidal flats. The other anthropogenic activity in the area, commercial fishing activities on the tidal flats for cockles and seed mussels, did have an impact on migrant birds. In the course of 1990 stocks of mussels declined to unprecedentedly low levels in the Dutch Wadden Sea. Hardly a wild mussel bed was left on the tidal flats as a consequence of three years (1988, 1989, 1990) with failing recruitment in combination with intensive fishing for seed mussels. During these three years recruitment of cockles also failed, whereas fishing was continued. Birds taking these bivalves as staple food, the oystercatcher and the eider, experienced food shortage. Significant numbers of eiders left the Dutch Wadden Sea area or died, whereas oystercatchers remained abundant throughout the winter in most of the Dutch Wadden Sea, but suffered from abnormally high mortality.



# EUTROPHICATION OF THE WESTERN DUTCH WADDEN SEA, A SHORT REVIEW

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## ABSTRACT

A short review is given on existing literature and data on the eutrophication of the western Dutch Wadden Sea. An extension is made of the previously published trends to the early nineties. Eutrophication is defined here as any increase in the rate of supply of nutrients or organic matter to an ecosystem. Effects of increased nutrient loads as *e.g.* increased algal blooms are not included in this review. Annual loads of total P and total N in the river Rhine at Spijk/Lobith have decreased since 1982-1987 to values comparable to those in the sixties and early seventies. Due to inputs in the Dutch part of the drainage basin of the Rhine, total nutrient loads from the Rhine to the North Sea have decreased substantially less during the last decade. The recent decrease in the nutrient loads from the Rhine is not reflected in the N and P concentrations in Dutch coastal waters close to the Wadden Sea. The total P and total N concentrations in the northern part of Lake IJssel as well as the discharges from the lake into the Wadden Sea follow a similar decrease as the loads of the Rhine since the mid-eighties, however with a time lag of a few years. At present, discharges into the Wadden Sea are as low as before the seventies. Concentrations of total P and total N in the western Wadden Sea followed the steep increase in the loads from Lake IJssel in the early seventies, but showed different trends hereafter. In contrast to Lake IJssel and the adjacent North Sea both N and P dropped since 1978-1983, *i.e.* some years before the onset of the decrease in the main nutrient sources, and stabilized at relatively low levels since then. This suggests a major role of internal processes in controlling nutrient levels in the Wadden Sea. At present the concentrations are comparable to those in the sixties and early seventies.

## 1. INTRODUCTION

Several definitions of eutrophications have been applied in the literature. Here we define eutrophication conforming to POSTMA (1985) as: "*any increase in the rate of supply of nutrients or organic matter to an ecosystem*". Eutrophication is mostly considered as being solely caused by anthropogenic nutrient loading, but it should be stressed that it may also have natural causes. Increased phytoplankton blooms, oxygen depletion and other possible effects of eutrophication are not included in the above definition, but obviously these are most

important for the functioning of the ecosystem and for water quality management. Basically, anthropogenic eutrophication of marine and estuarine waters started at the introduction of agriculture through increased land run-offs (HOWARTH *et al.*, 1993). During the last decades, nutrient inputs to Dutch coastal waters sharply increased (*e.g.* POSTMA 1985) due to loads of domestic and industrial origin and due to intensivated cattle-farming in the drainage basins of the main rivers.

Eutrophication of the Dutch Wadden Sea has received considerable attention in the scientific literature during last years. A recent review is

presented by DE JONGE & VAN RAAPHORST (1994). The earliest reliable data sets on phosphorus and nitrogen compounds in the two most westerly basins (Marsdiep en Vlie) are those of POSTMA (1954) and DUURSMA (1961) for 1949-1951 and 1956-1957, respectively. A more complete data set on nitrogen compounds was presented by POSTMA (1966) for the years 1962-1963. Regularly measurements on nutrient concentrations started in the early seventies, first by DE JONGE & POSTMA (1974) and HELDER (1974), and later by the monitoring programme of the Rijkswaterstaat. Based on these data and comparable data on the main nutrient sources, VAN DER VEER *et al.* (1989) made a reconstruction of the history of the external N and P loading to the western Dutch Wadden Sea and the development of the change in nutrient concentrations in this area for the period 1950-1985.

In this paper we will give a short review on the eutrophication of the western Dutch Wadden Sea since the early fifties. Long term data sets published so far in the literature will be updated until the early nineties (based on data of the Rijkswaterstaat). Effects of eutrophication as increased algal blooms, oxygen depletions and increased biomasses of benthic fauna are not discussed here. For this we refer to *e.g.* DE JONGE (1990), BEUKEMA (1992), RIEGMAN *et al.* (1992), CADÉE & HEGEMAN (1993) and the review of DE JONGE & VAN RAAPHORST (1994). A review on the eutrophication of the North Sea adjacent to the Wadden Sea has been given by KLEIN & VAN BUUREN (1992).

## 2. AREA DESCRIPTION

The western Dutch Wadden Sea is divided into two tidal basins: the Marsdiep basin and the Vlie basin. These basins have mean tidal depths of 3.9 and 2.6 m, respectively. Total surface areas are  $743 \times 10^6$  m<sup>2</sup> for the Marsdiep basin and  $672 \times 10^6$  m<sup>2</sup> for the Vlie basin, of which respectively 15% and 40% is covered by intertidal flats. The freshwater input to the area is dominated by the discharge from the adjacent Lake IJssel, which in turn is fed by the river IJssel, a branch of the river Rhine. Flushing time of the freshwater is approximately 10-12 days (RIDDERINKHOF *et al.*, 1990). The

freshwater discharges together with the North Sea provide the most important nutrient sources to the basins (POSTMA 1954; VAN RAAPHORST & VAN DER VEER, 1990). Local inputs from *e.g.* villages and canals are of minor importance in the overall nutrient budgets of the area (VAN MEERENDONK *et al.*, 1988; VAN RAAPHORST & VAN DER VEER, 1990).

## 3. EUTROPHICATION OF THE WESTERN WADDEN SEA

### 3.1. RHINE AND COASTAL NORTH SEA

Since both main nutrient sources of the area (coastal North Sea, Lake IJssel) are strongly influenced by the river Rhine, it is worthwhile to first consider the nutrient loads of this river. Total P (tP) loads at the German border (Spijk/Lobith) increased steadily from the early fifties until the seventies and early eighties (Fig. 1). After 1982 the loads of tP decreased to values in 1990 close to those in the early sixties. A similar pattern is observed for dissolved inorganic P (DIP). The loads of the nitrogen compounds, however, developed differently (Fig. 2). The largest increase in the total N (tN) loads occurred before 1965, the maximum loads were reached in 1987 and the values in 1990 are comparable to those in the period 1965-1975. Nitrate forms the largest pool of nitrogen compounds in the river Rhine at the German border after 1965-1970. The concentrations and loads at the German border are not fully representative for the inputs into the coastal North Sea or into Lake IJssel. According to KLEIN & VAN BUUREN (1992) the load of DIP at the German Border fell about 75% over the period 1980-1990, whereas the load fell only 45% at the entrance of the North Sea near Maassluis. Similarly, the tP load at Maassluis dropped only 16% in the period 1985-1989 when compared to the period 1980-1984. Since the tN load remained unchanged during this 10 year period, the atomic N:P ratio in the loads increased from approximately 25:1 in 1981 to 31:1 in 1989 (KLEIN & VAN BUUREN, 1992).

The development of the nutrient concentrations in the coastal North Sea are less well described. For the Wadden Sea,

concentrations near the tidal inlets are most important. Based on the reconstruction of VAN DER VEER *et al.* (1989) it seems that both tN and tP at a station 2-4 km off the coast at Callantsoog continuously increased between 1950 and 1980 and subsequently stabilized. Winter concentrations of tN and tP are similar or only slightly lower in the Dutch coastal zone in 1989-1991 compared to 1976-1980 (KLEIN & VAN BUUREN, 1992). Apparently, the changes in the inputs from the river Rhine were not reflected in the tP and tN concentrations in the coastal North Sea. Only the winter concentrations of DIP seem to have decreased substantially from their maximum in the early eighties until 1990-1991 (KLEIN & VAN BUUREN, 1992).

#### LAKE IJssel

The long term trend of the mean annual nutrient concentrations in Lake IJssel differs from that of the Rhine, particularly in the northern part near the Afsluitdijk bordering the lake from the Wadden Sea. VAN DER VEER *et al.* (1989) conclude that the river IJssel, feeding Lake IJssel, showed a similar increase in nutrient loads as the Rhine before 1980. In the northern part of the lake this increase was observed only after the early seventies. The development of increased levels of nutrients in Lake IJssel is well documented by DE WIT (1980). He clearly showed that it took from 1973 until 1978/1979 before the 'front' of increased concentrations of DIP moved from the mouth of the river IJssel in the south to the Afsluitdijk in the north. Apparently Lake IJssel acted as a trap for the increased nutrient loadings from the river IJssel in the seventies. The decrease in tP and tN concentrations in the northern IJsselmeer started also a little later, *i.e.* after 1985, than the comparable decrease in the rivers Rhine and IJssel (DE JONGE & VAN RAAPHORST, 1994). Although some possible explanations for the time lags in the development of the nutrient concentrations in Lake IJssel were given by DE WIT (1980), particularly for the seventies, the true mechanisms remain unsolved at present. Further research seems necessary to fully understand the nutrient buffering and retention capacity of Lake IJssel as an intermediate

between the river Rhine and the Wadden Sea. Because tP has decreased more than tN, atomic N:P ratios in Lake IJssel increased from about 34:1 in 1981 to 50:1 in 1989 (KLEIN & VAN BUUREN, 1992).

#### WESTERN WADDEN SEA, INPUTS AND CONCENTRATIONS

Inputs of organic matter and nutrients to the western Wadden Sea occur through discharges from Lake IJssel at the two sluices in the Afsluitdijk (Den Oever and Kornwerderzand), by the tidal exchange with the adjacent North Sea and through atmospheric deposition (VAN MEERENDONK *et al.*, 1988; VAN RAAPHORST & VAN DER VEER, 1990; DE JONGE & VAN RAAPHORST, 1994). The atmospheric loadings are not well quantified, but the available data suggest that it is of minor importance in the overall N and P budgets of the Wadden Sea (VAN MEERENDONK *et al.*, 1988). Particularly the exchange with the North Sea is not easily quantified and has been the subject of some debate in the past literature (POSTMA, 1954; DE JONGE & POSTMA, 1974; CADÉE, 1980; VAN DER VEER *et al.*, 1989; VAN RAAPHORST & VAN DER VEER, 1990). Although in reality the exchange processes at the tidal inlets are far more complicated (RIDDERINKHOF & ZIMMERMAN, 1992), they may be simplified into 3 terms: dispersive exchanges driven by tidal mixing and the concentration gradients in the tidal inlets, advective transport due to the residual current in the basins, and the 'pseudo' advective or residual transport of particulate matter into the basins which is driven by the fact that in the inlets the flood transport of suspended matter is larger than the corresponding ebb transport (POSTMA, 1954; GROEN, 1967). Based on this division VAN RAAPHORST & VAN DER VEER (1990) analysed the phosphorus budget of the Marsdiep basin in the period 1950-1985. It was concluded that almost 50% of the tP input to the Marsdiep basin originates from the adjacent Vlie basin, which in turn is fed by the North Sea and Lake IJssel. Before 1970 exchange with the North Sea seemed to dominate the P budget of the area, mainly through the imports of particulate P compounds at the tidal inlet. From approximately 1975 to 1979 the 'pseudo'

advective input of particulate P sharply increased, but the net transport through the inlet turned into an export to the North Sea. Since the mid eighties, the dispersive export of particulate P seems to compensate for the 'pseudo' advective import of particulate P. In all years there has been a net export of DIP at the tidal inlets to balance inputs of particulate P from the North Sea and the inputs from Lake IJssel. Although a comparable budget analysis is not available for nitrogen, we may expect similar patterns for the transports of the N compounds.

Trends in the nutrient loadings from Lake IJssel are presented in Fig. 3 and 4 which are extensions of the reconstruction made by VAN DER VEER *et al.* (1989). Although total water discharges vary from year to year, the observed pattern of the nutrient loads is basically similar to that of the concentrations in the northern Lake IJssel. At present, discharges of tN and tP into the Wadden Sea are as low as in the sixties.

Long-term trends of nutrients in the western Wadden Sea can be found in Figs. 5 to 12 for the first and third quarter of the year, respectively. Data are included from 2 stations in the Marsdiep basin and 2 stations in the Vlie basin. Apparently, spatial variations are minor when compared to the long-term variations of the entire area. In the first quarter of the year, all nutrient concentrations sharply increased in the early seventies as a response on the increased loadings from Lake IJssel (VAN DER VEER *et al.*, 1989; VAN RAAPHORST & VAN DER VEER, 1990). Winter concentrations of tN reach their maximum in 1975 and subsequently decreased to values slightly above those before 1970. This decrease is not visible in the trend of nitrate or ammonium (DE JONGE & VAN RAAPHORST, 1994), but seems mainly caused by lower values of organic N compounds since the second half of the seventies. The phosphorus compounds tP and DIP reached their maxima during the first 3 months of the year in 1979-1980, and as tN steadily decreased since. The trends of the concentrations in the third quarter of the year differ somewhat from those in January-March. Maxima of tP and DIP were reached some years later in 1983, then sharply decreased to

stabilize at values comparable to the early seventies. Nitrate reached exceptionally high levels in the third quarter of 1977, probably caused by a slightly later onset of N limitation of the phytoplankton during that year. After 1986, nitrate concentrations in the Wadden Sea were close to zero during summer. The most striking trend seemed to have appeared in tN, which showed relatively large station to station variations before 1975, but only very minor spatial differences since. After the deep minimum in 1971, tN in the third quarter of the year increased to the highest values measured in 1977 and then decreased in 1978 to concentrations as low as those in the sixties. As in winter, this decrease is caused by the lowering of the measured amount of organic N compounds in the Wadden Sea at the end of the seventies.

Nutrient concentrations in the Wadden Sea are controlled by external inputs, export to the North Sea and by internal processes. Apparently, nutrient levels responded to the increased discharges from Lake IJssel in the early seventies. The trend since the early seventies seems, however, not only determined by the corresponding trends in the main external nutrient sources. Only the observed general decrease in annual tN and tP loadings from Lake IJssel after the mid eighties were reflected in decreasing nutrient concentrations in the western Wadden Sea. The decrease in the Wadden Sea started, however, well before the maximum inputs from Lake IJssel occurred. Sediment-water exchanges may counter-balance or reinforce changed nutrient concentrations in the overlying water through adsorption processes, denitrification and burial (VAN RAAPHORST *et al.*, 1988, 1992; KIESKAMP *et al.*, 1991; VAN RAAPHORST & KLOOSTERHUIS, 1994). DE JONGE & VAN RAAPHORST (1994) present winter (December to February) and summer (May to July) averaged concentrations of N and P compounds in the western Wadden Sea as a function of salinity for the early fifties, early sixties, early seventies and mid eighties. They show that nitrate behaved conservatively during winter in all years, but was consumed in the interior of the basin in the summer of 1986 but not in the summer of the other years. In the summer of 1986 a net production of both

ammonium and DIP occurred. In 1972, a net consumption of ammonium was observed during summer, while in the early fifties an uptake of DIP occurred in the Wadden Sea basins. Thus, DE JONGE & VAN RAAPHORST (1994) conclude that in the low salinity regions of the Wadden Sea limitation of the summer production may have changed over past decades from DIP in 1950 and probably also in 1961 to ammonium in the early seventies. In 1986 consumption of nitrate seems most important. These shifts in limitations and transformations from *e.g.* ammonium to nitrate are not fully determined by the external nutrient inputs, but apparently are controlled by internal processes. This is consistent with the present tN:tP ratios in the area. In winter, the atomic tN:tP ratio is close to 30:1 which is lower than in Lake IJssel but well comparable to the coastal North Sea. In the third quarter of the year this ratio is lowered to 10 à 15:1, pointing at preferential removal of nitrogen in the basins. Denitrification could be the responsible removal mechanism, but apparently is not very high in summer (KIESKAMP *et al.*, 1991). The available data on denitrification may be underestimated severely, however, particularly in summer due to shortcomings in the measurement techniques (LOHSE *et al.*, in prep.). Another mechanism could be a different transport and deposition of particulate organic N and P compounds in the Wadden Sea. POSTMA (1954) already demonstrated that deposition of organic matter originating from the North Sea and the subsequent mineralization in the sediments of the Wadden Sea are most important in controlling nutrient availability to the Wadden Sea ecosystem. We may extend this to particulate organic matter imported from Lake IJssel (CADÉE, 1980) and to locally produced organic materials, both in the water column and in the sediment. VAN RAAPHORST & VAN DER VEER (1990) concluded from their budget analysis that the 'pseudo' advective import of particulate P through the Marsdiep tidal inlet is linearly related to the concentration of particulate P in the inlet, which in turn is determined by the North Sea and by internal processes in the Wadden Sea. Annual wind conditions and current patterns in the coastal North Sea are important factors for the

transport of particulate nutrients and organic matter towards the Wadden Sea and likely fluctuate from year to year. Similarly, we expect the retention capacity of the Wadden Sea for these particulate matters to show annual variability. We conclude that internal processes rather than decreasing anthropogenic nutrient inputs have stimulated the onset of de-eutrophication of the Wadden Sea. Thus, in addition to changes in the external nutrient inputs from *e.g.* Lake IJssel, non-anthropogenic mechanisms seem to have played a substantial role in the nutrient budgets and concentrations of the Wadden Sea during past decades.

Acknowledgements.—We are indebted to the Dutch Rijkswaterstaat for supplying their monitoring data (through Dr. V.N. de Jonge, RIKZ, Haren).

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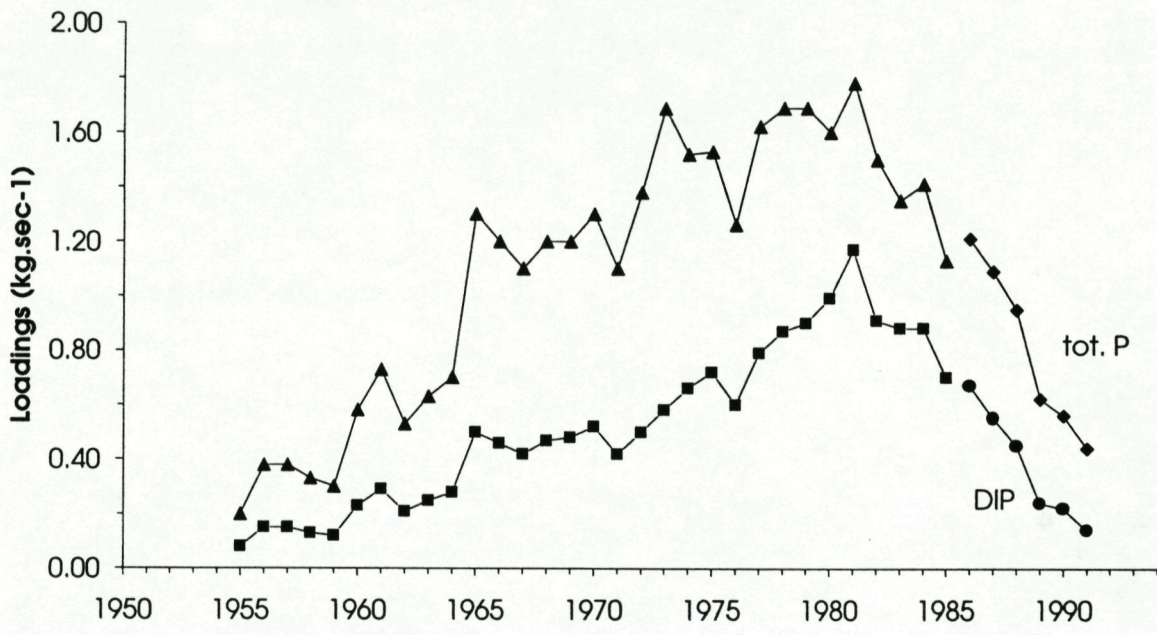


Fig.1. Annual Rhine discharge since 1955, upper curve total P (tP), lower curve dissolved inorganic P (DIP) The figure is an extension of the reconstruction presented by VAN DER VEER *et al.* (1989) with data obtained from the Rijkswaterstaat (period after 1985). For details of the trends before 1985 see the original publication by VAN DER VEER *et al.*

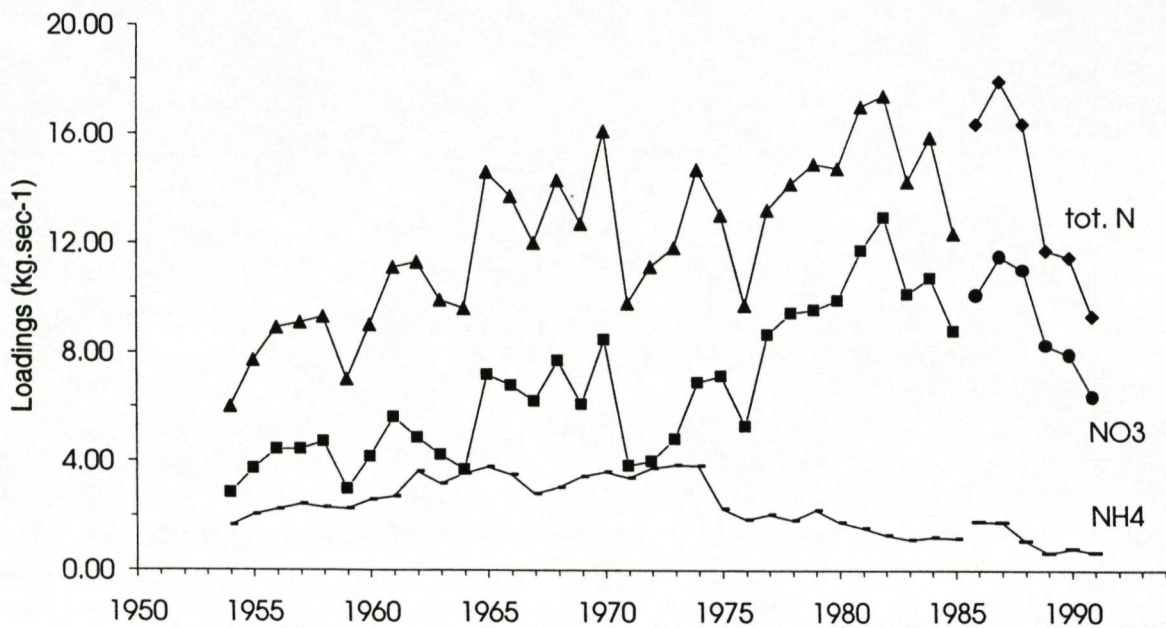


Fig. 2. As Fig. 1, but for total N (tN) in the upper, nitrate in the middle and ammonium in the lower curve.

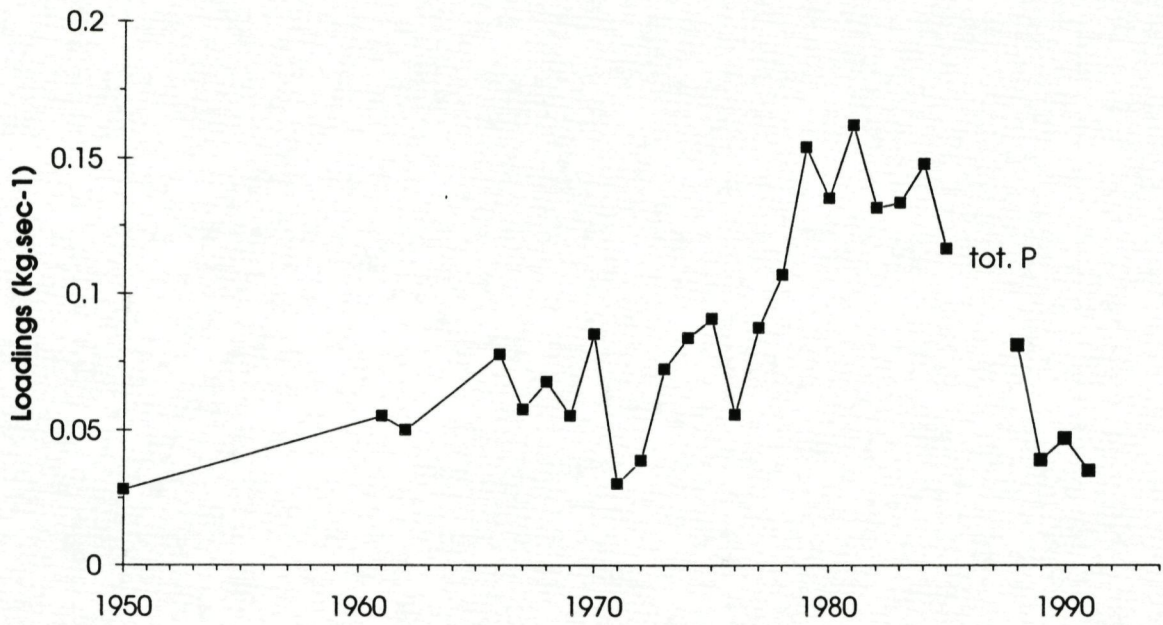


Fig. 3. As Fig. 1, but for the discharge of total P (tP) from Lake IJssel into the Wadden Sea.

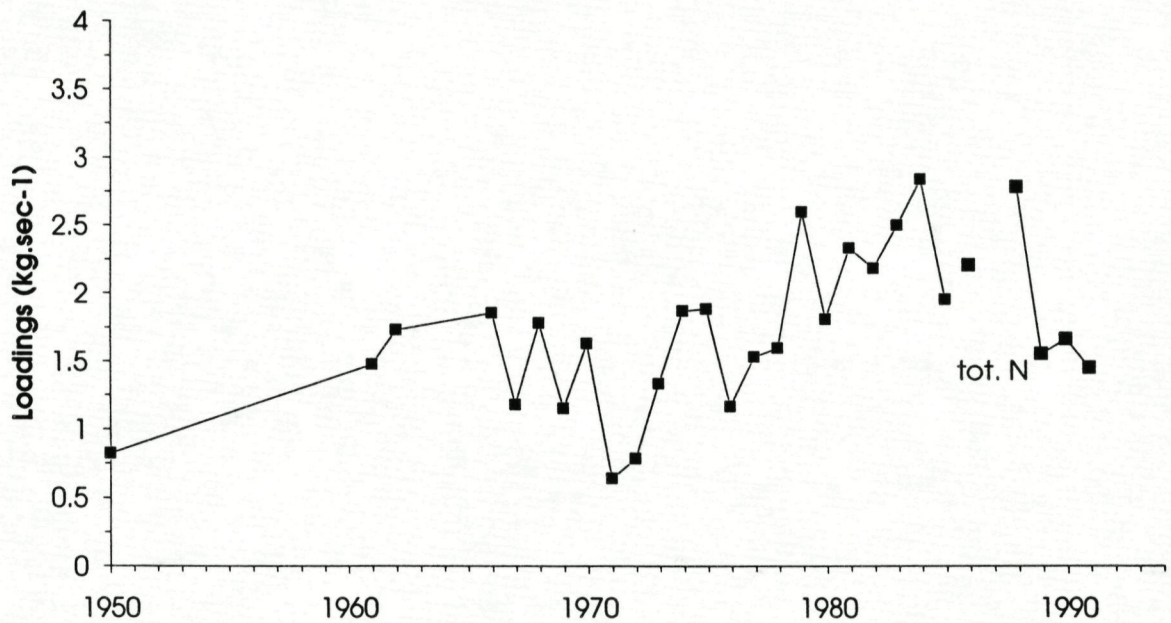


Fig. 4. As Fig. 3, but for the discharge of total N (tN) from Lake IJssel into the Wadden Sea.

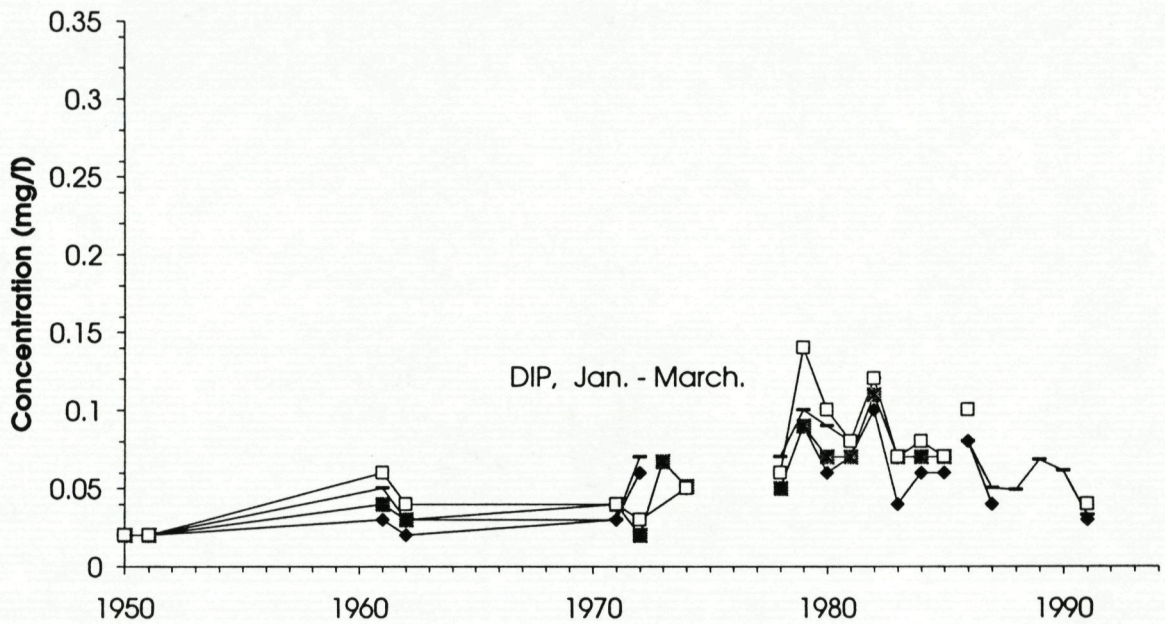


Fig. 5. As Fig. 1, but for the concentration of dissolved inorganic P (DIP) at 4 stations in the western Dutch Wadden Sea. Concentrations are averaged over the first quarter of the year. Stations are Vlie tidal inlet, Blauwe Slenk, Marsdiep tidal inlet and Doove Balg.

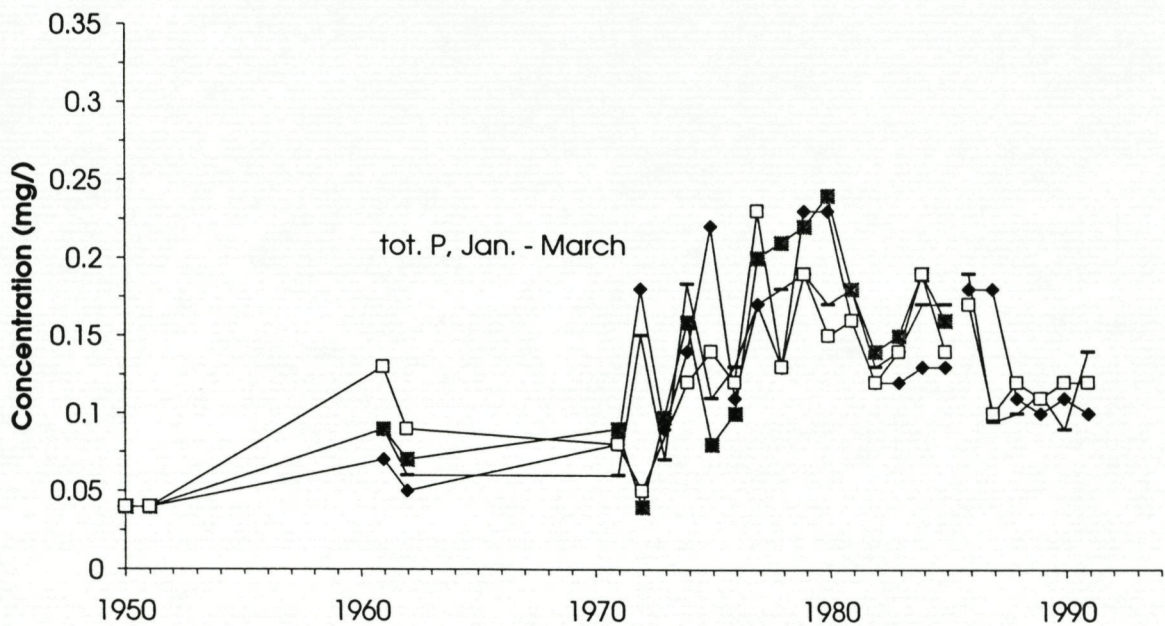


Fig. 6. As Fig. 5, but for total P (tP).

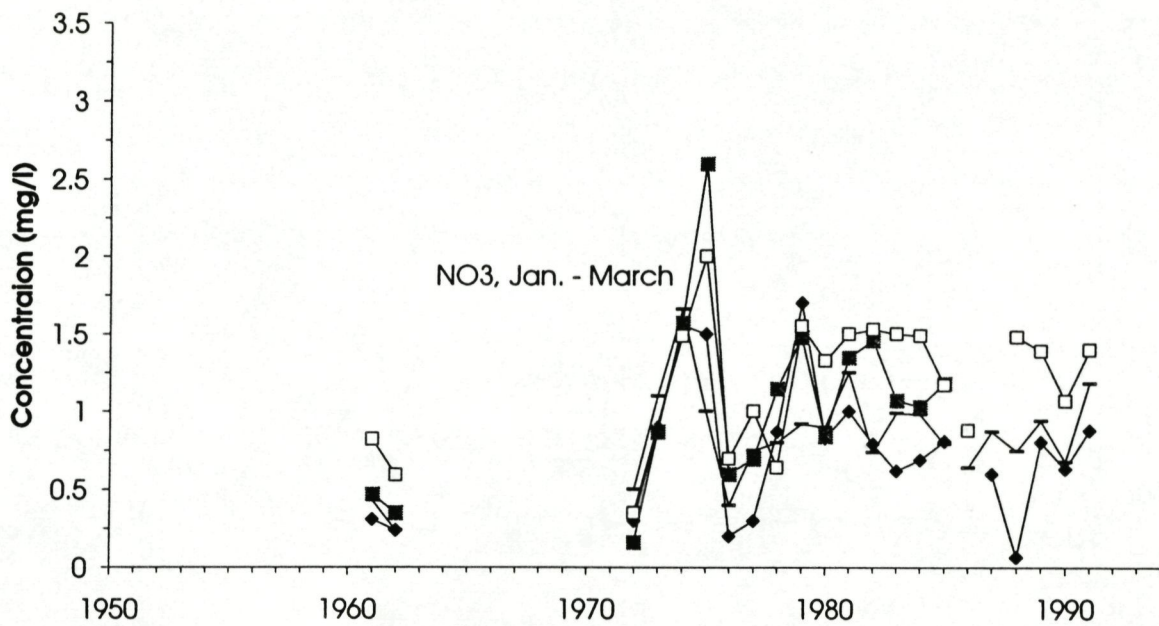


Fig. 7. As Fig. 5, but for nitrate.

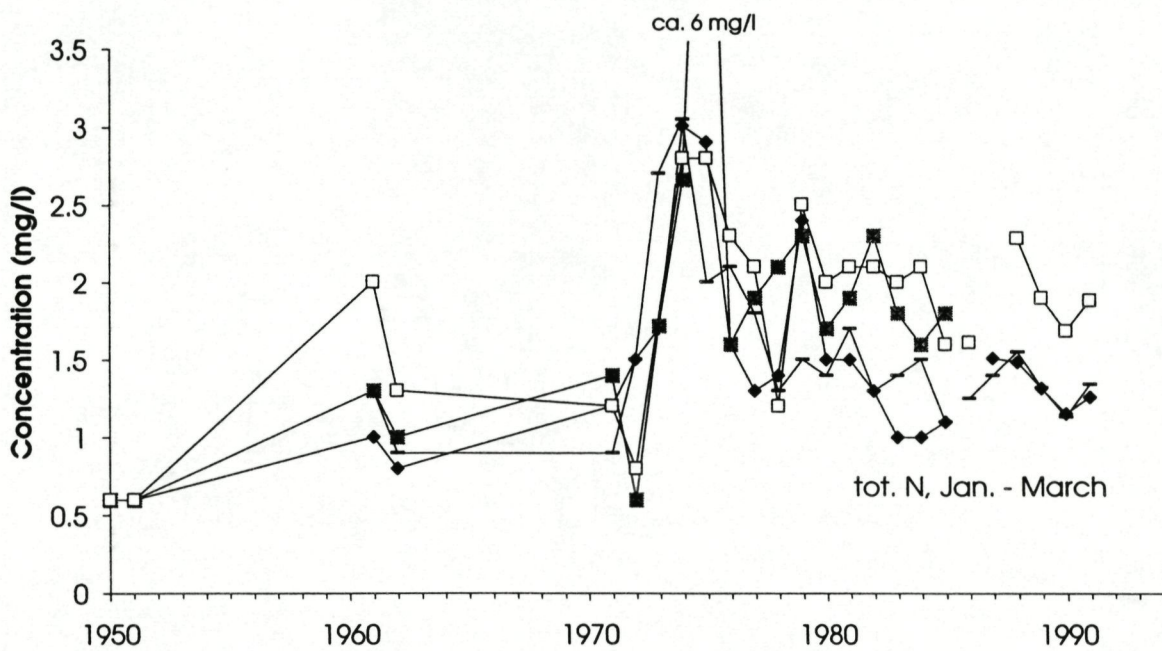


Fig. 8. As Fig. 5, but for total N (tN).

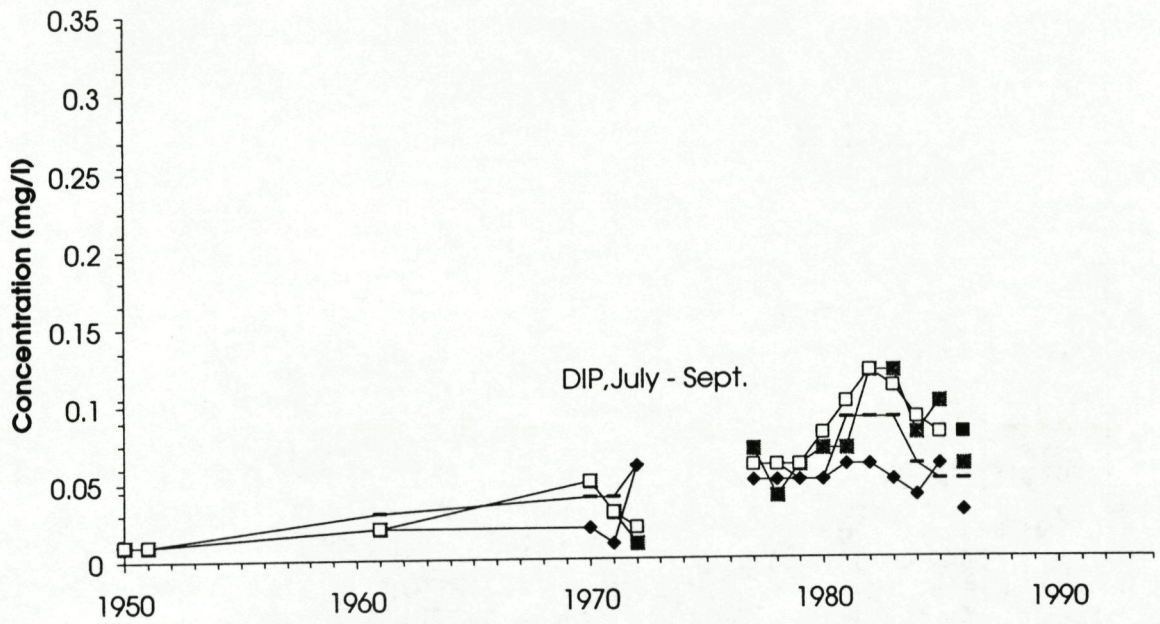


Fig. 9. As Fig. 5, but for the third quarter of the year

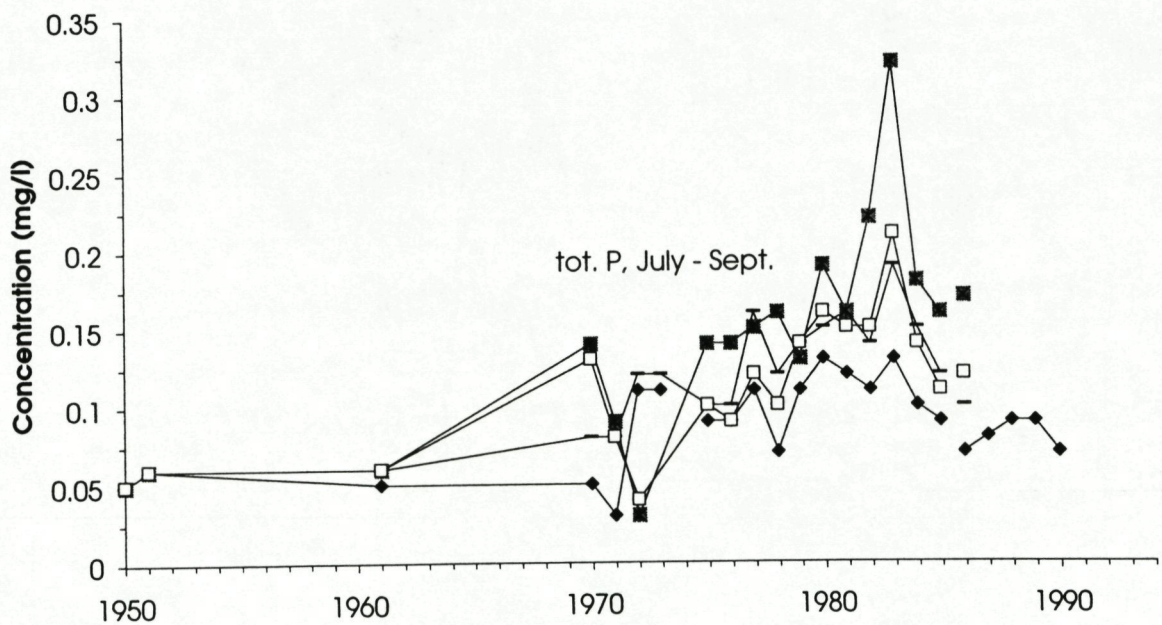


Fig. 10. As Fig. 9, but for total P (tP).

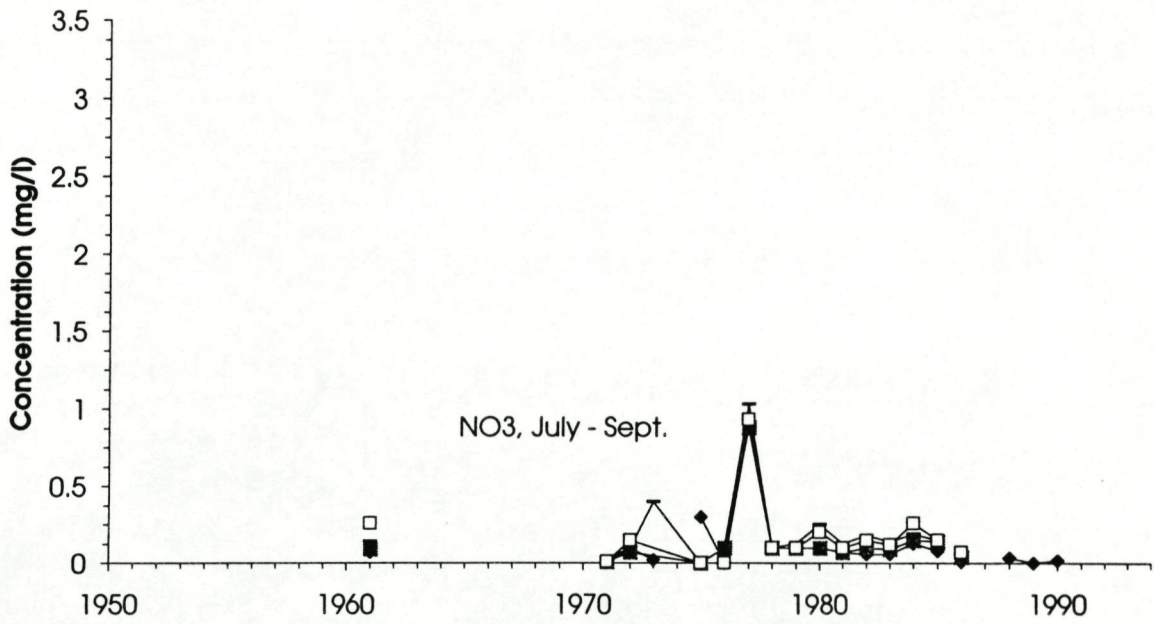


Fig. 11. As Fig. 9, but for nitrate.

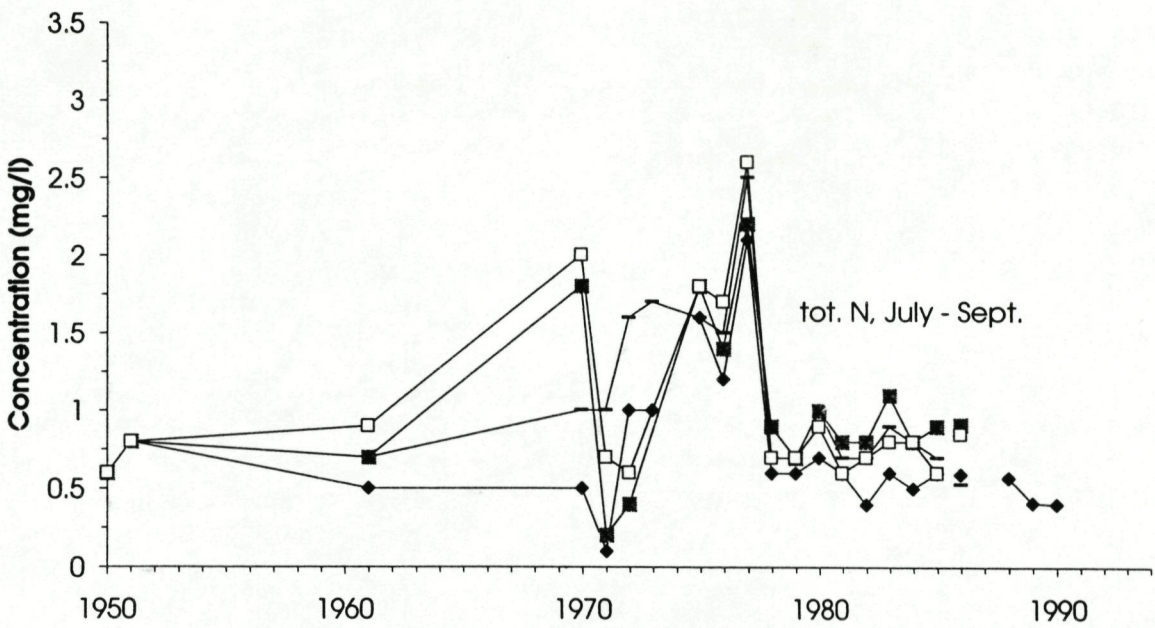


Fig. 12. As Fig 9, but for total N (tN).

# HIGH LEVELS OF PRIMARY PRODUCTION AT DECLINING PHOSPHATE CONCENTRATIONS IN THE DUTCH COASTAL AREA (MARSDIEP)

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## ABSTRACT

Phytoplankton primary production in the Marsdiep estimated regularly in 1991 and 1992 showed values as high as measured during the peak years in the mid-1980s. Lowering of P-inputs from the Rhine since 1981 caused an almost simultaneous but less marked decrease in phosphate concentrations in the Marsdiep, resulting in winter concentrations during 1991 and 1992 that were ca 40% lower than those during the peak in the early 1980s. Apparently, the P-concentration reaches values limiting primary production only for a short period during the phytoplankton spring bloom. It is concluded that the decline of the P-load of the river Rhine does not yet reduce the productivity in the Marsdiep area. 1.

## INTRODUCTION

In a provocative paper, BODDEKE & HAGEL (1991) called the eutrophication of the North Sea continental zone during the last decades a 'blessing in disguise'. In the Dutch coastal zone, these authors observed recent decreases in stocks of brown shrimp, some bivalves and demersal fish species all living in the coastal zone or using it as a nursery. They related these decreases to a lower input of phosphate to the coastal zone, a consequence of the successful lowering of phosphate load of the Rhine since 1981 (ANONYMOUS, 1991; Fig. 1).

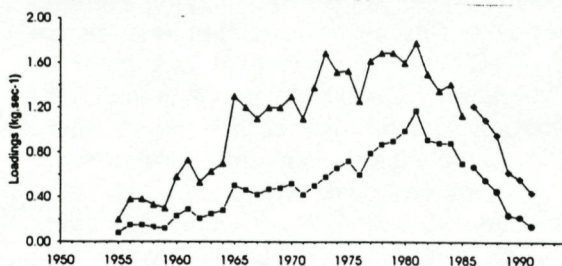


Fig. 1. Rhine discharge since 1955, upper curve total P, lower curve PO<sub>4</sub>-P, based on data by Rijkswaterstaat. Figure prepared by H.W. v.d. Veer (NIOZ) being an extension of fig. 3a in VAN DER VEER *et al.*, 1989.

They point to negative consequences of further cleaning of the Rhine in accord with their claim that eutrophication of the coastal zone enhances productivity of the system and hence fishery yield. The authors assume that the recent lower discharge of phosphate into the coastal zone has already led to lower primary production of phytoplankton and thus to less food for suspension-feeding bivalves and herbivorous copepods. As a consequence less food would be available for the zooplankton-eating brown shrimps and the juveniles of several North Sea demersal fish species (which use the coastal area as a nursery).

Boddeke & Hagel's assumption of a decreased phytoplankton primary production in the coastal zone can be tested by comparison of published earlier primary production values for the Marsdiep, the westernmost inlet of the Wadden Sea (POSTMA & ROMMETS, 1970; CADÉE & HEGEMAN, 1974, 1991a, b; CADÉE 1986, 1992a, b), with recent observations in 1991 and 1992. The Marsdiep is influenced by Rhine discharges along two routes viz. via the coastal North Sea current and via Lake IJssel/Wadden Sea (VAN BENNEKOM *et al.* 1974; DE JONGE, 1990; VAN RAAPHORST & VAN DER VEER, 1990). Our routine sampling at the Netherlands Institute for Sea Research (NIOZ)

Marsdiep pier is thought to be representative of Rhine-influenced Dutch Coastal Zone Water.

## 2. MATERIAL AND METHODS

Sampling of phytoplankton for primary production measurements was done during high water at the NIOZ-pier in the Marsdiep tidal inlet (Fig. 2). Measurements were performed almost every week in spring and summer and less frequently during the rest of the year (see Fig. 3). Methods for measuring primary production were exactly the same as those used before, thus obtaining comparable data. Water samples were incubated with  $^{14}\text{C}$  under constant light in the laboratory at in situ temperatures for 3 hours. Samples were filtered and activity of the filters measured with liquid scintillation; for further details see CADÉE & HEGEMAN (1974) and CADÉE (1986). Temperature, salinity, turbidity, chlorophyll *a*, and phytoplankton cell numbers were measured simultaneously by the same methods as used earlier (see CADÉE & HEGEMAN, 1974; CADÉE, 1986). Nutrients were analysed by the chemical department of NIOZ, using a Traacs-800 autoanalyser.

## 3. RESULTS AND DISCUSSION

In 1991, the seasonal variation in phytoplankton composition was similar to earlier years, showing a marked spring peak of diatoms followed by a peak in *Phaeocystis* with maximum cell numbers of  $150\,000\text{-cm}^{-3}$  (Fig. 3 ab). In 1992 the pattern differed: the diatom spring peak was present but the following *Phaeocystis* peak was less pronounced, cell numbers decreasing after a first peak of only  $33\,000\text{ cells-cm}^{-3}$ . In late April and early May very low numbers were found (in 1991 this was the peak period of *Phaeocystis*). In late May a second peak developed with a maximum of  $70\,000\text{ cells-cm}^{-3}$  (Fig. 3 ef).

Despite these differences in phytoplankton composition, chlorophyll *a* seasonal curves showed less difference between 1991 and 1992. Peak values for both years were around  $40\text{ mg-m}^{-3}$  and coincided with the *Phaeocystis* spring peak in 1991, whereas in 1992 it

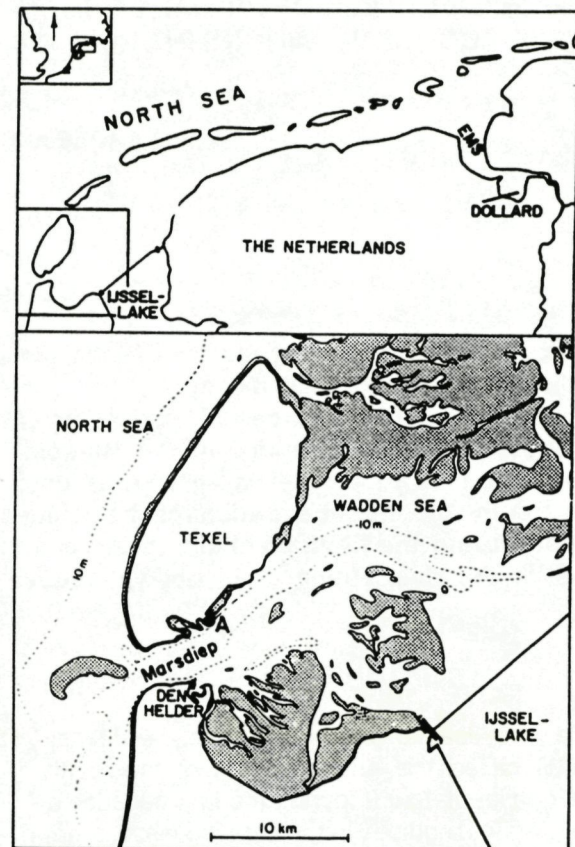


Fig. 2. The Marsdiep area and the NIOZ-pier sampling locality (A).

occurred when diatoms were more important (Fig. 3 cg).

Primary production for 1991 and 1992 showed annual curves (Fig. 3 dh) roughly paralleling the chlorophyll curves. Highest production values ( $5$  to  $6\text{ gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) were obtained during the *Phaeocystis* peaks, a second lower and broader peak of ca  $2\text{ gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  occurred in July/August in both years. As the maximum concentrations of *Phaeocystis* occurred later in 1992, spring and summer primary production peaks merged in 1992 to one broad peak, whereas in 1991 the two primary production peaks were separated by a dip. Annual primary production values derived from these data amounted to  $385\text{ gC}\cdot\text{m}^{-2}$  in 1991 and  $370\text{ gC}\cdot\text{m}^{-2}$  in 1992. The high primary production values were not due to abnormally high solar radiation. This was measured in Den Helder, just south of the Marsdiep, by the Royal Dutch Meteorological

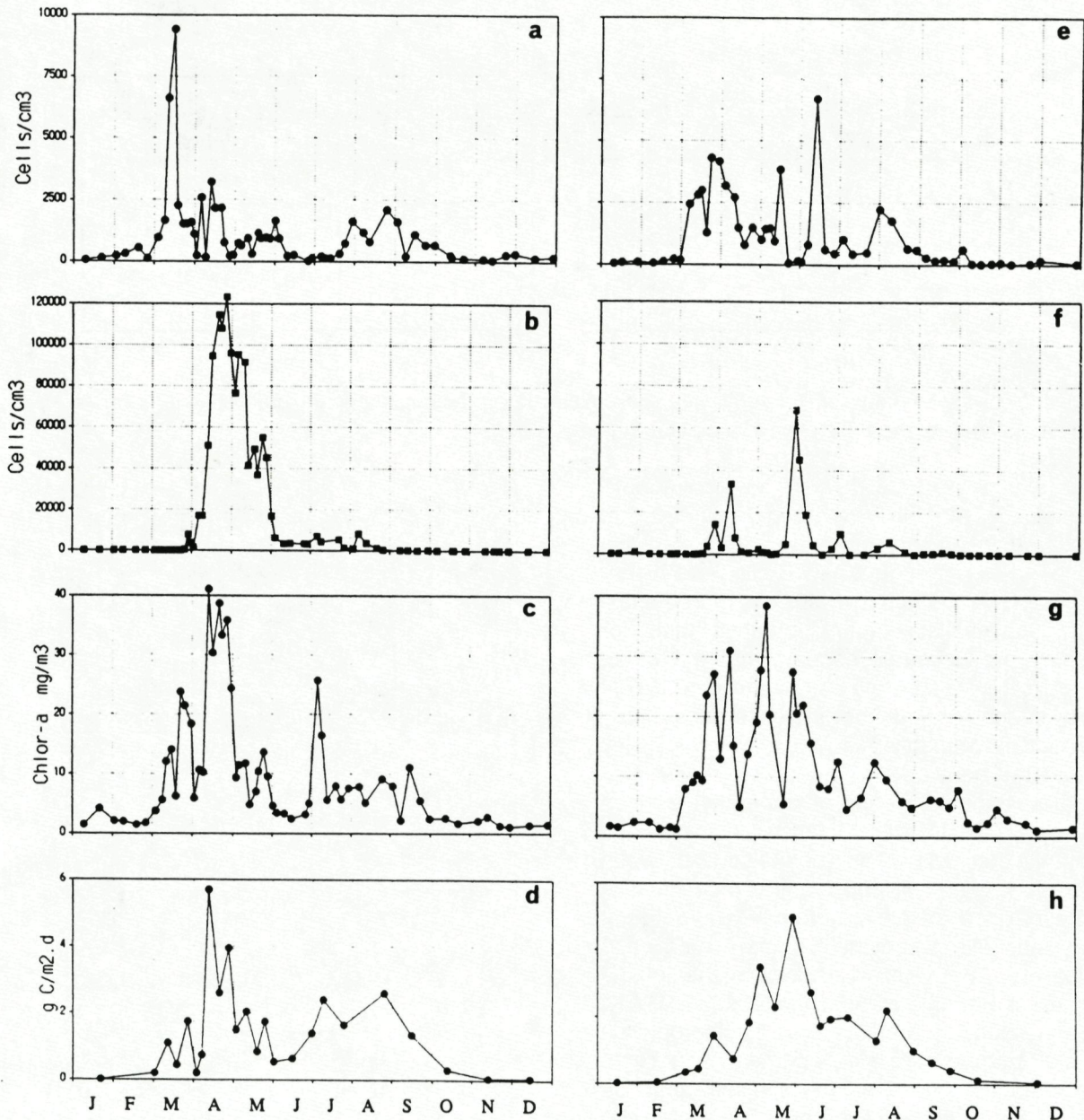


Fig. 3. Seasonal variations in phytoplankton in 1991 (a, b, c, d) and 1992 (e, f, g, h): (a, e) diatom cell numbers in  $\text{cells}\cdot\text{cm}^{-3}$ ; (b, f) *Phaeocystis* cell numbers in  $\text{cells}\cdot\text{cm}^{-3}$ ; (c, g) Chlorophyll a in  $\text{mg}\cdot\text{m}^{-3}$ ; (d, h) Primary production in  $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ .

Institute (KNMI). Annual solar radiation for 1991 was 4% below the long-term average and for 1992 1% above it (KNMI, 1991, 1992).

In Fig. 4a these annual production data are compared with production values for earlier years. Annual values amounted to 150-200  $\text{gC}\cdot\text{m}^{-2}$  in the 1960s, and early 1970s. A doubling took place in the early 1980s, and

values have remained high since. Primary production in 1990 was relatively low (250  $\text{gC}\cdot\text{m}^{-2}$ ) but the values for 1991 and 1992 were as high as those in the mid-1980s. Clearly, a recent lowering, as assumed by BODDEKE & HAGEL (1991), has not taken place.

Annual average chlorophyll data are available for a shorter period (since 1972), but for every

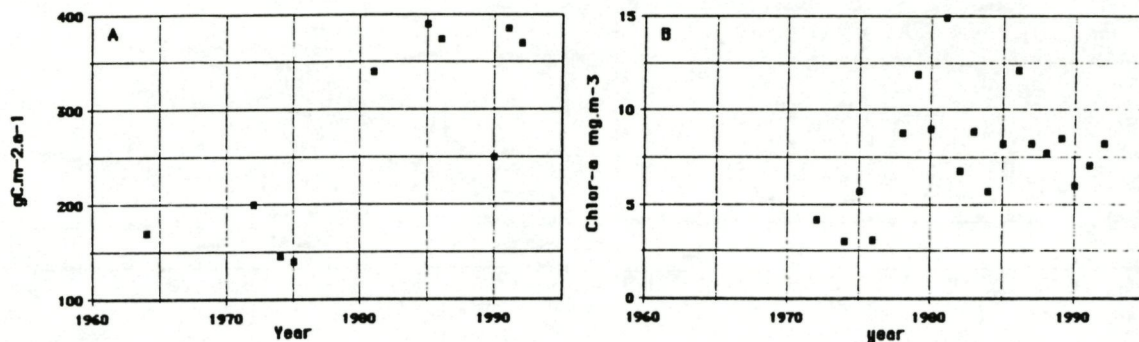


Fig. 4. Year-to-year variation in the Marsdiep phytoplankton (a) for annual primary production in  $\text{gC}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ; (b) for annual average chlorophyll a in  $\text{mg}\cdot\text{m}^{-3}$ .

year (except 1973 and 1977). These chlorophyll a data (Fig. 4b) show a trend similar to that observed in primary production (Fig. 4a): low values in the early and mid-1970s, and higher values in the 1980s and 1990s. As more annual data are available for chlorophyll than for primary production, it appears that the steep increase took place already in the late 1970s. This suggests that the increase in primary production probably also took place already before the early 1980s. The suggestion in Fig. 4b of a gradual lowering of chlorophyll a since the early 1980s is not statistically significant (ANOVA,  $p > 0.1$ ). The correlation between average chlorophyll and primary production is not very good (ANOVA,  $n=9$ ,  $r=+0.67$ ,  $p < 0.05$ ). The year with the highest primary production value (1985) did not coincide with that of the highest mean chlorophyll concentration (1981). This indicates that annual average chlorophyll a is only a crude estimate of primary production. For instance, phytoplankton species composition and available light will influence the production/chlorophyll ratio.

Phosphate data for the Marsdiep based on POSTMA (1954), DE JONGE & POSTMA (1974), CADÉE (1986) and data for 1991 and 1992 (measured by NIOZ chemical department) are summarized in Fig. 5. In the Marsdiep lower P values were observed in 1991 and 1992 than in the early 1980s; the winter values were ca 40% lower (Fig. 5). A trend of lowering P values in the Marsdiep was also reported by VAN RAAPHORST & VAN DER VEER (1990) and was found in a larger part of the Dutch coastal zone by KLEIN & VAN BUUREN (1992) and JANSSEN

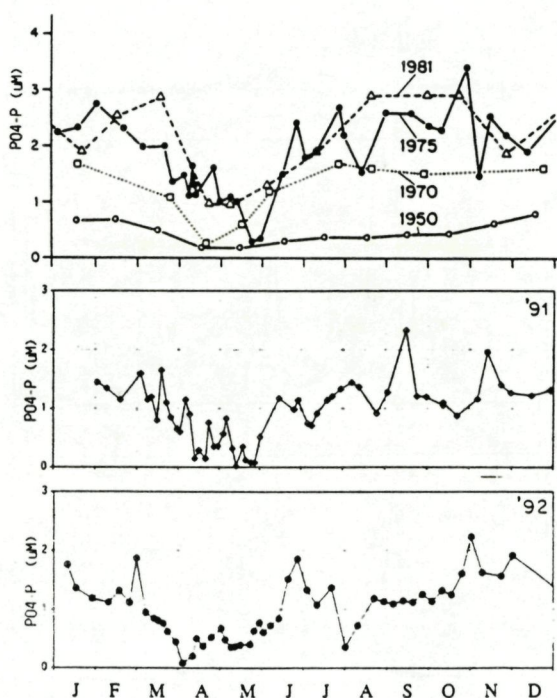


Fig. 5. Phosphate concentration in the Marsdiep for 1991 and 1992 in  $\text{mM}$ , compared with earlier data based on POSTMA (1954), DE JONGE & POSTMA (1974) and CADÉE (1986).

(1993). Phosphate discharges from the Rhine measured by Rijkswaterstaat at the German/Dutch boundary at Lobith decreased significantly during the last decade (ca 80% both as  $\text{PO}_4\text{-P}$  and Total-P, ANONYMOUS, 1991; Fig. 1).

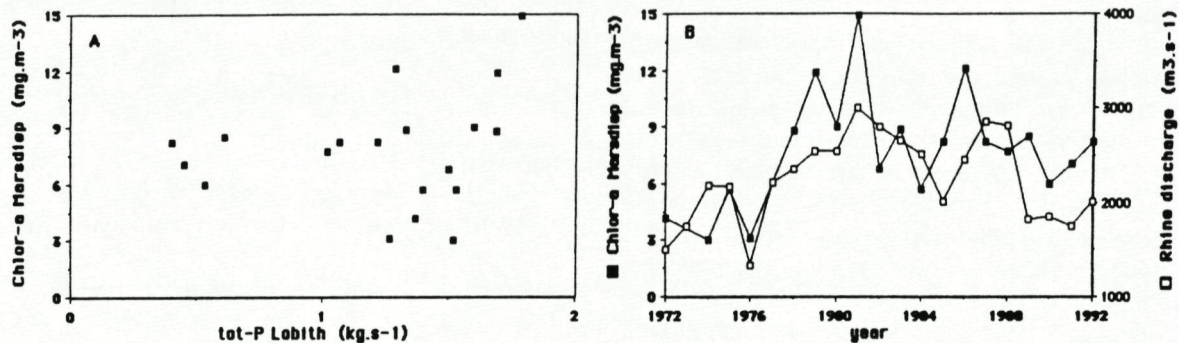


Fig. 6. (a) Relation between annual average chlorophyll *a* (mg·m<sup>-3</sup>) of the Marsdiep and Rhine run-off at Lobith (total P discharge in kg·s<sup>-1</sup>), (b) year-to-year variation in annual chlorophyll *a* Marsdiep (solid points, mg·m<sup>-3</sup>) and annual average Rhine water discharge (open points, in m<sup>3</sup>·s<sup>-1</sup>).

However, the decline in the coastal zone was less than observed in the Rhine at Lobith, partly because of extra inputs from fertilizer plants in the Rotterdam area (KLEIN & VAN BUUREN, 1992; JANSSEN, 1993). The lowering of P has not clearly affected primary production in the Marsdiep area. During most of the year phosphate concentrations still appear to be above limiting values; only during short periods with peak values of phytoplankton concentration, do phosphate concentrations decline to near-0 levels.

Phytoplankton biomass in the Dutch coastal waters is not correlated with P discharge in the Rhine at Lobith (Fig. 6a,  $r=0.2$ ), contrary to the assumption by BODDEKE & HAGEL (1991). It is also highly unlikely that P discharge from the Rhine would be the only factor regulating phytoplankton growth in Dutch coastal waters as implicitly assumed by BODDEKE & HAGEL (1991). Lowering of phosphate in the Marsdiep area was coincident with changes in N/P and NH<sup>4+</sup>/NO<sup>3-</sup> ratios, and a shift from P-limitation before 1977 to N-limitation after 1977 (RIEGMAN *et al.*, 1992). In the relatively turbid Dutch coastal waters, light is a limiting factor for phytoplankton growth during most of the year (CADÉE & HEGEMAN, 1974; PEETERS *et al.*, 1993). In Dutch coastal waters, phytoplankton growth limitation is alternately limited (in space and time) by such factors as light, P, N and Si (RIEGMAN *et al.*, 1990; PEETERS *et al.*, 1993).

Notwithstanding the above, there is a relation between phytoplankton in Dutch coastal water and Rhine discharges. SCHAUB & GIESKES (1991) observed a positive relationship between spring and summer biomass (chlorophyll *a*) in Dutch coastal waters and Rhine water discharge in the same periods. CADÉE (1992a) found a relation between annual Rhine water discharge and annual average chlorophyll *a* for the Marsdiep (ANOVA,  $r=0.61$ ,  $n=15$ ,  $p<0.01$ ). In Fig. 6b the 1991 and 1992 data are added to those published in CADÉE (1992a); they do not change the relation observed earlier. High rainfall apparently increases N leaching from nutrient-saturated agricultural areas (not P): annual total-N discharge was highly correlated with annual water discharge (ANOVA,  $r=0.93$ ,  $n=21$ ,  $p<0.0005$ ), whereas for total P no correlation was found ( $r=0.07$ ) (CADÉE, 1992a: Fig. 5). This high N-input keeps Dutch coastal phytoplankton at high levels despite lowered P discharges. The years 1991 and 1992 were relatively dry, with Rhine discharges lower than normal (1753 and 2012 m<sup>3</sup>·s<sup>-1</sup>, respectively, against 2200 m<sup>3</sup>·s<sup>-1</sup> on average, data Rijkswaterstaat). Wetter years with higher Rhine water discharges might have resulted in even higher primary production in Dutch coastal waters than measured in 1991 and 1992.

Lowering of shrimp and demersal fish landings, and mussel and cockle biomass in the Wadden Sea, therefore, cannot be traced back

directly via primary production and phytoplankton abundance to a lower input of phosphate from the Rhine. The suggested relation, is not a causal one but must be accidental. Other factors must have caused the recent decrease in mussel and cockle biomass in the Wadden Sea. A succession of mild winters caused low recruitment during a series of years (BEUKEMA, 1992). Overfishing diminished the remaining already low stocks dramatically, leading in 1991 to food shortage for some bird species in the Wadden Sea. As a consequence the number of eiders declined by 35% (some 15000 were found dead; VAN DER KUIP, 1991; SWENNEN & DUIVEN, 1992). Overfishing in the 12-miles coastal zone might be responsible for the decrease of shrimp and demersal fish (DEN HEYER, 1992).

Any recommendation to stop further cleaning of the Rhine, in order to enrich the coastal zone again, cannot be justified. In fact this would even be disastrous for Dutch freshwater habitats which for a large part receive Rhine water (BLUMENTHAL *et al.*, 1986) and are still far too eutrophic. Intensive cleaning and biomanipulations are in operation and necessary to make Dutch freshwater habitats less eutrophic (*e.g.* VAN DONK & GULATI, 1989; VAN IERSEL & RIP, 1992).

#### 4. CONCLUSIONS

Primary production data for the Marsdiep do not indicate a lowering in recent years. This undermines the assumption by BODDEKE & HAGEL (1991) that lower discharges of the Rhine are responsible for lowering of stocks of suspension-feeding bivalves, brown shrimps and demersal fish in the coastal zone. So far, there is no reason to stop further reductions of nutrient discharges to the Rhine and obviously such a policy would be harmful to Dutch freshwater habitats.

Acknowledgements.—We are very grateful to K.M.J. Bakker, A. van Koutrik and J.L. van Ooyen (chemical department NIOZ) for analysing nutrient samples, to J.J. Beukema and W.W.C. Gieskes for very useful comments and to R.W.P.M. Laane for providing the latest Rhine-discharge data. The long-

term monitoring data of Dutch coastal waters and Rhine discharges by Rijkswaterstaat have proved indispensable.

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# TRENDS IN SETTLEMENT AND GROWTH OF JUVENILE FLATFISH AND SHRIMPS AT THE TIDAL FLATS IN THE WESTERN DUTCH WADDEN SEA IN RELATION TO ANTHROPOGENIC ACTIVITIES

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## ABSTRACT

Time-series over the period 1974-1993 on settlement and growth of juvenile flatfish (*Pleuronectes platessa* and *Platichthys flesus*) and juvenile brown shrimp (*Crangon crangon*) at the Balgzand, a tidal flat area in the western part of the Dutch Wadden Sea are analysed, with the aim to determine the possible impact of anthropogenic activities on the productivity of juvenile flatfish and shrimp in this area. Two types of anthropogenic activities could be determined: (1) a eutrophication of the area from the 1960-ties onwards with maximum nutrient loadings in the 1980-ties, followed by a de-eutrophication from the mid 1980-ties onwards, and (2) an (variable) fishing activity in the area for bivalves (mussels and cockles). Both anthropogenic activities are acting indirectly (eutrophication) or directly (fishing) on the abundance of the macrozoobenthic, the main food source for both flatfish and shrimps. Despite large year-to-year fluctuations in macrozoobenthic biomass, no effect on settlement and growth of flatfish and shrimps could be detected. Year-class strength of both flatfish and shrimps appeared to be determined by other factors than the carrying capacity of the area where the juveniles grow up. For both groups, growth was only determined by prevailing water temperatures. At present, there is no indication of an impact of eutrophication on biomass or productivity of the major epibenthic predators at the Balgzand intertidal area.

## 1. INTRODUCTION

Tidal flat systems, such as the estuarine Wadden Sea, are important nursery areas for fish species and crustaceans (a.o. ZIJLSTRA, 1972; ZIJLSTRA *et al.*, 1982; KUIPERS & DAPPER, 1981; 1984; VAN DER VEER *et al.*, 1990; 1991; BEUKEMA, 1991; 1992). Each spring, a mass invasion and settlement of juvenile flatfish, gobidae, shrimps and crabs occur, each with its specific timing (KUIPERS & DAPPER, 1984). Due to the favourable food conditions at the tidal flats, high growth rates in all these species are found during the subsequent growing seasons. These tidal-flat populations form an important contribution to the ultimate adult stock in at least a number of these species, such as plaice *Pleuronectes platessa* L. (ZIJLSTRA, 1972; ZIJLSTRA *et al.*, 1982; VAN DER VEER, 1986) and shrimps (BEUKEMA, 1992).

Already for a long time, anthropogenic activities have influenced the coastal zone and the estuarine Wadden Sea (a.o. WOLFF & ZIJLSTRA, 1980). Nutrient loadings into the western Wadden Sea have increased considerably in the 1970-ties and 1980-ties (o.a. VAN DER VEER *et al.*, 1989; VAN RAAPHORST & MOM, 1994). It has been suggested that due to this eutrophication, both primary and secondary production also have increased (BEUKEMA & CADÉE, 1986), whereas the biomass of the benthic fauna doubled and its composition changed (BEUKEMA, 1991b). As a consequence, the carrying capacity of the area might have increased during that period. During this period of eutrophication, food and growth conditions of juvenile flatfish and shrimp appeared to have been optimal and not food limited (ZIJLSTRA *et al.*, 1982; KUIPERS & DAPPER, 1981; VAN DER VEER, 1986).

Recently, the nutrient loadings from the mainland are decreasing (VAN DER VEER *et al.*, 1989; CADÉE, 1993; VAN RAAPHORST & MOM, 1994) and BODDEKE & HAGEL (1991) suggest that this may have negative effects on the production of fish and shellfish in the S-E North Sea. However, in contrast CADÉE & HEGEMAN (1993) found persisting high levels of pelagic primary production in the Wadden Sea even in recent years (1991-1992). In this study, the suggestion of BODDEKE & HAGEL (1991) is investigated as far as the productivity of juvenile flatfish and shrimps at the tidal flats in the Dutch Wadden Sea is concerned. For both species, abundance estimates and growth data are available over a relatively long time period. Sampling of juvenile plaice started by KUIPERS (1977) in 1974 and was continued by ZIJLSTRA *et al.* (1982) and by VAN DER VEER (1986) until 1982. Additional sampling occurred in 1992 and 1993. The population dynamics of juvenile shrimps are being studied from 1983 onwards and data for the period 1983-1990 were published by BEUKEMA (1992).

## 2. MATERIAL AND METHODS

### 2.1. AREA OF STUDY

The Balgzand intertidal area is situated in the westernmost part of the Dutch Wadden Sea. It has an area of about 52 km<sup>2</sup>, and it is surrounded by 5 to 20 m deep tidal channels in the north and east and by dikes to the west and south. At high water the water depth depends on prevailing weather conditions and varies between 0.5 and 1.5 m. The tidal flats are intersected by small gullies through which the water recedes during the later phase of the ebb tide to the tidal channels. Sediment composition of the flats varies from mud and fine sand in the sheltered southern areas to coarse sand in the exposed northern part, with a median grain size of about 150 µm and a mean silt content of about 5% (DAPPER & VAN DER VEER, 1981). Most of the area consists of barren tidal flats, with a variable amount of mussel beds, particularly in the western part.

### 2.2. JUVENILE FLATFISH SAMPLING

High water sampling was carried out at 36 stations spread out regularly over the Balgzand area (Fig. 1). From 1974 to 1982 and in 1993, sampling was done at fixed time intervals (14 d) between February and October. In 1991 sampling was done only twice: at the beginning of the growing season in May and in August. Fishing was done by a 1.9-m beam trawl (mesh size 5 x 5 mm) towed by a rubber dinghy with a 25-hp outboard motor, and a speed of ca. 35 m. min<sup>-1</sup>, according to RILEY & CORLETT (1966). Sampling was restricted to a period of 3 h around high water during daytime, when the distribution of the flatfish appeared to be random (KUIPERS, 1973). The length of the hauls (at least 100 m each) was assessed with a meter wheel fitted to the trawl. All material was preserved either in 4% formalin seawater solution or deep-frozen. Subsequently, it was sorted out in the laboratory within a few days. All individuals were counted and measured to the nearest mm total length. All numbers caught were corrected for net efficiency, using data of KUIPERS (1975) and DAPPER (1978). The corrected numbers were converted into densities per 1000 m<sup>2</sup> and the arithmetic mean was calculated for each survey to be used as an index of abundance. For more details see VAN DER VEER, 1986 and VAN DER VEER *et al.*, 1991.

### 2.3. JUVENILE SHRIMP SAMPLING

Different sampling square plots of 1000 m<sup>2</sup> each were selected (Fig. 1). From 1983 to 1993 samples were taken at low water, 2 to 4 times a month during the period mid-April to late-October. At each sampling per plot 40 core samples of 80 cm<sup>2</sup> each were taken to a depth of 5 cm (total area sampled: 1.056 m<sup>2</sup>). All cores were sieved in the field on 1-mm mesh screens and sorted out alive in the laboratory. All shrimps were counted and total length (mm) was measured to the nearest mm from the tip of the rostrum to the tip of the telson. For all sampling dates, mean numbers and mean length per m<sup>2</sup> was estimated. For more information see BEUKEMA (1992).

### 3. RESULTS

#### 3.1. JUVENILE FLATFISH

Figure 2 shows the seasonal abundance of juvenile flatfish at the Balgzand at high water. A total of four 0-group flatfish species were found: plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*), sole (*Solea solea*) and dab (*Limanda limanda*). The 1993 sampling illustrated the sequence in settling of the different species. 0-group plaice settled from March onwards until May, followed by flounder in April, sole in May-June and dab in June-July. The rank order of abundance was similar to the sequence in settling. Although sampling took place only twice in 1991, a difference in pattern among the two years could be observed. For 0-group plaice, flounder and sole, densities were higher in 1991 compared with 1993, and maximum numbers seemed to occur later in 1991 than in 1993, suggesting a difference in the timing of larval settling. In 1991 also just-settled 0-group dab was found at some locations during the June sampling.

Mean length increase of the various 0-group flatfish populations is presented in Fig. 3. The sequence in larval settling was reflected in the differences in mean length increase during the growing season. Due to the differences in timing of settling, the mean length at the end of the growing season differed between the species. In August, 0-group plaice reached a mean length of about 75-80 mm, whereas for 0-group flounder and sole these values were 40 and 35 mm respectively. For both 0-group plaice and 0-group flounder the rate of increase in mean size (steepness of the growth curve) was similar in 1991 and in 1993.

In Fig. 4 the increase in mean length of 0-group plaice in 1991 and 1993 is compared with that in a number of years in the period 1975-1982. No difference could be found between the rates of increase in size of 0-group plaice of the two periods. In 0-group flounder again no differences could be detected in growth rates between the period 1979-1982 and 1991-1993 (Fig. 5).

#### 3.2. JUVENILE SHRIMP

The seasonal abundance in small juvenile shrimp at low water at the tidal flats is presented in Fig. 6. The overall pattern among years was rather similar. Densities were almost zero in spring and increased from early April onwards. Maximum densities could be found between late May and the end of July. Rather large year-to-year differences in maximum abundance were present of between 50 to 225 individuals per m<sup>2</sup>.

Due to the continuous immigration of newly-settled individuals and the emigration of larger ones, it is difficult to estimate growth of the field population. Only a few times a distinct shift in size-frequency distribution between two successive sampling dates could be found. These shifts (over variable time periods) were converted into daily growth estimates and related to water temperature (Fig. 7). A rather large variability in growth estimates could be observed. In general, growth increased with water temperature. The estimates for growth during 1991 and 1993 did not differ from those for the other years (1983-1989). For these juvenile shrimp, only water temperature appeared to determine the growth rate. Shrimp density and initial size were not significantly influencing growth rate (Table 1).

### 4. DISCUSSION

#### 4.1. TRENDS IN MACROZOOBENTHOS

The Wadden Sea is an important nursery area for a number of fish and crustacean species and as a staging area for especially wading birds (ZIJLSTRA *et al.*, 1972; SMIT & WOLFF, 1983). The macrozoobenthos forms the main food source for both groups of predators (DE VLAS, 1979; SMIT & WOLFF, 1983). The benthic community has been sampled from the beginning of the 1970-ties onwards (BEUKEMA, 1976; 1989; 1994) and this has resulted in information on the year-to-year variability in biomass. During this time period, a strong variability in biomass could be observed from

between about 5 to about 40 g ash free dry weight (AFDW) per m<sup>2</sup>. Part of these fluctuations in biomass are due to natural variability, caused by highly variable recruitment in combination with the on average short life span of the species, as for instance the sensitivity of species to low winter temperatures (BEUKEMA *et al.*, 1988; BEUKEMA, 1990). However, BEUKEMA & CADÉE (1986) suggest that anthropogenic activities might also have affected the trends in benthic biomass. Especially, eutrophication of the Wadden Sea was thought to have enhanced the biomass of the macrozoobenthos in the beginning of the 1980-ties. Nutrient loadings from the mainland are decreasing in recent years (VAN RAAPHORST & MOM, 1993), and as a consequence, BODDEKE & HAGEL (1993) expect a decrease in the productivity of the benthos and its predators. Recently, BEUKEMA (1993) showed that other anthropogenic activities such as intensive bivalve fishing on mussels and cockles can also negatively affect the macrozoobenthic biomass in the Wadden Sea.

The trend in macrozoobenthic biomass for the time period 1971-1993 can be compiled after BEUKEMA (1994). The high level during the 1980-ties coincided with maximum levels of nutrients and chlorophyll. The low value found in early 1991 (Fig. 8) was partly a consequence of intensive fishing in the area in 1990 (BEUKEMA, 1993). In more recent years, 1992 and 1993, values increased again to an all-time maximum of more than 35 g AFDW.m<sup>-2</sup> in early 1993. Thus, there is no indication of a consistent decrease in macrozoobenthic biomass of the tidal flats as a consequence of decreasing nutrient loadings of the western Dutch Wadden Sea (VAN RAAPHORST & MOM, 1993).

#### 4.2. TRENDS IN PRODUCTIVITY OF PREDATORS

The productivity of the area as nursery area of flatfish and shrimps will be determined by a number of aspects, among which the carrying capacity of the area will be the main factor (VAN DER VEER & BERGMAN, 1987). The carrying capacity of the area will be reflected in the numbers of individuals and in their growth.

Fig. 9 shows the year-class strength of both juvenile flatfish and shrimps at the tidal flats of

Balgzand. Estimates of year-class strength is based on peak abundance, following the method of VAN DER VEER (1986). Both in juvenile flatfish and in juvenile shrimp, large year-to-year fluctuations were observed. In plaice, year-class strength appeared to be inversely related with temperature conditions during spawning (VAN DER VEER, 1986). The factors and/or processes determining year-class strength in flounder are unknown (VAN DER VEER *et al.*, 1991). However in both flatfish species year-class strength is thought to be generated during the pelagic egg- and larval stages (VAN DER VEER, 1986; VAN DER VEER *et al.*, 1991). This means that for juvenile flatfish the carrying capacity of the Balgzand will not be reached and that the limiting factor might be larval immigration through the tidal inlets (BERGMAN *et al.*, 1989). The processes determining the year-class strength in juvenile shrimp are also unknown (BEUKEMA, 1992). The timing of larval immigration and subsequent peak abundance appears to be determined by winter temperatures (BEUKEMA, 1992). However, there is no clear relationship between year-class strength of shrimps and winter temperature (Fig. 10). Neither was year-class strength of juvenile shrimp related to the macrozoobenthic biomass (Fig. 11). This might suggest that also in shrimp, the carrying capacity is not reached and that year-class strength is determined by other factors.

The observations on growth of juvenile flatfish and shrimp support the view that for both groups the carrying capacity was not reached. Growth estimates in the present period of decreasing nutrient loadings of the area (VAN RAAPHORST & MOM, 1993) did not differ from growth rates observed in previous time periods. Even in 1991, with all-time lowest macrozoobenthic biomasses, growth rates in flatfish and shrimps were similar with those for other years. Growth of 0-group plaice at Balgzand it thought to be determined by water temperature only (ZIJLSTRA, 1972; VAN DER VEER, 1986; VAN DER VEER *et al.*, 1990). In general, food quality seems to affect growth, whereas density-dependent effects, indicating competition and hence a limitation by the carrying capacity of the area, has never been observed (VAN DER VEER & WITTE, 1993). Also, the growth of

shrimps seemed to be determined by prevailing water temperatures only and not affected by shrimp density (Table 1). This means that despite the large fluctuations in food availability, the abundance and growth of juvenile flatfish and shrimps were never food-limited at Balgzand. Consequently, so far there seems to be no relationship between productivity of the Balgzand area for juvenile shrimp and flatfish and the decreasing nutrient loadings of the western Wadden Sea.

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TABLE 1

Statistical evaluation (ANOVA) on influence of water temperature (TEMP), shrimp density (DENSITY) and mean length of the shrimps (LENGTH) on growth of juvenile shrimp (GROWTH) at Balgzand intertidal area during the period 1983 - 1983. Growth estimates were based on Peterson method. Data after BEUKEMA (1992) and unpublished.

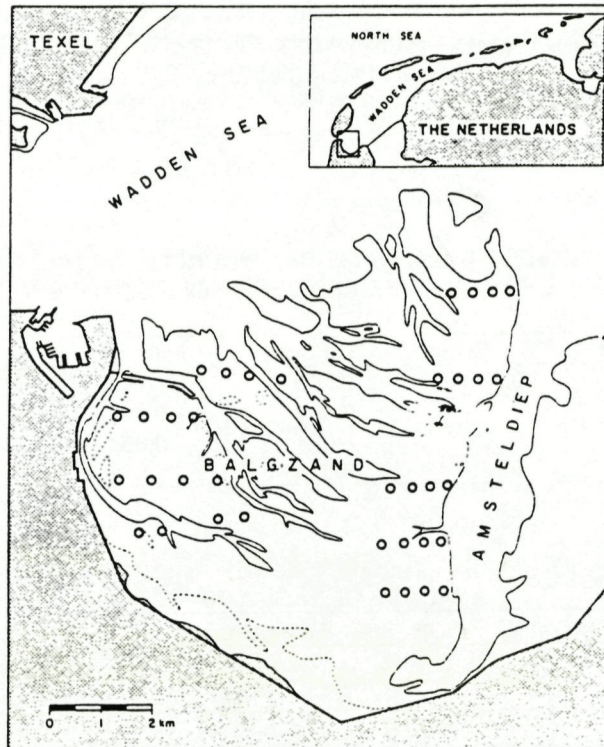
2 CASES DELETED DUE TO MISSING DATA

DEP VAR: GROWTH N: 29 MULTIPLE R: .803 SQUARED MULTIPLE R: .645  
 ADJUSTED SQUARED MULTIPLE R: .602 STANDARD ERROR OF ESTIMATE: 0.327

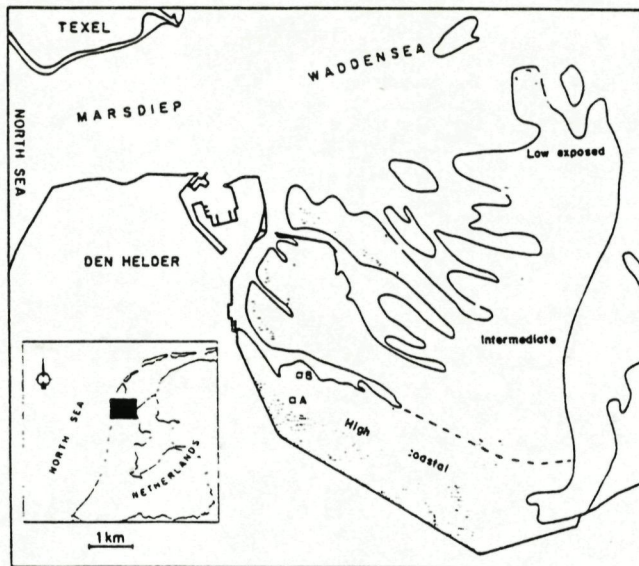
Variable	Coefficient	Std Error	Std Coef	Tolerance	T	P (2 Tail)
Constant	-3.227	0.396	0.000		-8.148	0.000
Temp	0.137	0.021	0.808	0.943	6.587	0.000
Density	-0.000	0.001	-0.024	0.894	-0.193	0.849
Length	0.001	0.022	0.008	0.935	0.068	0.946

ANALYSIS OF VARIANCE

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Regression	4.848	3	1.616	15.130	0.000
Residual	2.670	25	0.107		



a



b

Fig. 1. The Balgzand intertidal area in the western Dutch Wadden Sea. a: High water sampling stations; b: low water sampling stations

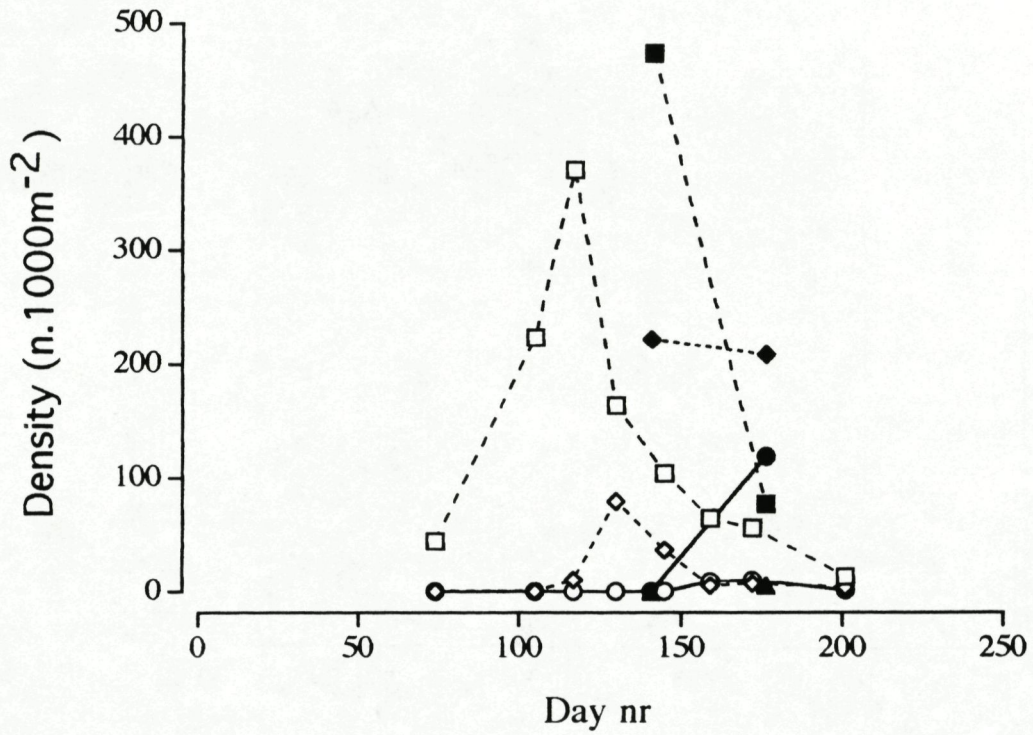


Fig. 2. Seasonal abundance (n.1000 m<sup>-2</sup>) of juvenile flatfish at the Balgzand at high water in 1991 (solid symbols) and 1993 (open symbols). ■ □ : plaice; ◆ ◇ : flounder; ● ○ : sole.

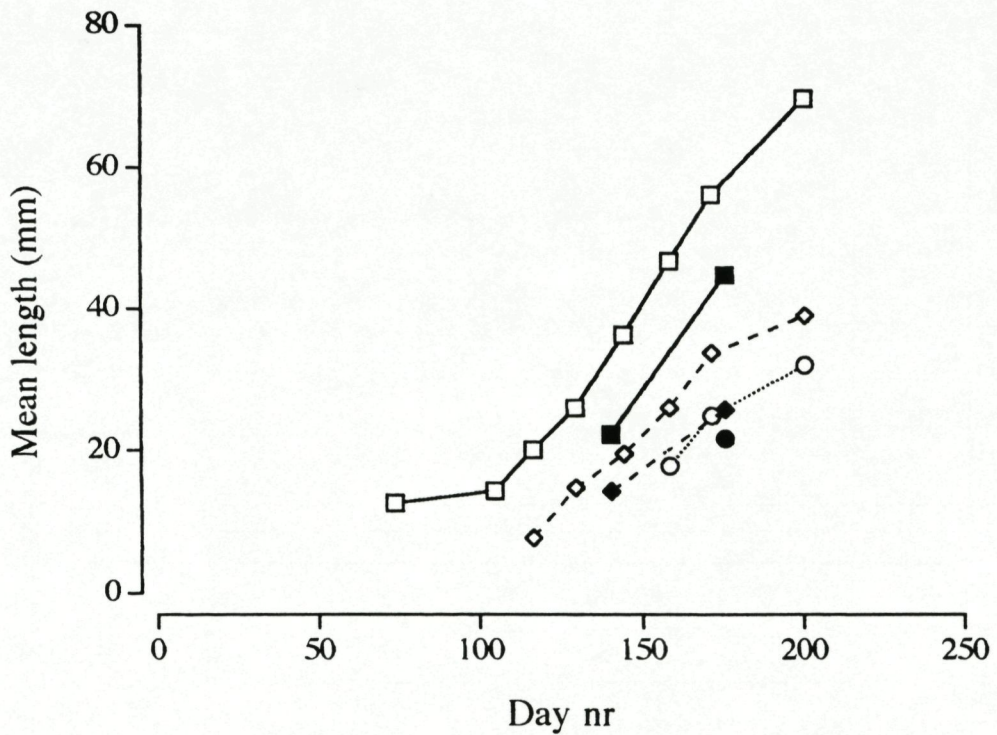


Fig. 3. Seasonal increase in mean length (mm) of juvenile flatfish at the Balgzand at high water in 1991 (solid symbols) and 1993 (open symbols). ■ □ : plaice; ◆ ◇ : flounder; ● ○ : sole.

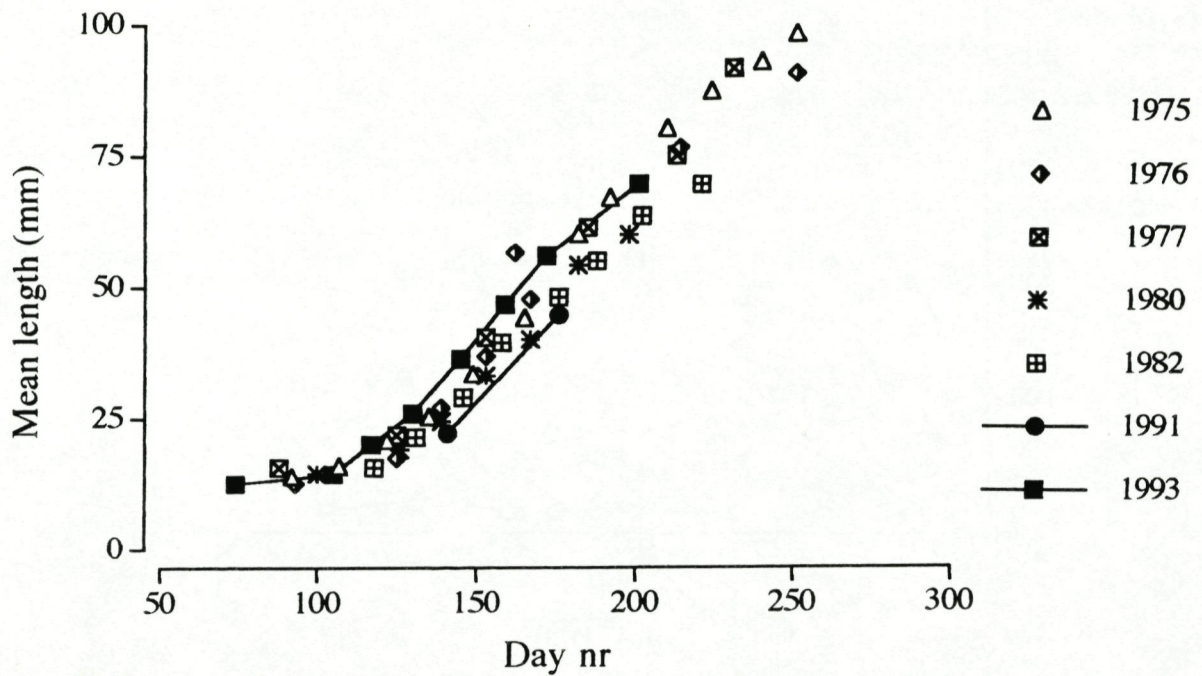


Fig. 4. Seasonal increase in mean length (mm) of juvenile plaice at the Balgzand at high water for a number of years: 1975-1993.

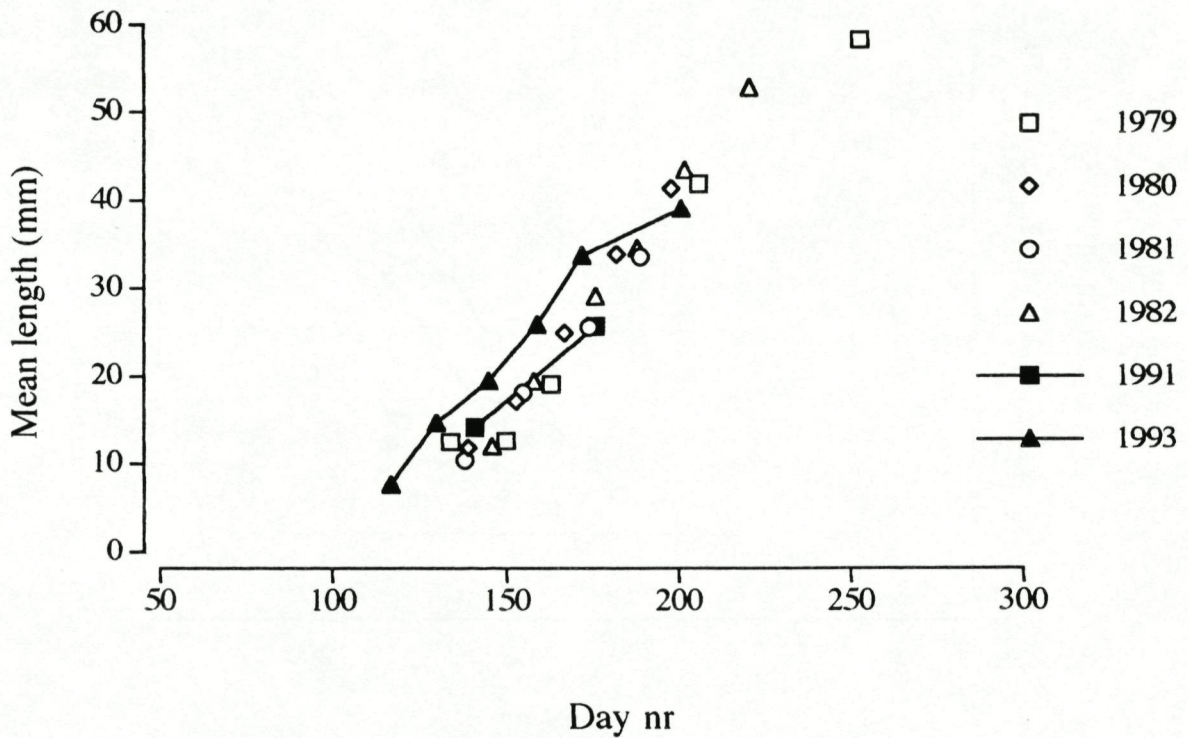


Fig. 5. Seasonal increase in mean length (mm) of juvenile flounder at the Balgzand at high water for a number of years: 1979-1993.

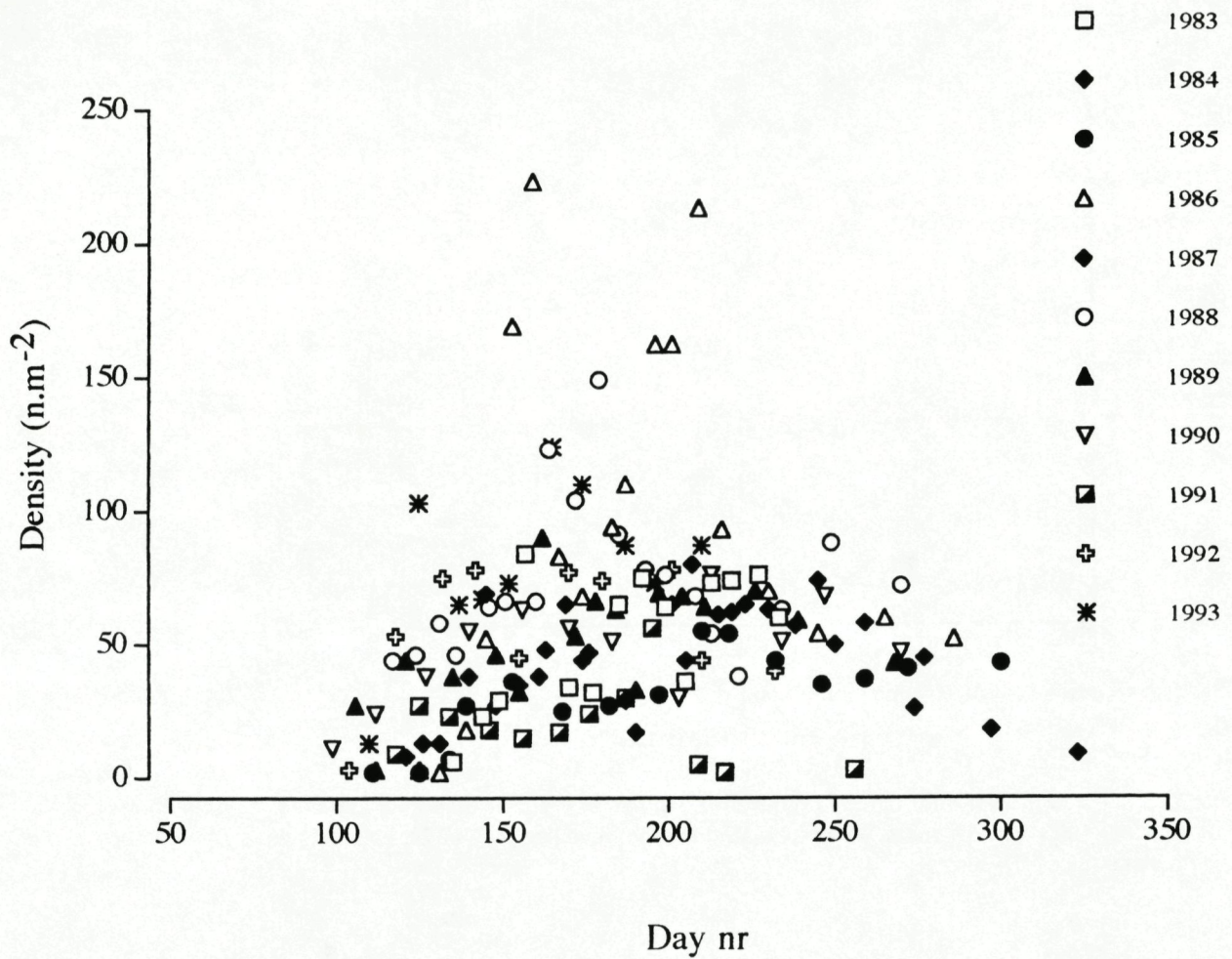


Fig. 6. Seasonal abundance (n.m<sup>-2</sup>) of juvenile shrimp at the Balgzand intertidal flat at low water for a number of years: 1983-1993.

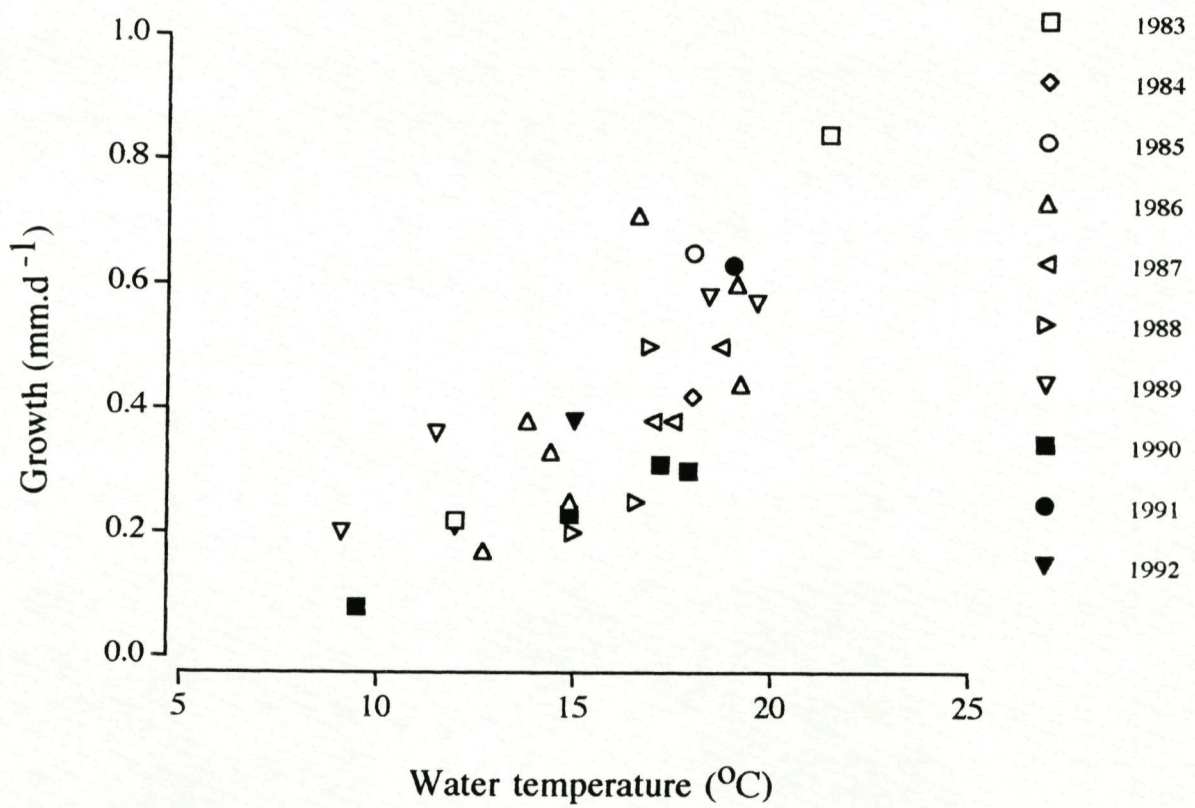


Fig. 7. Estimated growth rate (mm.d<sup>-1</sup>) of juvenile shrimps at the Balgzand intertidal area for a number of years: 1983-1993 in relation to water temperature, as revealed by means of shifts in size-frequency distributions (by eye).

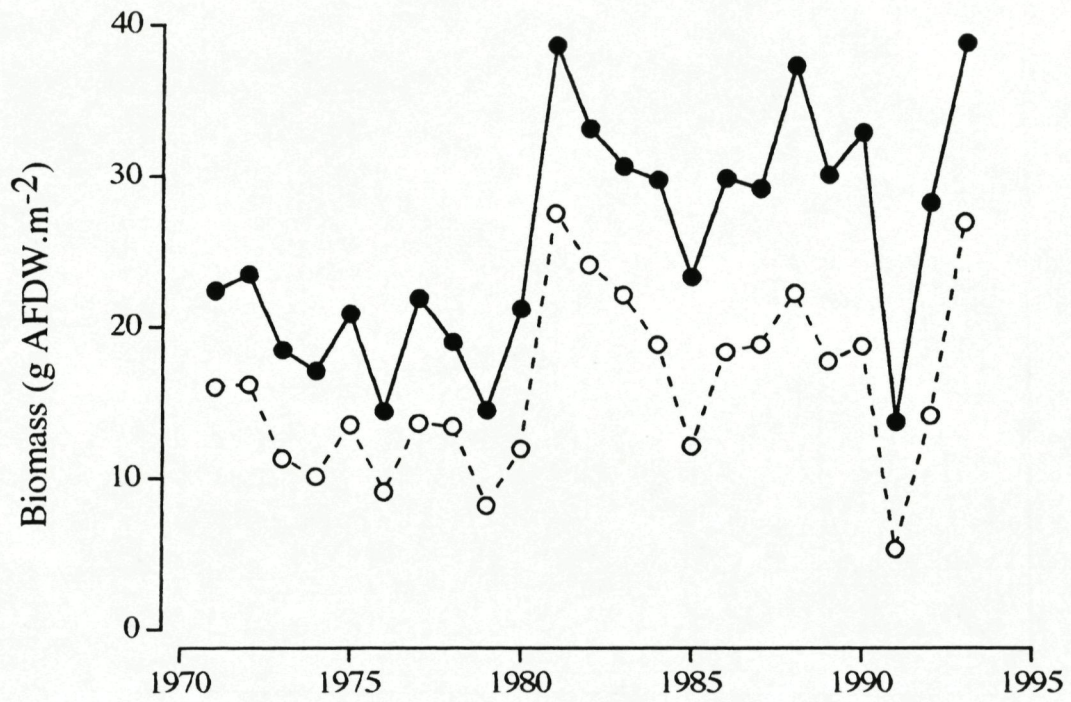


Fig. 8. Year-to-year variability in macrozoobenthic biomass (g AFDW.m<sup>-2</sup>) at the Balgzand intertidal area in spring during the period 1971-1993. Total biomass: solid symbols; bivalve biomass: open symbols. Data after: BEUKEMA (1994).

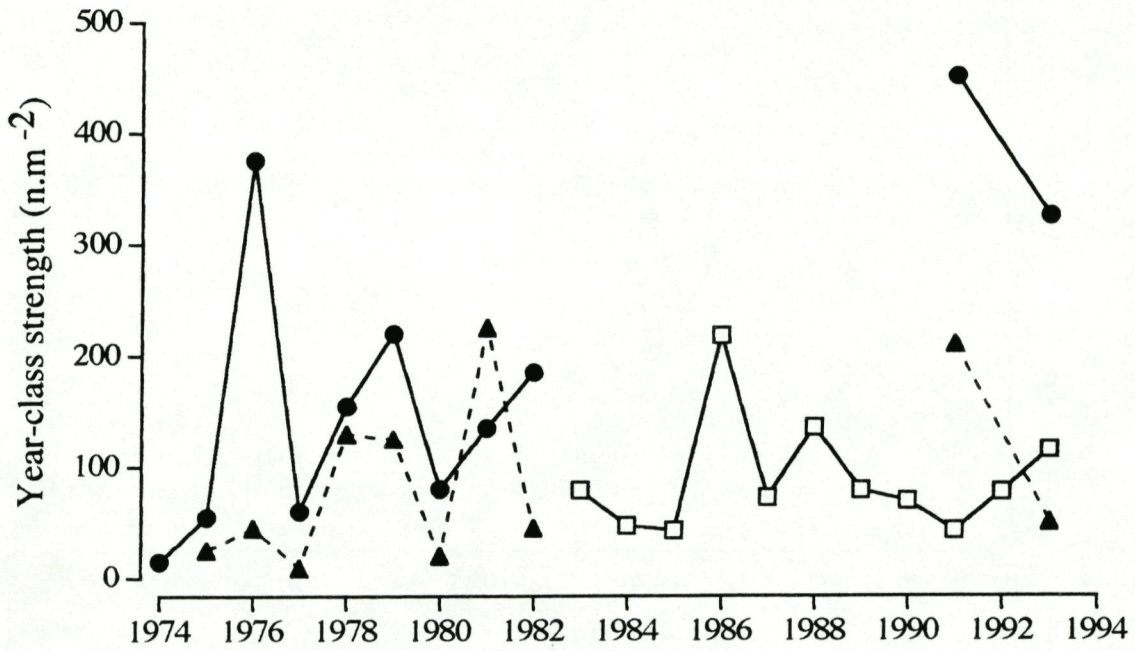


Fig. 9. Year-class strength of juvenile flatfish ( $n.1000\ m^{-2}$ ) and juvenile shrimp ( $n.m^{-2}$ ) at the Balgzand intertidal over the period 1974-1994, estimated as mean peak abundance of two successive surveys (flatfish) and maximum mean June or July density (shrimps). Shrimp: open symbol; plaice solid points; flounder solid triangles. Shrimp data after BEUKEMA (1992 and unpubl.).

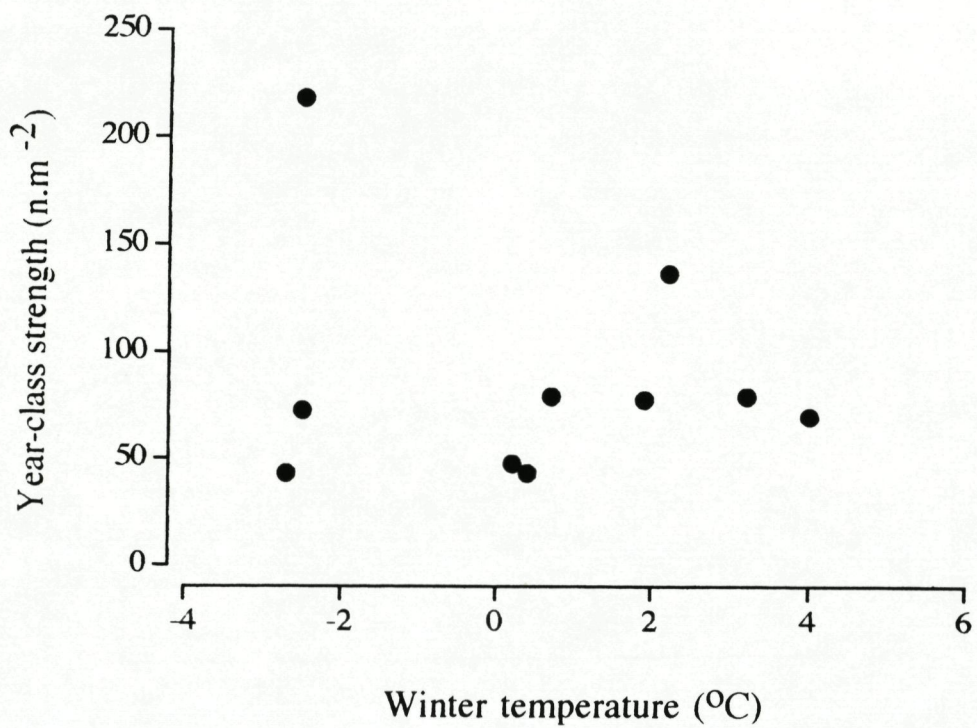


Fig. 10. Relationship between year-class strength of juvenile shrimp at the Balgzand intertidal and previous relative winter temperature (°C deviation from long-term average). Data after BEUKEMA (1992 and unpubl.).

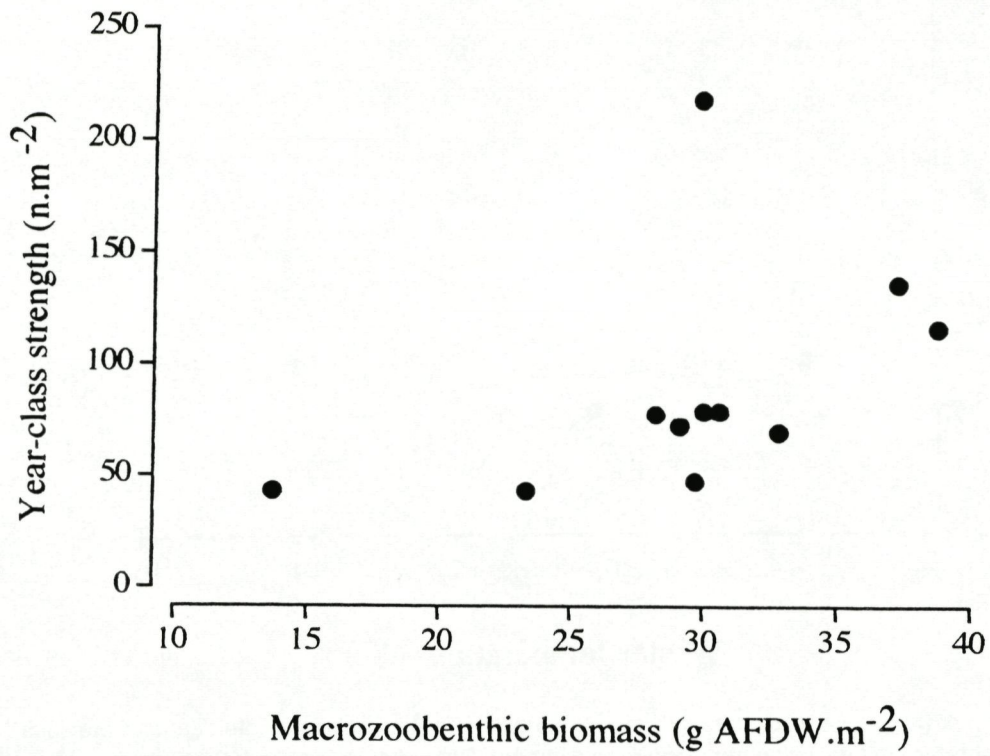


Fig. 11. Relationship between year-class strength of juvenile shrimp at the Balgzand intertidal and macrozoobenthic biomass. Data after BEUKEMA (1992 and unpubl.).

# INCREASED MORTALITY IN ALTERNATIVE BIVALVE PREY DURING A PERIOD WHEN THE TIDAL FLATS OF THE DUTCH WADDEN SEA WERE DEVOID OF MUSSELS\*

16482

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## ABSTRACT

In the course of 1990, stocks of mussels (*Mytilus edulis*) declined to unprecedentedly low levels in the Dutch Wadden Sea. Hardly a wild mussel bed was left on the tidal flats as a consequence of three years (1988, 1989, and 1990) with failing recruitment and intensive fishing for seed mussels. During these three years, recruitment of cockles (*Cerastoderma edule*) also failed, whereas fishing was continued. Bird species taking these bivalves as staple food, the oystercatcher (*Haematopus ostralegus*) and the eider (*Somateria mollissima*), experienced food shortage. Significant numbers of eiders left the Dutch Wadden Sea area or died, whereas oystercatchers remained abundant throughout the winter in most of the Dutch Wadden Sea.

Alternative prey species of oystercatchers experienced unusually high mortality rates in the appropriate size classes. This was so in all other common species of bivalves, viz. first-year and older cockles, adult *Macoma balthica*, and juvenile *Mya arenaria*. This led to minimal stocks of food for oystercatchers in the late winter of 1991. In March 1991, cockles were depleted and the combined stocks of *Mya* and *Macoma* would soon have run out of food supply to the overwintering oystercatcher population. Apparently, oystercatchers are able to reduce the stocks of their various bivalve prey species to very low levels.

## 1. INTRODUCTION

The benthic food stocks available to predators in the Wadden Sea are generally high, but they fluctuate significantly and may occasionally decline to low levels. Numbers and biomass in some species of benthic animals are notoriously unstable by a combination of highly variable recruitment and a short life span. In some years, low densities may arise and these extend over hundreds to thousands of km<sup>2</sup> (BEUKEMA & ESSINK, 1986; BEUKEMA *et al.*, 1993). Among these unpredictable food sources, two important bivalves stand out, as judged from their high contribution to benthic biomass (BEUKEMA, 1976; DEKKER, 1989). These are the cockle (*Cerastoderma edule* (L.)) and the blue mussel (*Mytilus edulis* L.). In particular the cockle may at times become scarce, especially after a severe winter when they die out almost completely on the tidal flats

of the Wadden Sea (BEUKEMA, 1979, 1985, 1990). Mussels are more resistant to severe winters, but are equally variable in their recruitment (BEUKEMA, 1982, 1992). In both species recruitment tends to fail after extraordinarily mild winters (BEUKEMA, 1992). A number of such failures in close succession result in small stocks of old specimens in the two species (BEUKEMA *et al.*, 1993). Such a simultaneous minimum in the abundance of cockles and mussels occurred in the Dutch Wadden Sea in 1990 and 1991. Consequences of the failing reproduction in 1988, 1989, and 1990 (BEUKEMA, 1992) were worsened by an irresponsible continuation of intensive fishery for mussels and cockles through 1990. In the Wash, in the western North Sea, densities of both cockles and mussels were also low in the early 1990s as a consequence of repeated recruitment failure in the foregoing years (CLARK, 1993).

The most important consumers in terms of biomass of benthic food in the Wadden Sea are the oystercatcher (*Haematopus ostralegus* L.) and the eider (*Somateria mollissima* L.) and both depend largely on cockles and mussels (HULSCHER, 1983; SWENNEN, 1983). In normal years, these species each consume about 2 g ash-free dry weight per m<sup>2</sup> (SMIT, 1983). For oystercatchers this amount is expressed per m<sup>2</sup> of the tidal flats and for eiders per m<sup>2</sup> of sublittoral bottom of the Dutch Wadden Sea, where eiders mainly take their food. These amounts are roughly equal to what all other bird species together consume annually in these areas. In years with food stocks around or above average, consumption by birds would amount to only low proportions of these stocks and their annual production. However, periods of low cockle abundance are not infrequent. They occur after all severe winters, *i.e.* at least once or twice per decade (BEUKEMA *et al.*, 1993). Oystercatchers and eiders then usually switch to mussels, which are generally abundant in the form of dense beds, both in the subtidal and in the intertidal parts of the Dutch Wadden Sea. The numerous mussel beds at sheltered locations on tidal flats of the Wadden Sea are very stable (DANKERS & KOELEMAIJ, 1989; OBERT & MICHAELIS, 1991; NEHLS & THIEL, 1993), occurring in the same areas since time immemorial. However, in the course of 1990 virtually all 'wild' mussel beds disappeared from the tidal flats of the Dutch Wadden Sea by intensive fishing (DANKERS, 1993).

Thus the year 1990/91 was characterized by coinciding scarcity in mussels and cockles. These two prey species are precisely the usual main food supply for the two largest consumers of bivalves in the Wadden Sea. The consequences of the coinciding low stocks of mussels and cockles in 1990/91 were dramatic for the eider population wintering in the Dutch Wadden Sea: they concentrated on the last mussel banks present, *i.e.* the culture plots, where they were regularly chased away. A significant proportion of the population in the Dutch Wadden Sea left the area or died (VAN DE KUIP, 1991; DANKERS, 1993). The number of eiders in the Dutch Wadden Sea in January 1991 was only about 65% of the average of the

20 foregoing years (SWENNEN, 1991). The oystercatchers, on the other hand, remained in high numbers in most of the Wadden Sea area in the 1990/91 winter (HULSCHER *et al.*, 1993). As far as they continued foraging on the tidal flats, they will have switched to other prey types, such as the bivalves *Macoma balthica* L. and *Mya arenaria* L. Such switching was indeed observed in an area without mussel beds in an earlier year (1979) when cockles became scarce (ZWARTS & WANINK, 1993). In early 1991, the alternative food stocks in the Dutch Wadden Sea must have been only just sufficient, as judged from the apparently poor condition of the oystercatchers, as demonstrated by the unexpectedly high numbers found dead (CAMPHUYSEN, 1993).

The aim of the present paper is to quantify the precarious 1990/91 food situation for bivalve-consuming birds on tidal flats in the westernmost part of the Wadden Sea (Balgzand), to compare this situation with other (more normal) years, and to study the effects of the shortage of mussels (and subsequently also of cockles) on the abundance and death rates of alternative prey species. Such data should provide answers to questions such as: 'Can bird predation seriously affect survival of benthic prey?' and 'To what extent can birds deplete stocks of various prey types?'

A long-term programme for the study of dynamics of macrozoobenthos on Balgzand provides the necessary data series to assess the exceptional state and fate of the benthic food supply in 1990/91.

## 2. METHODS AND MATERIAL

Quantitative data on bivalves in the Balgzand area were obtained from a long-term sampling programme for macrozoobenthos, details of which are described in earlier papers (*e.g.* BEUKEMA, 1974). Biannual sampling (in February-March and in August-September) started in the early 1970's. In this paper, generally only biomass data obtained in 1977 or later will be used, because no earlier bird data are available. In the earlier years, the August samples were taken to a depth of only about 15 cm, as opposed to a consistent about-30 cm in

March. Therefore, generally only winter samples will be used for deep living species such as the lugworm.

Balgzand is a 50-km<sup>2</sup> tidal flat area in the westernmost part of the Wadden Sea. Physical characteristics and benthic fauna are described in BEUKEMA (1988). Fixed sampling stations were scattered over the tidal flats, covering all types of sediment and all intertidal levels. Samples were taken by sieving cores: 50 along each of 12 transects of 1 km length and 18 within each of three squares of 900 m<sup>2</sup>.

Abundance of benthic animals is expressed in mean number per m<sup>2</sup> (from samples taken at 15 stations with a total area sampled of about 14 m<sup>2</sup> in late winter and about 9 m<sup>2</sup> in late summer) or in biomass units: g per m<sup>2</sup> ash-free dry weight (AFDW) of the soft parts.

Numbers of birds were obtained from annual reports on Balgzand issued by the Dutch Society for Bird Protection (Nederlandse Vereniging tot Bescherming van Vogels), Zeist, the Netherlands. They contain monthly counts of birds at high-tide roosts, as reported ever since 1977 by the keeper of the Balgzand bird sanctuary Mr M. Otter.

### 3. RESULTS

#### 3.1. BIVALVE STOCKS IN LATE WINTER

##### a. Year-to-year fluctuations

Minimal biomass values on the tidal flats occur in late winter (BEUKEMA, 1974; ZWARTS & WANINK, 1993). Moreover, a smaller proportion of total biomass is available to birds in winter than in other seasons (EVANS & DUGAN, 1984; ZWARTS & WANINK, 1993), since several species live relatively deep in the sediment in winter and rarely rise to the sediment surface, making them inaccessible to most bird species (ESSELINK & ZWARTS, 1989; ZWARTS *et al.*, 1992; ZWARTS & WANINK, 1993). Food demands of individual birds are maximal in winter (PIENKOWSKI *et al.*, 1984; KERSTEN & PIERSMA, 1987), so food stocks in cold late-winter periods are critical.

During the 1977-1993 period, bivalve biomass in March on the tidal flats of Balgzand fluctuated between 5 and 28 g AFDW per m<sup>2</sup> (upper line of Fig. 1a). If only the size classes

that are taken as food by the oystercatcher (the main avian predator on the tidal flats) are considered (using criteria derived from ZWARTS *et al.*, in press), the fluctuations of this 'suitable' fraction of biomass were even more violent (lower line of Fig. 1a): from less than 3 to about 22 g AFDW per m<sup>2</sup>. The lowest value recorded so far on Balgzand occurred in March 1991.

Figs 1b, c, and d show how much the various bivalve species contributed to total biomass each year. High total-bivalve biomass values were observed in the early 1980s after the birth of an exceptionally strong year class of cockles in the summer of 1979. Low values were observed after cold winters (the first months of 1979, 1985, 1986, and 1987) due to the (almost complete) disappearance of cockles during such winters (Fig. 1b). However, 1991 was far from a cold winter (compare fig. 7a of BEUKEMA *et al.*, 1993). Therefore, the exceptionally low biomass value observed in the late winter of 1991 asks for a different explanation (see c).

##### b. The minimal stocks in early 1991

Note that exceptionally low bivalve-biomass values in early 1991 were not only observed in mussels and cockles (Fig. 1b), but also in *Mya* and *Macoma* (Fig. 1c). It was the coincidence of low biomass values in all important bivalve species that made total biomass of bivalves extremely low in early 1991.

Mussels have invariably been present in the samples ever since the start of the benthos-monitoring programme around 1970, but were completely absent in March 1991 (Fig. 1b). Even additional searching, outside the 13.5 m<sup>2</sup> routinely sampled, revealed only very few specimens. Mean density must have been <0.01 per m<sup>2</sup> VAN STRALEN & KESTELOO-HENDRIKSE (1992), who sampled at no less than 1471 locations all over the shallow parts of the Dutch Wadden Sea, also found hardly any mussels in the spring of 1991.

Cockles were exceptionally scarce in early 1991, with a mean biomass of only 0.16 g AFDW per m<sup>2</sup> (Fig. 1b), being the lowest value of the 25-y data series of the 1969-1993 period. In March 1991, the mean numerical density of adult (>30 mm) cockles amounted to only 0.2 per m<sup>2</sup>, that of small (less than 1-y-old) only to

about 4 per m<sup>2</sup> (including only 0.5 per m<sup>2</sup> of such cockles >10 mm).

Gaper clams (*Mya*) too were relatively scarce in early 1991 with a mean biomass of 1.7 g AFDW per m<sup>2</sup> (including all size classes) (Fig. 1c). This again was a species with the lowest value of the 25-y data set to be found in early 1991. The amount of *Mya* actually available to oystercatchers (the 15-45 mm size class) in early 1991 amounted to no more than about 0.3 g per m<sup>2</sup>, or 1.2 individuals per m<sup>2</sup>.

In 1991, the minimum biomass of *Macoma balthica* was reached in the first half of March and amounted to 2.0 g AFDW per m<sup>2</sup> (Fig. 1c). Lower values were only observed before 1979, but never during the 1979-1993 period. In early 1991, the amount of adult-sized *Macoma* was 2.0 g or 65 individuals per m<sup>2</sup>.

Finally, the amounts of other molluscs, mainly *Scrobicularia plana* (Da Costa), *Angulus tenuis* (Da Costa) and *Ensis directus* (Conrad), were usually low. In early 1991 these amounts were negligible (Fig. 1d).

### c. Causes of the low stocks in 1990/91

The extremely low biomass values of the above mentioned bivalves observed in early 1991 arose from a number of factors. The primary cause was the failure of recruitment in all important bivalve species in three successive years, viz. the summers of 1988, 1989, and 1990, probably as a consequence of the extraordinarily mild winters preceding these summers (BEUKEMA, 1992). During the 1988-1990 period, the densities of the strong cockle and mussel year classes born in 1987 gradually diminished. Due to the high individual weights of these old animals, biomass values in early 1990 were still relatively high and not far from the long-term averages. However, in the summer of 1990, biomass values of mussels had declined to close to nil, instead of showing the normal increase at this time of the year, and the normally strong seasonal increase of cockle biomass was only weak in 1990. Thus already in August 1990, biomass values were much lower than the long-term summer average in the two species (Fig. 2). At the following sampling, in March 1991, the summed biomass values of cockles and mussels were close to 0 (Fig. 2). In the next paragraph, I argue that

intensive fishery was decisive for the abnormal and rapid decline of practically the entire mussel and most of the cockle stocks on Balgzand in the course of 1990.

Stocks of wild mussels are fished annually to seed culture plots. In early 1990, they had become exhausted throughout the subtidal parts of the Dutch Wadden Sea, where the last successful spat fall had been in 1987. That is why mussel fishery in 1990 concentrated on the remaining mussels of any size in the intertidal. Some fishermen even used shallow-draught cockle vessels to exploit the beds at the higher intertidal levels, where they had rarely, if ever, fished before. Already in the summer of 1990, all mussel beds on Balgzand had been turned into ploughed sand flats with only some scattered empty shells remaining. The same was true in late summer for part of the cockle banks. Other causes of death must have been relatively unimportant, since only a few empty shells were left (indicating a natural death by e.g. predation). Moreover, fishing trails were clearly visible (see photographs in VAN DE KUIP, 1991). Such intensive fishing on tidal flats was also reported from other parts of the Dutch Wadden Sea in 1990, where mussel and cockle banks also disappeared almost completely. Attempts to stop this disastrous fishing in 1990 by governmental measures failed. On the contrary, after judges had decided in the fishermen's favour, fishing on tidal flats became virtually unrestricted, even destroying several seagrass beds and some so-called 'eco-plots' used for monitoring the fauna (DANKERS & DE VLAS, 1992; REVIER, 1993). Cockles survived only in areas with low densities and in a few (apparently overlooked) banks. Large mussel beds disappeared in areas where they had been present since time immemorial. Mussels survived only on culture plots, on a few very small banks, which were apparently overlooked (DANKERS & DE VLAS, 1992), and locally on dikes (which were in some places illegally scraped for seed mussels).

### 3.2. OYSTERCATCHERS AND THEIR FOOD DEMANDS

Long-term averages of monthly counts of birds at their high-tide roosts bordering Balgzand

revealed high numbers (means between 10 and 20000) of oystercatchers during the September-March periods and low numbers in the remainder of the year (Fig. 3). Though the tidal flats of Balgzand (about 50 km<sup>2</sup>) comprise only about 4% of the total tidal-flat area of the Dutch Wadden Sea (about 1300 km<sup>2</sup>), in winter they harbour between 3 and 22% (average 8%, weighted average 7%) of the total numbers of oystercatchers in the Dutch Wadden Sea (11 January counts, 1980-1990, Table 7 of ZEGERS & KWINT, 1992). Data included in Table 18 of HULSCHER (1983) suggest a Balgzand share of about 10% of the numbers wintering in the Dutch Wadden Sea and of about 5% of those of the entire international Wadden Sea. Expressed per km<sup>2</sup> of tidal flats, winter densities of oystercatchers on Balgzand were above the Dutch Wadden Sea average in 10 out of the 11 years 1980-1990.

Annual mean numbers counted on Balgzand slightly increased from about 8000 during the late 1970s to about 10000 during the 1980s, and the increase is still continuing. This will reflect a general increase in numbers of oystercatcher counted in western Europe (SMIT, 1989; ZEGERS & KWINT, 1992). During most of the 12 months July 1990 to June 1991, numbers were above the long-term average (Fig. 3), the February 1991 numbers (31 600) were higher than ever observed on Balgzand in winter. However, between mid-February and mid-March 1991 numbers of oystercatcher on Balgzand declined steeply and reached very low levels in spring (Fig. 3). Both the April and May numbers were the second-lowest for these months in the entire 16-y period of observation. In March, absolute numbers were not yet exceptionally low, but as a proportion of the February numbers they were: 16% in 1991 as opposed to between 20 and 90% in other years. Thus, an extraordinarily high proportion of the oystercatchers wintering on Balgzand left the area in 1991 between mid-February and mid-March.

Monthly food demands of the oystercatcher population were calculated for the August 1990 to August 1991 year using an estimate of daily consumption per individual of 55 g AFDW in winter (Nov.-April) and 40 g in the remainder of the year, based on field data summarised in

Appendix 1 of HULSCHER (1982). These figures are slightly higher than the detailed estimates by KERSTEN & PIERSMA (1987) of oystercatchers' food intake in outdoor cages, amounting to about 35 g at temperatures above ca. 10°C and increasing to about 50 g at below-0 temperatures. The higher activity levels of birds living in the field will justify the use of the higher estimates.

The estimates of total food intake by oystercatchers (number of bird-days times daily intake per bird) were divided by the area of the Balgzand tidal flats (50 km<sup>2</sup>) to express the predation pressure exerted by oystercatchers in g per m<sup>2</sup>. The thus estimated monthly consumption by the oystercatcher population increased during autumn and early winter, reaching a maximum of 1.0 g AFDW per m<sup>2</sup> in February 1991 (Fig. 4). A comparison of this consumption rate with the amounts of food left in early March on Balgzand (Fig. 4) shows how close the bivalve consumers were to total food depletion.

Total estimated oystercatcher consumption during the year 1990-91 amounted to 4.3 g AFDW per m<sup>2</sup>, more than half of which was taken in only three months (Dec.-Jan.-Feb.). The total consumption by oystercatchers between the two sampling occasions in August 1990 and March 1991 will have amounted to 4.1 g AFDW per m<sup>2</sup>.

Some other bird species also consume significant amounts of bivalves of sizes overlapping with those of oystercatcher prey, viz. eiders (mussels and cockles) and knots (*Macoma*). It is unknown to what extent eiders derive their food intake from tidal flats (SMIT, 1983), but they were feeding in considerable numbers above tidal flats of Balgzand at high tides in 1990/1991. In this area they were relatively numerous according to counts made in January 1991 (SWENNEN, 1991). Knots (*Calidris canutus*) were relatively numerous on Balgzand in the autumn of 1990, viz. around 40000 during the counts in November and December. Calculations of knots' consumption were made in the same way as in oystercatchers, but started from a daily food intake of 10 g per individual (compare WIERSMA & PIERSMA, in press). Between August 1990 and March 1991, total amounts consumed by knots

will have amounted to about 0.5 g AFDW per m<sup>2</sup>. Most of this must have consisted of *Macoma*, as other prey of knots (ZWARTS & BLOMERT, 1992; PIERSMA *et al.*, 1993) such as *Hydrobia* and small cockles were scarce on Balgzand in that period.

### 3.3. DEATH RATES OF ALTERNATIVE PREY

The main food items of oystercatchers feeding on tidal flats are molluscs, in particular the larger-sized cockles, mussels and *Macoma*. To a lesser extent, and particularly in summer, also worms and crustaceans are taken (HULSCHER, 1983). When mussels are lacking, as was already the case in the summer of 1990, cockles are preferred as an alternative food source. When these are scarce too (as occurred in the course of the winter 1990/91), *Macoma* is a usual alternative (HULSCHER, 1982, 1983), particularly in spring and summer (see appendix of HULSCHER, 1982) when this species lives close to the sediment surface (ZWARTS & WANINK, 1993). Individual birds may specialize on other specific prey types (BOATES & GOSS-CUSTARD, 1992), such as worms (*Arenicola marina* and *Nereis diversicolor*), various clams (such as *Mya arenaria*, *Scrobicularia plana* and *Angulus tenuis*), snails (*Littorina littorea*), or crabs (*Carcinus maenas*). Not all of these possible alternatives can have been important during the 1990/91 period. *Littorina*, *Scrobicularia* and *Angulus* are rare on Balgzand. On the tidal flats, *Carcinus* are numerous in summer only. *Arenicola* and *Nereis* appear to be important prey items only in summer, because they live deeply buried and are hardly active near the sediment surface in winter (ESSELINK & ZWARTS, 1989). Therefore, the bivalves *Cerastoderma*, *Macoma* and *Mya* will have been the most plausible alternatives for the lacking *Mytilus*, but *Arenicola* and *Nereis* cannot be excluded.

The following paragraphs deal with the fate of the various species of alternative prey. Long-term (1977-1993) averages of mortality rate were calculated and compared with the values observed in 1990-1991, *i.e.* the period with extremely low densities of mussels (and later also of cockles). Moreover, the amounts of biomass of the various species disappearing

between August 1990 and March 1991 were assessed to obtain an estimate of the amounts that could maximally have been removed from the Balgzand tidal flats by birds.

#### a. *Cerastoderma edule*

Oystercatchers generally prefer larger cockles, so data were used of cockles of >15 mm length. In August 1990, cockles of at least one year old (with lengths of about 20 mm or more) were present on Balgzand in an average density of 11 per m<sup>2</sup>. This estimate is close to the average number of 10.1 such cockles per m<sup>2</sup> for the shallow part of the entire Dutch Wadden Sea (1414 sampling locations), observed in spring 1990 by VAN STRALEN (1990). About 5% of Balgzand showed densities of adult cockles of at least about 50 per m<sup>2</sup>, whereas the areas with densities >100 per m<sup>2</sup> occupied only about 1%. Threshold densities below which oystercatchers cannot profitably feed on pure stands of cockles appear to be close to about 50 big cockles per m<sup>2</sup> (HORWOOD & GOSS-CUSTARD, 1977; SWENNEN, pers. comm.). The proportion of the adult cockles present in August 1990 at densities of at least 50 per m<sup>2</sup> was 30% of the total stock of 5.4 g AFDW per m<sup>2</sup> or 1.6 g per m<sup>2</sup> (both biomass estimates averaged over the entire Balgzand).

Only 0.2 per m<sup>2</sup> (2%) of these adult cockles were left in March 1991. A decline in numbers of adult cockles between August and March of as much as 98% was unique during the 25-y period of observation of benthos on Balgzand. Even after the four coldest winters, 5 to 20% of the adult cockles were still alive in March (Fig. 5), whereas in years with normal or mild winters survival in adult cockles was generally much higher (mostly between 30 and 80%).

First-year cockles were relatively scarce (0.2 g AFDW per m<sup>2</sup> in August 1990) and will not have played any significant role as an alternative source of food for oystercatchers. Some of this youngest age group of cockles were larger than 10 mm in August. They experienced a similar, abnormally high, rate of mortality between August 1990 and March 1991, *viz.* 98%. Only 0.5 per m<sup>2</sup> (0.03 g per m<sup>2</sup>) of 0-group cockles with a length >15 mm were left in March 1991. Small cockles became an

important food source during periods of scarcity of bigger cockles in Northern Ireland (O'CONNOR & BROWN, 1977), but cannot have played this role on Balgzand, because of their scarcity.

Expressed in units of weight, the decline in cockle biomass between August 1990 and March 1991 amounted to 5.2 g AFDW per m<sup>2</sup> (viz. 5.4 g present in August and 0.2 g left in March). It is unknown which part of this loss between August and March should be attributed to predation by birds (in particular oystercatchers and eiders). Though the normal weight loss of specimens of this species in winter (BEUKEMA, 1974; ZWARTS, 1991; ZWARTS & WANINK, 1993) was unusually low during 1990/91, the contributions of cockle fishery (taking place mainly in the late summer of 1990) and a cold spell (in early February 1991) are unknown.

#### **b. *Macoma balthica***

Adult (>10 to 11 mm) *Macoma* are an important food type for oystercatchers in the Wadden Sea (HULSCHER, 1982, 1983), whereas these birds reject smaller *Macoma* (HULSCHER, 1982; ZWARTS *et al.*, in press). By far most (spring and summer) to about half (winter) of the individuals of this bivalve species live buried at depths sufficiently shallow to make grasping by oystercatchers easy (ZWARTS & WANINK, 1993; ZWARTS *et al.*, in press). They can be exploited successfully wherever their density in the intertidal is above about 200 per m<sup>2</sup> in winter and above about 50 in early summer (figure 27 of HULSCHER, 1982). Densities above 100 adults per m<sup>2</sup> (which could probably be profitably exploited in late summer and autumn) were generally present on significant parts of Balgzand: during the 1977-1993 period the proportion of the sampling areas (100-m stretches of the 12 transects of 1 km each) with such densities varied between 13 and 80%, with an average ( $\pm$  s.e.) of  $38 \pm 5\%$  (n=17). In August 1990, this proportion amounted to 24% of Balgzand, declining to 20% in March. However, densities >200 per m<sup>2</sup> were absent in March 1991. Thus, *Macoma* can be considered to be an exploitable alternative food source for oystercatchers feeding on Balgzand throughout the summer of 1990, but only during part of the

period August 1990/ March 1991. Unfortunately, no direct observations on feeding behaviour of oystercatchers on Balgzand are available. Death rates of *Macoma*, however, can be calculated from biannual (March and August) density estimates at 15 stations. If the *Macoma* population suffered extra mortality in 1990/91, this would be an indication of their wide-scale use as an alternative food for the lacking mussels and cockles.

Both during the spring/summer half year March - August 1990 and during the autumn/winter half year August 1990 - March 1991, the survival rates of adult *Macoma* were lower than in any other corresponding half-year period during the 16 years 1977-1993 (Fig. 6).

Since *Macoma* were numerous at all stations in all years, with particularly high numbers in the larger March samples, it is meaningful to calculate standard errors of mean annual death rates for March-to-March periods. To this end, death rates were expressed in instantaneous rates of mortality  $z$  ( $= \ln n$  in  $y(t+1)/ n$  in  $y(t)$ ). The 16-y mean annual death rate of the entire Balgzand population of adults amounted to  $0.46 \pm 0.02 \text{ y}^{-1}$  (the standard error reflecting the between-year variability). Between March 1990 and March 1991,  $z$  amounted to  $0.69 \text{ y}^{-1}$ , being 1½ times the long-term average and three standard deviations higher than this average. For the half-year period between August 1990 and March 1991,  $z$  amounted to 0.24, being again 1½ times the long-term average for this season.

The above mortality rates were calculated for the entire Balgzand population (from totals of the 15 sampling areas). To evaluate statistically the year-to-year differences in mortality, annual 15-station means (with standard errors reflecting the place-to-place variability) were also calculated. The mean for March 1990/ March 1991 amounted to  $0.70 \pm 0.08 \text{ y}^{-1}$ . In all other years of the 1977-1993 period, these means ranged from 0.30 to 0.51 with standard errors between 0.04 and 0.07. Thus, the 1990/91 value was significantly higher than any other mean value found so far.

Expressed in units of weight, the biomass decline between August 1990 and March 1991 amounted to about 1.2 g AFDW per m<sup>2</sup> (viz. 3.1 g in August and 1.9 g in March). This is an

estimate of the maximum amount of *Macoma* that predators such as oystercatchers and knots could have removed from Balgzand during this period, because this bivalve does not grow between August and March, but rather loses weight (BEUKEMA, 1974; BEUKEMA & DE BRUIN, 1977; ZWARTS, 1991). During the half year between August 1990 and March 1991 this individual weight loss was only modest (less than about 20% of the August weights), leaving a maximum of about 0.7 g per m<sup>2</sup> for predators.

### c. *Mya arenaria* and other molluscs

Oystercatchers feeding on *Mya* select specimens 15 to 40 mm long, rejecting sizes <15 mm and being unable to catch the deeply burrowed specimens of >40 mm length (ZWARTS & WANINK, 1984). Occasionally, however, they appear to grasp siphons of *Mya* bigger than 40 mm (ZWARTS *et al.*, in press). Therefore, the 'proper' (harvestable) size class was defined as the *Mya* of between 15 and 45 mm length.

Because age determination in *Mya* is difficult, mortality was studied only as changes in density of the three 10-mm size classes between 16 and 45 mm during the half-year periods with little growth, *i.e.* between August and March. Only data collected in 1984 or later were used, because August samples taken in 1983 or earlier were too shallow to include all of the bigger *Mya*. The proportions of the August numbers surviving to March varied strongly from year to year and were minimal in all three size classes in 1990/1991 (Fig. 7). Note that the size class of smaller *Mya* (16-25 mm) showed lower survival than the bigger ones in all years. In each of the three size classes, the survival rate in 1990/91 was the lowest of the 1984-1993 period.

Expressed in z units, the mortality of the 16-25 mm size group amounted to 2.2 in 1990/91, which is more than double the average (1.0) of the remaining 8 years of the 1984-1993 period. For the 26-35 and the 36-45 mm size groups this was similar: a more than 2 times higher-than-normal mortality in 1990/91.

In accordance with the more than doubling of the long-term mean mortality rates in 1990/91, the biomass of the 15-45 mm *Mya* declined by 61% between August 1990 and March 1991, as

compared to a long-term average of 28% for such half-year periods. It was the highest value of the 10-y period 1984-1993. Expressed in weight units, the decline between August 1990 and March 1991 amounted to 0.4 g AFDW per m<sup>2</sup> (*viz.* the difference between 0.7 g in August and 0.3 g in March). This loss can be attributed fully to mortality, as the usual (BEUKEMA, 1974; ZWARTS, 1991) individual weight losses in winter were absent in 1990/91.

Other molluscs that might serve as food for oystercatchers (such as *Scrobicularia plana*, *Angulus tenuis*, *Ensis directus* and *Littorina littorea*) are generally scarce on Balgzand. In August 1990, the biomass values of these species were all <0.1 g AFDW per m<sup>2</sup>. Taken together, the biomass of members of this group of a suitable size for oystercatchers amounted to only 0.2 g AFDW per m<sup>2</sup>, about half of which may have been taken by birds.

### d. Worm species

Most worm species living on tidal flats of the Dutch Wadden Sea are either too small (AFDW < 10 mg in most adult individuals; compare BOATES & GOSS-CUSTARD, 1989, for sizes preferred by oystercatchers) or occur at too low densities to serve as an important food source for oystercatchers (compare Table 1 of BEUKEMA, 1976, for a quantitative overall picture of numbers and biomass of the tidal-flat macrozoobenthos of the Dutch Wadden Sea). The only species with big specimens occurring at relatively high densities are lugworms, *Arenicola marina*, and the adults of the ragworm, *Nereis (Hediste) diversicolor*.

Adult *Nereis* are not expected to be an important prey for oystercatchers in winter. They live too deeply burrowed to be available as food for short-billed waders (ESSELINK & ZWARTS, 1989). Biomass values of this species declined by 50% between August 1990 and March 1991 and this value is close to the long-term average of 46% (n = 13: the years 1980-1993). Stronger declines than 50% were observed in 5 out of the 13 years.

Lugworms also live deeply buried. Oystercatchers cannot reach them as long as they stay in the deeper parts of their burrows. Occasionally, however, lugworms have to rise to the sediment surface to defecate. In the

Dutch Wadden Sea, they do so almost year-round, including mild periods in winter (CADÉE, 1976). Thus, lugworms may have been a potential prey for specialized oystercatchers during the 1990/1991 period. In August 1990, lugworms were relatively abundant on Balgzand: mean density amounted to 22 per m<sup>2</sup> and biomass values ranged from 0 to 23 g AFDW per m<sup>2</sup>, with an average of 8 g per m<sup>2</sup>. These averages declined to 14 individuals and 4 g per m<sup>2</sup> in March 1991. Both values were the lowest encountered on Balgzand since March 1977 and March 1980, respectively.

Because lugworms could not be aged above an age of one year, annual survival could be estimated only by comparing the numbers of all (juvenile + adult) worms in year  $n$  with the numbers of adults in year  $n+1$  (compare BEUKEMA & DE VLAS, 1979). March numbers were used for these estimates, as reliable summer numbers were not available for the earlier years. The annual survival rates thus estimated averaged 81% during the 1977-1993 period, but amounted to only 49% in 1990/1991. This was the lowest value of the 16 annual estimates and it was two standard deviations below the long-term average. Thus lugworm mortality between March 1990 and March 1991 was exceptionally high, amounting to  $51/19 = 2.7$  times the long-term mean. Between August 1990 and March 1991, the decline in lugworm biomass amounted to about 4 g AFDW per m<sup>2</sup>, including about 1 g accounted for by individual weight losses, thus leaving maximally 3 g per m<sup>2</sup> for predators.

Unfortunately, no direct observations are available on the prey choice and feeding locations of oystercatchers during the 1990/1991 winter, impeding any serious guess of the possible contribution of worms to the diet of birds normally for the greater part specialized in bivalves.

#### 4. DISCUSSION

In the course of 1990, both mussels and cockles became scarce on the tidal flats all over the Dutch Wadden Sea (DANKERS, 1993). On Balgzand, a fisherman cleared the last intertidal mussel beds completely in the early summer of 1990. In the summer of 1990, cockle stocks on

Balgzand were already below their long-term average (compare Fig. 2). The subsequent decline was dramatic: 98%, to an all-time low of 0.2 g per m<sup>2</sup> in March 1991. As argued above (part 3.3.a), the relative contributions to this decline of various factors could not be assessed. A significant part of the relatively low stock of cockles, and particularly of the denser banks, was probably removed already in late summer by cockle fishery. Cockle shortage for birds may thus have started already in late summer.

It is unlikely that birds could have taken more than about half of the total of 5.2 g AFDW per m<sup>2</sup> of cockles disappearing from Balgzand between August 1990 and March 1991, as cockle fishery (in late summer and early autumn) and other causes of mortality (in particular a cold spell in February 1991) took their (unknown) share as well. Probably no more than 2 or 3 g of cockles per m<sup>2</sup> can therefore have been taken by birds. This is one reason why oystercatchers (with a food demand estimated at 4.1 g per m<sup>2</sup>) and eiders will have needed alternative food in this period. The second reason is that no more than 1.6 g cockles per m<sup>2</sup> were available at densities above a threshold of 50 adult individuals per m<sup>2</sup>. Such areas, where profitable feeding on cockles was possible, were already small in August 1990 and will subsequently have disappeared quickly.

The need for alternative food of the numerous birds (oystercatchers, eiders) normally taking mussels and cockles as staple food, offers an obvious explanation for the enhanced mortality rates observed in each of the other two bivalve species that were both sufficiently numerous and of the right size for profitable consumption by these birds, viz. *Macoma* (Fig. 6) and *Mya* (Fig. 7). Maybe, the lower survival in lugworms in 1990/1991 was also caused by unusually high predation pressure exerted by birds.

A maximal estimate of the contribution of other bivalves than cockles and mussels to the food supply of bivalve consumers is about 0.7 (*Macoma*) + 0.4 (*Mya*) + 0.1 (other species) = 1.2 g AFDW per m<sup>2</sup>. Again, the actual amounts taken by birds must have been lower, because there will have been other causes of mortality. The maximal amounts of bivalves that could be removed by birds of 1.2 (alternative bivalves) +

5.2 (cockle) = 6.4 g per m<sup>2</sup> should be compared with the needs of the birds, amounting to 4.1 (oystercatcher) + 0.5 (knot) + unknown (eider) = at least about 5 g per m<sup>2</sup>. This would leave only about 1 g per m<sup>2</sup> (about 20% of the total bivalve losses) for other mortality factors, including fishery, abiotic factors, and biotic factors other than bird predation. Only if an improbable maximum of 3 g per m<sup>2</sup> of lugworms were taken by the oystercatchers, would maximally removable amounts of food between August 1990 and March 1991 increase to 9.4 g per m<sup>2</sup>, lowering the share of predation by the above three bird species to 55 instead of 80% of the decline of the biomass of the group of affected prey species.

It will be an extraordinary situation when bird predation accounts for a share of as much as 55 to 80% of total mortality over a longer period and a vast area. Usually, consumption by birds does not contribute much to mortality in tidal-flat fauna. The total annual food intake by birds on tidal flats was estimated by SMIT (1983) to amount to about 5 g AFDW per m<sup>2</sup>. Even if it has meanwhile increased to about 6 g per m<sup>2</sup> (due to higher numbers of birds in the Wadden Sea in recent years, compare ZEGERS & KWINT, 1992), this is only a modest share of the total annual macrozoobenthic production, estimated at 30 g per m<sup>2</sup> in the 1970's (BEUKEMA, 1983), but about 60 g per m<sup>2</sup> during the 1980's (compare BEUKEMA, 1991). However, birds may exert a higher predation pressure on tidal-flat macrozoobenthos in two conditions:

- (a) locally on concentrations of highly preferred and easily detectable food, such as mussel beds. Examples are reviewed by MEIRE (1993B). ZWARTS & DRENT (1981) describe an example of depletion by birds of such a food resource.
- (b) over vast areas if the preferred staple food is scarce and the birds have to concentrate on any (small) population of staple or alternative food still present. This may have happened in 1990/91 with the Balgzand populations of *Cerastoderma* (Fig. 5), *Mya* (Fig. 7) and *Macoma* (Fig. 6).

The extreme depletion of cockles observed on Balgzand in 1990/91 is remarkable in view of the widely accepted existence of threshold densities below which profitable foraging is

impossible (for oystercatchers and cockles, see HORWOOD & GOSS-CUSTARD, 1977; for oystercatchers and *Macoma*, see HULSCHER, 1982). Such threshold densities may often have been overestimated, because (a) birds may leave an area long before they reach the lowest threshold there or (b) birds may not always work with maximal effort (SWENNEN *et al.*, 1989). Nevertheless, threshold prey densities will exist for a bird foraging on a single prey species at a time. However, tidal flats generally supply a multispecies prey assemblage and birds will not reject an encountered cockle when searching for (a generally less preferred) *Macoma*. HULSCHER (1982) observed such mixed feeding in one of his field experiments: with 140 *Macoma* plus 62 *Cerastoderma* per m<sup>2</sup> available, the oystercatcher supplemented its *Macoma* intake with cockles. As long as the total prey density (e.g. *Cerastoderma* + *Macoma* + *Mya*) is above the threshold for profitable feeding, I expect that the prey most preferred or easiest to tract can be depleted to close-to-zero levels. This may have been the case in particular with cockles on Balgzand in 1990/91. Compare also figure 4A of MEIRE (1991) or the almost identical figure 7 of MEIRE (1993a), indicating the presence of oystercatchers (albeit in low densities) on tidal-flat plots with extremely low biomass of cockles and absence of mussels. Thus, a sharp threshold in cockle density might be absent if there is sufficient alternative prey in the same area.

The unprecedentedly low bivalve densities in early 1991 will have led to a precarious situation for birds specialized on bivalves. At the end of the winter, not only the areas with above-threshold prey densities had almost disappeared, but also the total amounts of food still present were almost exhausted. Fig. 2 shows that the amount of *Mya* in March could have met at most one or two weeks of food demand of oystercatchers at the February level, whereas the stock of *Macoma* would have been consumed in about two such months. Of course, the birds dependent on bivalves would have to leave Balgzand long before complete prey depletion, because of lack of areas with food densities above the threshold for profitable feeding. Actually, bivalve food stocks should be considered depleted by early March 1991.

There are indeed indications that birds left the tidal flats of the Dutch Wadden Sea by the end of the 1990/1991 winter: the unusually strong reduction in numbers of oystercatcher between the February and March counts at the high-tide roosts of Balgzand and the high numbers foraging in inland areas at that time (TANGER, 1993). This response to poor food stocks at tidal flats was also observed in subsequent years in various parts of the Wadden Sea (HULSCHER *et al.*, 1993) and around the Wash (CLARK, 1993). So far, mussels beds in most of the intertidal of the Dutch Wadden Sea did not recover. A high proportion of the eiders normally wintering in the Dutch Wadden Sea also left the area in the course of the 1990/1991 winter (VAN DE KUIP, 1991), a.o. to forage on *Spisula* in off-shore North Sea areas (LEOPOLD, 1993). A high proportion of shore crabs (*Carcinus maenas*) in their diet will have enhanced their parasite load, leading to higher mortality (VAN DE KUIP, 1991).

Birds that eat bivalves were in a poor condition in the 1990/1991 winter. In the first months of 1991, both eiders (VAN DE KUIP, 1991) and oystercatchers (CAMPHUYSEN, 1993; LAMBECK, pers. comm.) were found dead in higher numbers than normal. Such high numbers of dead oystercatchers are usually reported only during severe winters, whereas the character of the 1990/1991 winter was close to normal.

The precarious situation on Balgzand in early 1991 was not restricted to this part of the Wadden Sea. Scarcity of mussels and cockles was observed all over the Dutch Wadden Sea (VAN STRALEN & KESTELOO-HENDRIKSE, 1992; DANKERS, 1993). In terms of zoobenthic biomass, the Balgzand tidal-flat area is among the richest parts of the western half of the Dutch Wadden Sea (see the cluster of above-median biomass values on Balgzand in figure 1 of BEUKEMA, 1976). Balgzand is particularly rich in *Macoma* and *Mya*. The relatively high numbers of oystercatchers (as compared to foregoing years) in 1990/1991 on Balgzand may be explained by even worse feeding conditions in other parts of the Dutch Wadden Sea.

Part of the results presented in this paper are relevant for present policy decisions aiming at safeguarding food supply for birds in the Dutch

Wadden Sea. Predictions of minimal densities of cockles to be reserved for birds can only be made at a known level of abundance of alternative prey. If mussels are scarce too, birds specialized in large bivalves run into difficulties even at close-to-average densities of such possible alternatives as *Macoma* and *Mya*. The risk of occurrence of a simultaneous scarcity of mussels and cockles appears to be far from remote in the Wadden Sea (BEUKEMA *et al.*, 1993). Therefore, any indication of a fixed minimal density level of cockles to be reserved for birds from cockle fishery would be tricky. For the time being, protection of sufficiently large areas against fishery on benthic animals is a prerequisite for safeguarding bird life in the Wadden Sea. DANKERS (1993) arrives at a similar recommendation.

Acknowledgements.-Several colleagues commented on an earlier draft of this paper or answered my questions. I am particularly grateful to Kees Camphuysen, Norbert Dankers, Bruno Ens, Jan Hulscher, Rob Lambeck, Meindert Otter, Theunis Piersma, Cor Smit, Kees Swennen, and Leo Zwarts, who corrected a great deal of my shortcomings in know-how on birds.

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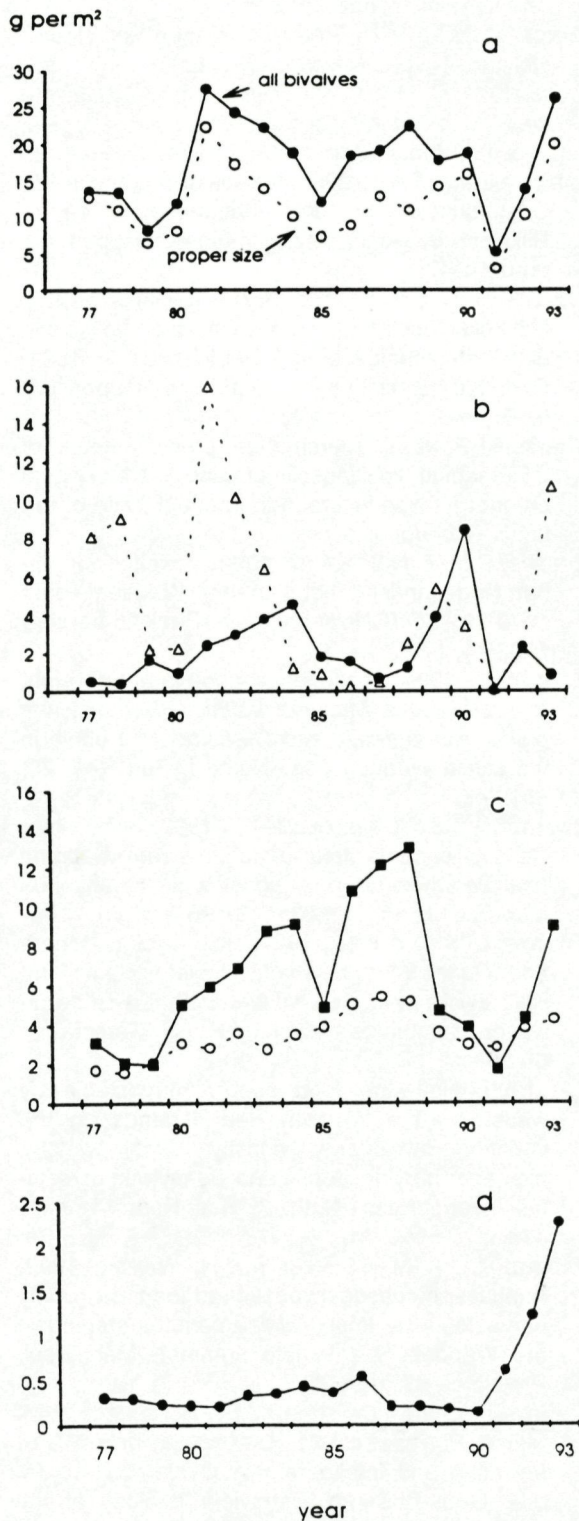


Fig. 1. Year-to-year changes of bivalve biomass in late winter during the 1977-1993 period on Balgzand (means of 15 stations).  
 (a) Totals of all size classes of all species (solid line) and (broken line) of those size groups that are suitable as food for oystercatchers, i.e. the sum of biomass estimates of (>10 mm) *Macoma balthica*, (>15 mm) *Cerastoderma edule*, (>20 mm) *Mytilus edulis*, and (15-45 mm) *Mya arenaria*.  
 (b) All *Mytilus* (solid line) and all *Cerastoderma* (broken line).  
 (c) All *Mya* (solid line) and all *Macoma* (broken line).  
 (d) Sum of all other bivalve species.

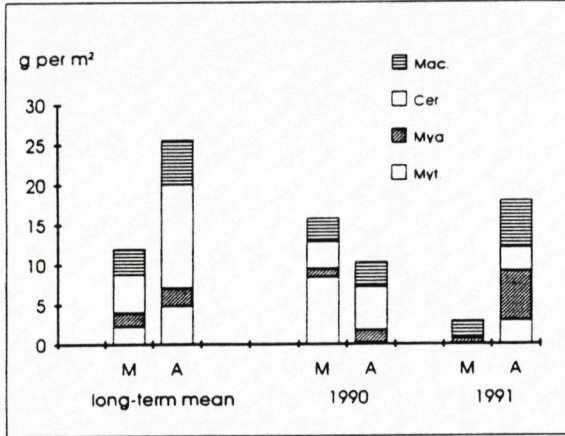


Fig. 2. Average (15-station) Balgzand values of biomass of bivalves suitable as food for oystercatchers (see legend of Fig. 1) in late winter (M = March) and in late summer (A = August) for three periods: means for the entire 16-y period 1977-1992 (long-term means), for 1990 and for 1991. The four important species are indicated by different shading.

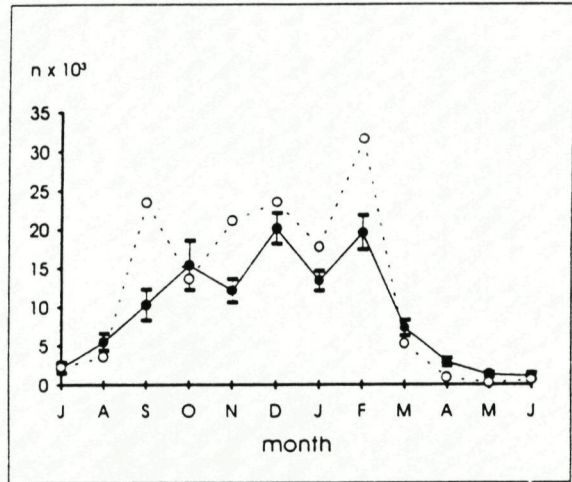


Fig. 3. Annual course of oystercatcher numbers counted monthly on Balgzand: (solid line) 15-year averages (1977-1991) with one standard error, and (broken line) numbers during the period July 1990-June 1991 (courtesy Ned. Ver. Bescherming Vogels and M. Otter).

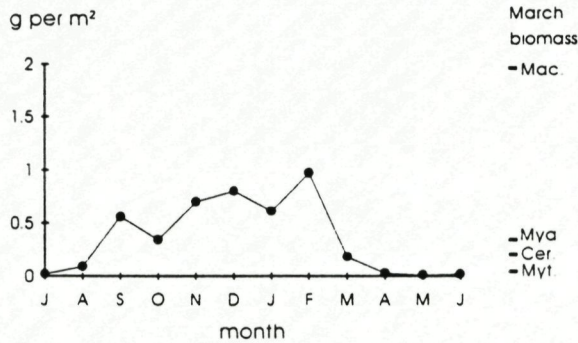


Fig. 4. Monthly estimates of total food intake per unit of area (expressed in g AFDW per m<sup>2</sup> per month) of the oystercatcher population on Balgzand during the period July 1990 to June 1991. At the right-hand side of this graph, the amounts of food still present in early March 1991 are indicated (in g AFDW per m<sup>2</sup>, proper-sized bivalves only).

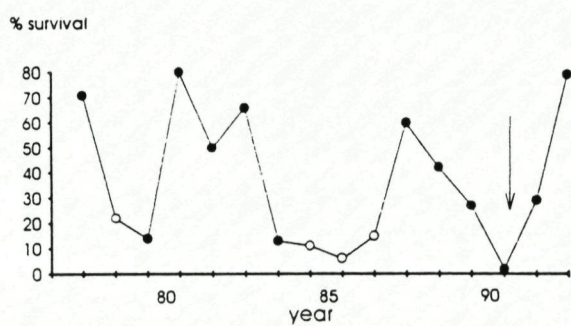


Fig. 5. Proportions (% of the number at the start of the period) of adult (1 or more y old) cockles, *Cerastoderma edule*, surviving between August and March in each of 16 years (1977-1993). Open points refer to periods including a cold winter. An arrow marks the point for 1990/91.

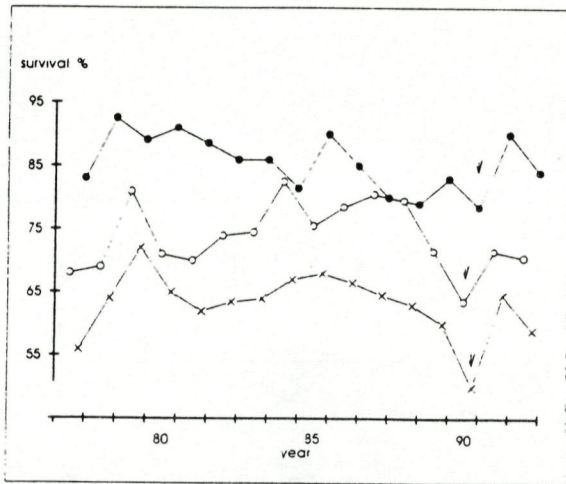


Fig. 6. Year-to-year changes during the 1977-1993 period in proportions (in % of initial numbers) of adult *Macoma balthica* surviving between August and March (●), between March and August (○), and between March and March (x). The points for the periods with extreme mussel and cockle scarcity marked by an arrow.

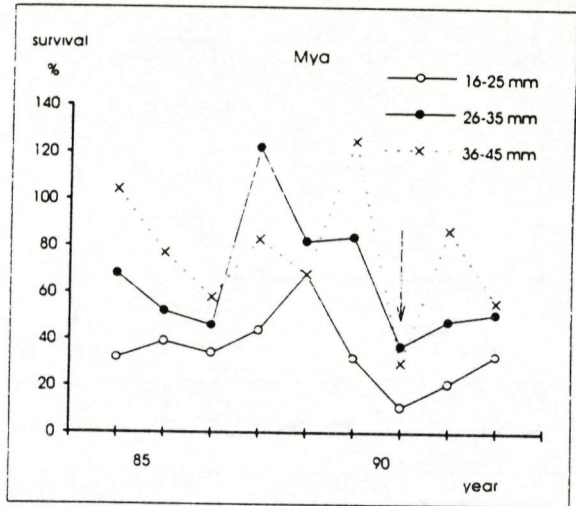


Fig. 7. Year-to-year changes during the 1984-1993 period in proportions (in % of initial numbers) of three size classes of *Mya arenaria* surviving between August and March. An arrow marks the points for 1990/91.

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