

The macrozoobenthos of an important wintering area of the common scoter (*Melanitta nigra*)

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In October 1994, 39 macrobenthic samples, divided between two areas, were taken on the western Belgian Coastal Banks. The two areas could not be clearly divided, concerning their macrobenthic communities. Multivariate techniques revealed five coherent communities, linked with typical sedimentological factors: (1) the *Barnea candida* community in a very compact muddy sediment (median 14 μm); (2) a second community characterized by the presence of spat of *Mytilus edulis*, with a medium sandy sediment (median 456 μm); (3) the *Lanice conchilega* community inhabiting a fine sandy sediment (median 211 μm); (4) the *Nephtys cirrosa*–*Echinocardium cordatum* community in a coarser fine sandy sediment (median 242 μm); and (5), closely related to the latter, the *N. cirrosa* community also occurring in a fine sandy sediment (median 224 μm). Only the *L. conchilega* community belongs to the diverse transition zone. The other four communities seem to be part of the heterogeneous, species-poor coastal zone associations. No open sea communities have been detected in the area.

On the western Coastal Banks only the *L. conchilega* community, because of the high numbers of *Abra alba*, *Tellina fabula*, and *Spisula subtruncata*, can be interesting as feeding grounds for the common scoter (*Melanitta nigra* (Aves: Mergini)). Comparison of the spatial distribution of the wintering common scoters and the *L. conchilega* community revealed no direct similarity. The factors possibly causing this dissimilarity have been discussed.

INTRODUCTION

On the Belgian continental platform several sandbank systems occur: (1) the Hinderbanks, about 35–60 km offshore; (2) the Zeelandbanks, some 15–30 km offshore; (3) the Flemish Banks, about 10–30 km offshore of the western Belgian coast; and (4) the Coastal Banks, parallel to the coastline and typical for the coastal zone between Oostende and De Panne.

These Coastal Banks are composed of a combination of: (1) a subtidal extension of the sandy beaches; and (2) a series of shallow (<8 m) sandbanks parallel to the coast. The latter can be subtidal as well as intertidal with mobile sandripples of different scales (De Moor, 1986; Ashley, 1990; Van Lancker & Jacobs, 1996). The sandbanks may be separated by trenches. Being shallow and having a highly variable and diverse topography, currents can change drastically within only tens of metres because of the compression of the water column (Van Veen, 1936). This implies a large variety of sediments (Bastin, 1974; Buchanan, 1984; Houthuys, 1989), with a patchy distribution over the area. Because of this very heterogeneous topography and the ensuring very diverse, patchy sediment texture, the macrozoobenthic communities, due to the close relation between the benthos and the sediments, will also be patchily distributed. So far, the benthos along the western Belgian coast has been poorly studied (Govaere, 1978; Govaere et al., 1980; Van Steen, 1978; Van Assche & Lowagie, 1991).

The area of the western Belgian Coastal Banks is an important wintering area for the common scoters

(*Melanitta nigra*) (Maertens et al., 1988, 1990), reflecting its ecological importance. The seaducks, whose diet consists of macrobenthos, mainly bivalves (Madsen, 1954; Glutz von Blotzheim & Bauer, 1980; Nilsson, 1972; Cramp & Simmons, 1977; Van Steen, 1978; Meissner & Bräger, 1990; Durinck et al., 1993), winter mainly on the Coastal Banks in front of Oostende (Stroombank and Balandbank) and/or in front of De Panne–Koksijde (Potje, Broersbank and Den Oever) (Maertens et al., 1988, 1990). The Ramsar convention (Kuijken, 1972; Skov et al., 1994, 1995) has therefore put the area of the western Coastal Banks under an international preservation convention. The western Belgian Coastal Banks were also put on the list of Belgian areas for the EC bird directive 79/4099/EEC (Van Vessem & Kuijken, 1986) and EC habitat directive 92/43/EEC (Anon., 1992). The area was skipped for the EC bird directive, but is still under consideration for the EC habitat directive.

Ecological information on the food resource of the common scoter will provide additional information: (1) on the potential distribution of the seaducks; and (2) on the food resource itself, the macrozoobenthos, as a component of the sandbank ecosystem. At this moment it is not clear to what extent the feeding grounds of the seaducks are linked with their wintering distribution.

In this paper the structural characteristics of the macrobenthic communities along the western Belgian coast will be investigated in relation to the granulometric characteristics of the sediments and will be correlated with the spatial distribution of the wintering common scoter. This knowledge should be of importance

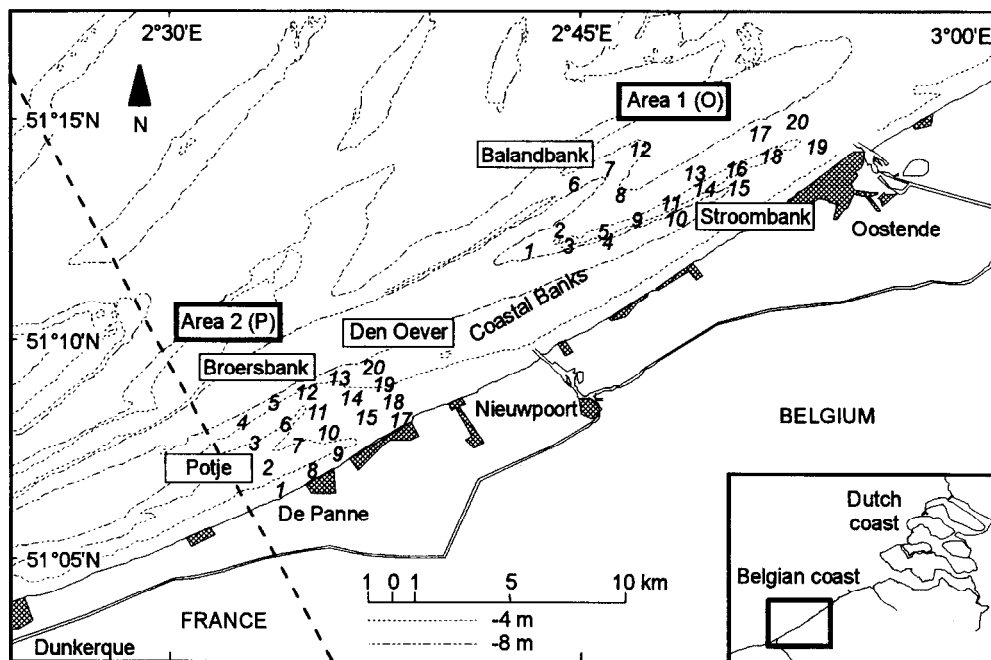


Figure 1. Geographical view on the western Belgian Coastal Banks, divided in area 1 and area 2; with indication of the 39 sampling sites.

to the management of the coast. Indeed, large-scale dredging on the sandbanks is planned within the framework of coastal defence to prevent further erosion of the coastline. This could affect scoter populations in a very negative way, not at least by damaging their food supply.

MATERIALS AND METHODS

Sampling site

The sampling area (Figure 1) covers the Stroombank and Balandbank, separated from the beach by a deep trench (area 1), and Potje, Broersbank and part of Den Oever, directly adjacent to the beach (area 2). These are the two most important wintering areas for the common scoter.

In October 1994, 39 macrozoobenthic samples were taken. In area 1, 20 stations cover the different geomorphological formations: the southern and northern flanks (4 and 6 respectively), and the top of the sandbanks (10). As area 2 is geomorphologically more differentiated, the 19 stations were placed in a grid covering the whole area.

Sampling method

Samples were taken with a Van Veen grab (sampling surface 0.12 m²) and sieved on board over a 1-mm sieve before fixation. The residual was preserved in a buffered 8% formaldehyde solution. Samples were decanted, stained with Bengal rose and the residuals were sorted under stereomicroscope. All the individuals were identified up to species level, except the oligochaetes.

Environmental parameters

Water depth was recorded while sampling and standardized to mean low water spring (MLWS). The grain size

analysis of a subsample was measured with a Coulter particle size analyser.

Data analysis

To identify groups of similar stations the density data were subjected to a two-way indicator species analysis (TWINSPAN), with cutlevels: 0, 9, and 40 ind m⁻², a TWINSPAN on the presence/absence data (Hill, 1979) and, after fourth root transformation, to a Bray–Curtis group-average cluster analysis (van Tongeren, 1987) and a canonical correspondence analysis (CCA) (Ter Braak, 1986).

The station groupings, resulting from the multivariate analyses, were characterized by their typical species composition, diversity indices (Hill numbers, N_0 , N_1 and N_{inf} , and Shannon–Wiener diversity index, H') (Hill, 1973; Shannon & Weaver, 1949) and the measured environmental variables.

Statistical differences for biotic and abiotic variables between groups were analysed by the Kruskal–Wallis test ($P < 0.05$). Significant differences were further analysed by *a posteriori* multiple comparisons (Conover, 1971).

RESULTS

The number of species per station varied between three and 29 species, with a mode of four species (Figure 2A). About 47% of the 71 identified species belong to the Polychaeta, 20% to the Bivalvia, 14% to the Amphipoda, 6% to the Decapoda, and another 11% belong to the remaining taxa (Figure 2B). The total density varied between 58 and 8350 ind m⁻² with a mode of 100–200 ind m⁻²; 18 stations have densities from 100–400 ind m⁻² (Figure 2C).

Multivariate analyses

In the different multivariate analyses the same stations were always grouped together, except for O13, O18 and

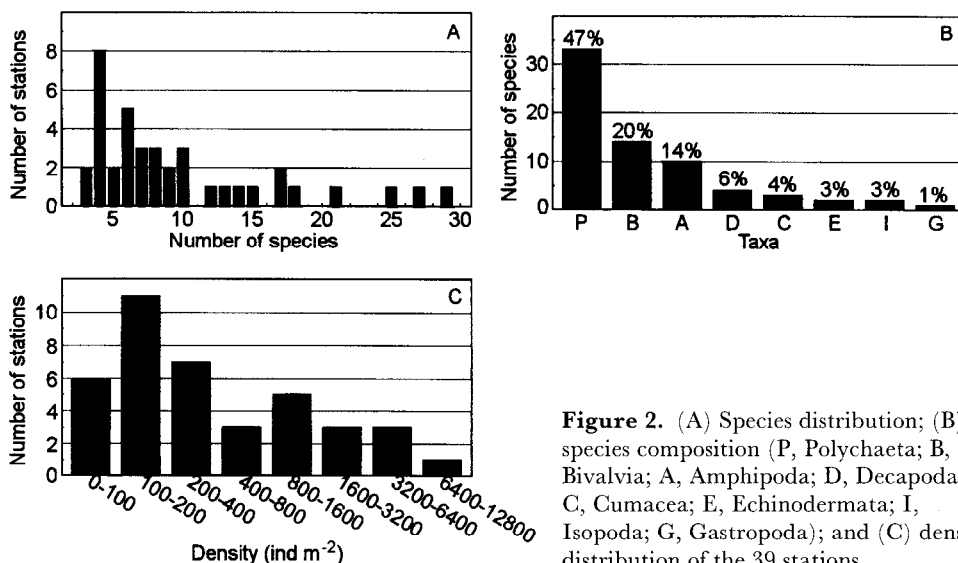


Figure 2. (A) Species distribution; (B) species composition (P, Polychaeta; B, Bivalvia; A, Amphipoda; D, Decapoda; C, Cumacea; E, Echinodermata; I, Isopoda; G, Gastropoda); and (C) density distribution of the 39 stations.

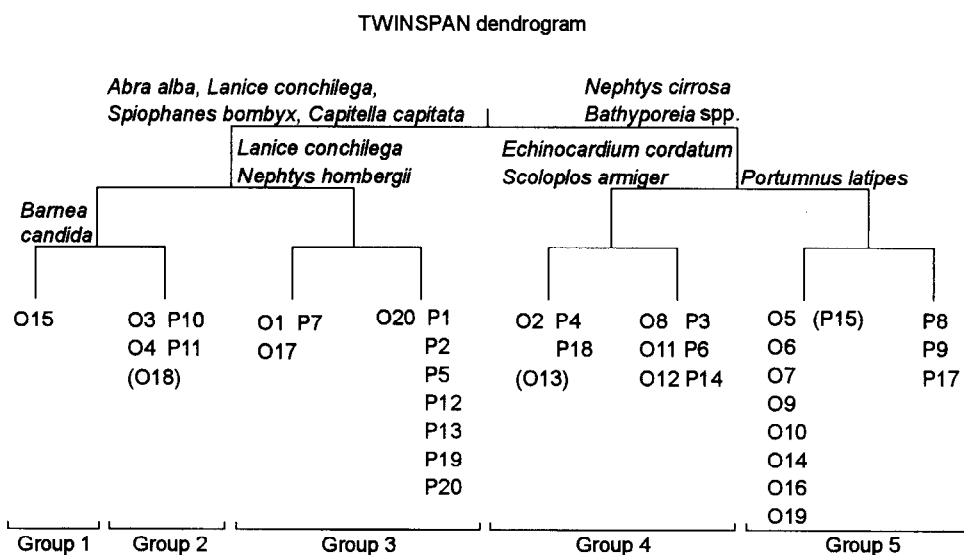


Figure 3. Presentation of the graphical result of one multivariate technique: TWINSPAN dendrogram of the presence/absence data; with indication of the five groups and their indicator species.

P15 (Figure 3). Station O13 was placed in group 2 in three of the four analyses. The stations O18 and P15 showed no preferences for a group and were kept out of further analyses.

Species composition

The ten most dominant species differ between the five groups as do their relative importance within groups (Table 1). In group 1 only *Barnea candida* (Linnaeus, 1758) occurs in quite high densities. The second group is dominated by *Microphthalmus similis* (Bobretzky, 1870) and spat of *Mytilus edulis* (Linnaeus, 1758). *Magelona papillicornis* (F. Müller, 1858), *Eumida sanguinea* (Oersted, 1843), *Lanice conchilega* (Pallas, 1766), *Abra alba* (S. Wood, 1802), and *Tellina fabula* (Gronovius, 1781) are very well represented in group 3. Group 4 has high densities of *M. papillicornis* and *Nephtys cirrosa* (Ehlers, 1868). Group 5 also has *M. papillicornis* and *N. cirrosa* as most dominant species.

The abundances of the indicator species of the TWINSPAN, presence/absence and absolute densities, were compared statistically in between groups (Table 2). Group 1 cannot be compared statistically with the other groups ($N=1$), but the presence of *B. candida*, which occurs only in group 1 is likely to be typical for that kind of environment. Group 2 is put apart by the abundance of juvenile specimens of *Mytilus edulis*. Group 3 differs from the other groups by the abundance of *A. alba* and *L. conchilega*. *Nephtys cirrosa* and *Echinocardium cordatum* (Pennant, 1777) are typical for group 4, and group 5 cannot be separated statistically by any TWINSPAN indicator, but possesses the highest number of *N. cirrosa*.

Thirteen species of bivalves were found in the whole area (Figure 4). Group 1 is characterized by *B. candida* and *Ensis* spp. Group 2 has only high densities of *M. edulis* spat. *Abra alba*, *T. fabula*, *Spisula subtruncata*, *Ensis* spp., and *Montacuta ferruginosa* are reaching high densities in group 3. Group 4 does not have a typical bivalve species

Table 1. The ten most abundant species per group with indication of the density (ind m^{-2}) and the percentage of occurrence in the stations of the different groups (%).

Group 1 Species	ind m^{-2}	%	Group 2 Species	ind m^{-2}	%
<i>Barnea candida</i>	117	100	<i>Microphthalmus similis</i>	237	60
<i>Ensis</i> sp.	33	100	<i>Mytilus edulis</i> spat	118	100
<i>Nephtys longissima</i>	25	100	<i>Nephtys cirrosa</i>	28	100
<i>Nereis succinea</i>	25	100	<i>Hesionura augeneri</i>	20	60
<i>Glycera capitata</i>	25	100	Oligochaeta	15	20
Oligochaeta	17	100	<i>Ensis</i> spp.	10	40
<i>Eteone longa</i>	17	100	<i>Scoloplos armiger</i>	7	60
<i>Upogebia deltaura</i>	8	100	<i>Glycera capitata</i>	7	40
Bivalvia indet.	8	100	<i>Spisula subtruncata</i>	7	40
<i>Anaitides mucosa</i>	8	100	<i>Ophelia limacina</i>	3	20
Group 3 Species	ind m^{-2}	%	Group 4 Species	ind m^{-2}	%
<i>Magelona papillicornis</i>	1392	64	<i>Magelona papillicornis</i>	72	77
<i>Eumida sanguinea</i>	344	82	<i>Nephtys cirrosa</i>	70	100
<i>Lanica conchilega</i>	228	64	<i>Echinocardium cordatum</i>	21	77
<i>Abra alba</i>	139	91	<i>Bathyporeia</i> spp.	16	66
<i>Tellina fabula</i>	104	64	<i>Scoloplos armiger</i>	7	55
<i>Pariambus typicus</i>	69	64	<i>Pontocrates altamarinus</i>	6	55
<i>Ensis</i> spp.	62	82	<i>Pseudoparatanaïs batei</i>	5	22
<i>Nephtys hombergii</i>	61	82	<i>Diastylis bradyi</i>	5	33
<i>Spisula subtruncata</i>	48	55	<i>Ensis</i> sp.	4	33
<i>Capitella capitata</i>	41	73	<i>Urothoe poseidonis</i>	4	33
Group 5 Species	ind m^{-2}	%			
<i>Magelona papillicornis</i>	125	75			
<i>Nephtys cirrosa</i>	93	100			
<i>Ensis</i> spp.	21	17			
<i>Donax vittatus</i>	11	25			
<i>Bathyporeia</i> spp.	7	50			
<i>Nephtys hombergii</i>	7	33			
<i>Portumnus latipes</i>	7	42			
<i>Urothoe poseidonis</i>	4	25			
<i>Eumida sanguinea</i>	4	8			
<i>Diastylis bradyi</i>	2	25			

Table 2. Densities (ind m^{-2}) of the differentiating species, with indication of the test statistic (H) of the Kruskal–Wallis test together with the P-level for differences between group 2, 3, 4, and 5.

	Group 1	Group 2	Group 3	Group 4	Group 5	H	P
<i>Barnea candida</i>	117	0	0	0	0	—	—
<i>Mytilus edulis</i> spat	0	118	5	0	0	28.682	<0.0001
<i>Abra alba</i>	0	2	139	0	0	28.861	<0.0001
<i>Lanice conchilega</i>	0	0	228	0	0	25.813	<0.0001
<i>Nephtys cirrosa</i>	0	28	25	70	93	14.365	0.0025
<i>Echinocardium cordatum</i>	0	0	2	21	0	18.968	0.0003

and no bivalve species has a density higher than 5 ind m^{-2} . Group 5 is also poor concerning bivalves, but *Donax vittatus* and *Ensis* spp. are found in low numbers. *Tellina tenuis*, *Macoma balthica*, *Spisula solida*, *Mactra corallina*, and *Venerupis pullastra* are only occurring in low densities (maximal 11 ind m^{-2}).

Diversity

Table 3 is indicating different diversity indices. Each group is characterized by some exclusive species. Group 3 has 23 exclusive species in a total of 54 species. On a total of only ten species found, group 1 has three exclusive

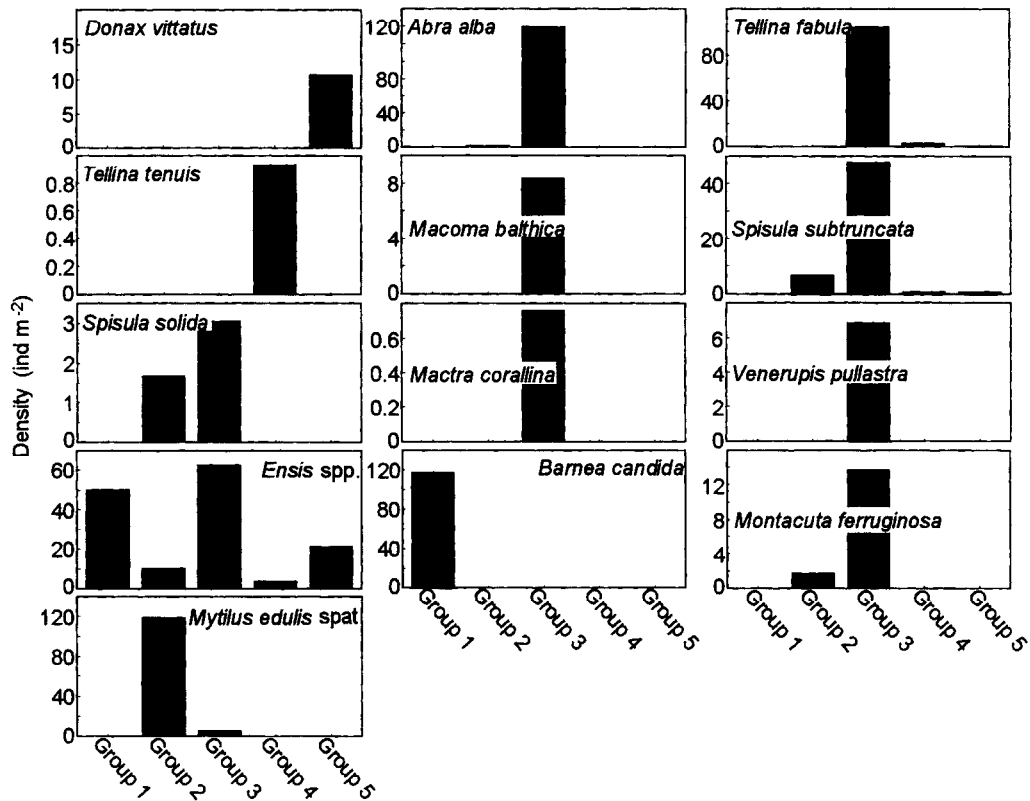


Figure 4.

Table 3. The number of exclusive species per group; the total number of species per group and different diversity indices of the five groups: (1) Hill numbers (N_0 , N_1 , N_2 and N_{inf}) and (2) Shannon–Wiener diversity index (H').

	Group 1	Group 2	Group 3	Group 4	Group 5
Exclusive species	3	3	23	4	1
Total number of species	10	21	54	24	15
N_0	10	8	18	8	5
N_1	6.8	5.0	6.8	5.2	3.2
N_2	4.9	4.2	4.4	4.0	2.5
N_{inf}	2.6	2.7	2.3	2.6	1.7
H'	1.9	1.6	1.7	1.6	1.1

Table 4. Average value of the measured environmental variables per group, with indication of the P-level of the Kruskal–Wallis test for differences between group 2, 3, 4 and 5, and the geographical distribution of the number of stations of the five groups over area 1 and area 2.

	Group 1	Group 2	Group 3	Group 4	Group 5	P-level
Depth	8.2	4.8	5.7	4.8	3.8	0.3698
Median	14	456	211	242	224	0.0005
MM-ratio	1.2	1.0	0.9	1.0	1.0	0.0393
% Mud	18	0	1	0	0	0.0004
% Silt	63	0	3	0	0	0.0004
% Very fine sand	8	1	4	1	3	0.0007
% Fine sand	6	9	65	57	63	0.0019
% Medium sand	4	54	22	43	33	0.0063
% Coarse sand	1	36	5	1	1	0.0010
% Gravel	0	11	0	0	0	<0.0001
Area 1:area 2	1:0	3:2	3:8	4:5	8:3	—

Depth, under MLSW; median, median grain size (μm); MM-ratio, sediment mean–median ratio; different sediment fractions in volume percentages; percentage gravel in mass percentage.

Table 5. Environmental variables indicating statistical differences between groups with an a posteriori test after a negative Kruskal–Wallis test.

	Group 2	Group 3	Group 4	Group 5
Group 2	—			
Group 3	1234567	—		
Group 4	167	12345	—	
Group 5	14567	234	no differences	—

1, median grain size; 2, mud; 3, silt; 4, very fine sand; 5, medium sand; 6, coarse sand; and 7, gravel content of the sediment.

Table 6. The most abundant macrobenthic species of other sandbank ecosystems on the Belgian continental platform. The species list of the Zeelandbanks is based on the species lists of samples from the Thornton Bank and Gootebank; the list of the Flemish Banks is based on samples from the Oostdijk, Buiten Ratel and Kwintebank (Meheus, 1981).

Zeelandbanks	Flemish Banks
<i>Spisula elliptica</i>	<i>Ophelia limacina</i>
<i>Nephtys cirrosa</i>	<i>Hesionura augeneri</i>
<i>Ophelia limacina</i>	<i>Oligochaeta</i>
<i>Nephtys longosetosa</i>	<i>Bathyporeia elegans</i>
<i>Nephtys caeca</i>	<i>Nephtys cirrosa</i>
<i>Scolelepis bonnierii</i>	<i>Spio filicornis</i>
<i>Bathyporeia guillamsoniana</i>	<i>Eteone longa</i>
<i>Thia scutellata</i>	<i>Bathyporeia guillamsoniana</i>
<i>Eteone longa</i>	<i>Nephtys hombergii</i>

Table 7. The distribution of the common scoter at the Belgian coast during winter 1994–1995, with distinction between area 1 and area 2 (*H. Offringa*, unpublished data, Institute of Nature Conservation).

	13.11.94	31.12.94	12.02.95	04.03.95
Area 1	52	1187	1366	184
Area 2	67	72	165	0
Total	343	1294	1585	188

ones. N_0 , which gives the group average of the number of species per station, indicates a very high number for group 3 (18). The other groups are having a N_0 varying from five (group 5) to ten (group 1). Taking into account the rest of the Hill numbers, generally group 1 is the most diverse group, followed by group 3.

Environmental variables and geographical community distribution

As group 1 is composed of only one station, statistical comparisons with other groups is impossible. However, the relatively greater depth (8.2 m), low median grain size (14 μm), and high volume percentage of silt (63%), differentiate group 1 from the other groups.

Statistical differences between the other four groups (Table 4) were found for: median grain size, volume percentage clay (<4 μm), silt (4–63 μm), very fine sand (63–125 μm), medium sand (250–500 μm) and coarse

sand (500–1000 μm), and mass percentage of gravel (>1000 μm). Depth, mean–median ratio, and volume percentage fine sand (125–250 μm) showed no differences. Most of the stations in group 3 (eight stations) occur in area 2, with only three stations in area 1 (Table 4). In all the other groups there are more stations in area 1 (groups 1 and 5) or about the same number of stations in the two areas (groups 2 and 4). The results of the Kruskal–Wallis a posteriori tests on the differentiating environmental variables between the groups 2, 3, 4 and 5 are given in Table 5.

In summary, group 1 has a typical very fine sediment, group 2 is characterized by a medium sandy sediment, group 3 by a fine sandy sediments, and the very similar group 4 and 5 by slightly coarser fine sandy sediments.

DISCUSSION

Macrobenthic communities

Govaere et al. (1980) described three macrobenthic communities occurring in the Southern Bight of the North Sea: (1) a very diverse open sea community; (2) a rather diverse transition zone community, where the following species are numerically dominant: *Lanice conchilega*, *Nephtys cirrosa*, *Spiophanes bombyx*, *Magelona papillicornis*, *Pectinaria koreni* (Malmgren, 1865), *Anaitides mucosa* (Oersted, 1843), *Tellina fabula*, *Eumida sanguinea*, and *Ophelia limacina* (Rathke, 1843); and (3) a species-poor, heterogeneous coastal zone community, dominated by *P. koreni*, *Macoma balthica*, *Nephtys hombergii* (Savigny, 1818), and *Abra alba*.

The presented study here, in the shallow subtidal part of the western Belgian coast, detected five macrobenthic communities, all characterized by a series of typical species and specific values of some environmental factors. As this study only results from an autumn campaign, differences with the communities described in Govaere et al. (1980), resulting from several campaigns, spread over several years, are expected (McIntyre et al., 1982).

As *Barnea candida* (besides *Ensis* spp. the only bivalve species in group 1) is exclusively found in group 1, this group can be defined as the *B. candida* community. This rather diverse community occurs in a muddy (median 14 μm), deeper lying (8.2 m) sediment, containing only high numbers of *B. candida* (117 ind m^{-2}). The species composition of this community does not resemble any of the three communities described in Govaere et al. (1980). However, due to the heterogeneous character of the coastal zone, with a typical deposition of fine sediments and a low number of species, the *B. candida* community possibly belongs to the coastal zone community complex. The very fine sediments, in contradiction to the generally high dynamic sandbanks with a consequently coarser sediment, and the depth indicate that this community is part of the communities occurring in the trenches in between, rather than on, the sandbanks. As this study aimed to sample the communities of the sandbanks, only one station belonging to the *B. candida* community has been encountered.

Group 2 could be differentiated by means of the presence of juvenile *Mytilus edulis*: the '*M. edulis*' community. This community is situated on top of the Broersbank

(area 2) and along the top of the Stroombank (area 1). The very coarse sediments, with an average median grain size of 456 μm , imply high hydrodynamic forces. The community is characterized by a low diversity. Except for the juvenile *M. edulis* specimens, no other bivalves occurred in high densities. Due to the low diversity and low number of species, this community could also be part of the coastal zone community complex. Because of the absence of adult specimens of *M. edulis*, this bivalve may not be a typical species over all the seasons. The juvenile specimens can attach to the coarse sediment particles, but when they grow the chance of being washed out increases, as adult *M. edulis* firmly attach to hard substrata.

A fine sandy sediment (median 211 μm) with typically high densities of *A. alba* and *L. conchilega* and a very high diversity are characteristic elements for group 3, defined as the *L. conchilega* community. This community contains the highest densities of bivalves. The *L. conchilega* community coincides very well with the transition zone community (Govaere et al., 1980). In fact the transition zone reaches the coast in front of De Panne and the *L. conchilega* community, in this study, is typical for the sandbank area at this place: eight of the 11 stations of the association are situated in area 2, only three transition zone stations can be found in area 1.

The groups 4 and 5, which are very similar, are occurring in a slightly coarser fine sandy sediment (median respectively 242 and 224 μm) with both a quite low diversity and low numbers of bivalves. *Echinocardium cordatum* and *N. cirrosa* are reaching high densities, respectively 21 and 70 ind m^{-2} , and are characteristic for group 4: the *N. cirrosa*-*E. cordatum* community. The fifth group contains only high numbers of *N. cirrosa* (93 ind m^{-2}) and can thus be defined as the *N. cirrosa* community. These two communities both have a low diversity and can also be considered as a type of the coastal zone community complex.

Some studies on the macrobenthos of the nearby, but deeper lying, Flemish and Zeeland Banks have been carried out (Rappé, 1978; Meheus, 1981; De Rijcke, 1982; Vanosmael et al., 1982). Generally these sandbanks have a typical open sea community, with affinities to the transition zone. The communities are relatively species-poor in comparison to the surrounding areas (Rappé, 1978) and no relation between the most abundant species of these Flemish and Zeeland Banks on the one hand and these of the Coastal Banks (this study) on the other hand could be detected (Table 6). The lack of high densities of bivalves is also in contrast with the Coastal Bank communities or at least with the *L. conchilega* community.

Craeymeersch et al. (1990a) described for the Voordelta area (the Netherlands), a shallow, sandy, subtidal marine area, five communities, related with typical abiotic parameters, of which the sedimentology seemed to be the most important (Craeymeersch et al., 1990b). Generally, the macrozoobenthos of the Voordelta area has higher densities (500–15,000 ind m^{-2}) and higher number of species (55–120 species) in comparison with the five communities of this study. Yet, a clear similarity between the median grain size of the richest communities of Craeymeersch et al. (1990a), namely 180–220 μm , and the median grain size of the rich *L. conchilega* community (average 211 μm) can be noticed. Biologically seen, among

the most abundant species are also *S. bombyx*, *L. conchilega*, *A. alba*, *Spio filicornis*, and *Mysella bidentata*. *Spisula subtruncata* occurs in high densities, but the lack of high densities of this bivalve species in the *L. conchilega* community is discussed below.

Van Steen (1978) surveyed area 2, with special attention to the bivalves. As only a selective part of the western Coastal Banks, mainly Potje, was sampled, the sediment analyses all resulted in a fine sandy sediment (median 170–240 μm). Yet, the high densities of *A. alba*, *T. fabula*, and *L. conchilega*, show a clear relationship with the *L. conchilega* community described here.

Sandbank systems are abiotically extremely diverse and a depth difference of 0.5 m in a shallow area affects the hydrodynamics very much. Consequently, extremely diverse hydrodynamics are expected. Because of the linkage between hydrodynamics and sedimentology (Gullentops et al., 1977; Buchanan, 1984), even within some tens of metres completely different types of sediment can be encountered, each with their own typical macrobenthic community. A large variety of communities can thus be expected. However, as the 39 stations (without the exceptional *B. candida* community) are only divided into four consistent communities, it is unlikely that a new community will be found when taking more samples in the same area.

Since the dynamics of the benthic system are a reflection of the distribution of residual and tidal currents and the load of suspended materials, the basic composition and distribution of the respective communities and their spatial distribution will remain stable (within the natural variability due to erratic recruitment and mortality) as long as the currents and the amount of suspended material carried do not change drastically (Govaere et al., 1980). A comparison of the geomorphology and sedimentology of area 2 between 1973 (Bastin, 1974) and 1994 (this study) reveals no substantial differences. This implies no drastic changes in hydrodynamic regime and, consequently, an over years rather constant spatial variation of the macrobenthic communities, even for a very high dynamic region such as the western Coastal Banks. No reasons could be found to presume a different situation in area 1.

Food availability for the common scoter

In total 13 bivalve species are found in this study. Yet, for the common scoter, not all bivalves at any density are a potential food resource: (1) the bivalves have to occur at a fairly high density, so the scoter is likely to find a bivalve specimen while diving; (2) the bivalve specimens cannot be too big for swallowing or too small, which make it energetically unfavourable diving for; and (3) may not be digging too deep, which make it unlikely to be found (Leopold, 1995; Leopold et al., 1995). Of the 13 species, only *Donax vittatus*, *A. alba*, *T. fabula*, *Tellina tenuis*, *M. balthica*, *S. subtruncata*, and *B. candida* are likely to be eaten by the wintering common scoter. Thus, the common scoters are expected to feed on the *L. conchilega* community, with fairly high densities of *A. alba*, *T. fabula*, and *S. subtruncata*, and to a lesser extent on the *B. candida* community. Although, morphologically seen, *B. candida* is a potential food resource for the common scoter, the

bivalve lives in a very compact muddy sediment (clay) and it is doubtful the common scoter could find these bivalves.

While studying the bivalves in an area just east of area 2, Van Assche & Lowagie (1991) encountered a community with very high densities of *S. subtruncata* (up to over 500 ind m⁻²), *M. balthica* (up to 500 ind m⁻²), *T. fabula*, and *A. alba*. This community would probably also act as a very important food resource for seaducks, but it has not been detected in this study.

Possibly, due to their irregular recruitment, the bivalve populations disappeared by: (1) natural mortality; (2) maybe predation by the common scoters; and (3) the lack of recruitment in the area for several years. Concerning *S. subtruncata*, the high number of individuals found in February 1991 (Van Assche & Lowagie, 1991) were probably all recruits from 1989 or earlier (personal observation from maximal shell length) and the present study reveals few individuals which were recruited in 1993, the low densities indicating that recruitment has taken place even earlier. Maybe, between 1990 and 1994, there has even been no successful recruitment at all, which could explain the extremely low densities of *S. subtruncata* in comparison with 1991. Unfortunately, between 1990 and 1994 no macrobenthic samples have been taken in the area to prove this idea.

The expected similarity between the spatial distribution of the macrozoobenthos (Nilsson, 1972), more specifically the *L. conchilega* community, and the wintering scoters (Table 7), as discussed above, cannot be detected. Most of the scoters are staying in area 1, whereas the highest densities of bivalves (*L. conchilega* community) are mostly found in area 2. Obviously there exist some problems when linking both spatial distributions.

The first problem is the difference in scales used. The macrozoobenthic species are, in comparison to the ducks, very sessile: one sampling campaign for the macrozoobenthos reveals already a detailed pattern, which normally is quite stable in time. As seaducks are a lot more mobile, for instance by flying and drifting (Winter, 1993) their spatial distribution can change significantly, even within some hours. Consequently, four seaduck counts during one winter half year do not necessarily show a detailed, temporally stable spatial pattern. It gives an idea about the total number in a large area, rather than their distribution over the area. This fact implies problems linking both distributions.

Secondly, groups of the seaduck can be found on places where it is too deep to dive for food (H. Offringa, personal communication) and research, trying to link the spatial distribution of the common scoter with the macrozoobenthos in the Netherlands, revealed an excess of *Spisula* banks: not all *Spisula* banks found constantly have a group of common scoters feeding on them (Leopold, 1995). These two facts create the idea that the common scoter does not always have to select the best feeding grounds. Sometimes 'suboptimal' or even 'bad' feeding places can be preferred. This can also be concluded from the presence of the scoters during winter 1994–1995 in area 1. What exactly or what combination of factors determines the ducks' spatial distribution is not known at this moment. Possibly a combination of food availability and the lack of disturbance, by fishing activities for instance

(Leopold & van der Land, 1996), determines their spatial distribution.

Still the protection of areas as wintering place for the common scoter is important. As tranquillity zones, e.g. marine protected areas, can be safeguarded against anthropogenic influences, such as shellfisheries and sand extraction, the establishment of these areas, rich in bivalves, will have a positive influence on and may even attract the common scoter. Even if the tranquillity zone is not visited by the common scoter every year, the area can act as a refuge in times of food shortage or disturbance.

The monitoring of the macrobenthos in these areas allows estimates of potential productivity of renewable resources and is thus a major component in determining sustainable levels of use, for instance in the case of the shellfisheries (Agardy, 1994).

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