Effect of sedimentological and hydrodynamical changes in the intertidal areas of the Oosterschelde estuary (SW Netherlands) on distribution, density and biomass of five common macrobenthic species: *Spio martinensis* (Mesnil), *Hydrobia ulvae* (Pennant), *Arenicola marina* (L.), *Scoloplos armiger* (Muller) and *Bathyporeia* sp.

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Key words: Oosterschelde, tidal flats, macrozoobenthos, population dynamics

Abstract

In order to evaluate the impact of the construction of the storm-surge harrier and secondary dams on macrobenthos of the tidal fiats in the Oosterschelde (SW Netherlands), changes in distribution, density and biomass offive common species *(Spio martinensis, Hydrobia ulvae, Arenicola marina, Scoloplos armiger* and *Bathyporeia sp)* were analysed.

Data on macrobenthos were collected from 1979 to 1989 on five different tidal fiats. Changes in sediment texture and hydrodynamic factors during the construction and after the completion of the coastal engineering project were taken into account.

Three severe winters in a row caused more disturbance in the population of the main predator of *S. armiger* than did the hydrodynamical changes. A temporary prolongation of the emersion time (in 1986 and 1987) caused a temporary decrease in juvenile *A. marina.* But afterwards they still occupy the same 'nursery grounds'. Increased wave action on the edges of the flats probably created new niches for *Bathyporeia sp.* and *Spio martinensis,* replacing other benthic species.

It is not yet clear what has caused the decline of *H. ulvae* in many places in the Oosterschelde estuary. Parasitic infestation is one of the possibilities.

Introduction

The distribution, abundance and biomass of intertidal macrobenthos species are related to various environmental factors such as height in the intertidal zone (immersion time) and sediment characteristics (Wolff, 1973; Gray, 1974; Beukema, 1982; Dankers & Beukema, 1983; Forbes & Lopez, 1990; Fortuin *et al"* 1989; Hummel *et al"* 1994).

Due to the construction of the storm-surge harrier and additional dams, some environmental conditions in the Oosterschelde have changed (Nienhuis & Smaal, 1994). For some tidal flats it has been shown that the amount of silt in the upper layer has decreased (Ten Brinke *et al"*

1994) and the bottom height has changed, because of changes in erosion/sedimentation processes (Mulder & Louters, 1994).

During construction, increased wave dynamics were observed on the edges of the tidal flats and a 'washing-out' of fine sediments during storms occurred, without replacement by sedimentation, because of the low percentage of silt in the water under the new conditions (Ten Brinke *et al.*, 1994). A slow erosion of the tidal flats, resulting in a net loss of 15% intertidal area within 30 years, is the dominant process now (Smaal & Nienhuis, 1992).

Apart from the impact of the coastal engineering project, the effect of severe winters or high summer temperatures on benthic populations can be substantial (Beukema, 1979; Beukema, 1985; Dörjes, 1980; Ziegelmeier, 1964). Seys *et al.* (1994) found the observed patterns in total biomass, total density and diversity to be largely determined by the alternation of severe and mild winters.

In order to evaluate the impact of the hydrodynamic and sedimentological changes on macrobenthos of the tidal flats in the Oosterschelde a monitoring programme was executed. Three approaches have been used to treat the data. This paper deals with analysis of the population dynamics at the species level. Meire *et al.* (1994) studied the same dataset from a community viewpont and Seys *et al.* (1994) assessed trends and patterns in total density, total biomass and diversity of the benthic community.

Material and methods

Sampling stations and methods

The analysis is based on three datasets: INTERECOS, COST and VIANE.

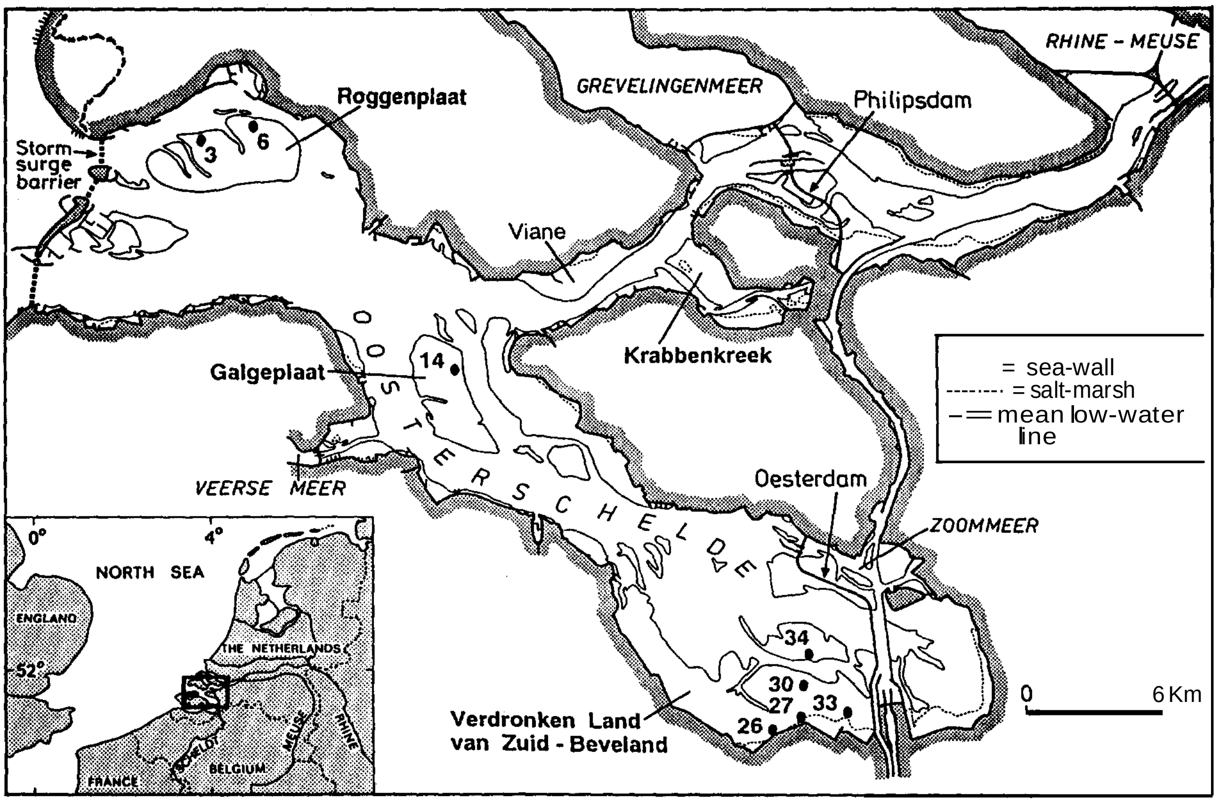


Fig. 1. Map of the Oosterschelde indicating sampling stations mentioned in the text.

The INTERECOS dataset consists of a macrozoobenthic survey in August/September 1985 (pre-harrier situation) and a similar one in 1989 (post-harrier situation) with 305 sampling stations distributed over three tidal fiats, *i.e.* in the western (Roggenplaat), central (Galgeplaat) and northern (Krabbenkreek) part of the Oosterschelde (Fig. 1). To compare the results of both years the Wilcoxon matched-pairs signed rank test (Siegel, 1956) was used. The sediment texture of the 3 large tidal fiats does show some variation in average values (Table 1). Sediments were very sandy with the fines content generally less than 5%. Roggenplaat and Galgeplaat showed little difference in percentages of silt and median grain size from 1985 to 1989. Only the Krabbenkreek shows a significant decrease in both (Table 1). The tidal elevation of the sampling sites varied between NAP (Dutch Ordnance Level) -1.6 m and NAP + 1.2 m in both years with means of NAP -0.14 m and NAP -0.24 m in 1985 and 1989 respectively. The decrease in 1989 was significant (Meire *et al.*, 1994: Table 1). The higher zones of the tidal fiats (up to NAP +0.75 m) were less silty in 1989 than in 1985 (Fig. 2).

The COST dataset comes from a monitoring programme in the period 1983-1989 based on two stations from the Roggenplaat in the west of the Oosterschelde and five at the eastern tidal fiats (Verdronken land van Zuid Beveland [Fig. 1]). Samples were initially (1983 and 1984) taken four times a year, and twice since then (1985-1989). The sediment in most of the permanent stations was silty sand with a median grain-size of 2.5-3.2 O (Seys *et al.*, 1993). Two stations higher in the intertidal zone in the east-

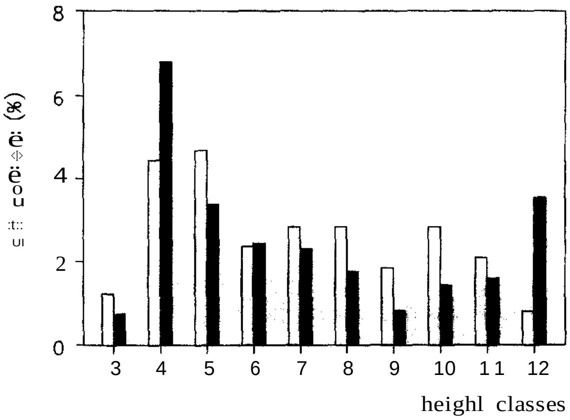


Fig. 2. Silt content in the sediment in relation to height in the intertidal zone of the tidal flats of the Oosterschelde in 1989. White bars = 1985; black bars = 1989. Height classes, legend: 3 = NAP-150 cm/NAP-125 cm; 4 = – 125/ – 100; 5 = – 100/ – 75; 6 = – 75/ – 50; 7 = – 50/ – 25; 8 = – 25/NAP; 9 = NAP/ + 25; 10 = + 25/ + 50; 11 = + 50/ + 75; 12 = + 75/ = 100.

ern part were more silty before the construction of the dams. The tidal elevation of the stations varied between NAP -0.70 and NAP + 1.1 m before the construction of the dams. In 1989 one station showed sedimentation (30 cm), three showed erosion (10-15 cm) (Seys *et al.*, 1994).

The VIANE dataset was derived from a monitoring programme (1979-1989) on 6 stations on a tidal fiat (The Slikken van Viane), situated in the northern part of the Oosterschelde (Fig. 1). Samples were taken (almost) yearly in late summer. Until 1986 the Viane stations had a higher percentage of silt (fraction < 53 µ), in the order of 5 to 10% (Seys *et al.*, 1994). In 1987 the percentage dropped to an average of 2.5 (except for station V-39). The tidal elevation of the stations

Table J. Mean values of percentage silt and median grain size of 3 intertidal areas in the Oosterschelde in 1985 and 1989 (excluding mussel plots and clay banks) {after Ten Brinke *et al.*, 1994}. * Difference 1989-1985 statistically significant according to Wikoxon signed ranks test (Siegel, 1956).

Area	% silt fraction < 53 μm				Median grain size			
	1985	1989	Diff.	Test	1985	1989	Diff.	Test
Roggenplaat	0.86	1.14	0.28		2.56	2.54	-0.02	*
Galgeplaat	1.01	0.76	-0.25	*	2.80	2.78	-0.02	
Krabbenkreek	4.47	2.86	-1.61	*	2.89	2.86	-0.03	*

varied between NAP -0.80 and NAP + 0.60 before the construction of the dams. In 1988 most stations showed erosion (10-15 cm) (Seys *et al.*, 1994).

In all the datasets, care-samples were taken and sieved on a 1 mm-mesh sieve. Numbers of animals are counted and identified and ash free dry weight (AFDW) is determined by drying, weighing, ashing and reweighing. For more details on sampling and laboratory methods see Meire *et al.* (1994), Craeymeersch *et al.* (1988) & Seys *et al.* (1993) and Meire & Dereu (1990) for the INTERECOS, COST and VIANE datasets respectively.

Results

In the Oosterschelde tidal flats, biomass and density are dominated by 10 to 15 species. Of these species very few reach mean densities above 1000 m^{-2} or mean biomass above 10 g AFDW m^{-2} (Meire *et al.*, 1994). The species in Figs 3 and 4 are the most abundant and dominant in biomass. For the purpose of this paper five species have been chosen from that list. *Cerastoderma edule* and *Mytilus edulis* are discussed in separate papers in this volume (Coosen *et al.*, 1994; Van

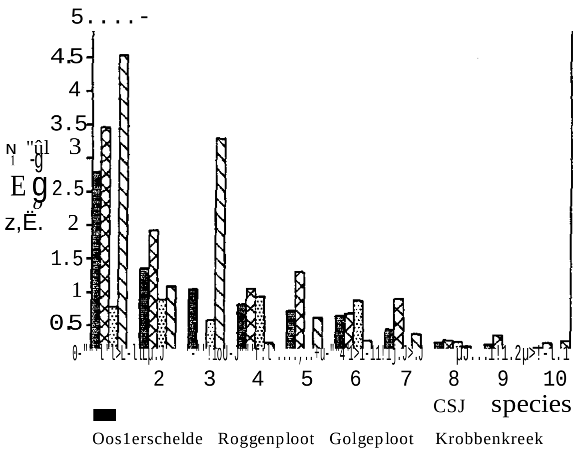


Fig. 3. Mean density of 10 most abundant species in the Oosterschelde, per area (1 = *Oligochaeta;* 2 = *Scoloplos armiger;* 3 = *Hydrobia ulvae;* 4 = *Tharyx marioni;* 5 = *Pygospio elegans;* 6 = *Spio martinensis;* 7 = *Bathyporeia pilosa;* 8 = *Cerastoderma edule;* 9 = *Capitella capitata;* 10 = *Nereis diversicolor).*

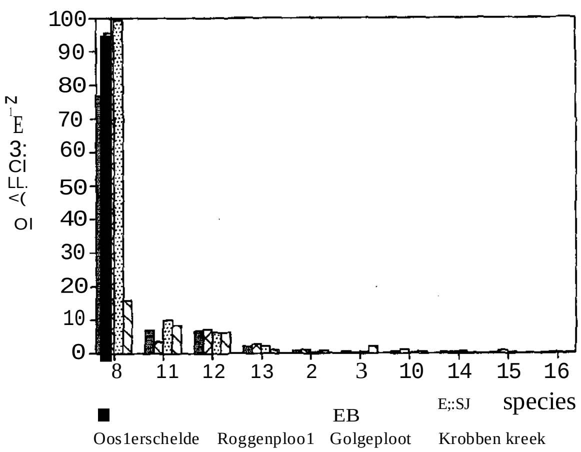


Fig. 4. Mean biomass of 10 most dominant species in the Oosterschelde, per sub-area; (2, 3, 8 & 10 = see figure 3; 11 = *Mytilus edulis;* 12 = *Arenicola marina;* 13 = *Macoma balthica;* 14 = *Nephthys hombergii;* 15 = *Lanice conchilega;* 16 = *Heteromastus filiformis.*

Stralen & Dijkema, 1994). From the group of small opportunistic polychaetes like *Pygospio, Capitella, Tharyx* and *Spio,* the last has been selected because of its remarkable density peaks in 1986 and 1989. The deposit-feeding lugworm *A. marina* is the polychaete species contributing most to the biomass. It is a very common inhabitant of the tidal flats, important as prey for wading birds and flatfish and known to have a life-cycle on different levels of the tidal flats (Reise, 1985). The herbivorous gastropod *H. ulvae* is very common on the tidal fiats and serves as food for Shelduck *(Tadorna tadorna)* and Redshank *(Tringa totanus)* and is a consumer of organic debris or the micro-organisms attached to it (Newell, 1965). Together with S. *armiger* (one of the most common species in the Oosterschelde) its distribution might be infiuenced by a change in sediments. *Bathyporeia sp"* an inhabitant of more exposed sites, can give an indication of the extent to which the new hydrodynamic properties of the Oosterschelde have infiuenced that habitat for benthic organisms.

Spio martinensis

The two INTERECOS surveys showed a remarkable increase in frequency of occurrence, mean

Table 2. INTERECOS data (number of samples, frequency of occurrence, mean density and mean biomass) of 5 species. t* = significant increase; i*significant decrease. Number of samples (1985 & 1989) Roggenplaat: 120; Galgeplaat: 110; Krabbenkreek: 75.

	Roggenplaat			Galgeplaat			Krabbenkreek		
	1985	1989	Sign	1985	1989	Sign	1985	1989	Sign
(a) *Spiu martinensis*									
Freq. of occurr. (%)	42	61		36	77		9	25	
Mean density N · m -2	150	691	î*	200	870	î*	270	430	î*
Mean bwmass g AFDW · m -2	0.02	0.114	t*	0.027	0.113	î*	0.027	0.039	
(b) *Hydrobia ulvae*									
Freq. of occurr. (%)	72	18		95	27		92	65	
Mean d.:nsity N · m -2	3550	75	i*	23000	580		17000	3000	i*
Mean biomass g AFDW · m -2	1.4	0.9	i*	4.5	4		4	2	P
(c) *Arenicola marina*									
Freq. of occurr. (%)	79	89		75	68		87	89	
Mean density N · m -2	31	30		22	15		68	41	!*
Mean biomass g AFDW · m -2	4.9	7.4	î*	3.8	6.5	i*	4.6	6.5	
(d) *Scoloplos armiger*									
Freq. of occurr. (/₀)	97	89		87	85		85	88	
Mean density N · m -2	770	1920	î*	600	900		1190	1090	
Mean biomass g AFDW · m -2	1.07	1.24		0.88	0.46		1.13	0.92	
(e) *Bathyporeia sp.*									
Freq. of occurr. (%)	52	18		44	4		31	29	
Mean density N · m -2	420	1020		140	25	!*	640	390	
Mean biomass g AFDW · m -2	0.08	0.15		0.05	0.013	i*	0.117	0.05	

biomass and mean density on all three tidal flats between 1985 and 1989 (Table 2a). Results from the permanent stations gave no evidence for a gradual pattern of increase: numbers at most permanent stations were only high in 1986 and 1989, shown for stations 3, 30 & 34 in Fig. 5.

A preference of *Spio* for sandy sediments (< 1% silt) is obvious from the INTERECOS data (Fig. 6a). The vertical distribution of *Spio*, however, has drastically changed from 1985 to 1989 (Fig. 6b). In 1985 it was most abundant in the zones below NAP, but in 1989 the higher zones were occupied too by this small polychaete.

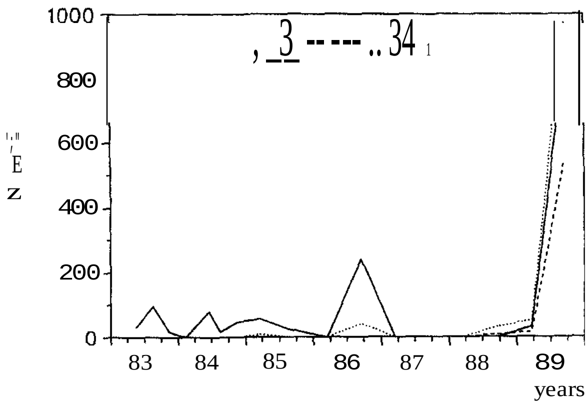
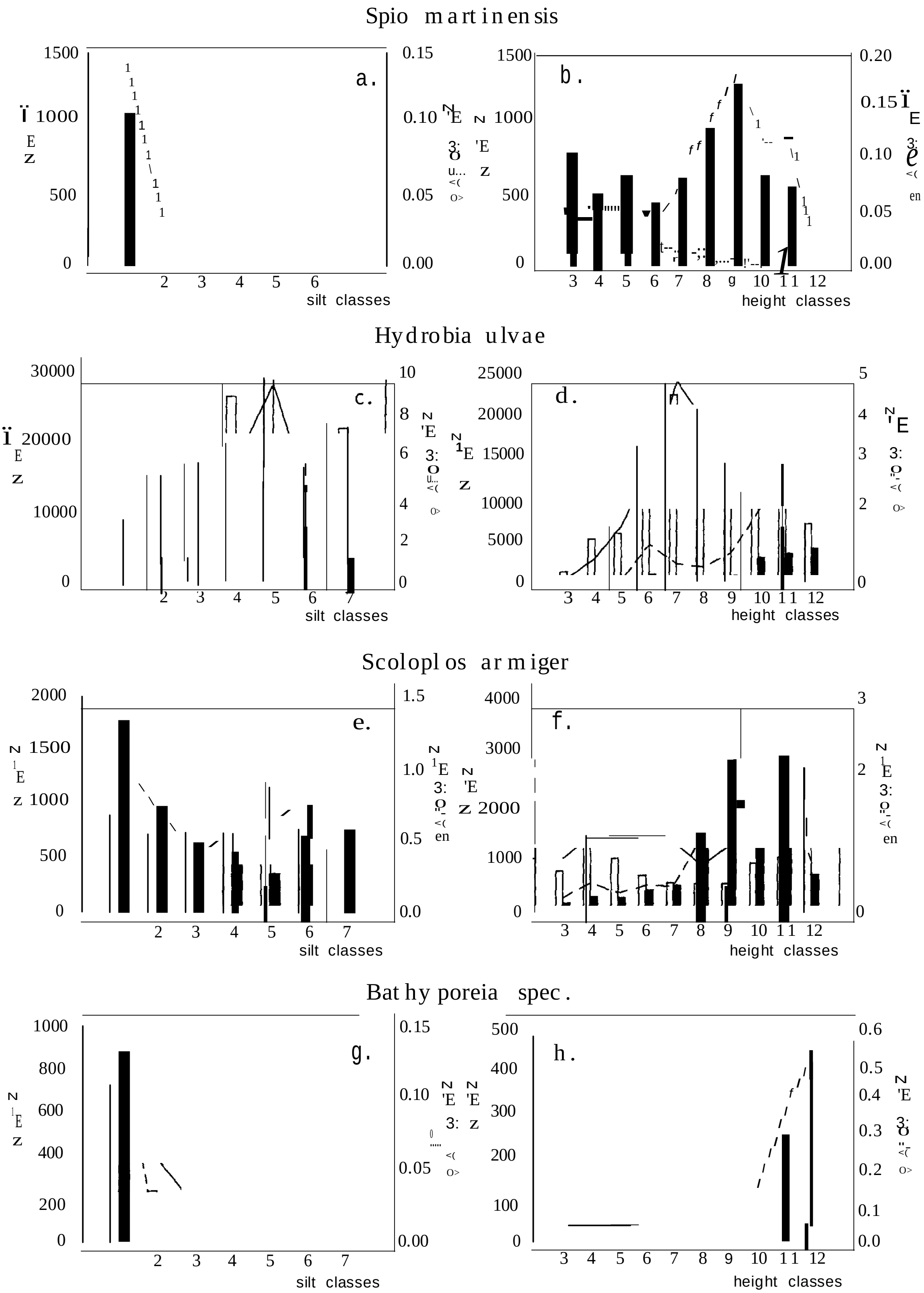


Fig. 5. Density (in N m $^{-2}$) of *Spio martinensis* at COST stations 3, 30 and 34.

Hydrobia ulvae

Comparing 1985 and 1989 (INTERECOS), frequency of occurrence, mean biomass and mean density decreased dramatically on the Roggenplaat and Galgeplaat (Table 2b), a pattem also found at most of the permanent stations there (Fig. 7a). The decrease in density and biomass occurs in all types of sediment (Fig. 6c) and in


Spio martinensis
a.
b.
silt classes
height classes
Hydrobia ulvae
c.
d.
silt classes
height classes
Scoloplos armiger
e.
f.
silt classes
height classes
Bathyporeia spec.
g.
h.
silt classes
height classes

most tidal areas (up to NAP + 0.5 m: Fig. 6d). At the Krabbenkreek the change in frequency of occurrence, mean biomass and mean density was less pronounced (Table 2b), but still significant. At the Slikken van Viane the mudsnail is dominant in the higher zones, with a distinct downward trend in biomass in station V32 (Fig. 7b). In the eastern part, the three permanent stations where *H. ulvae* is common show a mixed development in biomass variation from year to year. At two stations a seasonal pattern with low spring biomass values and higher autumn values is found during the whole period of investigation, except in autumn 1985 when low values were recorded (Fig. 7c). At the third station (34) *H. ulvae* almost disappeared from autumn 1987 onwards.

Arenicola marina

The surveys of 1985 and 1989 do not show a significant change in the distribution pattern of this species. It was present in 70 to 90% of the samples in both years (Table 2c). On the Roggenplaat mean biomass increased between 1985 and 1989, mean densities remained stable. The results from the permanent stations on the Roggenplaat (3 & 6) showed a normal seasonal pattern, with lower biomass values in spring and higher values in autumn, except in 1985 and 1988 at station 6 (Fig. 8a). Densities were fairly constant: (25-30 m^{-2}) in 1983 to 1984 and again in 1988 to 1989, but were three times as high in autumn 1985 and 1987. In the centra!part overall mean biomass values increased from 1985 to 1989 (Table 2c); densities decreased. In the eastern part of the Oosterschelde densities were higher at the higher, more silty stations (27 and 33) than in the lower stations (26, 30 and 34) (Figs 8b and 8c). The former represent typical 'nursery grounds', since autumn values were mostly high, together with low individual weights in stations 27 and 33. In contrast, individual weights in stations 30 and 34 showed higher values in autumn and numbers are fairly constant compared to stations 27 and 33.

Scoloplos armiger

The surveys of 1985 and 1989 show no significant change in the distribution pattern of S. *armiger*. The species is present in almost 90 % of the samples taken at the three tidal flats (Table 2d). Mean biomass was usually low and stayed the same, except on the Galgeplaat, where it decreased in 1989. Mean density only increased at the Roggenplaat (Table 2d).

Time series at the permanent stations show in general low numbers from 1980 to 1984, an increase in 1985 in the eastern part, followed in the western and centra! part with a peak in 1986. At most stations 1988 and 1989 showed high numbers too (Fig. 9). Biomass values usually remain around 1 g AFDW m^{-2}, hut occasionally reach 2 g AFDW m^{-2}. On the higher zone in the eastern part of the Oosterschelde (stations 27, 33 and 34) the seasonal pattern was interrupted in autumn 1986: density and biomass decreased and the species was absent until spring 1988 (Fig. 9b). S. *armiger* does not seem to have a real preference for one type of sediment (Fig. 6e), although it is slightly more abundant in less silty sediments in 1989. Data from the same survey showed that densities on the higher parts of the intertidal zones increased (Fig. 6f).

Fig. 6. Biomass and density of four species in relation to different silt classes of the sampling plots in the INTERECOS surveys of 1985 and 1989. Silt = fraction < 53 μ. Class l = S 1%; 2 = 1-2 ; 3 = 2-3%; 4 = 3-4% ; 5 = 4-5%; 6 = 5-10%; 7 = > 10 · Left vertical aids: White bars = density 1985; black bars = density 1989. Right vertical axis: solid line = biomass 1985; broken line = biomass 1989. a = *Spio martinensis;* c = *Hydrobia ulvae;* e = *Scoloplos armiger;* g = *Bathyporeia sp*. Biomass and density of four species in relation to different height classes of the sampling plots in the INTERECOS surveys of 1985 and 1989. Height classes, legend: 3 = NAP-150 cm/NAP-125 cm; 4 = – 125/ – 100; 5 = – 100/ – 75; 6 = – 75/ – 50; 7 = – 50/ – 25; 8 = – 25/NAP; 9 = NAP/ + 25; 10 = + 25/ + 50; 11 = + 50/ + 75; 12 = + 75/ + 100. Left vertical axis: White bars = density 1985; black bars = density 1989. Right vertical axis: solid line = biomass 1985; broken line = biomass 1989. b = *Spio martinensis;* d = *Hydrobia ulvae;* f = *Scoloplos armiger;* h = *Bathyporeia sp*.

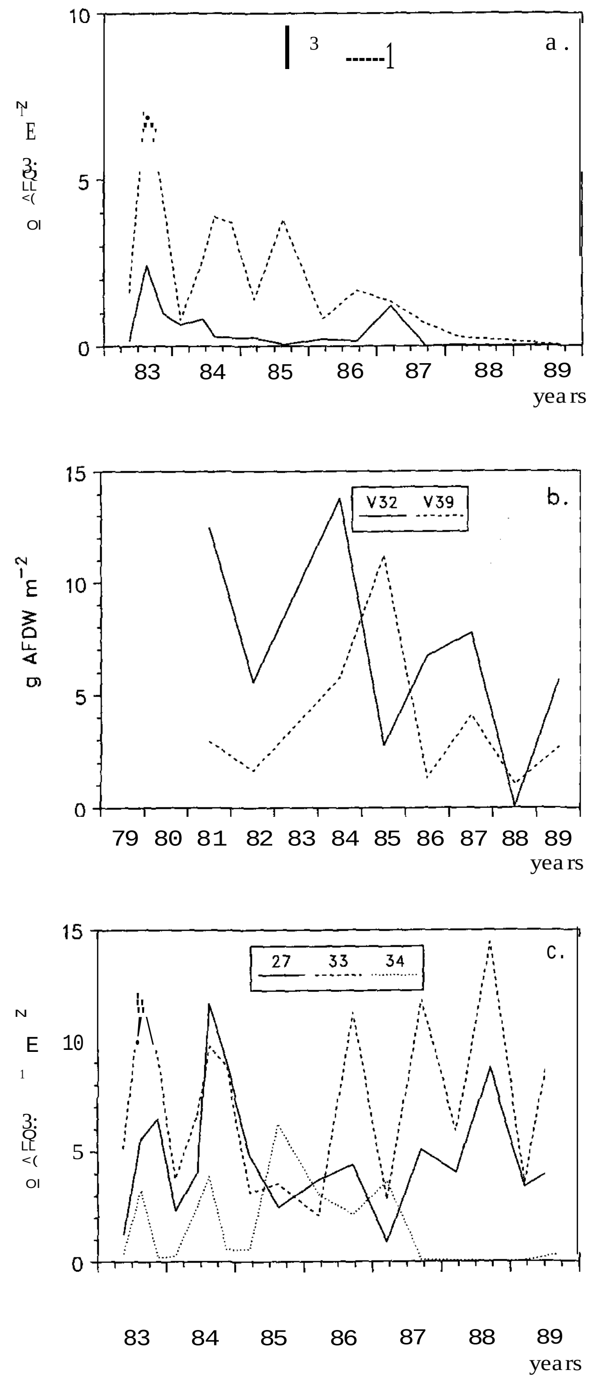


Fig. 7. Biomass (in g AFDW m $^{-2}$) of *Hydrobia ulvae* at COST stations 3 and 6 (a); at Viane stations V32 and V39 (b); at COST stations 27, 33 and 34 (c).

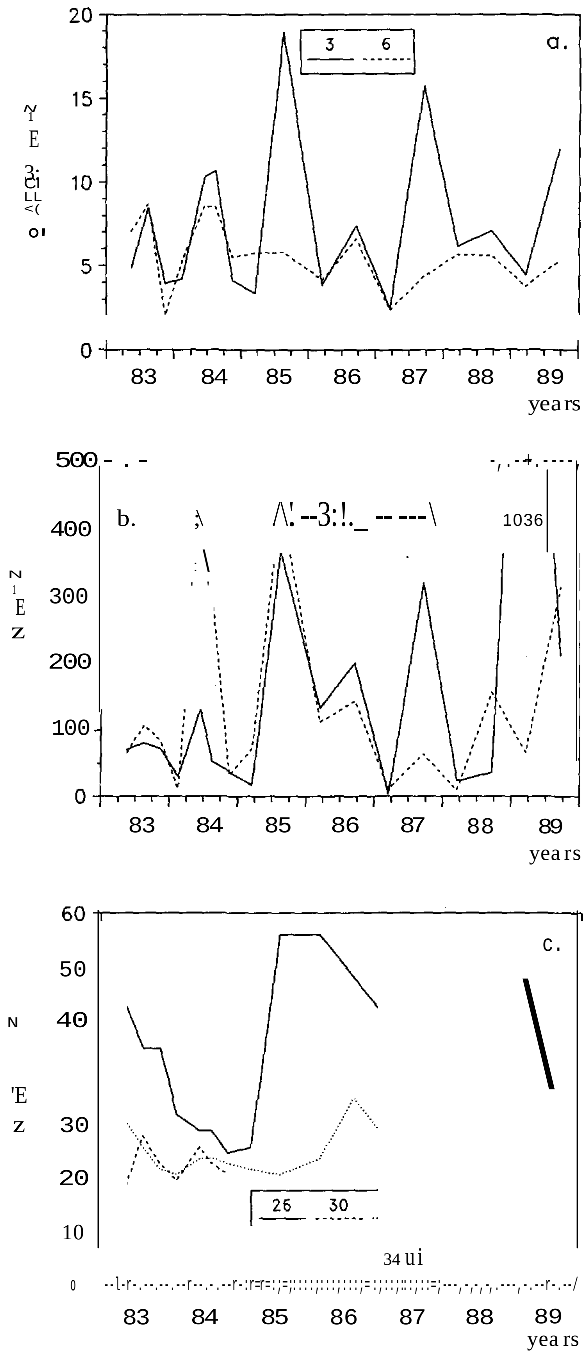


Fig. 8. Biomass (in g AFDW m $^{-2}$) of *Arenicola marina* at COST stations 3 and 6 (a); Density (in N m $^{-2}$) of *Arenicola marina* at COST stations 27 and 33 (b); at COST stations 26, 30 and 34 (c).

*Bathyporeia sp_*

The Amphipods *Bathyporeia pilosa* (Lindström) and *B. sarsi* (Watkin) are both more or less abundant on the tidal flats of the Oosterschelde. Since identification problems can arise, all animals were grouped as *Bathyporeia sp.* The survey of 1989

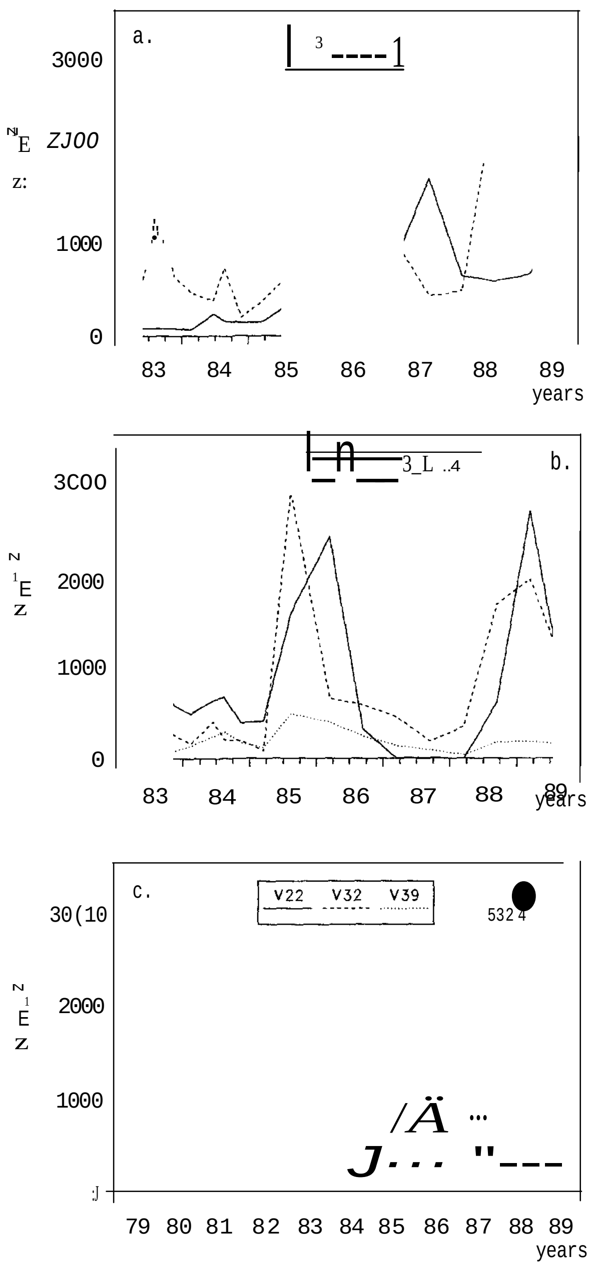


Fig. 9. Density (in N m-^{2}) of *Scoloplos armiger* at COST stations 3 and 6 (a); at COST stations 27, 33 and 34 (b); at Viane stations V22, V32 and V39 (c);

showed a negative change in the distribution pattern of *Bathyporeia sp.* on the Roggenplaat and the Galgeplaat compared with the survey of 1985. The species was present in almost 50% of the samples taken at these two tidal flats in 1985

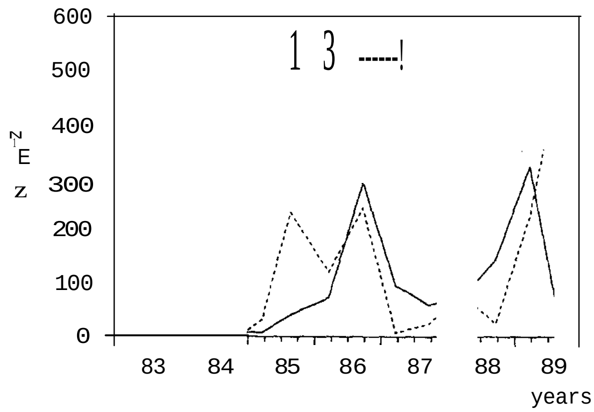


Fig. 10. Density (in N m-^{2}) of *Bathyporeia sp.* in COST stations 3 and 6.

(Table 2e). In 1989 *Bathyporeia sp.* was found in only 18% (Roggenplaat) and 4% (Galgeplaat) of the samples. In the Krabbenkreek it was still present in 30% of the samples. Mean biomass was usually very low on all three locations, not more than 0.15 g AFDW m-^{2} and mean density varies between 25 and 1000 m-^{2}. They only decreased on the Galgeplaat. The preference for sandy sediments is obvious in both years (Fig. 6g).

Overall, the change in distribution between 1985 and 1989 indicates a change of biomass and density towards the higher intertidal zones (Fig. 6h). In the permanent stations where this amphipod was found, rather low numbers were recorded in 1980-1984. Density increased temporarily in 1985-1986 and again in 1988-1989 (Fig. 10).

Discussion

Sediments and height

Ten Brinke *et al.* (1994) assume that the decrease in percentage silt and median grain size found in the Krabbenkreek is representative of all landward tidal flats (also for the Verdronken Land van Zuid Beveland). This assumption corresponds with the decrease at the higher stations 27 and 33, but not with the observations at the low lying station 30 (Seys *et al"* 1994). So, a genera! pattern of change in sediment texture is hard to give on the basis of the available data. The decrease in height between 1985 and 1989 is significant for all tidal fiats examined (Mulder & Louters, 1994). Consequently, the emersion periods for most sites have changed. Due to the reduced tidal amplitude emersion period also changed, resulting in a decrease above mid tidal level and an increase below. But overall, the range of observed emersion periods on the tidal fiats of the Oosterschelde did not change, so benthic organisms still have to deal with the same variation in exposure and submersion.

The ongoing shift of sediment from the higher to the lower intertidal parts (Mulder & Louterse, 1994) will lead to a substantial decrease in exposed total tidal fiat area during low tide.

Macrobenthos

The density-peaks of *Spio martinensis* in 1986 and 1989, especially on the higher dynamic zones of the tidal fiats, cannot both be explained as a response to the hydrodynamic changes that took place in 1986. The opportunistic life style with two to four reproductive periods in a year, together with a short life span of one year (Gudmundsson, 1985) makes an immediate reaction possible, but the factor that caused the 3-fold increase in 1989 was not of hydrodynamic nature.

Although the higher zones of the tidal fiats became less silty after the completion of the engineering works, *S. martinensis* <lid not increase immediately. The settlement in 1989 in the higher zones of *Spio* may be explained by lack of competition or predators. At the Krabbenkreek and the Galgeplaat, where the decrease in silt fraction was significant, the frequency of occurrence increased from 9 to 25% and from 36 to 77% respectively, but also on the Roggenplaat this species became more common.

The high spatial variability in density and biomass is quite common in *Hydrobia* populations. Beukema & Essink (1986) and Dörjes *et al.* (1986) found almost exclusively non-coinciding density tluctuations in the Wadden Sea; this was explained by the active migration of the species.

Four possible explanations for the decline of the mudsnail in the Oosterschelde will be discussed:

(a) hydrodynamic changes due to the engineering works;
(b) intluence of cold winters on recruitment;
(c) parasitic infestation.

(a) Since *H. ulvae* is known to favour silty sediments (Newell, 1965; Fenchel, 1975, Barnes & Greenwood, 1978), a lowering of the percentage of silt in the upper layers could be one of the reasons for the observed decline in 1989. During the higher wave impact of 1986 (Mulder & Louters, 1994) the sediment of the lower intertidal zone, including the mudsnails, could have been 'washed out'. That habitat would than be less suited to larvae of the mudsnail.

On the tidal fiats examined, the silt fraction was lower in 1989 than in 1985, but only on the Krabbenkreek were the differences in percentage silt and median grain size significant (Table 1; Ten Brinke *et al.*, 1994), compared with the temporal variability. On that intertidal fiat, the decrease in silt in the sampling stations was not correlated with the decrease in biomass of the mudsnail in the same stations (Fig. 11). Other taxa that are favoured by silty sediments, like *Heteromastus filiformis* and *O/igochaeta*, did not show any decrease from 1985 to 1989. The de-

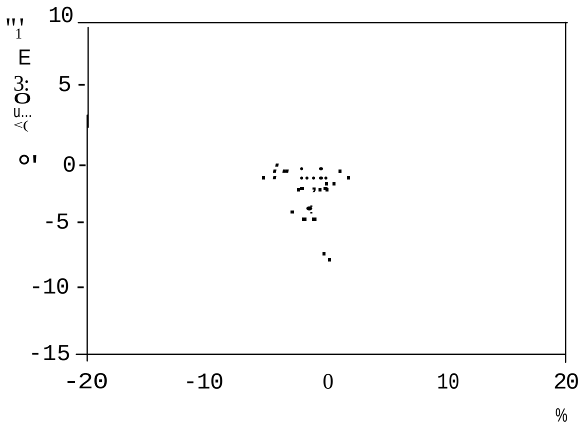


Fig. 11. Decrease/increase in biomass of *Hydrobia ulvae* in relation to decrease/increase of silt content in sediments from the Krabbenkreek (1989 *vs* 1985).

cline of *H. ulvae* is just as strong in the parts of the tidal fiats that still have a high percentage of silt (Fig. 6c).

There are more facts that refute the 'washing out'-hypothesis. If the animals are 'washed away' by hydrodynamic forces, the chance of this happening must have been greatest in the period October 1986, since at that time the storm surge harrier was closed during a severe storm. No collapse of the population (in numbers and/or biomass) was found in spring 1987, however (Fig. 7). At three of the stations (3, 6 and 34) the decrease starts in autumn 1987 and at the Slikken van Viane autumn 1988 gave the lowest values of the study period. The observed low value in spring 1987 at station 27, high in the intertidal of the eastern part of the Oosterschelde, is probably related to the preceeding period of reduced immersion times (Hummel *et al.,* 1994), because in autumn 1987 numbers were high again and biomass was back to previous levels. The higher zones of the INTERECOS surveys also showed a minimum change in biomass (Fig. 6d). The ability of *Hydrobia* to disperse easily points towards a non-hydrodynamical factor to explain the decrease in numbers and biomass on many locations, but it is possible that the permanent increased wave impact bas an effect on the settlement oflarvae on a small zone of the tidal flats.

It seems that the disappearance of *H. ulvae* did not happen in the entire Oosterschelde and where it happened it was not simultaneous.

(b) *H. ulvae* is not very sensitive to cold winters (Beukema, 1979), but it could well be that the cold winter of 1984/1985 caused a decrease in numbers of its predators *(i.e.* shore crabs), so allowing the new settlement of 1985 of *H. ulvae* to spread all over the estuary. On the other hand, warm summers can cause low egg production and hence a small recruitment (Barnes & Greenwood, 1978). The summer temperature of 1989 was indeed above normal (KNMI – weather reports). Recruitment success is one of the determining factors that govern density fluctuations. It could well be that the INTERECOS survey of 1985 coincided with a remarkable strong settlement.

The mudsnail is known for its variable pattem of strong and weak year classes (Fish & Fish, 1974, 1977). Data from the Slikken van Viane and one of the eastern stations (34) support this view, but other stations show highest numbers of juveniles in other years. Again, the dispersion of *Hydrobia* is an important phenomena explaining density differences. A comparison of the mean individual weights of the mudsnails in 1985 and 1989 (Table 3) indicates smaller specimens in 1985. The observed biomasses (including shell) in 1985 (0.20 to 0.45 mg AFDW) suggest a strong dominance of 0 -year individuals, if compared with the weights found by Wolff & de Wolf (1977) in the former Grevelingen estuary. Dekker (1979) also found comparable weights (0.20-0.60 mg AFDW) in the Western Dutch Wadden Sea.

(c) Parasitic infestation.

H. ulvae is an important intermediate host for several trematodes (Kinne, 1980; Rothschild, 1936; Ankel, 1962; Morrisey, 1990; Jensen & Mouritsen, 1992). Infestation rates can vary from place to place, from only a few individuals to over 90% of the population (Kinne, 1980). There are no data on parasitic infestation of *H. ulvae* in the Oosterschelde. At several stations, however, high individual weights were recorded in 1987 to 1989. This may point to infestation. The destruction of the gonads results in changes in physiological and hormonal mechanisms, causing the specimens to grow bigger than normal (gigantism) and make them sterile. A mortality of 40% in the Danish Wadden Sea in 1990 was attributed to infestation with trematodes. High temperatures were suggested as a triggering factor for the mass development of the trematodes in *Hydrobia* (Jensen & Mouritsen, 1992).

Table 3. Mean individual biomass (mg AFDW, including shell) of *H. ulvae* on three tidal flats in the Oosterschelde in 1985 and 1989.

Tidal flats	1985	1989
Roggenplaat	0.45	1.14
Galgeplaat	0.20	1.06
Krabbenkreek	0.23	0.73

The conclusion must be, with Barnes (1988), that population limiting factors and their differential effects on juveniles and adults are still contentious or unknown. The occurrence of a strong year class in 1985, coinciding with different factors that caused a decline in the population at many places, does not allow a proper assessment of the impact of the engineering works.

Living rather deep in the sediment, the adult *Arenicola marina* is not very sensitive to hydrodynamic disturbances. lts ecological amplitude is broad, but very soft sediments are not favoured, certainly not by adults (De Wilde & Farke, 1981). Severe winters have no infiuence on the size of the population (Dörjes *et al.*, 1986; Beukema, 1982). Large density fiuctuations from year to year do not occur (Reise, 1985; Beukema, 1982), presumably because the number of juveniles that settles between the adults is limited by the number of adults (Farke & Berghuis, 1979). Only on typical juvenile settlement places ('nursery fiats') on the higher shore do large numbers occur. The developments of *A. marina* in the Oosterschelde over the period 1983-1989 do not deviate from studies elsewhere. Only on the higher zones, juvenile settlement was interrupted in the period of reduced tidal amplitude.

Longbottom (1970) has shown that the abundance of *A. marina* can be correlated with the abundance of organic matter in the sediment. The changes in fine sediment content that occurred on some places did not infiuence its distribution on the Oosterschelde, however.

Scoloplos armiger is widespread in subtidal and intertidal areas in all sorts of sediments (Wolff, 1973), but particulary common in fine to muddy sands (Gibbs, 1968). The increase in numbers and biomass from 1985 onwards occurred in other coastal areas too, such as the Wadden Sea (Beukema & Essink, 1986). This indicates that the development in the Oosterschelde is probably not caused by local environmental changes, hut by larger scale events such as weather or climate. *S. armiger* is a northern species, not very sensitive to severe winter temperatures (Beukema, 1989), whereas one of its major predators *Nephtys hombergii* is then subject to a high mortality (Beukema, 1987). In the permanent plots *N. hombergii* declined sharply between 1984-1987 (severe winters 1984-1985, 1985-1986 and 1986-1987). Recolonisation did not start until 1989 (Seys *et al"* 1994). Moreover, although *S. armiger* is known to be sensitive to langer exposure times (Fortuin *et al"* 1989) and it is therefore not likely to occur at the highest intertidal level (Schöttler & Grieshaben, 1988), it was most abundant in 1989 in the higher zones (Fig. 6f). At the same time *N. hombergii* became re-established higher on the tidal fiats (Fig. 12). This is an indication that the pattern of distribution of *S. armiger* in the Oosterschelde is temporally and spatially (under the normal immersion regime) infiuenced by the occurrence of the predator *N. hombergii*.

B. pilosa and *B. sarsi* live in the upper layers of unstable, sandy tidal fiats (<2 % silt content, median grain size 150-220 μ; Kharyallah & Jones, 1980). There they find enough water movement (oxygen supply) and the sediment structure that enables them to dig and feed in their typical way (Nicolaisen & Kanneworff, 1969).

The tempora! density pattern of *Bathyporeia sp.* in the Oosterschelde is neither related to severe winter temperatures (1984-1985 to '86-'87), nor to manipulations of the storm surge harrier

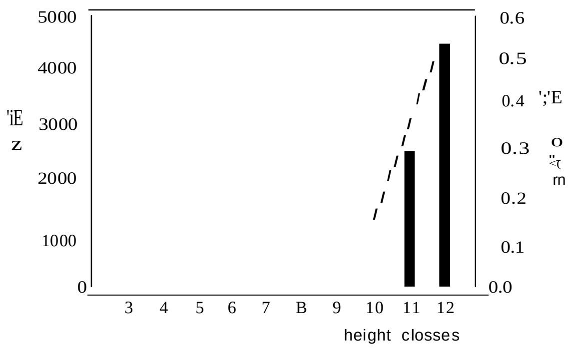


Fig. 12. Biomass and density of *Nephthys spec.* in relation to different height classes of the sampling plots in the INTER-ECOS surveys of 1985 and 1989. legenda: 3 = NAP-150 cm/ NAP-125 cm; 4 = −125/−100; 5 = −100/−75; 6 = −75/ −50; 7 = −50/−25; 8 = −25/NAP; 9 = NAP/+25; 10 = +25/+50; 11 = +50/+75; 12 = +75/+100. Left vertical axis: White bars = density 1985; black bars = density 1989. Right vertical axis: solid line = biomass 1985; broken line = biomass 1989.

(1986-1987). However, the shift towards higher tidal levels on a spatial scale and the increase in density and biomass at the Roggenplaat indicate that local changes in hydrodynamics may play a role. Nicolaisen & Kanneworff (1983) found rather large seasonal and year to year variations in absolute and relative numbers in a Danish coastal area, and they mention water movement as one of the most important environmental factors for the distribution of the species. In the Westerschelde *Bathyporeia sp.* is one of the most common species of the high dynamic sand flats (Ysebaert & Meire, 1991). In the Oosterschelde current velocities decreased on average by 33% (Ten Brinke *et al.*, 1994) while in a limited range (NAP + 50 cm to NAP + 100 cm) of the tidal area the impact of wave-stress increased (Mulder & Louters, 1994). This range is just the range where *Bathyporeia sp.* is still present in high or even higher densities.

Conclusions

Various fiuctuations in the distribution, density and biomass of some common species of the tidal fiats have been observed before, during and after the construction and presence of the storm-surge harrier and secondary dams, but only little of that variation could be explained by the changes in hydrodynamic factors or sediment characteristics. It seems to be restricted to a tempora!decline in numbers on the higher zones of the flats during the period ofreduced immersion (1986-1987). Tidal conditions and sediment variation are still of the same order as before, but the current velocities are lower in many places. The effect of the new hydrodynamica! conditions on transport and settlement of pelagic larvae was not studied. It is however unlikely that the mechanica! properties of the sediment have altered in such a way that the growth of juveniles is restricted. Transport of food to the bottom may be affected on the long run. The erosion process of the tidal flats may eventually cause a shift in benthic communities: further observations on a large scale of all benthic organisms can give answers to the many questions that still remain.

Acknowledgements

We wish to thank A. van den Dool, J. Dereu, E. C. Stikvoort, E. Brummelhuis and E. Wessel who assisted in the sampling, the determination and the recording of the data. J. Buijs and E. C. Stikvoort carefully handled the data and prepared the figures. We would also like to thank R. H. D. Lambeck for his helpful comments on the draft. Communication No. 699 of NIOO-CEMO, Yerseke, The Netherlands.

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