Estuaries Vol. 15, No. 4, p. 538–548 December 1992

Eutrophication, Water Management, and the Functioning of Dutch Estuaries and Coastal Lagoons

PIETER H. NIENHUIS
Netherlands Institute of Ecology
Vierstraat 28
4401 EA Yerseke
The Netherlands

ABSTRACT: A number of major European rivers (especially the Rhine) have a prevailing influence on the nutrient cycling of most Dutch estuaries. Owing to the increased loading of the estuaries with nitrogen and phosphorus compounds, effects of eutrophication on the biological communities are most evident in the tidal Western Wadden Sea and in a nontidal brackish lagoon, Veerse Meer. Whether the relation between changed nutrient loadings and changed biomass and production of primary and secondary producers in the turbid tidal Dutch ecosystems should be considered as a causal relation is questionable. The very widespread practice of lagoon modification confuses the effects of nutrient loading.

Introduction

Generally, temperate estuaries are open, inconstant ecosystems characterized by extensive natural spatial and temporal variability. Increased human activities in the 20th Century led to significant changes in the estuaries around the North Sea. In Dutch estuaries, a tremendous increase in mussel culture, fisheries, bottom trawling, sand dredging, recreation, and flood control construction took place after the Second World War. These activities resulted in habitat loss and disturbance of coastal communities (Heip 1989). Fishery activities introduced alien species, such as the "oyster thief," the brown alga *Colpomenia peregrina,* the slipper limpet, *Crepidula fornicata,* and recently the Japanese oyster, *Crassostrea gigas,* the Japweed, *Sargassum muticum,* and many others. Dutch estuaries receive fresh water from a number of rivers, which are loaded with nutrients and pollutants from agricultural, urban, and industrial land uses within the watersheds. Reducing eutrophication, the process of increasing loads and concentrations of inorganic nutrients, mainly nitrogen and phosphorus, is therefore one of the primary concerns of present-day water management. In this paper I try to link the trends in the development of estuarine communities to the chronic effects of eutrophication and to other natural and man-induced changes in Dutch estuaries.

Eutrophication of Dutch Estuaries

All Dutch estuaries (Fig. 1) are strongly influenced by discharge from the Rhine, Meuse, and Scheldt rivers. The average discharge of the Rhine and Meuse together is 2,580 m^{-3} s^{-1}. The Scheldt has an average discharge of only 112 m^{-3} s^{-1} (de Ruyter et al. 1987). About 80% of the water of the Rhine runs via Nieuwe Waterweg and Hollands Diep-Haringvliet into the North Sea. Residual currents along the Dutch coast transport Rhine water in a northerly direction. Roughly 6% of the original Rhine water enters the Wadden Sea (Ridderinkhof 1990). Via the IJssel, the northern branch of the Rhine, 8–15% of the Rhine water flows into the IJsselmeer, and eventually into the Western Wadden Sea (van der Veer et al. 1988).

The nitrogen, ammonium, and nitrate loads of the Rhine and Meuse have increased 2-fold to 4-fold, over the period 1950–1985, whereas the phosphorus load has increased 5-fold to 7-fold (Fig. 2; van der Veer et al. 1988). As a result of the reduced pollution of the rivers, nitrogen and phosphorus loads decreased somewhat after 1980. In the past, concentrations of nutrients increased even more markedly than the load: a 5-fold increase for N and a 10-fold increase for P, with recently a slight decrease. The increased concentrations of nutrients in the Rhine-Meuse water resulted in a 3-fold to 5-fold increase in N and P concentrations in Dutch coastal waters (van der Veer et al. 1988). The increase in nutrient concentrations and loads in Westerschelde estuary showed a comparable dramatic trend over the past 30 to 40 years (van Buuren 1988), but the impact of the Scheldt River on the North Sea is negligible, owing to its small discharge of fresh water.

Because of the northerly-directed residual cur-

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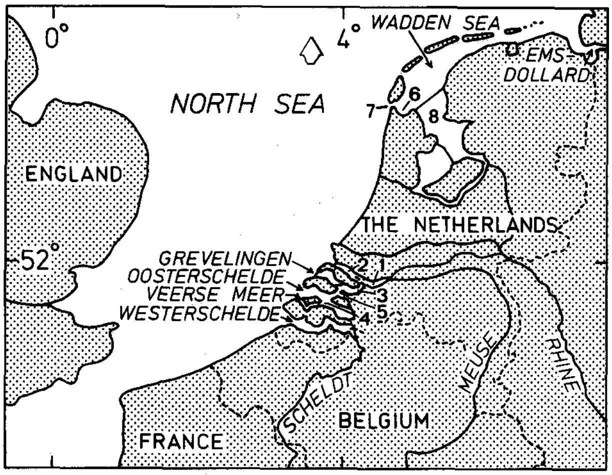

Fig. 1. The geographic position of the Dutch estuaries. Additional geographic names mentioned in the text: 1 = Hollands Diep; 2 = Haringvliet; 3 = Volkerak; 4 = Zandkreek; 5 = Krabbenkreek; 6 = Balgzand; 7 = Marsdiep; 8 = IJsselmeer.

rent along the coast, less than 5% of the original Rhine-Meuse water reaches the estuaries and brackish lagoons in the southwest Netherlands. Oosterschelde, Grevelingen, and Veerse Meer are therefore mainly loaded with nutrients from diffuse sources, such as agricultural run-off, treated waste water, and drainage canals. The saline water bodies in the southwest Netherlands are spatially separated (compartmentalization) by dikes and sluices constructed during the "Deltaworks," a civil engineering scheme that was in operation between 1957 and 1987, and aimed to restrict the sea-born flow of the main estuaries for safety reasons. Consequently, each of these (former) estuaries has its own eutrophication history and its own specific water regime. These characteristics mean that each unit has to be managed according to its particular conditions (Nienhuis 1989a).

Some properties of present-day Dutch estuaries vary considerably (Table 1). The residence time of the water masses in nontidal Grevelingen and Veerse Meer is long compared to the same characteristic in tidal estuaries. The net freshwater load directly derived from the Rhine and Meuse rivers on Oosterschelde, Veerse Meer, and Grevelingen is very small: 1% to 2% of the discharge of the rivers. The Wadden Sea received approximately 400 $m^3 s^{-1}$ of water from the Rhine; Westerschelde and Ems-Dollard each receive 100 to 150 $m^3 s^{-1}$ of fresh water from their tributaries. Veerse Meer experiences almost permanent stratification, whereas in Grevelingen and Ems-Dollard only a few deep channels are stratified during summer. The Westerschelde (marine section), Oosterschelde, and Wadden Sea estuaries are completely-mixed tidal systems. Westerschelde and Ems-Dollard are extremely turbid, Grevelingen has very clear water, and Oosterschelde, Veerse Meer, and Wadden Sea are in-between (Table 1).

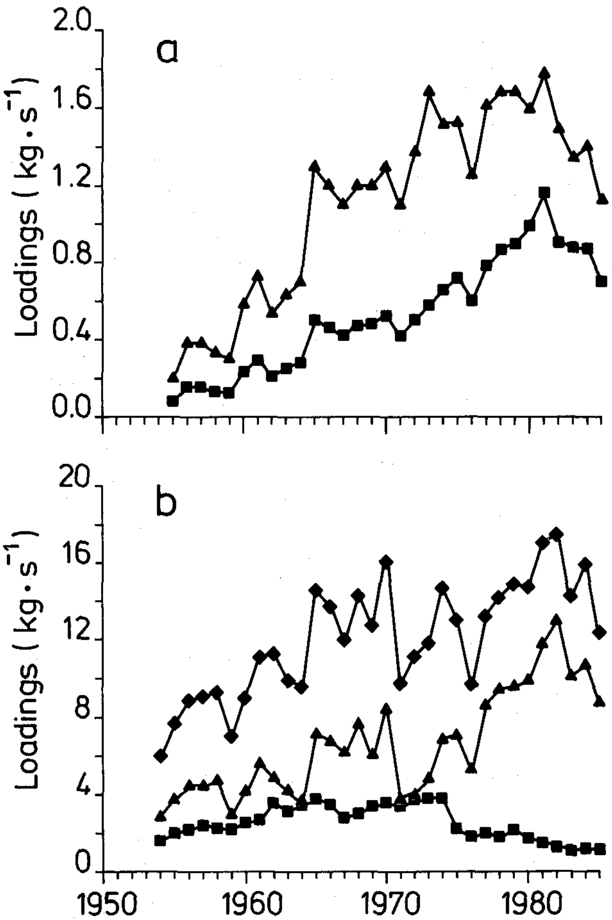

Fig. 2. a. Loadings of total phosphorus (triangles), orthophosphate (squares); (b) total nitrogen (diamonds), nitrate (triangles), and ammonium (squares) of the Rhine River near the German-Dutch border (van der Veer et al. 1988).

There is no one specific factor that limits growth of algae in Dutch estuaries. In the turbid Westerschelde the availability of light limits phytoplankton dynamics. In part of the Western Wadden Sea phosphate may be potentially limiting (Veldhuis 1987). Nitrogen may be the limiting factor for phytoplankton growth in Oosterschelde and Grevelingen (de Vries et al. 1988a; Wetsteyn et al. 1990), and occasionally also in Veerse Meer.

The range of nutrient concentrations in Dutch estuaries differs greatly. Values above 1 mg l^{-1} for N, P, and Si seldom occur in Oosterschelde and Grevelingen and nutrient concentrations frequently approach zero during blooms of phytoplankton. Veerse Meer has higher maximum values for N and Si, but depletion occurs during the growing season (Daemen 1985; de Vries et al. 1988b). Westerschelde and Ems-Dollard have the highest nu-

TABLE 1. Properties of the Dutch estuaries, derived from Wollast (1988) and Bokhorst (1988) for Westerschelde, from Projectgroep Balans (1988) and Wetsteyn and Peperzak (1988) for Oosterschelde, from Nienhuis (1985) and de Vries et al. (1988a) for Grevelingen, from Daemen (1985) and Stronkhorst et al. (1985) for Veerse Meer, from EON-projectgroep (1988) for Wadden Sea, and from Rijkswaterstaat (1985) for Ems-Dollard. Load = freshwater load.

	Westerschelde	Oosterschelde	Grevelingen	Veerse Meer	Ems-Dollard	Wadden Sea
Area (km^2)	300	350	108	22	460	1,200
Residence time (d)	30–90	5–40	180–360	±180	14–70	8–15
Load ($m^3 s^{-1}$)	100	20	5	3	150	400
Tides	+	+	–	–	+	+
Stratification	–	–	±	+	±	–
Extinction coefficient (m^{-1})	0.5–7	0.4–1.5	0.2–0.5	0.3–1.4	1–7	0.5–3
Chlorinity (‰)	0–17	15–17	14–16	8–12	0–17	10–17

trient concentrations, never approaching zero during spring and summer and reaching high values during winter (8 mg l^{-1} N, 4 mg l^{-1} P, and 9 mg l^{-1} Si) (Rijkswaterstaat 1985; Baretta and Ruardy 1988a; Bokhorst 1988).

The total nitrogen loadings to Dutch coastal waters vary two orders of magnitude (4–235 g N m^{-2} yr^{-1}, Table 2). Mean N concentrations show a much smaller range of 0.5–4.6 mg l^{-1}. Obviously nitrogen loads of 40–200 g N m^{-2} yr^{-1} do not give rise to extremely high chlorophyll concentrations during summer in the turbid Dutch estuaries and in the coastal waters. In such places light availability rather than nutrient supply may limit net primary production. In the clear waters of Veerse Meer, a load of 34 g N m^{-2} yr^{-1} results in high chlorophyll concentrations (100 mg chl *a* m^{-3}, or even higher; de Vries et al. 1988b). Production of phytoplankton biomass in Veerse Meer, and consequent deposition of particulate organic carbon on the bottom sediments, was large enough during 1980–1983 to increase the area of anaerobic sediment from 4% to 25% of the bottom surface (Stronkhorst et al. 1985). Veerse Meer Lagoon is vulnerable to eutrophication because of the long residence time of the water mass, the low extinction coefficient, and the almost permanent stratification.

Oosterschelde has a very low N loading, and correspondingly low chlorophyll concentrations (Table 2). Owing to the design of the Deltaplan, Oosterschelde has been largely separated from flow of the Rhine. Oosterschelde is mainly influenced by marine coastal water which contains low concentrations of total nitrogen (less than 0.5 mg N l^{-1}; Brockmann et al. 1988). Mathematical model calculations revealed that a reduction of 50% of the nitrogen load of the Rhine River would only lead to a reduction of less than 6% of the N concentration in Oosterschelde (Simulation Model Oosterschelde Ecosystem; H. Scholten personal communication).

TABLE 2. Nitrogen and chlorophyll in Dutch estuaries and coastal waters. Data derived from de Vries et al. (1988b); SMOES-model calculations (H. Scholten, personal communication; Rijkswaterstaat 1985).

	Load (g N m^{-2} yr^{-1})	Mean Winter Concentration N-NH_4^+ N-NO_3^- (mg l^{-1})	Mean Chlorophyll Concentration Summer (mg Chl. *a* m^{-3})
North Sea coastal	40	0.5	15
Dollard	61	3.5	40
Wadden Sea	50	1.2	30
Westerschelde	235	4.6	30
Oosterschelde	5	1.0	5
Grevelingenmeer	4	0.7	5
Veerse Meer	34	3.0	100

Grevelingen Lagoon has a low N loading (4 g N m^{-2} yr^{-1}, Table 2) in contrast with Veerse Meer. Mathematical model simulations (de Vries et al. 1988a) suggested that production of phytoplankton in Grevelingen is limited by nitrogen rather than by light availability. In addition, the N:P ratio of dissolved nutrients in Grevelingen Lagoon during winter is 2 to 4, pointing to a surplus of phosphate, notwithstanding the dominance of nitrogen in the discharge water entering the lagoon (N:P = 22:1). Model calculations showed a high turnover of nitrogen in the water column. The chain of processes, nutrient uptake by phytoplankton, to formation of organic matter in algal cells, to mineralization of dead algae, to regeneration of nutrients, etc., repeats about eight times per year in Grevelingen. This implies that about 90% of the annual primary production of phytoplankton is supported by regenerated nutrients, especially NH_4 (de Vries and Hopstaken 1984; de Vries et al. 1988a).

Biological Effects of Eutrophication and Water Management

Effects on Primary Producers

In Fig. 3 a tentative carbon budget of the main categories of primary producers in all Dutch estuaries is given. It has to be realized that the "pies" depict average, annual, integrated data, useful for reasons of comparison, but do not reflect temporal and spatial variability. Phytoplankton are the dom-

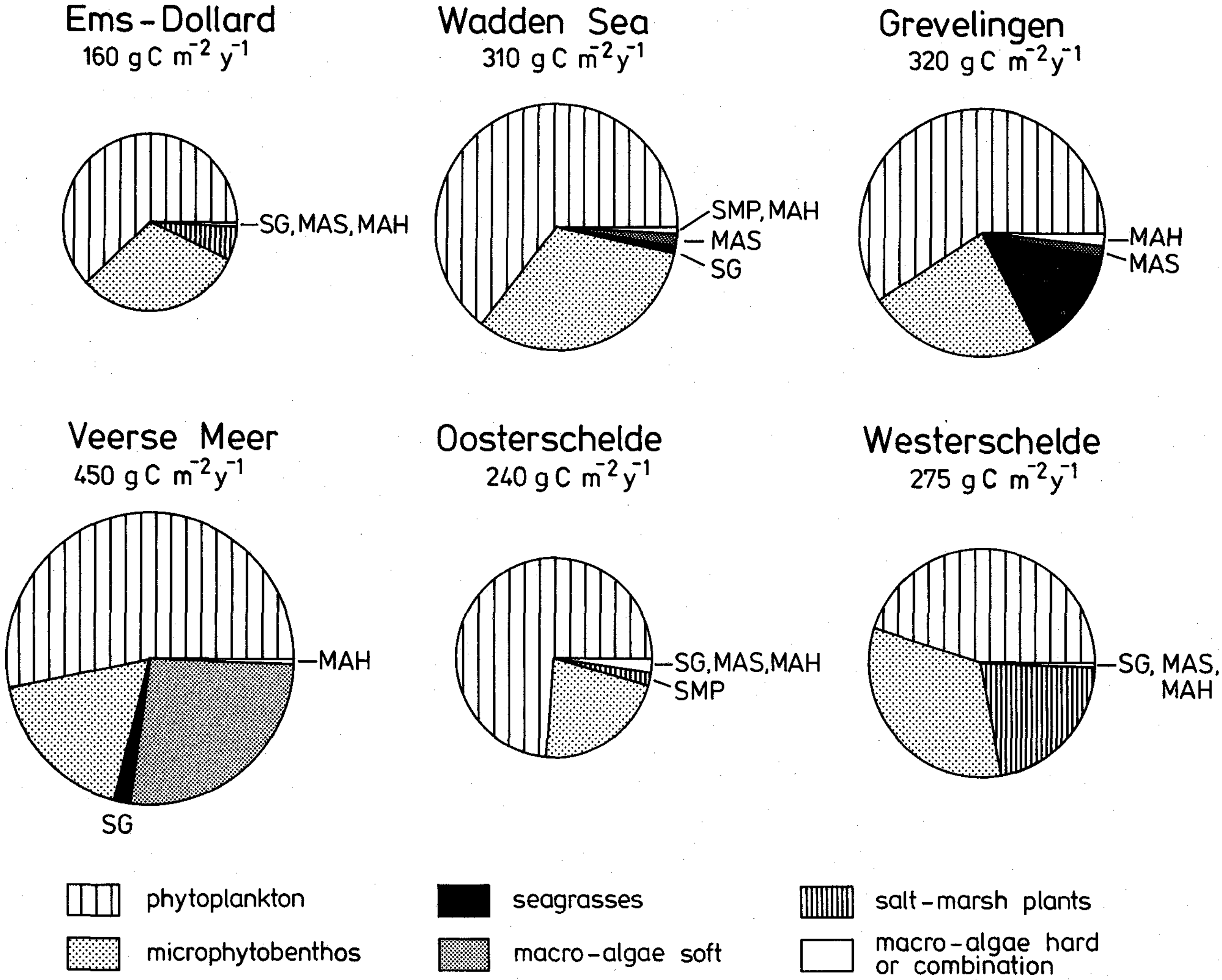

Fig. 3. Preliminary average annual carbon budget of primary producers in Dutch estuaries (Nienhuis 1989a; Rijkswaterstaat 1985; Baretta and Ruardy 1988a [Ems-Dollard]; de Wilde and Beukema 1984; Vosjan 1987; Baretta and Ruardy 1988b [Wadden Sea]; Wetsteyn et al. 1990 [Oosterschelde]; and Coosen et al. 1990 [Veerse Meer]). SG = seagrass; MAS = macroalgae on soft substrates; MAH = macroalgae on hard substrates; SMP = salt-marsh plants.

inant primary producers in Dutch estuaries, contributing 45% to 71% to the overall annual budget of organic material (Fig. 3). Notwithstanding the large differences in nutrient loadings of the separate waters, primary production of phytoplankton only shows a 2.4-fold difference between the light-limited, turbid Ems-Dollard (100 g C m^{-2} yr^{-1}) and Westerschelde (125 g C m^{-2} yr^{-1}), and the clear, presumably not nutrient-limited Veerse Meer (240 g C m^{-2} yr^{-1}). Production levels in Wadden Sea, Oosterschelde, and Grevelingen are intermediate.

Production of microphytobenthos (benthic diatoms, green algae, etc.) is roughly 30% to 70% of the production of phytoplankton. In Westerschelde estuary the relative share of benthic microphytes is high, based on a P/B ratio derived from very high biomass data, sampled on intertidal flats (D. J. de Jong personal communication, Dienst Getijdewateren).

Both production and biomass of microphytobenthos in the Western Wadden Sea show an increasing trend over the period 1968–1981, possibly related to the increasing eutrophication of the Western Wadden Sea. The interpretation of causes is confused by large tidal, seasonal, and year-to-year variability in the Wadden Sea, together with changes in the stations caused by dredging. Moreover, improvements in the measuring methods of organic matter, chlorophyll, and primary production interfere seriously with the assessment of any long-term trend in input of nutrients to the Western Wadden Sea (Cadeé 1980).

In several reports by water managers the suggested positive relation between primary produc-

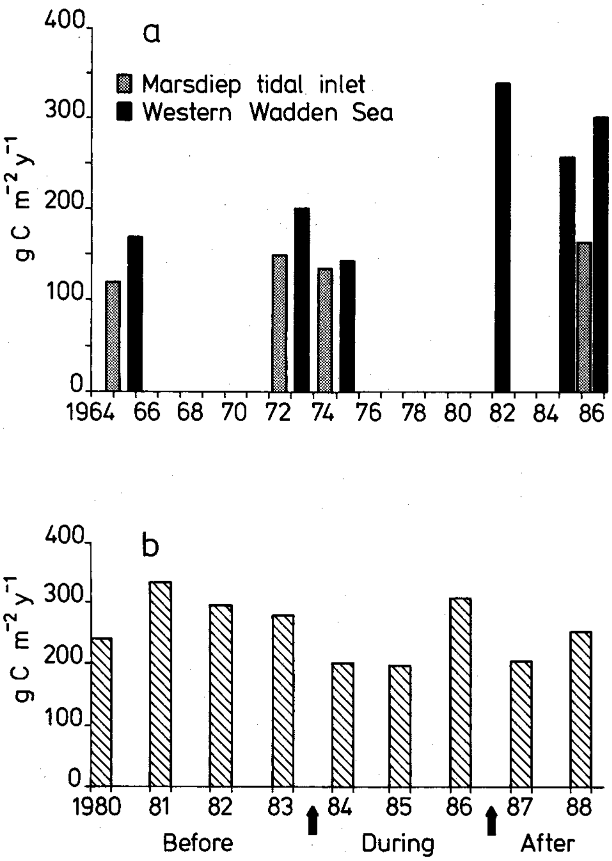

Fig. 4 a) Annual ^{14}C phytoplankton primary production, integrated over the water column, at two stations in the Western Wadden Sea, Marsdiep tidal inlet, and inner Western Wadden Sea (compilation derived from van der Veer 1988), and (b) at one station in eastern Oosterschelde before, during, and after the construction of the storm surge barrier (data derived from Vegter and de Visscher 1987 [data for 1985]; Nienhuis 1989b; Wetsteyn et al. 1990).

tion and eutrophication in the Western Wadden Sea has been mentioned, sometimes as a causal relation (Rijkswaterstaat 1989), sometimes as a noncausal, suggested relation (Rijkswaterstaat 1990).

It may be questioned whether increasing nutrient loading of the water mass of the Western Wadden Sea should necessarily give an increase in production and biomass of microphytobenthos. Or stated otherwise, the relation between an increasing nutrient load of the water mass and increasing microphytobenthos activity suggests a limiting role for these nutrients before eutrophication started. This is unlikely in the Western Wadden Sea, since nutrient concentrations in the interstitial water of subtidal and intertidal flats are far higher than in the water column because of the accumulation of decomposing organic matter in shallow-water sediments. In Oosterschelde estuary which is less eutrophic than the Wadden Sea (Table 2), de Jong et al. (1990) found that nutrient supply from interstitial water in the sediment is not limiting the growth rate of intertidal microphytobenthos.

Phytoplankton productivity should reflect more directly a possible effect of an increasing trend in nutrient loadings than microphytobenthos production. Phytoplankton productivity in the Western Wadden Sea increased during 1965–1986 (Fig. 4a; data derived from van der Veer et al. 1988). However, owing to the scanty data, the large variation in the data set, and the methodological changes in the course of time (Cadée 1980, 1984, 1986; Cadée and Hegeman 1974a, b, 1977), the significance of the increase is unclear.

Although current velocities, visibility of the water mass, nutrient load, and seston quantities (Wetsteyn et al. 1990) in the Oosterschelde estuary changed dramatically after the construction of a storm surge barrier and two auxiliary dams, annual phytoplankton primary production did not change notably (Fig. 4; Vegter and de Visscher 1987; Wetsteyn et al. 1990). Neither an increasing nor a decreasing trend is detected. The construction of the storm surge barrier was finished in 1986, but no break in the production data could be observed (Fig. 4b). Wetsteyn et al. (1990) and Scholten et al. (1990) thought that the decreased nutrient loading of Oosterschelde estuary was compensated by an increase in light penetration through the water column, resulting in almost the same integrated level of primary production of phytoplankton on an annual basis.

Data from Oosterschelde show how cautiously "correlations" should be drawn between environmental parameters and phytoplankton productivity. Obviously, the integrated parameter primary production is a robust characteristic of the pelagic estuarine ecosystem, showing large resilience against changes in the environment (cf. Herman and Scholten 1990).

High turbidity and exposure to waves and tides prevents the potential sediment habitats in Westerschelde and Ems-Dollard from being invaded by macrophytes. Oosterschelde and Western Wadden Sea have only local growth of macrophytes on sediment substrates in sheltered regions, such as Balgzand, Zandkreek, and Krabbenkreek embayments (Fig. 1). In the brackish lagoons Grevelingen and Veerse Meer, macroalgae (mainly green algae) and seagrasses contribute significantly to the carbon budget. In Grevelingen the rooted seagrass *Zostera marina* covers 20% of the surface area of the lagoon and has a net production of 150 g C m^{-2} yr^{-1}. The eelgrass contributes only 14% to the annual carbon budget, while phytoplankton provides 60% (Fig. 4).

In eutrophic waters, such as Veerse Meer, macroalgae become more prominent. Here seagrasses cover only 3% of the surface area of the lagoon while macroalgae—mainly *Ulva*—cover 20% (Hannewijk 1988). The lagoon is dominated by *Ulva* species during summer, producing roughly 500 g C m^{-2} yr^{-1} in shallow areas. The contribution to the annual carbon budget of Veerse Meer is 120 g C m^{-2} yr^{-1}, which is 27% of the lagoon's budget (Fig. 3). The high nitrogen load of Veerse Meer not only results in a high production of phytoplankton, but also in mass growth of *Ulva* in shallow areas.

Light remains the dominant factor for production processes. Veerse Meer, eutrophic and clear, has the highest total primary production of all estuaries in The Netherlands, roughly 450 g C m^{-2} yr^{-1}, and light-limited Ems-Dollard estuary has the lowest value, roughly 160 g C m^{-2} yr^{-1}.

A number of biological effects have been linked to the increasing eutrophication in the Dutch coastal waters and the Western Wadden Sea (see for summary Nelissen and Stefels 1988): an increasing biomass and production of microalgae and an increasing dominance of flagellates over diatoms. Whether there exists a cause–effect relation between eutrophication and algal blooms remains unresolved. Cushing (1990) postulated that in the western North Sea, between the 1950s and 1970s, phytoplankton production was reduced considerably owing to the occurrence of strong northerly winds and gales that delayed the time of the onset of production in spring. The interaction between physical climatic factors (temperature, wind), acting on a time scale of decades to centuries, and the regional or local factors (eutrophication, pollution), acting on a time scale of weeks to decades, makes interpretation of biological phenomena very complicated.

According to Richardson (1989), blooms of phytoplankton, toxic or nontoxic species, are a natural phenomenon in the coastal and central parts of the North Sea. However, eutrophication from anthropogenic sources gives rise to an increase in the intensity and frequency of such algal blooms in the coastal areas, possibly stimulating the frequency of oxygen depletion, and thus seriously affecting ecosystem functioning.

The relation between eutrophication and microalgal production, mentioned for Dutch coastal and Wadden Sea waters, can hardly be achieved for the estuaries and lagoons in the southwestern Netherlands. Veerse Meer and Grevelingen have their own specific eutrophication stories, starting respectively in 1961 and 1971, when the estuaries were closed off from the sea. Long-term series, such as those published for the Wadden Sea by Beukema and Cadée (1986), are not available for Oosterschelde estuary. For Westerschelde, Bokhorst (1988) summarized a series of physico-chemical characteristics over the period 1982 to 1988. In Westerschelde estuary the time series of chlorophyll concentrations in the water column show a rising trend. This trend can partly be explained by variations in the spring light extinction. The remaining part to be interpreted is unclear and can hardly be due to an increase in nutrient concentrations (Herman and Hummel 1989). Effects of eutrophication of the delta waters have been obscured (except for Westerschelde) by the execution of the Deltaplan, which drastically altered the hydrography of the area.

Effects on Higher Trophic Levels

Phytoplankton are the dominant primary producers in all Dutch estuaries. Roughly 10% to 20% of the phytoplankton net production in Dutch estuaries is grazed by herbivorous zooplankton (C. Bakker personal communication). Generally, in deeper coastal waters a much larger part is consumed by zooplankton (Valiela 1984).

The prominent food link in Grevelingen, Oosterschelde, and the Wadden Sea is dominated by phytoplankton to benthic filter feeders such as mussels and cockles. The turnover rate of nutrients in these ecosystems is determined by the filtering capacity of benthic filter feeders. Theoretically, every 5 to 10 days the entire volume of water of the estuaries mentioned circulates through the filtering apparatus of the suspension feeders. Filter feeders act as natural controllers of eutrophication processes (Officer et al. 1982); they transfer organic material from the water column onto the bottom sediments. Moreover, they accelerate the regeneration of nutrients from the deposited particulate organic matter, thereby enhancing the primary production of phytoplankton, as was assumed for Grevelingen (de Vries et al. 1988a).

The chain of processes—partly measured, partly theoretical—from biodeposition to regeneration of nutrients and the coupling between nitrification and denitrification is directed by the load of organic material to the sediment. In this context, denitrification is undoubtedly a significant process in estuarine ecosystems. Rates of gaseous losses of nitrogen in the range of 5 mg N m^{-2} d^{-1} to 70 mg N m^{-2} d^{-1} were determined in Belgian, Dutch, and Danish coastal sediments, representing 8% to 23% of the amount of nitrogen mineralization in the benthic subsystem (Billen and Lancelot 1987). However, when the increasing load of organic material on the bottom exceeds the capacity of aerobic mineralization, anaerobic conditions will prevail in the sediment, leading to death of bottom fauna and a disconnection of nitrification and denitrifi-

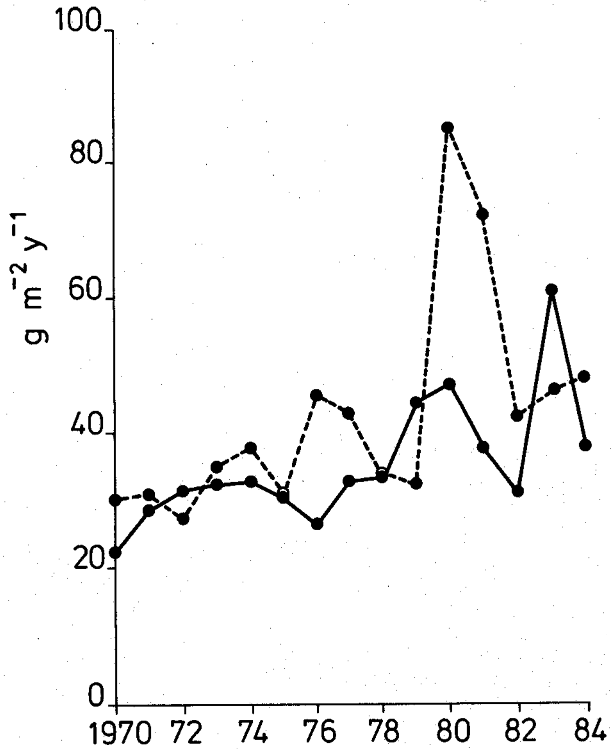

Fig. 5. Changes in total macrozoobenthos production (in g AFDW m^{-2} yr^{-1}) during a 15-yr period in a tidal flat in the Western Wadden Sea; estimates based on samples taken along 12 transects (interrupted lines) and in three permanent plots (uninterrupted lines) (Beukema and Cadée 1986).

cation. Mathematical model calculations simulate that a loading of approximately 10 g N m^{-2} yr^{-1} or more uncouples the eutrophication controlling processes (de Vries et al. 1988a).

Veerse Meer experiences a N load of 34 g m^{-2} yr^{-1} in combination with a long residence time of the water, permanent stratification mainly in the eastern section, and clear water during a considerable part of the year. Obviously, the chlorophyll concentrations in this lagoon cannot be controlled by the bottom fauna, although a substantial benthic biomass is available (Coosen et al. 1990).

Beukema and Cadée (1986) suggested that increased nutrient concentrations in Dutch coastal waters and in the Western Wadden Sea induced increased primary production, which, in turn, increased secondary production. Both authors are careful enough not to exclude several alternative factors that may have contributed to the observed trends, such as the decrease during the last decades of various toxic substances, like heavy metals and insecticides in the Rhine River and in the Dutch Wadden Sea (Dijkzeul 1982; Essink 1985), an increase in the concentration of suspended organic material, and an increase of the sedimentation rate at many of the tidal flats in the Western Wadden Sea. According to Beukema and Cadée (1986), it appears to be virtually impossible to estimate the contribution of these factors to the observed increases in productivity.

Decomposing algal stocks may deplete dissolved oxygen. Low oxygen concentrations were observed in the 1970s during summertime in the Western Wadden Sea (Tijssen and van Bennekom 1976), and in the 1930s in seagrass beds during the night (Broekhuysen 1935). No negative effects on the zoobenthos were observed during the past 20 years. Local mass mortalities of zoobenthos may be related to forced mineralization of deposited algal blooms (Beukema and Cadée 1986). Accumulation of decomposing macroalgal material causes local death to macrozoobenthos, for example, in places where much *Ulva* and *Enteromorpha* drift ashore (cf. Reise 1984).

Macrozoobenthos production and biomass at Balgzand, a tidal flat area in the westernmost part of the Wadden Sea, doubled over a period of 15 years (Fig. 5; Beukema and Cadeé 1986). Focussing, however, on the period 1970–1980, the period of the most severe eutrophication of the Rhine River (Fig. 2), no increasing trend can be detected in macrozoobenthos biomass; a "normal" year-to-year variation between 15 g AFDW m^{-2} and 26 g AFDW m^{-2} is observed (Beukema 1982).

Data from the Wadden Sea reveal how strongly macrozoobenthos biomass and production values vary over time and in space. Many biological and abiological factors modify these processes: density-dependent and density-independent population regulation, lethal effects of severe winters, impact of the building of large civil engineering constructions and manipulations with the tidal factor (Oosterschelde), fisheries activities (Oosterschelde) and presumably eutrophication (Wadden Sea). We know far too little to attribute causal explanations to these variations (cf. Beukema 1989; de Jonge and Essink 1991).

Besides the arguments mentioned, caution is needed in exemplifying a positive relation between benthos production and biomass and eutrophication, because this relation presupposes the existence of food limitation for the benthos. It is unlikely that in a eutrophicated system further addition of nutrients might enhance the productivity of filter feeders. Model calculations for Oosterschelde estuary showed that a doubling of the nutrient load on the ecosystem only increased benthic filter-feeder biomass by 2.5% (Herman and Scholten 1990). From budget calculations based on estimates of community metabolism, de Wilde and Beukema (1984) suggested that a shortage rather than an abundance of organic matter as food existed for the benthic fauna in the Western

Wadden Sea because about 90% of the primary food available will be mineralized in the bottom sediments, either aerobically (68%) or anaerobically (21%).

Beukema and Nienhuis (1985) came to a contrasting conclusion: rather than a shortage in food supply, the availability of suitable habitats, predation pressure, and the quality of the food (organic material) may decide whether macrozoobenthos biomass expansion is limited.

Going through the estuarine food web, at the level of the secondary consumers, the energy from the sun, substantiated in primary organic matter, is so far fractioned and dissipated that in terms of consumption and production only a few g C m^{-2} yr^{-1} is left. Many carnivores occur in the estuarine ecosystem, and all of them have their own specialized ways of catching their prey, consuming their food, and assimilating what is necessary for growth, respiration, and reproduction. It is impossible to couple eutrophication to the occurrence of top predators.

At low water, tidal flats are a very well-laid table for a wealth of waterfowl (waders, ducks, geese), each having their own feeding strategy. Oosterschelde estuary can be taken as an example. Over 200,000 migratory birds, mainly carnivorous waders (max. 150,000) and herbivores (max. 40,000), use the estuary as wintering grounds. Oystercatcher (*Haematopus ostralegus*) and dunlin (*Calidris alpina*), with maximum numbers in winter of 87,000 and 53,000 respectively, are the dominant waders (data Rijkswaterstaat, Middelburg; Meire et al. 1989). Meire and Coosen (1985) calculated that roughly 20% of the macrozoobenthos biomass is consumed annually by birds.

Grevelingen Lagoon: A Case Study

Grevelingen Lagoon offers an excellent example of long-term changes in the numbers and biomass of secondary consumers following the closure of the estuary in May 1971. Before 1971 when Grevelingen was still a tidal estuary, a considerable population of migratory marine flatfish (plaice, dab, sole) lived in the estuary. The closure of the estuary meant a blockade for the remaining population of flatfish. Their migratory behavior was counteracted and hence their usual way of reproduction. The seawalls surrounding the lagoon prevented them from returning to their spawning grounds in the North Sea. Figure 6 shows a gradual decline in the number of flatfish to a very low level at the end of the 1980s.

Migratory birds, carnivorous waders exploited the intertidal flats in Grevelingen estuary before May 1971. Owing to the closure of the estuary the water level was fixed, and consequently all inter-

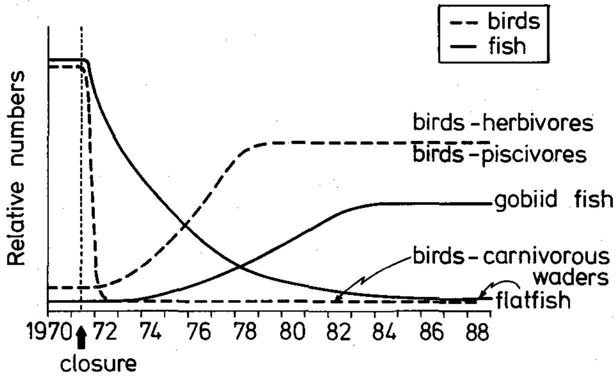

Fig. 6. Long-term changes in relative numbers of dominant groups of primary and secondary consumers in Grevelingen Lagoon, following the closure of the estuary in 1971 (derived from Nienhuis 1985). Only qualitative trends are given; annual fluctuations have been left out.

tidal flats changed into either permanently submerged sediments or permanently dry terrestrial shore areas. These changes were followed by a dramatic drop in the numbers of waders directly after 1971 (Fig. 6).

The sudden change in May 1971 induced several other changes on the tertiary trophic level. The numbers of small gobiid fish (*Pomatoschistus minutus, P. microps, Gobius niger*) and small pelagic fish (*Gasterosteus aculeatus, Sprattus sprattus, Atherina presbyter*) increased gradually after the closure (Fig. 6). All these fish species took advantage of the decreased exposure of the lagoon, the availability of suitable breeding habitats, and proper food (Doornbos 1987). The closure of Grevelingen estuary resulted also in a major increase in the numbers of piscivorous birds (great crested grebe, *Podiceps cristatus*; cormorant, *Phalacrocorax carbo*; red-breasted merganser, *Mergus serrator*). This change in numbers is related to the much higher transparency of the water (the birds are visual predators) and the availability of prey items. The prey taken by grebes and mergansers are usually small: 60% of the fresh weight of the stomach contents of these birds consisted of gobiid fish (Doornbos 1984).

Migratory herbivorous birds (geese, ducks, mute swan [*Cygnus olor*], and coot [*Fulica atra*]) took also great advantage of the new situation in Grevelingen Lagoon after May 1971, which brought them food and shelter (Slob 1989).

Eelgrass, *Zostera marina*, a rooting, submerged phanerogam, found an open niche—the sheltered subtidal sand flats—after May 1971. The species colonized the lagoon from the original pre-1971 sites, reached a maximum distribution in 1978, and showed a fluctuating pattern thereafter owing to complex causes beyond the scope of this review (cf.

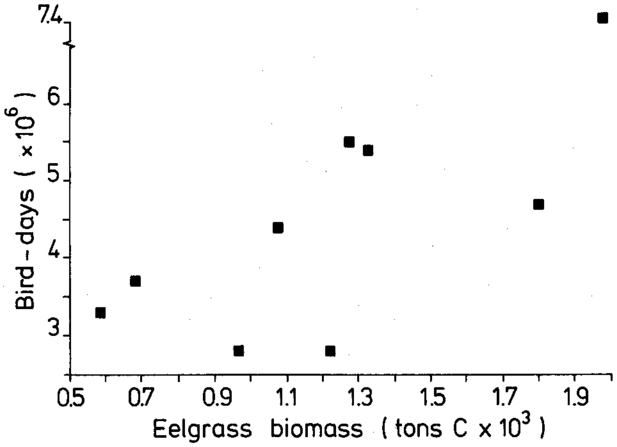

Fig. 7. Relation between maximum aboveground biomass of *Zostera marina* in Grevelingen Lagoon during July–August and the number of bird-days of herbivorous waterfowl in Grevelingen Lagoon in the subsequent autumn and winter over the period 1973–1987; $n = 9$; $r = 0.74$; $p < 0.025$.

Nienhuis 1983). *Zostera marina* is the dominant macrophyte food source in Grevelingen Lagoon. The maximum aboveground biomass of *Zostera marina* in July–August, over the period 1973 to 1988, showed a significant correlation with the number of bird-days of herbivorous birds (*Fulica atra, Anas penelope, Anas plathyrhynchos, Anas crecca, Branta bernicla, Cygnus olor*) in the subsequent autumn and winter ($r = 0.74$, $p < 0.025$, $n = 9$; Fig. 7). Although the birds only consume 4% of the annual aboveground primary production of eelgrass (Nienhuis and Groenendijk 1986), that is, 11% of the peak standing crop in August, the correlation between the numbers of birds present and their preferred food source is significant. Obviously a large part of the peak standing crop is not available to the birds because it is beyond the reach of their bills, or because the arrival of the birds does not coincide with maximum standing stock of the macrophytes; when most birds arrive later in the year, the larger part of the seagrass biomass has already decomposed.

Final Remarks

The effects of water management in Grevelingen Lagoon are clearcut (Figs. 6 and 7) following a sudden change in environmental circumstances. The chain of arguments in favor of a relation between eutrophication and food chain functioning is far more diffuse. Eutrophication is a slow and gradual process, loading the estuary with nutrients, presumably giving rise to higher primary production and, far less convincing, to higher secondary production and biomass (cf. examples from the Wadden Sea). Does a higher secondary production, that is, more food for waders, also lead to a larger population of migratory birds?

The effects of chronic eutrophication, like anaerobiosis, toxic algal blooms, mass kills of benthic and epibenthic animals and changes in species patterns, are all too obvious in many estuarine areas in the world (e.g., Baltic, Rosenberg 1985; northern Adriatic, Sfriso et al. 1987; Black Sea, Bologa 1989). Nontidal areas with a long residence time of the water mass and prevailing sedimentation and stratification appear to be most vulnerable to eutrophication. Once the unwanted, negative effects of eutrophication emerge, the process is very difficult to stop. Subsequent delivery of nutrients from underwater sediments may extend the process for many years.

Fortunately the situation along the Dutch coast is, as yet, not as pronounced as that sketched for the brackish areas abroad. As long as we do not know in detail the long-term effects of eutrophication on estuarine ecosystem functioning, the precautionary principle (Portman 1989) should be supported: avoiding excessive inputs of nutrients and reducing future loadings to Dutch estuaries and coastal waters. Political decisions in favor of that precautionary principle have already been taken by the governments of the countries bordering the North Sea. By 1995 these countries will have implemented a phosphorus- and nitrogen-removal capacity leading to a reduction of effluent loads of 50% (Third International Conference on the Protection of the North Sea 1990).

Acknowledgments

The author thanks Dr. P. G. Harrison (University of British Columbia, Vancouver, Canada), J. de Leeuw, and R. H. D. Lambeck (DIHO, Yerseke) for their comments on an earlier draft of the manuscript. Dr. I. Valiela (Woods Hole, Massachusetts, USA) considerably improved the manuscript. This paper is communication no. 616 of the NIOO, Yerseke, The Netherlands.

Literature Cited

Baretta, J. W. and P. Ruardy (eds.). 1988a. Tidal Flat Estuaries. Springer-Verlag, Berlin. 353 p.

Baretta, J. W. and P. Ruardy. 1988b. Enhanced benthic–pelagic coupling in the Western Wadden Sea model, p. 105–111. *In* EON-Projectgroep: The Ecosystem of the Western Wadden Sea: Field Research and Mathematical Modelling. Ecologisch Model Onderzoek Waddenzee II—Netherlands Institute for Sea Research Report 1988-11.

Beukema, J. J. 1982. Biologische produktie in de ondiepe, rijke randen van de zee, p. 32–53. *In* W. J. Wolff (ed.), Wadden, duinen, delta. Pudoc, Wageningen.

Beukema, J. J. 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. *Helgoländer Meeresuntersuchungen* 43:405–415.

Beukema, J. J. and G. C. Cadée. 1986. Zoobenthos responses to eutrophication of the Dutch Wadden Sea. *Ophelia* 26:55–64.

BEUKEMA, J. J. AND P. H. NIENHUIS. 1985. Processen in oecosystemen, p. 323–348. *In* K. Bakker et al. (eds.), Inleiding tot de oecologie. Bohn, Scheltema and Holkema, Utrecht.

BILLEN, G. AND C. LANCELOT. 1987. Modelling benthic microbial processes and their role in nitrogen cycling of temperate coastal ecosystems, p. 341–378. *In* H. T. Blackburn and J. Sorensen (eds.), Nitrogen in Coastal Marine Environments. Scope, Wiley, New York.

BOKHORST, M. 1988. Inventarisatie van een aantal abiotische factoren in de Westerschelde. Delta Instituut voor Hydrobiologisch Onderzoek Studentenverslagen D6-1988. (report in Dutch) 22 p.

BOLOGA, A. S. 1989. Present status of seaweed production along the Romanian Black Sea shore. *Vie et Milieu* 39:105–109.

BROCKMANN, U., G. BILLEN, AND W. W. C. GIESKES. 1988. North Sea nutrients and eutrophication, p. 348–389. *In* W. Salomons, B. L. Bayne, E. K. Duursma, and U. Förstner (eds.), Pollution of the North Sea. An Assessment. Springer-Verlag, Berlin.

BROEKHUYSEN, G. J. 1935. The extremes in percentages of dissolved oxygen to which the fauna of a *Zostera* field in the tidal zone at Nieuwediep can be exposed. *Archives Neerlandaises de Zoologie* 1:339–346.

BUUREN, J. T. VAN. 1988. De Noordzee en eutrofiëring. *H_2O* 21:591–595.

CADÉE, G. C. 1980. Reappraisal of the production and import of organic carbon 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 part of the Dutch Wadden Sea increased during the last decades? *Netherlands Institute for Sea Research Publication Series* 10:71–82.

CADÉE, G. C. 1986. Increased phytoplankton primary production in the Marsdiep area (Western Dutch Wadden Sea). *Netherlands Journal of Sea Research* 20:285–290.

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

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

CADÉE, G. C. AND J. HEGEMAN. 1977. Distribution of primary production of the benthic microflora and accumulation of organic matter on a tidal area, Balgzand, Dutch Wadden Sea. *Netherlands Journal of Sea Research* 11:24–41.

COOSEN, J. P., P. M. MEIRE, J. J. STUART, AND J. SEYS. 1990. Trophic relationships in brackish Lake Veere: The role of macrophytes, p. 404–423. *In* M. Barnes and R. N. Gibson (eds.), Trophic Relationships in the Marine Environment. Proceedings of the 24th European Marine Biology Symposium, Aberdeen University Press, Scotland.

CUSHING, D. H. 1990. Recent studies on long-term changes in the sea. *Freshwater Biology* 23:71–84.

DAEMEN, E. A. M. J. 1985. Literatuuronderzoek met betrekking tot de oecologie van het Veerse Meer. Delta Consult, Kapelle. (report in Dutch) 116 p.

DIJKZEUL, A. 1982. De waterkwaliteit van de Rijn in de periode 1970–1981. RIZA Report 82-061. (report in Dutch) 112 p.

DOORNBOS, G. 1984. Piscivorous birds on the saline lake Grevelingen, The Netherlands: Abundance, prey selection and annual food consumption. *Netherlands Journal of Sea Research* 18: 457–479.

DOORNBOS, G. 1987. The fish fauna of Lake Grevelingen (SW Netherlands). Ph.D. Thesis, University Amsterdam, Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke. 169 p.

EON-PROJECTGROEP. 1988. The ecosystem of the Western Wadden Sea: Field research and mathematical modelling. Netherlands Institute for Sea Research Report 1988-11. 139 p.

ESSINK, K. 1985. Monitoring of mercury pollution in Dutch coastal waters by means of the teleostean fish *Zoarcus viviparus*. *Netherlands Journal of Sea Research* 19:177–182.

HANNEWIJK, A. 1988. De verspreiding en biomassa van macrofyten in het Veerse Meer, 1987. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, Rapporten en Verslagen 1988-2. (report in Dutch) 25 p.

HEIP, C. H. R. 1989. The ecology of the estuaries of Rhine, Meuse and Scheldt in The Netherlands, p. 457–463. *In* J. D. Ros (ed.), Topics in Marine Biology. *Scientific Marine* 53.

HERMAN, P. M. J. AND H. HUMMEL. 1989. Project group Westerschelde, p. 51–52. *In* C. H. R. Heip and E. S. Nieuwenhuize (eds.), Progress Report Delta Institute for Hydrobiological Research. Dutch Royal Academy of Sciences, Amsterdam.

HERMAN, P. M. J. AND H. SCHOLTEN. 1990. Can suspension-feeders stabilise estuarine ecosystems? p. 104–116. *In* M. Barnes and R. N. Gibson (eds.), Trophic Relationships in the Marine Environment. Proceedings of the 24th European Marine Biology Symposium, Aberdeen University Press, Scotland.

JONG, S. A. DE, P. A. G. HOFMAN, A. J. J. SANDEE, AND E. J. WAGENVOORT. 1990. Primary production of benthic microalgae in the Oosterschelde estuary (SW Netherlands). Dienst Getijdewateren, Middelburg; Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke, BALANS report 43. 262 p.

JONGE, V. N. DE AND K. ESSINK. 1991. Long-term changes in nutrient loads and primary and secondary producers in the Dutch Wadden Sea, p. 307–316. *In* M. Elliott and J.-P. Ducrotoy (eds.), Estuaries and Coasts: Spatial and Temporal Intercomparisons. Olsen and Olsen, Fredensborg.

MEIRE, P. M. AND J. COOSEN. 1985. Benthos and bird communities in a changing estuary. Proceed. *Progress in Belgian Oceanographic Research,* Brussels 1985:292–303.

MEIRE, P. M., J. SEYS, T. YSEBAERT, P. L. MEININGER, AND H. J. M. BAPTIST. 1989. A changing delta: Effects of large coastal engineering works on feeding ecological relationships as illustrated by waterbirds, p. 109–146. *In* J. C. Hooghart and C. W. S. Posthumus (eds.), Hydro-ecological Relations in the Delta Waters of the Southwest Netherlands. TNO Communications Hydrological Research Proceedings and Information 41.

NELISSEN, P. H. M. AND J. STEFELS. 1988. Eutrophication in the North Sea, a literature survey. Netherlands Institute for Sea Research-Report 1988-4. 100 p.

NIENHUIS, P. H. 1983. Temporal and spatial patterns of eelgrass (*Zostera marina* L.) in a former estuary in The Netherlands, dominated by human activities. *Marine Technology Society Journal* 17:69–77.

NIENHUIS, P. H. (ED.). 1985. Het Grevelingenmeer. Van estuarium tot zoutwatermeer. Natuur en Techniek, Maastricht, Brussels. 177 p.

NIENHUIS, P. H. 1989a. Eutrophication of estuaries and brackish lagoons in the southwest Netherlands, p. 49–70. *In* J. C. Hooghart and C. W. S. Posthumus (eds.), Hydro-ecological relations in the delta waters of the southwest Netherlands. TNO Communications Hydrological Research Proceedings and Information 41.

NIENHUIS, P. H. 1989b. Introduction—Research group estuarine foodchains, p. 8–9. *In* C. H. R. Heip and E. S. Nieuwenhuize (eds.), Progress Report 1988. Delta Institute for Hydrobiological Research, Dutch Royal Academy of Sciences, Amsterdam.

NIENHUIS, P. H. AND A. M. GROENENDIJK. 1986. Consumption of eelgrass (*Zostera marina* L.) by birds and invertebrates: An annual budget. *Marine Ecology Progress Series* 29:29–35.

OFFICER, C. B., T. J. SMAYDA, AND R. MANN. 1982. Benthic

filter feeding: A natural eutrophication control. *Marine Ecology Progress Series* 9:203–210.
PORTMAN, J. E. 1989. The chemical pollution status of the North Sea. *Dana* 8:95–108.
PROJECTGROEP BALANS. 1988. Voedsel in de Oosterschelde. Rijkswaterstaat—Dienst Getijdewateren, Middelburg and Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke. (report in Dutch) 53 p.
REISE, K. 1984. Indirect effects of sewage on a sandy tidal flat in the Wadden Sea. *Netherlands Institute for Sea Research Publication Series* 10:159–164.
RICHARDSON, K. 1989. Algal blooms in the North Sea: The good, the bad and the ugly. *Dana* 8:83–93.
RIDDERINKHOF, H. 1990. Residual currents and mixing in the Wadden Sea. Ph.D. Thesis, State University, Utrecht. Publication 12 Ecological Research North Sea and Wadden Sea. 91 p.
RIJKSWATERSTAAT. 1985. Biological research Ems-Dollard estuary. Rijkswaterstaat Communication, Den Haag 40:1–182.
RIJKSWATERSTAAT. 1989. Water voor nu en later; Derde nota waterhuishouding, samenvatting. Rijkswaterstaat, Den Haag. (report in Dutch) 66 p.
RIJKSWATERSTAAT. 1990. Interim report on the quality status of the North Sea. Third International Conference on the Protection of the North Sea, March 7–8, The Hague, Rijkswaterstaat, Den Haag. 48 p.
ROSENBERG, R. 1985. Eutrophication—The future marine coastal nuisance? *Marine Pollution Bulletin* 16:227–231.
RUYTER, W. P. M. DE, L. POSTMA, AND J. M. DE KOK. 1987. Transport Atlas of the Southern North Sea. Rijkswaterstaat Tidal Waters Division, Delft Hydraulics, Den Haag. 34 p.
SCHOLTEN, H., O. KLEPPER, P. H. NIENHUIS, AND M. KNOESTER. 1990. Oosterschelde estuary (SW Netherlands): A self-sustaining estuary? *Hydrobiologia* 195:201–215.
SFRISO, A., A. MARCOMINI, AND B. PAVONI. 1987. Relationships between macroalgal biomass and nutrient concentrations in a hypertrophic area of the Venice Lagoon. *Marine Environmental Research* 22:297–312.
SLOB, G. J. 1989. 15 jaar vogelontwikkelingen in het afgesloten Grevelingenbekken. Staatsbosbeheer, Goes. (report in Dutch) 50 p. + appendices.
STRONKHORST, J., R. N. M. DUIN, AND H. A. HAAS. 1985. Primaire produktie onderzoek in het Veerse Meer (1982–1983). Nota Delta Dienst Milieu Onderzoek, 85.01, Middelburg. (report in Dutch) 52 p.
THIRD INTERNATIONAL CONFERENCE ON THE PROTECTION OF THE NORTH SEA. 1990. The implementation of the ministerial declaration of the Second International Conference on the Protection of the North Sea. Executive Summary, 8 March 1990. Ministry of Transport and Public Works, The Hague, The Netherlands. 64 p.
TIJSSEN, S. B. AND A. J. VAN BENNEKOM. 1976. Lage zuurstofgehaltes in het water op het Balgzand. *H_2O* 9:28–31.
VALIELA, I. 1984. Marine ecological processes. *In* D. E. Reichle (ed.), Springer Advanced Texts in Life Sciences. Springer, New York. 546 p.
VEER, H. W. VAN DER, W. VAN RAAPHORST, AND M. J. N. BERGMAN. 1988. Eutrophication of the Dutch Wadden Sea—External nutrients loadings of the Marsdiep and Vliestroom basins, p. 113–122. *In* EON-projectgroep: The Ecosystem of the Western Wadden Sea: Field Research and Mathematical Modelling. Ecologisch Model Onderzoek Waddenzee II—Netherlands Institute for Sea Research Report 1988-11.
VEGTER, F. AND P. R. M. DE VISSCHER. 1987. Nutrients and phytoplankton primary production in the marine tidal Oosterschelde estuary (The Netherlands). *Hydrobiological Bulletin* 21:149–158.
VELDHUIS, M. J. W. 1987. The ecophysiology of the colonial alga *Phaeocystis pouchetii.* Ph.D. Thesis, University Groningen, Van Denderen Groningen. 127 p.
VOSJAN, J. H. 1987. A sketchy outline of the fate of organic matter in the Dutch Wadden Sea. *Hydrobiological Bulletin* 21: 127–132.
VRIES, I. DE AND C. F. HOPSTAKEN. 1984. Nutrient cycling and ecosystem behaviour in a salt-water lake. *Netherlands Journal of Sea Research* 18:221–245.
VRIES, I. DE, F. HOPSTAKEN, H. GOOSSENS, M. DE VRIES, H. DE VRIES, AND J. HERINGA. 1988a. GREWAQ: An ecological model for Lake Grevelingen. Report T-0215-03, Rijkswaterstaat Dienst Getijdewateren, Den Haag, Delft Hydraulics, Delft. 159 p. + 83 p.
VRIES, I. DE, W. VAN RAAPHORST, AND N. DANKERS. 1988b. Extra voedingsstoffen in zee: Gevolgen, voordelen, nadelen. *Landschap* 5:270–285.
WETSTEYN, L. P. M. J., J. C. H. PEETERS, R. N. M. DUIN, F. VEGTER, AND R. P. M. DE VISSCHER. 1990. Phytoplankton primary production and nutrients in the Oosterschelde (The Netherlands) during the pre-barrier period 1980–1984. *Hydrobiologia* 195:103–177.
WETSTEYN, L. P. M. J. AND L. PEPERZAK. 1988. Abiotische variabelen, primaire produktie en kwalitatieve fytoplanktonsamenstelling en -successie in de Oosterschelde in 1987. Nota GWAO-88.1009. Rijkswaterstaat DGW, Middelburg. (report in Dutch) 59 p.
WILDE, P. A. W. J. DE AND J. J. BEUKEMA. 1984. The role of zoobenthos in the consumption of organic matter in the Dutch Wadden Sea. *Netherlands Institute for Sea Research Publication Series* 10:145–158.
WOLLAST, R. 1988. The Scheldt estuary, p. 183–193. *In* W. Salomons, B. L. Bayne, E. K. Duursma, and U. Förstner (eds.), Pollution of the North Sea—An Assessment. Springer, Berlin.

Received for consideration, September 1, 1990
Accepted for publication, March 13, 1992