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Macrofaunal diversity on beds of the Pacific oyster (*Crassostrea gigas*) in the Oosterschelde estuary

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Abstract

The Pacific oyster (Crassostrea gigas) is a marine exotic species that has successfully been introduced into the Oosterschelde estuary in the Netherlands in the 1960's. It is still spreading, and can now be considered a part of the local ecosystem. Along with C. gigas other exotic species have been introduced. C. gigas influences its environment through the formation of oyster beds. An oyster bed alters the local environment by influencing current flow, filtering food particles from the water column, by providing structural complexity and by locally enriching the sediment through faeces and pseudofaeces deposition.

The aim of this study was to investigate how the presence of a Pacific oyster bed affects local macrofaunal diversity. Along a transect from the center of the oyster bed to the adjacent mudflat, sediment and oysters were sampled to determine the occurrence of species and their abundances. Two oyster beds were sampled.

In total, 38 species were found. Polychaeta dominated, and together with Bivalvia and Malacostraca comprised 76% of all specimens identified to species level. Considerably higher biodiversity and abundances per unit area were found on the oyster beds than on the mudflats. This may be due to the structural complexity of the oyster beds, providing many microhabitats, and by organic enrichment of the sediment. The total number of specimens found increased from the center of the oyster bed to the transition zone, where the oyster bed and mudflat overlap. Both deposit/suspension feeders and carnivore/omnivores showed this pattern. This may be explained by the heterogeinity in habitat types of the transition zone. The transition zone may provide an optimal compromise between nutrient availability, shelter and living space for deposit/suspension feeders. Carnivore/omnivores may feed on these, and thus show a similar pattern. Total diversity also increased from the center to the transition zone on one oyster bed, but this was not shown conclusively for the other oyster bed.

The implications of the spreading of the Pacific oyster in Dutch waters may be profound. Locally the spreading of Pacific oyster considerably increased biodiversity and abundances. However, the extent of the implications of this to the ecosystem as a whole remain to be investigated.

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Introduction

1. Marine introduced species

Introduced species are an important phenomenon in the marine environment. Human traffic has become more frequent over larger distances in modern times, creating opportunities for the introduction of exotic species in a large number of marine habitats. Vectors for the introduction of marine exotics include fouling on ships' hulls, ships' ballast water, and deliberate introductions for commercial purposes. Human-introduced marine exotics can today be found in marine areas all over the world. The share of exotics in the North Sea biota increases from the offshore part towards the coast, and increases further from the open coast towards the estuaries (Reise et al., 1998). In Dutch estuaries, the percentage of exotic species is up to 6% (Wolff, 1998).

An exotic species, when introduced, can sometimes permanently establish itself in the receiving ecosystem. Exotic species can subsequently dominate the receiving ecosystem (Ricciardi and MacIsaac, 2000). Occasionally an exotic species, through lack of natural inhibitors such as predators, spreads to such an extent that it can be considered a pest (Bax et al., 2003; Ricciardi et al., 1998).

The Pacific oyster (*Crassostrea gigas*) is a marine exotic species that has successfully been introduced into the Oosterschelde estuary in the Netherlands and has firmly established itself in the local ecosystem. *C. gigas*' origin lies in North-East Asia. Other exotic species have been introduced into various parts of the world together with *C. gigas* (Reise et al., 2002; Wolff and Reise, 2002). Many invertebrate species and algae live on or in the oyster shell, or close enough to it to be transported together with the oyster. Introductions with *C. gigas* into the Netherlands may help explain a peak of newly recorded species in the 1970s (Reise et al., 1998). However, components of antifouling paints may also explain this peak (see Box 1).

C. gigas forms oyster beds. Oyster beds can form on hard substrata such as artificial piers and dikes, common structures in the Netherlands, or on soft substrata by attaching to a piece of hard material and then using the first oyster(s) as a substratum. An oyster bed alters the local environment by influencing currents, filtering food particles from the water column, forming hard substratum for it and other species to attach to, and by locally enriching the sediment. These factors will be discussed in more detail.

Box 1: Does TBT explain the 1970's peak in newly recorded species?

There is a peak in the record of newly recorded species in the North Sea in the 1970s, which may partly be explained with imports of *C. gigas* and its associated organisms (Reise et al., 1998). These imports occurred in the 1960s to 1970s. However, this could also in part be explained by the changeing of components of antifouling paints in the 1970s. The new hull coating which contained tributyltin (TBT) might be more effective compared to previously used compounds. This may have prevented a further increase in the rate of introductions since the mid 1970s (Minchin & Sheehan 1995 in (Reise et al., 2002)), thus explaining the peak in the record. However, Minchin and Gollasch (2003) in a later study conclude that although organotin antifouling paints such as TBT have reduced settlement on hulls, fouling has not been eliminated. Ships have also become larger and faster, visiting more ports in a shorter time, thus creating new opportunities for species to tag along and spread.

2. Historical developments in the Netherlands

Due to large-scale mortality of the native flat oyster *Ostrea edulis* in the winter of 1963, which caused a population decline from 120 million to 4 million individuals in the Oosterschelde (Drinkwaard A.C., 1999), culture of *O. edulis* was no longer commercially viable. An alternative was sought and found in the Pacific oyster, which was subsequently imported as a small shipment of spat in 1964 from British Columbia by a Dutch oyster grower. It was believed that *C. gigas* would not be able to reproduce in Dutch waters due to cold temperatures. Also, the Oosterschelde estuary would be made a fresh water system by the completion of the Dutch Delta Works. However, the Delta Works plans were modified from a permanently closed dam to a storm surge barrier and the Oosterschelde estuary remained saline. *C. gigas* was able to reproduce. The first spawning that yielded high recruitment was observed in 1976.

Flat oyster-farmers were concerned about their livelihood, and their political lobby helped prohibit *C. gigas* imports at the end of 1976. A second large natural larval outburst in July 1982 definitively established the Pacific oyster in the Netherlands. From that time onwards it was considered established fauna in Zeeland (Drinkwaard A.C., 1999). Nearly all oyster growers started the commercial farming of Pacific oyster.

3. Current situation

The Pacific oyster has permanently settled in Dutch waters and is expanding rapidly. Figure 1 shows the current distribution of littoral oyster beds in the Oosterschelde estuary. In the Wadden Sea, the Westerschelde estuary and Lake Grevelingen (Drinkwaard A.C., 1999) the Pacific oyster is also spreading. From reconstruction of aerial photographs, and the annual oyster survey conducted by RIVO-Center for Shellfish Research, coverage by littoral oyster beds in the Oosterschelde was estimated to have increased from 0.25 km^2 in 1980 to 6.40 km^2 in 2002 (Kater B.J. et al., 2002). For 2003 an oyster-covered area of 7.66 km^2 was estimated. It is assumed that a similar cover of oysters is present in the sublittoral (Gelderman E., 2004). It is estimated that *C. gigas* currently occupies 50% of the available hard substratum in the Oosterschelde estuary (Aquasense, 2003).

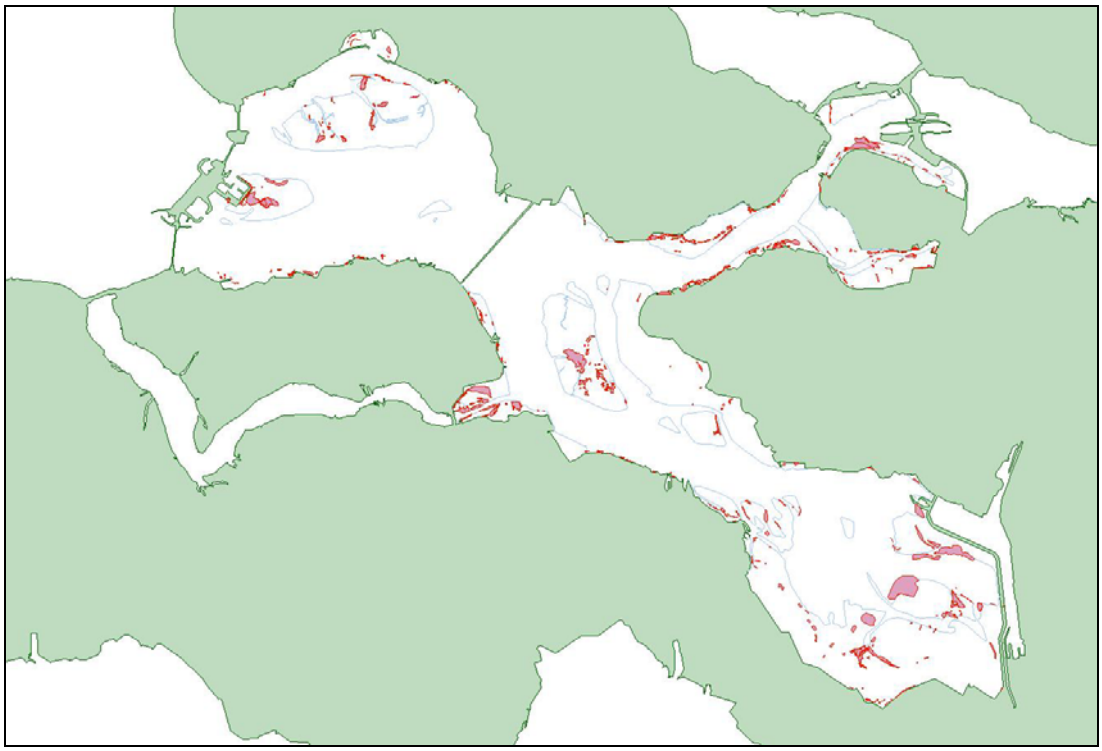

Figure 1: Littoral oyster beds in the Oosterschelde estuary (Image by RIVO-CSO) are shown in red. Oysters in other water bodies in the figure are not shown.

Box 2: Biology and ecology of *C. gigas*

Figure 2: *C. gigas* individual as occurring on an oyster bed

Figure 2 shows a Pacific oyster *in situ* on an oyster bed. The oyster is angular and irregular in shape, and often has a number of barnacles attached to it. The purple-streaked edge of the oyster that can be seen in the figure is recent growth of the shell, probably over the past year. *C. gigas* is a bivalve, oviparous hermaphroditic mollusc, developing first as a male and later functioning as a female. Its natural habitat is an open coast ecosystem or rocky shore. Its rapid growth shows an annual cycle with growth occurring from April - October, peaking in June (Walne & Mann 1975; Walne & Spencer 1975 in Kater, 2002). Spawning on the northern hemisphere occurs in July and August (Reise, 1998), but can also occur in June and September (Arakawa 1990 in Kater, 2002). A single oyster can produce between 1 million and 100 million eggs of 50 µm (Reise, 1998). Both eggs and sperm are released into the water column, where fertilization takes place. The larvae are free-living for 15 – 30 days and are moved by water currents. The larvae develop a foot, and on the seafloor search a suitable substratum to settle on. Often the substratum will be dead or live shells, such as mussels, cockles or other oysters. Although the larva needs to settle on hard substratum this can also be a piece of shell material in a sandy environment.

The oysters can survive and grow well in lower salinity, which enables them to grow in estuaries. No growth occurs in coastal waters with a salinity of less than 10 ‰ or more than 30‰. Spawning can occur between 10‰ and 42‰ (Mann et al. 1991 in Kater, 2002). Oysters are limited in their dispersal also by the minimum water temperature that is required for spawning. Therefore they are seldom encountered further north than the southwest coast of Norway (www.zeeuwseoesters.nl).

The Pacific oyster is a filter feeder. It has a large filtering capacity; the water pumping activity of a square meter of an oyster bed per hour has been estimated from literature values by Kater (2002) to be 677 l/h. Part of the filtered material reaches the intestine, is digested and the remainder is expelled as faeces, but the majority is expelled as pseudofaeces.

The Pacific oyster might be able to outcompete mussels and cockles by either settling on mussel beds, or by trophic competition for suspended organic matter. The American oyster *Crassostrea virginica* consumes larvae of many taxonomic groups including bivalve and gastropod veliger larvae (even their own). This could negatively impact the ecosystem, and thus mussel and cockle fisheries. Most birds for example are unable to crack the Pacific oyster's hard shell, while their normal prey may decrease in number.

4. Habitat-altering effects of C. gigas beds

Enhanced structural complexity

Aggregations of oysters can form oyster beds (see Box 2) that gradually replace bare mudflat by a habitat with distinctly different characteristics. This may, through several mechanisms, cause a profound change in the epi- and infaunal species assemblage. Oyster beds are structurally much more complex than mudflats, and sediment characteristics are very different below the oyster bed compared to the mudflat sediment. Mean grain size is smaller and organic content is much higher (see 'sediment organic enrichment' p.7). Figure 3 shows the difference between a mudflat and an oyster bed in the Oosterschelde estuary. Most oyster beds typically are not entirely covered with oysters, but have bare patches. There is also no sharp border between the oyster bed and the adjacent mudflat, but there is a transition zone. This is a zone of overlap between the oyster bed and the adjacent mudflat. I defined the point where the oyster cover clearly becomes thinner as the edge of the oyster bed. The transition zone starts there and continues to the point where the oyster cover reaches (almost) zero.

Figure 3: Left: mudflat in Oosterschelde. Right: oyster bed in Oosterschelde

Effects of structural complexity

Figure 4 shows the structural complexity of an oyster bed. The oysters on top often stand erect, with many other oysters making up lower layers. Seaweeds can attach to oysters and drifting seaweeds often become trapped by the oyster bed or by byssus threads from mussels, where some subsequently settle. As oyster beds expand, structural complexity on many locations is considerably enhanced. This may provide new opportunities or difficulties to the various species living there.

Figure 4: close-up photograph of an oyster bed with Wakame seaweed (*Undaria pinnatifida)*, another human-introduced species originally from Japan

The new structurally complex habitat may offer increased shelter to various organisms from for example predation, turbulence, and exposure to air (in the intertidal). Beukers and Jones (1998) showed that, on a coral reef, structurally more complex habitats provided significantly better juvenile survivorship for damselfish (*Pomacentrus moluccensis*) than structurally less complex habitats. However, increased habitat complexity may at the same time increase intermediate predator foraging efficiency through mechanisms that decrease intra- and interspecific aggression or competition. Hence, mechanisms driving increased predator foraging efficiency within complex habitats could counteract habitat complexity driven benefits to prey survival (Grabowski and Powers, 2004).

Increased physical structure in the habitat also creates more microhabitat types, and therefore a greater total niche space, which may allow the coexistence of competitors and the persistence of both predators and their prey (Smith, 1972 and Crowley, 1978 in Crowder and Cooper, 1982).

Oysters can also enhance sedimentation of fine particles through their trophic activity (Castel et al., 1989), or by altering hydrodynamic forces in such a way that sedimentation increases (Kirby 1994 in De Grave et al., 1998).

Sediment organic enrichment

Another major change in the habitat caused by the appearance of an oyster bed is organic enrichment of the sediment. This effect was shown for mussels (*Mytilus edulis*) by Kautsky and Evans (1987), by Grenz et al. (1990), and by Mattson and Linden (1983). Grenz et al. (1990) also showed increased bacterial production in mussel enriched sediments. Several studies have shown organic enrichment by oyster cultivation (Sornin et al. 1983 in De Grave et al., 1998); (Castel et al., 1989); (Hayakawa et al., 2001). Hayakawa et al. (2001) also suggest high degradation rates

of biodeposits at the sediment-water interface. The recycling of important quantities of organic matter in large oyster aggregations increases the oxygen demand and the hypoxic conditions can lead to ammonification (Lerat et al. 1985 in Castel et al., 1989).

Organically enriched and chemically altered sediment on oyster beds may have positive or negative effects on epi- and infauna. Castel et al. (1989) found meiofaunal densities near oyster farms to be higher compared to nearby sandflats, but macrofaunal densities to be lower. They argue that biodeposition by oysters enriches the substratum for meiofauna, but is detrimental to macrofauna as oxygen concentrations are lowered due to increased oxygen demand. However, de Grave et al. (1998) found no negative effect of oyster farming on the macrofaunal community.

Predation from refuge habitat

Using caging experiments Summerson and Peterson (1984) found evidence implying that predation by large epibenthic consumers was the major cause of between-habitat differences in infaunal densities. They proposed that epibenthic predators remain inside seagrass beds and other refuges during daylight, and restrict their predation on sand-flat infauna to the night, when risk of higher-order predation is reduced. This hypothesis implies that the importance of epibenthic predation on the infauna should decline as a function of increasing distance from the nearest seagrass-bed refuge. In a mussel transplant experiment by Ragnarsson and Raffaelli (1999), mobile epibenthic crustaceans colonized mussel transplant plots, but were absent at all times from the adjacent sandflat sediments. This may indicate that they hide on the mussel bed. This may also be the case on oyster beds.

Altered food web

Leguerrier et al. (2004) modeled the impact of oyster culture on a mudflat food web. They argue that the presence of oysters, which are direct trophic competitors of other filter feeders, modifies benthic-pelagic coupling by forcing a shift from pelagic consumers to benthic consumers. Increasing the surface area of cultivated oysters caused secondary production to increase, providing food for top predators (in particular juvenile nekton), reinforcing the nursery role of the mudflat in the ecosystem, and altering the species composition available to the top predators.

The Pacific oyster may also regulate zooplankton; it has been shown that *M. edulis* has a strong regulating effect on the development of microzooplankton, especially in summer (20-200µm) (Horsted et al. 1998 in Kater, 2002). An altered food web may provide new opportunities or difficulties to various species.

5. Effects on shellfish farming / tourism industry

C. gigas may have a negative impact on the mussel industry (*M. edulis*) through trophic competition and through predation of *C. gigas* on veliger larvae (van Stee, 2000 and Been, 2001 in Kater, 2002). Spat of Pacific oyster attached to mussels also reduces their market value. The tourism industry may be negatively impacted as surfers, swimmers and divers come into contact with the sharp edges of the oyster shells more frequently.

6. Research questions

To be able to predict what the consequences may be as *C. gigas* spreads, it is vital to understand oyster beds. Facilitation of establishment of new biota by non-native species capable of creating physical complexity in ecosystems may be a major and predictable consequence of biological invasions (Crooks and Khim, 1999). The new habitat provided by *C. gigas* beds has an associated flora and fauna, which may include native species that already lived on the mudflat, or native species that normally live on for example mussel beds or other hard substrata, or species that were introduced with or independently of the Pacific oyster. The oyster beds' epi- and infauna specifically is the subject of this study. Expansion of Pacific oyster may have a negative impact on some species that are unable to live on oyster beds, or are outcompeted. Other species may find a very suitable environment on oyster beds.

This study aimed to investigate how the presence of a Pacific oyster bed on soft substratum affects local faunal diversity. I investigated which species were positively influenced and which negatively, and where diversity was highest. I grouped collected species into taxonomic and trophic groups, and plotted mobile epibenthic crustaceans separately, to identify explanatory patterns. Aquasense (2003) investigated C. gigas beds on hard substrata. The current study focuses on oyster beds on soft substratum (mud or sand). To obtain an estimate of variability two oyster beds were sampled. Samples were taken along a transect from the center of the oyster bed to the transition zone and the adjacent mudflat. Epi- and infauna were identified and their abundances determined. In order to make general inferences about the effects of the spreading of oyster beds it is important to know the variability between oyster beds. Two oyster beds with different characteristics were compared. I hypothesized that diversity would be higher on the oyster beds due to enhanced structural complexity and organic enrichment of the sediment. This is contrary to the effect of oyster reef formation on hard substrata, which resulted in a decrease of diversity (Aquasense, 2003). The transition zone may harbour the highest diversity since it combines elements of both habitats, or it may harbour intermediate diversity since it may be an altogether less suitable habitat for species from both habitats.

Materials and Methods

1. Site selection

A number of oyster beds were visited. Two oyster beds were selected: Sint Annaland and Neeltje Jans (figure 5). These beds were deemed most suitable for this study because of their accessibility, relative undisturbedness, clear layout, clear transition from oyster bed through transition zone to mudflat (explained later in this chapter), and their similar tidal height. Furthermore, it was possible to take samples parallel to the low water line at the same tidal height.

One of the selected beds was located far inland in the Oosterschelde off Sint Annaland. It therefore received a flood current that already passed many other filter feeders, causing lowered food levels in the water column. Also daily water replacement was relatively low. The other was located off the estuary-side of the largely man-made island of Neeltje Jans, which was created to facilitate construction of the Oosterschelde storm surge barrier. It was the closest oyster bed to the mouth of the Oosterschelde and therefore received the freshest flood current, with the highest food levels and the largest daily water replacement.

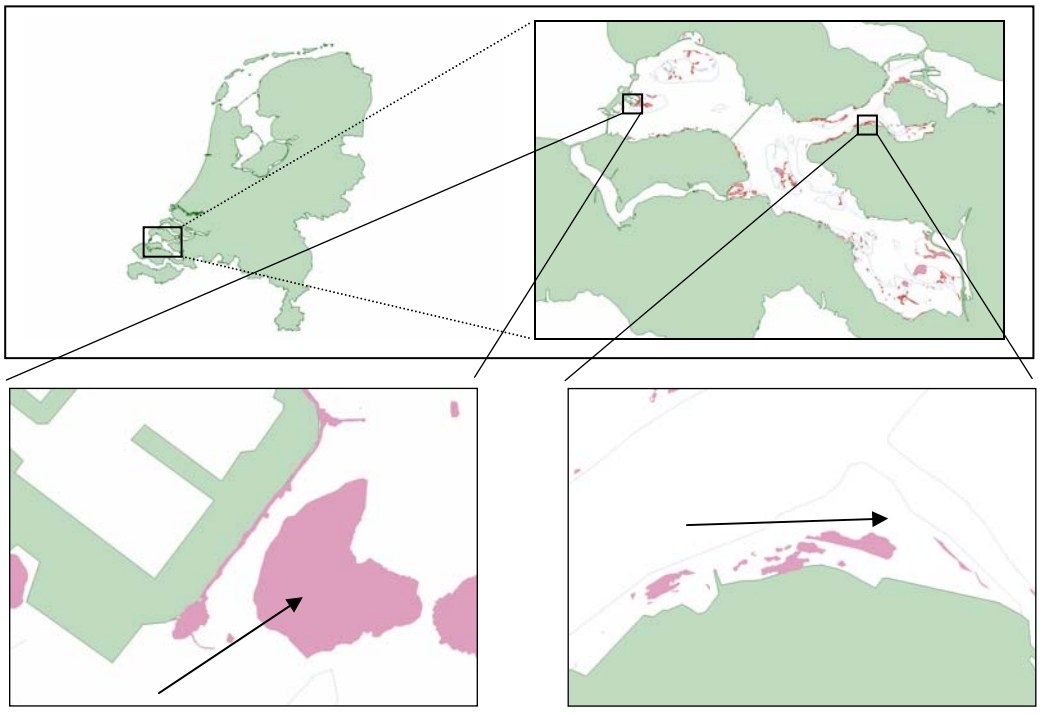

Figure 5: Geographic locations of the Sint Annaland and Neeltje Jans oyster beds. Oyster beds are shown in pink. Arrows indicate approximate direction of flood current. (Images by RIVO-CSO)

2. Sampling locations on oyster beds

To determine a gradient in faunal species richness and diversity, a sampling transect was employed from the center of the oyster bed to the mudflat, using five sampling locations (A – E, figure 6). On locations A - C both oyster-covered mudflat and bare mudflat were present (hereafter named 'oyster patches' and 'mud patches') – both were sampled as shown in figure 6. On locations D and E by definition only bare mud was present.

A: the oyster bed center
B: the edge of the oyster bed
C: the transition zone
D: approximately 5 m from the furthest patch of oysters
E: approximately 20 m from the furthest patch of oysters

Saier (2002) found that in the non-attached epifaunal community of mussel beds (*M. edulis*) the tidal level effect within a range of metres was strong, while the spatial variability in a much wider (kilometre) range but at the same tidal elevation was negligible. In order to eliminate the potential influences of distance from the low water line and tidal elevation these sampling locations were selected parallel to the low water line, and at the same tidal elevation. The tidal elevation was determined by repeated observation; locations were reached simultaneously by water during flood.

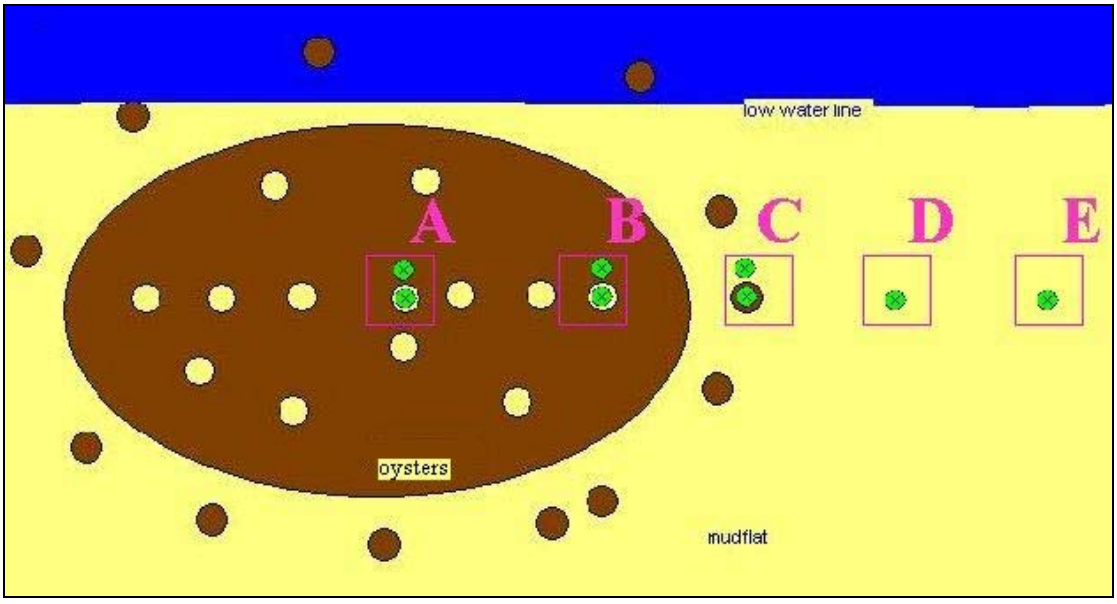

Figure 6: Location of sample points on a schematic representation of an oyster bed in top-down view. Capital letters and squares represent the sampling transect points. Green circles represent sampling locations. Brown: oysters; Blue: water; Yellow: mudflat.

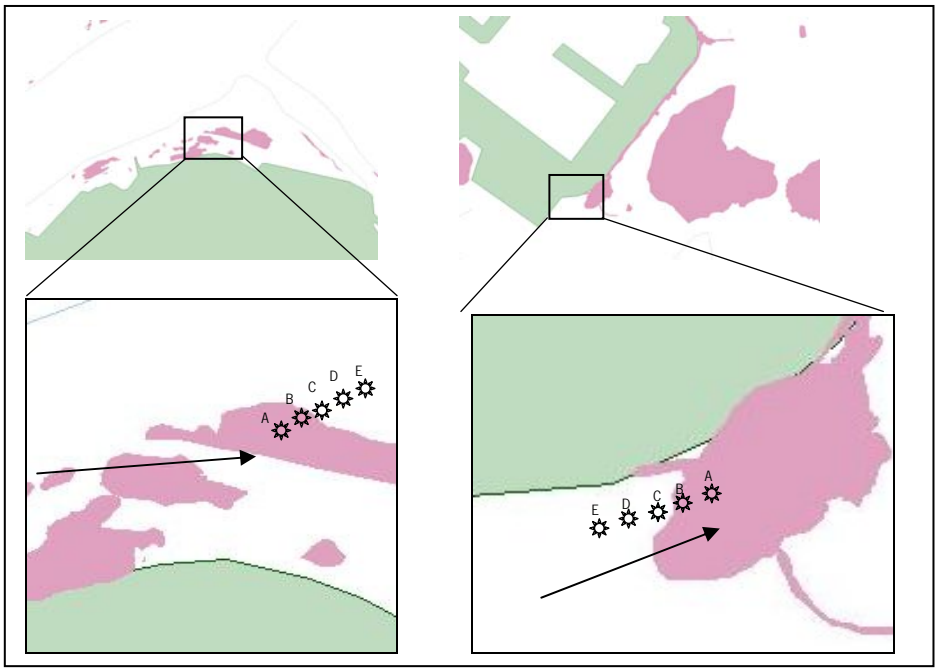

Figure 7: Sampling points on the oyster beds, depicted by stars. Oyster beds are shown in pink. Left: Sint Annaland. Right: Neeltje Jans. Arrows indicate approximate direction of flood current. (Images by RIVO-CSO)

3. Sampling

All samples were taken in the period from 02-09-2003 to 10-11-2003. To minimize bias due to seasonal effects this period was kept as short as possible. Three methods were used to take samples; hand corers, quadrats and collection of separate oysters. To sample the sediment, core samples were taken on all sampling locations. Two different-sized hand corers were used to collect sediment samples on all locations: a small corer ∅ 3.8 cm, height 22 cm (vol. 998 cm^3) to extract small specimens (500 µm – 1 mm) from, and a large corer ∅ 10 cm, height 24 cm (vol. 7540 cm^3) to collect larger specimens (> 1 mm). Oysters and other protruding items were cleared to ground level before core samples were taken.

On mudflat covered by oysters, the oysters and other fauna partly live above ground level and trap sediment above ground level. For a complete inventory all material in a 1/16 m^2 quadrat was also sampled on all sampling locations with oyster cover. Larger, readily identifiable specimens such as *Carcinus maenas* were identified alive and released in the Oosterschelde estuary. The remainder of the material was taken to the laboratory for analysis. The quadrat samples yielded a considerably larger amount of sediment than the core samples.

Some organisms live on or bore in the shell of live oysters, and to complete the inventory live oysters were collected to obtain these organisms. On locations A and B on the Neeltje Jans oyster bed separate oysters were collected at least 1 m apart, nine and eight oysters respectively.

The sediment obtained through hand coring and quadrat sampling was sieved to discard shell material, sand and silt and to isolate fauna. All specimens were stored in 70 % ethanol solution and stored at 4 °C for later analysis. To isolate macrofauna

only specimens that did not pass through a 500 µm mesh size sieve were analyzed. Four size fractions were created through stepwise sieving to facilitate analysis of fauna:

1:	500 µm – 1 mm	from the small core
2:	1 mm – 2 mm	from the large core
3:	2 mm – 5 mm	
4:	> 5 mm	

The separately collected oysters were kept cool and dry for two days, and were then placed in natural sea water under a dissection microscope. Following this procedure facilitates removal of most specimens because they partly come out of their shelter. All specimens were removed and stored cooled in 70% ethanol solution for later analysis.

4. Analysis

All specimens were identified using a dissection microscope and a microscope, to species level if possible. If this was not possible due to missing parts or other damage, the specimen was identified to the highest taxonomic level possible and only included in analyses where applicable. The main reference work used for species identification was The Marine Fauna of the British Isles and North-West Europe by Hayward & Ryland (1990).
For each location two indices were calculated. Perhaps the simplest index of diversity in use, Species Richness equals the number of species at a certain location. To give a better representation of diversity, the Shannon Index of diversity (H; formula 1) was calculated (Shannon C.E. and Weaver W., 1949).

$$H = -\sum_{S-1}^{S} Pi \ln P_i \qquad (1)$$

Where S = number of species
P_I = proportion of total number of individuals made up by the *i*th species

The Shannon Index is a widely used index of diversity in recent literature, and gives much more information about diversity than Species Richness since it incorporates the relative abundance of species. Note that H=0 when S=1.

Results

1. Overview

In all samples combined, 38 species were found (for more information see appendix). Of these, the 16 most abundant species are shown in figure 8.

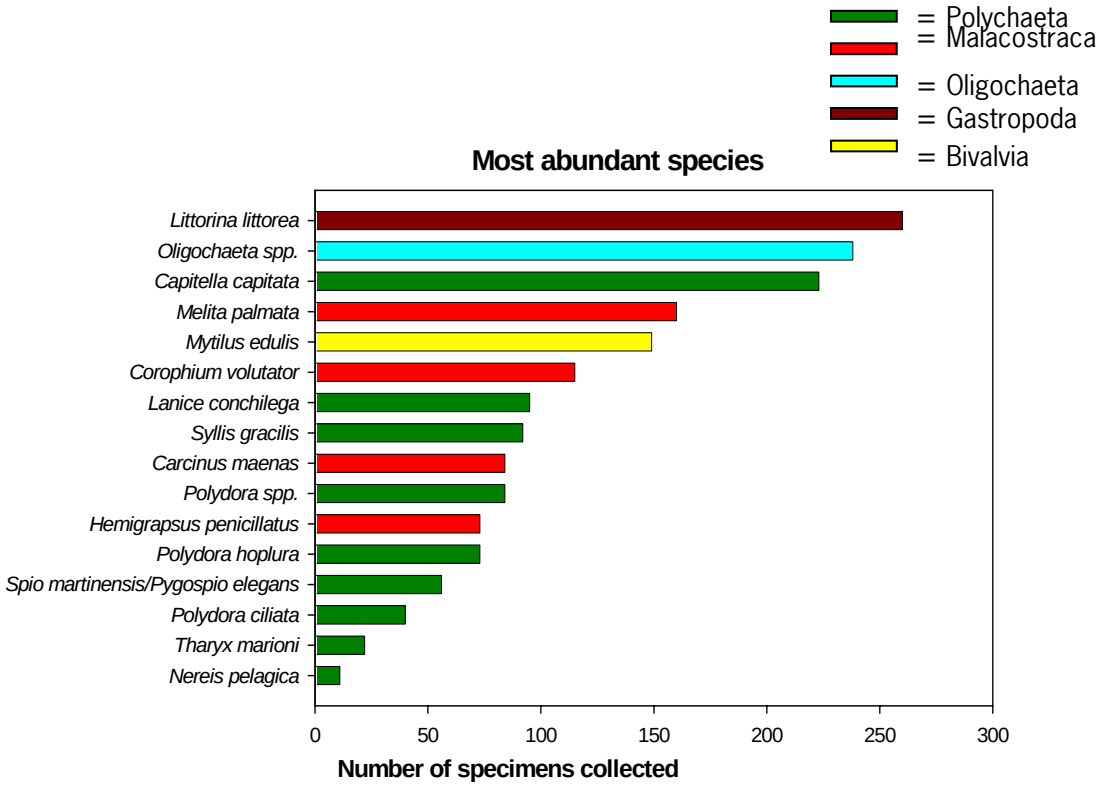

Figure 8: Number of individuals collected of the most abundant species, from all samples. The colours of the bars correspond with the species' taxonomic class (see legend). C. gigas are not shown.

The most abundant species was the periwinkle *Littorina littorea* (Dutch: alikruik), a gastropod. Note that the second most abundant group shown in the graph, the oligochaetes, were not identified to species level, but were treated as one group. *Polydora spp.* is also a combined group, including all *Polydora* species that could not be identified to species level. These bars therefore do not represent a single species but multiple, individually less abundant species. The third most abundant species was *Capitella capitata*, a polychaete.

Of the 38 species identified in total, 22 were polychaetes, therefore the group containing the most species. Malacostracans were represented by 8 species, which was therefore the second most speciose group.

The total number of specimens identified to species level was 2132, of the total number of 2361 specimens that were captured (90%). Polychaeta were the most abundant group, followed by Malacostraca and Bivalvia, Gastropoda and Oligochaeta (figure 9). Polychaeta, Bivalvia and Malacostraca together comprise 76% of specimens.

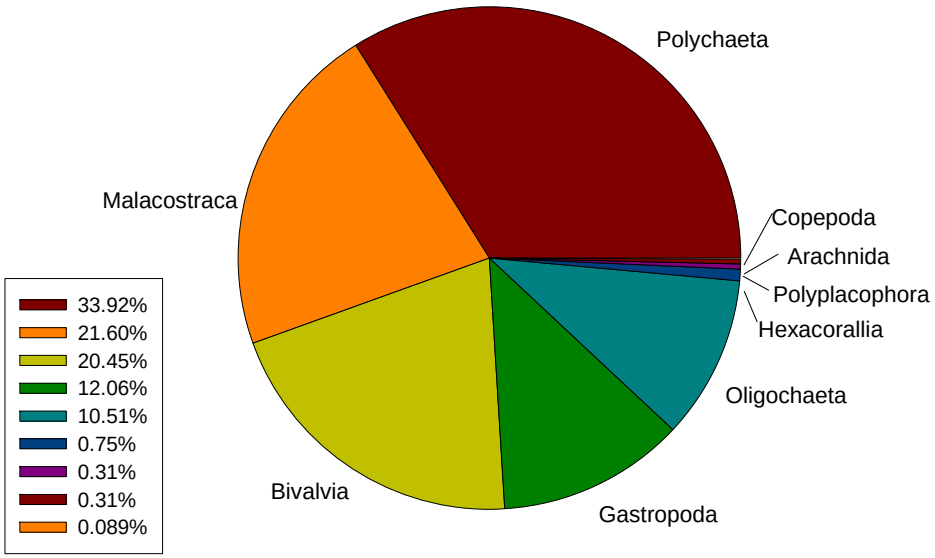

Figure 9: Relative abundances of taxonomic classes, from all samples.

2. Transect

On both oyster beds, the number of individual specimens collected from the quadrat samples increased from the center of the oyster bed to the transition zone (figure 10).

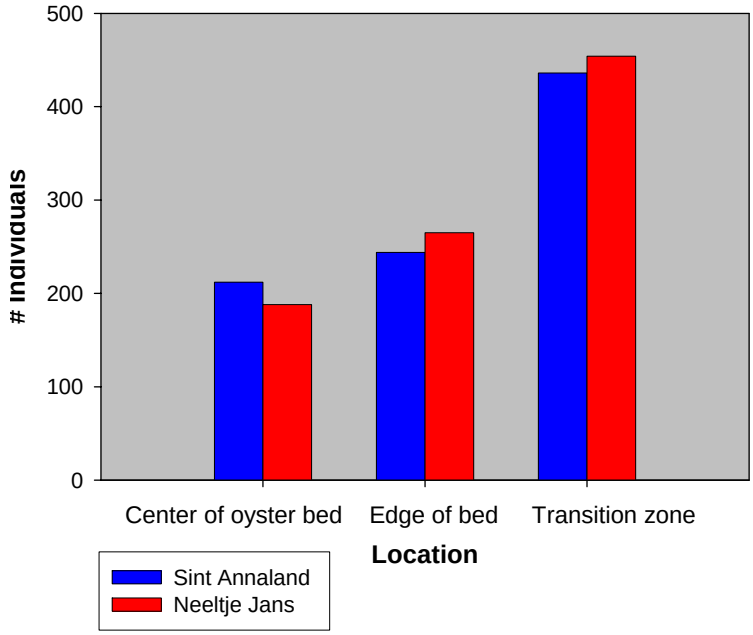

Figure 10: Number of specimens collected from quadrat samples, per location.

For each species the relative abundance at each location was calculated from the quadrat samples (data shown in figures 12,13). Subsequently for each location the relative abundances of all species were averaged. This places the same weight on each species, regardless of its absolute numbers. This analysis shows that species, on average, are most abundant on the transition zone on both oyster beds (figure 11).

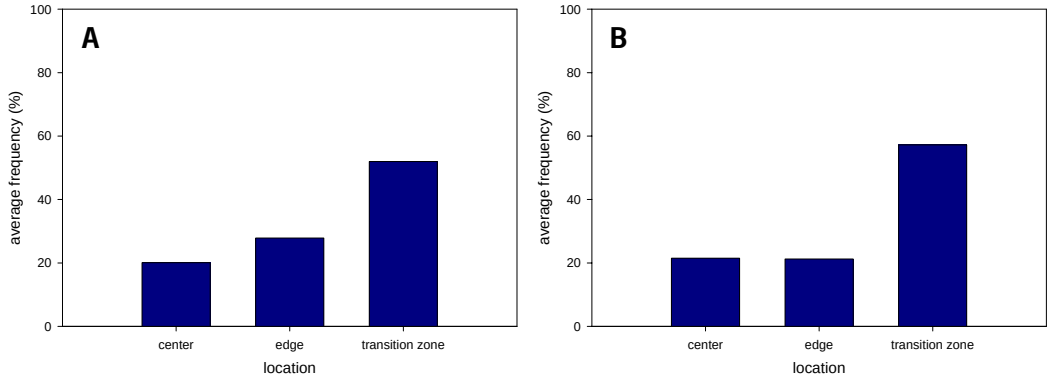

Figure 11: Average frequencies of all species from quadrat samples. A: Sint Annaland; B: Neeltje Jans.

Figure 12 shows the relative abundances of species, mentioned above. On Neeltje Jans many species were most abundant on the transition zone. Of the 13 species of which > 10 individuals were collected, 9 were most abundant on the transition zone. Furthermore, 7 of these were found in greater number on the transition zone than on the center and the edge of the bed combined. Of all polychaetes (except *Polydora ciliata* which was only found on the edge), only a fraction of the number found on the transition zone was found on the center and the edge of the bed. These effects were less pronounced on Sint Annaland.

Low numbers of individuals were found in the core samples (figure 13). The numbers were too low to perform similar analyses as shown for quadrat samples (figures 10,11). No clear pattern could be distinguished for either oyster bed.

3. Transect – Species Richness and Diversity

Species Richness (number of species) and the Shannon Index (diversity) were calculated separately for the quadrat samples (figure 14), and for the core samples (figures 15,16).
In quadrat samples from Neeltje Jans both species richness and diversity increased from the center of the oyster bed to the transition zone (figure 14b), whereas on Sint Annaland only species richness increased (figure 14a).

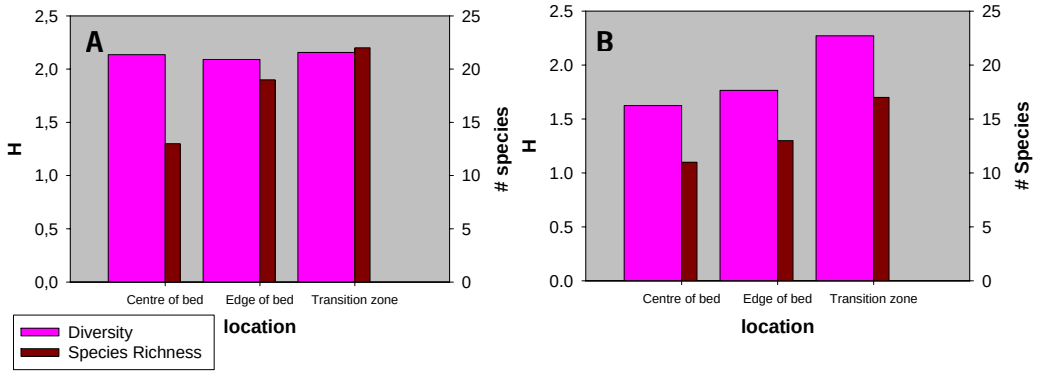

Figure 14: Diversity and Species Richness per location, from quadrat samples. A: Sint Annaland; B: Neeltje Jans.

Both diversity and species richness from all core samples (figures 15,16) showed considerably lower values than for the quadrat samples. Diversity from the core samples on oyster covered patches increased from the center of the oyster bed to the transition zone on both oyster beds (figure 15), but species richness increased only on Sint Annaland.

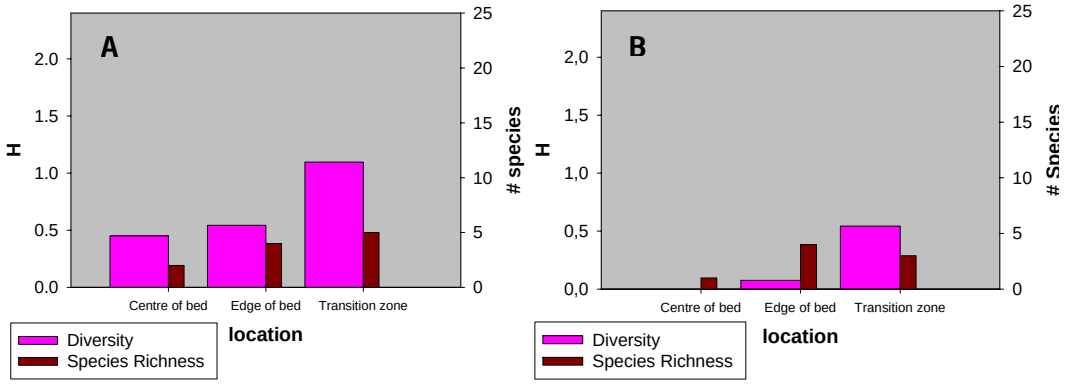

Figure 15: Diversity and Species Richness per location, from core samples on oyster covered patches. A: Sint Annaland; B: Neeltje Jans.

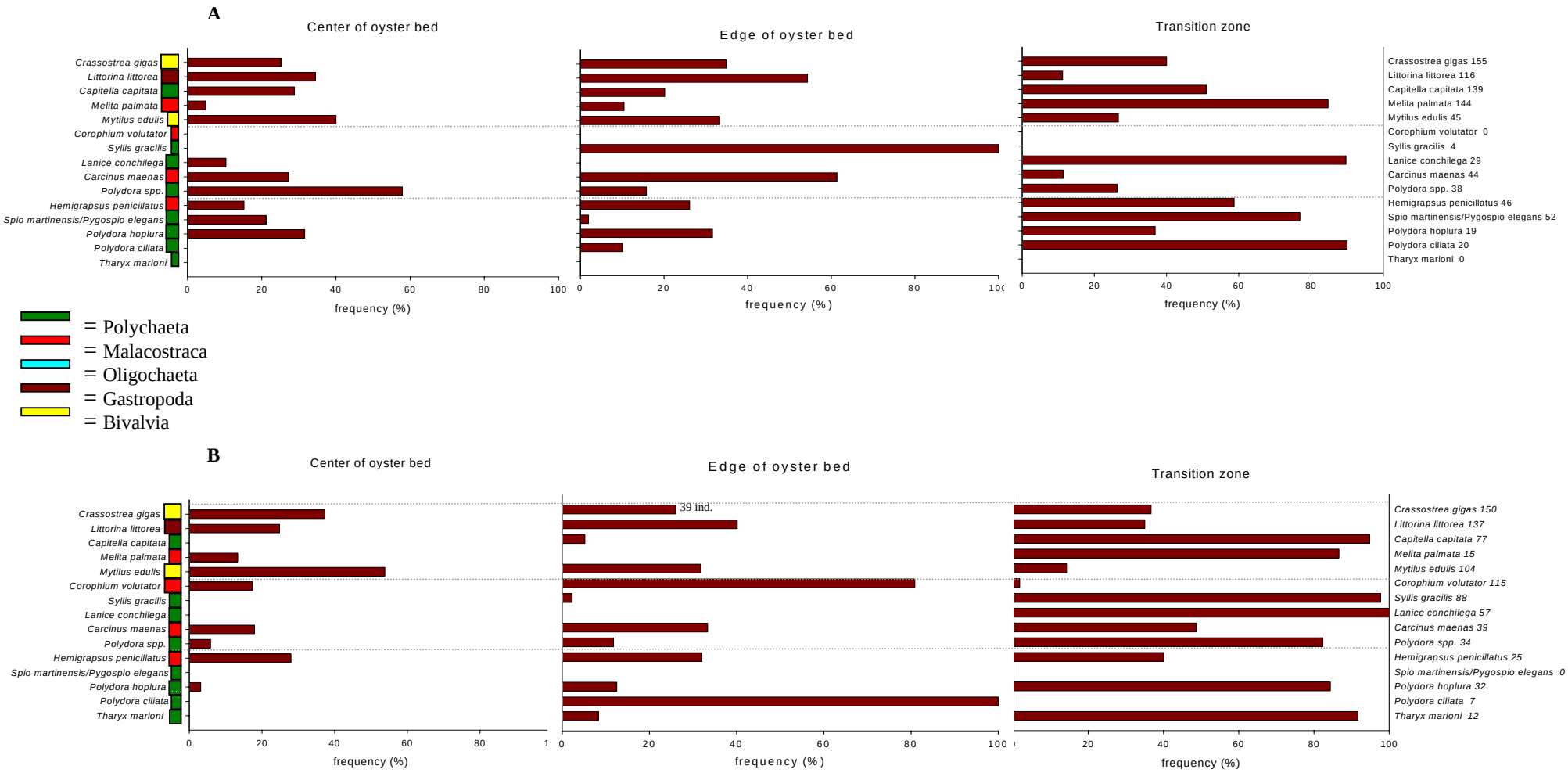

Figure 12: Species' occurence at specific sampling locations, from quadrat samples. Only species of which > 10 individuals were found are shown. The numbers of individuals found are shown to the right of the species' name. The colours of these numbers correspond to the species' taxonomic class. A: Sint Annaland; B: Neeltje Jans. In addition numbers of *C. gigas* collected are shown in the figures.

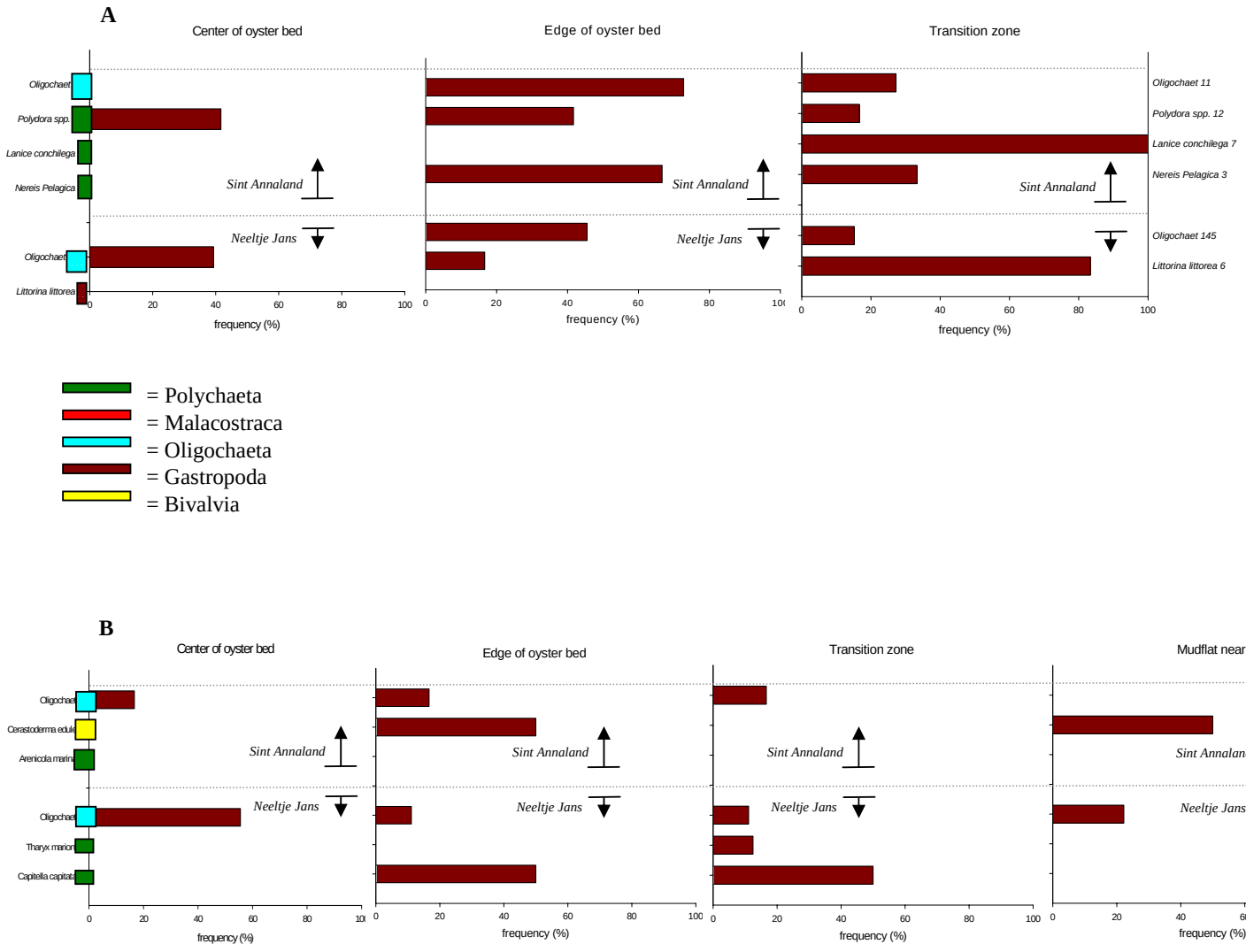

Figure 13: species' relative frequencies per location. Only species of which > 3 individuals were found in oyster and mud core samples combined are shown. The numbers of individuals found are shown to the right of the species' name. The colours of these numbers correspond to the species' taxonomic class (see legend). A: oyster covered patches; B: bare mud patches.

For the core samples on bare mud patches, diversity increased from the center of the oyster bed to the transition zone only on Neeltje Jans, as did species richness (figure 17). Diversity and species richness on Neeltje Jans were relatively low on the mudflat compared to the transition zone (figures 15b,16b). Diversity and species richness on Sint Annaland were lower on the mudflat (figure 16a) than on the transition zones' oyster patches (figure 15a). However, they were slightly higher than on the transition zones' bare mud patches (figure 16a).

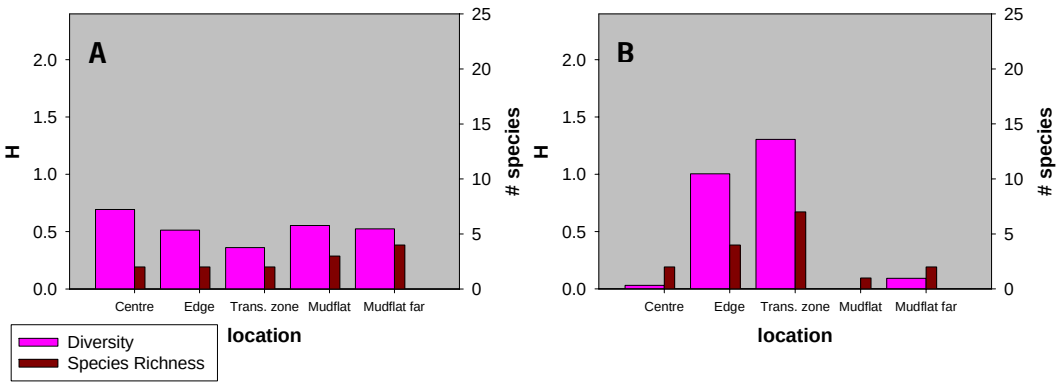

Figure 16: Diversity and Species Richness per location, from core samples on bare mud patches. A: Sint Annaland; B: Neeltje Jans.

The separately collected oysters showed higher species richness and diversity on the edge of the oyster bed than in the center (figure 17).

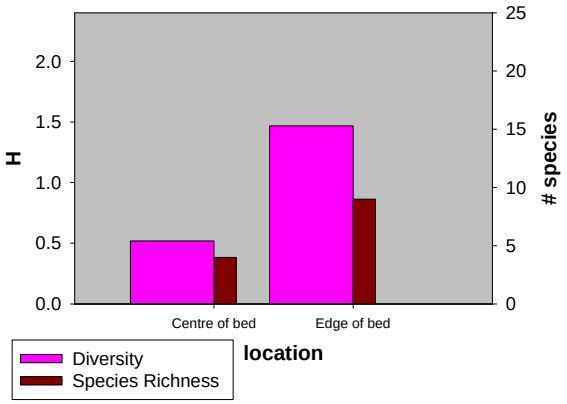

Figure 17: Diversity and Species Richness per location, from oysters collected on Neeltje Jans. Center of oyster bed: n=9 oysters; edge of oyster bed: n=8 oysters.

4. Transect - taxonomic / trophic groups

Figure 18 shows highest abundances on the transition zones of both oyster beds for Polychaeta. Bivalvia showed an opposite distribution. Gastropoda were most abundant on the edge of both oyster beds. Malacostraca showed a clear difference between both oyster beds.

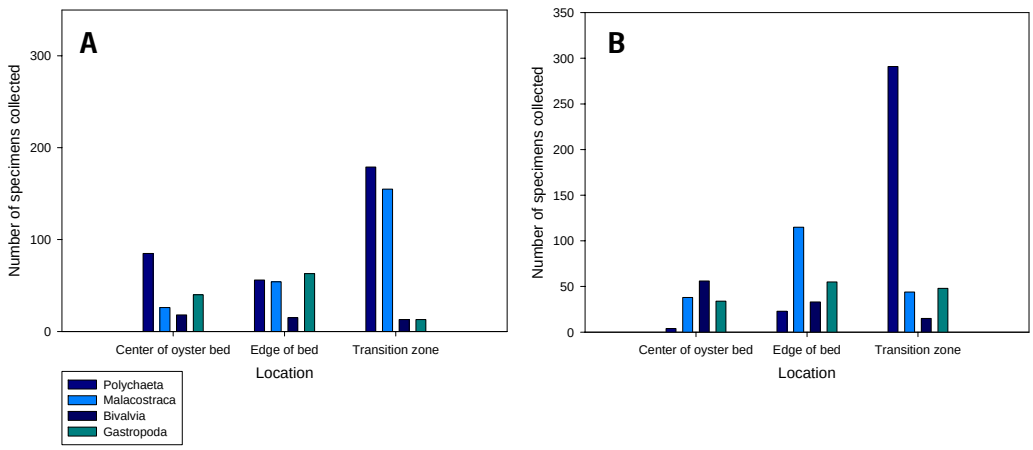

Figure 18: Numbers of collected specimens of most abundant taxonomic groups from quadrat samples. A: Sint Annaland; B: Neeltje Jans. The group Bivalvia is shown without C. gigas.

Average frequencies of the most abundant taxonomic classes from the quadrat samples were plotted separately in figure 19, in the same way as figure 11. The core samples covering the entire length of the transect, from the center of the oyster bed to the mudflat, produced too low numbers of specimens to perform the same analyses as for the quadrat samples. Polychaeta, the most abundant taxonomic group collected in this study, showed the same pattern on both oyster beds as the average frequencies in figure 11. Malacostraca and Bivalvia both showed an almost opposite pattern on one oyster bed and a similar pattern to the Polychaeta on the other. Gastropoda were most abundant on the edge of the oyster bed.

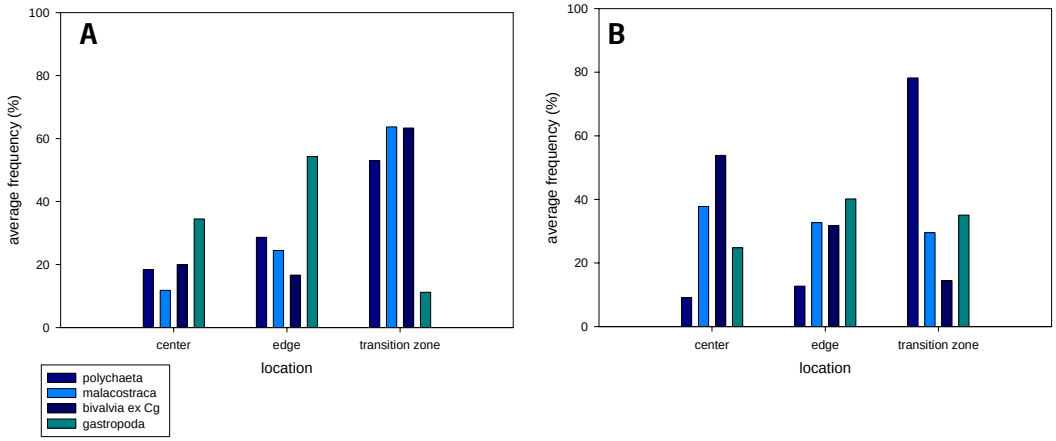

Figure 19: Average frequencies of most abundant taxonomic groups from quadrat samples. A: Sint Annaland; B: Neeltje Jans. The group Bivalvia is shown without *C. gigas.*

Figure 20 shows very similar distributions on both oyster beds. Deposit/suspension feeders and carnivore/omnivores were most abundant on the transition zones, and herbivores were most abundant on the edges of the beds.

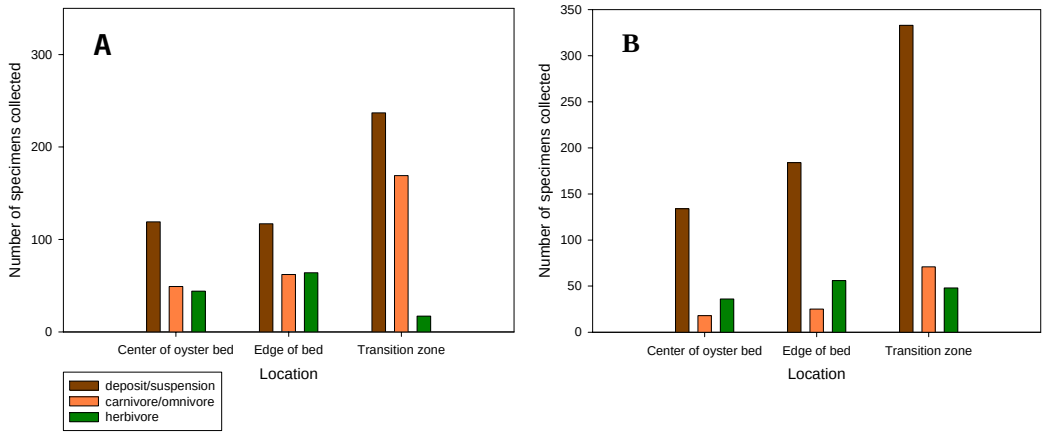

Figure 20: Numbers of specimens collected of trophic groups from quadrat samples. A: Sint Annaland; B: Neeltje Jans.

I grouped the species into three trophic groups based on their diet: deposit/suspension feeders, carnivores/omnivores, and herbivores (for more information see Appendix). On both oyster beds all three trophic groups occurred in relatively low numbers on the center of the bed, and most on the transition zone, the only exception being the herbivores on Neeltje Jans (figure 21). The herbivores showed an almost opposite pattern between both oyster beds.

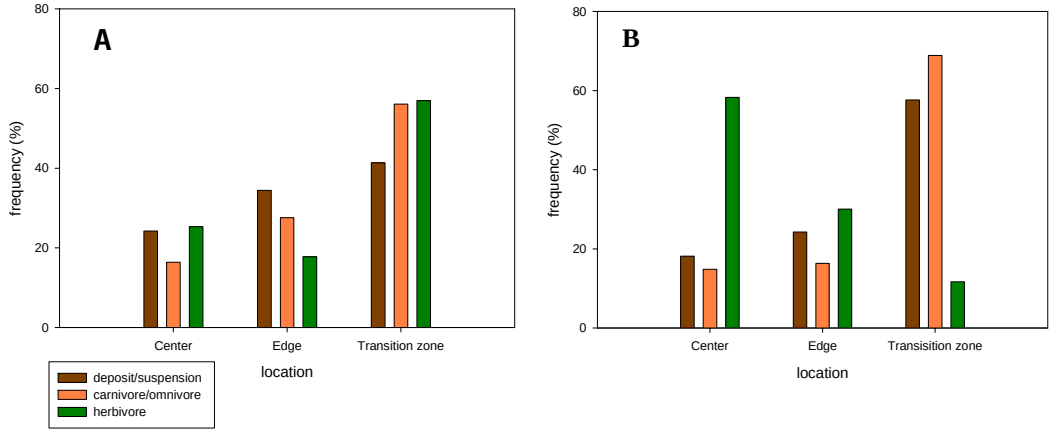

Figure 21: Average frequencies of trophic groups from quadrat samples. A: Sint Annaland; B: Neeltje Jans.

The average frequencies for two of the putatively most mobile species, the crab species *Hemigrapsus penicillatus* and *C. maenas*, were plotted in figure 22. Both species were most abundant on the transition zone, except *C. maenas* on Sint Annaland.

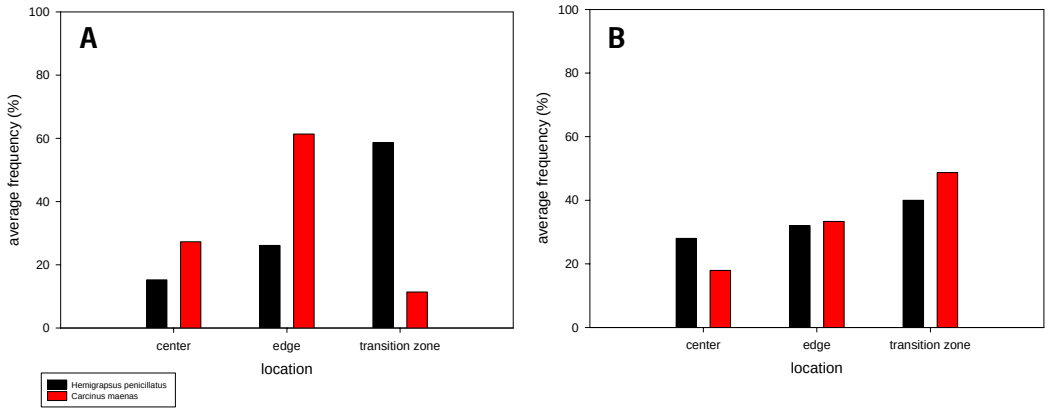

Figure 22: Frequencies of two crab species. A: Sint Annaland; B: Neeltje Jans.

Discussion and Conclusions

1. Overview

I collected macrofauna from two oyster beds, along a transect from the center of the oyster bed to the mudflat. The core samples covered the entire transect (oyster bed, transition zone and mudflat), whereas the quadrat samples covered only the oyster bed and transition zone. The core samples yielded considerably lower numbers of specimens than the quadrat samples. This was probably due to smaller sample size. Also the sediment that was sampled using quadrats may have contained more specimens per unit volume than the sediment from the core samples; the density of organisms appeared to be greater near the surface than deeper in the sediment (personal obs.). This sediment appeared to be the most organically enriched by oysters; faeces and pseudofaeces of oysters can get trapped between oyster shells and become part of the sediment (see Introduction) (Castel et al., 1989; Hayakawa et al., 2001). The accumulation and enrichment of this trapped sediment may be one of the most important effects of oyster beds on the local environment, producing a rich, novel habitat for large numbers of organisms.

2. Transect - general

First I will discuss the part of the transect that comprised the center of the oyster bed, the edge and the transition zone. On both oyster beds numbers of specimens, numbers of species, and diversity generally increased from the center of the oyster bed to the transition zone. This was not explained by the number of oysters in the quadrats; although numbers of oysters increased from the center of the oyster bed to the transition zone on one bed, they did not on the other (numbers in figure 12). This trend was clearer on Neeltje Jans than on Sint Annaland. On Neeltje Jans it was supported by nearly all analyses: number of specimens in quadrat samples (figure 10), average frequency of species (figure 11), all but one values for species richness (table 1), and all values for diversity (table 1).

On Sint Annaland this trend was supported by the same analyses minus: diversity of quadrat samples, and diversity of core samples on bare mud patches. Diversity on quadrat samples showed approximately constant values for all three locations. Therefore, although not supported equally strongly, the same trend was shown for both oyster beds. Aquasense (2003) concluded that on hard substrates, when oyster cover exceeded 60%, diversity was lower than at lower oyster coverage. Possibly relatively low oyster cover on transition zones allows the coexistence of multiple habitat types, thus increasing diversity.

Table 1: Summary of diversity and species richness patterns, from the center of the oyster bed to the transition zone. A: Sint Annaland; B: Neeltje Jans. Symbols for an increasing pattern are shown in green for ease of reference.

A

Sample type	diversity (H)	species richness (# species)
Quadrat	□	+
core oyster	+	+
core mud	-	□

B

Sample type	diversity (H)	species richness (# species)
Quadrat	+	+
core oyster	+	^
core mud	+	+
Oysters	+	+

LEGEND	
-	Decrease
□	Stable
+	Increase
^	Peak at B

Secondly, I discuss the entire transect, from the center of the oyster bed to the mudflat. Only core samples were taken over the entire transect. For all core samples on both beds - except Sint Annaland's bare mud patch samples - the relatively low values outside the oyster bed were very similar in magnitude to the values on the center of the oyster bed (figures 15;16). On Sint Annaland, bare mud patch values on the mudflat showed relatively high values compared to the other sample series. However they were relatively not very dissimilar from the values at the center of the bed. Therefore it appears that on both oyster beds, diversity and species richness of the sediment below ground level were about the same magnitude at the center of the oyster bed as on the mudflat.

Combining these results with the results from the sediment trapped between oyster shells (quadrat samples) showed that, in total, diversity on the mudflat was clearly lower than on the oyster beds and on the transition zones for both oyster beds. This was directly caused by the production of very rich interstitial sediment on the oyster beds. This sediment can support many more organisms than the unenriched bare mudflat. No strongly adverse effect on fauna from organic enrichment, such as found by Castel et al. (1989) for hypoxic conditions or such as found by Lerat et al. (1985 in Castel et al., 1989) for ammonification, appeared likely from the findings in this study. However, a comparison with their findings was difficult since confounding effects of the composition of the original bare mudflats cannot be excluded.

3. Transect - taxonomic / trophic groups

Polychaeta were clearly most abundant on the transition zone. This was shown both in absolute numbers of specimens collected, and in average distribution of all polychaete species (figure 19). Malacostraca, in the same way, were most abundant on the transition zone on one of the oyster beds. Bivalvia (excluding C. gigas) occurred in

relatively low numbers, and their abundance decreased from the center of the beds to the transition zone. Gastropoda were most abundant on the edge of the oyster bed; the reason for this is unclear.

Deposit/suspension feeders and carnivore/omnivores showed the same pattern of increase from the center of the oyster bed to the transition zones as the Polychaeta. This was shown both in absolute numbers and in average distribution of species (figure 21). For deposit/suspension feeders this similarity was probably due to the fact that the most abundant deposit/suspension feeders were polychaetes. For the carnivore/omnivores however, this similarity, especially on Sint Annaland, was peculiar. This group was largely made up of malacostracans, that showed a markedly different distribution on Sint Annaland. This indicates that the transition zone is a richer feeding ground for carnivore/omnivores; possibly the deposit/suspension feeding polychaetes are their prey and thus cause this pattern.

Herbivores, in absolute numbers, were most abundant on the edge of the oyster bed, but showed opposite patterns in their average preference. However, the average preference was strongly influenced by several species of which only a few individuals were found.

4. Variability between oyster beds

Relatively little difference between the oyster beds was found in total number of specimens (figure 10). Taxonomic groups showed much variability, trophic groups less; only the herbivores show a distinctly different pattern. The faunal community as a whole is virtually the same size on both beds, and shows little difference in trophic roles, but the individual species composition differs. This suggests that different species, even from different taxonomic groups, may fulfil the same role on different oyster beds.

The differences at some points between oyster beds necessitate caution in the wider interpretation of the results from this study. My data suggest that diversity was lowest on the center of the oyster bed and highest on the transition zone. However, on one of the oyster beds this was not shown unequivocally. A potential confounding effect may have been the direction of the flood current. The Neeltje Jans oyster bed received a fresh flood current, whereas the Sint Annaland oyster bed received a flood current that had already passed over the oyster bed for a considerable distance before reaching the sample site (figure 5). This may have caused some irregularity in the results on Sint Annaland. To accurately determine the magnitude of variability between oyster beds, more beds would need to be sampled.

5. Comparison with mussel bed studies

Few comparable studies on diversity in oyster beds have been carried out previously. However, a number of studies have investigated diversity in beds of several species of mussel. Mussel beds have many features in common with oyster beds, making a comparison a logical step. Increased diversity and abundances on beds were also found in multiple mussel studies. Günther (1996) concluded that the number of taxa and diversity were higher on M. edulis beds than on the adjacent sandy areas of the same tidal elevation. Crooks (1998), working with another species of mussel, the byssal mat forming Musculista senhousia, also found higher densities of all

macrofaunal individuals as well as species richness inside than outside mussel mats. However, the opposite effect has also been described occasionally. Dittmann (1990) found that from a sandflat to a mussel bed (M. edulis) mean species densities of macrofauna did not differ significantly, while abundances were significantly lower in the mussel bed than in the sandflat.
The underlying mechanisms of the effects of mussel beds on the occurrence of macrofaunal groups have also been investigated. Ragnarsson and Rafaelli (1999) concluded that the effects of mussels on infauna were probably caused by a combination of biodeposition and filtration by the mussels, and the provision of a structurally complex habitat. Hartstein and Rowden (2004) argued that findings of mussel farm effect studies generally follow the pattern first identified by Mattson and Linden (1983), where the original shallow water macrofaunal assemblage of soft sediments is replaced by one dominated by small opportunistic polychaetes. The parameters that best explained the difference in macroinvertebrate assemblage were sediment total organic matter and number of mussel shells.

Conclusions of mussel bed studies generally agree with the results of this study. Diversity and abundances were generally higher on mussel beds than on the adjacent mudflats. This was often explained by structural complexity of the mussel bed habitat, and by organic enrichment of the sediment, suggesting that the same mechanisms may be responsible for the patterns observed in this study.

6. Causes for patterns of diversity

From mussel bed studies two main potential causes for patterns of diversity are frequently identified: structural complexity of the habitat, and organic enrichment of the sediment. In this section I discuss additional literature concerning these topics.
Many studies have correlated physical structure and number of habitat types with increased diversity. Smith (1972) and Crowley (1978), both in (Crowder and Cooper, 1982), concluded that increased physical structure creates more microhabitat types. The presence of epibenthic microhabitats results in a variety of trophic groups co-occurring in a mussel bed (Dittmann, 1990). This supports my finding that diversity is higher on the oyster bed than on the adjacent mudflat. The center of the oyster bed has the greatest amount of structural complexity (personal obs.). However, transition zones may harbour more microhabitat types than the center of the oyster bed, since they combine attributes of two habitat types; oyster bed and mudflat. Zajac et al. (2003) showed, on a larger scale (50-200 m width), that transition zones add considerably to variation in infaunal abundance. This supports the trend to highest diversity on the transition zone, identified in this study.

Various studies have investigated the effects of enhanced habitat structure on specific types of fauna. Prey survival often increases with enhanced habitat structure (Beukers and Jones, 1998; Crowder and Cooper, 1982; Diehl, 1988;Grabowski, 2004; Heck and Thoman, 1981; Schriver et al., 1995; Summerson and Peterson, 1984). The prey that tend to be associated most closely with dense structure or other refuges are larger, higher utility prey and those most vulnerable to predation (Crossman, 1959; Charnov et al., 1976; Stein, 1977 and Van Dolah, 1978, all in Crowder and Cooper, 1982). However, increased habitat complexity may at the same time increase intermediate predator foraging efficiency through mechanisms that decrease intra- and interspecific aggression or competition. Smith (1972 in Crowder and Cooper, 1982) and Crowley (1978 in Crowder and Cooper, 1982) argue that because increased physical structure in the habitat also creates more microhabitat

types, and therefore a greater total niche space, this may allow the coexistence of competitors and the persistence of both predators and their prey. Thus, mechanisms driving increased predator foraging efficiency within such complex habitats could counteract habitat complexity driven benefits to prey survival (Grabowski and Powers, 2004). Indeed both prey and predator diversity and abundance were higher on the transition zones than on the centers of the oyster beds in this study. Increased total niche space and variability may have benefited both predator and prey.

The higher diversity and abundances on the oyster bed than on the mudflat may also, be caused by organic enrichment of the sediment (see Introduction) (Castel et al., 1989; Hayakawa et al., 2001) of the sediment. It may be a combination of biodeposition and structural complexity of the habitat that may be responsible for the observed effects; however, the relative importance of both factors would need to be investigated further.

In addition, another cause for the high abundance of deposit/suspension feeders on the transition zone may simply be the available living space. Most polychaetes collected in this study are infaunal, and as such require sediment to live in. On the center of the oyster bed the density of oysters may be too great. The transition zone may provide the best compromise between nutrient availability, shelter, and space.

7. Predation from oyster bed

Shrimps en crabs appeared to hide on oyster bed and venture out onto the mudflat during high tide (personal obs.). Collecting accurate inventories of mobile predators during high tide and low tide on the mudflat proved to be beyond the scope of this study. However, two very mobile predators were collected on the oyster beds: H. penicillatus and C. maenas. Figure 22 shows that H. penicillatus was most abundant on the transition zone, and C. maenas was most abundant there on one of the oyster beds. However, whether they forage from the oyster beds onto the mudflats cannot be concluded since many other, less mobile species were also found in greatest numbers on the transition zone. This would need to be investigated more specifically.

8. Implications of spreading C. gigas in Dutch waters

The implications for Dutch estuarine waters of the spreading of C. gigas beds may be substantial. Locally the implications are most obvious. Seafloor physical structure is enhanced and faunal abundance and diversity are considerably increased. The possible future extent of this enhancement is not known however, since the carrying capacity of Dutch waters for C. gigas beds, or for filter feeders in general, is not known. Furthermore the result of competition for food and space with other species is not yet clear. C. gigas competes for space with M. edulis and Mya arenaria, and is capable of displacing these species (Shatkin 1997 in Kater, 2002). It also competes with the polychaete Lanice conchilega for suspended food particles (Kater, 2002), and possibly with other suspension-feeding (in-)fauna. Consequently the extent of future spreading cannot yet be accurately predicted. The biota as a whole may change, but to what extent remains to be investigated.

9. Conclusion

Diversity and macrofaunal abundance were shown to be considerably higher on oyster beds than on the adjacent mudflats. Spreading of oyster beds, and thus, frequently, replacement of mudflats, locally changed and enriched the faunal assemblage. A combination of biodeposition and the structural complexity of the habitat are the most probable causes for the increased diversity and abundances on oyster beds. Diversity was generally greatest on the transition zone; this was probably caused by the aforementioned two factors plus an overlap in habitat types from the mudflat and from the oyster bed. Deposit/suspension feeders were most abundant on the transition zone. This probably caused a similarly increased abundance of carnivore/omnivores there by providing a richer feeding ground. The transition zone may provide the best compromise for deposit/suspension feeders between nutrient availability, shelter and living space. My findings agree with the conclusion drawn by Zajac et al. (2003); transition zones may be ecologically important areas in seafloor environments. The invading species C. gigas clearly has and expresses the ability to locally change its environment, and in so doing has a considerable impact on the local biota.

10. Recommendations

Although trends have been identified in this study, further research is needed for a more complete understanding of the mechanisms underlying community structuring on oyster beds, and to be able to make predictions about future invasions of habitat-altering invaders.

In a future study, sample size on the mudflat would need to be much greater to produce higher numbers of specimens. This would allow a better comparison between mudflat and oyster bed. Another topic for future research would be investigating the relative contributions of oyster biodeposition and the provision of a structurally complex habitat to the observed patterns of diversity. This could include experimental patches of oyster reef using nutrient depleted sediment, or strictly structural complexity and no living oysters.

Sampling oyster beds at multiple tidal heights would probably yield interesting results, as Saier (2002) found that in the non-attached epifaunal community of M. edulis beds the tidal level effect within metres was strong, while the spatial variability in a much wider (kilometre) range but at the same tidal level was negligible. Sampling more than two oyster beds would allow a more reliable determination of variability between beds. As mentioned before, predation by predators hiding inside the oyster bed may depress faunal abundances in the vicinity. This effect should be investigated and possibly sampling needs to be continued further away from the oyster bed. Potentially, even the furthest-away sampling point (E) may not represent the base situation of a mudflat. Predator activity outside the oyster beds could be measured by catching predators at different phases of the tidal cycle.

This study investigated macrofauna (> 500 µm). Including meiofauna could improve our understanding of C. gigas beds. However, this may only be possible by the use of other isolation techniques than the sieving method employed here, since my trials with smaller mesh size failed due to sediment grain size. Possibly density separation methods can be used, for example using colloidal silica (de Jonge V.N., 1977).

Long term studies would give a more complete picture. This study represents a single state in time of the faunal community on the oyster beds. All samples were taken in as short a period as possible, to exclude seasonal effects. However, seasonal changes in faunal assemblage might be an interesting subject for further study. Apart from seasonal effects, changes over the course of years may also take place. On M. edulis beds on hard substrata, Okamura (1986) found that faunal communities can change drastically over seasons and over years. The age of an oyster bed may also be an important factor for the faunal community as found by Günther (1996) for M. edulis beds; possibly a succession of faunal communities occurs.

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Appendix

Species	# found	Diet	Species	# found	Diet
Crassostrea gigas	305	d/s	*Cerastoderma edule*	6	d/s
Littorina littorea	260	h	*Jaera albifrons*	4	h
Oligochaeta	238	?	*Pygospio elegans*	3	d/s
Capitella capitata	223	d/s	*Nereis diversicolor*	3	d/s
Melita palmata	160	c/o	*Nepthys hombergi*	2	c/o
Mytilus edulis	149	d/s	*Arenicola marina*	2	d/s
Corophium volutator	115	d/s	*Lepidonotus squamatus*	2	c/o
Lanice conchilega	95	d/s	*Eumida sanguinea*	2	c/o
Syllis gracilis	92	d/s	*Anaitides maculata*	2	c/o
Polydora spp.	84	c/o	*Platynereis dumerilii*	2	h
Carcinus maenas	84	c/o	*Urothoe poseidonis*	1	c/o
Spio martinensis/Pygospio elegans	56	d/s	*Mysta picta*	1	c/o
Polydora hoplura	73	d/s	*Odostomia spp.*	1	p
Hemigrapsus penicillatus	73	c/o	*Eteone longa*	1	c/o
Polydora ciliata	40	d/s	*Jaera forsmani*	1	h
Tharyx marioni	22	d/s	*Jaera praehirsuta*	1	h
Nereis Pelagica	11	d/s	*Nereis fucata*	1	?
Streblospio spp.	8	d/s	*Laophonte brevicornis*	1	?
Lepidochitona cinereus	7	h	*Nereis virens*	1	c/o

Appendix: Number of individual specimens from all samples identified to species level, per species. Abbreviations for diet: d/s: deposit/suspension feeder; c/o: carnivore/omnivore; h: herbivore; p: parasitic.