The ecology of the estuaries of Rhine, Meuse and Scheldt in the Netherlands*

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SUMMARY: Three rivers, the Rhine, the Meuse and the Scheldt enter the North Sea close to each other in the Netherlands, where they form the so-called delta region. This area has been under constant human influence since the Middle Ages, but especially after a catastrophic flood in 1953, when very important coastal engineering projects changed the estuarine character of the area drastically. Freshwater, brackish water and marine lakes were formed and in one of the sea arms, the Eastern Scheldt, a storm surge barrier was constructed. Only the Western Scheldt remained a true estuary. The consecutive changes in this area have been extensively monitored and an important research effort was devoted to evaluate their ecological consequences. A summary and synthesis of some of these results are presented. In particular, the stagnant marine lake Grevelingen and the consequences of the storm surge barrier in the Eastern Scheldt have received much attention. In lake Grevelingen the principal aim of the study was to develop a nitrogen model. After the lake was formed the residence time of the water increased from a few days to several years. Primary production increased and the sediments were redistributed but the primary consumers suchs as the blue mussel and cockles survived. A remarkable increase of Zostera marina beds and the snail Nassarius reticulatus was observed. The storm surge barrier in the Eastern Scheldt was just finished in 1987. Predicted consequences have been modeled and include decreased current velocity, smaller amounts of suspended material and less extinction of light and increased primary production. The smaller tidal volume will decrease the surface of intertidal flats available to wintering birds. This is a special concern since the delta area is of international importance for certain wader species. The Western Scheldt has not changed hydrodynamically but is polluted by industrial and organic waste. Bacterial processes involving the consecutive exhaustion of different electron acceptors, from oxygen to sulphate, are dominant in the freshwater river. There are several indications that impacts in the estuary exist as well despite the important dilution by the tides.

Key words: estuaries, Rhine, Meuse, Scheldt, ecology

INTRODUCTION

Three main European rivers, the Rhine, the Meuse and the Scheldt, enter the North Sea close to each other in the so-called Delta area in the south west of the Netherlands. The Rhine is by far the largest of the three rivers, with a length of 1326 km and a drainage area of 224,000 km². The river originates in the northwestern part of the Alps and by the time it crosses the Swiss-German border near Basel its water flow already averages more than 1000 m³ s⁻¹. When it enters the Netherlands this amount has more than doubled to 2200 m³ s⁻¹. The Meuse originates on the Langres plateau in eastern France and has a total length of 925 km and a drainage area of 33,000 km². Its flow is much more erratic than that of the Rhine and at the Dutch-Belgian border averages about 270 m³ s⁻¹. The smallest of the three rivers is the Scheldt

with a total length of 355 km. It originates on the Saint Quentin plateau at the southwestern border of the North European Plain and drains about 19,500 km², mainly Flanders' low-lying plains. The input into the estuary at the Dutch-Belgian border is estimated as $105 \text{ m}^3 \text{ s}^{-1}$ on average.

The intricate pattern of estuarine branches in the delta area (Fig. 1) resulted from a series of transgressions of the North Sea creating a rapidly changing system in which many islands were surrounded by large sea arms maintained by the tides. Since the seventeenth century, the general geography of the area has changed less, due to human constructions. Four large estuaries are recognizable on all maps over the past four hundred years: from north to south they are what are now called the Haringvliet, the Grevelingen, the Oosterschelde and the Westerschelde.

The last unhindered invasions by the sea of the

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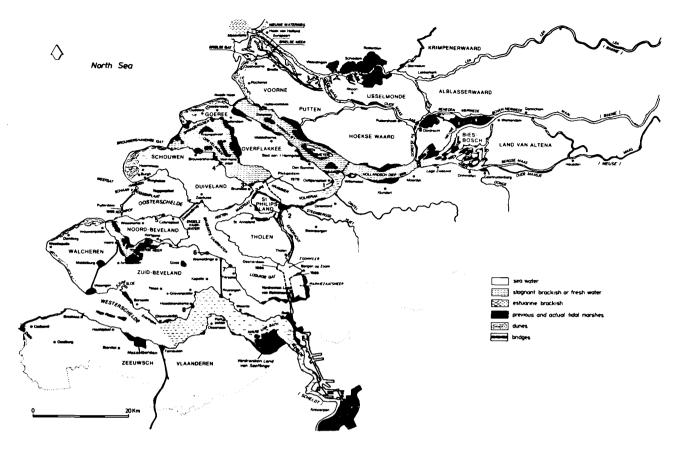


Fig. 1. — Map of the Delta area.

area took place from the 3th till the 14th century during the Dunkirk II and III transgressions. Only in the fourteenth century dyke building, which had already started in the tenth and eleventh centuries, became a large scale operation but despite of dyke construction a long series of catastrophic storm floods is known: the Saint Elisabeth flood in 1421, the Saint Felix flood in 1530 and the All Saints Day flood in 1570 are the best documented. Each of these floods was responsable for the death of thousands of people and the loss of large areas of land, including whole villages.

From the seventeenth century onwards, increasing wealth and better social organisation improved the protection from the rising sea level and the islands in the area became more or less consolidated. More than 60,000 ha of new land were acquired as well. Although storm floods continued to occur their impact was relatively small. Then came the storm flood disaster of 1 February 1953, inundating 150,000 ha of land and causing the death of 1835 people. It had a huge impact on public opinion and politics in the Netherlands and as a consequence the delta plan was adopted by the Dutch Parliament in 1957. In the original plan the complete closure of three of the four main estuaries (only the Westerschelde had to remain open) and construction of a series of secondary dams

was intended, creating a system of freshwater lakes.

Due to increasing awareness of the environmental issues involved the original plan was not carried through and instead a rather unique combination of new habitats was created. The Haringvliet, as originally intended, became a freshwater lake, stagnant when river flow is low and serving as a "safety valve" in cases of large Rhine discharge, when its sluices to the North Sea are opened. The Grevelingen was completely closed off from the sea in 1971 but a new connection was made in 1978 and it became a rather unique area in Europe, a saline, marine lake. The Oosterschelde was maintained as a tidal marine embayment but it was protected from storm floods through one of the most ambitious coastal engineering projects ever undertaken, the construction of the storm surge barrier, finished in 1986. The Westerschelde remained the only unchanged estuary in the delta area. With the closing of a secondary dam in April 1987 the delta project, involving nearly thirty years of work and representing probably the most extensive coastal engineering work ever undertaken, was finished.

From the original situation of four comparable estuaries many ecologically very different water bodies have now been created. The environmental impact of the constructions was huge and since the beginning of execution of the delta plan this impact has been monitored, though the approach has greatly changed over the years. As examples of the environmental impact studies in this paper some ecological changes are described and the actual main ecological features of three former estuaries (the freshwater Haringvliet will not be considered) are compared: the production of organic matter and its consumption mainly by benthos and bacteria. In such a simple picture many of the important components of real ecosystems are lost, e.g. zooplankton, birds and salt marshes. A paper of this size cannot possibly be exhaustive and the review is mainly intended as an introduction to the general features of these estuaries and to the large body of (grey and other) literature on the delta area.

THE ORIGINAL SITUATION

The geomorphology of the delta area has resulted from a long series of regressions and transgressions of the North Sea. About 2000 years ago the area was part of a Wadden Sea extending from Cap Blanc Nez near the Strait of Dover to the mouth of the Elbe (VAN VEEN, 1950). The area was similar to the present day Wadden Sea between the Frisian Isles and the mainland in the Netherlands and Germany.

Tidal currents in the Southern Bight of the North Sea are strong and the sea arms in between the islands were large, deep and long. Only a few of them caught the mouth of a major river: besides the three rivers dealt with, the Ems, the Weser and the Elbe. When the mouth of a river was caught, the tidal current could penetrate much deeper inland and the channels were maintained in spite of the progressive silting up of the Wadden sea due to sediments brought in by the tidal current entering the Wadden sea and by the rivers.

The main change of the area over the past centuries has been the disappearance of the northern Rhine-Meuse mouth. Haringvliet and Grevelingen received most of the Rhine and Meuse water from the eighteenth century until 1868 when the Nieuwe Waterweg that connects Rotterdam with the sea was finished. Through the Krammer-Volkerak system some of that water reached the Oosterschelde as well but since its connection with the Westerschelde was closed off in 1867 this estuary was far less influenced by fresh water than the others.

The mixing of the freshwater inflow from the rivers and North Sea water entering the estuary with the tides created a salinity gradient which was responsable for many of the ecological features of the estuarine system. Such a system still exists in the Westerschelde and some of these features will be discussed there. This original situation has been described extensively by WOLFF (1967), NIENHUIS (1975), PEELEN (1967) and others. Most of the huge water influx in the delta area is derived from the Rhine, with an average flow of over 2000 m³ s⁻¹ and maximum water flows of sometimes over 13,000 m³ s⁻¹. Since the Nieuwe Waterweg was constructed it receives about half of the average flow through the Lek $(400 \text{ m}^3 \text{ s}^{-1})$ and Merwede $(700 \text{ m}^3 \text{ s}^{-1})$. About 900 m³ s⁻¹ of Rhine water, through the Waal and Nieuwe Merwede, and about 300 m³ s⁻¹ of Meuse water reached the North Sea either through the Haringvliet $(1150 \text{ m}^3 \text{ s}^{-1})$ or via the Volkerak through the Grevelingen (65-70 $\text{m}^3 \text{ s}^{-1}$). The average inflow from the Scheldt is about 100 m³ s⁻¹, reaching the sea exclusively through the Westerschelde estuary.

LAKE GREVELINGEN

In 1964 the connection between the Grevelingen estuary and the rivers was cut off through the construction of the Grevelingen-dam and a semi-enclosed estuary was left. In 1971 the mouth was closed off as well by the Brouwersdam and Lake Grevelingen was created. The tideless lake has a surface area of 108 km² and a mean depth of 5.3 m. It was nearly completely isolated and through evaporation and inflow of rainwater and polderwater discharges a slow but persistent decrease of salinity occurred over the years. To counteract this decrease the connection with the North Sea was restored in 1978 by the construction of a underwater sluice through the Brouwersdam with a capacity of 100-140 m³ s⁻¹. At the same time a siphon under the Grevelingendam was constructed.

The immediate results of the disappearance of the tides in 1971 were, of course, dramatic. On the 29 km² of intertidal area it is estimated that about 400 million lugworms (Arenicola), 500 million cockles (Cerastoderma), 30 billion Lanice and 100 billion mud snails (Hydrobia) perished over a few weeks (LAMBECK, 1985).

The long-term changes in the lake are however of more interest. The residence time of the water increased from a few days in the estuary to 3-6 years in the completely enclosed lake, then decreased again to several months after 1978. Currents became wind driven and much weaker. In consequence, the amount of suspended matter in the water decreased from more than 100 mg l⁻¹ to less than 10 mg l⁻¹ in the lake. Light penetration thus became much deeper and primary production increased.

Phytoplankton development starts in spring. After the enclosure the dominance of diatoms decreased and cryptomonad flagellates, growing rapidly in non-turbulent water, took over in early spring since light conditions became favourable earlier in the year. In 1979 when the lake was flushed again with North Sea water and salinity increased to 17 ‰ Cl⁻, diatoms became relatively more important again (BAKKER & DE VRIES, 1984).

Primary production by phytoplankton was studied from 1976 onwards and showed a remarkable increase from 80 g C m⁻² y⁻¹ in 1976 to 225 g C m⁻² y⁻¹ in 1981 (VEGTER & DE VISSCHER, 1984). Benthic primary production increased as well. The increased light penetration made an increased primary production possible by microphytobenthos, mainly diatoms, that in the estuary would mainly fotosynthesize in intertidal areas at low tide. This primary production was estimated variably as between 35 g C m⁻² y⁻¹ (NIENHUIS & DE BREE, 1984) and 70 g C m⁻² y⁻¹ (LINDEBOOM *et al.*, 1984). Increasing siltation through the absence of strong currents additionally induced the considerable extension of the sea grass *Zostera marina* in the system, which became an important primary producer of about 50 g C m⁻² y⁻¹.

The long residence time of the water increased the 'memory' of the system. Orthophosphate concentrations increased strongly immediately after the closure and showed a persistent long term increase till 1978 (BANNINK et al., 1984). During May and August phosphate is mobilized from the sediments where it accumulates during the rest of the year (KELDERMAN, 1984). However, phosphate is always present in excess and primary production in the lake is nitrogen (and probably silicon, not discussed here) limited.

The sediments are predominant in the nitrogen cycle. Interstitial nitrate values are highest in the top layer, whereas ammonium has minimum values there, probably due to nitrification in the top layer and denitrification deeper down (KELDERMAN, 1984). Seasonal variations in ammonium concentration are due to mineralisation in the deeper areas and by primary production in the shallow sediments. The benthic primary producers are therefore probably direct competitors with the phytoplankton for nutrients.

The sediments in lake Grevelingen have been redistributed after the closure of the estuary, with transportation of the fine particles towards the deeper gullies (KELDERMAN et al., 1984a). In 1977 the main suspension feeder in the benthos of Lake Grevelingen was the blue mussel Mytilus edulis. In natural mussel beds an average biomass of 240 g dwt m⁻² has been found, representing 6 g C m⁻² for the entire lake. The cockle, Cerastoderma edule, still occurs in water depths of about 1-2 m and also the lugworm Arenicola, also normally an intertidal species, is found in those strata with an average biomass of 2.3 g C m⁻². For the whole lake the macrobenthic biomass has been estimated as 8 g C m⁻²

for suspension feeders and 6 g C m⁻² for deposit feeders (DE VRIES, 1984). The impact of these suspension feeders on the lake is important: on average the entire water column of the lake is filtered every 4-5 days by benthic suspension feeders. This induces high mortality of phytoplankton and transport of suspended particles towards the sediments by production of pseudofaeces and faeces. On the other hand, the growth of mussels and other suspension feeders is limited by primary production. There seems to have been no recruitment at all of mussels between 1977 and 1981. Both cockles (Cerastoderma edule and C. lamarcki) and ovsters (Ostrea edulis) maintained important populations in the lake. Of particular interest is the explosion of the snail Nassarius reticulatus who from 1977 onwards reached densities of more than 100 per m².

THE OOSTERSCHELDE

The Oosterschelde is a nearly marine embayment (28.6-32.2 salinity) with a low freshwater influx of 55 m³ s⁻¹, which has become even lower after closure of the Krammer. It is the center of the Dutch shellfish industry. Until 1986 it had a volume of 417 million m³, an intertidal surface of 158 km² and a subtidal surface of 330 km². Its average depth is 8.1 m. The Oosterschelde is clearly structured along its main longitudinal axis where a gradient in physical and chemical characteristics exists. The average water depth in the eastern, sheltered part of the embayment is 4 m and half of the total surface area is exposed at low tide. The average depth in the western, more exposed part is 12 m and only 20 % of the shoals are exposed at low tide. The resident time of the water is 47 days inland, decreasing to 16 days towards the sea. The turbidity also decreases eastward, with 20-30 mg l^{-1} to 15-20 mg l^{-1} of seston. The average concentration of seston (25 mg l^{-1}) is very low.

Primary production in the water column follows the east-west gradient. The values found are lowest in the east (195 g C m⁻² y⁻¹), intermediate in the centre (280 g C m⁻² y⁻¹) and highest in the west (336 g C m⁻² y⁻¹). The phytoplankton is diatom-dominated but in May a predominant species is the flagellate *Phaeocystis pouchetii*, entering the Oosterschelde from the North Sea and moving landinward. Nitrogen is high in winter and early spring (1.5 mg l⁻¹) and low after the spring-bloom and in summer (0.1 mg l⁻¹). As in the Grevelingen, benthic primary production, mainly through diatoms, is important: average values range between 103 (west) and 195 (east) g C m⁻² y⁻¹. In extremely sheltered, shallow parts of the embayment seagrasses and macroalgae dominate with a locally important

primary production estimated at 116 g C m⁻² y⁻¹ and 56 g C m⁻² y⁻¹ respectively.

Zooplankton, mainly consisting of copepods but with a considerable component of meroplankton at times, grazes up to 25 % of the primary production in the water column. Since grazing is selective, the availability of material with the highest nutritional value for benthic filter feeders is restricted. Nevertheless, as in the Grevelingen, most of the organic matter is eventually grazed by the benthos. Two species are of paramount importance in the system: Mytilus edulis, mainly in subtidal areas, and Cerastoderma edule, mainly in intertidal areas. The impact of the commercially exploited mussel beds on the ecology of the Oosterschelde is important and enonomic and marketing constraints on the shellfish exploitation are to be taken into account when describing the ecology of the Oosterschelde.

Biomass of the mussels is determined by the mussel farmers (SMAAL et al., 1986). The western part of the embayment is used as a culture area where mussels are grown to commercial size. In these areas the biomass reaches 116 g adwt m⁻² (juveniles) and 340 g adwt m⁻² (adults). In the middle part the spat is seeded, with 12 g m⁻² (juveniles) and 230 g m⁻² (adults). The inner area is used for stocking autochtonous and imported (from the Waddensea) mussels during several weeks before consumption and for stocking mussels when the market price is unfavourable. Here the biomass is about 211 g adwt m⁻² (adults only).

The cockle Cerastoderma edule occupies mainly the intertidal flats and their subtidal slopes. Their average biomass on the flats decreases from 63 g adwt m⁻² in the west over 35 g adwt m⁻² in the middle to 20 g adwt m⁻² in the east, subtidal biomass on the slopes of the sandbanks being about three times lower (SMAAL et al., 1986).

Whereas filter feeders predominate in the western part, the benthic deposit feeders, mainly polychaetes such as *Arenicola marina* and *Heteromastus filiformis*, and grazers such as *Hydrobia* have their highest biomass in the eastern intertidal areas.

Much of the intertidal biomass is consumed by birds and the Oosterschelde, supporting a large quantity of benthic animals, is an important wintering area for palearctic birds. Oystercatcher (Haematopus ostralegus) and dunlins (Calidris alpina) are the most important species and birds consume about 20 % of the macrobenthos each year.

Transport processes play a major role in the Oosterschelde ecosystem, in contrast to the Grevelingen that can be modeled as a single, depth zonated system. The transport of dissolved substances may be modelled in estuarine environments taking the salinity distribution as a lead. The situation is more difficult for the transport of particulate matter, since par-

ticles settle and are resuspended according to the tide, resulting in a residual movement that is very different from the water movement. Modeling efforts for processes in the Oosterschelde make use of five compartments, three of which encompass the main embayment.

A large part of the observed sediment transport can be attributed to sand, which makes up more than 96 % of the bottom sediment. Sand transport is mainly due to movement of sand waves along the bottom of the tidal channels. The sedimentation and erosion of fine particles has been calculated by TEN BRINKE (1987) and show a remarkable constant export of clay towards the sea.

The construction of the storm surge barrier has been done with the intention of maintaining as much of the original marine character of the Oosterschelde as possible. The dam is made up of 65 concrete piers that support steel gates which can be dropped like portcullises to close off the estuary in case of danger. Each pier is 53 m high and weighs 18,000 tonnes. The piers are joined together with beams to make a single construction. More than 60 gates, each 42 m long, can be raised and lowered independently.

However, some important changes in the hydrological regime of the Oosterschelde will result: the volume of water entering with each tide decreases, and with it the current speed, the tidal amplitude and the surface of intertidal areas. The delta works also entrain an important loss of salt marshes.

The possible effects of the storm surge barrier have been the subject of much research, mainly on macrobenthic animals and salt marshes. Most of the salt marsh plants withstand an inundation of 4-8 days but immersion tolerance decreases with temperature (GROENENDIJK, 1985). Permanent submersion during 14 days did not affect intertidal benthic animals but permanent emersion caused mortality after 1-2 days at either high or very low temperatures (HUMMEL et al., 1986). Small polychaetes were more susceptible to desiccation than larger worms.

THE WESTERSCHELDE

The Westerschelde is the last true estuary remaining in the delta region, with an important salinity gradient. Between the mouth at Vlissingen (Flushing) and Walsoorden the estuary has a multiple channel system and is completely mixed; between Walsoorden and Gent, where the tidal regime stops, there is only a single channel and only partial mixing with small horizontal and vertical salinity gradients. Although the differences are small they have important consequences for the transport of material upstream.

PETERS & STIRLING (1976) divide the Scheldt

river in three zones: the maritime zone is 70 km long, including the part permanently submerged in the North Sea. In this zone a complex sediment transport exists through deep and large channels separated by large sand banks. The central part of the estuary, between Walsoorden and the mouth of the river Rupel, is about 50 km long. Mixing is less strong and a floculation zone exists close to Antwerpen. The fluvial part of the tidal river is upstream from the Rupel mouth and is characterized by a rapid and large penetration of the tides.

The total volume of the estuary between Vlissingen and Zandvliet is 2.5 billion m³; from the Scheldt river only 9 million m³ enters the estuary each day. The residence time of the water between the Belgian-Dutch border and the mouth at Vlissingen is consequently rather large, about 75 days or 150 tidal cycles. For this reason the dilution of seawater is gradual and stable. Salinity zones in the estuary are relatively stable as well and are maintained in more or less the same position throughout a tidal cycle, though more important shifts may occur over a year according to the freshwater inflow.

Fine particles are a highly characteristic feature of estuaries and they are derived both from the sea and from land. Their deposition is controlled by current speed and by salinity: since clay particles tend to adhere to each other in salt water settlement speed is increased in the brackish water zone of a river, creating the flocculation zone and turbidity maximum (POSTMA, 1967) where the inward flow of marine water along the bottom stops and the sediments rise to mix with the surface fresh water. According to WOLLAST (1976) more than 1 million tons of fine material from continental origin settle in the middle part of the river, a further 200,000 tonnes are deposited in the seaward zone where a further 800,000 tonnes of marine sediments are deposited. With the suspended matter a high load of pollutants is deposited as well: deposition within the estuary thus limits the export of these substances to the sea but has important consequences for the estuary itself since these substances may be incorporated into the estuarine food web.

Important modifications of the physical and chemical characteristics of the water are due to the mixing of fresh and salt water. These modifications entrain a whole series of transformations of the chemical species present in the water which affects their distribution. These chemical changes are enhanced further by the long residence times in the Scheldt. The important load of organic matter in the Scheldt river catalyses an intense heterotrophic bacterial activity which rapidly exhausts the oxygen in the river. Other oxydants are then used for anaerobic respiration: manganese, nitrate, iron and ultimately sulphate. When all electron acceptors are exhausted sulphate reduction thus may become the

dominant process in the river. Due to flocculation the organic matter content decreases and with it the bacterial activity. Only when mixing with sea water becomes important the oxygen content of the water rises again and a system based on autotrophic production instead of allochtonous import of organic matter takes over: this happens about at the Dutch-Belgian border (but see HUMMEL et al., 1988).

The Westerschelde has been less studied that the other delta waters (HUMMEL et al., 1988). The valuable studies of DE PAUW (1975) are mainly qualitative in nature and describe the water column of the estuary as it was twenty years ago (1967-1969). Primary production in the estuary was studied in 1983 by BILLEN et al. (1985). Highest production was observed in the freshwater and oligohaline parts. At Doel and at Hansweert, as elsewhere, a maximum primary production of about 1 g C m⁻² d⁻¹ was observed in July, with very low values for the rest of the year. Total primary production at Doel was estimated as 85 g $\overset{\frown}{C}$ m⁻² y⁻¹, at Hansweert probably somewhat higher. This low value is due to the high amount of suspended matter and the high extinction of light in the water.

Nitrogen is probably never limiting in the Westerschelde. Due to nitrification in the presence of oxygen the amounts of nitrate are always elevated. In fact, due to the importance of denitrification in the anaerobic part of the river, this amount would actually increase when water quality would improve to such a point that the river would be aerobic around Antwerpen (BILLEN et al., 1985) and would be a major exporter of nitrogen to the North Sea.

Little is known on the importance of other processes in the estuary. The benthos in the seaward part seems to be rather typical for the N. W. European area, with only the remarkable scarcity of harpacticoid copepods (VAN DAMME et al., 1984) and the polychaete Scoloplos armiger (HEIP et al., 1986) as possible consequences of pollution. Benthic biomass is certainly much lower than in the Oosterschelde and has been estimated as 2-3 g C m⁻² by HUMMEL et al. (1988).

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REFERENCES

- BAKKER, C. & DE VRIES, I. 1984. Phytoplankton- and nutrient dynamics in saline Lake Grevelingen (SW Netherlands) under different hydrodynamical conditions in 1978-1980. Neth. J. Sea Res., 18 (3/4): 191-220.
- BANNINK, B. A., VAN DER MEULEN, J. H. M. & NIENHUIS, P. H. 1984. Lake Grevelingen: from an estuary to a saline lake. An introduction. Neth. J. Sea Res., 18 (3/4): 179-190.
- BILLEN, G., SOMVILLE, M., DE BECKER, E. & SERVAIS, P. 1985. A nitrogen budget of the Scheldt hydrographical basin. Neth. J. Sea Res., 19 (3/4): 223-230.
- DE PAUW, C. 1975. Bijdrage tot a kennis aan milieu en plankton in het Westerschelde-estuarium. Doct. thesis. State University, Gent
- VRIES, I. 1984. The carbon balance of a saline lake (Lake Grevelingen, The Netherlands). Neth. J. Sea Res., 18 (3/4): 511-528
- GROENENDIJK, A. M. 1984. Consumption of eelgrass (Zostera marina L.) by the isopod Idotea chelipes (Pallas) in Lake Grevelingen, after the growing season. Neth. J. Sea Res., 18 (3/4): 384-394.
- GROENENDUK, A. M. 1985. Ecological consequences of tidal management for the salt marsh vegetation. Vegetatio, 62: 415-424.
- HEIP, C., HERMAN, R. & CRAEYMEERSCH, J. 1986. Diversiteit, densiteit en biomassa van het macrobenthos in de Westerschelde: 1978-1985. R. U. Gent. Inst. v. Dierkunde, sektie Mariene Biologie, 1986. 12 pp.
- HUMMEL, H., MEYBOOM, A. & DE WOLF, L. 1986. The effects of extended periods of drainage and submersion on condition and mortality of benthic animals. J. Exp. Mar. Biol. Ecol., 103: 251-266.
- HUMMEL, H., MOERLAND, G. & BAKKER, C. 1988. The concomitant existence of a typical coastal and a detritus food chain in the Western Scheldt estuary. Hydrobiol. Bull, 22:35-41.
- KELDERMAN, P. 1984a. Sediment-water exchange in Lake Grevelingen under different environmental conditions. Neth. J. Sea Res., 18 (3/4): 286-311.
- KELDERMAN, P. 1984b. Nutrient concentrations in the interstitial water of Lake Grevelingen sediment: effects of sediment redistribution and benthic primary production processes. Neth. J. Sea Res., 18 (3/4): 312-336.
- KELDERMAN, P., NIEUWENHUIZE, J., MEERMAN-VAN DE REPE,

- A. M. & VAN LIERE, J. M. 1984. Changes of sediment distribution patterns in Lake Grevelingen, an enclosed estuary in the SW Netherlands. Neth. J. Sea Res., 18 (3/4): 273-285
- LAMBECK, R. H. D. 1985. Leven zonder getij. Bodemdieren in het Grevelingenmeer. Natuur en Techniek, 53 (12): 916-931
- LINDEBOOM, H. J., DE KLERK, H. A. J. & SANDEE, A. J. J. 1984. Mineralization of organic carbon on and in the sediment of Lake Grevelingen. Neth. J. Sea Res., 18 (3/4): 492-510.
- NIENHUIS, P. H. 1975. Biosystematics and ecology of Rhizoclonium riparium (Roth) Harv. (Chlorophyceae: Cladophorales) in the estuarine are of the rivers Rhine, Meuse and Scheldt. Doct. Thesis. University of Groningen.
- NIENHUIS, P. H. & DÉ BREE, B. H. H. 1984. Carbon fixation and chlorophyll in bottom sediments of brackish Lake Grevelingen, The Netherlands. Neth J. Sea Res., 18 (3/4): 337-359.
- NIHOUL, J. C. J. & WOLLAST, R. (Eds.) 1976. L'Estuaire de l'Escaut. Project Mer. Rapport final. Bruxelles. Service du Prem-
- ier Ministre, 10: 1-239.

 PEELEN, R. 1967. Isohalines in the Delta area of the rivers Rhine, Meuse and Scheldt. Classification of waters in the Delta area according to their chlorinity and the changes in these waters. Neth. J. Sea Res., 3: 575-597
- PETERS, J. J. & STERLING, A. 1976. Hydrodynamique et transports de sédiments de l'Estuaire de l'Escaut. In: L'Estuaire de l'Escaut. Projet Mer. Rapport final. (Nihoul, J. C. J. & Wollast, R., eds.) 10: 1-70. Bruxelles, Service du Premier Mini-
- POSTMA, H. 1967. Sediment Transport and Sedimentation in the estuarine environment. In: Estuaries. (LAUFF, G. H., ed.): 83:336-340. Am. Ass. Adv. Sci.
- SMAAL, A. C., VERHAGEN, J. H. G., COOSEN, J. & HAAS, H. A. 1986. Interaction between seston quantity and quality and benthic suspension feeders in the Oosterschelde, The Netherlands. Ophelia, 26: 385-399.
- TEN BRINKE, W. B. M. 1987. The input of fine sediment into the Oosterschelde system by erosion of old clay deposits. In: Progr. Rep. Delta Inst. 1986 (Beeftink, W. G. & Nieuwenhuize, E. S., eds.): 32-34.
- VAN DAMME, D., HEIP, C. & WILLEMS, K. A. 1984. Influence of pollution on the harpacticoid copepods of two North Sea estuaries. Hydrobiologia, 112: 143-160.
- VAN VEEN, J. 1950. Eb- en vloedschaarsystemen in de Nederlandse getijwateren. Tijdschr. Kon. Ned. Aard Gen., 67: 303-325.
- WOLFF, W. J. 1973. The estuary as a habitat. An analysis of data of the estuarine area of the rivers Rhine, Meuse and Scheldt. Zoöl. Verhand. Leiden, 126. Thesis.
- WOLLAST, R. 1976. Transport et accumulation de pollutants dans l'estuaire de l'Escaut. In: L'Estuaire de l'Escaut. Projet Mer. Rapport final. (Nihoul, J. C. J. & Wollast, R., eds.), 10: 191-218. Bruxelles. Service du Premier Ministre.