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Changes in the sublittoral hard substrate communities in the Oosterschelde estuary (SW Netherlands), caused by changes in the environmental parameters

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Abstract

In order to assess the effects of the execution of the Delta Project, the sessile sublittoral communities on hard substrates in the Oosterschelde estuary and the environmental parameters were quantitatively investigated from 1985 till 1990. During the construction period of the barrier, three communities were sampled in the photic zone and four in the aphotic zone. The distribution of the communities in the photic zone seemed to be determined by the exposition to water movement and depth, while the communities in the aphotic zone were restricted to geographic areas, with differences in tidal current velocities: the mouth of the estuary, the Hammen, the central part and the Zijpe. Two years after the completion of the enclosure works, the community structure changed rapidly, caused by decreases of tidal current velocities, increases of the amounts of sedimentation, especially of fine sediments, and an increase of the transparency of the water. Changes within the associated vagile animals showed the same tendency as the sessile communities: under less exposed conditions the number of organisms remained the same or increased, while at some locations this increase was nullified by increasing amounts of sedimentation.

Introduction

Recently a growing interest is shown in the use of the structure of sublittoral benthic communities on hard substrate for ecological monitoring. Partly this interest was stimulated by the development of SCUBA techniques, which enables marine biologists to survey the communities in their natural habitat and partly because of the increasing acceptance of the importance of the benthic hard substrate communities for the entire ecosystem. Even on the artificial rocky shores in the Oosterschelde estuary, benthic hard substrate organisms stand for 32.7% of the total benthic

biomass (Leewis & Waardenburg, 1989). To use these hard substrate communities for ecological monitoring, a reproducible description of both communities and environmental parameters should be available. Because of this reproducibility, the communities should be studied as a whole, including both floral and faunal components, and, if possible, the associated vagile fauna as well. Secondly, the data must be quantified as much as possible. A regulation model for sublittoral communities by the environmental parameters is proposed by De Kluijver (1989). However, testing these models brings forth a problem, because most studies contributing to the development of

these models were carried out in stable marine environments (e.g., De Kluijver, 1991), wherein it is difficult to assess the impact of the individual environmental parameters. The large scale engineering works in the southern Delta area (SW Netherlands) provide a unique situation in which it is possible to follow the effects of changing parameters.

The engineering works in the Oosterschelde estuary were completed in 1987. The effects of the construction of the storm-surge barrier in the mouth of the estuary and of two compartmentalisation dams in the eastern part on the marine environment are revealed by Wetsteyn *et al.* (1990) and Nienhuis & Smaal (1994). Before the completion of the Delta works, the sublittoral communities were studied by Leewis & Waardenburg (1989; 1990) and De Kluijver (1989). To evaluate the effects of the engineering works,

the quantitative data of De Kluijver (1989) were used.

Material and methods

During the years of 1985 and 1986 (construction period) 79 stations were investigated along the dikes of the southern Delta area (De Kluijver, 1989). During the post-barrier period (1987–1990) another 175 stations were investigated in the same area. The locations of the stations are shown in Fig. 1.

The communities were sampled using quadrats, in which the percentages of coverage in vertical projection of all sessile macro-organisms were estimated. At each station a minimal sampling area (Weinberg, 1978) of 31 dm², as determined in the construction period, was sampled. Vagile organisms, which are able to move around,

Fig. 1. Map of the study area showing the sampled locations (dots) and the four different regions found in the construction period: M (mouth), H (Hammen), C (central part) and Z (Zijpe).

were scored qualitatively within the stations, but were not used for cluster analysis. Cluster analysis was carried out using the computer program CLUSTAN1 C2 (Wishart, 1978), with logarithmically transformed data. The average-linkage method (Sokal & Michener, 1958) was used in combination with the Bray-Curtis coefficient. With the results of the normal analysis an inverse analysis was performed, which procures information concerning the species composition of the clusters. With the program SRTORD (Kaandorp, 1986) the distribution of the quantities of the species over the clusters was calculated. Characteristic species were distinguished at a concentration level of 90% within a community. To be distinguished as dominant or characteristic species, the species had to be present in at least 67% of the stations in the community concerned. Characteristic species were restricted to just one community, while dominant species were abundant (5% percentage cover or more) and occurred in more communities. The communities, here defined as assemblages of species which inhabit a specific set of environmental parameters and remain stable in time and space, consist of different structural layers. In the studied area a distinguishable top layer (TL) of thalli of large brown algae of the genera *Laminaria* and *Sargassum* may be developed. A middle layer (ML) is formed by organisms growing erect from the substrate, but which do not reach the canopy of the top layer. Also epiphytic and epizoid organisms belong to this layer. The encrusting layer (EL) consists of organisms totally adhering to the substrate, e.g., algae and bryozoans. As a result of the changing environmental parameters, the assemblages of species changed in such a way that either new communities could be distinguished or the assemblages could be regarded as a variant of an existing community. The difference between a community and its modified variant is frequently related to the abundance of species.

The most important environmental parameters were measured.

- Depth was referred to NAP, the Dutch Ordinance Level, which approximately corresponds

to mean sea level. The tidal difference increases towards the east. In the central part, during the construction period, it reached 3.5 m at spring-tide.

- The submarine daylight was measured using a relative 'Underwater Hemispherical Irradiance Meter' (UHIM). The spectral sensitivity of this meter (peak value 480 nm; band-width 60 nm) roughly corresponds to the transmission characteristics of the water. By these measurements, the vertical extinction coefficient (k in m^{-1}) was calculated.
- The exposure of the communities to water movement was determined using erosion of gypsum blocks and the composition of the bottom sediments. The erosion of the gypsum blocks is expressed as the weight loss (g h^{-1}) during one lunar day (24.45 hours). The erosion values obtained in the construction period were statistically tested on the current velocities measured by the Tidal Waters Division (current velocities (in cm s^{-1}) = 806.1, erosion values (g h^{-1}) = 41.5; correlation coefficient = 0.99). Sediment characteristics were determined using 7 graded sieves (2.8–0.053 mm). The characteristics were expressed as the proportional contribution of the dry weights of the different sieved fractions.
- The potential sedimentation in the communities was measured using sediment traps. Simple cylinders were used with an inner diameter of 11.7 cm and a length to diameter ratio of 5:1. Sedimentation was expressed in $\text{g m}^{-2} \text{d}^{-1}$ dry weight, measured over one month.
- Temperature was measured using a modified mercury thermometer.

During 1988 and 1989 monthly colonization and succession experiments were carried out on artificial concrete substrates at two locations in the mouth and in the eastern part of the estuary.

Results

Based on the distribution of the sublittoral communities during the construction period (De Kluijver, 1989; Leewis & Waardenburg, 1989;

Fig. 2. Simplified dendrogram resulting from the cluster analysis of the data collected during 1985–1990. The communities and variants distinguished are marked on the horizontal axis (explanation see text).

1990), the Oosterschelde estuary was divided into four different regions (Fig. 1). A simplified dendrogram of the 254 sampled stations during 1985–1990 is shown in Fig. 2. The communities restricted to the photic zone are marked Aa1 through Ac. These communities are dominated by algae in the middle structural layer. The communities restricted to the aphotic zone are marked M, H, C or Z, corresponding with the main distribution in the regions of Fig. 1. Communities distributed within more regions of the eastern part of the estuary are marked C as well.

Communities restricted to the photic zone

The photic zone is the depth zone in which the communities are dominated by foliose algae in the middle structural layer. In addition to this, a top layer of thalli of large brown algae of the genera *Laminaria* and *Sargassum* and an encrusting layer of red algae may be developed. This zone extends from the tidemark during the lowest water during spring tide to depths where 10% of the surface light intensity is available (measured by 480 nm). In the construction period (1985–1986) three dif-

ferent communities were found in the Oosterschelde estuary (Figs 3, 4, 5 & 6). Dominant species, which were present in at least 67% of the

Fig. 3. Distribution of the communities in the photic zone of the mouth of the Oosterschelde estuary. On the x-axis the different years are shown (1985–1990), on the y-axis the relative richness of all sessile species present in at least 67% of the stations and on the z-axis the proportional contribution of the communities per year (length of axis is 100%).

Fig. 4. Distribution of the communities in the photic zone of the Hammen. For an example see Fig. 3.

Fig. 5. Distribution of the communities in the photic zone of the central part. For an explanation see Fig. 3.

stations of one of the communities, are listed in Table 1.

Community Aa1 was found in all four regions, between 2 and 3.5 m minus NAP. The middle structural layer of this community was dominated by the red algae *Ceramium rubrum*, *Phyllophora pseudoceranoides* and *Polysiphonia nigrescens* and the brown alga *Dictyota dichotoma* and the tenuous form of the green alga *Codium fragile*. The

Fig. 6. Distribution of the communities in the photic zone of the Zijpe. For an explanation see Fig. 3.

bryozoan *Electra pilosa* was found epiphytic within this structural layer. The top layer was mainly formed by *Sargassum muticum* and sporadically by *Laminaria saccharina*. An encrusting layer, formed by *Phymatolithon lenormandi*, was hardly developed.

Community Aa2 was found at exposed locations in the Hammen and the central part, between 2.7 and 3.5 m minus NAP. The community possessed a well developed canopy of *Laminaria saccharina*. The middle structural layer was dominated by the red algae *Ceramium rubrum*, *Phyllophora pseudoceranoides*, *Polysiphonia nigrescens* and *Gracilaria verrucosa* and the tunicate *Styela clava*. Like in community Aa1, *Electra pilosa* was found epiphytic again on these algae.

Community Aa3 was also sampled in the Hammen and in the central part, between 2.7 and 4.0 m minus NAP. A top layer was not developed within this community. The middle structural layer was, besides the red alga *Hypoglossum woodwardii*, dominated by heterotrophic elements from the aphotic zone (e.g., the tunicate *Styela clava*, the anthozoan *Diadumene cincta*, the sponge *Haliclondria panicea* and barnacles). The bryozoan *Electra pilosa* is found epiphytic and epizoic on the other species.

During the first two years of the post-barrier

Table 1. Percentage coverage of the dominant species in the communities in the photic zone. Species which are found in at least 67% of the stations of one community are marked with an asterisk.

Community	Aa1	Aa2	Aa3	Ab1	Ab2	Ab3	Ab4	Ac
<i>Antithamnion plumula</i> (Ellis) Thur. in Le Jolis	1.7*	–	0.1	1.1*	0.3*	13.3*	–	3.3*
<i>Ceramium rubrum</i> (Huds.) C. Ag.	15.2*	35.0*	2.4*	15.6*	14.1*	–	2.4*	–
<i>Dumontia contorta</i> (Gmel.) Rupr.	0.1	–	–	–	0.1	–	8.6*	–
<i>Gracilaria verrucosa</i> (Huds.) Papenf.	0.1	5.8*	0.1	0.3	–	–	–	–
<i>Hypoglossum woodwardii</i> Kützting	4.4*	4.4*	6.7*	2.0*	0.7*	0.7*	–	0.6
<i>Phyllophora pseudoceranoides</i> (Gmel.) N. et T.	4.6*	28.7*	0.3*	16.5*	0.7*	0.7*	17.5*	–
<i>Polysiphonia nigrescens</i> (Huds.) Grev.	13.0*	4.6*	2.5*	7.1*	17.5*	1.3*	4.2*	1.0
<i>Dictyota dichotoma</i> (Huds.) Lamour.	7.4*	–	–	6.8*	0.2	1.3*	0.1	–
TL- <i>Laminaria saccharina</i> (L.) Lamour.	0.1	14.7*	–	–	–	–	–	–
<i>Bryopsis hypnoides</i> Lamour.	0.6	0.4	0.7	3.1*	–	22.7*	0.3*	1.4
<i>Bryopsis plumosa</i> (Huds.) C. Ag.	2.3*	0.5	0.1	1.1	–	7.3*	0.7*	0.2*
<i>Codium fragile</i> (tenuos) Hariot	5.1*	1.9*	0.6*	0.4	–	–	–	–
<i>Ulva lactuca</i> L.	1.2*	1.0*	0.4	5.6*	11.6*	–	11.5*	0.6
<i>Diadumene cincta</i> Stephenson	0.9*	1.6*	8.8	0.7*	0.2	5.0*	0.2*	0.1
<i>Styela clava</i> Herdman	3.2	4.8*	5.1*	0.3	–	–	–	3.7*
<i>Halichondria panicea</i> (Pallas)	0.7	2.4*	7.7	0.1	0.1	–	–	–
<i>Electra pilosa</i> (L.)	7.9*	16.3*	11.4*	7.2*	1.0*	1.0*	0.6*	0.3
<i>Crassostrea gigas</i> (Thunberg)	2.9	–	0.1	4.4	0.2	28.7*	7.7*	32.5*
<i>Cirripedia</i>	2.8*	2.5*	8.3*	0.3	2.7	–	5.4	1.6*
Bare substrate	28.2	31.7	29.1	40.0	53.3	28.3	30.9	29.2
Number of stations	12	3	4	11	2	1	2	2
Number of sessile species	69	43	44	57	34	25	33	35
Number of vagile species	13	7	5	23	4	2	5	5

period (1987–1988) no changes in the community structure were noticeable. Communities Aa1 and Aa2 showed the same distribution pattern.

After 1988 the species composition of the communities changed quickly, the Aa communities were no longer sampled, instead a new community (Ac) and a number of variants (Ab) of community Aa1 were found. Many species strongly decreased in percentage cover (e.g., the sponge *Halichondria panicea*, the bryozoan *Electra pilosa* and the hydrozoans *Sertularia cupressina* and *Calicella syringa*), while other species, characteristic for the tideless Lake Grevelingen communities (see de Kluijver, 1989), became more abundant (e.g., the sponge *Halichondria bowerbanki*, the tunicates *Botryllus schlosseri* and *Asciidiella aspersa* and the algae *Bryopsis hypnoides*, *Dumontia contorta* and *Callithamnion byssoides*).

Variant Ab1 was found in the Hammen and the central part, between 1.7 and 3.1 m minus NAP. This variant is dominated by the same algae as in

community Aa1 and the green alga *Ulva lactuca*. The main difference between Aa1 and Ab1 is a reduction in species richness of 17% and an increase of 42% silt covered substrate.

Variant Ab2 was found in the mouth of the estuary, between 1.7 and 1.9 m minus NAP. This variant is dominated by the red algae *Polysiphonia nigrescens* and *Ceramium rubrum* and the green alga *Ulva lactuca*. The variant must be regarded as a further decline of variant Ab1. Species richness, compared to variant Ab1, is reduced 40% and the silt covered substrate is increased with 33%, up to 53% of the total available hard substrate surface.

Variant Ab3 was found in the Hammen at 3.7 m minus NAP. The middle structural layer was dominated by the algae *Bryopsis hypnoides*, *Bryopsis plumosa*, *Antithamnion plumula*, the anthozoan *Diadumene cincta* and the bivalve *Crassostrea gigas*.

Variant Ab4 was found in the Hammen and the

Fig. 7. Distribution of the communities in the aphotic zone of the mouth of the Oosterschelde estuary. For an explanation see Fig. 3.

central part at 1.8 m minus NAP. The middle structural layer is dominated by the algae *Ulva lactuca*, *Phyllophora pseudoceranoides*, *Dumontia contorta*, the bivalve *Crassostrea gigas* and by barnacles. Species composition indicates that this variant must be considered as an impoverished derivative of community Aa1.

Community Ac was found in the Zijpe at 3.9 m minus NAP. Algae were not dominant in the middle structural layer, but this layer was totally dominated by the bivalve *Crassostrea gigas*. Besides many algae with low percentage covers, this layer consists of many animals which are characteristic for the tideless Lake Grevelingen (e.g., the tunicates *Ascidia aspersa*, *Botryllus schlosseri* and *Ciona intestinalis*, the sponge *Haliclona xena* and scyphistomae of the jelly-fish *Aurelia aurita*).

Communities restricted to the aphotic zone

The aphotic zone is the depth zone which is limited by a 10% illumination boundary and extends to depths where no hard substrate is available. A top layer is absent in these communities and an encrusting layer may consist of bryozoans. The communities consist of heterotrophic animals, independent of the available light. In the construction period four different communities were found.

During the construction period of the barrier, in the mouth of the estuary especially community M1 was abundant (Fig. 7). The middle layer of this community was dominated by the anthozoan *Metridium senile* and the sponge *Halichondria panicea* (Table 2). During this period two variants of community M1 were found. In addition to the dominant species of community M1, variant M3 was also dominated by the polychaete *Lanice conchilega*. Most of the substrate was covered with a thick layer of sediment. Variant M2 was totally dominated by the anthozoan *Metridium senile* and compared to community M1 the species richness was decreased by 35%.

In the Hammen, during the construction period, community H1 was abundant (Fig. 8). This community was dominated by the sponge *Halichondria panicea*, the anthozoan *Diadumene cincta* and the hydrozoan *Halecium halecinum* (Table 3). Near its eastern boundary, community C1 was

Table 2. Percentage coverage of the dominant species in the communities in the mouth of the estuary in the aphotic zone. For explanation see Table 1.

Community	M1	M2	M3	M4	M5	M6
<i>Diadumene cincta</i> Stephenson	3.5*	0.5*	—	6.2*	9.7*	0.2
<i>Metridium senile</i> (L.)	43.2*	45.0*	21.0*	0.3*	51.7*	60.5*
<i>Ciona celata</i> Grant	1.3	—	—	—	5.3*	—
<i>Halichondria panicea</i> (Pallas)	12.0*	0.8*	16.8*	—	—	1.8
<i>Lanice conchilega</i> (Pallas)	0.1	—	13.5*	—	—	—
Bare substrate	33.6	49.4	41.3	85.0	40.0	36.5
Number of stations	36	7	1	1	1	5
Number of sessile species	28	18	21	19	10	10
Number of vagile species	27	13	7	8	3	9

Fig. 8. Distribution of the communities in the aphotic zone of the Hammen. For an explanation see Fig. 3.

sampled in 1985 and in 1986 community C3 was found, which became common in the post-barrier period.

In the central part community C1 was common (Fig. 9). The middle structural layer was dominated by the anthozoan *Diadumene cincta*, the tunicate *Styela clava* and the sponges *Halichondria panicea* and *Haliclona oculata* (Table 4). *Electra pilosa* was found epizoic. Other variants of community C1, sampled in this period were C2 and C3, both becoming more important during the post-barrier period.

Fig. 9. Distribution of the communities in the aphotic zone of the central part. For an explanation see Fig. 3.

In the Zijpe only community Z1 was sampled during the construction period (Fig. 10). The middle structural layer was dominated by the bi-valve *Crassostrea gigas*, the tunicate *Styela clava*, the anthozoan *Diadumene cincta* and the sponges *Halichondria panicea* and *Haliclona oculata* (Table 5).

During the first two years of the post-barrier period (1987–1988), changes in community structure were of minor importance, comparable with the photic zone.

In the mouth of the estuary 80% of the sampled stations still belonged to community M1, while

Table 3. Percentage coverage of the dominant species in the communities in the Hammen in the aphotic zone. For explanation see Table 1.

Community	H1	C1	C3	H2	C4	C5
<i>Haliclona oculata</i> (Pallas)	2.7*	5.1*	2.9*	0.9*	1.1*	0.6
<i>Diadumene cincta</i> Stephenson	14.2*	15.1*	12.2*	29.6*	11.0*	14.4*
<i>Ciona intestinalis</i> (L.)	2.7	0.1	1.3*	0.4	5.6*	1.1*
<i>Styela clava</i> Herdman	2.7*	13.0*	7.3*	1.9*	3.3*	2.2
<i>Halichondria panicea</i> (Pallas)	33.3*	7.2*	5.9*	7.2*	3.4*	2.5*
<i>Electra pilosa</i> (L.)	1.0*	14.8*	0.7*	0.6*	0.5*	0.6*
<i>Eudendrium</i> spec. Ehrenberg	0.3	0.1	0.5	5.4*	0.2	—
<i>Halecium halecinum</i> (L.)	4.9*	1.6	4.7*	6.9*	1.1	0.1
<i>Crassostrea gigas</i> (Thunberg)	—	—	0.1	0.7	9.9*	4.8*
Bare substrate	32.6	30.2	34.1	34.8	41.8	59.2
Number of stations	21	8	12	7	18	2
Number of sessile species	29	43	56	37	37	24
Number of vagile species	23	7	23	20	26	7

Table 4. Percentage coverage of the dominant species in the communities in the central part in the aphotic zone. For explanation see Table 1.

Community	C1	C2	C3	C4	C5	C6
<i>Haliclona oculata</i> (Pallas)	5.1*	5.2*	2.9*	1.1*	0.6	0.1
<i>Diadumene cincta</i> Stephenson	15.1*	26.6*	12.2*	11.0*	14.4*	2.5*
<i>Styela clava</i> Herdman	13.0*	16.2*	7.3*	3.3*	2.2	1.6*
<i>Ostrea edulis</i> L.	0.1	2.4*	2.6*	1.8	—	7.7
<i>Ciona intestinalis</i> (L.)	0.1	0.2	1.3*	5.6*	1.1*	6.8*
Cirripedia	2.2*	6.6*	2.2*	0.5*	—	—
<i>Halichondria panicea</i> (Pallas)	7.2*	14.2*	5.9*	3.4*	2.5*	0.2
<i>Electra pilosa</i> (L.)	14.8*	2.6*	0.7*	0.5*	0.6*	0.6*
<i>Crassostrea gigas</i> (Thunberg)	—	2.5*	0.1	9.9*	4.8*	0.1
Bare substrate	30.2	23.5	34.1	41.8	59.2	70.0
Number of stations	8	12	12	18	2	2
Number of sessile species	43	33	56	37	24	27
Number of vagile species	7	18	23	26	7	6

Fig. 10. Distribution of the communities in the aphotic zone of the Zijpe. For an explanation see Fig. 3.

the other stations belonged to variant M6. This variant displayed an even higher dominance of the anthozoan *Metridium senile* than variant M2 and species richness had decreased another 44%.

In the Hammen community H1 remained dominant, but in 1988 variants C3 and H2 were sampled, especially H2 became important later in the post-barrier period.

In the central part variants C2 and C3 became more important. Variant C2 was dominated by the anthozoan *Diadumene cincta*, the tunicate *Styela clava*, barnacles and the sponges *Halichondria panicea* and *Haliclona oculata*. Compared to community C1 the species richness decreased

Table 5. Percentage coverage of the dominant species in the communities in the Zijpe in the aphotic zone. For an explanation see Table 1.

Community	Z1	C4
<i>Haliclona oculata</i> (Pallas)	5.6*	1.1*
<i>Diadumene cincta</i> Stephenson	10.9*	11.0*
<i>Styela clava</i> Herdman	15.3*	3.3*
<i>Ciona intestinalis</i> (L.)	0.1	5.6*
<i>Halichondria panicea</i> (Pallas)	15.7*	3.4*
<i>Crassostrea gigas</i> (Thunberg)	28.2*	9.9*
Bare substrate	21.4	41.8
Number of stations	7	18
Number of sessile species	29	37
Number of vagile species	10	26

with 23%. Variant C3 was dominated by the anthozoan *Diadumene cincta*, the tunicate *Styela clava* and the sponge *Halichondria panicea*. Besides these species, the middle structural layer consisted of many floral elements general in the photic zone (e.g., the algae *Griffithsia devoniensis*, *Polysiphonia nigra*, *Ceramium deslongchampsii*, *Dictyota dichotoma* and *Callithamnion byssoides*). In the western part community H1 was sampled and in 1988 variant C4 was sampled.

In the Zijpe, only community Z1 was sampled during the years of 1987 and 1988.

After 1988 the species composition of the com-

munities changed quickly. In the mouth of the estuary community M1 was mainly found at greater depths, while at shallow places the variants M2, M4, M5 and M6 were found.

Variant M5 was dominated by the anthozoans *Metridium senile* and *Diadumene cincta* and the sponge *Cliona celata*. Variant M4 was dominated by *Diadumene cincta* while *Metridium senile* became sparse. In both variants the sponge *Halichondria panicea* was totally absent.

In the Hammen, community H1 was found only once, mostly this community was replaced by variant H2. Compared to community H1, the percentage cover of *Diadumene cincta* had doubled, while the cover of *Halichondria panicea* had strongly decreased. The hydrozoans *Halecium halecinum* and *Eudendrium* spec. were dominant. Other variants sampled in this period were C3, C4 and C5. Variant C5 was dominated by *Diadumene cincta* and the bivalve *Crassostrea gigas*. This variant had the lowest species richness of all variants in the eastern part. In the western part of the Hammen, at the bottom of the tideway, community M1 was sampled.

In the central part variant C3 was still found in 1989. In 1990 only the variants C4, C5 and C6 were sampled. In addition to *Diadumene cincta*, variant C4 was dominated by the tunicate *Ciona intestinalis* and the bivalve *Crassostrea gigas*. Variant C6 was dominated by *Ciona intestinalis* and the bivalve *Ostrea edulis*.

In the Zijpe community Z1 was totally replaced by the variant C4, caused by strong decreases in the percentage covers of the tunicate *Styela clava*, the sponges *Halichondria panicea* and *Haliclona oculata* and the bivalve *Crassostrea gigas*.

The numbers of vagile species found in the different communities are listed in Tables 1, 2, 3, 4 and 5.

In the photic zone the shore crab *Carcinus maenas* was common during both construction and post-barrier period. The starfish *Asterias rubens*, the crustacean *Caprella linearis* and the seaspider *Pycnogonum littorale* were especially common during the construction period, while the brittlestar *Ophiotrix fragilis*, the velvet swimming crab *Necora puber*, the mollusc *Crepidula fornicata* and

the black goby *Gobius niger* were more common during the post-barrier period. With the exception of variant Ab1, all variants in the post-barrier period accommodated less vagile animals than the variants in the construction period did.

The same holds for the variants in the apothic zone in the mouth of the estuary. *Ophiotrix fragilis* and *Necora puber* became more common during the post-barrier period, while nudibranchs (e.g., *Janolus cristatus*, *Dendronotus frondosus* and *Aeolidia papillosa*) became rare in this period. In the Hammen the number of vagile species did not change during both periods. In most variants *Caprella linearis*, *Asterias rubens* and the crustacean *Pagurus bernhardus* were common, but *Ophiotrix fragilis*, *Necora puber*, *Gobius niger*, and the crustacean *Macropodia* spec. became more abundant in the post-barrier period. In the central part the number of vagile species slightly increased. *Asterias rubens*, *Ophiotrix fragilis*, *Pagurus bernhardus*, *Macropodia* spec. and *Necora puber* became more common in the post-barrier period, while *Caprella linearis*, *Carcinus maenas* and nudibranchs became less abundant. In the Zijpe the number of vagile species strongly increased during the post-barrier period. *Asterias rubens* and *Carcinus maenas* were common in both periods, while *Ophiotrix fragilis*, *Pagurus bernhardus*, *Macropodia* spec., *Crepidula fornicata* and *Necora puber* became more abundant in the post-barrier period and the abundance of *Caprella linearis* and *Homarus gammarus* declined.

Environmental parameters

Changes in the sublittoral environment are connected to human activities in the southern Delta area. Since the start of the execution of the Delta Project, the Oosterschelde estuary became isolated from river influences and from adjoining estuaries (Nienhuis & Smaal, 1994). The successive operations gradually changed the water exchange with the North Sea, the mean velocity of the tidal currents and the fresh-water load of the estuary, which led to changes in the other environmental parameters (e.g., submarine daylight,

Table 6. Comparison of environmental parameters in the construction- and post-barrier period. Erosion values marked with asterisk are obtained through extrapolation of data of Tidal Waters Division. Sediment characteristics are given of bottom sediments, sampled at 10 m minus NAP, particle size given in mm.

	mouth	Hammen	central part	Zijpe	Grevelingen
Construction period:					
Erosion value (g h^{-1})*	0.17	0.17	0.14	0.20	—
k (in m^{-1})	0.78	0.57	0.57	—	—
Sediment characteristics	0.30–0.15	0.15–0.09	0.15–0.09	0.30–0.15	—
Post-barrier period:					
Erosion value (g h^{-1})	0.13	0.12	0.11	0.08	0.07
k (in m^{-1})	0.52	0.45	0.40	0.39	0.32
Sediment load ($\text{g m}^{-2} \text{ day}^{-1}$)	430–3130	270–1450	230–760	30–1150	10–1160
Sediment characteristics	0.15–0.09	< 0.09	< 0.09	0.15–0.09	0.30–0.09

sediment load and sediment characteristics). In Table 6 the changes of the most important environmental parameters are summarized.

Although the current velocities had already changed during the construction period, the data obtained using gypsum blocks corresponded with the flow velocities given by Wetsteyn *et al.* (1990): maximum current velocities were found in the mouth of the estuary, in the Hammen and in the Zijpe and less severe conditions were found in the central part. In the post-barrier period a decrease of 31% was found in the mouth of the estuary and a diminution of 25% in the central part (Wetsteyn *et al.*, 1990). Due to the construction of the Philipsdam, the current velocity in the Zijpe decreased even more, comparable to values measured in tideless water basins. Within the estuary, a periodicity in current velocities existed, with maximum current velocities in autumn and minimal values during winter. This periodicity is also displayed by the sedimentation and composition of the bottom sediments (Fig. 11).

All through 1980–84, turbidity was measured by Wetsteyn *et al.* (1990) using a Secchi disc and different energy cells. The highest vertical extinction coefficients (k in m^{-1}) were measured during autumn and winter, the lowest during spring and summer. During 1986–90, the UHIM was used only during spring and summer. During the construction period the highest values were measured in the western part of the estuary and lower values in the central and eastern parts. In the post-

barrier period the vertical extinction coefficient decreased in the whole estuary, but shortterm fluctuations became larger, especially in the western part.

At shallow locations, the particle size of the deposited material in the construction period was characterized by a dominance of silt and clay fractions (< 0.05 mm). At most deeper locations in the tidal channels in the mouth of the estuary and in the Zijpe, the sediments were dominated by the sand fraction between 0.3–0.15 mm, and in the Hammen and the central part the sediments were dominated by the fine-grained sand fraction (0.15–0.05 mm). Since 1988 an increase of the smaller fractions took place. In the mouth of the estuary, the original sand fraction was found below 15 m minus NAP, while at most shallow places fine-grained sand, silt and clay were dominant. The Hammen was totally dominated by the fine-grained sand, silt and clay fractions. In the central part and in the Zijpe the sediments were dominated by the fine-grained sand fraction, but silt and clay fractions started to become more dominant. The already noted periodicity in current velocities was also found in the particle size (Fig. 11).

The disturbance of the estuary is most clearly shown by the sediment load. The gradient in sediment load ranges from west to east from 430–3130 till 30–1150 $\text{g m}^{-2} \text{ d}^{-1}$ dry weight, while the gradient in erosion values ranges from 0.07–0.20 until 0.06–0.14 g h^{-1} . The variation in sedi-

Fig. 11. Environmental parameters in the mouth of the estuary at the location Plompetoren, 4.5 m minus NAP, during the post-barrier period. The upper graph shows the potential sedimentation ($\text{g m}^{-2} \text{d}^{-1}$) and the input of *Ophiotrix fragilis* (shaded). Underneath the composition of the bottom sediments is given. Type V is dominated by the 0.3–0.15 mm fraction, type VI by 0.15–0.09 mm fractions, VII by 0.09–0.05 mm fractions and type VIII is dominated by fractions ≤ 0.05 mm. The next graph shows the total amount of water movement (EV. in g h^{-1}). The bottom graph shows the water temperature (T in $^{\circ}\text{C}$).

ment load was mainly caused by the periodicity of the current velocities (Fig. 11). Periods with strong sedimentation, coincided with periods with strong and weak water movement, with maximal sedimentation during weak tidal currents. Compared to periods with weak tidal currents, coarse-grained sediments were deposited during strong tidal currents. The contradiction between current velocities and sedimentation was partly caused by the reduction of the tidal volume in relation to the cross section of the different regions and partly by the supply of sediments (see Mulder & Louters, 1994). Sand import from the North Sea has been measured to be $1.10^6 \text{ m}^3 \text{ y}^{-1}$, while the total sediment deficit is calculated to the amount of $400\text{--}600 \cdot 10^6 \text{ m}^3$ (Kohsiek *et al.*, 1987). A deficit of 40% of this amount exists in the mouth of the estuary, leading to bottom sediments characterized by sand fractions. The fine-grained sand, clay and silt fractions, deposited in areas with weak current velocities, probably originated from the erosion of tidal flats.

Temperature displayed a gradient in the Oosterschelde estuary. In the period 1988–1990 the temperature in the mouth of the estuary (measured at 4.5 m minus NAP) ranged between 5.5°C and 20.5°C . In the same period in the Zijpe (measured at 6.0 m minus NAP) temperature reached higher values during summer (21.0°C) and lower values during winter (4.5°C).

Discussion

The three sublittoral communities in the photic zone, found during the construction period (1985–1986), did not change during the first two years of the post-barrier period (1987–1988). Community Aa1 was common in all regions, while community Aa2 was found under exposed conditions. Measurements, using gypsum blocks during south-west winds, showed erosion values between 0.10 and 0.12 g h^{-1} for community Aa1 and 0.25 g h^{-1} for community Aa2. At deeper places community Aa3 occurred. When, after 1988, the species composition of these commu-

nities changed, the algal composition was unaffected in variants Ab1, Ab2 and Ab4. On the other hand, some of the faunal components, especially sponges, hydrozoans and bryozoans, suddenly disappeared. Only the bivalve *Crassostrea gigas* became more abundant in the variants Ab3 and Ab4 and community Ac. In variant Ab3 algae and the in community Ac faunal components characteristic for the tideless Lake Grevelingen, became more abundant.

It is not likely that changes in current velocities are directly responsible for the changes in community Aa1, because this community was found in all regions on both north and south shores of the estuary. The strength of the water movement in the photic zone is strongly dependent on the geographical position relative to prevailing winds. It is unlikely as well, that these changes are caused by predation or grazing activities of the vagile associated fauna. Except in variant Ab1, the number of vagile organisms found in the Ab-variants was less than found within the Aa-communities.

The decrease of sessile species richness was probably caused by the increased amounts of fine-grained sediments on the substrate. Especially sponges (e.g., *Prosuberites epiphytium* and *Halichondria panicea*), hydrozoans and bryozoans seem to be sensitive to strong sedimentation. The increase of elements characteristic for the tideless Lake Grevelingen, in variant Ab3 and community Ac, is probably a direct result of decreasing current velocities. The tunicates (*Ciona intestinalis*, *Botryllus schlosseri* and *Asciidiella aspersa*) are characteristic for other sheltered environments in the North Sea (De Kluijver, 1991).

Although the most important changes in the communities in the aphotic zone took place after 1988, since 1985 (construction period) minor changes in species composition were already detectable. Initially, community M1 dominated the mouth of the estuary, H1 the Hammen, C1 and partly C2 the central part and Z1 the Zijpe. In all these communities the sponge *Halichondria panicea* was dominant. In the mouth of the estuary *Metridium senile* was a dominant species, while in

all communities eastwards *Diadumene cincta* was dominant. A dominant species in the Hammen community was the hydrozoan *Halecium halecium*. The tunicate *Styela clava* was dominant in both central part and the Zijpe. The difference between C1 and C2 was a domination of *Electra pilosa* and *Lanice conchilega* in community C1, and barnacles besides *Haliclona oculata* in variant C2. The community Z1 in the Zijpe was further dominated by *Crassostrea gigas* and *Haliclona oculata*. The species richness (only those species were considered which were present in at least 67% of the stations of a community) in this initial stage was 28 species in the mouth of the estuary, 29 in the Hammen, 43 in the central part and 29 in the Zijpe (Tables 2, 3, 4 and 5). In 1986 variant M2 was sampled in the mouth of the estuary. This variant, only dominated by *Metridium senile*, showed a low species diversity (species richness = 18). In the Hammen and the central part, community C3 was found (species richness = 56), which consisted, besides the dominant species of H1, of many algae general in the photic zone. The penetration of algae into the aphotic zone is only possible in case of a lower vertical extinction coefficient in the Hammen and central part. In preceding studies it was found that algal dominance stopped at a depth of a 10% illumination level (De Kluijver, 1989, 1991).

In 1987, shortly after completion of the compartmentalization dams, variant M6 was found in the mouth of the estuary, mainly dominated by *Metridium senile* (species richness = 10). In the other regions the same communities were found as during the construction period. In 1988 a new community in the Hammen (H2) was sampled. Compared to H1 *Eudendrium* spec. also became dominant and the species richness increased to 37. In the central part, variant C4 was found dominated by *Diadumene cincta*, *Ciona intestinalis* and *Crassostrea gigas* (species richness = 37).

In 1989 in the mouth of the estuary 50% of the sampled stations belonged to the derivative variants of community M1, variant C4 was found eastwards, in the Hammen, the central part and in the Zijpe. In the Zijpe, it totally replaced the existing community Z1. In 1990 in the mouth of

the estuary mainly variants were found, dominated by *Metridium senile* or *Diadumene cincta* or both. In the Hammen, mainly H2 was found, dominated by *Diadumene cincta*, *Halichondria panicea*, *Halecium halecinum* and *Eudendrium spec.*. In the central part and the Zijpe, mainly variant C4 was found, dominated by *Diadumene cincta*, *Ciona intestinalis* and *Crassostrea gigas*.

In the construction period the mouth of the estuary was an exposed environment with a residence time of 10 tides. In the post-barrier period, tidal currents decreased with 30% and the tidal residence increased 100% (Wetsteyn *et al.*, 1990). At shallow places (<15 m) the increased sedimentation fragmented the original M1 community into derivative variants. The bottom sediments in the new variants were dominated by fractions <0.15 mm (broken line in Fig. 12). At greater depths (>15 m), community M1 was still found, but variant M2 was abundant as well. The bottom sediments were dominated by the sand fraction (0.3–0.15 mm). Colonization experiments during 1988 and 1989 showed that settlement mainly occurred in the period from April till September. Species colonizing artificial substrates in the shallow aphotic zone were barnacles, the anthozoan *Sagartia troglodytes* and the bivalve *Mytilus edulis*. The dominant *Metridium senile*, only colonized new substrates by asexual reproduction and migration. Under these stress

conditions (high sedimentation and strong tidal currents) it is not likely that other species are able to establish themselves at shallow places in this region. Furthermore most of the hard substrates are covered with thick layers of sediment. Whether community M1 is able to maintain itself at greater depths, will depend on the particle size of deposited sediments and the availability of hard substrates at greater depths.

In the Hammen, the central part and the Zijpe, a heterogeneous community will remain for a longer period, dominated by *Diadumene cincta* and *Crassostrea gigas*, with local differences: hydrozoans and bryozoans especially in the western part and tunicates in the central and eastern part. Colonization experiments in the Zijpe already showed the settlement of the tunicates *Botryllus schlosseri*, *Asciidiella aspersa* and *Ciona intestinalis*. Compared to the initial communities in the Hammen and the Zijpe, this community has a higher species richness but remains the same in the central part. In the post-barrier period tidal currents are less severe and thus potentially more species are able to settle, but increased sedimentation, of especially the fine-grained silt and clay fractions, prevents many species from doing so. Species, like *Halichondria bowerbanki*, which can survive sedimentation (Vethaak *et al.*, 1982) will become more abundant in this community.

It is remarkable that changes in most commu-

Fig. 12. Depth distribution of community M1 (squares), variant M2 (triangles) and the other M variants (diamonds) in the mouth of the estuary during the consecutive years. Black symbols indicate a dominance of the sand fractions (0.15–0.3 mm) in the bottom sediment. Open symbols indicate a dominance of fractions ≤ 0.15 mm.

nities after completion of the Delta Project occur with a considerable time-lag. This is also found in the total biomass (Leewis *et al.*, 1994). As already stated, three executive parameters were responsible for these changes: 1) the decrease of the vertical extinction coefficient, which enabled some algae to penetrate into the aphotic zone; 2) the decrease of tidal current velocities, which enabled other species, not adapted to extreme conditions, to settle in the mouth of the estuary, the Hammen and the Zijpe; 3) the increase of sedimentation, which prevented settlement and survival of species in certain regions.

Due to the execution of the Delta Project, parameter 3 was already effective in 1985, covering hard substrates in the mouth of the estuary, including the benthic communities, with a thick layer of sediment (see variant M3). Parameter 1 expressed itself in 1986, showing some algae to penetrate into the aphotic zone (see variant C3). In 1989 parameters 2 and 3 cooperated, causing a deterioration of sessile animals in both photic and aphotic zone and the introduction of new species into the eastern part of the Oosterschelde estuary. It took the communities two years to react on the most important changes (2 and 3). Partly this might be explained by the slow response of a biological system. Colonization is only possible during a short period of the year (April-September) and the existing community must deliver possibilities for the settlement of new species. On the other hand it is possible that it took some time for the redistribution of the fine-grained sediments to reach a lethal effect on the species which have disappeared.

The distribution of vagile animals does not indicate any regulation by these organisms. Together with the richness of sessile organisms in the photic zone and aphotic zone in the mouth of the estuary, the richness in vagile organisms decreased. In the central part species richness remained the same and in the Hammen and Zijpe richness increased. The increase in abundance of *Ophiotrix fragilis*, *Necora puber* and *Macropodia* spec. is caused by mild winters since 1987. In Fig. 12 the increase of *Ophiotrix fragilis* during summertimes is clearly visible. The increases in

abundance of *Crepidula fornicata* and *Gobius niger* are caused by the decrease of tidal current velocities. These species were characteristic for the tideless Lake Grevelingen. The increase of the *Ophiotrix fragilis* population is not responsible for the changes in the benthic communities, because the new variants were already established before the brittlestar reached its maximum density. Furthermore, this kind of population explosions occurred frequently in the past, without lasting changes in benthic community structure. The role of vagile organisms in the regulation of the community structure is probably negligible in the southern Delta area, and it is likely that their distribution is also determined by the environmental parameters (L.A.M. Aerts, pers. comm.).

Conclusions

The sublittoral hard substrate communities of the southern Delta area are mainly governed by the environmental parameters. After the completion of the Delta Project in 1987, these environmental parameters changed and subsequently the communities changed dramatically. A number of executive parameters caused changes in the communities in the photic and aphotic zone:

- A decrease of tidal volume of 30%, leading to decreases of tidal current velocities, enabled species, not adapted to extreme tidal currents, to colonize other regions. Examples are some algae and tunicates which were characteristic for the tideless Lake Grevelingen, but became dominant in the post-barrier period in some communities in the Oosterschelde estuary.
- The decrease of tidal volume also disturbed the relation between the cross section of the tideways and tidal currents in the different regions, causing a sediment deficit within the Oosterschelde estuary. Increased sedimentation and a redistribution of the sediments caused a deterioration of some animals, while other organisms came in a more favourable position.
- A decrease of the vertical extinction coefficient

enabled some algae to penetrate into the aphotic zone.

After a time-lag of two years the seven initial communities changed rapidly. In the photic zone, some faunal elements disappeared, while elements characteristic for the tideless Lake Grevelingen, became dominant. The net result of the changes was a decrease in species richness. Correlated with increased sedimentation, the original community in the aphotic zone in the mouth of the estuary, fragmented into a number of derivated variants, all with a low species richness. In the three regions eastwards a new variant is in development. In the Hammen and in the Zijpe species richness increases, correlated with a severe decrease of tidal current velocities, while in the central part the species richness remains equal or decreases.

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