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Was total primary production in the western Wadden Sea stimulated by nitrogen loading?

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Abstract Borum and Sand-Jensen (1996) described empirical relationships between nitrogen (N) loadings from land and total (benthic + pelagic) primary production rates in shallow coastal marine waters. We applied these relationships to N loadings of the western Wadden Sea system, and compared the production estimates with actually observed primary production rates of autotrophic components (phytoplankton, microphytobenthos, macroalgae and seagrasses) for those years for which field data were available. During the 1980s and early 1990s, primary production values appear in good agreement with those derived from the empirical relationships. During the 1960s and early 1970s, however, these relationships substantially overestimated the total primary production in the western Wadden Sea. Based on ambient nutrient concentrations and the Redfield ratio, production in that period was considered not to be limited by N but by phosphorus (P) during most of the time. It is concluded that primary production is not invariably stimulated by N loading from land. If other factors (i.e. additional nutrient sources, N:P ratios, internal nutrient dynamics and co-limiting effects of nutrients and light) are not taken into account, management regulations that are targeted at diminishing the effects of eutrophication hold the risk of seriously under- or overestimating nutrient reductions that are thought necessary to achieve their goals.

Key words Nitrogen loading · Wadden Sea · Primary production · Eutrophication · Nutrient enrichment

Introduction

The fundamentals of eutrophication phenomena in coastal waters are best understood by including the effects of nu-

trient enrichment on all autotrophic components, i.e. phytoplankton, microphytobenthos, macroalgae and seagrasses. Nutrient enrichment in coastal waters is often accompanied by a shift from large slow-growing macrophytes to small fast-growing microalgae (Borum 1996; de Vries et al. 1996). Both in the field and the laboratory, eutrophication usually results in an increase in biomass of phytoplankton (Doering et al. 1989; Keller et al. 1990; Sullivan and Banzon 1990; Carlsson and Granéli 1993; Hofmann and Höfle 1993), microphytobenthos (Nilsson et al. 1991) and ephemeral macroalgae (Sfriso et al. 1989; Nilsson et al. 1991). Concurrent with these changes, the abundance of seagrasses and perennial macroalgae has been observed to decline (Borum 1983; Cambridge et al. 1986; Kautsky et al. 1986).

Primary producers obviously respond in different ways to nutrient enrichment, most probably depending on their specific life-history characteristics such as growth curves and storage capacities (Grover 1997). Slow-growing marine macrophytes such as seagrasses seem well adapted to coastal areas of low inorganic nutrient availability. Although microphytes such as phytoplankton have high specific growth rates, the macrophytes are better capable of meeting nutrient requirements because of their adequate uptake mechanisms, exploitation of internal stores and, for some species, internal nutrient cycling (Grover 1997). Hence, large macrophytes experience shorter periods of nutrient-limited growth than small, fast-growing plants. Small plants, such as planktonic algae, depend more on the immediate nutrient concentrations in the water column and require a constant and rich nutrient supply to sustain a high biomass and production (Borum 1996).

The eutrophication-induced shift towards more phytoplankton biomass often coincides with an increase in pelagic primary production (Oviatt et al. 1986; Sampou and Oviatt 1991; Borum and Sand-Jensen 1996). However, although eutrophication may change the species composition of a marine vegetation drastically, the summed primary production by all autotrophic components was stated not to be affected (Borum and Sand-

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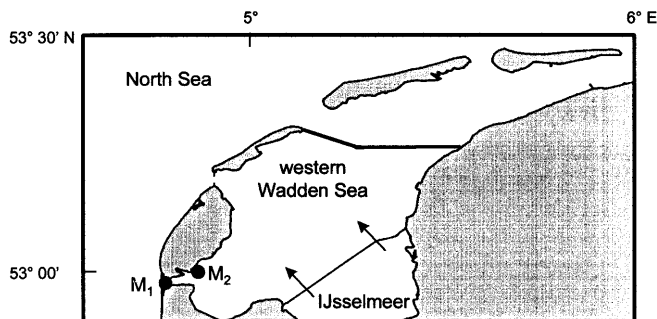


Fig. 1 Map of the western part of the Dutch Wadden Sea, showing locations of sampling stations of nutrient loadings from the freshwater lake IJsselmeer (arrows), and nutrient concentrations (M_1) and phytoplankton production (M_2) in the Marsdiep tidal inlet

Jensen 1996). In many shallow coastal marine waters (mean depths of less than 40 m), either phytoplankton or macrobenthic primary production (perennial macrophytes such as kelps and seagrasses) is high. Combined primary production rates, averaged across the entire ecosystem, remain more or less constant within a broad range of nitrogen (N) loadings (Borum and Sand-Jensen 1996).

In this paper, we examine the relationship between primary production and nutrient enrichment in the western part of the Dutch Wadden Sea (Fig. 1). This area experienced a gradual increase in N and phosphorus (P) loadings during the last decades (de Jonge and Postma 1974; van der Veer et al. 1989). We examine how different plant components responded to this nutrient enrichment, first according to the empirical relationships found by Borum and Sand-Jensen (1996) and then by comparing resulting estimates of primary production (pelagic, benthic and total) rates with actually observed values for those years for which field data were available. We discuss the applicability of the empirical relationship for our waters, other limiting factors, and address the implications for management regulations that aim to diminish the effects of eutrophication.

Methods and results

Production estimates

Estimates of total ($\text{PrimProd}_{\text{total}}$) and pelagic ($\text{PrimProd}_{\text{pelagic}}$) primary production rates ($\text{gC m}^{-2} \text{ year}^{-1}$) were based on total-N loadings ($\text{mol N m}^{-2} \text{ year}^{-1}$) according to the empirical relationships described by Borum and Sand-Jensen (1996) for shallow marine coastal waters:

$$\text{PrimProd}_{\text{total}} = 398 + 21 \log(N_{\text{loading}})$$

$$\text{PrimProd}_{\text{pelagic}} = 244 + 175 \log(N_{\text{loading}})$$

$$\text{PrimProd}_{\text{benthic}} = \text{PrimProd}_{\text{total}} - \text{PrimProd}_{\text{pelagic}}$$

Nutrient loadings were calculated by multiplying water-transport rates with corresponding nutrient concen-

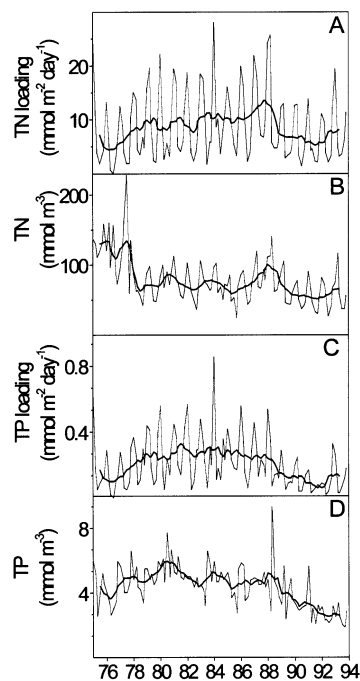


Fig. 2A–D Bi-monthly averaged time-series and 12-month running means in the western Wadden Sea from 1975 to 1993. **A** Total N loadings ($\text{mmol m}^{-2} \text{ day}^{-1}$); **B** total N concentrations (mmol m^{-3}); **C** total P loadings ($\text{mmol m}^{-2} \text{ day}^{-1}$); and **D** total P concentrations (mmol m^{-3}). Time series were taken from the water quality monitoring database (DONAR) of the Dutch Ministry of Transport and Public Works

trations. Data on transport rates and concentrations were taken from the water-quality monitoring database (DONAR) of the Dutch Ministry of Transport and Public Works. Loadings of the western Wadden Sea were determined as the summed outputs by the two sluices from the freshwater lake IJsselmeer (Fig. 1) divided by the surface area of the western part of the Dutch Wadden Sea ($1415 \cdot 10^6 \text{ m}^2$; Ridderinkhof et al. 1990).

Applying the empirical relationships on local N loadings (Fig. 2A), the total primary production in the western Wadden Sea was estimated to have been approximately $410 \text{ gC m}^{-2} \text{ year}^{-1}$ between 1974 and 1994 (Fig. 3A). Pelagic production rates would have been approximately $310 \text{ gC m}^{-2} \text{ year}^{-1}$ in the mid-1970s, $340 \text{ gC m}^{-2} \text{ year}^{-1}$ around the 1980s and roughly $320 \text{ gC m}^{-2} \text{ year}^{-1}$ during the early 1990s (Fig. 3B). Consequently, the coincident benthic production must have been almost $100 \text{ gC m}^{-2} \text{ year}^{-1}$, $70 \text{ gC m}^{-2} \text{ year}^{-1}$ and around $90 \text{ gC m}^{-2} \text{ year}^{-1}$, respectively (Fig. 3C).

Production measurements

Phytoplankton

Most field data on phytoplankton production in the western Wadden Sea were derived from a long-term sampling programme in the Marsdiep tidal inlet during high tide

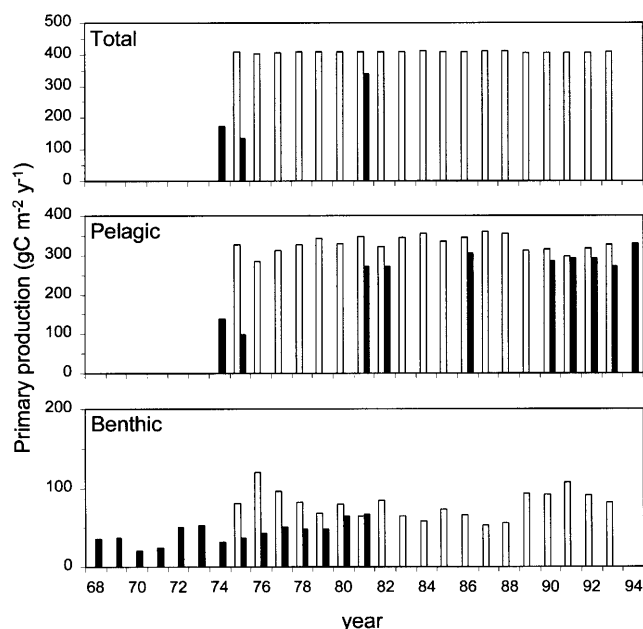


Fig. 3 Total (A; upper panel), pelagic (B; middle panel) and benthic (C; lower panel) primary production in the western Wadden Sea between 1968 and 1994. White bars indicate the production estimates as derived from N loadings from the freshwater lake IJsselmeer according to empirical relationships for shallow marine coastal areas supplied by Borum and Sand-Jensen (1996); solid bars show actual production values as measured in the study area

(M_2 in Fig. 1). Sampling frequency was generally once or twice a month, and more frequently, up to twice a week, during phytoplankton spring blooms. Primary production was measured in the laboratory in an incubator kept at in situ temperature, using a constant light source and the ^{14}C method (Cadée and Hegeman 1974a). In situ primary production was calculated from incubator production data, day length and depth of the euphotic zone (3 times Secchi depth), using the empirical formula of Cadée and Hegeman (1974a). In the Marsdiep tidal inlet, pelagic production was approximately $150 \text{ gC m}^{-2} \text{ year}^{-1}$ during the 1970s, and more than $300 \text{ gC m}^{-2} \text{ year}^{-1}$ in the 1980–1990s. From additional data on chlorophyll contents and algae densities in the Marsdiep tidal inlet, it was concluded that the doubling of pelagic production most probably occurred rather suddenly between 1976 and 1978 (Cadée 1986, 1992).

During the 1970s, phytoplankton production near the Marsdiep tidal inlet was approximately $150 \text{ gC m}^{-2} \text{ year}^{-1}$ (Cadée and Hegeman 1974a) and in the water column over the tidal flats around $20 \text{ gC m}^{-2} \text{ year}^{-1}$ (Cadée and Hegeman 1974b). Considering the geomorphologic properties of the western Wadden Sea (77% subtidal areas and 23% tidal flats; Hoppema 1991), we calculated the pelagic primary production rate of the western Wadden Sea to be $120 \text{ gC m}^{-2} \text{ year}^{-1}$ ($(150 \times 77 + 20 \times 23) / 100$) which is 80% of the production measured at the Marsdiep tidal inlet (Fig. 3B). Applying this ratio to Marsdiep measurements, resulted in pelagic production rates for the western Wadden Sea of less than $100 \text{ gC m}^{-2} \text{ year}^{-1}$ in the mid-

1970s, and more than $280 \text{ gC m}^{-2} \text{ year}^{-1}$ thereafter (Fig. 3B).

Microphytobenthos

Due to scarcity of measurements and methodological difficulties, primary production by benthic microflora in the study area is a very uncertain factor. In the top layer of the sediment at a monitoring station on a tidal flat in the western Wadden Sea, both the concentrations of chlorophyll and the rates of primary production of microphytobenthos increased between 1968 and 1981 from $100 \text{ gC m}^{-2} \text{ year}^{-1}$ to more than $200 \text{ gC m}^{-2} \text{ year}^{-1}$ (Cadée 1984). For the early 1970s, production by microphytobenthos was found to be $100 \text{ gC m}^{-2} \text{ year}^{-1}$ on tidal flats, $10 \text{ gC m}^{-2} \text{ year}^{-1}$ in relatively shallow waters and close to $0 \text{ gC m}^{-2} \text{ year}^{-1}$ in relatively deep subtidal areas (Cadée and Hegeman 1974b; Cadée 1980). Corrected for the geomorphologic properties of this particular area (Hoppema 1991) in a similar way as for pelagic production, the average primary production by benthic microflora in the western Wadden Sea is considered to be approximately 27% of the rates measured at the monitoring station. Applying this ratio to Marsdiep measurements resulted in microbenthos production rates for the western Wadden Sea of more than $40 \text{ gC m}^{-2} \text{ year}^{-1}$ in the mid-1970s, and almost $60 \text{ gC m}^{-2} \text{ year}^{-1}$ during the early 1980s.

Macroalgae

Measurements at a sheltered tidal flat in the western Wadden Sea resulted in an estimate of annual macroalgae production of approximately $15 \text{ gC m}^{-2} \text{ year}^{-1}$ (Goedheer 1977). Although on sheltered tidal flats macroalgae (mainly *Ulva* and *Enteromorpha*) may form a dense vegetation during summer in some years (e.g. 1969 and 1971; J.J. Beukema, personal communication), their average contribution to the total Wadden Sea primary production is considered to be relatively small, approximately $5 \text{ gC m}^{-2} \text{ year}^{-1}$ during the mid-1970s (Goedheer 1977; van den Hoek et al. 1979; Cadée 1980). Since no obvious changes in densities of macroalgae occurred in the western Wadden Sea thereafter (J.J. Beukema, personal communication; G.C. Cadée, personal observation), we assumed that primary production by the macroalgae remained more or less constant around $5 \text{ gC m}^{-2} \text{ year}^{-1}$ during the entire study period.

Seagrasses

At present, intertidal seagrass stands (mainly *Zostera noltii*) cover less than 1 km^2 in the western Wadden Sea (Philippart and Dijkema 1995). Based on a species-specific productivity range of dense seagrass stands of $190\text{--}800 \text{ gC m}^{-2} \text{ year}^{-1}$ (Hillman et al. 1989) and other

Table 1 Annual primary production ($\text{gC m}^{-2} \text{ year}^{-1}$) by autotrophic components in the western Wadden Sea as measured at a sampling station or averaged for several stations within an area. The location of the sampling station Marsdiep is presented in Fig. 1

Component	Period	Station/Area	Production	Source	
Phytoplankton	early 1950s	Marsdiep	20–40	Postma 1954; de Jonge 1997	
	1963–1965	Marsdiep	152 ^a	Postma and Rommets 1970	
	1963–1965	Interior western WS	93 ^a	Postma and Rommets 1970	
	1974	Marsdiep	172	Cadée (unpublished)	
	1975	Marsdiep	123	Cadée (unpublished)	
	1981–1982	Marsdiep	340	Cadée 1986	
	1986	Marsdiep	379	Cadée (unpublished)	
	1986	Western Wadden Sea	303	Veldhuis et al. 1988	
	1990	Marsdiep	354	Cadée (unpublished)	
	1991	Marsdiep	365	Cadée (unpublished)	
	1992	Marsdiep	365	Cadée (unpublished)	
	1993	Marsdiep	339	Cadée (unpublished)	
	1994	Marsdiep	412	Cadée (unpublished)	
	Micro-phytobenthos	1968	Tidal flat	111	Cadée 1984
1969		Tidal flat	116	Cadée 1984	
1970		Tidal flat	57	Cadée 1984	
1971		Tidal flat	68	Cadée 1984	
1972		Tidal flat	170	Cadée 1984	
1973		Tidal flat	176	Cadée 1984	
1974		Tidal flat	101	Cadée 1984	
1975		Tidal flat	116	Cadée 1984	
1976		Tidal flat	139	Cadée 1984	
1977		Tidal flat	169	Cadée 1984	
1978		Tidal flat	162	Cadée 1984	
1979		Tidal flat	160	Cadée 1984	
1980		Tidal flat	220	Cadée 1984	
1981		Tidal flat	230	Cadée 1984	
1968–1972		Tidal flat	100	Cadée and Hegeman 1974b; Cadée 1978	
1968–1972		Shallow subtidal	10	Cadée and Hegeman 1974b; Cadée 1978	
1968–1972		Deep subtidal	0	Cadée and Hegeman 1974b; Cadée 1978	
Macroalgae		1970s	Mok	5–26	Goedheer 1977
		1970s	Western Wadden Sea	1–10	Cadée 1980
Seagrasses	1950–1960	Western Wadden Sea	<1	van den Hoek et al. 1979	
	1972–1973	Western Wadden Sea	<1	van den Hoek et al. 1979	

^a After correction by Cadée and Hegeman (1974b)

estimates (see Table 1), we assume that the average primary production of seagrasses in the western Wadden Sea was close to $0 \text{ gC m}^{-2} \text{ year}^{-1}$ during the entire study period.

Comparison of production estimates and measurements

During the 1980s and 1990s, both the pelagic and total production estimates were in good agreement with the actual field data on primary production in the western Wadden Sea (Fig. 3B). In general, the phytoplankton production estimates of on average $330 \text{ gC m}^{-2} \text{ year}^{-1}$ were higher (by about 15%) than the actual measurements (actual mean value $280 \text{ gC m}^{-2} \text{ year}^{-1}$). In 1981, the estimate of the total production was approximately 20% higher than the sum of the actual production rates of phytoplankton, microphytobenthos and macroalgae (Fig. 3A).

During the 1970s, however, the estimated pelagic production of more than $300 \text{ gC m}^{-2} \text{ year}^{-1}$ was much higher than actually measured production for phytoplankton during this period, i.e. less than $100 \text{ gC m}^{-2} \text{ year}^{-1}$ (Fig. 3A). Because pelagic production represented the

main part of total production (>75%), similar differences between estimated ($400 \text{ gC m}^{-2} \text{ year}^{-1}$) and measured ($150 \text{ gC m}^{-2} \text{ year}^{-1}$) rates of total production were observed.

The measured values of pelagic production in the 1960s and early 1970s were more or less constant (about $150 \text{ gC m}^{-2} \text{ year}^{-1}$ for the Marsdiep tidal inlet) and consistent with chlorophyll and algae density data (Cadée 1986, 1992). We believe, therefore, that the model strongly overestimated the pelagic as well as the total production in the western Wadden Sea during the beginning of the study period.

Discussion

Growth-limiting nutrients for phytoplankton

During the 1980–1990s, the total and pelagic production estimates based on annual N loadings appear to be in good agreement with actually observed production rates in the western Wadden Sea (Fig. 3) and lie well within the range found for other shallow coastal marine waters (Borum and Sand-Jensen 1996). During the 1960–1970s,

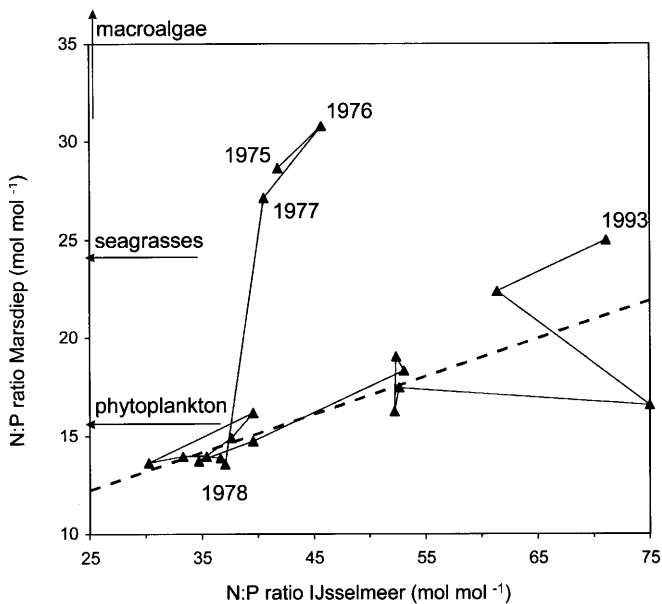


Fig. 4 Relationship between total N:P ratio of the nutrient loadings from the freshwater lake IJsselmeer and that of the concentrations in the Marsdiep tidal inlet from 1975 to 1993 (see Fig. 2). The *stippled line* indicates the linear relationship between these ratios for the period from 1978 to 1993 ($N:P_{\text{conc}} = 7.5 + 0.19 N:P_{\text{loading}}$; $P < 0.001$; $n = 16$)

however, the total- and pelagic-production estimates based on local N loadings were much too high compared with actual field values. This difference suggests that (1) primary production was probably not related to the supply of this particular nutrient but to another factor during the beginning of the study period, and (2) the Borum and Sand-Jensen model was not applicable to this situation, e.g. because primary production was not stimulated by N loading from land.

Loadings and concentrations

The N:P ratios of the discharged freshwater from IJsselmeer into the western Wadden Sea always exceeded the Redfield ratio of 16 (Fig. 4). However, this does not imply that P rather than N was the limiting factor for algal growth in these shallow marine waters (contra de Jonge et al. 1996). Due to mixing with other water masses and denitrification, the N:P ratios of ambient nutrient concentrations ($\text{ratio}_{\text{Marsdiep}}$) were generally lower than those of the loadings from land ($\text{ratio}_{\text{IJsselmeer}}$) between 1978 and 1993 (Fig. 4). Only between 1975 and 1977 were the N:P ratios of the ambient nutrient concentrations almost as high as those of the loadings.

Furthermore, nutrient budget calculations of the western Wadden Sea implied that before 1978 the nutrient loadings originating from the freshwater lake IJsselmeer

Fig. 5 Annual averages of P (A; upper panel) and N (B; lower panel) mass fluxes ($\text{mmol m}^{-2} \text{day}^{-1}$) of the western Wadden Sea between 1975 and 1993. The nutrient budget calculations were based on the hydrodynamic model by Ridderinkhof et al. (1990), and data on freshwater inputs and nutrient concentrations (114 bi-monthly averages) were taken from the water quality monitoring database (DONAR) of the Dutch Ministry of Transport and Public Works. The division into three different periods was based on indices for trophic state (indicated by annual averaged chlorophyll *a* concentrations) and TN:TP ratio (Philippart et al., 2000)

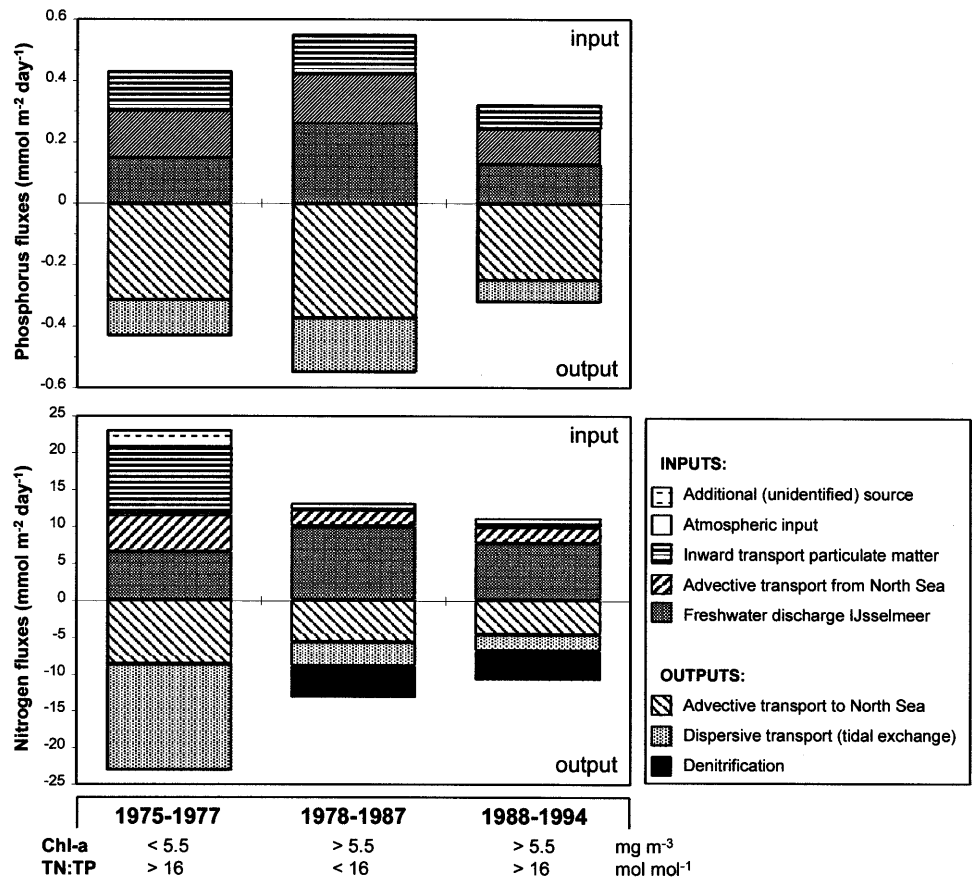


Table 2 Atomic N:P ratios in various marine autotrophic components

Component	Median value	<i>n</i>	Range	Source
Phytoplankton	16		–	Redfield et al. 1963
	17 ^a	69	–	Duarte 1992
Macroalgae	31 ^{b,c}	77	9–182	Atkinson and Smith 1983
	49	125	–	Duarte 1992
	71 ^a	125	–	Duarte 1992
Seagrasses	18 ^{b,d}	40	5–61	Atkinson and Smith 1983
	20 ^{b,e}	22	9–48	Atkinson and Smith 1983
	24 ^e	62	–	Duarte 1990
	27 ^a	135	–	Duarte 1992

^a Derived from empirical relationships (after correction of intercept values; $y=10^a x^b$)

^b Calculated from data supplied

^c Macroalgae include Chlorophyta, Cyanophyta, Phaeophyta and Rhodophyta

^d All parts of seagrass plants included

^e Restricted to seagrass leaves

comprised only a relatively small portion of the total nutrient input into the system, i.e. 35% for P and 28% for N (Philippart et al., 2000). At that time, the inward transport of organic matter from the North Sea was an important additional source of nutrients, i.e. more than 30% of total P inputs and almost 40% of total N inputs (Fig. 5). This flux remained more or less stable for P (about $0.11 \text{ mmol m}^{-2} \text{ day}^{-1}$), but its importance was substantially reduced for N from 1978 onwards, decreasing from 9.1 to $0.5 \text{ mmol m}^{-2} \text{ day}^{-1}$. From 1978 onwards, nutrient loadings from IJsselmeer represented 45% of the total P and 75% of the total N inputs.

Growth-limiting nutrients

The nutrient that limits primary production in a particular area is generally identified by a comparison of the ratio of the concentrations of the local nutrients in the water column with the contents of these nutrients in the specific autotrophic component. By comparing the ambient nutrient ratios and the Redfield ratio (N:P=16) which is generally considered to approximate phytoplankton composition (Redfield et al. 1963), it appears that phytoplankton growth in the western Wadden Sea was probably more limited by ambient P than by N concentrations before 1978 and after 1987 (Riegman et al. 1992; Philippart et al., 2000).

When examining growth-limiting nutrients for the other autotrophic components, it has to be considered that nutrient contents of marine macroalgae and seagrasses may deviate markedly from those of phytoplankton (see Table 2). Assuming that the N:P ratio of the nutrient contents of phytoplankton is 16 (Redfield et al. 1963), of macroalgae is 49 (Duarte 1992) and of seagrass is 24 (Duarte 1990), the limiting nutrient in the western Wadden Sea differed between years and between autotrophic components throughout the study period (Fig. 4). It has to be remembered that even relatively small differences in the taxonomic outcome of resource competition for nutrients may be followed by secondary and tertiary

effects which enhance the shift within autotrophic components. For example, elevated phytoplankton biomass decreases the photosynthetic activity of seagrasses and thereby affects their ability to reduce the toxic sulphide in the sediment (Hemminga 1998).

Co-limitation effects

Total primary production will not only depend on ambient nutrient concentrations but also on other properties of the study area such as morphometry, light climate and hydraulics (Nienhuis 1992; de Vries et al. 1996; Colijn 1982). Changes in these assets may therefore result in changes of the total primary production. In 1932, the former Zuiderzee was closed off from the western Wadden Sea by means of the Afsluitdijk. Because this engineering work had a severe effect on several properties such as the morphodynamics and hydraulics of the study area (Dijkema et al. 1980), we have to be cautious when extrapolating present production values to the period before 1932. From the 1930s onwards, however, no such major modifications were made and, as far as we know, neither were significant changes observed in freshwater discharges, salinity and water temperatures (e.g. van der Hoeven 1982; Cadée 1984; de Jonge 1997).

Possible changes in turbidity of Dutch Wadden Sea waters since the 1930s are still under discussion. Monitoring results at several sampling stations from the 1970s to the 1990s suggests an increase in suspended-matter concentrations up to the beginning of the 1980s followed by a decrease (de Jonge and de Jong 1992; de Jonge et al. 1996). However, part of these observed trends can be satisfactorily explained by systematic changes in sampling procedures (Maiwald and Verhagen 1991). Moreover, the Secchi-disk readings which were consistently taken at high tide in the Marsdiep tidal inlet by the second author between 1974 and 1990 did not indicate such changes in turbidity (Cadée and Hegeman 1991).

Furthermore, it has to be noted that during nutrient-limited growth at non-saturating irradiance levels, algae

enhance their nutrient quota and growth is sustained at higher substrate concentrations (Zevenboom et al. 1980; Rhee and Gotham 1981; Healey 1985; Riegman and Mur 1985; Riegman et al. 1985). From these studies, it can be concluded that in coastal areas where suboptimal light conditions prevail during summer periods due to high suspended matter levels, nutrients can still be limiting the specific growth rate at higher concentrations compared with waters with lower turbidity, as a consequence of co-limitation effects (R. Riegman, personal communication). Some indication for this mechanism is already apparent: during the past decade the P-discharge into the area has been gradually reduced by 50%, but a significant reduction in the average chlorophyll *a* during summer periods has not been observed until now (Cadée and Hegeman 1993; de Jonge 1997; R. Riegman, personal communication).

Conclusions

Although the production estimates derived from the empirical relationships as described by Borum and Sand-Jensen (1996) were in good agreement with actual production rates in the western Wadden Sea during the last two decades, the relationships substantially overestimated pelagic production during the 1960s and early 1970s. Our results strongly suggest that these relationships cannot be applied to the estimation of primary production in those coastal environments (1) in which other factors than the ambient N concentrations limit primary production, and (2) where availability of the actual limiting resource is not reflected in the N loadings from land.

For example, primary production in shallow marine waters may also be related to additional nutrient sources (e.g. inputs from the open sea), ambient concentrations of other nutrients (P, Si), co-limitation effects between nutrients and light, and rates of biochemical processes that affect nutrient loadings (e.g. denitrification rates). In addition, total primary production will be governed by the species composition, life-history characteristics and stoichiometry of the autotrophic components present. If these factors are not taken into account, management regulations that aim to diminish the effects of eutrophication hold the risk of seriously under- or overestimating the nutrient reductions which are thought necessary to obtain their goals.

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