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The importance of sediments in the transformation and turnover of nutrients and organic matter in the Wadden Sea and German Bight

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Summary

From 1994 through 1996 transformation processes in the water column of the German Bight and the adjacent Wadden Sea were investigated in the projects TRANSWATT and KUSTOS. On the basis of a review of carbon and nutrient budgets we examine the role of processes in the sediment for overall carbon and nutrient cycling in the Wadden Sea and adjacent German Bight. We distinguish two aspects: the sediment as the site where organic matter is rapidly turned over and the sediment as the site where organic matter and nutrients are immobilized. The relative importance of the sediment for the remineralisation of organic matter depends on the water depth: The review of carbon budgets suggests that in the Wadden Sea (2 - 3 m) about 50% of the remineralisation occurs in the sediment. In the German Bight (20 m) , 10 - 20% of the primary production is remineralised in the sediment. The budgets further show that the Wadden Sea is heterotrophic. About 100 gC m^{-2} y^{-1} is imported from the coastal zone. This implies a net autotrophy of the coastal zone, which is in line with the results from the projects TRANSWATT and KUSTOS. Within the Wadden Sea, organic matter has to be turned over two to three times and in the German Bight three to four times to explain the annual primary production. This is lower than in the offshore North Sea where annual turnover rates up to five have been found. Several processes remove nutrients on longer time-scales from the biogeochemical cycle. The importance of the local formation of phosphorus containing minerals like apatite as a phosphorus sink is shown. A discussion of several denitrification estimates concludes that in the German Bight and adjacent Wadden Sea on average about 8 - 16% of the total nitrogen influx (from the coastal zone, from rivers and via the atmosphere) is lost to the atmosphere.

Bedeutung der Sedimente in Umsatzprozessen von Nährstoffen und organischen Substanzen im Wattenmeer und der Deutschen Bucht (Zusammenfassung)

Von 1994 bis 1996 wurden Transformationsprozesse in der Wassersäule der Deutschen Bucht und des angrenzenden Wattenmeers im Rahmen der Projekte TRANSWATT und KUSTOS untersucht. Aufgrund eines Reviews von Kohlenstoff-und Nährstoffbudgets wurde die Bedeutung der Umsatzprozesse im Sediment des Wattenmeeres und der angrenzenden Deutschen Bucht erörtet. Zwei Aspekte wurden unterschieden: Das Sediment als der Ort, wo organische Substanz schnell umgesetzt wird, und das Sediment als der Ort, wo organische Substanz und Nährstoffe für längere Zeiträume festgelegt werden. Die relative Bedeutung von Sedimenten für den gesamten Kohlenstoffumsatz nimmt mit zunehmender Wassertiefe ab. Im flacheren Wattenmeer (2-3 m) wird etwa 50% des Kohlenstoffs in den Sedimenten veratmet, in der Deutschen Bucht (etwa 20m) nur noch 10-20 %. Die Budgets zeigen, dass das Wattenmeer heterotroph ist. Etwa 100 g C m^{-2} a^{-1} wird aus der Nordsee importiert. Die Implikation, daß die Küstenzone autotroph ist, stimmt mit den Ergebnissen von TRANSWATT und KUSTOS überein. Im Wattenmeer muß organische Substanz etwa 2 bis 3 mal und in der Deutschen Bucht etwa 3 bis 4 mal umgesetzt werden, um die annuelle Primärproduktion erklären zu können. Diese Raten sind niedriger als in der offenen Nordsee, wo annuelle Umsatzraten von etwa 5 mal gefunden wurden. Verschiedene Prozesse entfernen Nährstoffe für längere Zeit aus dem biogeochemischen Kreislauf. Im Wattenmeer werden phosphorhaltige Mineralien wie Apatite geformt, die eine bedeutende Phosphatsenke sind. Eine Diskussion der Denitrifikation in der Deutschen Bucht und im Wattenmeer zeigt, daß im Schnitt etwa 8 – 16% der gesamten Stickstoffimport in die Deutsche Bucht (via der Atmosphäre, durch Flüsse und durch Advektion aus dem Westen) an die Atmosphäre abgegeben wird.

1 Introduction

The remineralisation of organic matter in the coastal zone is dominated by water column processes accounting on average for 70 % of total carbon respiration (SMITH AND HOLLIBAUGH [1993]). In shallow areas, the importance of benthic processes can increase up to 50–60 % of total carbon metabolism (HEIP et al. [1995]). Although a large proportion of the organic matter is remineralised in the water column, the biogeochemical cycle of nutrients contained in the organic matter is strongly affected by processes within the sediment. For example, denitrification in sediments of the North Atlantic Ocean continental shelf and adjacent estuaries is thought to exceed the fluvial nitrogen input (GALLOWAY et al. [1996]), and formation of authigenic phosphorus minerals like apatites in shelf sediments has been suggested as an important phosphorus sink (RUTTENBERG AND BERNER [1993]; SLOMP et al. [1996a]).

In two interdisciplinary projects (TRANSWATT and KUSTOS) the transformation and transport of organic matter and nutrients was studied in the German Bight and adjacent Wadden Sea (SÜNDERMANN et al. [this volume]). The investigations focussed on water column processes. The aim of this contribution is to examine the importance of sediments for overall carbon and nutrient cycling in the Wadden Sea by means of a review of carbon and nutrient budgets. Our focus will be on annual budgets. In some cases (organic matter turnover, denitrification) our view will be extended to the German Bight.

As a guide through the budgets we will follow a simple black model: Carbon (in the form of organic matter) and nutrients are imported via atmosphere, via rivers and via the western borders of the German Bight or via the tidal inlets in the case of the Wadden Sea. Within the black box transformation of nutrients and organic matter takes place. These processes include primary production, remineralisation of imported and locally produced organic matter, transformation of nutrients and burial. Export takes place via the atmosphere, through sedimentation and via the northern border of the German Bight or via the tidal inlets. We assume a steady state when discussing budgets: For instance, release of nutrients from organic matter that accumulated during the previous season may enhance the productivity during the next season, but we will assume that during that season a similar amount will be retained.

Carbon budgets will be used to quantify the role of sediments in overall organic matter turnover. Several aspects, like the influence of depth on the relative amount of organic matter remineralised within sediments, import of organic matter and annual organic matter turnover rates will be discussed. Two aspects of organic matter cycling in sediments will be distinguished in the present study: the sediment as the site of organic matter turnover (on short time scales within one year) and the sediment as the site where organic matter and especially nutrients are immobilized on time scales of years and more. In regarding the sediment as a nutrient sink we will first discuss the short time retention of P by adsorption onto iron hydroxides. Then we will focus on the long term removal of P and N from the coastal biogeochemical cycle through the formation of P containing minerals and through denitrification. Both processes counteract to a certain extent anthropogenic input of nutrients into the coastal zone.

2 Study area

2.1 German Bight

The German Bight (Fig. 1) is situated in the southeastern part of the North Sea. The topography of the German Bight is dominated by the Elbe Rinne – an old river bed formed during the last ice age – which runs in an approximate southeast-northwest direction. The depth of the German Bight ranges from 10 m along the Wadden Sea to 43 m in the Elbe Rinne. The German Bight is characterized by a complicated hydrography (see KRAUSE et al. [1986]). Basically, a mixture of Atlantic water and continental runoff (mainly Rhine) enters the German Bight from the west and leaves to the north. The circulation patterns strongly depend on the wind pattern. The major rivers discharging into the German Bight are Ems, Weser and Elbe (see below). In the shallow parts along the Wadden Sea, the water column is permanently mixed due to strong tidal currents. The central part is seasonally stratified. The vertical density gradient is due to both thermal and salinity differences (see BECKER et al. [this volume]).

2.2 Wadden Sea

The Wadden Sea is a shallow coastal sea along the Dutch, German and Danish North Sea coast. The seaward border of the Wadden Sea is defined by the 10 m isobath. It has a length of approximately 450 km and covers an area of about 8000 km^2. Its width varies between 10 and more than 30 km. Twice daily the tidal flats, which comprise about 50 % of the entire region, are flooded during high tide. Along most of its length the inner Wadden Sea is protected from the North Sea by barrier islands. However, in the inner German Bight, where the tidal range exceeds 2.9 m, such barrier islands are missing. The Wadden Sea is intersected by several rivers, the most important of which are the Ems (mean discharge: 106 m^3 s^{-1}), the Weser (mean discharge: 327 m^3 s^{-1}) and the Elbe (mean discharge: 718 m^3 s^{-1}, LENHART et al. [1996]). The main freshwater discharge into the Dutch Wadden Sea is the IJsselmeer (726 m^3 s^{-1}). The German Wadden Sea is subdivided into the East Frisian Wadden Sea between the Ems estuary and the Elbe estuary and the North Frisian Wadden Sea between the Elbe estuary and the island of Sylt in the north (Fig. 1).

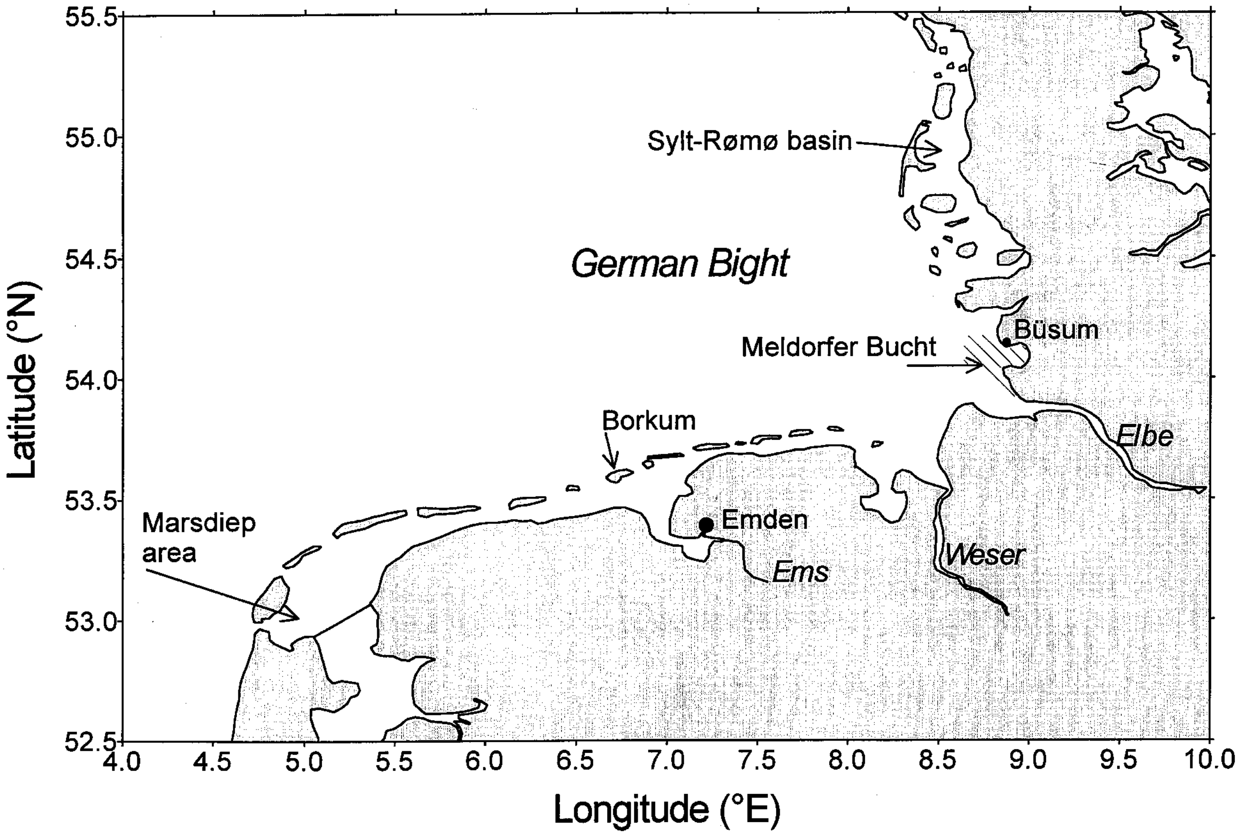

Fig. 1: Map of the German Bight and adjacent Wadden Sea showing the sites for which carbon budgets are presented.

3 Sediment as the site of organic matter turnover

In the German Bight proper most of the organic matter remineralisation (86 %: VON WESTERNHAGEN et al. [1986]) occurs in the water column. The importance of Wadden Sea sediments in overall organic matter turnover will be discussed on the basis of a review of carbon budgets. From these budgets the influence of depth on the amount of organic matter remineralised in the sediment and the amount of organic matter imported from the adjacent coastal zone into the Wadden Sea will be inferred. Furthermore, an estimate of the annual turnover rate of organic matter will be given.

3.1 Carbon budgets of the Wadden Sea and German Bight

One of the characteristics of the Wadden Sea is that it remineralises more organic matter than is locally produced (POSTMA [1954; 1984]). This hypothesis has been supported by phosphorus and carbon budgets from several parts of the Dutch Wadden Sea (DE JONGE AND POSTMA [1974]; DE WILDE AND BEUKEMA [1984]; BARETTA AND RUARDIJ [1988]; HOPPEMA [1991]). Other budgets were inconclusive (EON [1988]). For the German Wadden Sea only one carbon budget for the intertidal zone of the Sylt-Rømø basin has been formulated (ASMUS et al. [1998a]; ASMUS AND AMSUS [1998]). In this section we will review the available carbon budgets. We will discuss a carbon budget for the Marsdiep basin (western Dutch Wadden Sea) during the eighties, a carbon budget for the entire Sylt-Rømø basin (nineties) and for the Wadden Sea near Büsum (Meldorfer Bucht, nineties). The Marsdiep budget is based on investigations carried out mainly by the NIOZ (EON [1988]). The Sylt-Rømø budget is based on the results from the SWAP Project (Sylter Wadden Sea Exchange Processes; GÄTJE AND REISE [1998]) and in particular on a carbon budget of the intertidal part of the Sylt-Rømø basin (ASMUS et al. [1998a]). The Büsum budget is largely based on own observations in the water column, which are extended to the entire system on the basis of the other budgets. In addition, a carbon budget for the Ems estuary exists which is addressed in the discussion.

3.1.1 Marsdiep carbon budget (western Dutch Wadden Sea)

The revised Marsdiep budget is largely based on EON [1988], where a carbon budget for the entire Western Dutch Wadden Sea for the mid-eighties was proposed. At that time, the eutrophication of the Wadden Sea reached its maximum (e.g. CADÉE AND HEGEMAN [1993]; DE JONGE [1997]). In some points (benthic primary production, benthic aerobic respiration) we propose a different interpretation than EON [1988]. In summary, we suggest that the mean primary production (all compartments) amounts to 298 gC m^{-2} y^{-1}. The mean remineralisation amounts to 450 gC m^{-2} y^{-1} indicating a net organic matter import of 152 gC m^{-2} y^{-1} (Table 1).

The budget was derived as follows: We followed the areal division proposed by EON [1988; Table 2] into an intertidal area (area between mean high water and mean low water level, LWL), the subtidal area (area between the LWL and 5 meters below LWL) and the channels (depth >5 m below LWL). All estimates are summarized in Table 2.

Pelagic primary production (^{14}C) in the subtidal and channel area (300 gC m^{-2} y^{-1}) was taken from VELDHUIS et al. [1988; 250 gC m^{-2} y^{-1}] and multiplied by 1.2 (EON [1988]) to account for DOC excretion which was not measured. Pelagic production above the intertidal flats was taken from EON [1988; 42 gC m^{-2} y^{-1}]. This figure is based on measurements in the early 70s by CADÉE AND HEGEMAN [1974a, b], corrected for excretion as above and multiplied by 2.5 to account for the increased primary production between the early 70s (about 120 gC m^{-2} y^{-1}) and the mid-80s (about 300 gC m^{-2} y^{-1}).

Benthic primary production (^{14}C) of the intertidal area was taken from CADÉE [1984]. There is some confusion concerning benthic primary production. EON [1988] multiplied the mean benthic production of 130 gC m^{-2} y^{-1} reported by CADÉE AND HEGEMAN [1974a] by a factor of 2.5 to account for a possible

Area	Production	Remineralisation	Import	% Remin. sediment	source
Marsdiep basin	298	450	152	48	see Table 2
Sylt Rømø basin	309	419	110	42	see Table 3
Büsum	200	280	80	72	see Table 4
Ems estuary	210	290	80	47	a
German Bight	250[b]–420[c]	n.a.	n.a.	14[d]	b, c, d

a BARETTA AND RUARDIJ [1988]
b JOINT AND POMEROY [1993]
c RICK et al. [this volume]
d VON WESTERNHAGEN et al. [1986]
n. a. not applicable

Table 1: Carbon budgets of the Wadden Sea and German Bight. All values are given in gC m^{-2} y^{-1}. Details are given in Tables 2–4

Major geographic characteristics	Surface (10^6 m^2)	Tidal mean volume (10^6 m^3)	
Intertidal	144		
Subtidal	471		
Channel	128		
Total	743	3000	
Carbon budget	(gC m^{-2} y^{-1})	Whole area (10^9 gC y^{-1})	Reference
Pelagic prod. Subtidal	300	174	a, b
Pelagic prod. Intertidal	42	6	b, c, see text
Benthic prod. Intertidal	200	22	d
Benthic prod. Subtidal	15	7	b, c
Total production (mean)	**298**	**216**	
Pelagic rem. (gC m^{-3} y^{-1})	58	174	e
Benthic rem. Aerobic	100	74	f, see text
Benthic rem. Anaerobic	47	37	b, see text
Benthic C demand	80	49	g
Total remineralisation (mean)	**447**	**335**	

a VELDHUIS et al. [1988]
b EON [1988]
c CADÉE AND HEGEMAN [1994]
d CADÉE [1984]
e VAN DUYL AND KOP [1988, cited in EON [1988]]
f VAN DUYL AND KOP [1990]
g DE WILDE AND BEUKEMA [1984]

Table 2: A carbon budget of the Marsdiep basin (western Dutch Wadden Sea)

underestimation due to the applied measuring technique. No evidence is available yet to support this view for the Western Dutch Wadden Sea. We used 200 gC m^{-2} y^{-1} as the most recent figure reported by CADÉE [1984] which is reasonable compared to other production data from the 80s and 90s (ASMUS et al. [1998b]. Benthic primary production in the subtidal area (15 gC m^{-2} y^{-1}) was taken from EON [1988], which is based on CADÉE AND HEGEMAN [1974a].

Pelagic remineralisation (58 gC m^{-3} y^{-1}) was taken from VAN DUYL AND KOP [1988].

Benthic O_2 consumption includes aerobic bacterial remineralisation, macrobenthic respiration and the oxidation of reduced compounds that originate from anaerobic decomposition. We estimated benthic aerobic remineralisation at 227 gC m^{-2} y^{-1}. This value is based on observations by de WILDE AND BEUKEMA [1984], who measured a mean benthic respiration by oxygen uptake of incubated sediment cores, and on unpublished results by VAN DUYL AND KOP [1988; cited by EON, 1988]. DE WILDE AND BEUKEMA [1984] already indicated that the total respiration as measured by incubated sediment cores was underestimated by a factor of 2–3 due to undersampling of the macrobenthos and due to inhibition of bioturbation. They estimated a carbon remineralisation by the macrobenthos of 80–100 gC m^{-2} y^{-1}. Later measurements indicate that aerobic bacterial remineralisation alone already amounts to 100 gC m^{-2} y^{-1} (VAN DUYL AND KOP [1990]). We added to this number an anaerobic respiration of 47 gC m^{-2} y^{-1} (EON [1988]) and a macrobenthic respiration of 80 gC m^{-2} y^{-1} (DE WILDE AND BEUKEMA [1984]), giving a total benthic respiration of 227 gC m^{-2} y^{-1}.

3.1.2 Sylt Rømø carbon budget

The Sylt Rømø carbon budget (Table 3) is based on data from the SWAP Project (ASMUS et al. [1998a, b]; KRISTENSEN et al. [1998]) which was carried out between 1990 and 1995. During the SWAP project special emphasis was put on carbon budgets of the intertidal zone, taking into account the different benthic communities (e.g. ASMUS AND AMUS [1998]). Here we extend this budget to the entire basin. An updated carbon budget of the entire Sylt Rømø basin including yet unpublished data will be discussed elsewhere (ASMUS AND ASMUS [in prep.]).

The mean production in the entire region amounts to 309 gC m^{-2} y^{-1} (ASMUS et al. [1998b]). We estimate the mean remineralisation in the entire region at 419 gC m^{-2} y^{-1} implying a net import of organic matter of about 110 gC m^{-2} y^{-1}.

The above budget was derived as follows, largely on the basis of a carbon budget for the intertidal zone compiled by ASMUS et al. [1998a]:

Annual mean benthic plus phytoplankton primary production (both measured with the O_2 incubation method) was 296 gC m^{-2} y^{-1}. Seegrass production amounts to 3 % of total production giving a total production of 309 gC m^{-2} y^{-1}.

Mean respiration in the water column was 110 gC m^{-3} y^{-1} (R. ASMUS [pers. comm.]; see Fig. 2 in ASMUS et al. [1998b]).

The aerobic and total microbial remineralisation in the intertidal zone is based on sulfate reduction rates and community respiration rates reported by KRISTENSEN et al. [1998] and ASMUS et al. [1998a] and was estimated for the entire tidal zone at 40 and 94 gC m^{-2} y^{-1} respectively.

The macrobenthic carbon respiration was estimated at 98 gC m^{-2} y^{-1} (AMUS et al. [1998a]).

No benthic respiration measurements were carried out in the subtidal zone and in the deep channels. We estimated a macrobenthic carbon demand of 37 gC m^{-2} y^{-1} on the basis of a biomass of 11 gC m^{-2} (REISE AND LACKSCHEWITZ [1998]) by using a mean respiration/biomass ratio of 3.4 reported by ASMUS et al. [1998a; Table 8]. The microbial remineralisation was estimated by using the lowest rates (as measured on the "Arenicola" sandflats; 33 gC m^{-2} y^{-1} aerobic and 77 gC m^{-2} y^{-1} anaerobic; KRISTENSEN et al. [1998]).

Taking into account the geography of the Sylt Rømø Bight we estimate a mean aerobic remineralisation of 35 gC m^{-2} y^{-1}, a mean anaerobic remineralisation of 83 gC m^{-2} y^{-1}, a mean macrobenthic carbon demand of 57 gC m^{-2} y^{-1}.

Major geographic characteristics	Surface (10^6 m^2)	Tidal Mean Volume (10^6 m^3)	
Intertidal	135		
Subtidal	231		
Channel	40		
Total	406	900	
Carbon budget	(gC m^{-2} y^{-1})	Whole area (10^9 gC y^{-1})	reference
Pelagic Phytoplankton Production	160	65	a, b
Pelagic Phytobenthos Production	136	55	a, b
benthic Seagrass production	13	5	a, b
Total Production (mean)	**309**	**125**	b
Pelagic Remin. (gC m^{-3} y^{-1})	110	99	b, c
Benthic Rem. Aerobic	35	14	b, d
Benthic Rem. Anaerobic	83	34	b, d, see text
Benthic C demand Macrobenthos	57	23	b, e, see text
Total Remineralisation (mean)	**419**	**170**	

a ASMUS et al. [1998a]
b ASMUS et al. [1998b]
c R. ASMUS, [personal communication]
d KRISTENSEN et. al. [1998]
e REISE AND LACKSCHEWITZ [1998]

Table 3: A carbon budget of Sylt-Rømø basin

3.1.3 The Meldorfer Bucht/Büsum carbon budget

The Meldorfer Bucht/Büsum carbon budget (Table 4) is based on regular measurements of phytoplankton primary production (150 gC m^{-2} y^{-1}) and water column respiration (38 gC m^{-2} y^{-1}) near Büsum by TILLMANN et al. [2000]. These data were extended to the area shown in Figure 1 by assuming a phytobenthos primary production of 200 gC m^{-2} y^{-1} (mean of the Western Dutch Wadden Sea, Ems, Elbe and Sylt-Rømø basin). The benthic respiration values are the means for the Western Dutch Wadden Sea and the Sylt-Rømø basin (see Table 4). The assumptions for the benthic compartment imply that the budget to some extent is forced to resemble the other Wadden Sea budgets.

3.1.4 Other budgets

Apart from the above discussed budgets three further budgets exist. For the Western Dutch Wadden Sea (1949–1951), POSTMA [1954] estimated, on the basis of chlorophyll data and phosphate gradients, a local primary production of about 80 gC m^{-2} y^{-1}, an import of organic matter of 80 gC m^{-2} y^{-1} and a remineralisation of about 160 gC m^{-2} y^{-1} (assuming a C:P weight ratio of 40:1). CADÉE [1980] discussed that the primary production estimate should be used with care. However, the data do indicate the order of magnitude.

DE JONGE AND POSTMA [1974] compared phosphorus data from the Western Dutch Wadden Sea from 1970–1971 with the former data (1949–1951).

Major geographic characteristics	Surface (10^6 m^2)	Tidal mean volume (10^6 m^3)	
Intertidal	248		
Subtidal	191		
Channel	0		
Total	439	896	
Carbon budget	(gC m^{-2} y^{-1})	Whole area (10^9 gC y^{-1})	Reference
Pelagic prod. Subtidal	150	29	Own observations
Pelagic prod. Intertidal	15	4	b, c, d; see text
Benthic prod. Intertidal	200	50	e
Benthic prod. Subtidal	30	6	
Total production (mean)	**200**	**88**	b
Pelagic remineralisation (gC m^{-3} y^{-1})	38	34	Own observations
Benthic rem. Aerobic	67	29	e
Benthic rem. Anaerobic	67	29	e
Benthic C demand Macrobenthos	69	30	e
Total remineralisation (mean)	**281**	**123**	

a CADÉE AND HEGEMANN [1974]
a GÄTJE [1992]
b BARETTA AND RUADIJ [1988]
c ASMUS et al. [1998b]
e Mean values Sylt-Rømø basin and Western Dutch Wadden Sea (Tables 2 and 3)

Table 4: A carbon budget of the Meldorfer Bucht near Büsum

They observed a twofold increase in particulate organic P concentrations and a threefold increase in phosphate release. DE JONGE AND POSTMA [1974] suggested that the import of organic matter from the North Sea into the Wadden Sea had tripled whereas the local production had remained unchanged. We hesitate to used their budget for the following reason. A large part of the phosphorus load into the North Sea is in the form of particulate Fe-bound P (SALOMONS AND GERRITSE [1981]; VAN BEUSEKOM AND BROCKMANN [1998]). This implies that estimates of organic matter import based on amounts of released phosphate overestimate the import of organic matter. The comparison by DE JONGE AND POSTMA [1974] unambiguously indicates the increased eutrophication of the Western Dutch Wadden Sea between 1950 and 1970. However, their suggestion of an increased organic matter import by a factor of three to 320 gC m^{-2} y^{-1} (calulated assuming a C:P weight ratio of 40 in organic matter) probably overestimated the import.

A third carbon budget available for the Wadden Sea is based on investigations in the Ems Dollard estuary between 1977 and 1982 (BARETTA AND RUARDY [1988]; COLIJN [1983]). These data are based on an ecosystem model and have been used as published.

3.2 Implications of the carbon budgets

The above carbon budgets will be used to discuss three aspects of the carbon cycle: 1) the influence of depth, 2) the import of organic matter and 3) the annual turnover of organic matter.

3.2.1 Influence of depth

The relative importance of the sediment as the site where organic matter is remineralised depends on the water depth. In the Wadden Sea (mean depth: 2–3 m) about 50 % of the system respiration occurs in the water column (range: 28–58 %; see Table 1). With increasing depth the importance of sediment in organic matter remineralisation decreases. VON WESTERNHAGEN et al. [1986] calculated that in the German Bight about 86 % of the total respiration occurs in the water column. BEDDIG et al. [1997] estimated that in the German Bight 90 % of the total respiration occurs in the water column based on extrapolated benthic nitrogen fluxes measured by LOHSE et al. [1993]. Figure 2 shows that the estimate of 50 % benthic respiration in the Wadden Sea and about 10 % benthic respiration in the German Bight fits within the general trend found by HEIP et al. [1995]. This trend indicates that the importance of sediment respiration decreases exponentially with depth. The rationale given by HEIP et al. [1995] for this relationship was that of a newly formed particle at the surface having a sinking velocity of about 2.3 m day^{-1} combined with an exponentially decreasing remineralisation rate.

3.2.2 Import of organic matter

The budgets are not for the same period of time, and therefore cannot be compared directly. We assume, however, that the function of the Wadden Sea as importer of organic matter has not changed. In Figure 3 the total annual primary production estimates for the different parts of the Wadden Sea have been plotted against total annual remineralisation. To put these data in a historic perspective, the first Wadden Sea budget proposed by POSTMA [1954] is included. Although his budget should be treated with care (see also CADÉE [1980]), it gives an idea of the changes that took place during the last decades (DE JONGE AND POSTMA [1974]; DE JONGE [1990]). Two trends are evident from Figure 3: Firstly, remineralisation is always larger than primary production (compare Table 1) and secondly, remineralisation is correlated with primary productivity.

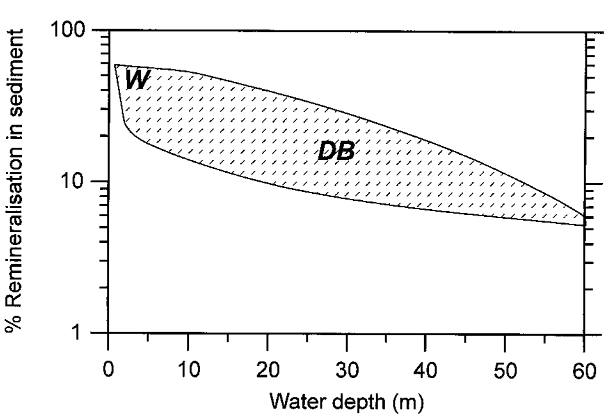

Fig. 2: Influence of water depth on the relative importance of sediment respiration compared to total respiration in sediment and in the water column (modified after HEIP et al. [1995]).
DB: German Bight
W: Wadden Sea

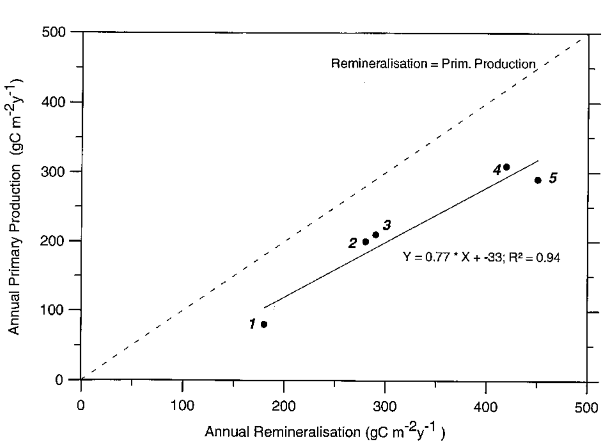

Fig. 3: Relationship between annual respiration and primary production in the Wadden Sea. 1: Western Dutch Wadden Sea 1949–1951 (POSTMA [1954]); 2: Meldorfer Bucht (Table 1, 4); 3: Ems Dollard Estuary (BARETTA AND RUARDIJ [1988]); 4: Western Dutch Wadden Sea (Table 1, 2); 5: Sylt Rømø basin (Table 1, 3).

Within the Wadden Sea a surplus of 80–150 gC m^{-2} y^{-1} is remineralised, implying an additional import of organic matter. Two sources have to be taken into account: import from the coastal zone and import from freshwater sources. In the Marsdiep area, import of organic matter from the IJsselmeer accounts for an organic matter remineralisation of 56 gC m^{-2} y^{-1} (HOPPEMA [1991]) or about 1/3 of the overall excess remineralisation (Table 1). This implies an organic matter import from the North Sea of about 100 gC m^{-2} y^{-1}. Model calculations for the Ems estuary indicate that in the late seventies about 65 % of the surplus organic matter remineralisation was due to import from freshwater sources, including waste water discharges into the Dollard. These discharges, which originated from potato mills, have ceased since 1991. At present, about one third of the organic matter import (as organic P) into the estuary is derived from freshwater sources and two-thirds is imported from sea (VAN BEUSEKOM AND DE JONGE [1998]; see Table 5). This is a similar ratio as in the Western Dutch Wadden Sea. It should be noted that the quality of organic matter that is imported via rivers into the Wadden Sea and its estuaries can range from readily degradable organic matter like freshwater phytoplankton blooms (e.g HOPPEMA [1991]; VAN BEUSEKOM AND BROCKMANN [1998]) to highly degraded dissolved organic matter that passes nearly unchanged through estuaries (LAANE [1980]).

For the Meldorfer Bucht area near Büsum, no data are available from which the relative contribution of marine and freshwater sources to the surplus remineralisation could be inferred. However, in the Sylt-Rømø Bight, freshwater input is negligible (ASMUS AND ASMUS [1998]) and it is safe to assume that the excess remineralisation (110 gC m^{-2} y^{-1}) is due to import from the North Sea.

We will use 100 gC m^{-2} y^{-1} as a first approximation of organic carbon of present-day import from sea into the Wadden Sea. This estimate is lower than the 200 gC m^{-2} y^{-1} proposed by POSTMA [1984], but constrained with several budgets. The uncertainty inherent in the budgets should be borne in mind. For instance, the scale of the incubation techniques significantly changes the outcome of the measurements (ASMUS et al. [1998c]). The estimate is based on budgets from different years and from different areas, which makes a comparison difficult. Year-to-year variation in offshore production may lead to interannual variability in the amount of organic matter imported into the Wadden Sea. Model calculations as for the Ems estuary) may show deviations from measured data (VELDHUIS et al. [1988]).

A net import of about 100 gC m^{-2} y^{-1} from the North Sea suggests that the coastal zone is autotrophic. The net autotrophy of the inner German Bight, the import of organic matter into the Wadden Sea and the heterotrophic nature of the Wadden Sea are supported by the measurements carried out in the TRANSWATT/KUSTOS project (RICK et al. [submitted]; DICK et al. [this volume]; REIMER et al. [this volume]).

3.2.3 Organic matter turnover

Primary production is fueled by advected nutrients (new production) and locally remineralised nutrients (regenerated production). The results of the KUSTOS/TRANSWATT experiments show that during summer remineralisation plays an important role in sustaining a high productivity in the German Bight (BROCKMANN et al. [this volume]; POHLMANN et al. [this volume]; REIMER et al. [this volume]; RICK et al. [submitted]). How important these processes are on an annual scale could not be assessed by direct measurements. In the following section evidence will be compiled that in the North Sea and adjacent Wadden Sea the annual turnover rate is between 2 and 5. In general, the annual turnover rate in turbid areas is lower than in clear, offshore regions.

A comparison of the annual primary production of the German Bight with nitrate stocks before the onset of the spring phytoplankton bloom and the import of nitrogen during the growth period suggests a turnover rate of three to four. This is derived as follows: In the German Bight the annual primary production amounts to 260–420 gC m^{-2} y^{-1} (JOINT AND POMROY [1993]; RICK et al. [submitted]). We will adopt a mean value of 340 gC m^{-2} y^{-1} equal to 60 gN m^{-2} y^{-1}, or 120 • 10^{10} gN y^{-1} for the entire German Bight. The depth-weighted average amount of NO_3 at the start of the growing season amounts to about 9 gN m^{-2} (10 • 10^{10} gN for the entire German Bight). During summer (April - September) about 10 • 10^{10} gN is additionally imported into the German Bight via the rivers Ems, Weser and Elbe (calculated from LENHART et al. [1996]). Input via the atmosphere (3 • 10^{10} gN, calculated from BEDDIG et al. [1997]) and denitrification (see below) at least cancel each other out. To explain a primary production of 120 • 10^{10} gN y^{-1} the available amount of nitrogen (28 • 10^{10} gN y^{-1}) has to be recycled about three to four times.

HYDES et al. [1999] compared the annual primary production in the entire southern North Sea (JOINT AND POMROY [1993]) in a similar way as described above with the amount of nitrate available in March before the onset of the spring phytoplankton bloom and the nitrogen load by rivers and atmosphere during the growth period. They concluded a turnover of five times for ICES Box 7' (central North Sea), ICES Box 4 (Dutch coastal zone) and ICES Box 5 (German Bight). In ICES Box 3b (English east coast) a lower factor of 2 was calculated. The latter low value was explained by the adverse light conditions suppressing primary production in this area.

Both estimates for the German Bight indicate a similar annual turnover rate (3–5). Possibly, the difference is related to the fact that our estimate (3–4) covers the entire (inner and outer) German Bight, whereas the turnover rate of five by HYDES et al. [1999] is based on the NERC Project which only covered the less turbid, outer German Bight.

HEIP et al. [1995] reviewed carbon budgets in temperate coastal zones and suggested that nutrients are turned over three to four times before they are removed from the system. Based on a plot of the net remineralisation against primary production, HEIP et al. [1995] discerned two types of coastal zones (Fig. 4): light limited and light saturated areas. In the light limited coastal areas annual primary production never exceeded 160 gC m^{-2} y^{-1}, irrespective of the amount of imported organic matter. In light sufficient areas a positive relation was found between surplus remineralisation (organic matter import) and primary production. To explain the annual primary production exclusively on the basis of nutrients from remineralized imported organic matter, nutrients had to be turned over three to four times. The annual turnover rates calculated by HEIP et al. [1995] did not take into account the amount of nutrients present before the onset of the spring bloom nor nutrient input from freshwater sources or from the sea. These are all nutrient sources that do not depend on imported and locally remineralised organic matter but which may contribute to local annual primary production.

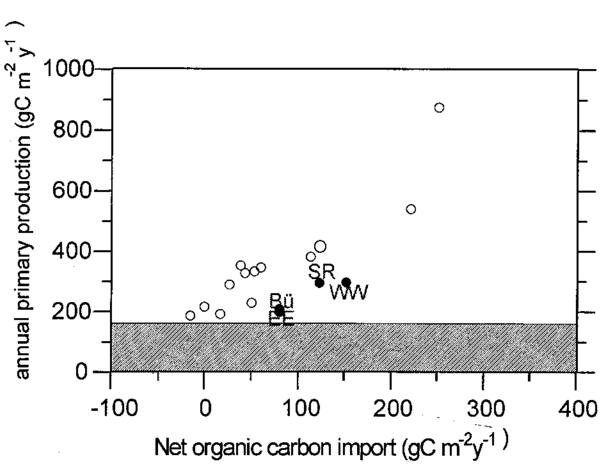

Fig. 4: Tentative relationship between net organic matter import and primary production (modified after HEIP et al. [1995], where the data used for this plot are listed). Below a level of 160 gC m^{-2} y^{-1} the annual primary production is assumed to be light limited (hatched area; see also HEIP et al. [1995]).

The Wadden Sea data show a relation between organic matter import (= excess remineralisation; see Fig. 3) and primary production. However, primary production is lower than the relationship suggested by HEIP et al. [1995; see Fig. 4] for light saturated areas, suggesting lower turnover rates for the the Wadden Sea.

Available Wadden Sea carbon budgets suggest a turnover time of about two to three times: A nutrient budget of the Ems estuary (VAN BEUSEKOM AND DE JONGE [1998]) showed that during summer the total nitrogen input (river and import from sea) could merely explain about 25–35 % of the primary production. This indicates that nutrients are turned over about two to three times within the estuary. Also the Sylt-Rømø basin budget supports a similar turnover rate: A three-fold turnover of the imported organic matter (about 100 gC m^{-2} y^{-1}) can acount for the annual primary production of 309 gC m^{-2} y^{-1}. Primary production based on available nitrogen in the water column is less important: The winter DIN concentrations amount to about 80 µM. Freshwater input is negligible (ASMUS AND ASMUS [1998a]). Given a mean depth of 2.5 m this enables a new production of 15 gC m^{-2} y^{-1}. Applying an annual turnover of about three, this biomass can only explain 20 % of the annual primary production of 309 gC m^{-2} y^{-1}. Of course, nitrogen release from organic matter that accumulated during the previous years can fuel local primary production. In the above calculation, however, we assumed steady state: On an annual basis, nitrogen release from the sediment is compensated for by an equal nitrogen flux into the sediment.

The above estimates suggest a gradient from the open North Sea, with annual turnover rates of about 5, to turnover times of about two to three in turbid coastal areas like the Wadden Sea. This gradient reflects the fact that in the Wadden Sea the local primary producers cannot take full advantage of the nutrient load. It is in line with the Wadden Sea primary production being light limited (e.g. COLIJN [1983]; VELDHUIS et al. [1988]; TILLMANN et al. [2000]). However, the positive relation between organic matter import and primary production (Fig. 3; see also the above mentioned Sylt Rømø budget) suggests that despite a certain level of light limitation, primary production is enhanced by increased nutrient input. The increased primary production in the Wadden Sea due to coastal eutrophication (CADÉE AND HEGEMAN [1993]; DE JONGE [1997]; ASMUS et al. [1998b]) supports this view. This suggests that at least during some stage in the seasonal cycle nutrient limitation occurs, which is supported by the very low nitrogen levels observed during summer in the Wadden Sea (HESSE et al. [1995]; VAN BEUSEKOM AND DE JONGE [1998]).

The turnover rates of about three for the Wadden Sea probably do not indicate a true rate in the sense that it expresses the degradability of the organic matter. Rather, it expresses the efficiency with which the primary producers can take advantage of the available nutrients. The low turnover rates suggest that the Wadden Sea productivity is very susceptible to changes in light regime (cf. DE JONGE et al. [1996]). Recently, CLOERN [1999] proposed an index for the relative importance of light and nutrient limitation in coastal areas as a measure for the susceptability to nutrient enrichment. He showed that in some areas a colimitation of nutrients and light can occur. It would be interesting to test whether his index also predicts a colimitation for the Wadden Sea.

The maximum annual turnover rates of primary produced organic matter in the North Sea are about five. These are annual averages: For instance, in the German Bight during spring a simple transformation from dissolved to particulate nutrients was observed. The rates of transformation were in good agreement with primary production. In summer, the primary production rates indicate an intense turnover on the order of days (BROCKMANN et al. 1999a, 1999b [this volume]; POHLMANN et al. [this volume]; REIMER et al. [this volume]; RICK et al. [submitted]).

4 Sediment as a sink for nutrients

In the previous section the importance of the sediment as a site of organic matter turnover was discussed. This section addresses the sediment as a sink for nutrients. We will not discuss carbon burial which is negligible in Wadden Sea carbon budgets (EON [1988]; BARETTA AND RUARDIJ [1988]). Most of the remineralised organic carbon is either exported as dissolved inorganic carbon or is exported as carbon dioxide to the atmosphere. This contrasts with the biogeochemical cycle of nutrients: In the following section it will be shown that biogeochemical cycles in the coastal zone are significantly altered by benthic processes. We will discuss two aspects of the biogeochemical phosphorus cycle: phosphorus retention on short time scales (months) through the adsorption to iron hydroxides and retention on longer time scales (years and more) through the formation of stable phosphorus minerals like apatites.

4.1 Short-term retention of phosphorus in sediments

The phosphorus cycle in the Wadden Sea has changed markedly during the past decades: in the Western Dutch Wadden Sea POSTMA [1954] observed a phosphate minimum in spring which gradually increased to a winter maximum. Two decades later, DE JONGE AND POSTMA [1974] observed a maximum in this area during summer . This maximum was explained by increased organic matter import and remineralisation and was illustrated by a budget. HICKEL [1989] observed a similar phenomenon in the Sylt-Rømø basin but with a delay of about 20 years. HESSE et al. [1995] observed a phosphate summer maximum in the Wadden Sea near Büsum. Observations during TRANSWATT (Fig. 5) also indicate the release of dissolved phosphate from the inner parts of the North Frisian Wadden Sea (DICK et al. [this volume]). The latter authors calculated an export rate of 0.7 tonnes PO_4 per tide and 100 km^2 during summer, equaling a release of about 0.4–0.5 mmol PO_4 m^{-2} day^{-1}. This value is in the range of release rates measured in other temporal coastal zones during summer: RUTGERS VAN DER LOEFF et al. [1981] observed a maximum release of about 1 mmol P m^{-2} day^{-1} in June in the inner part of the Ems estuary (Dollard). During the other seasons, these authors found no significant phosphate efflux from the sediment. Sometimes an influx into the sediment was observed. JENSEN et al. [1995] studied phosphorus cycling in Aarhus Bay and observed a maximum phosphate efflux of 0.5 mmol PO_4 m^{-2} day^{-1} which occurred during a short period in June. During the other seasons, the PO_4 efflux was mostly below 0.2 mmol PO_4 m^{-2} day^{-1}. In winter even an influx into the sediment was observed. The annual average DIP efflux amounted to 0.1 mmol m^{-2} day^{-1}. ASMUS AND ASMUS [1998b] stressed the importance of benthic communities for the exchange of matter between sediment and water. They found a mean release of 7 mM m^{-2} day^{-1} in the Sylt Rømø basin on the basis of flume measurements. Since unfiltered samples were analysed, this value probably overestimates the true dissolved phosphate release. However, the authors noticed that intertidal flats were particle traps suggesting that they indeed found a high dissolved phosphate release. They also observed very high nitrogen release rates with the flume technique as compared to other, small scale incubation methods and explained the difference by stating that large scale incubation allows hydrographic factors like current speed and wave action to enhance the exchange rates (ASMUS et al. [1998c]). They compiled evidence that measured exchange rates increase with the surface of the incubated sediment. If we regard the whole tidal basin, the exchange rates with the adjacent coastal zone are probably lower than observed on the tidal flats because in the deeper channels phytoplankton uptake will remove part of the released nutrients.

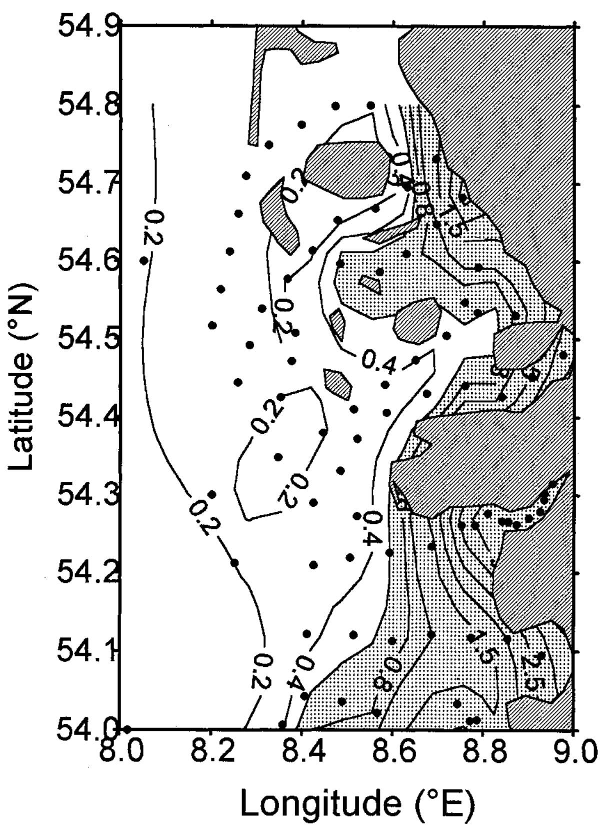

Fig. 5: Dissolved inorganic phosphorus (μM) in the North Frisian Wadden Sea during July 1994 (Transwatt 3). In the hatched area concentrations exceed 0.6 μM.

In the North Sea, SLOMP et al. [1998] also observed very high PO_4 efflux rates in August, ranging between 0.02–1.7 mmol PO_4 m^{-2} d^{-1}. The two highest values (0.17–1.7 mmol PO_4 m^{-2} d^{-1}) were observed in the German Bight. The maximum value of 1.7 mmol m^{-2} d^{-1} was observed in the Elbe Rinne, where the sediments were almost completely anoxic. During winter, DIP fluxes were substantially lower, ranging from –0.03 to +0.04 mmol PO_4 m^{-2} d^{-1}. Note that in winter many sediments acted as a sink for DIP.

The dynamics of phosphorus recycling in coastal sediments depend to a large extent on the interaction between dissolved phosphorus and iron hydroxides (KROM AND BERNER [1981]; SUNDBY et al. [1992]; JENSEN et al. [1995]). These hydroxides have a large capacity to adsorb dissolved phosphorus (VAN RAAPHORST AND KLOOSTERHUIS [1994]) and to retain phosphorus within the sediment. Under anoxic conditions, however, iron hydroxides are reduced and the adsorbed phosphorus is released. Iron hydroxides, therefore, mainly act as a temporal phosphorus buffer.

The seasonal phosphorus dynamics in German Wadden Sea sediments have not been studied yet. But the phosphorus cycle is probably similar to the cycle described by JENSEN et al. [1995] in sediments from the Aarhus Bay (Fig. 6): During winter Fe/P ratios in ironhydroxides from the oxic sediment layer of about 10 prevail. These ratios represent an equilibrium under marine conditions (SUNDBY et al. [1992]; DE JONGE et al. [1993]; SLOMP et al. [1996b]; VAN BEUSEKOM AND BROCKMANN [1998]). During and after the spring bloom, large amounts of organic matter are transferred to the sediment where they are remineralised. Part of the released P is adsorbed onto iron hydroxides, decreasing the Fe/P ratios in the oxic zone. Due to remineralisation, the depth of the oxic zone decreases, iron hydroxides are reduced and dissolved Fe^{2+} and PO_4 are released. If all dissolved Fe and PO_4 were to diffuse upward into the oxic zone and reprecipitate there, this would have no effect on the Fe/P ratios in iron hydroxides of the oxic zone. However, part of the reduced Fe is lost as FeS. This results in a decreased ratio between Fe^{2+} and PO_4 and, after precipitation in the oxic zone, in decreased Fe/P ratios in iron hydroxides. In Aarhus Bay the Fe/P ratio in iron hydroxides continuously decreased from 10 in winter to about 2 during summer. The PO_4 efflux was positively related with the Fe/P ratio in iron hydroxides. The Fe/P ratio of 2 was interpreted by JENSEN et al. [1995] as the ratio where the buffer capacity of the sediment was exhausted. The above scenario can explain why phosphorus release is observed only during a limited period of time. It is important to note that in the North Frisian Wadden Sea a PO_4 export was observed as early as in spring (BROCKMANN et al. [this volume]; DICK et al. [this volume]).

4.2 Long-term retention of phosphorus in sediments

In the previous section it was shown that the seasonal cycle of phosphorus is modified by the interaction with iron hydroxides, which can buffer phosphorus for some months. The high phosphorus concentrations that occur in the sediment at the oxic-anoxic interface (Fig. 6) open up the possibility of authigenic Ca–P mineral precipitation (e.g. apatites, cf. VAN CAPPELLEN AND BERNER [1988]; RUTTENBERG AND BERNER [1993]; SLOMP et al. [1996a]). Once formed, these minerals are very stable and are a long term phosphorus sink (RUTTENBERG AND BERNER [1993]).

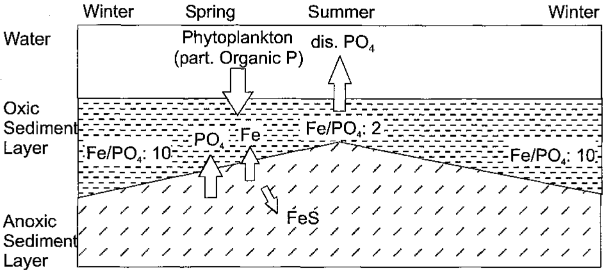

Fig. 6: The phosphorus cycle in the coastal zone (after JENSEN et al. [1995]).

DE JONGE et al. [1993] showed that Ca–P minerals are the major form of phosphorus in Wadden Sea sediments. It remains to be shown whether these compounds are imported into the Wadden sea or whether they are formed locally. We present two lines of evidence that local precipitation of authigenic Ca-P minerals in the Wadden Sea plays a key role in the phosphorus cycle of the Wadden Sea:

1. Apatite concentrations in suspended matter from the German Bight and from rivers are lower than in the Wadden Sea.
2. Budget calculations for the Ems estuary indicate local formation of authigenic Ca-P minerals.

Figure 7 presents the proportion of authigenic Ca-P minerals in suspended particulate phosphorus from the German Wadden Sea and adjacent German Bight during winter. The highest proportions are found in the Wadden Sea area and the lowest once in the German Bight, which suggests that authigenic Ca-P minerals are not imported from the sea. The relative proportion of authigenic Ca-P minerals in the Ems estuary reaches a maximum in the middle part of the estuary and supports local authigenic Ca-P mineral formation in the Ems estuary (Fig. 8). A maximum of Ca-P minerals in the middle reaches of the Elbe estuary (VAN BEUSEKOM AND BROCKMANN [1998]) also indicates local formation of Ca-P minerals.

Further evidence for local Ca-P mineral precipitation is given by a particulate phosphorus budget of the Ems estuary (VAN BEUSEKOM AND DE JONGE [1997; 1998]). Results of these authors have been updated on the basis of recent observations from the Ems estuary (Table 5). The budget shows that in the Ems estuary particulate phosphorus is mainly imported as organic P or as Fe-bound P. The dominant phosphorus form that is buried in the sediment is Ca-bound phosphorus. This indicates that part of the phosphorus that is released during the remineralisation of organic matter or after reduction of iron-hydroxides is precipitated within the sediment as Ca-P minerals like apatite. The annual phosphorus flux in the the Ems estuary amounts to about 45 10^6 mol P (VAN BEUSEKOM AND DE JONGE [1998]) a quarter of which is retained as Ca-P minerals. Once formed these minerals apparently do not easily redissolve. Therefore, their formation is important in removing phosphorus from the coastal biogeochemical cycle on longer, geological time scales (RUTTENBERG AND BERNER [1993]).

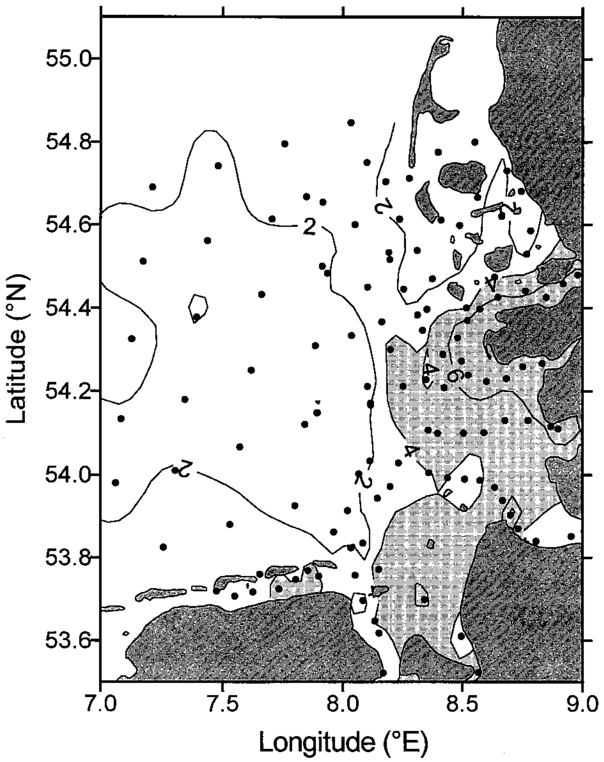

Fig. 7: Relative contribution of apatite-bound phosphorus to total phosphorus in suspended matter during winter (TRANSWATT 7/KUSTOS III, March 1996). Methods are described by VAN BEUSEKOM AND BROCKMANN [1998]. In addition, before the last HCl extraction, apatites were extracted in 1M Na acetate, pH 4 during 2 hours (see also RUTTENBERG [1992[).

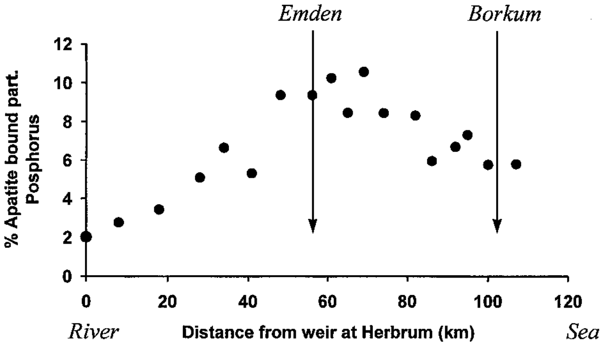

Fig. 8: Relative contribution of apatite-bound phosphorus to total phosphorus in suspended matter from the Ems estuary during February 1997 (see Fig. 1). See Fig. 7 for methods.

P-Fraction	Import river (10^6 mol P y^{-1})	Import sea (10^6 mol P y^{-1})	Total (10^6 mol P y^{-1})	Sedimentation (10^6 mol P y^{-1})
Organic P	2.9	6.1	9.0	2.7
Fe-bound P	11.2	3.2	14.4	2.7
Ca-bound P	0.6	0.8	1.4	11.7
Other	1.5	1.8	3.3	0.9
Total	16.2	11.9	28.1	18.0

Table 5: A particulate phosphorus budget of the Ems estuary

4.3 Nitrogen transformation

Denitrification occupies a special position in coastal nutrient cycling because it immobilizes nitrogen and counteracts coastal eutrophication. Few denitrification measurements have been carried out in the German Bight (LAW AND OWENS [1990]; LOHSE et al. [1993]; LOHSE et al. [1996]). In the framework of the SWAP Project (Sylter Wadden Sea Exchange Processes) denitrification was studied by JENSEN et al. [1996] and BRUNS et al. [1998] in the northern part of the Wadden Sea. KIESKAMP et al. [1991] investigated denitrification in the Western Dutch Wadden Sea.

Before discussing the importance of denitrification for nitrogen budgets in the German Bight and the adjacent Wadden Sea, a short discussion of the methods used to assess denitrification is necessary. A commonly used method is the Acetylene Blocking Method (ABM). This method uses the finding that acetylene blocks the reduction of N_20 to N_2, and denitrification is estimated by measuring the evolution of N_20. The AB-method has some disadvantages. Among others, it severely underestimates denitrification if nitrate concentrations are low and if a tight coupling between nitrification (NH_4 -> $N0_3$) and denitrification exists (LOHSE et al. [1996]). Low nitrate concentrations occur in summer in large parts of the German Bight and in the Wadden Sea. Recently, LOHSE et al. [1996] compared the AB-method with a new method based on the replacement of the bottom water ^{14}N nitrate with ^{15}N nitrate and which measures the evolution of $^{14}N^{15}N$ and $^{15}N^{15}N$ di-nitrogen (hence ion pairing, IP; NIELSEN [1992]). Their study, which was performed with North Sea sediments, indicates that the AB method underestimates the denitrification rates between 2 and 10 times. The underestimation depends on the incubation duration. During short incubations (<60 minutes) the AB method underestimates by a factor of 2. However, normally an incubation of about 6 hours is used and then the bias can be much larger: Compared to earlier rates measured with the AB-method at the same locality, the IP-method yielded 10 times higher rates. The degree of underestimation is a matter of debate: It is certainly larger than 2 because of the 6-hour incubation time but lower than 10. We will apply a factor of 5 as best guess to convert the rates inferred from the AB method to "true" denitrification rates.

The IP method probably also underestimates denitrification (VAN LUIJN et al. [1994]). Uncertainties exist also in the way denitrification is calculated from the IP measurements (MIDDELBURG et al. [1996a]; NIELSEN et al. [1994]) but the uncertainty involved is probably less than 10 %. The best way to estimate denitrification is to directly measure changes in N_2. SEITZINGER [1988] pioneered this approach. Her method involves the removal of N_2 from the overlying water in order to measure significant changes in N_2. The drawback of the method is the danger of contamination with atmospheric N_2. KANA et al. [1994] proposed a mass spectrometric method with such high precision measurements of N_2 that direct measurements of denitrification without pretreatment of the incubated cores are possible. In general, the direct denitrification measurements give the highest estimates indicating that the ABM method and the IP method underestimate denitrification (e.g. VAN LUIJN et al. [1994]; CORNWELL et al. [1999]). It is interesting to note that independent estimates of denitrifcation in a lake with a nitrogen mass balance and with the direct measurement of N_2 changes gave similar results (VAN LUIJN et al. [1994]). Direct measurements of denitrification using the above N_2 methods have not yet been made in the German Bight and Wadden Sea. These methods promise new insight into the magnitude of denitrification in these areas.

BEDDIG et al. [1997] proposed a nitrogen budget for the German Bight (Table 6). The budget included import of N via the atmosphere, via rivers and via the western boundary of the German Bight. N was removed by burial, by denitrification and by transport through the northern boundary of the German Bight. Because of the large uncertainties in estimating the different fluxes the budget was assumed to be closed although total output was about 10 % lower than total input. Based on the above discussion about measuring denitrification we will propose an updated nitrogen budget for the German Bight and the adjacent Wadden Sea.

Pathway	Fluxes (Gmol y^{-1}) (after BEDDIG et al. [1997])		Fluxes (Gmol y^{-1}) Revised	
	Input	Output	Input	Output
Rivers	10.7		10.7	
Atmosphere	4.9		4.9	
Seaward boundaries	64.3	71.4	64.3	71.4
Estuarine denitrification		0.5		0.5
Denitrification		0.7		2.7–4.1
Wadden Sea (WS)				
Denitrification		0.3		2.6
North Sea (NS)				
Denitrification WS + NS + Estuaries				6.3 – 13
Sedimentation		1.0		1.0
Total	79.9	73.9	79.9	78.7 – 85.4
Difference	–6.0			–1.2 – +5.5

Table 6: A nitrogen budget of the German Bight and adjacent Wadden Sea

LAW AND OWENS [1990] observed a denitrification rate of 7–9 µmol N m^{-2} day^{-1} in the German Bight during summer (June/July) using the ABM method. But since the incubation time was very long (about 10 hours) we will not use these data. LOHSE et al. [1993] found a denitrification of 5–46 µmol N m^{-2} day^{-1} in August, and 31–196 µmol N m^{-2} day^{-1} in winter (ABM method, incubation: 1–4 hours). Given a 5-fold underestimation with the AB method, an annual denitrification rate of about 130 mmol m^{-2} y^{-1} or 2.6 Gmol for the entire German Bight is calculated. We note that also the IP method on which the above conversion factor is based underestimates denitrification. A denitrification of 130 mmol m^{-2} y^{-1} therefore is a conservative estimate: HYDES et al. [1999] estimated a mean denitrification of 260 mmol m^{-2} y^{-1} on the basis of a nitrogen mass balance of the North Sea. SMITH et al. [1997] estimated a denitrification rate of about 180 mmol m^{-2} y^{-1} with an ecosystem model.

In the Western Dutch Wadden Sea KIESKAMP et al. [1991] reported a denitrification rate of 110 mmol m^{-2} y^{-1} as measured with the AB-method. Based on a nitrogen budget for the Ems estuary, van BEUSEKOM AND DE JONGE [1998] estimated a denitrification of 900 mmol m^{-2} y^{-1}. Assuming that KIESKAMP et al. [1991] underestimated the "true" denitrification by a factor of 5, both estimates give comparable results (about 600–900 mmol m^{-2} y^{-1}). In the Sylt-Rømø basin much lower denitrification rates were observed with the IP method of about 50 mmol m^{-2} y^{-1} (JENSEN et al. [1996]; BRUNS et al. [1998]). These low values are probably due to nitrate limitation. Low summer nitrate concentrations are typical of the North Frisian Wadden Sea (BROCKMANN et al. [1998]). We will assume a value of 600 mmol m^{-2} y^{-1} for the entire Wadden Sea. A revised denitrification estimate shows that about 6 Gmol N can be removed by denitrification. This is similar to the amount of N not accounted for in the "Beddig" budget.

An overall estimate of the North Sea plus Wadden Sea denitrification can be made applying the relationship put forward by SEITZINGER AND GIBLIN [1996]. They estimated for North Atlantic shelf sediments that approximately 13 % of the nitrogen taken up by phytoplankton was denitrified. This implies for the Wadden Sea and North Sea a denitrification of 13 Gmol y^{-1} or about 260 mmol m^{-2} y^{-1} (PP North Sea = 340 gC m^{-2} y^{-1}, PP Wadden Sea = 250 gC m^{-2} y^{-1}; mean PP = 320 gC m^{-2} y^{-1}; CN ratio = 6.625). A separation between the Wadden Sea and the German Bight proper is not useful because part of the primary production in the German Bight is remineralised within the Wadden Sea.

In summary, estimates for the denitrification rate in the German Bight and adjacent Wadden Sea range between 6 and 13 Gmol y^{-1}. The revised denitrification estimate is substantially higher than the original estimate by BEDDIG et al. [1997] and leads tot the conclusion that denitrification removes between 8 and 16 % of the total nitrogen flux into the German Bight and adjacent Wadden Sea, which equals 40–80 % of the total river plus atmospheric input. Other nitrogen budgets for the North Sea support the importance of denitrification. HYDES et al. [1999] showed that the North Sea is a sink of nitrogen (denitrification is larger than river + atmospheric input). This supports the conclusion by GALLOWAY et al. [1996] that the North Atlantic shelf region is a nitrogen sink. MIDDELBURG et al. [1996b] stressed the importance of denitrification in the global nitrogen cycle. The above discussion and the relevance of nitrogen to coastal eutrophication indicates that the role of denitrification in the German Bight and in the Wadden Sea should be investigated in more detail.

5 Summary

* The Wadden Sea is a heterotrophic area importing about 100 gC m^{-2} y^{-1} from the North Sea annually.
* Within the investigated area (German Wadden Sea and German Bight) organic matter turnover within the water column prevails (30–90 %).
* The contribution of the sediment to total organic matter degradation increases from about 50 % in the Wadden Sea (mean depth: 2–3 m) to 90 % in the German Bight (mean depth 26 m).
* The turnover rate of organic matter to cover the nitrogen need of the annual primary production decreases from five in the open North Sea to three to four in the German Bight and two to three in the Wadden Sea. The turnover rate reflects the efficiency with which the primary producers can use remineralized nutrients and not the degradability of the organic matter. The gradient reflects an increasing light limitation towards the Wadden Sea.
* The low annual turnover rate in the Wadden Sea on the one hand and the increased primary production in the Wadden Sea on the other hand indicate that primary producers are colimited by both light and nutrient availability.
* The formation of Ca-P containing minerals within the sediment is an important phosphorus sink in the Wadden Sea which can remove up to 25 % of the phosphorus input.
* Denitrification removes on average 8–16 % of the total nitrogen flux through the German Bight, which is equal to 40–80 % of the combined river and atmospheric input.

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References

ASMUS, H. AND R. ASMUS, 1998a: The role of macrobenthic communities for sediment-water material exchange in the Sylt Rømø tidal basin. *Senckenbergiana Maritima,* **29**, 111–119.

ASMUS, R. M. AND H. ASMUS, 1998b: Bedeutung der Organismengemeinschaften für den benthopelagischen Stoffaustausch im Sylt Rømø Wattenmeer. In: Gätje C., Reise, K. (eds.) Ökosystem Wattenmeer: Austausch-, Transport- und Stoffumwandlungsprozesse. Berlin: Springer, p. 257–302.

ASMUS, H., D. LACKSCHEWITZ, R. ASMUS, G. SCHEIFFARTH, G. NEHLS AND J.-P. HERRMANN, 1998a: Transporte im Nahrungsnetz eulittoraler Wattflächen der Sylt-Rømø Bucht. In: Ökosystem Wattenmeer: Austausch-, Transport- und Stoffumwandlungsprozesse. C. Gätje and K. Reise (eds.). Berlin: Springer, p. 393–420.

ASMUS, R., M.H. JENSEN, D. MURPHY AND R. DOERFFER, 1998b: Primärproduktion von Mikrophytobenthos, Phytoplankton und jährlicher Biomasseertrag des Makrophytobenthos im Sylt-Rømø Wattenmeer. In: Ökosystem Wattenmeer: Austausch-, Transport- und Stoffumwandlungsprozesse. C. Gätje and K. Reise (eds.). Berlin: Springer, p. 367–392.

ASMUS, R. M., H. ASMUS, M. H. JENSEN, K. M. JENSEN, E. KRISTENSEN AND A. WILLE, 1998c: The role of water movement and spatial scaling for measurement of dissolved inorganic nitrogen fluxes in intertidal sediments. *Estuarine, Coastal and Shelf Science,* **46**, 221–232.

BARETTA, J. AND P. RUARDIJ, 1988. Tidal Flat Estuaries. Ecological studies, 71. Berlin: Springer, 353 pp.

BECKER, G. A., H. GIESE, K. ISERT, P. KÖNIG, H. LANGENBERG, TH. POHLMANN, AND C. SCHRUM, 1999: Mesoscale structures, fluxes and the water mass variability of the German Bight as exemplified in the KUSTOS-experiments and numerical models. This volume, 155-180.

BEDDIG, S., U. BROCKMANN, W. DANNECKER, D. KÖRNER, T. POHLMANN, W. PULS, G. RADACH, A. REBERS, H.-J. RICK, M. SCHATZMANN, H. SCHLÜNZEN, M. SCHULZ, 1997: Nitrogen fluxes in the German Bight. *Marine Pollution Bulletin,* **34**(6), 382–394.

BROCKMANN, U., T. RAABE, K. HESSE, K. VIEHWEGER, S. RICK, A. STARKE, B. FABISZISKY, D. TOPCU, AND R. HELLER, 1999a: Seasonal budgets of the nutrient elements N and P at the surface of the German Bight during winter 1996, spring 1995, and summer 1994. This volume, 267-292.

BROCKMANN, U., K. VIEHWEGER, T. RAABE, S. RICK, H.-J. RICK, AND R. HELLER, 1999b: Conversion of nutrients in the Elbe river plume during drift experiments in the German Bight during spring 1995, and summer 1994. This volume, 293-312.

BRUNS, R., K.M. JENSEN, M.H. JENSEN, E. KRISTENSEN AND L.-A. MEYER-REIL, 1998: Benthische Stickstoffumsätze und ihre Bedeutung für die Bilanz gelöster anorganischer Stickstoffverbindungen. In: Ökosystem Wattenmeer: Austausch-, Transport- und Stoffumwandlungsprozesse. C. Gätje and K. Reise (eds), , Berlin: Springer, p. 219–232.

CADÉE, G.C., 1980: Reappraisal of the production and import of organic matter in the western Wadden Sea. *Netherlands Journal of Sea Research,* **14**, 305–322.

CADÉE, G.C., 1984: Has input of organic matter into the western Dutch Wadden Sea increased during the last deacdes? Netherlands Institute of Sea Research - Publication Series 10, 71–82.

CADÉE, G.C. AND J. HEGEMAN, 1974a: Primary production of the microflora living on the tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research,* **8**, 260–291.

CADÉE, G. C., J. HEGEMAN, 1974b: Primary production of phytoplankton in the Dutch Wadden Sea. *Netherlands Journal of Sea Research,* **8**, 240–259.

CADÉE, G. C. AND J. HEGEMAN, 1993: Persisting high levels of primary production at declining phosphate concentrations in the Dutch coastal area (Marsdiep). Netherlands Journal of Sea Research 31, 147–152.

CLOERN, J. E., 1999: The relative importance of light and nutrient limitation of phytoplankton growth: a simple index of coastal ecosystem sensitivity to nutrient enrichment. *Aquatic Ecology,* **33**, 3–16.

COLIJN, F., 1983: Primary production in the Ems Dollard estuary. PhD Thesis, State University Groningen, Groningen, 123 pp.

CORNWELL, J. C., W.M. KEMP AND T.M. KANA, 1999: Denitrification in coastal ecosystems: methods, environmental controls and ecosystem level controls, a review. *Aquatic Ecology*, **33**, 41–54.

DE JONGE, V. N., 1990: Response of the Dutch Wadden Sea ecosystem to phosphorus discharges from the River Rhine. *Hydrobiologia,* **195**, 49–62.

DE JONGE, V. N., 1997: High remaining productivity in the Dutch Western Wadden Sea despite decreasing nutrient inputs from riverine sources. *Marine Pollution Bulletin,* **34**, 427–436.

DE JONGE, V.N. AND H. POSTMA, 1974: Phosphorus compounds in the Dutch Wadden Sea. *Netherland Journal of Sea Research,* **8**, 139–153.

DE JONGE, V. N., M. M. ENGELKES, J. F. BAKKER, 1993: Bio-availability of phophorus in sediments of the western Dutch Waddden Sea. *Hydrobiologia,* **253**, 151–163.

DE JONGE, V. N., J. F. BAKKER, M. VAN STRALEN, 1996: Recent changes in the contributions of river Rhine and North Sea to the eutrophication of the Western Dutch Wadden Sea. *Netherlands Journal of Aquatic Ecology,* **30**, 27–39.

DE WILDE, P.A.W.J. AND J.J. BEUKEMA, 1984: The role of the zoobenthos in the consumption of organic matter in the Dutch Wadden Sea. Netherlands Intitute for Sea Research - Publication Series 10, 145–148.

DICK, S., U.H. BROCKMANN, J.E.E. VAN BEUSEKOM, B. FABISZISKY, M. GEORGE, U. HENTSCHKE, K.-J. HESSE, B. MAYER, TH. NITZ, TH. POHLMANN, K. POREMBA, K. SCHAUMANN, W. SCHÖNFELD, A. STARKE, U. TILLMANN, AND G. WEIDE, 1999: Exchange of matter and energy between the Wadden Sea and the coastal waters of the German Bight – Estimations based on numerical simulations and field measurements. This volume, 181-220.

EON, 1988: The ecosystem of the western Wadden Sea: field research and mathematical modelling. NIOZ rapport 11, 1-139.

GALLOWAY, J.N., R.W. HOWARTH, A.F. MICHAELS, S.W. NIXON, J.M. PROSPERO AND F.J. DENTENER, 1996: Nitrogen and phosphorus budgets of the North Atlantic Ocean and its watershed. *Biogeochemistry,* **35**, 3–25.

GÄTJE, C., 1992. Artenzusammensetzung, Biomasse und Primärproduktion des Mikrophytobenthos des Elbe-Ästuars. PhD Thesis, University of Hamburg, Hamburg, 210 pp.

GÄTJE, C. AND K. REISE (Editors), 1998: Ökosystem Wattenmeer: Austausch-, Transport- und Stoffwandlungsprozesse. Berlin: Springer, 567 pp.

HESSE, K.-J., U. TILLMANN AND U. BROCKMANN, 1995: Nutrient-phytoplankton relations in the German Wadden Sea. ICES C.M. T:8.

HEIP, C.H.R., N.K. GOOSEN, P.M.J. HERMAN, J. KROMKAMP, J.J. MIDDELBURG AND K. SOETAERD, 1995: Production and consumption of biological particles in temperate tidal estuaries. Oceanography and Marine Biology: an Annual Review, 33, 1–149.

HICKEL, W., 1989: Inorganic micronutrients and the eutrophication in the Wadden Sea of Sylt (German Bight, North Sea). In: Proceedings of the 21st EMBS. Gdansk: Polish Academy of Science, 309–318.

HOPPEMA, J.M.J., 1991: The oxygen budget of the western Dutch Wadden Sea, The Netherlands. *Estuarine, Coastal and Shelf Science,* **32**, 483–502.

HYDES, D. J., B.A. KELLY-GERREYN, A.C. LE GALL AND R. PROCTOR, 1999: The balance of supply of nutrients and demands of biological production and denitrification in a temperate latitude shelf sea - a treatment of the southern North Sea as an extended estuary. *Marine Chemistry,* **68** (1-2), 117-131.

JENSEN, H.S., P.B. MORTENSEN, F.O. ANDERSEN, E. RASMUSSEN AND A. JANSEN, 1995: Phosphorus cycling in coastal marine sediment, Aarhus Bay, Denmark. *Limnology and Oceanography,* **40** (5), 908–917.

JENSEN, K.M., M.H. JENSEN AND E. KRISTENSEN, 1996: Nitrification and denitrification in Wadden Sea sediments (Königshaven, Island of Sylt, Germany) as measured by nitrogen isotope pairing and isotope dilution. *Aquatic Microbial Ecology*, **11**, 181–191.

JOINT, I. AND A. POMROY, 1993: Phytoplankton biomass and production in the southern North Sea. *Marine Ecology Progress Series,* **99**, 179–182.

KANA, T.M., C. DARKANGELO, M.D. HUNT, J.B. OLDHAM, G.E. BENNETT AND J.C. CORNWELL, 1994: Membrane inlet mass spectrometer for rapid high-precision determination of N2, O2 and Ar in environmental water samples. *Analytical Chemistry,* **66**, 4166–4170.

KIESKAMP, W.M., L. LOHSE, E. EPPING AND W. HELDER, 1991: Seasonal variation in denitrification rates and nitrous oxide fluxes in intertidal sediments of western Wadden Sea. *Marine Ecology Progress Series,* **72**, 145–151.

KRAUSE, G., D. BUDÉUS, K. GERDES, K. SCHAUMANN AND K.-J. HESSE, 1986: Frontal systems in the German Bight and their physical and biological effects. In: Marine Interface Dynamics. J.H.C. Nihoul (Ed.). Amsterdam: Elsevier, 119-140.

KRISTENSEN, E., M.H. JENSEN AND K.M. JENSEN, 1998: Sulfur dynamics in sediments of Königshafen. In: Ökosystem Wattenmeer: Austausch-, Transport- und Stoffwandlungsprozesse. C. Gätje and K. Reise (eds.). Berlin: Springer, p. 233–256.

KROM, M.D. AND R.A. BERNER, 1981: The diagenesis of phosphorus in a nearshore marine sediment. *Geochimica et Cosmochimica Acta,* **45**, 207–216.

LAANE, R.W.P.M., 1980: Conservative behaviour of dissolved organic carbon in the Ems Dollart estuary. *Netherlands Journal of Sea Research,* **14**, 192–199.

LAW, C.S. AND N.J.P. OWENS, 1990: Denitrification and nitrous oxide in the North Sea. *Netherlands Journal of Sea Research,* **25** (1/2), 65–74.

LENHART, H.-J., J. PÄTSCH AND G. RADACH, 1996: Daily nutrient loads of the european continental rivers for the years 1977–1993. Berichte aus dem Zentrum für Meeres- und Klimaforschung. Reihe B: Ozeanographie 22, 1–159.

LOHSE, L., H.T. KLOOSTERHUIS, W. VAN RAAPHORST AND W. HELDER, 1996: Denitrification rates as measured by the isotope pairing method and by the acetylene inhibition technique in continental shelf sediments of the North Sea. *Marine Ecology Progress Series,* **132**, 169–179.

LOHSE, L., J.F.P. MALSCHAERT, C.P. SLOMP, W. HELDER AND W. VAN RAAPHORST, 1993: Nitrogen cycling in North Sea sediments: interaction of denitrification and nitrification in offshore and coastal areas. *Marine Ecology Progress Series,* **101**, 283–296.

MIDDELBURG, J. J., K. SOETAERT AND P. M. J. HERMAN, 1996a: Evaluation of the nitrogen isotope-pairing method for measuring benthic denitrification: a simulation analysis. *Limnology and Oceanography,* **41**, 1839–1844.

MIDDELBURG, J. J., K. SOUTAERT, P.M.J. HERMAN AND C.H.R. HEIP, 1996b: Denitrification in marine sediments: a model study. *Global Biogeochemical Cycles,* **10**, 661–673.

NIELSEN, L. P., 1992: Denitrification in sediment determined from nitrogen isotope pairing. *FEMS Microbial Ecology,* **86**, 357–362.

NIELSEN, L. P., N.R.S. RISGAARD-PETERSEN AND T.H. BLACKBURN, 1996: Reply to the comment by Middelburg et al.. *Limnology and Oceanography,* **41**, 1846–1847.

POHLMANN, TH., TH. RAABE, R. DOERFFER, S. BEDDIG, U. BROCKMANN, S. DICK, M. ENGEL, K.-J. HESSE,P. KÖNIG, B. MAYER, A. MOLL, D. MURPHY, W. PULS, H.-J. RICK, R. SCHMIDT-NIA, W. SCHÖNFELD, AND J. SÜNDERMANN, 1999: Combined analysis of field and model data: A case study of the phosphate dynamics in the German Bight in summer 1994. This volume, 331- 353.

POSTMA, H., 1954: Hydrography of the Dutch Wadden Sea. *Archives néerlandaises de Zoologie,* **10**, 405–511.

POSTMA, H., 1984: Introduction to the symposium on organic matter in the Wadden Sea. Netherland Institute for Sea Research Publication Series, 10, 13–22.

REIMER, A., S. BRASSE, R. DOERFFER, C.-D. DÜRSELEN, S. KEMPE, W. MICHAELIS, H.-J. RICK, AND R. SEIFERT, 1999: Carbon cycling in the German Bight: An estimate of transformation processes and transport. This volume, 313-330.

REISE, K. AND D. LACKSCHEWITZ, 1998. Biota des Wattenmeeres zwischen Sylt und Rømø. In: Ökosystem Wattenmeer: Austausch, Transport und Stoffwandlungsprozesse. C. Gätje and K. Reise (Eds.). Springer, Berlin, p. 393–420.

RICK, H.-J., M. E. M. BAUMANN, J. BEIL, S. BRASSE, U. H. BROCKMANN, F. BUCHHOLZ, S. DIEL-CHRISTIANSEN, C.-D. DÜRSELEN, U. FEHNER, U. GÄRTNER, M. GEORGE, A. GÖBEL, K.-J. HESSE, C. KABATNIK, A. KLAWON, R. KOPP, P. KOSCHINSKI, M. KRAUSE, N. LADWIG, C. MEHRKÜHLER, R. MÜLLER, K. POREMBA, T. RAABE, A. REIMER, T. RIELING, S. RICK, K. SCHAUMANN, M. SCHÜTT, J. SÜNDERMANN, A. TILLMANN, U. TILLMANN, A. WEBER, G. WEIDE AND C. WOLFF, submitted to Dt. hydrogr. Z.: Balances and imbalances of production and respiration in German Bight pelagic systems.

RUTGERS VAN DER LOEFF, M.M., F.B. VAN ES, W. HELDER AND R.T.P. DE VRIES, 1981: Sediment water exchanges of nutrients and oxygen on tidal flats in the Ems-Dollard estuary. *Netherlands Journal of Sea Research,* **15** (1), 113–129.

RUTTENBERG, K.C., 1992: Development of a sequential extraction method for different forms of phosphorus in marine sediments. *Limnology and Oceanography,* **37**(7), 1460–1482.

RUTTENBERG, K.C. AND R.A. BERNER, 1993: Authigenic apatite formation and burial in sediments from non-upwelling continental margins. *Geochimica et Cosmochimica Acta,* **57**, 991–1007.

SALOMONS, W., R. G. GERRITSE, 1981: Some observations on the occurence of phosphorus in recent sediments from western Europe. Th*e Science of the total Environment,* **17**, 73–49.

SEITZINGER, S. P., 1988: Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. *Limnology and Oceanography,* **33**, 702–724.

SEITZINGER, S.P. AND A.E. GIBLIN, 1996: Estimating denitrification in North Atlantic continental shelf sediments. *Biogeochemistry,* **35**, 235-260.

SLOMP, C.P., E.H.C. EPPING, W. HELDER AND W. VAN RAAPHORST, 1996a: A key role for iron-bound phosphorus in authigenic apatite formation in North Atlantic continental platform sediments. *Journal of Marine Research,* **54**, 1179–1205.

SLOMP, C.P., S.J. VAN DER GAAST AND W. VAN RAAPHORST, 1996b: Phosphorus binding by poorly crystalline iron in North Sea sediments. *Marine Chemistry,* **52**, 55–73.

SLOMP, C.P., J.F.P. MALSCHAERT AND W. VAN RAAPHORST, 1998: The role of sorption in sediment-water interaction of phosphate in North Sea continental margin sediments. *Limnology and Oceanography,* **43**, *832-846.*

SMITH S.V., P.R. BOUDREAU AND P. RUARDIJ, 1997: NP Budget for the Southern North Sea. http://data.ecology.su.se/MNODE/Europe/NORTHSEA.HTM

SMITH, S.V. AND J.T. HOLLIBAUGH, 1993: Coastal metabolism and the oceanic carbon balance. *Reviews of Geophysics,* **31**, 75–89.

SUNDBY, B., C. GOBEIL, N. SILVERBERG AND A. MUCCI, 1992: The phosphorus cycle in coastal marine sediments. *Limnology and Oceanography,* **37**, 1129–1145.

SÜNDERMANN, J., K.-J. HESSE, AND S. BEDDIG, 1999: Coastal mass and energy fluxes in the southeastern North Sea. This volume, 113-132.

TILLMANN, U., K.-J. HESSE AND F. COLIJN, in press: Planktonic primary production in the German Wadden Sea. *Journal of Plankton Research.*

VAN BEUSEKOM, J.E.E. AND U.H. BROCKMANN, 1998: Phosphorus transformation in the Elbe estuary. *Estuaries,* **21**(4a), 518–526.

VAN BEUSEKOM, J.E.E. AND V.N. DE JONGE, 1998: Retention of phosphorus and nitrogen in the Ems estuary. *Estuaries,* **21**(4a), 527–539.

VAN BEUSEKOM, J.E.E. AND V.N. DE JONGE, 1997: Transformation of phosphorus in the Wadden Sea: apatite formation. *Dt. Hydrogr. Z.*, **49** (2/3), 297–305.

VAN CAPPELLEN, P. AND R.A. BERNER, 1988: A mathematical model for the early diagenesis of phosphorus and fluorine in marine sediments:apatite precipitation. *American Journal of Science,* **288**, 289–333.

VAN DUYL, F.C. AND A.J. KOP, 1988: Temporal and lateral fluctuations in production and biomass of bacterioplankton in the western Dutch Wadden Sea. *Netherlands Journal of Sea Research,* **22**, 51–68.

VAN DUYL, F.C. AND A.J. KOP, 1990: Seasonal patterns of bacterial production and biomass in intertidal sediments of the western Dutch Wadden Sea. *Marine Ecology Progress Series,* **59**, 249–261.

VAN LUIJN, F., P.C.M. BOERS AND L. LIJKLEMA, 1996: Comparison of denitrifcation rates in lake sediments obtained by N2 flux method, the 15N isotope paring technique and the mass balance approach. *Water Research,* **30**, 893–900.

VAN RAAPHORST, W. AND W.T. KLOOSTERHUIS, 1994: Phosphate sorption in superficial intertidal sediments. *Marine Chemistry,* **48**, 1–16.

VELDHUIS, M.J.W., F. COLIJN, L.A.H. VENEKAMP AND L. VILERIUS, 1988: Phytoplankton primary production and biomass in the western Wadden Sea (The Netherlands): A comparison with an ecosystem model. *Netherlands Journal of Sea Research,* **22**(1), 37–49.

VON WESTERNHAGEN, H., W. HICKEL, E. BAUERFEIND, U. NIERMANN AND I. KRÖNCKE, 1986: Sources and effects of oxygen deficiencies in the south-eastern North Sea. *Ophelia,* **26**, 457–473.

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