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Zooplankton biomass in the Oosterschelde (SW Netherlands) before, during and after the construction of a storm-surge barrier

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Key words: zooplankton biomass, copepods, *Temora*, *Pleurobrachia*, benthic larvae, phytoplankton, seston food quality, Oosterschelde, retention time

Abstract

The hydrodynamic consequences of large coastal engineering (barrier-construction) works in the Oosterschelde were: prolonged residence times of the water, increased sinking of particulate material, and higher water transparencies. This strongly influenced the phytoplankton (Bakker *et al.*, 1990; 1994) and phytoplankton biomass increased in the shallow Eastern compartment of the Oosterschelde (Bakker & Vink, 1994) while phytoplankton concentration of the seston rose.

Zooplankton biomass, especially of copepods (*Temora*) and meroplankton (barnacle larvae) increased during the post-barrier period in the Eastern compartment. It is hypothesized that this is caused by the improved feeding conditions and the increased retention times in this area.

The barrier years 1985 and 1986 were characterized by low current velocities. In the Eastern compartment, this may have favoured the development of the rotifer *Synchaeta* (Bakker, 1994) and of the important copepod predator *Pleurobrachia* (Ctenophora).

In the Western compartment, zooplankton developments in the post-barrier years were rather similar to those in the pre-barrier period. This led to the disappearance of the previously existing biomass gradients West-East (maxima in West). At present a trend in the opposite direction (maxima in East) is observed.

Introduction

In the Oosterschelde (Fig. 1), a tidal inlet (*ca* 350 km^2) of the southern North Sea, a large-scale hydraulic engineering project was carried out. This involved the construction of a storm-surge barrier in the mouth (1982–86), and dams in the Eastern part (Oesterdam, 1982–86) and in the Northern compartment (Philipsdam, 1985–87) (Fig. 1). For further details cf. Nienhuis & Smaal (1994).

The construction of the barrier and the accompanying works seriously affected tidal amplitude and current velocities (Wetsteyn *et al.*, 1990; Smaal & Nienhuis, 1992). Current velocities decreased, especially in the shallow Eastern area, suspended matter concentrations declined (Wetsteyn & Bakker, 1991) and water transparency rose concomitantly (Bakker *et al.*, 1990). This caused the phytoplankton assemblage to extend its growth season both earlier and later in the year (Bakker *et al.*, 1990).

During the post-barrier years a changed light-nutrient-salinity regime (*i.e.* high water trans-

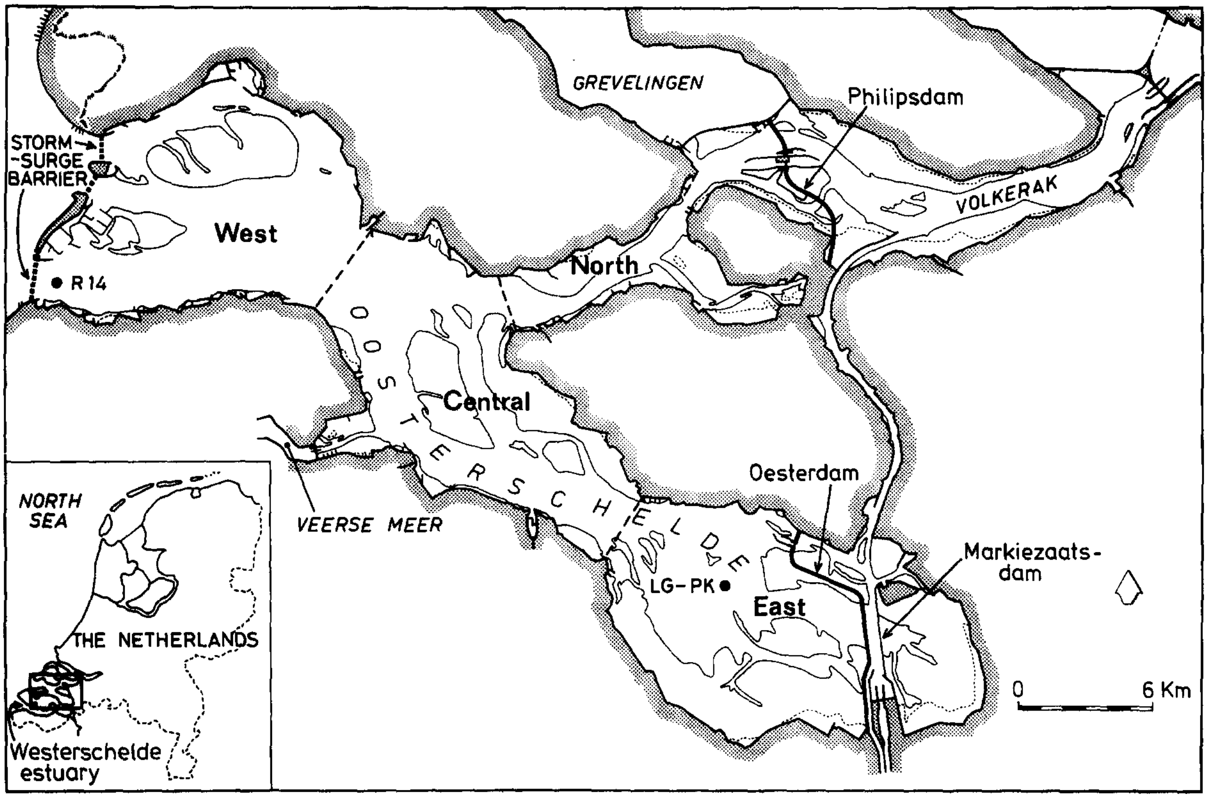

Fig. 1. Map of the Oosterschelde with indications (broken lines) of the 4 compartments and the sampling localities in West (R14) and East (LG-PK).

parency, limitation of nitrate, high salinity) was established during an extended summer season, without the gradual transitions characterising the pre-barrier period (Bakker *et al.*, 1994). In summer, biomass of diatoms decreased but biomass of flagellates increased in the Eastern compartment (Bakker & Vink, 1994). Annual primary production of the pre-barrier years, as reported by Vegter & De Visscher (1987), did hardly change in the post-barrier period (Wetsteyn & Kromkamp, 1994): slightly decreased values were observed for the Western- and similar values for the Eastern compartment.

Data on the zooplankton species composition of the Oosterschelde are given by Bakker (1994). Population dynamics and trophic relations were studied in the eighties, with special reference to the copepods. Bakker & Van Rijswijk (1987) determined the development time and growth rate of *Temora longicornis* as related to the local food conditions. At the same time Tackx *et al.* (1989, 1990) performed grazing experiments using the copepods *Acartia* spp., *Temora longicornis* and *Centropages hamatus* as well as the nauplius larvae of *Balanus* spp., dominating in the Eastern area. They demonstrated size- and species-selective feeding in the copepods, and quantified the grazing pressure in the Western and Eastern parts of the Oosterschelde. Van Rijswijk *et al.* (1989) continued the *Temora* studies with the estimation of daily fecundity as influenced by temperature and food. Tackx *et al.* (1991, 1994) studied size distributions of phyto- and zooplankton for the analysis of the trophic relations in the pelagic subsystem in the basin. Finally, Klepper (1989) and Van der Tol & Scholten (1992) integrated all field data of the Oosterschelde in a dynamical ecosystem model in an attempt to quantify the impact of the hydraulic works on the foodweb.

The aim of the present paper is to detect a possible response of the dominant zooplankton species, notably the copepods, to the environmental conditions in the present-day Oosterschelde.

As in the phytoplankton papers (Bakker *et al.*, 1990, 1994; Bakker & Vink, 1994) the attention is focussed on the Eastern part of the sea-arm as changes were most pronounced in that area. Eastern and Western compartments are further indicated as E and W, respectively.

Methods

Samples were taken at two locations: station LG-PK in E (depth 20 m) and station R14 in W (depth 40 m, near the storm-surge barrier) (Fig. 1). During the period March to October sampling was carried out weekly, during the rest of the year less frequently.

Sampling and counting

Zooplankton was collected by pumping with a Pleuger submersible system, capacity 200 l min^{-1}. Generally, 100 l of water were filtered, through a net of 63 μm mesh gauze, retaining all copepod stages (smallest nauplii and eggs included), cladocerans, appendicularians and the majority of meroplankton (larvae of mollusks, polychaete worms, barnacles). The 63 μm mesh did not retain quantitatively rotifers and protozoans. Sampling was always done around half tide, when maximum current velocities prevailed, causing approximately homogeneous vertical distributions of zooplankton in the water column (unpublished data of a precedhng pilot study). During the years 1982–84 all samples were taken at mid depth, in the period 1985–88 samples were collected at depths of 2.5, 7.5, 12.5, 17.5 and 22 m and in W also at 27.5 and 32 m depth. At both stations, samples taken at all depths were pooled. Zooplankton was preserved with borax-buffered formalin to a final concentration of 4% exactly (Steedman, 1976). In the laboratory a subsample was taken, representing 100 l of the original field sample. Adult copepods and copepodid stages were counted under a binocular microscope. For the copepod nauplii and the rest of the zooplankton a subsample was taken representing 10 l of water of the original field sample and the organisms were counted using an inverted microscope.

Pleurobrachia pileus (Ctenophora) was sampled at mid depth with a 200 μm mesh-sized high-speed sampler during tows of *ca* 5 minutes, filtering 50–100 m^3 of water. Total numbers of comb-jellies were counted on board the ship (without determining the size), in order to obtain an impression of the abundance of this predator, potentially of importance in controlling copepod densities.

Biomass determination and calculations

Copepods were sorted and divided in the following groups: small copepodid stages (I–III, 3 x 40 individuals, large copepodids (IV–V, 3 x 30 ind.), adult females (3 x 10 ind.) and males (3 x 10 ind.). Cephalothorax lengths were measured. The animals were put in aluminum combustion vessels of 10 x 4 x 3 mm (Perkin-Elmer). Vessels were pre-dried and vessels plus animals dried in an oven at 50 °C for 24 hours. A Cahn electrobalance (model 29, accuracy 0.1 μg) was used for the determination of copepod dry weight. For corrections of dry weight values and further details: cf. Bakker & Van Rijswijk, 1987). For *Oikopleura* the length-weight relation according to King *et al.* (1980) was used. For the remaining species and groups weights were determined after calculation of volume and conversion of wet- to dry weight.

Further calculations

Weekly averages of the biomass of the two main components of the zooplankton (copepods and meroplankton) were calculated for the 3 periods of investigation: pre-barrier- (1982–83), barrier- (1984–86) and post-barrier- (1987–88) period

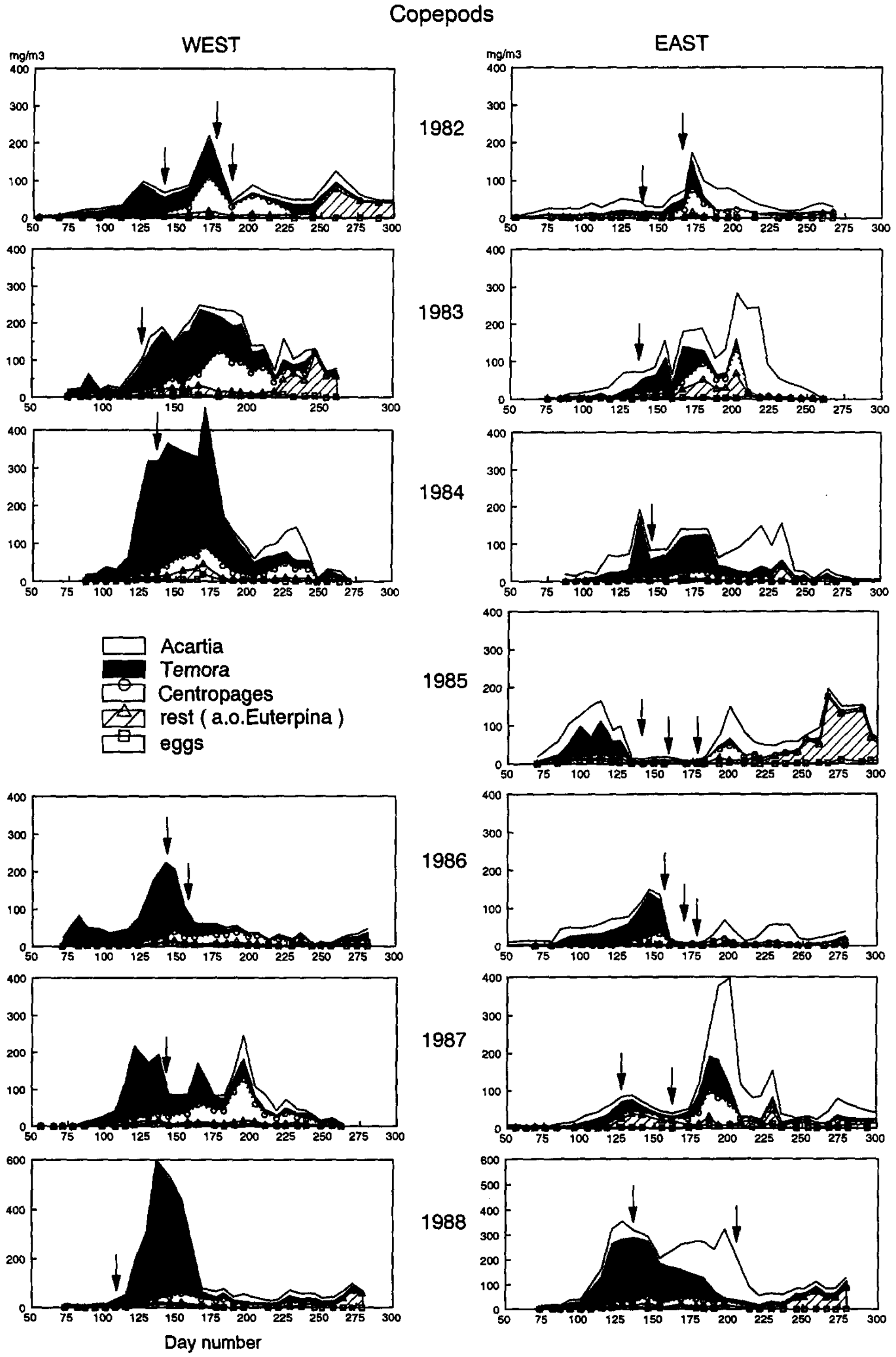

Fig. 2. Seasonal distribution of copepod biomass (mg drw m^{-3}) in the Western and Eastern compartments of the Oosterschelde, 1982–88. Arrows indicate peaks of *Pleurobrachia*. (Note the different scale in 1988).

(Fig. 8). Bakker *et al.* (1990) argumented the inclusion of 1984 in the barrier construction period, on the basis of the already increasing transparencies.

Although phytoplankton is considered to be the main food for suspension-feeding (meso)-zooplankton, microzooplankton like ciliates and rotifers may also be consumed by these animals (Stoecker & Egloff, 1987). Therefore total microplankton carbon (*i.e.* phytoplankton- and microzooplankton carbon added) was calculated (based on the data of Bakker & Vink, 1994, and on unpublished data of these authors), as monthly averages for the 3 periods of investigation (Fig. 10).

In the Oosterschelde suspended matter concentrations and particulate organic carbon concentrations decreased, from the barrier period onwards (Wetsteyn & Bakker, 1991). Consequently, the ratio of microplankton carbon to POC seemed of importance as a measure of (changing) food quality. This ratio was also calculated as monthly averages for the 3 periods of investigation (Fig. 11).

Results

Copepod biomass (Figs 2–3)

In spring, the most abundant copepod genera were *Temora* and *Acartia*; during summer *Centropages*, *Acartia* and *Euterpina* were found, the latter however only abounding during the barrier year 1985 in E (Fig. 2). Generally, *Pseudocalanus*, *Paracalanus* and *Euterpina* did not reach high densities and were lumped to the rest group in Figs 2–3. The seasonal distributions of copepod biomass at both stations (Fig. 2) and the average annual biomass values (Fig. 3) show *Temora longicornis* to be the dominating copepod in W throughout the entire period of investigation with *ca* 50–75% of total biomass. In E, *Acartia* spp. were more abundant, representing *ca* 40–60% of

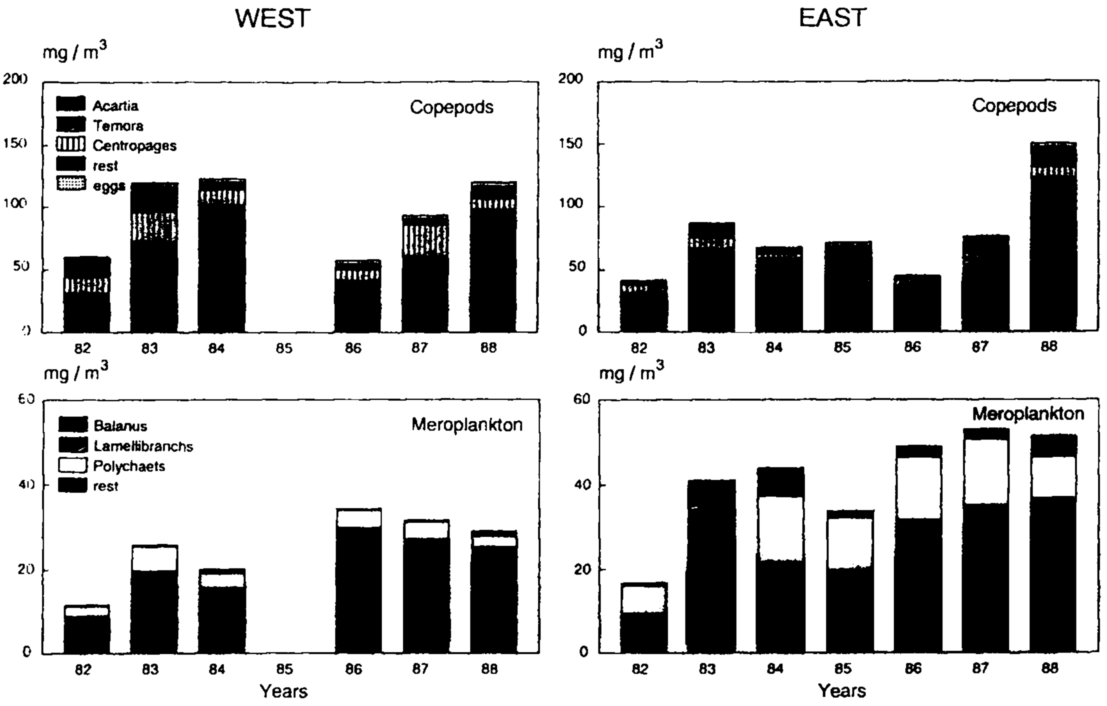

Fig. 3. Annual average copepod (top) and meroplanktonic (bottom) biomass (mg drw m^{-3}) in the Western and Eastern compartments of the Oosterschelde, 1982–88.

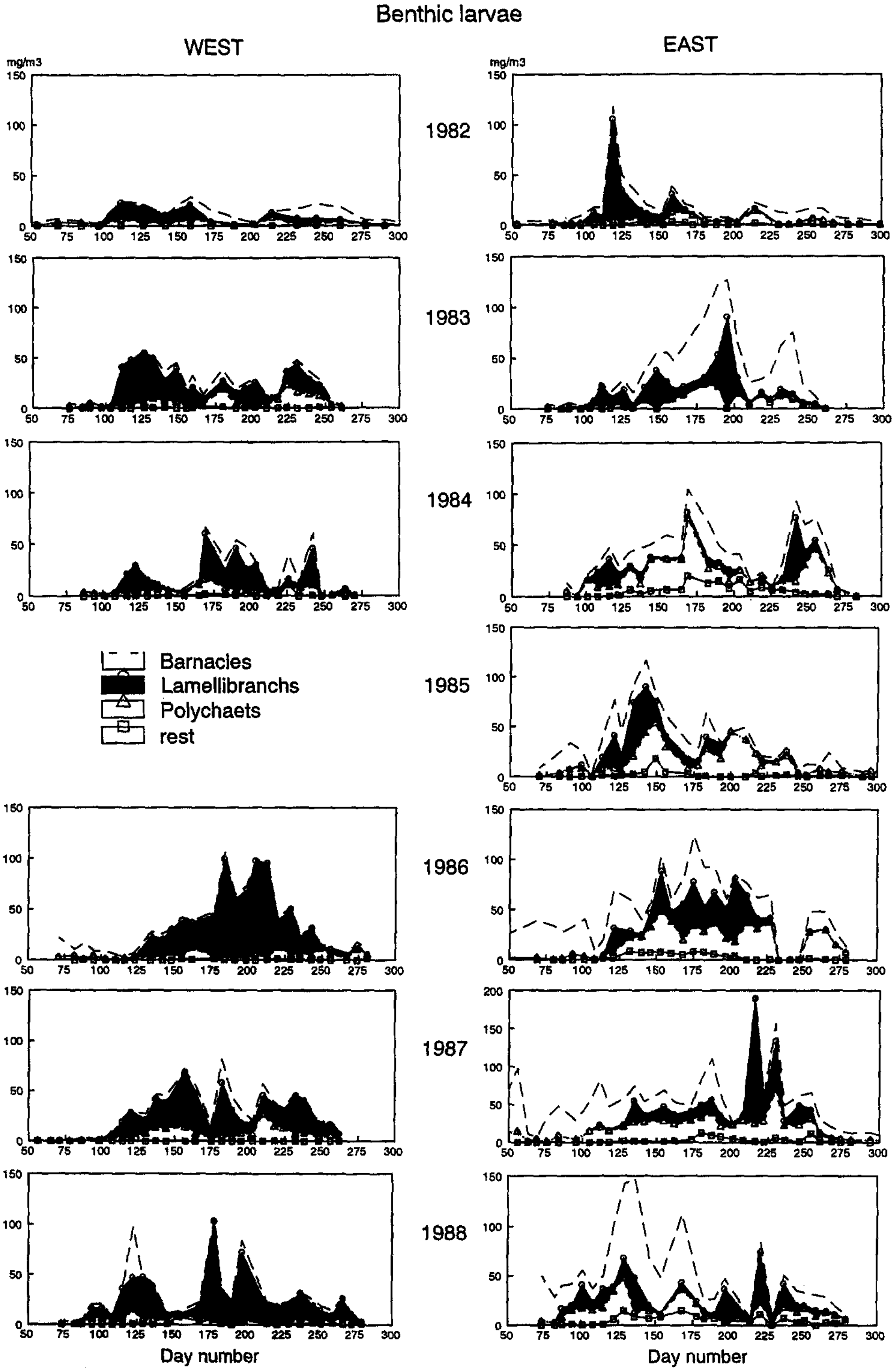

Fig. 4. Seasonal distribution of meroplanktonic biomass (mg drw m^{-3}) in the Western and Eastern compartments of the Oosterschelde, 1982–88.

total biomass. During the postbarrier year 1988 *Temora* reached an unprecedentedly high biomass in E. Consequently, total copepod biomass rose considerably in this area in 1988 (Fig. 3). In W such an increase did not occur: average biomass of 1988 was similar to that of 1983–84 (Fig. 3). Late winter–early spring densities of *Temora* in W were larger than those in E in 1982 till 1986, but this tendency disappeared in 1987–88. Consequently, *Temora* tended to peak earlier in W than in E, but this trend was reversed in 1988.

Acartia always demonstrated much larger late-winter biomass and earlier peaks in E than near the barrier. Here, *Acartia* development was often very poor.

Peaks of *Centropages* biomass were modest, if present, and times of occurrence of peaks were similar in both areas. Late winter–early spring densities were always very small or negligible. *Centropages* generally followed *Temora*, but always had much smaller biomass.

All copepod species showed a more or less fixed pattern of seasonal occurrence, except for *Euterpina*. In W during 1982–83, this species developed well, but it could hardly be observed in 1984–87 (Fig. 2). In E a dense *Euterpina* population occurred only in 1985 (Fig. 2). In this barrier year, when current velocities began to decrease, copepod developments were strikingly different from those in all other years of investigation in this area. *Temora* peaks, for instance, were already seen around day 100, while the usual maxima around days 150–175 were completely lacking in 1985 (Fig. 2).

Eggs (of all copepod species together) always contributed very sparsely to total copepod biomass.

Meroplankton biomass (Figs 3–4)

Meroplankton (benthic larvae) in the Oosterschelde consisted mainly of barnacle larvae (*Balanus* spp.), bivalve larvae (mussels, cockles, oysters) and polychaete larvae. Other groups recorded were gastropods (periwinkles, mud snails, slipper limpets) and tunicates (tadpole larvae).

The meroplankton group composition differed considerably between the two compartments. Barnacle- and polychaete larvae were found in a 2–5 times higher biomass in E than in W. Barnacle larvae could reach high densities in E already in the pre-barrier period (1983), decreased during 1984–85 and continuously increased again from 1986 onwards (Figs 3, 4). Polychaetes, mostly comprising a substantial biomass in E, had a remarkably low density in 1983 (Fig. 3). Bivalve larvae accounted for *ca* 25% of total benthic biomass in E. In W extended mussel beds occur, causing the major benthic contribution to total larval biomass in that area, especially from 1986 onwards, when biomass values amounted to >20 mg m^{-3}, equalling those of barnacle larvae in E (1983, 1988). Other groups of minor importance were stronger represented in E. In W the first larvae peak, in spring, was produced by mussels; the summer peaks (Fig. 4) originated from cockle larvae. In this area in 1986, exceptionally, summer biomass strongly exceeded the spring values here (Fig. 4). In E high cockle larvae peaks were observed during summer 1987 (Fig. 4).

Ctenophora (Pleurobrachia) densities (Figs 5–6)

Figure 5 gives the *Pleurobrachia* densities (N m^{-3}) from 1982 onwards at both stations. As a rule, highest densities were observed in W (1982, 1983, 1984, 1987). During 1985 and 1988 highest maxima were registrated in E, while in 1986 (barrier construction year) E started and finished higher than W, although the absolute peak was found in the latter area. In 1984, 1985 and 1988 W demonstrated relatively low maxima (≤ 10 m^{-3}) while during the other years numbers fell within the range of >20–>50 m^{-3}). *Pleurobrachia* development became visible from March–April onwards and most maxima were situated in May.

During the pre-barrier years a W–E gradient in *Pleurobrachia* density was observed which disappeared in the barrier period but returned in the post-barrier years. In 1988 (May) however, this gradient reversed due to a steady increase of

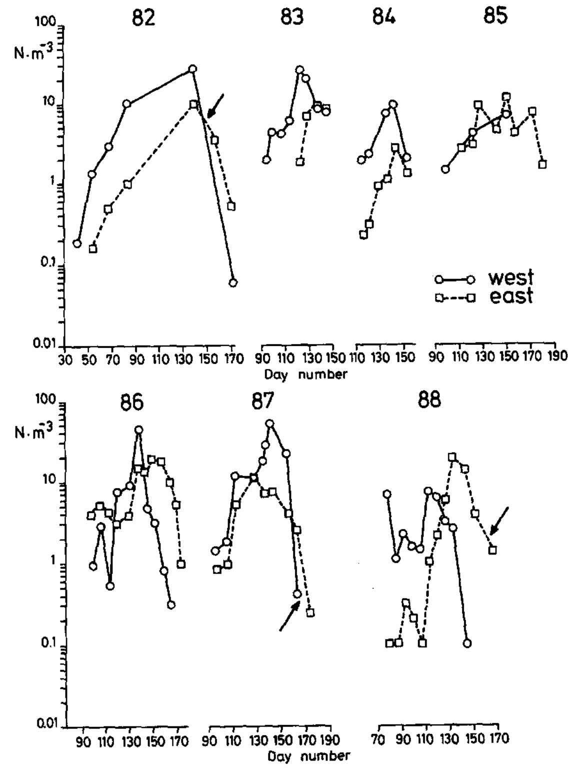

Fig. 5. Densities of *Pleurobrachia pileus* (N m^{-3}) in Western and Eastern compartments of the Oosterschelde during the years 1982–88. Arrows indicate presence of *Beroe gracilis*.

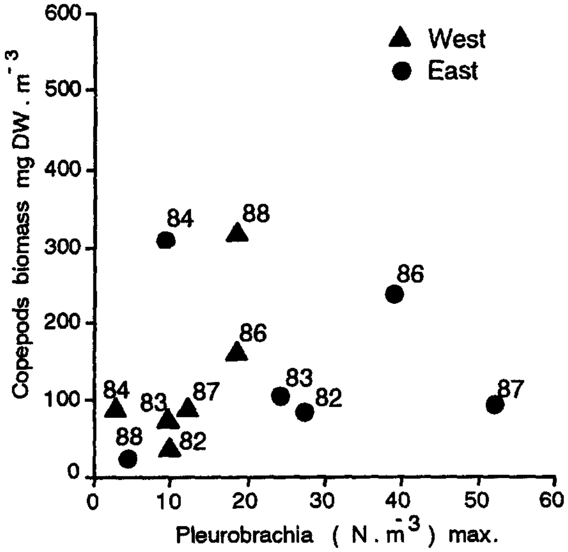

Fig. 6. Maxima (N m^{-3}) of *Pleurobrachia* and co-occurring copepod biomass (mg drw m^{-3}) in the Oosterschelde (1982–1988) in the Western (circles) and Eastern (crosses) compartments.

Pleurobrachia numbers in E, coinciding with a decline in West. Figure 6 shows that no correlation existed between the maximum density of *Pleurobrachia* and the co-occurring total copepod biomass. However, comparing Fig. 5 with Fig. 2, the following details can be noticed. In 1984 *Pleurobrachia* reached low peak numbers in W while at the same time (day 142) copepod (*Temora*) biomass was very large and still rose further after the definite wane of the predator. In E, 1985 was characterized by scarcity of copepods from day 130 onwards which coincided with a relatively high and long-lasting (although fluctuating) abundance of *Pleurobrachia*. From day 170 onwards when *Pleurobrachia* decreased definitely, summer copepods (mainly *Acartia*) developed. In E, 1986, the possibly predatory influence of *Pleurobrachia* shifted to June when its numbers still rose and copepod biomass strongly declined. In W, 1986, copepod biomass did not increase further when *Pleurobrachia* was at its maximum (day 140). In W, 1987, the drop of *Temora* on day 140 may be influenced by the *Pleurobrachia* maximum at the same time. In E, 1987, it was not earlier than day 170 when *Pleurobrachia* (as well as other gelatinous predators: *Aurelia*) had disappeared completely, that a strong copepod development started. In E, May 1988, copepod biomass levels decreased or flattened (*Temora*) when *Pleurobrachia* reached maximum abundance. In W, 1988, the high peak in copepod biomass developed when *Pleurobrachia* was nearly absent.

Biomass during pre-barrier-, barrier- and post-barrier periods (Figs 7–8)

Annual average total zooplankton biomass (Fig. 7). Biomass in W during the pre-barrier period (*ca* 75–*ca* 150 mg drw m^{-3}) was generally higher than in E (*ca* 60–*ca* 100 mg drw m^{-3}). During the years 1985–86 biomasses in W and E were similar and amounted to *ca* 100 mg drw m^{-3}. During the post-barrier period E reached the largest values measured in 1988 (> 200 mg drw m^{-3}), while the values of W maintained the 1983–84 level (*ca* 150 mg drw m^{-3}). During

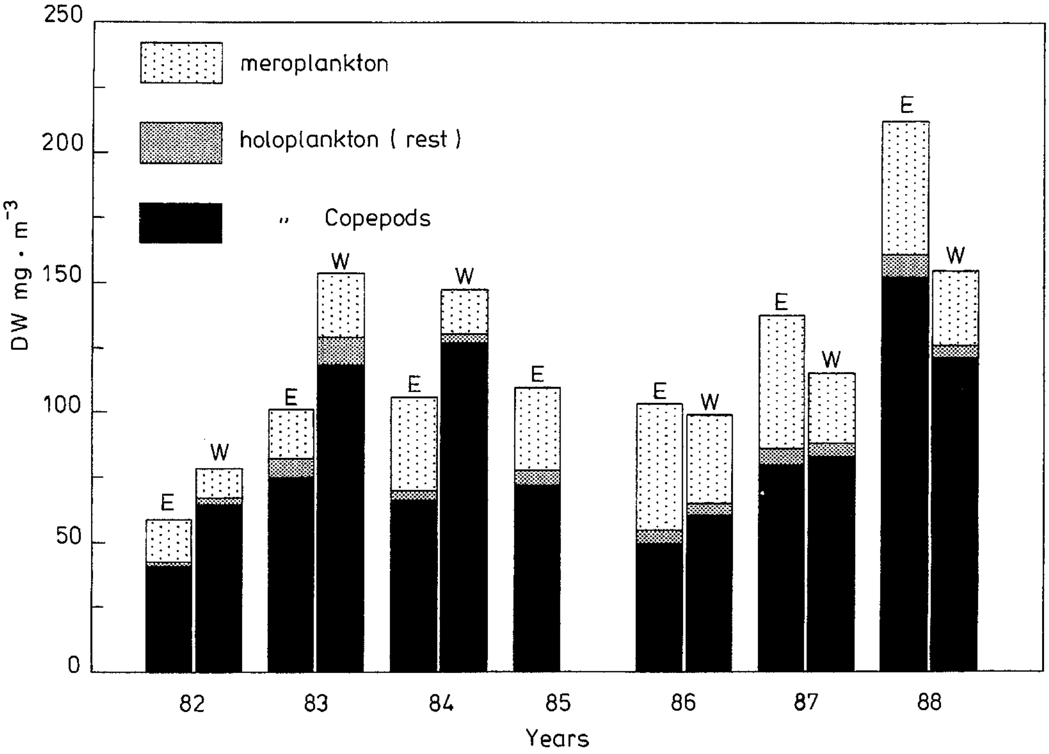

Fig. 7. Annual average values of total zooplankton biomass (mg drw m^{-3}, main contributing groups indicated) in Western (right bar) and Eastern (left bar) compartments of the Oosterschelde, 1982–88.

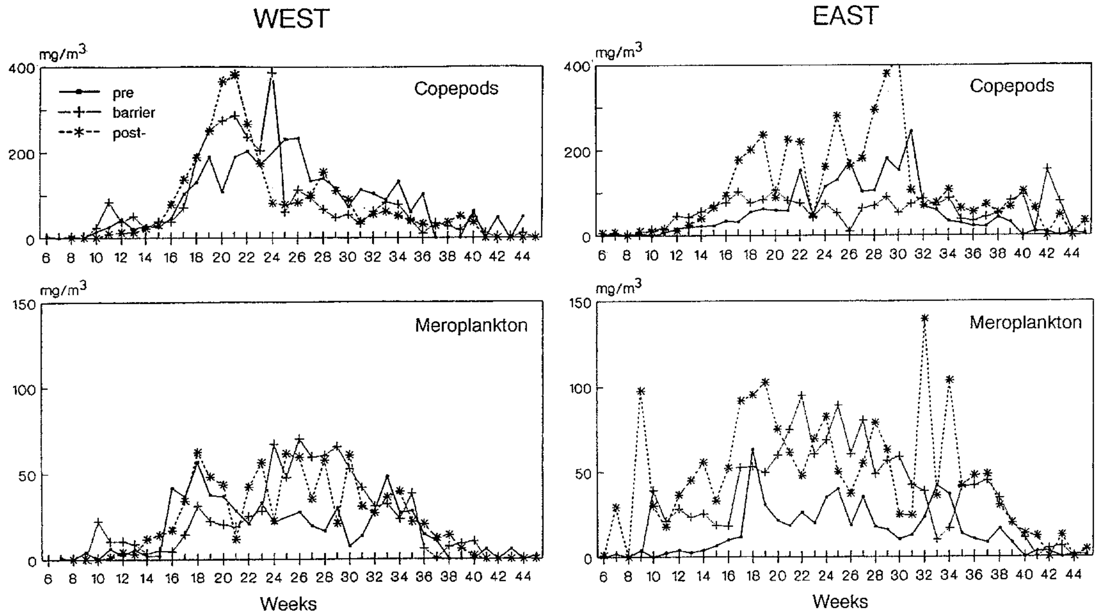

Fig. 8. Seasonal distribution of copepod (top) and meroplanktonic (bottom) biomass (mg drw m^{-3}) averaged for pre-barrier-, barrier- and post-barrier years in the Oosterschelde, Western and Eastern compartments.

1987–88 total annual biomass in W was smaller than in E, so that the previous biomass gradient W–E was reversed (on a per m^3 basis).

Seasonal distribution patterns for copepods and meroplankton are shown in Fig. 8, where average weekly biomass values are given during the three periods separately, for the two compartments.

Copepods. In the post-barrier period in W, copepods demonstrated a series of higher spring but lower summer values than previously, leading to approximately similar annual averages, except 1982 (Fig. 7). In E on the other hand, copepods in the post-barrier years reached higher values than before, nearly all over the year. The years of barrier construction showed very low values in summer (weeks 24–31).

Meroplankton. In W higher values in barrier- as well as in post-barrier years were reached during summer, as compared to the pre-barrier situation. In E a similar trend was observable during nearly the whole year.

Discussion

The main change observed in this study is the important increase in zooplankton biomass during the post-barrier period in E. This led to the reversal of the previous biomass gradient W–E during the major part of the growth season in these years (1987–88). However, we face the objection that the complete zooplankton data for the last period only comprise 1988, the first complete post-barrier year, and not 1989, a year still included indeed in the phytoplankton studies. And as zooplankton biomass, especially of *Temora longicornis*, was unprecedentedly high in E during 1988, the question arises whether this increase was an incidental phenomenon only. Zooplankton samples of 1989 have been collected and analysed with regard to *Temora*. Results of the counting of the numbers of the adult animals are presented in Fig. 9, for both 1988 and 1989 (after Darboe, 1992). Maximum *Temora* densities of 1989 were as high as those of the foregoing year. The duration of the entire period of occurrence was even longer in 1989 (Fig. 9). Moreover, the 1989 (and 1988) *Temora* adults reached heavier individual weights than during the pre-barrier period (Bakker & Van Rijswijk, unpubl.; Darboe, 1992). This supports the impression that the increase of copepod (notably *Temora*) biomass is a characteristic phenomenon for the post-barrier years. Also the model calculations by Van der Tol & Scholten (1992) indicate an increased zooplankton biomass and an overall increase in carbon fluxes with regard to the zooplankton during the post-barrier period.

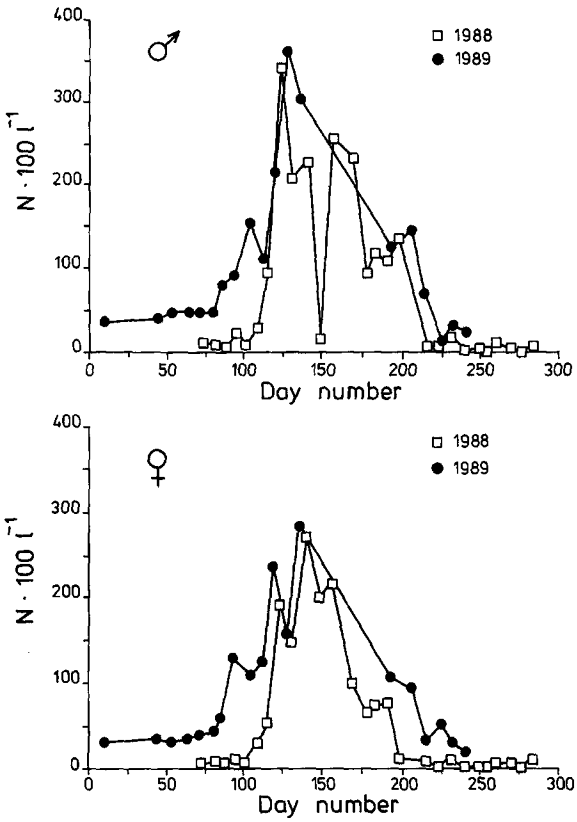

Fig. 9. Seasonal distribution of adult *Temora longicornis* densities in the Eastern compartment of the Oosterschelde in 1988 and 1989 (after Darboe, 1992).

Environmental factors in the Oosterschelde influencing the annual fluctuations in zooplankton abundance comprise both the hydrodynamical changes (specific for this basin) and the cyclic physical, chemical and biological alterations, partly of general nature, partly strengthened or weakened by the infrastructural works. Because several factors demonstrated the most conspicuous changes in E, the phytoplankton in this area were influenced most distinctly too (Bakker *et al.*, 1994; Bakker & Vink, 1994).

In relation to the zooplankton biomass increase in E, the following factors are of importance:

1. Increased residence times during barrier- and post-barrier years (cf. Wetsteyn *et al.*, 1990; Vroon, 1994). Larger residence times lead to stronger retention of zooplankton which is of importance during the growth season as the populations are allowed to stay and reproduce for a prolonged time in a smaller area than before. This may result in higher population densities during the propagative period of a species. For copepods this can also lead to higher numbers of resting eggs sedimenting on a certain bottom area and, consequently, to higher naupliar densities in the next spring period. The strongly decreased current velocities during the barrier years were most favourable for the rotifer *Synchaeta* spp., reaching peak abundances during this period (Bakker, 1994).

2. Increased phytoplankton biomass. A shift in phytoplankton composition during the barrier period was demonstrated (Bakker *et al.*, 1990), continuing in the post-barrier period (Bakker *et al.*, 1994). It is difficult to evaluate a possible influence of a change in phytoplankton composition *per se* on the zooplankton, but when also phytoplankton biomass increases (Bakker & Vink, 1994; Wetsteyn & Kromkamp, 1994), the food conditions for the zooplankton will improve, especially when the enlarged biomass of the phytoplankton is composed of preferred species in favourable size classes (Tackx *et al.*, 1989). There are good reasons to assume that this is true indeed, as flagellate biomass increased from 1985 onwards (Bakker & Vink, 1994) and also a number of smaller diatom species appeared (Bakker *et al.*, 1994). For the copepods also microzooplankton (rotifers, ciliates) represent good food (Stoecker & Egloff, 1987). Therefore total micro-

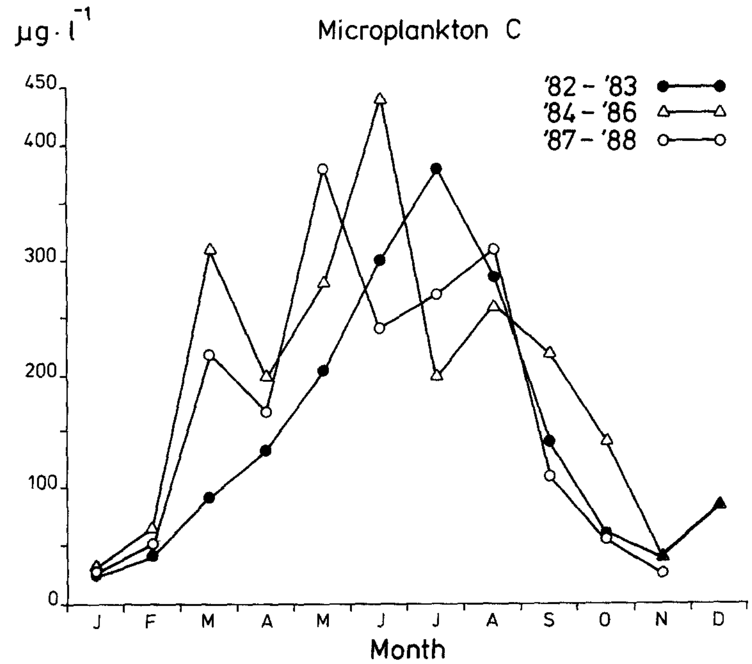

Fig. 10. Microplankton carbon (*i.e.* phytoplankton- plus microzooplankton carbon) in the Eastern compartment of the Oosterschelde, calculated as average monthly values during pre-barrier- (1982–83), barrier- (1984–86) and post-barrier (1987–88) periods.

plankton carbon (including microzooplankton) was calculated to illustrate the changed food quantities in the Oosterschelde during the 3 periods (Fig. 10). For the pre-barrier period a regular increase of microplankton carbon can be seen from winter to summer, with a distinct summer peak, followed by a (steeper) decrease in late summer and autumn. The barrier- and post-barrier years, characterized by higher transparencies in the water column enabling an earlier start of phytoplankton development, demonstrated much larger biomass in late winter and spring. In summer, however, carbon biomass values were smaller than previously: this may be partly due to nitrogen limitation (Bakker & Vink, 1994), partly to increased grazing pressure exerted by the larger zooplankton biomass (Fig. 8).

3. Increased food quality during barrier- and post-barrier years. Suspended matter concentrations decreased significantly from the barrier period onwards (Wetsteyn & Kromkamp, 1994; Bakker & Vink, 1994). Particulate organic carbon concentration was found to behave similarly as suspended matter concentration (Bakker & Wetsteyn: unpubl.). During the major part of the growth season in barrier- and post-barrier periods, the microplankton carbon/POC ratio changed in favour of the living component of the POC (Fig. 11). (Only during a short summer period (July) the situation was similar to the pre-barrier period). This improvement of the food value of the seston, in combination with the increased microplankton biomass *per se*, may result in a more favourable energy balance as the animals have to spend less energy and/or time to select preferred food items. This may have led to a larger productivity, of the holoplankton as well as of the benthos, and, consequently to the increased biomass and total zooplankton densities. The decrease of indigestible material in the zooplankton diet was not explicitly modelled by van der Tol & Scholten (1992).

4. Increased sinking rate during the barrier period, when current velocities and tidal amplitude continuously decreased to minimum values at the end of 1986 and the first months of 1987 (cf. Vroon, 1994). The demonstrated increased sedimentation of total suspended matter might also have comprised living organisms, zooplankton included. *Temora* abundance was rather low during 1986. Barnacle larvae, on the other hand, were more abundant than previously (Fig. 4) and notably these animals are expected to respond strongly to decreased current velocities with increased sinking, due to slower swimming movements (compared to copepods) according to their littoral character. For the copepods, an intensified vertical migration rather than increased sink-

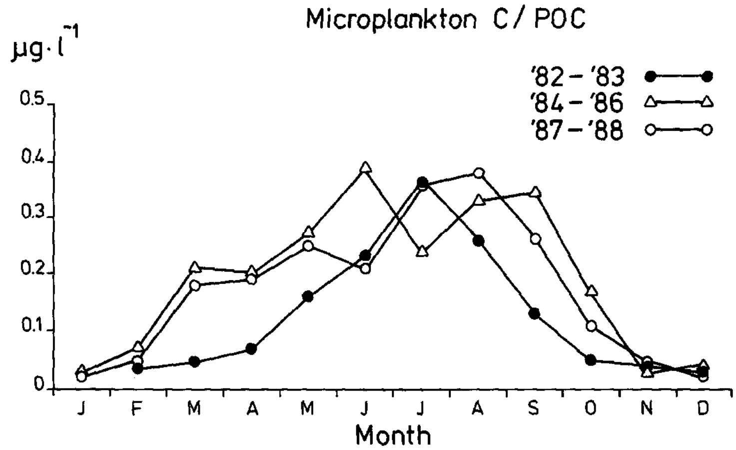

Fig. 11. The ratio microplankton carbon: particulate organic carbon in the Eastern compartment of the Oosterschelde, calculated as average monthly values during pre-barrier- (1982–83), barrier- (1984–86) and post-barrier (1987–88) periods.

ing rates might be held responsible for the smaller biomass observed, as the decreased tidal water movements were accompanied by increased transparencies (cf. Dodson, 1990).

5. *Predatory control of mesozooplankton populations by invertebrate macrozooplankton.* In the open North Sea, Daan (1989) demonstrated that predation, as a regulating factor, is only of importance when feeding conditions for the copepods are sub-optimal. In the coastal zone, however, other situations may prevail and predators like *Ctenophora* can reduce copepod population densities to a high extent (a.o. Greve, 1971; Deason & Smayda, 1982). (See further).

6. *Water temperature, especially during winter.* Influence of water temperature in zooplankton reproduction, notably of copepods, has been studied thoroughly. In our region a significant correlation was established between *Temora* fecundity and temperature in spring (Van Rijswijk *et al.*, 1989; Fransz *et al.*, 1989). Colebrook (1982, 1985) was the first to document that winter periods are often crucial for the variation between years, through differential survival of the stocks. After mild winters copepod development starts earlier and may proceed more rapidly, while after extreme winters development is strongly retarded (Fransz *et al.*, 1991). Remarkably, during the barrier period three colder winters occurred successively. Air temperature during the months January–March were 1–3 °C lower than the long-term mean (Data Dutch Meteorological Inst., unpubl.). (See further).

We assume that the effects of increased residence times, increased phytoplankton biomass and improved food quality all have influenced the zooplankton development positively during the barrier construction period. Moreover, larger volumes of Grevelingen (Fig. 1) water were discharged into the Oosterschelde in those years (Nienhuis & Smaal, 1993) and several phytoplankton- and microzooplankton organisms were introduced that found favourable conditions for development, especially in E (Bakker *et al.*, 1994; Bakker, 1994). Increased sinking rates of large phytoplankton and stronger predatory control, on the other hand, may have counteracted the favourable effects. Also the lower winter temperatures may have had negative influences. However, when we account for the strong early development of *Temora* in E in 1985 (Fig. 2), it seems that the winter effect can be neglected here and that the positive effects of food quality and -quantity prevailed.

Copepod production of resting eggs

The persistence of a neritic copepod population over successive years may depend on the ability of producing resting eggs. Overwintering eggs of *Temora longicornis* were discovered by Lindley (1986) who found that these eggs could remain viable for more than a year (Lindley, 1990). *Temora* in E probably developed autochthonous populations via increasing densities of resting eggs when exchange between the compartments decreased and retention of animals plus eggs increased. Moreover, resuspension and subsequent transport of eggs will have mainly occurred during flood, via the deeper channels in eastern direction, because the strength of the ebb current in E was reduced more strongly in barrier- and post-barrier years than the strength of the flood current (Vroon, 1994) and thus transport of eggs in seaward direction might have decreased, probably leading to accumulation of eggs in E.

Copepods (Temora) *and Ctenophora* (Pleurobrachia)

Pleurobrachia abundance in coastal embayments, at the start of its growth season, is often dependent on import (immigration) from the sea (Van der Veer & Sadée, 1984). The Oosterschelde data (Fig. 5) suggest a similar picture, cf. the W–E gradient of *Pleurobrachia* densities in the pre-barrier years.

The sudden appearance of high numbers of the comb-jellies in coastal areas is ascribed to migration of already developed populations from elsewhere (Reeve & Walter, 1978), or to massive resuspension of overwintering stages on the sea floor (De Wolf, pers. comm.). *Pleurobrachia* adopts the planktonic phase when a water temperature of *ca.* 10 °C is exceeded (De Wolf, idem) and at the same time food is present in sufficient quantities. The massive recruitment from bottom stages partly explains the patchy occurrence of *Pleurobrachia*, although many other plankton organisms show patchiness phenomena (De Wolf, 1989). Once in the water phase and in favourable food conditions, propagation of the species proceeds rapidly and in the adjacent waters of the southern North Sea the peak is generally reached in May (Greve, 1971; Van der Veer & Sadée, 1984; Kuipers *et al.*, 1990; this paper).

Fraser (1970) found 80–97% of the diet to consist of crustaceans with copepods as dominating constituent. Depletion of copepod standing stocks by Ctenophora is observed regularly (Greve, 1971; Kremer, 1976; Deason & Smayda, 1982; Frank, 1986; Suthers & Frank, 1990). However, also in coastal systems the predatory impact of *Pleurobrachia* on copepod abundance is sometimes very small (Kuipers *et al.*, 1990; Dutch Wadden Sea, 1983). Moreover, negative correlations between *Pleurobrachia*- and copepod abundance, as reported in the literature, often are not significant (Miller & Daan, 1989). But when a patchy Ctenophora distribution would coincide with a uniform copepod distribution, correlations although existing, might not be demonstrated (Suthers & Frank, 1990).

We did not find a correlation between *Pleurobrachia* maxima and copepod densities at the same time (Fig. 6), but for the W compartment there were strong indications that the height of the *Pleurobrachia* maximum was influenced by either the preceding copepod maximum, or might influence (in its turn) the following copepod maximum (Fig. 12). A choice, however, between cause and consequence cannot be made. Moreover, an exact correlation can hardly be expected as the timings of the start of both prey and predator are independent of each other (see also Kuipers *et al.*, 1990). When *Pleurobrachia* comes first and food is still lacking, mortality of the Ctenophora will be high and subsequent copepod development may be prosperous. A good example of this sequence may be the situation of W in 1988 (Fig. 2). In case of the reverse, *i.e.* when *Temora* starts first and develops rapidly, the later arriving *Pleurobrachia* finds a well provided table and may quickly graze down the copepod stock. This could have occurred in E, 1985, when after a cold winter, phytoplankton started its growth very early and *Temora* responded immediately, in spite of the lower water temperature. Afterwards, continued high abundance of *Pleurobrachia* may have caused the unusual disappearance of the copepod in May. In many cases development of predator and prey may run more or less parallel, e.g. in 1986, in both compartments; this was also observed by Kuipers *et al.* (1990). In W, *Temora* biomass of 1984 was the largest measured in this area during the entire period of observation and the combination of high densities of suitable phytoplankton (Bakker & Van Rijswijk, 1987) and low abundance of *Pleurobrachia* (Fig. 5) can be held responsible.

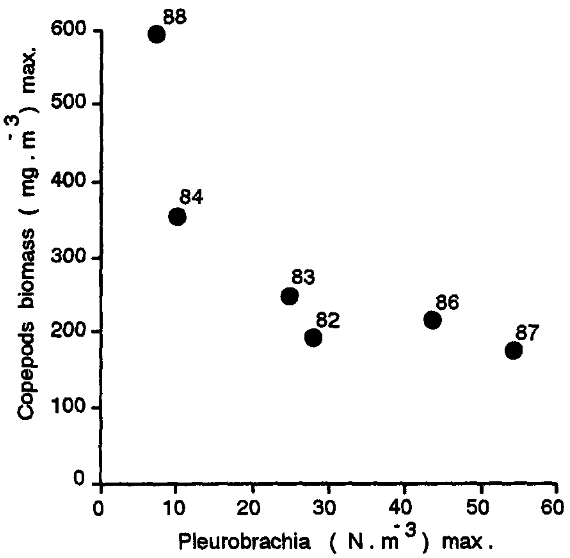

Fig. 12. Maxima (N m^{-3}) of *Pleurobrachia* and copepod biomass maxima (mg drw m^{-3}) before, during or after the *Pleurobrachia* peak in the Oosterschelde, Western compartment, 1982–1988.

The (ctenophoran) predator on *Pleurobrachia*, often causing the final decline of the latter, is

Beroe gracilis (e.g. Greve, 1971). We paid no special attention to *Beroe*, but in case this species was observed, this always occurred during the wane of *Pleurobrachia* (cf. the arrows in Fig. 5 for 1982, 1987 and 1988).

Meroplankton

Copepods use to dominate in W (to *ca* 70% of total zooplankton biomass; Bakker & Van Rijswijk, 1987; Tackx *et al.*, 1990) and benthic larvae demonstrate higher biomass values in East, as follows from the detailed comparisons of Figs 2, 3 and 4.

Generally, tidal estuaries and sea-arms show an increase of depth of the channels in seaward direction. In the Oosterschelde a large difference between the compartments exists in depth-volume ratios: average depth in W is *ca* 12 m and in E *ca* 4 m. (For the main hydrographical features cf. Vroon, 1994). Consequently, in E a relatively larger bottom surface provides a relatively small water volume with many benthic larvae, especially those of barnacles and polychaetes, while in W comparable numbers of larvae are continuously distributed over a much larger water volume. Nevertheless, the abundance of a particular group of meroplankton, the lamellibranch larvae, is still larger in W, which is due to the localization of the majority of the mussel culture plots in this (and the central) area of the sea-arm (van Stralen & Dijkema, 1994).

In coastal marine and estuarine areas suspension-feeding zoobenthos may largely control phytoplankton biomass (Cloern, 1982; Herman & Scholten, 1990). This holds also for the Oosterschelde with its dense beds of cockles and (cultivated) mussels, implying high filtering activity (Prins & Smaal, 1994; Van Stralen & Dijkema, 1994; Herman & Scholten, 1990, Van der Tol & Scholten, 1992). The increased residence times during barrier- and post-barrier years will have been responsible for a stronger retention than before of the numerous larvae released and this explains the increased biomass of lamellibranch larvae during these periods in W (Figs 3, 4). The copepods have to compete with the mussels for phytoplankton food and did not succeed to increase their biomass during these years (Figs 2, 3).

In E, however, there is virtually no mussel culture, and it was here, that the copepods (Figs 2, 3, 7, 8) as well as the non-selective (Tackx *et al.*, 1989) barnacle larvae (Figs 3, 4, 7) could profit completely from the improved food conditions. Consequently, total zooplankton biomass here increased during nearly the entire growth season of the post-barrier period (Figs 7, 8).

During the pre-barrier period, as a rule, mussel veligers were present from the beginning of April onwards (Fig. 4). After the colder winters of the barrier years, however, development of larval populations started later. In 1988 the larvae could be observed again in April. It seems therefore that the lower water temperatures in early spring retarded mussel reproduction. For barnacle reproduction, on the other hand, a retarding effect of low temperatures during spring 1985–87 could not at all be discovered: a large larval stock was already present in March, while during the same period in 1982–84 only a few larvae were found. In 1988 at the same time many larvae occurred. For barnacles, therefore, food availability seems decisive for the early development, even in case of low winter temperatures. During the pre-barrier years, when suspended matter concentration was high due to a large contribution of non-living particulate matter, barnacle larvae, contrary to copepods not able to efficient phytoplankton selection (Tackx *et al.*, 1989), did not occur in very high abundances. It seems therefore that these organisms, even more than the copepods, profited from the new situation with increased phytoplankton concentration of the seston, making selection less necessary.

Final remarks

The increased zooplankton biomass in E (post-barrier years) will exert a stronger grazing pressure on the phytoplankton. During summer phytoplankton biomass was much smaller than previously (Bakker & Vink, 1994) indeed. Beside the role of zooplankton, the increasing nutrient limitation (especially of nitrogen) can be held responsible for the phytoplankton decline in summer (Bakker & Vink, 1994).

Tackx *et al.* (1994) calculated phyto- and zooplankton biomass distributions in E during the entire period of observation. They used these data to test the model of Sheldon *et al.* (1977; predicting biomasses at higher from those at lower trophic levels) and showed that observed standing stock ratios of zooplankton to phytoplankton agreed well with the model predictions in pre-barrier- and barrier periods. In 1988, however, the model predictions became invalid because of important changes in the zooplankton, *i.e.* the increased biomass of mainly *Temora* and *Balanus* nauplii.

We concluded that the new hydrographic regime in the Oosterschelde (via reduced current velocities, increased sinking of suspended matter and increased transparencies) influenced phytoplankton composition (Bakker *et al.*, 1990; 1994), phytoplankton biomass (Bakker & Vink, 1994) and -primary production (Wetsteyn & Kromkamp, 1994) directly. Correspondingly, we hypothesize that increased retention time, increased phytoplankton biomass and improved food quality of the seston have resulted in an increase of zooplankton biomass from 1988 onwards. These phenomena were most clearly observed in E. In this area also some changes in species composition were observed (Bakker, 1994). Future research in the Oosterschelde will reveal if this new trends of the zooplankton development will persist.

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References

Bakker, C. & P. van Rijswijk, 1987. Development time and growth rate of the marine calanoid copepod *Temora longicornis* as related to food conditions in the Oosterschelde estuary (Southern North Sea). Neth. J. Sea Res. 21: 125–141.

Bakker, C., P. M. J. Herman & M. Vink, 1990. Changes in seasonal succession of phytoplankton induced by the storm-surge barrier in the Oosterschelde (SW-Netherlands). J. Plankton Res. 12: 947–972.

Bakker, C., P. M. J. Herman & M. Vink, 1994. A new trend in the development of the phytoplankton in the Oosterschelde (SW Netherlands) during and after the construction of a storm-surge barrier. Hydrobiologia 282/283: 79–100.

Bakker, C. & M. Vink, 1994. Nutrient concentrations and planktonic diatom-flagellate relations in the Oosterschelde (SW Netherlands) during and after the construction of a storm-surge barrier. Hydrobiologia 282/283: 101–116.

Bakker, C., 1994. Zooplankton species composition in the Oosterschelde (SW Netherlands) before, during and after the construction of a storm-surge barrier. Hydrobiologia 282/283: 117–126.

Cloern, J. E., 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? Mar. Ecol. Progr. Ser 9: 191–202.

Colebrook, J. M., 1982. Continuous plankton records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. J. Plankton Res. 4: 435–462.

Colebrook, J. M., 1985. Continuous plankton records: overwintering and annual fluctuations in the abundance of zooplankton. Mar. Biol. 84: 261–265.

Daan, R., 1989. Predation and cannibalism as regulating processes in North Sea copepod populations. Ph. D. Thesis Univ. Amsterdam, 62 pp.

Darboe, F. S., 1992. Comparison of the *Temora longicornis* (Copepoda Calanoida) population in pre- and post-barrier Oosterschelde, the Netherlands. M. Sc. Thesis Free Univ. Brussels, 43 pp.

Deason, E. E. & T. J. Smayda, 1982. Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. J. Plankton Res 4: 203–217.

De Wolf, P., 1989. The price of patchiness. Helgoländer Meeresunters. 43: 263–273.

Dodson, S., 1990. Predicting diel vertical migration of zooplankton. Limnol. Oceanogr. 35: 1195–1200.

Frank, K. T., 1986. Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. Can. J. Fish. aquat. Sci. 43: 211–222.

Fransz, H. G., S. R. Gonzalez & W. C. M. Klein Breteler, 1989. Fecundity as a factor controlling the seasonal population cycle in *Temora longicornis* (Copepoda, Calanoida). In J. S. Ryland & P. A. Tyler (eds), Reproduction, genetics and distributions of marine organisms. Olsen & Olsen: 83–90.

Fransz, H. G., J. M. Colebrook, J. C. Gamble & M. Krause, 1991. The zooplankton of the North Sea. N. J. Sea Res. 28: 1–52.

Fraser, J. H., 1970. The ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters. J. Cons. Int. Explor. Mer 33: 149–168.

Greve, W., 1971. Ökologische Untersuchungen an *Pleurobrachia pileus* I. Freilanduntersuchungen. Helgoländer wiss. Meeresunters. 22: 303–325.

Herman, P. M. J. & H. Scholten, 1990. Can suspension-feeders stabilise estuarine ecosystems? In M. Barnes & R. N. Gibson (eds.). Trophic Relationships in the Marine Environment, Aberdeen University press: 104–116.

King, K. R., J. T. Hollibaugh & F. Azam, 1980. Predation-prey interactions, between the larvacean *Oikopleura dioica* and bacterioplankton in enclosed water columns. Mar. Biol. 56: 49–57.

Klepper, O., 1989. A model of carbon flows in relation to macrobenthic food supply in the Oosterschelde estuary (S.W. Netherlands). Thesis, Wageningen.

Kremer, P., 1976. Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In M. Wiley (ed.), Estuarine processes I. Uses, stresses and adaptation to the estuary. New York Academic Press: 197–215.

Lindley, J. A., 1986. Dormant eggs of calanoid copepods in sea-bed sediments of the English channel and southern North Sea. J. Plankton Res. 8: 399–400.

Lindley, J. A., 1990. Distribution of overwintering calanoid copepod eggs in sea-bed sediments around Southern Britain. Mar. Biol. 104: 209–217.

Miller, R. J. & R. Daan, 1989. Planktonic predators and copepod abundance near the Dutch coast. J. Plankton Res. 11: 263–282.

Nienhuis, P. H. & A. C. Smaal, 1994. The Oosterschelde estuary, a case study of a changing ecosystem: an introduction. Hydrobiologia 282/283: 1–14.

Prins, Th. & A. Smaal, 1994. The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde estuary (The Netherlands). Hydrobiologia 282/283: 413–429.

Reeve, M. R. & M. A. Walter, 1978. Nutritional ecology of ctenophores – a review of recent research. Adv. Mar. Biol. 15: 249–287.

Sheldon, R. W., W. H. Sutcliffe & M. A. Paranjape, 1977. Structure of pelagic food chain and relationship between plankton and fish production. J. Fish. Res. Bd Can. 34: 2344–2353.

Smaal, A. C. & P. H. Nienhuis, 1992. The Eastern Scheldt (The Netherlands), from an estuary to a tidal bay: a review of responses at the ecosystem level. Neth. J. Sea Res. 30: 161–173.

Steedman, H. F., 1976 (ed.). Zooplankton fixation and preservation. The Unesco Press, Paris.

Stoecker, D. K. & D. A. Egloff, 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. J. exp. mar. Biol. Ecol. 110: 53–68.

Suthers, I. M. & K. I. Frank, 1990. Zooplankton biomass gradient off south-western Nova Scotia: nearshore ctenophore predation or hydrographic separation? J. Plankton Res. 12: 831–850.

Tackx, M. L. M., C. Bakker, J. W. Francke & M. Vink, 1989. Size- and phytoplankton selection by Oosterschelde zooplankton. Neth. J. Sea Res. 23: 35–43.

Tackx, M. L. M., C. Bakker & P. van Rijswijk, 1990. Zooplankton grazing pressure in the Oosterschelde (The Netherlands). Neth. J. Sea Res. 25: 405–415.

Tackx, M. L. M., J. W. Francke, P. Van Rijswijk, M. Vink & J. Rijk, 1991. Size distributions and trophic relationships of the pelagic ecosystem in the Oosterschelde (S.W. Netherlands). Hydrobiol. Bull. 25: 9–14.

Tackx, M. L. M., P. M. J. Herman, P. Van Rijswijk, M. Vink & C. Bakker, 1994. Plankton size distributions and trophic relations before and after the construction of the storm-surge barrier in the Oosterschelde estuary. Hydrobiologia 282/283: 145–152.

Van Rijswijk, P., C. Bakker & M. Vink, 1989. Daily fecundity of *Temora longicornis* (Copepoda, Calanoida) in the Oosterschelde estuary (SW-Netherlands). Neth. J. Sea Res. 23: 293–303.

Van Stralen, M. R. & R. Dijkema, 1994. Mussel culture in a changing environment: the effects of a coastal engineering project on mussel culture (*Mytilus edulis*) in the Oosterschelde (SW Netherlands). Hydrobiologia 282/283: 359–379.

Van der Tol, M. W. M. & H. Scholten, 1992. Response of the Eastern Scheldt ecosystem to a changing environment: functional or adaptive? Neth. J. Sea Res. 30: 175–190.

Van der Veer, H. W. & C. F. M. Sadée, 1984. Seasonal occurrence of the ctenophore *Pleurobrachia pileus* in the western Dutch Wadden Sea. Mar. Biol. 79: 219–227.

Vegter, F. & P. R. M. De Visscher, 1987. Nutrients and phytoplankton primary production in the marine tidal Oosterschelde estuary (The Netherlands). Hydrobiol. Bull. 21: 149–158.

Vroon, J., 1994. Hydrodynamic characteristics of the Oosterschelde in recent decades. Hydrobiologia 282/283: 17–27.

Wetsteyn, L. P. M. J., J. C. H. Peeters, R. N. M. Duin, F. Vegter & P. R. M. de Visscher, 1990. Phytoplankton primary production and nutrients in the Oosterschelde (The Netherlands) during the pre-barrier period 1980–1984. Hydrobiologia 195: 163–177.

Wetsteyn, P. M. J. & C. Bakker, 1991. Abiotic characteristics and phytoplankton primary production in relation to a large-scale coastal engineering project in the Oosterschelde (The Netherlands): a preliminary evaluation. In: M. Elliott & J. P. Ducrotoy (eds.). Estuaries and coasts: spatial and temporal inter-comparisons. Proc. ECSA 19 Symp., 1989. Olsen & Olsen, p. 365–373.

Wetsteyn, L. P. M. J. & J. Kromkamp, 1994. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (The Netherlands) before, during and after a large-scale coastal engineering project (1980–1990). Hydrobiologia 282/283: 61–78.