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ECOLOGY OF COASTAL LAGOONS IN THE NETHERLANDS (VEERSE MEER AND GREVELINGEN)

P.H. NIENHUIS

Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology,
Vierstraat 28, 4401 EA Yerseke, The Netherlands

THE NETHERLANDS
COASTAL LAGOON
NUTRIENT DYNAMICS
EUTROPHICATION
FOODWEB

ABSTRACT – The Netherlands are for the larger part situated around the estuaries of the rivers Rhine, Meuse and Scheldt. During the period 1960-1980 several estuaries have been closed off from the sea and transformed into artificial lagoons. The hydrography, nutrient dynamics and trophic relations of two large coastal lagoons, mesotrophic Grevelingen and eutrophic Veerse Meer are the subject of this review. Nitrogen and phosphorus loadings on Grevelingen lagoon are only small compared to the loadings on Veerse Meer lagoon. The key-element in the cycling of organic matter in both lagoons is nitrogen, limiting the rates of primary production. Veerse Meer has a relatively high biomass and production of phytoplankton and loose-lying *Ulva* spp., whereas Grevelingen has a relatively high biomass and production of eelgrass, *Zostera marina*. In both lagoons large quantities of benthic macrophytes are consumed by herbivorous birds. Veerse Meer is more susceptible to anoxia owing to the high concentrations of labile and refractory organic matter, both in the water column and in the bottom sediments.

PAYS-BAS
LAGUNE CÔTIÈRE
DYNAMIQUE DES SELS NUTRITIFS
EUTROPHISATION
RÉSEAUX TROPHIQUES

RÉSUMÉ – Les Pays-Bas s'étendent en grande partie entre les estuaires du Rhin, de la Meuse et de l'Escaut. Au cours des années 1960 à 1980, plusieurs estuaires ont été endigués et transformés en lagunes artificielles. L'hydrographie, la dynamique des sels nutritifs et les relations trophiques des 2 grandes lagunes côtières, le Grevelingen (à caractère mésotrophique) et le Veerse Meer (à tendance eutrophique), constituent le sujet de cette revue. Les apports exogènes en azote et en phosphore sont bien plus faibles pour le Grevelingen que pour le Veerse Meer. Pour ces deux écosystèmes l'azote, principal facteur limitant pour la production primaire, constitue l'élément clé du cycle de transformation de la matière organique. Le Veerse Meer est caractérisé par une biomasse végétale et une production primaire relativement élevée, principalement attribuables au phytoplancton et aux Algues dérivantes du genre *Ulva spp.*, tandis que dans le Grevelingen, les herbiers à *Zostera marina* constituent une part prépondérante des biomasse et production végétales. Dans ces 2 lagunes une grande quantité de macrophytes benthiques sont consommés par des oiseaux herbivores. Le Veerse Meer est, en raison de ses fortes concentrations en matières organiques (labile et réfractaire), plus susceptible de présenter des crises anoxiques se développant aussi bien dans le sédiment que dans la colonne d'eau.

INTRODUCTION

The Netherlands are a small, low-lying country, for the larger part situated around the estuaries of the rivers Rhine, Meuse and Scheldt (Fig. 1). Natural coastal lagoons do not occur in the Netherlands, but many brackish water systems exist, originated in the course of the history of the country. Repeated flooding by the sea, progressive land reclamation and embankment, left many smaller and larger man-made brackish inland waters. Many of these water-bodies can hydrographically be characterized as isolated brackish lakes and some of them as coastal lagoons, viz. water-bodies with a semi-permanent connection with the open sea, mainly by man-operated sluices. Most inland water-bodies are small in surface area (< 100 ha), varying in depth from over 10 m to very shallow marshy wetlands, and varying in salinity from oligohaline (0.3-3 ‰ Cl), via mesohaline (3-10 ‰ Cl) to polyhaline (10-16.5 ‰ Cl). Owing to

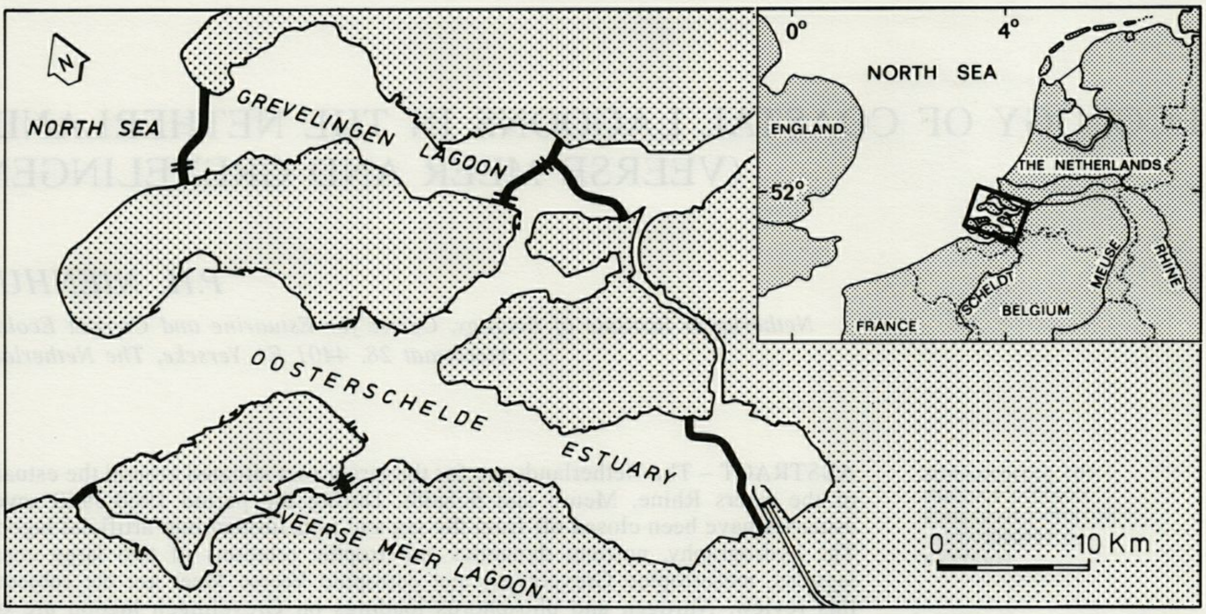

Fig. 1. – Veerse Meer lagoon and Grevelingen lagoon in the SW Netherlands. Man-operated sluices connect the artificial lagoons with adjoining tidal estuaries. Insert : The SW Netherlands in the lower drainage basin of the rivers Rhine, Meuse and Scheldt.

their topographic isolation and large variation in environmental characteristics, these inland waters often contain interesting biological communities with specific combinations of plants and animals. Brackish waters are poor in species and a significant phenomenon is the relation between the variation in salinity of the water mass and the number of species : the larger the fluctuation in salinity, the smaller the number of species (De Jonge, 1974; Barnes, 1980).

Mesohaline waters are the most characteristic brackish waters in the Netherlands; small in surface area and shallow, containing an impoverished but specific flora and fauna, a.o. the submersed macrophyte *Ruppia cirrhosa*, the bryozoan *Electra crustulenta*, the bivalve *Cerastoderma lamarcki*, the gastropods *Hydrobia ventrosa* and *H. stagnorum*, the polychaete *Nereis diversicolor*, the crustaceans *Neomysis integer*, *Palaemonetes varians*, *Sphaeroma rugicauda* and *S. hookeri*. Obviously these species are physiologically well adapted as they can stand strongly fluctuating concentrations of environmental parameters.

Polyhaline wate-bodies are rare in the Netherlands. Two of them fall in the category "coastal lagoon", viz. Veerse Meer lagoon and Grevelingen lagoon, large water systems (> 2 000 ha), now blind estuaries, closed off from the sea by seawalls and transformed into artificial lagoons with a semi – permanent connection with the open sea. This chapter will focus on the specific ecology of these two larger artificial lagoons in the SW Netherlands meso-polyhaline Veerse Meer lagoon and polyhaline Grevelingen lagoon (Fig. 1).

HYDROGRAPHY

1. Veerse Meer

Veerse meer lagoon originated in 1960-1961, after the embankment of an estuarine branch of the Rhine-Scheldt. Man-operated sluices connect the lagoon with the tidal Oosterschelde estuary. Table 1 gives hydrographical data on the Veerse Meer lagoon. The surface area of the lagoon is 21 km^2 during summer, but during winter the lagoon serves mainly as a receiving water-body for nutrient-rich agricultural run-off (83 x 10^6 m^3 yr^{-1}). To facilitate this function, the water level is maintained at MSSL (Mean Standard Sea Level) in summer and MSSL – 0.70 m in winter (surface area during winter 18 km^2).

The ratio between the annual fresh-water load and the volume of the lagoon is roughly 1. Each year in April 67 x 10^6 m^3 of salt water from Oosterschelde estuary is introduced into the lagoon via the locks/sluices in the eastern dam (Fig.1) and each year in September/October the same volume of water is exchanged again with the adjoining estuary. The yearly average residence time of the water is about 180 days. This regime resulting in a high water level in summer and a low level during winter is contrasting with the "natural" fluctuation in water levels in isolated water-bodies in the cold temperature climate areas with a precipitation surplus in winter and an evaporation surplus in summer.

Salinity of the water is dependent on the water-management, and fluctuates between 8 and 12 ‰ Cl. The inlet of saline water in April is situated in the eastern dam, implying a permanent stratification at a water-depth of 5-6 m. In the central part of the lagoon the depth of the stratification layer varies between 5 and 15 m, only in summer, and in the western part of the lagoon the water-mass is mostly well mixed or incidentally stratified with a mixing depth varying between 6 and 25 m (Coosen *et al.* 1990). This regime has its consequences for the benthic infaunal communities. Tides are absent and currents are weak : particles settle easily and consequently the stagnant water of the lagoon, containing a low amount of silt particles is clear, but plankton blooms may colour the water mass occasionally (maximum extinction coefficient 1.4). The substantial input of nutrient-rich fresh/oligohaline water from the surrounding agricultural grounds causes a moderate phosphorus load (6 g P m^{-2} yr^{-1}) and a high nitrogen load (34 g N m^{-2} yr^{-1}) resulting in considerable concentrations of ammonium and nitrate at the end of the winter, before the phytoplankton spring bloom starts (3 mg l^{-1}). Chlorophyll a concentrations, derived from phytoplankton, vary considerably between years, mainly in spring. The mean value of 100 mg Chl a m^{-3} is often exceeded by higher values, mainly in the eastern part of the lagoon (Coosen *et al.*, 1990).

2. Grevelingen

Grevelingen lagoon, the largest polyhaline lagoon in the Netherlands, originated in 1964-1971. In 1964 the eastern dam was closed, isolating the estuary from the main influx of fresh-water of the river Rhine (Fig. 1). In 1971 the connection with the North Sea was interrupted by the construction of a dam through the western mouth of the estuary and Grevelingen became a stagnant, non-tidal lagoon with only wind driven currents. The water-level is maintained at MSSL – 0.20 m, both during summer and winter. Fluctuations in water-level due to wind effects, evaporation and precipitation are a few decimeters at a maximum. Table 1 shows hydrographical data on Grevelingen lagoon. The surface area of the lagoon is 108 km^2, with an average depth of 5.3 m. About 64 % of the lake has a depth of less than 5 m and 46 % of less than 2.5 m. During the period 1971-1978 Grevelingen was an almost completely closed brackish-water lake, with only a small shipping lock in the eastern dam, connecting the water-body with the adjoining Oosterschelde estuary. Owing to this almost complete isolation from the surrounding water-masses Grevelingen changed gradually : salinity decreased from 17 to 13 ‰ Cl, phosphate increased from 0.2 to 0.8 mg l^{-1}. In 1978 the connection between the North Sea and Grevelingen lagoon was effected again by means of a sluice (100 m^3 sec^{-1}) in the western Brouwersdam, implying restricted entrance of full sea-water into the brackish lagoon, only during winter, thus preventing stratification during summer.

In 1983 another siphon-type sluice system in the eastern dam re-established the connection between Oosterschelde estuary and Grevelingen lagoon. Salinity increased again to 16 ‰ Cl; phosphate decreased to 0.15 mg l^{-1} nitrate remained low (0.15 mg l^{-1}) and ammonium remained extremely low (0.07 mg l^{-1}). Circulation of water from the North Sea via the sluices in the western dam, through the lagoon and finally through the sluice-system in the eastern dam into the Oosterschelde estuary is now one of the management options.

Grevelingen lagoon has a much more favourable ratio between the volume of fresh-water discharged on the system and the volume of the lagoon proper (1 :27) than Veerse Meer (1 :1). Consequently, nitrogen and phosphorus loadings on Grevelingen are but small compared to the loadings on Veerse Meer. Grevelingen lagoon can be characterized as "mesotrophic" in contrast to "eutrophic" Veerse Meer lagoon. The water of Grevelingen lagoon is extremely clear for Dutch standards (extinction coefficient 0.2-0.5 m^{-1}) and turbidity is only seldom seriously affected by plankton blooms (mean chlorophyll a concentration 5 mg m^{-3}).

Owing to the newly established hydro-dynamical conditions the process of redistribution of bottom-sediments is still continuing : the exposed (former) tidal flats are leveled by continuous erosion and the (former) tidal gullies are gradually filled with silt and sand. This balance between erosion and deposition has also been observed in Veerse Meer lagoon.

NUTRIENT DYNAMICS

The range of nutrient concentrations in Veerse Meer and Grevelingen lagoon differs considerably. Concentrations in Grevelingen lagoon reach only seldom values above 1 mg l^{-1} for N, P and Si, and nutrient concentrations frequently approach zero during heavy blooms of phytoplankton in these ecosystems. Veerse Meer has higher maximum values for N and Si, but depletion occurs during the growing season (De Vries *et al.*, 1988 b). Although phosphate is often coined as the lim-

Tabl. I. – Hydrographical and hydrochemical properties of Veerse Meer lagoon and Grevelingen lagoon in the SW Netherlands (data derived from Nienhuis, 1992).

	Veerse Meer	Grevelingen
Area (km^2)	22 (18)	108
Volume (m^3.10^6)	89	575
Maximum depth (m)	25	48
Average depth (m)	4.5	5.3
Residence time (d)	± 180	180-360
Fresh-water load (m^3.10^6 yr^{-1})	83	21
Volume: Load	1 : 1	27 : 1
Tides	no	no
Stratification	yes	yes/no
Extinction coefficient (m^{-1})	0.3-1.4	0.2-0.5
Chlorinity (‰)	8-12	14-16
Nitrogen load (g N m^{-2} yr^{-1})	34	4
Winter conc. N-NH$_4$ + N-NO$_3$ (mg l^{-1})	3.0	0.7
Phosphorus load (g P m^{-2} yr^{-1})	6.0	0.4
Autumn conc. P-PO$_4$ (mg l^{-1})	0.8	0.3
Summer chlorophyll conc. (mg Chl a m^{-3})	100	5

iting nutrient in fresh – and brackish-water systems, this component seems available in excess in the non-tidal stagnant lagoons in the SW Netherlands. The availability of inorganic phosphate to estuarine primary producers depends on microbial and physical processes both in the water and in the sediment. Phosphate is taken up and released by both aerobic and anaerobic sediments, although most exchange occurs between water and anaerobic sediments. Also, more exchange occurs with disturbed than undisturbed sediments (Kelderman, 1985). As oxygen slowly diffuses into sediments it is rapidly consumed by the benthic community. As the oxygen concentration is depleted with depth in the underwater sediment, dissimilatory sulphate reduction dominates, producing sulfide, which decreases the redox potential, causing a solubilization of inorganic phosphate (Fenchel and Riedl, 1970). If the overlying water is anoxic, as is the case in stratified estuaries, the phosphate may enter the water column, stimulating photosynthesis. If the surface of the sediment remains aerobic, much of this phosphate is again made insoluble as it diffuses, or as it is bioturbated, into the aerobic zone. Besides oxygen availability a temperature-mediated process of mobilization and accumulation of sediment-bound phosphates makes the picture more complicated, as was shown by Kelderman (1980) in the Grevelingen lagoon; in 1974-1977 he found a net P-mobilization during the period April-September, and a net accumulation during the rest of the year.

In Grevelingen lagoon these microbial and physical processes resulted in a steady increase in phosphate concentrations during the period 1971-1978 (from 0.2 mg PO_4-P l^{-1} to 0.8 mg PO_4-P l^{-1}), and a consequent decrease in the period thereafter (to a level of 0.2 mg PO_4-P l^{-1}), when the connection with the North Sea was reopened. In Veerse Meer the relative load with fresh-water is larger than in Grevelingen (Tabl. I) and hence the concentrations of phosphate have always been substantial (PO_4-P 0.1-0.9 mg l^{-1}).

Instead of phosphorus it is assumed that nitrogen is limiting primary production processes in the Grevelingen (De Vries *et al.*, 1988 a) and occasionally in the Veerse Meer. In the clear water 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.*, 1988 b). This large production of phytoplankton biomass in Veerse Meer, and the consequent deposition of particulate organic carbon on the bottom sediments, resulted during the period 1980-1983 in an increase of the anaerobic sediment surface area from 4 to 25 % of the bottom surface. Obviously, Veerse Meer is vulnerable to eutrophication, owing to the long residence time of the water mass, the low extinction coefficient and the almost permanent stratification.

Grevelingen has an extremely low N-loading (4 gN m^{-2} yr^{-1}; Table I), in contrast with Veerse Meer. Simulations in a mathematical model (de Vries *et al.* 1988 a) revealed that the production of phytoplankton in Grevelingen is limited by nitrogen availability and not by light. The N :P ratio of the dissolved nutrients in the water column of Grevelingen lagoon during winter is 2 to 4, pointing into the direction of a surplus of phosphate, notwithstanding the dominance of nitrogen in the discharge water, loading the lagoon (N :P = 22 :1). Model calculations showed a higher turnover of nitrogen in the water column. The chain of processes : nutrient uptake by phytoplankton – formation of organic matter in algal cells – mineralization of dead algae – regeneration of nutrients – etc. runs 8 times a year in Grevelingen lagoon. This implies that roughly 90 % of the annual primary production of phytoplankton occurs on the basis of regenerated nutrients, especially NH_4 (De Vries *et al.*, 1988 a).

In many shallow estuarine waters the main food chain is dominated by phytoplankton and benthic filter feeders (mussels, cockles), just as is the case in Grevelingen and Veerse Meer lagoons. 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 lagoons mentioned, circulates through the filtering apparatus of the suspension feeders. Filter feeders act as natural controllers of eutrophication processes (Officer *et al.*, 1982) : they deposit 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 the Grevelingen lagoon (De Vries *et al.*, 1988 a).

The chain of processes – partly measured, partly theoretical – from biodeposition to regeneration of nutrients and the coupling between nitrification and denitrification, is controlled by the load of organic material to the sediment. Denitrification is a key-process in the nitrogen cycle of lagoonal ecosystems. Rates of gaseous losses of nitrogen in the range from 5 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 load of organic material on the bottom increases faster than the process of aerobic mineralization, anaerobic conditions will prevail in the sediment, leading to death of bottom fauna and a disconnection of nitrification and denitrification. Mathematical-model calculations by De Vries *et al.* (1988 a) simulate that a loading of approximately 10 gN m^{-2} yr^{-1} or more uncouples the eutrophication controlling processes and consequently, may have negative effects on the benthic animal communities.

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. According to the model calculations of De Vries *et al.* (1988 a) the chlorophyll concentrations in this lagoon cannot be controlled by the bottom fauna, although a substantial filter-feeding benthic biomass is available (Coosen *et al.*, 1990).

Tabl. II. – Production in g C m^{-2} y^{-1} (P = net or gross production, or value in between, depending on the method used; P_n = net production) and consumption (C) in Veerse Meer and Grevelingen lagoon, SW Netherlands (from Nienhuis, 1992).

	Veerse Meer	Grevelingen
PRIMARY PRODUCERS		
- phytoplankton (P)	240	190
- microphytobenthos (P)	80	75
- macrophytobenthos (P)	120	50
PRIMARY CONSUMERS		
- macrozoobenthos (C)	120	118
- id (Pn)	12	14
- birds (herbivores) (C)	5	2
SECONDARY CONSUMERS		
- fish + invertebrates (C)	3	3
- birds (carnivores) (C)	2	± 1
- man (C)	<<1	<<1

PRIMARY PRODUCERS

In Table II a tentative carbon budget of the main categories of primary producers in Grevelingen and Veerse Meer lagoons is given. Phytoplankton is the dominant primary producer contributing 53 to 59 % to the overall annual production of organic material. The figures in Table II depict average, annual, integrated data, useful for reasons of comparison. However, phytoplankton primary production in coastal lagoons is not a continuous process over the course of the year. Earlier than in turbid estuaries it usually starts with the spring bloom in March, showing peaks and troughs during spring, summer and autumn, depending on water temperature, insolation, nutrient availability, competition between plankton species and other factors. This implies that year to year changes in phytoplankton production may be rather substantial.

Production of microphytobenthos (benthic diatoms, green algae, etc.) comprises a very rough estimate (Nienhuis and De Bree, 1984) and is roughly 18 to 23 % of the total primary production. Macrophytobenthos comprises both rooting phanerogams and macro-algae. In the brackish lagoons Grevelingen and Veerse Meer, macrophytes living on or rooting in sediment, respectively macro-algae (mainly green algae) and seagrasses, offer a significant share to the carbon budget. In the mesotrophic Grevelingen the rooting seagrass *Zostera marina* dominates, covering

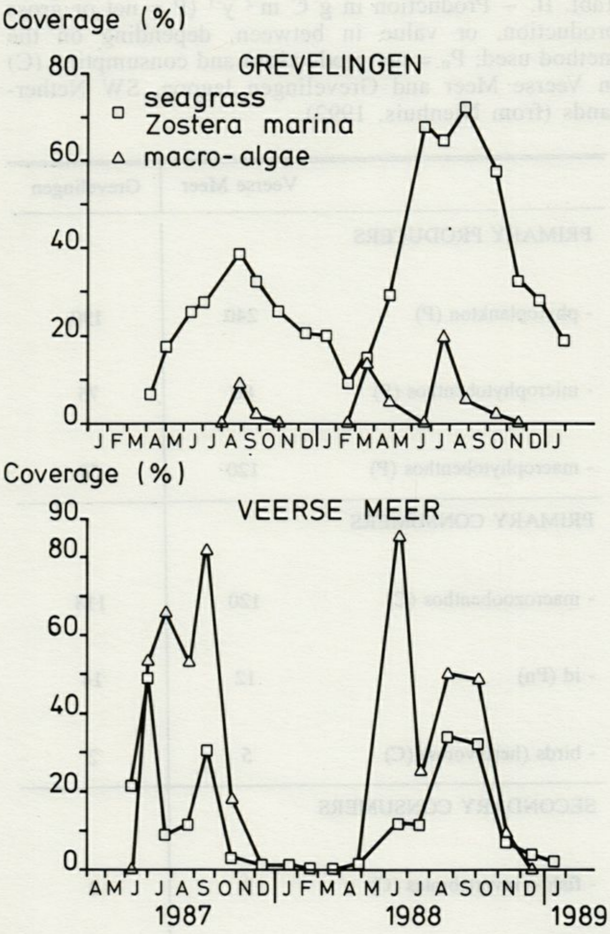

Fig. 2. – Percentage coverage of *Zostera marina* and macro-algae in vertical projection on the sediment in permanent sample plots in Veerse Meer lagoon and Grevelingen lagoon. Size of sample plots is 15 x 15 m^2, waterdepth in both localities is 1.25 m (Nienhuis, 1989).

20 % of the surface area of the lagoon and showing a within-habitat production of 150 g C m^{-2} yr^{-1}, but contributing only 14 % to the annual carbon budget, owing to the lower annual average P/B ratio of 3, compared to phytoplankton.

In Veerse Meer lagoon seagrasses cover only 3 % of the surface area (Hannewijk, 1988) and have to compete with green algae – mainly *Ulva* – for space and light. The lagoon is dominated by *Ulva* spp. during summer, showing a roughly estimated production of 500 gC m^{-2} yr^{-1} in shallow areas. The contribution of *Ulva* to the annual carbon budget of Veerse Meer is roughly 120 gC m^{-2} yr^{-1}, which is 27 % of the lagoon's budget (Table II); *cf.* Fig. 8 where *Ulva* production is estimated at 30 gC m^{-2} yr^{-1}. The high nitrogen load of Veerse Meer not only results in a relatively high production of phytoplankton, but also in mass growth of *Ulva* in shallow areas.

Fig. 2 shows the increase and decrease in biomass of macrophytes, expressed as percentage coverage, in a permanent sample plot in the Grevelingen and in the Veerse Meer. In the Grevelingen the annual cycle of changes in biomass of seagrass is not disturbed by macro-algae, which have only a low presence. In the Veerse Meer the seagrass plot becomes completely dominated by quickly growing *Ulva*, suppressing the growth of *Zostera*.

For fresh-water ecosystems a tentative model has been developed, describing the relation between the relative dominance of primary producers connected to the availability of nutrients, and the successive phases in the process of increasing eutrophication (Fig. 3, upper panel). The model has been adapted by me for estuarine and lagoonal situations (Fig. 3, lower panel), based on data from the Grevelingen and Veerse Meer. The model is only applicable to stagnant brackish lagoons and extremely sheltered parts of tidal estuaries. In "healthy" saline waters, waterplants – such as seagrasses – dominate. Nitrogen load and concentrations are low and the relative importance of phytoplankton in the shallow seagrassbeds is insignificant; the Grevelingen lagoon is an example of phase I. In brackish waters where eutrophication increases, revealed by higher nitrogen loads and nitrogen concentrations and lower, instable salinities, waterplants are outcompeted by macro-algae. Epiphyte growth on seagrasses in-

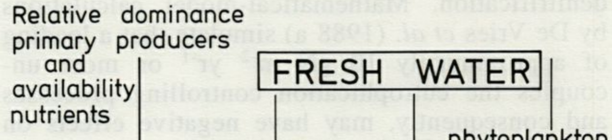

Fig. 3. – Tentative model depicting the relation between primary producers and nutrients, and the successive stages in the process of eutrophication (Nienhuis, 1989).

creases considerably together with the relative dominance of phytoplankton. The resilience of the aquatic communities decreases, which makes the system less constant in time and less predictable for water-quality managers; the Veerse Meer lagoon is an example of phase II. In hyper-eutrophicated systems (phase III) heavy uncontrolled phytoplankton blooms alternate with mass growth of macro-algae. Nutrient concentrations are continuously high. Rooting waterplants have completely disappeared. Bottom sediments suffer from permanent anoxia. The inshore parts of the lagoon of Venice is an example of phase III, where *Ulva* biomass reaches values of 1.5 kg dry weight m^{-2} (Sfriso *et al.*, 1987) which is 6 times higher as in the Veerse Meer.

Two remaining categories of macrophytobenthos have to be mentioned, viz. higher plants in supratidal wetlands and epilithic macro-algae. Supratidal wetlands overgrown with higher plants, salt marshes, form one of the natural habitats, fringing tidal estuaries in the temperate climatic zones. Salt marshes have an extremely high net primary production, roughly 400 to 1200 C m^{-2} yr^{-1}, above – and below – ground production taken together (Huiskes, 1988; Groenendijk, 1984). Owing to the impact of man, many of the original salt marshes along the Dutch estuaries have been transformed in the past centuries into agricultural land and surrounded by sea-walls. Grevelingen lagoon and Veerse Meer lagoon are non-tidal systems, and the wetlands surrounding the lagoons, although covered by extensive vegetations of higher plants, are functionally separated from the water mass. Far out the larger part of the organic matter of the wetland vegetation decomposes in the marshes proper, and perhaps a very small part of marsh-detritus is transported into the lagoon. Their contribution to the carbon budget in Table 2 is ignored.

The lagoons in the SW Netherlands lack natural rocky substrates. The only stony habitats are the man-made sea-walls and stone-clad dikes surrounding the lagoons. Consequently, macrophytes (epilithic macro-algae) attached to those substrates contribute only very little to the carbon budget of the entire water-bodies, notwithstanding their high primary production per m^2 of habitat.

TROPHIC RELATIONS AND FOOD-WEBS

1. *Veerse Meer lagoon*

The phytoplankton community of Veerse meer lagoon is poor in species. In spring a diatom bloom of *Skeletonema costatum* produces most of the biomass. The zooplankton community is also poor in species, and is dominated in early spring

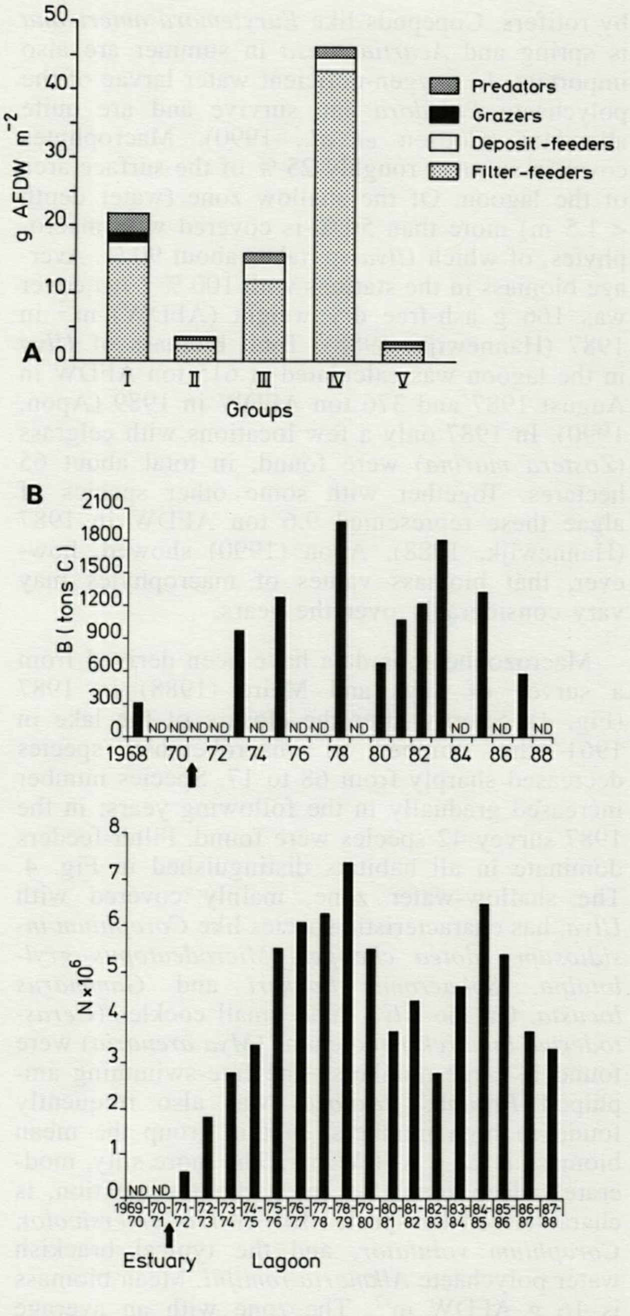

Fig. 4. – A, average biomass per macrozoobenthos group in Veerse Meer lagoon in 1987 (Seys and Meire, 1988). Group I : shallow, sandy, abundant macrophytes; Group II : moderately shallow, sandy, macrophytes present; Group III : moderately shallow, sandy, no macrophytes; Group IV : deep, silty, no macrophytes; Group V : deep, muddy, no macrophytes. B, upper panel : long-term trend in integrated biomass (above-ground peak standing stock in July-August) of eelgrass, *Zostera marina*, in entire Grevelingen lagoon, in tons organic carbon, over the period 1968 to 1988. ND = no data collected. Arrow indicates closure of Grevelingen estuary in 1971. Lower panel : numbers of annual (July to July) bird-days (= number of birds times the number of days the birds are present) of (mainly) migratory herbivorous waterfowl in Grevelingen lagoon, over the period 1971 to 1988. ND = no data collected (Nienhuis, 1992).

by rotifers. Copepods like *Eurytemora americana* is spring and *Acartia tonsa* in summer are also important. In oxygen-deficient water larvae of the polychaete *Polydora* can survive and are quite abundant (Coosen *et al.*, 1990). Macrophytes cover in summer roughly 25 % of the surface area of the lagoon. Of the shallow zone (water depth < 1.5 m) more than 50 % is covered with macrophytes, of which *Ulva* sp. takes about 90 %. Average biomass in the stations with 100 % *Ulva* cover was 166 g ash-free dry weight (AFDW) m^{-2} in 1987 (Hannewijk, 1988). Total biomass of *Ulva* in the lagoon was calculated at 615 ton AFDW in August 1987 and 376 ton AFDW in 1989 (Apon, 1990). In 1987 only a few locations with eelgrass (*Zostera marina*) were found, in total about 65 hectares. Together with some other species of algae these represented 9.6 ton AFDW in 1987 (Hannewijk, 1988). Apon (1990) showed, however, that biomass values of macrophytes may vary considerably over the years.

Macrozoobenthos data have been derived from a survey of Seys and Meire (1988) in 1987 (Fig. 4). Shortly after the closure of the lake in 1961 the number of macrobenthic species decreased sharply from 68 to 17. Species number increased gradually in the following years; in the 1987 survey 42 species were found. Filter-feeders dominate in all habitats distinguished in Fig. 4. The shallow-water zone, mainly covered with *Ulva*, has characteristic species like *Corophium insidiosum, Idotea chelipes, Microdeutopus gryllotalpa, Sphaeroma hookeri* and *Gammarus locusta*. On the *Ulva* thalli small cockles (*Cerastoderma lamarcki*) and clams (*Mya arenaria*) were found in large numbers. The free-swimming amphipod *Praunus flexuosus* was also frequently found in high numbers. In this group the mean biomass is 22 g AFDW m^{-2}. The more silty, moderately deep zone (5-9 m) without vegetation, is characterized by species like *Nereis diversicolor, Corophium volutator*, and the typical brackish water polychaete *Alkmaria romijni*. Mean biomass is 16 g AFDW m^{-2}. The zone with an average depth of 6 to 10 m, mostly in the western, more saline part, contains the blue mussel (*Mytilus edulis*) as the dominant species. Associated with the mussel beds are tunicates (*Molgula manhattensis*) and anthozoans. Mean biomass is high : 46 g $AFDW^{-2}$.

After the closure of the lake in 1961 the number of marine fish species decreased from 35 to 18 (Vaas, 1970). Nowadays eel (*Anguilla anguilla*), three-spined stickleback (*Gasterosteus aculeatus*), black goby (*Gobius niger*), and sand smelt (*Osmerus eperlanus*) are the most abundant species. For angling purposes, trout (*Salmo trutta*) is introduced into the lake (about 3 000 kg yr^{-1}). In summer and autumn gobiids are observed in the *Ulva* vegetation; in winter they migrate to the deeper parts. The pelagic fish observed by echo sounder and by divers appeared to be only shoals of the three-spined stickleback.

When comparing the numbers of birds per 10 ha between Veerse Meer lagoon and Grevelingen lagoon, Veerse Meer appears to have the highest numbers for more than two thirds of the investigated species (Stuart, 1988). The importance of Veerse Meer lagoon for birds expresses itself in its function as a resting and foraging ground during migration and in winter. The large quantity of food and easy availability is the key to this role. Compared with Grevelingen lagoon however, the water quality of Veerse Meer lagoon is negative, as was pointed out in preceding paragraphs.

Coosen *et al.*, (1990) focus on the relationships between the trophic groups, including birds, in order to unravel this apparent paradox. All the data used in the quantification of these relationships were collected in the season 1987-1988. During the winter (September-April) 1987-1988 a total number of 5 381 000 bird-days were spent in the lake. More than 80 %, or 4 413 000 bird-days, was accounted for by the herbivores. A small percentage of coots feed on benthos. Wigeon (*Anas penelope*) and mallard (*Anas platyrhynchos*) also feed on grassland (Stuart, 1988). Of the total consumption of 294 tons AFDW, 76 % consists of macrophytes taken from the shallow zone of the lake.

The benthos-eating birds like tufted duck (*Aythya fuligula*), goldeneye (*Bucephala clangula*), shelduck (*Tadorna tadorna*) and the waders feed from near the shore to about 4 m water-depth, and consume a considerable amount of the benthos in the lake. The total consumption of these birds in the winter of 1987-1988 was estimated at 56 tons AFDW.

Fish eating birds (great crested grebe [*Podiceps cristatus*] and red-breasted merganser [*Mergus serrator*]) are probably entirely dependent on three-spined sticklebacks and gobiids. The consumption in fresh weight in the winter 1987-1988 was 45.8 tons or 8.4 tons AFDW. This corresponds to 2.5 g FW m^{-2} yr^{-1} (= 0.5 g AFDW), very much like the figure found in Lake Grevelingen in 1984-1985 (Doornbos, 1987).

From these calculations it follows that the shallow zone is by far the most important area when consumption by birds is considered. In September 1987 about 93 % of the total amount of birds (except gulls) present at that time in Veerse Meer lagoon foraged in the shallow zone. In January this was about 58 %. The deeper parts of the lake are feeding grounds for fish-eating birds like the cormorant, great crested grebe and the majority of the red-breasted merganser; these birds usually do not feed deeper than 4 m. As the area below 4-5 m water-depth is of no direct importance to the birds, all problems with chlorinity and temperature stratification only affect the feeding grounds of benthos-eating birds in very warm, windless summers, when the stratification is at a depth of about 4 m. For the bottom-dwelling fish, like the gobiids, low oxygen is, of course, a hazard. The impact of this on the population size of gobiids, and hence on the food supply for the piscivores is not known (Coosen *et al.*, 1990).

2. Grevelingen lagoon

Grevelingen estuary was closed in 1971, and gradually changed into an artificial brackish lagoon. This change drastically affected the numbers of species present. Within a number of plant and animal groups (sea-anemones, bristle worms, lobsters and crabs, molluscs, echinoderms, fishes, macro-algae and some plankton groups) the overall number of species decreased with 24 %. Together with this decrease concomitant shifts in numbers of individuals per species could be established : species that occurred only occasionally before 1971 became common, and also the reverse could be observed (Nienhuis, 1978). Within certain taxonomical groups, species with a broad ecological tolerance against changes in environmental factors generally remained in the lake. Two examples may illustrate this. Out of 10 lobster and crab species occurring in the Grevelingen estuary only two species remained after the closure. One of them is *Carcinus maenas*, the common shore crab. Out of 28 fish species occurring in the estuary only 16 remained, and among them is *Gasterosteus aculeatus*, the three-spined stickleback. Both species tolerate drastic changes in salinity and complete their life cycle in brackish water. In contrast with the loss of a considerable number of marine species (approximately 75 within the groups mentioned) only a few immigrants characteristic for stagnant brackish water were found after the closure e.g. the crustacean *Idotea chelipes*, the molluscs *Hinia reticulata* and *Cerastoderma lamarcki* and the fish *Gobius niger*.

An important fact underlying the disappearance of species is that their life cycles were interrupted. The prevailing conditions in Grevelingen lagoon, viz. lack of currents and low salinity of the water, may block the life cycle of certain animals in its initial phase. The unsuccessful reproduction of flatfish in the lake may act as an example. Under normal marine conditions the eggs of flatfish like plaice, flounder and dab, float in the water after spawning, and hatch to pelagic larvae. In Grevelingen lagoon it may be presumed that, among other reasons, the rapid sinking of the eggs after deposition prevents them of being fertilized adequately (Vaas, 1978).

Elimination of the tides caused a strong decrease of the amounts of suspended matter available in Grevelingen lagoon, and, above that, the particle size diversity diminished. Owing to accelerated sinking and settlement in non-tidal water, coastal marine-pelagic diatoms live now benthically in Grevelingen. The larger and more silicified marine diatoms settled in stagnant water; they were permanently withdrawn from the pelagic zone and are consequently no longer available as food for planktonic herbivores (Bakker, 1978). This is well illustrated by small, pelagic copepods with a life cycle consisting of more than 10 stages. The gradually increasing size of the stages may imply parallel changes in food relations in the course of development of these zooplankton organisms. Notwithstanding a certain flexibility in prevailing food demands, there is a real chance that a certain particle size lacks for a certain developmental stage (Bakker, 1978).

The same is true for larger animals. The survival rate of larvae and young individuals is determining the size of a population. This may be illustrated by the blocked life cycle of the jellyfishes (Scyphozoa) in Grevelingen lagoon. The animals were common in the Grevelingen estuary. The larvae settle on the seafloor to develop a small hydroid-like organism, the scyphistoma stage. The scyphistoma buds repeatedly, giving rise to ephyra larvae which then develop into the characteristic adults. There are indications that the scyphistoma stages of *Aurelia aurita* occur commonly in Lake Grevelingen. Larger jellyfishes, however, are seldom seen in the course of the year, an indication that normal development of the young stages is seriously hampered, possibly owing to lack of adequate food (Bakker, 1978).

Another significant impact on the life cycle of many species is the fact that their migration routes

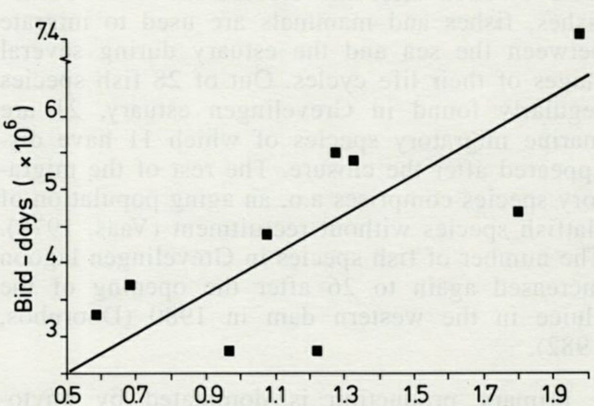

Fig. 5. – Relation between maximum above-ground biomass of *Zostera marina*, Grevelingen lagoon in July/August and the number of bird days of herbivorous waterfowl in Grevelingen lagoon in subsequent autumn and winter over the period 1973 to 1987 (data derived from Fig. 5); $n = 9$; $r = 0.74$; $p < 0.025$ (Nienhuis, 1992).

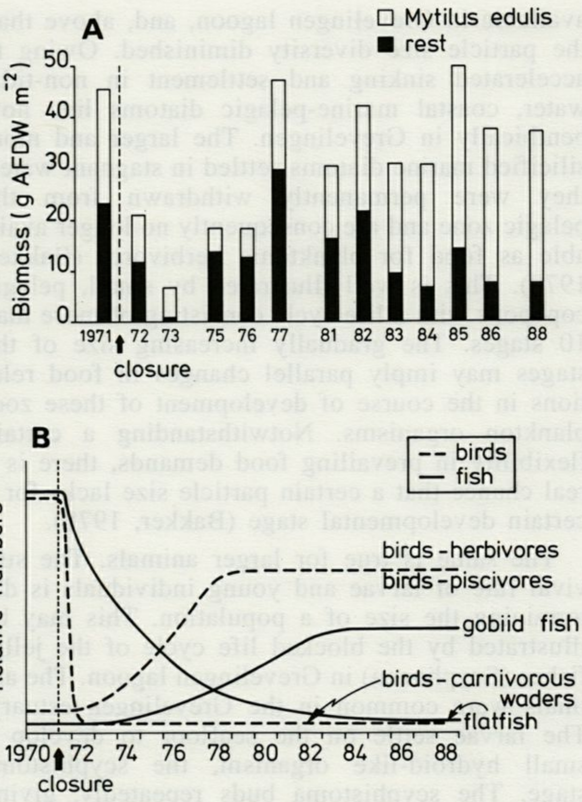

Fig. 6. – A, long-term changes (1971-1988) in macrozoobenthos biomass, averaged over a number of sampling plots, > 1.5 m waterdepth, in Grevelingen lagoon (Lambeck *et al.*, 1989). B, long-term changes in relative numbers of dominant groups of primary and secondary consumers in Grevelingen lagoon, following the closure of the estuary in 1971. Only qualitative trends are given; annual fluctuations have been left out (Nienhuis, 1985; 1992).

were blocked after the closure in 1971. Cuttlefishes, fishes and mammals are used to migrate between the sea and the estuary during several stages of their life cycles. Out of 28 fish species regularly found in Grevelingen estuary, 21 are marine migratory species of which 11 have disappeared after the closure. The rest of the migratory species comprises a.o. an aging population of flatfish species without recruitment (Vaas, 1978). The number of fish species in Grevelingen lagoon increased again to 26 after the opening of the sluice in the western dam in 1980 (Doornbos, 1982).

Primary production is dominated by phytoplankton (Table 2) as is the case in all the other tidal and non-tidal estuaries and lagoons in The Netherlands. In spring the diatom *Skeletonema costatum* predominates and in summer both the flagellate *Cryptomonas* and the diatom *Chaetoceros* are prevailing. The zooplankton grazing on phytoplankton comprises the copepod *Acartia tonsa*, but also rotifers (*Synchaeta*) and protozoan species (Bakker, 1978).

A specific characteristic of Grevelingen is the extensive perennial population of eelgrass, *Zostera marina*, covering large areas, but declining recently. *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 spots, reached a maximum distribution in 1978 and showed a fluctuating pattern thereafter (Fig. 4) (Nienhuis, 1983 a). *Zostera marina* is by far the dominant macrophyte food source in Grevelingen lagoon. The maximum above-ground 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, A. platyrhynchos, A. crecca, Branta bernicla, Cygnus olor*) in the subsequent autumn and winter (Fig. 6). Although the birds only consume 4 % of the annual above-ground primary production of eelgrass (Nienhuis and Groenendijk, 1987), that is 11 % of the peak standing crop in August, the correlation between the numbers of birds present and their obligate 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 timing of the birds does not match 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.

Lambeck (1981), Lambeck and Brummelhuis (1985), Lambeck and Pouwer (1986), Lambeck and De Smet (1987) and Lambeck *et al.* (1989) described the changes in macrozoobenthos biomass and population dynamics after the closure of Grevelingen estuary from 1971 until 1988. In 1971 the intertidal and subtidal populations of macrozoobenthos became isolated from the tidal movements, and consequently large changes set in. The number of benthic polychaete species decreased by 20 % in the years following the closure of the estuary. Many species however extended their distribution areas owing to the less exposed and more uniform conditions in the sediments. The number of mollusc species (23) hardly changed after the closure of the estuary. During the period 1984-1989 a rather stable number of 45 macrozoobenthos species were counted in the entire lagoon, which means a slightly higher number than in Veerse Meer lagoon.

Fig. 6 shows an overall picture of macrozoobenthos biomass, averaged over a number of sampling spots. In 1971, before the closure, macrozoobenthos biomass was dominated (80 %) by *Mytilus edulis* and *Cerastoderma edule*. A strong decrease set in and showed a minimum in 1973 (only 5 g AFDW m^{-2}). Thereafter biomass recovered and showed a varying pattern between approximately 30 and 50 g AFDW m^{-2} over the

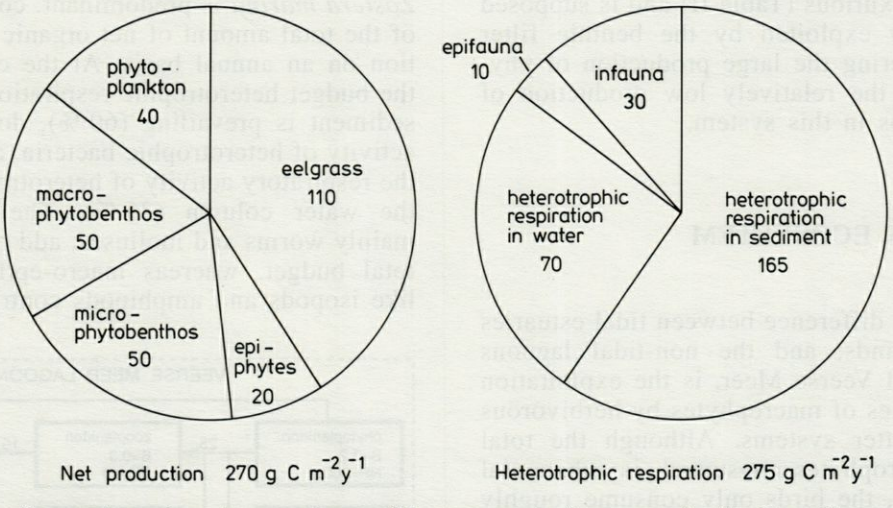

Fig. 7. – Budget of organic carbon in an eelgrass (*Zostera marina*) community in Grevelingen lagoon (1-1.5 m waterdepth), averaged over 1978 and 1979 (Nienhuis, 1983 b).

period 1977 to 1988. The spatial and temporal changes in the populations of the individual macrozoobenthos species showed a dynamic pattern, of which most max and wane is up to now only poorly understood.

Mytilus edulis, although dominant only during the period 1971 to 1977, since then steadily declined (biomass in 1986-1988 only 4 g AFDW m^{-2}). *Cerastoderma edule* decreased in biomass directly after the closure in 1971, but is still present. Its sibling species, *Cerastoderma lamarcki*, characteristic for stagnant, brackish habitats, emerged already in 1973 and increased since then to 2 – 5 g AFDW m^{-2}. Any data about competition between the two cockle species are lacking. *Hinia reticulata*, a carnivorous gastropod, was first discovered in 1975; after an initial success, expressing itself in an increase in biomass up to 7 g AFDW m^{-2}, the species recently showed a failing recruitment. Since 1983 the colonizer *Crepidula fornicata*, a filter-feeding mollusc, showed a rapid increase to a biomass in 1988 of 10 to 15 g AFDW m^{-2}. Although the overall level of macrozoobenthos biomass shows since 1981 a "normal", stable pattern, the population structure is highly dynamic, and new colonizers – opportunists – may still et their chance.

Grevelingen offers an example of long-term changes in the numbers and biomass of secondary consumers after a sudden intervention. Fig. 6, (derived from Nienhuis, 1985) summarizes a number of qualitative trends, reproduced in smooth lines; annual fluctuations have been left out. Before May 1971, when Grevelingen was still a tidal estuary, a considerable population of migratory marine flat fish (plaice, dab, sole) lived in the estuary. The sudden closure of the estuary meant a physical and biological blockade for the remaining population and Fig. 6 shows a gradually declining number of flat fish to a very low level at the end of the eighties. Migratory birds, carnivorous waders, used to exploit the intertidal flats in Grevelingen estuary before May 1971. Owing to the closure of the estuary the water level was fixed, and consequently all intertidal flats changed into either permanently submerged sediments or permanently dry terrestrial shore areas. Fig. 6 shows the dramatic fall of the numbers of waders directly after 1971. 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; cormorant – *Phalacrocorax carbo*; red-breasted merganser). This change in numbers is related to the much higher transparency of the water (the birds are catching their prey "on sight"), and the availability of considerable amounts of prey. 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, as was shown by Doornbos (1984) in 1981 and 1982. 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 (Fig. 6), which brought them food and shelter.

In the Grevelingen lagoon macrozoobenthos production may be limited by a restricted supply of microalgae (Table II), which in turn are nitrogen-limited (De Vries and Hopstaken, 1984). The supply of phytoplankton in eutrophicated Veerse

Meer is more luxurious (Table II) and is supposed to be not fully exploited by the benthic filter feeders, considering the large production of phytoplankton and the relatively low production of macrozoobenthos in this system.

THE LAGOON ECOSYSTEM

An important difference between tidal estuaries in the Netherlands, and the non-tidal lagoons Grevelingen and Veerse Meer, is the exploitation of large quantities of macrophytes by herbivorous birds in the latter systems. Although the total amount of macrophytes consumed, is substantial in both lagoons, the birds only consume roughly 5 % of the annual macrophyte production (*cf.* 14 % consumption calculated by Coosen *et al.*, [1990] but presumably based on too low macrophyte production estimates).

Among the secondary consumers the levels of organic carbon consumption – man excluded – are almost the same, when tidal estuaries are compared with non-tidal lagoons, notwithstanding the fact that the consumer populations show large qualitative differences (viz. herbivores in lagoons and carnivorous waders in tidal estuaries; Nienhuis, 1992). Carnivorous birds in Grevelingen consume mainly small fish (approximately 60 % of the available biomass in 1981-1982; Doornbos, 1984). Almost 20 % of the macrozoobenthos production may potentially be consumed by fish and larger invertebrates (Doornbos, 1987). In Veerse Meer the consumption by fish and invertebrates is unknown. The much higher consumption by carnivorous birds in Veerse Meer (Coosen *et al.*, 1990), as compared to Grevelingen (Doornbos, 1987), is explained by the fact that Veerse Meer harbours several times higher densities of zoobenthos-eating diving ducks (Meire *et al.*, 1989). The question whether the carrying capacity of macrozoobenthos in both lagoons fills the needs of the secondary consumers, seems to be answered positively, although carnivorous birds may be food-limited owing to the unpredictable year to year variations in the production of small fish.

Primary production and mineralization of organic matter, including consumption by animals and respiration, are roughly in a status of equilibrium in the Dutch coastal lagoons Veerse Meer and Grevelingen. This means that on an annual basis no significant deposition of organic matter, peat formation, occurs as is the case in shallow fresh-water lakes. Fig. 7 may illustrate this phenomenon. It shows an organic carbon-budget of a dominant habitat in Grevelingen lagoon, the eelgrassbed (Nienhuis, 1983 b). Besides eelgrass, epiphytes, macroalgae, microphytobenthos and phytoplankton are presented as primary producers. *Zostera marina* is predominant, contributing 40 % of the total amount of net organic carbon production on an annual basis. At the consumerside of the budget heterotrophic respiration in the bottom sediment is prevailing (60 %), dominated by the activity of heterotrophic bacteria, and followed by the respiratory activity of heterotrophic bacteria in the water column (25 %). The macro-infauna, mainly worms and molluscs, add only 11 % to the total budget, whereas macro-epifaunal elements like isopods and amphipods contribute only 4 %.

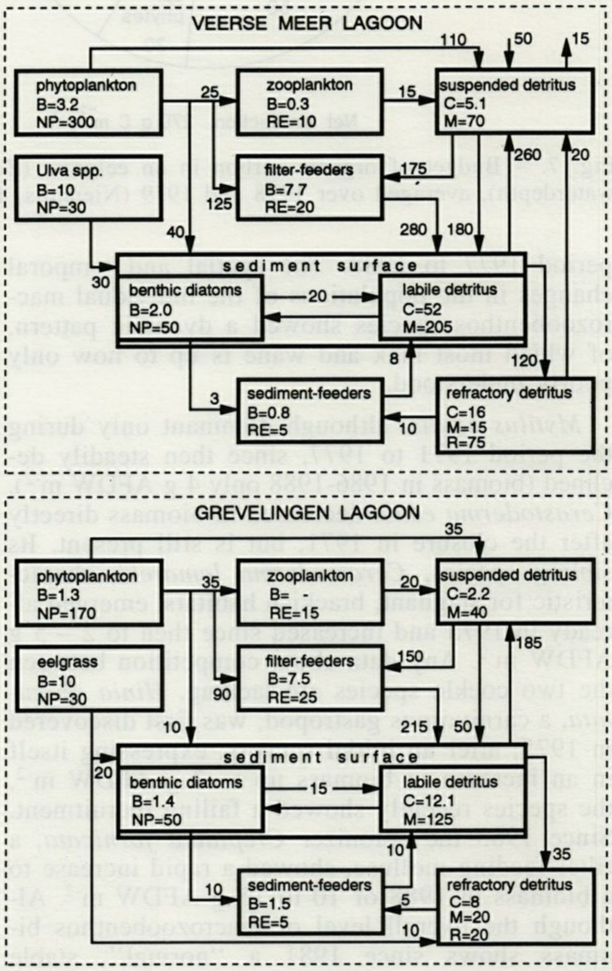

Fig. 8. – Averaged annual cycle of organic carbon, based on mathematical model calculations, derived from field data (De Vries *et al.*, 1989). Biomass (B) in g C m^{-2} and fluxes (arrows) in g C m^{-2} yr^{-1}; NP = net production (g C m^{-2} yr^{-1}); RE = respiration and excretion (g C m^{-2} yr^{-1}); M = heterotrophic mineralization (g C m^{-2} yr^{-1}); C = concentration (g C m^{-2}); R = refractory (g C m^{-2}).

The high mineralization rate in the bottom sediment indicates a relatively high load with organic material. The aerobic upper 2 to 3 mm of the sediment contain 0.5 to 2 % particulate organic matter. Below a depth of 3 mm into the sediment, the bottom is almost completely anoxic, except close to the rootsystem of the eelgrass. A much higher load with organic material and nutrients, as is the case in Veerse Meer lagoon, shifts the balance between primary production and mineralization into the direction of loose-lying macroalgae (*Ulva* species), flourishing on completely anoxic sediments, where rooting submerged phanerogams are no longer able to survive.

Two mathematical models describe the functioning of the aquatic ecosystems, respectively GREWAQ for Grevelingen lagoon (De Vries *et al.*, 1988 a) and VEERWAQ for Veerse Meer lagoon (De Vries *et al.*, 1989). The average annual cycle of organic carbon is depicted in Fig. 8. The dominant compartments distinguished in both models are in the water column : phytoplankton, macrophytobenthos, zooplankton, suspended detritus and filter-feeders; and in the sediment : microphytobenthos (mainly benthic diatoms), sediment-feeders, labile detritus with connected bacteria and stable detritus in the upper millimeters of the sediment of which a considerable part is inert.

The key-element in the cycling of organic material in both lagoons is nitrogen, limiting the rates of primary production. The surface area of the bottom sediments is the central part of the model. The top-layer of the sediment contains small anoxic patches connected to superficially aerated sediment, implying an efficient coupling of aerobic, heterotrophic mineralization of organic matter, aerobic nitrification and anaerobic denitrification. A considerable part of the thus mineralized nitrogen compounds will be released to the atmosphere as gaseous N_2.

Notwithstanding the large differences in internal loading with nutrients, the calculated carbon cycles of Grevelingen lagoon and Veerse Meer lagoon show a remarkable similarity, both with regard to the biomass levels of several important functional groups, and to the size of the rates connecting the compartments. The main differences indicate for the primary producers of Veerse Meer, compared to Grevelingen, a higher biomass and production of phytoplankton and the loose-lying high biomass of *Ulva* versus the rooting *Zostera* (*Ulva* primary production in Veerse Meer is estimated far too low in the model). The high level of detritus both in the water column and in the bottom-sediments, where four times more particulate organic matter is refractory in Veerse Meer lagoon, compared to Grevelingen lagoon, makes Veerse Meer more susceptible to anoxia. For the secondary producers the lower contribution of sediment-feeders in Veerse Meer, compared to Grevelingen, is significant.

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