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An ecosystem study in Lake Grevelingen, a former estuary in the SW Netherlands*

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Abstract

A working group of the Delta Institute at Yerseke, The Netherlands, studies the ecosystem of saline lake Grevelingen, a former estuary. The theme of the group is the cycling of organic matter in the two phases of the Grevelingen. The pool of particulate organic matter in the Grevelingen estuary (385 g C m^{-2} yr^{-1}) was fed from various sources. The amount of organic carbon from the North Sea, entering the estuary as detritus equalled the in situ primary production. After the closure of the estuary the import of organic matter from the North Sea was completely cut off. Overall yearly production of the phytoplankton was not notably influenced by the closure, notwithstanding the large changes in environmental conditions. The significance of the phytobenthos production increased considerably. The total amount of organic matter available for consumers, decreased by roughly 40% to a level of 235 g C m^{-2} yr^{-1}. In the estuary net production of macrozoobenthos was estimated at 28 g C m^{-2} yr^{-1}. This production was almost divided by a factor two after the closure, just as the amount of food available. Changes in the feeding habits of birds may reflect the often less striking changes in the lower parts of the foodchains. Herbivore bird consumption has increased more than 20 fold after the closure. Consumption of zoobenthos showed a threefold decrease whereas the predation by fish-feeding birds increased about a 30 fold after the closure. The change from an estuarine into a stagnant saline ecosystem, bordering the North Sea, resulted in a sharp decrease in the amount of organic matter available as food, and a shift in the relative significance of predominant species.

Zusammenfassung

Eine Ökosystemstudie im Grevelingensee, einem ehemaligen Ästuar im Südwesten der Niederlande

Eine Arbeitsgruppe des Delta Instituts von Yerseke (Niederlande) untersucht das Ökosystem des salzigen Grevelingensees, eines ehemaligen Ästuars. Das Thema der Gruppe ist der Kreislauf der organischen Substanz im Grevelingensee, im unabgedämmten und im abgedämmten Zustand. Der Bestand an partikulärer organischer Substanz im Grevelingen-Ästuar (385 g C m^{-2} $Jahr^{-1}$) wurde aus verschiedenen Quellen gespeist. Der Menge an organischer Substanz aus der Nordsee, die in das Ästuar als Detritus eindringt, entspricht der in situ Primärproduktion. Nach der Abdämmung des Ästuars war der Eintrag an organischem Material aus der Nordsee völlig ausgeschaltet. Insgesamt war die Jahresproduktion an

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Phytoplankton nicht sonderlich durch diesen Abschluß beeinflußt, trotz beträchtlicher Änderungen der Umweltbedingungen. Die Bedeutung der Phytobenthosproduktion stieg beträchtlich an. Die für Konsumenten verfügbare Gesamtmenge an organischer Substanz sank um ungefähr 40% auf ein Niveau von 235 g C m^{-2} $Jahr^{-1}$. Im Ästuar wurde eine Nettoproduktion des Makrozoobenthos von 28 g C m^{-2} $Jahr^{-1}$ berechnet. Nach der Abdämmung wurde die Produktion entsprend dem Gehalt an verfügbarer Nahrung fast halbiert. Änderungen in den Ernährungsgewohnheiten der Vögel dürften die oft weniger ins Auge fallenden Veränderungen auf den niederen Niveaus der Nahrungsketten widerspiegeln. Die Konsumtion durch herbivore Vögel stieg nach der Abdämmung auf mehr als das 20fache an. Die Konsumtion durch das Zoobenthos zeigte eine 3fache Abnahme, wobei der Wegfraß durch fischfressende Vögel nach der Abdämmung auf über das 30fache anstieg. Die Umformung vom Ästuar zu einem stagnierenden Salzsee-Ökosystem, der an die Nordsee angrenzt, hat eine starke Abnahme im Gehalt der als Nahrung verfügbaren organischen Substanz und einen Wechsel in der relativen Bedeutung der dominanten Arten zur Folge gehabt.

Introduction

The southwestern part of the Netherlands has been shaped by the North Sea and by three large rivers, Rhine, Meuse and Scheldt (Fig. 1 a). In 1953 about 1800 people were killed by an extreme storm flood, inundating more than half of the inhabited area. In order to avoid repetition of the flooding disaster, it was decided to close the main estuaries by high dikes.

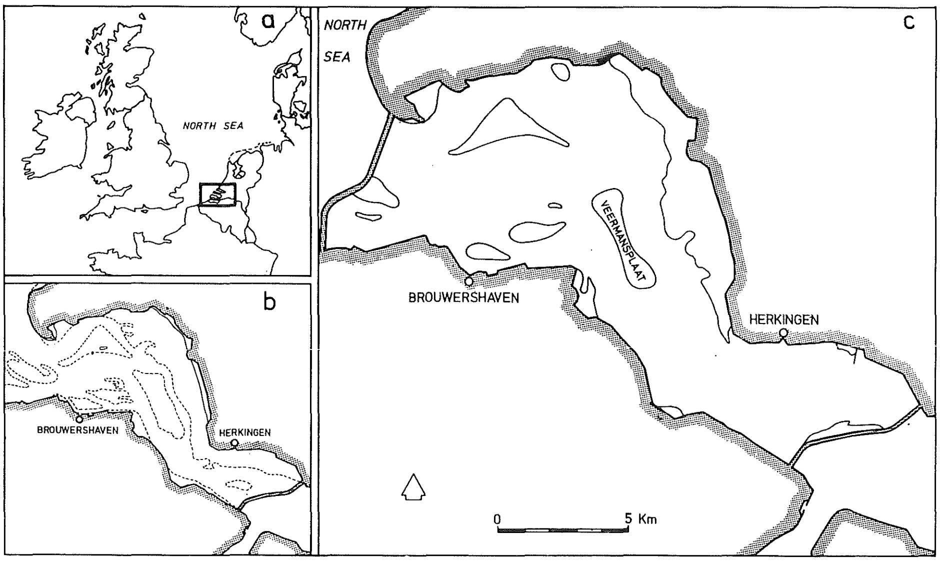

Figure 1

a) The SW Netherlands in W Europe; b) The Grevelingen estuary between 1964 and 1971; c) Lake Grevelingen after the closure in 1971

The Grevelingen was one of those estuaries, before 1971 in open connection with the river Rhine and with the North Sea (Fig. 1b). In 1971 a dam was closed in the mouth of the estuary, excluding influences both from the rivers and from the sea: lake Grevelingen originated (Fig. 1c).

In 1972 it was decided to set up an ecosystem study centred around the cycling of organic matter in the two phases of the Grevelingen: the tidal estuary and the salt-water lake. The study of the carbon cycle is important because energy used to support the structure and function of an ecosystem is transmitted via carbon fluxes through the food chains. The working group consists of a team of 25 biologists, chemists and assistants. The group covers a number of aspects of the organic matter cycle, viz. productivity measurements of phytoplankton, biomass estimations of phytoplankton, microphytobenthos and macrophytes; within the broad scope of the secondary producers attention is paid to zooplankton biomass, and biomass and production of macrozoobenthos. Further, studies are performed on meiozoobenthos and benthic and pelagic fishes. In relation to the efforts on production level, up to now, only little attention is paid to decomposition and mineralisation processes. Fig 2 shows a box model of the Grevelingen carbon cycle.

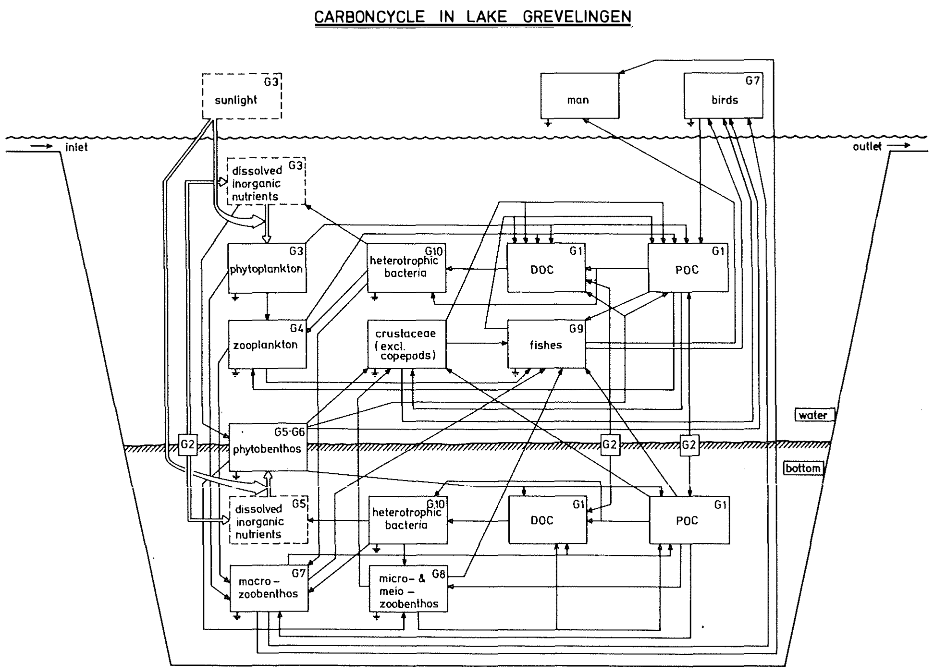

Figure 2

The carboncycle in Lake Grevelingen. The projects (compartments) in which investigations are carried out have been numbered (G 1–G 10)

Environment

Grevelingen estuary was a turbulent tidal system; chlorinity of the water fluctuated around 15‰, with occasional minimum values of 9‰ Cl^-. After the closure of the dam in 1971 the tidal movements dropped out, resulting in sedimentation of particles and consequent increase in transparency of the water. Table 1 summarizes some environmental variables. The Grevelingen is now a stagnant salt-water lake, with only wind driven currents. In this land-locked basin, surrounded by manbuilt dikes precipitation approximately equals evaporation. Salinity is rather high and stable but shows a slight decrease over the years (from 16 to 13‰ Cl^-). The influence of the adjacent polders and tidal waters via sluices is but small: only 10% of the total volume is exchanged per year (KLOMP and SPEKSNIJDER, 1973, 1974). The surrounding area is sparsely populated and waste water discharge of some importance is not present. Therefore the water is relatively clean and the yearly nutrient load is small.

Table 1

Summary of environmental parameters in Lake Grevelingen, SW Netherlands

Surface area		10800	ha
Volume		575.10^6	m^3
Average depth		5.3	m
Maximum depth		48	m
Length		23	km
Width		4–10	km
Secchi disc visibility		1 – 7	m
Suspended matter	>	0 –30	mg/l
Clorinity		13 –16	‰
$N-NH_4$		0.0–0.3	mg/l
$N-NO_3$		0.0–0.4	mg/l
$P-PO_4$		0.1–0.6	mg/l
Si	>	0 – 1	mg/l

Orthophosphate concentrations in the lake are rather high (maximum 0.6 mg/l), possibly caused by continuous release of phosphorus compounds from the bottom. The concentrations of inorganic nitrogen compounds and reactive silicate approach to zero in spring (NIENHUIS, 1977).

Anaerobic conditions, connected with a stable stratification, obligate features in the Baltic, do not occur in Lake Grevelingen. The lake is shallow and anoxic conditions only temporarily occur in the deepest gullies during summer. The bottom of the lake consists of fine grained sand with a relatively low amount of silt. There is no brackish water system in Western Europe completely comparable with Lake Grevelingen. Features in common with the Baltic are the high stable salinity and the absence of tides.

Biological results and discussion

The production of organic matter was quantified along various ways. Phytoplankton production was measured with the ^{14}C method (VEGTER, 1976, 1977). As regards benthic productivity, on the strength of a yearly average chlorophyll- a content in the topsoil some extrapolations could be made to the production of benthic micro-algae (NIENHUIS, unpublished). Production of macrophytes, like eelgrass and larger algae, was estimated using data on changes in biomass (NIENHUIS and De BREE, 1977).

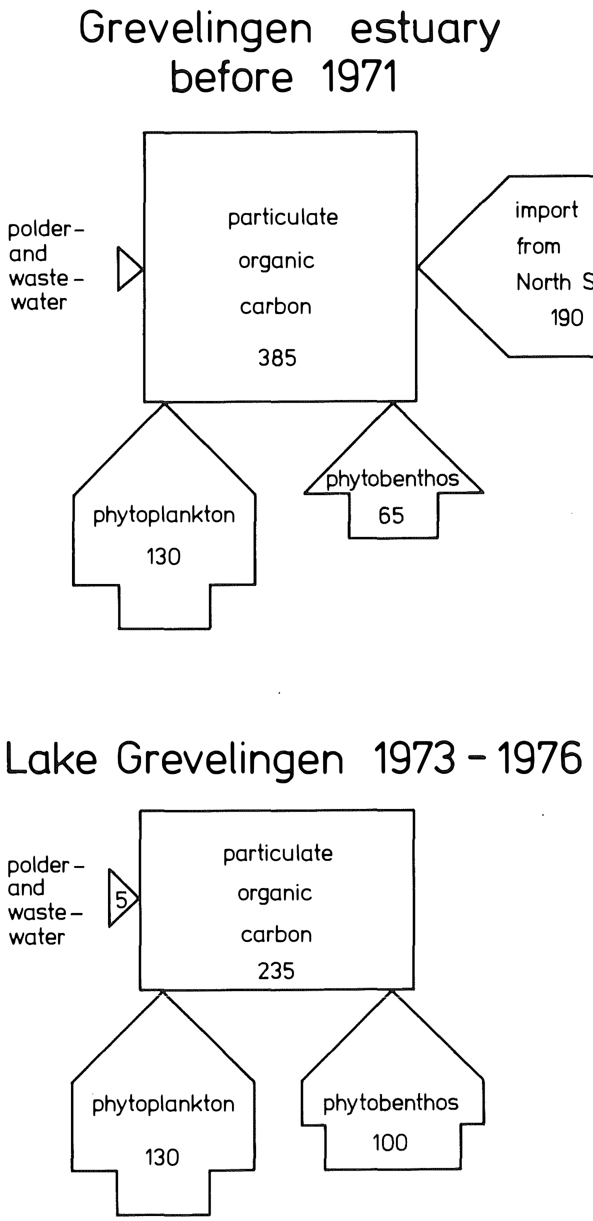

Figure 3
Survey of the amount of particulate organic carbon available in the water column, expressed in g C · m^{-2} · yr^{-1} (rectangles). Origin and size of the sources replenishing the stock are indicated by arrows

The pool of particulate organic matter in the Grevelingen estuary was fed from various sources (Fig. 3). The amount of organic carbon from the North Sea, entering the estuary as detritus, equalled the in situ primary production. Production in the estuary was by far dominated by the phytoplankton share, approximately 130 g C m^{-2} yr^{-1}. Phytobenthos production played a minor role and was roughly estimated at 65 g C m^{-2} yr^{-1} (WOLFF, 1977).

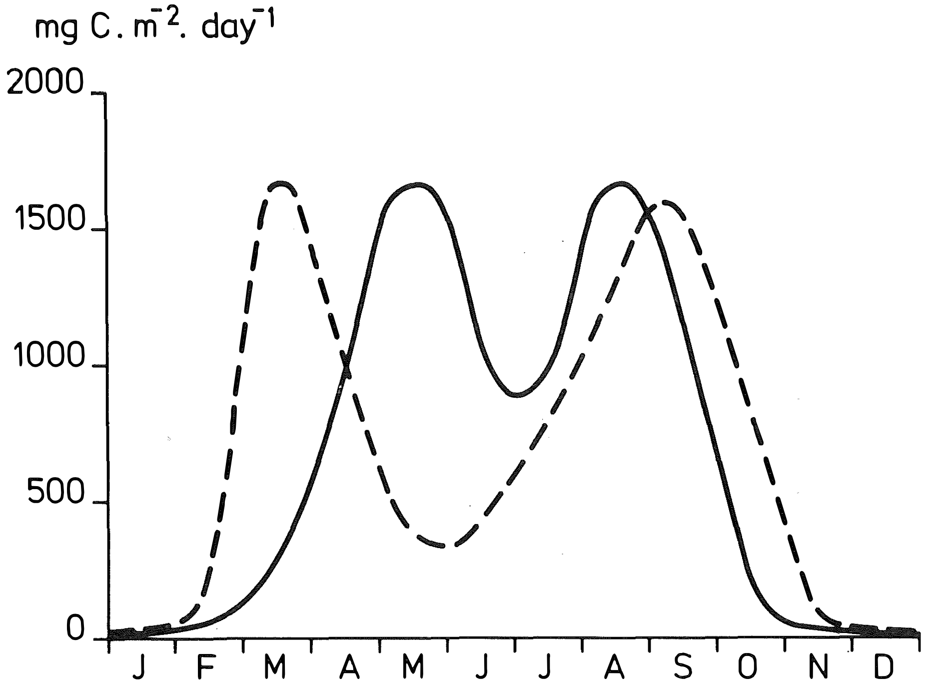

Figure 4

Rough outline of phytoplankton primary production in the Grevelingen estuary, between 1964 and 1970 (solid line) and in Lake Grevelingen between 1971 and 1976 (broken line)

After the closure of the estuary the import of organic matter from the North Sea was completely cut off. Overall yearly production of the phytoplankton was not notably influenced by the closure, notwithstanding the large changes in environmental conditions (VEGTER, 1977; WOLFF, et al., 1976). The picture of the production curve however changed drastically: production starts earlier (February), and stops later (November) than before the damming up (Fig. 4). In contradistinction with the situation before the closure there is evidence that nitrate and ammonium are limiting factors now for phytoplankton development in late spring and summer.

After the damming up the significance of the phytobenthos production increased considerably, roughly estimated from 65 g C to 100 g C m^{-2} yr^{-1}. Especially the role of the macrophytes became obvious in the clear water of the sheltered lake, and increased from less than 10 g C before the closure to 36 g C m^{-2} yr^{-1} at present (De BREE, NIENHUIS and VERSCHUURE, 1973; NIENHUIS and De BREE, 1977). Local peaks of approximately 200 g C m^{-2} yr^{-1} were calculated in eelgrass fields. Organic matter imput from polder- and waste water is insignificant.

The relative significance of the *in situ* primary production increased strongly after the closure, owing to the fact that the subsidy of organic matter from the North Sea was brought to an end. The total amount of organic matter available for consumers, decreased by roughly 40%, calculated on a yearly basis (Fig. 3).

With regard to the heterotrophs in the Grevelingen ecosystem, by far most results were gathered in the macrozoobenthos field (WOLFF, 1977; WOLFF et al., 1976; WOLFF et al., 1976; WOLFF and de WOLF, 1977). WOLFF and de WOLF's (1977) calculations were based on monthly sampling; the results for each yearclass of each benthos species were expressed as average ash-free dry weight per individual and average number of individuals per m^2. In the Grevelingen estuary the net production of the macrozoobenthos was estimated at 28 g C m^{-2} yr^{-1} (WOLFF and de WOLF, 1977). More than 80% of the production was on account of suspension feeders, mainly *Mytilus edulis* and *Cerastoderma edule*. Deposit feeders and grazers took less than 20 %.

A secondary production of 28 g C is high for an estuary. In a comparable area, like the Dutch Wadden Sea, benthic secondary production amounts to 10–15 g C m^{-2} yr^{-1} (BEUKEMA, 1975). In the adjacent North Sea production is several times lower. The amount of food available for the benthos is negatively correlated with the depth of the watercolumn, and a high production in an estuary like the Grevelingen, indicates that the energy flow through the bottomfauna is of large importance, in contradistinction to the situation in deeper seas. The amount of particulate organic carbon, available as food in the Grevelingen estuary was relatively large and this explains the closely connected high benthic secondary production (WOLFF, 1977). If all food of 385 g C m^{-2} yr^{-1} was used by the benthos, this would result in an ecological efficiency of 7%. This hypothetical low efficiency indicates that the food supply was sufficient for a high benthic secondary production (WOLFF and de WOLF, 1977).

How is the situation in Lake Grevelingen? The organic matter supply decreased with 40%. Benthic filter feeder production was established in 1973 on approximately 14 g C m^{-2} yr^{-1} (mainly mussels and cockles) (WOLFF, et al., 1976; WOLFF et al., 1976). For 1974 and 1975 the same tendency was observed (WOLFF, personal communication). As the benthic filter feeders still count for more than 80% of the benthic biomass, we may conclude that benthic secondary production was almost reduced by a factor two after the closure, just as the amount of food available. If we assume that the complete stock of food (235 g C m^{-2} yr^{-1}) is available to the zoobenthos, then it is used with an ecological efficiency of 6%; that means the same order of magnitude as before the closure.

Table 2

Food uptake by various groups of birds in the Grevelingen estuary and the Lake Grevelingen. All values expressed as g ash-free dry wt.m^{-2}.yr^{-1} (WOLFF, van HAPEREN, SANDEE, BAPTIST & SAEIJS, 1976)

Group	Estuary	Lake
Herbivores	0.130	2.712
Zoobenthos feeders	3.420	0.997
Piscivores	0.012	0.352

Changes in food web relations in the Grevelingen ecosystem will be further illustrated by means of a well studied group of animals, viz. the birds (WOLFF, et al., 1976). Changes in the feeding habits of birds may reflect the often less striking changes in the lower parts of the food chain. In Table 2 the food uptake by birds in the estuary and in the lake is summarized. The data were based on frequent bird countings before and after the closure. Data on the amount of food actually consumed by birds are lacking and therefore the calculated predation pressure is only a relative measurement. To determine the consumption, the standard metabolism of a bird was estimated on the basis of its weight. Body weights were taken from the literature. To obtain the consumption per bird the standard metabolism was multiplied by a constant factor five.

According to the data of WOLFF et al. (1976) herbivore consumption has increased more than 20 fold after the closure. The increase in production of larger algae and eelgrass amounted to about five times the production before the closure, but this is out of all proportion to the enormous increase in bird consumption. Tentatively it may be concluded that the absence of tides favours herbivore consumption, especially because a number of species (such as mute swan, coot and ducks), which appeared in the lake, hardly occurred in the estuarine area.

On account of the 1975 and 1976 data IERLAND (1977) calculated in a more accurate way herbivore consumption of eelgrass during the growing season. Only 5 out of 91 g $C.m^{-2}.yr^{-1}$, that means about 6%, of the eelgrass production was consumed by animals. Of that total consumption only 26% was on account of birds, which means that birds (mainly mute swan) took only 1.6% of the eelgrass production during the period April to September. Notwithstanding the rapidly increased birds' consumption after the closure of the estuary in 1971 it must be concluded that the impact on eelgrass biomass is only very small. By far the largest part of the eelgrass enters detritus food chains.

Consumption of zoobenthos showed a threefold decrease after the closure (Table 2). In the estuary zoobenthos feeders consumed 6% of the zoobenthos production. In the lake the consumption amounts to 3%. Apparently tidal movements favour the predation of zoobenthos. This also appears from the enormous decrease of specialized predators on zoobenthos, such as oystercatcher and grey plover, after the closure of the estuary, and the concomitant disappearance of the extensive tidal flats.

The predation by fish-feeding species increased about a 30 fold after the closure. Although we have no accurate data on changes in fish biomass before and after the closure, it seems improbable that this 30 fold increase reflects an increase in fish production of the same magnitude. We assume that the greatly increased transparency of the water in the determining factor. A greater water transparency obviously results in a better localization of the preys by fish eating species like great crested grebe and cormorant (WOLFF et al., 1976).

It may be concluded that the presence or absence of tides greatly influences the way in which birds may exploit a marine environment. A shift from secondary and tertiary consumers to primary consumers is predominant. In summary, the change from an estuarine into a stagnant saline ecosystem, bordering the North Sea, results in (a) a sharp decrease in the amount of organic matter available as food, and (b) a shift in the relative significance of predominant species.

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