

# Effects of an area closed to fisheries on the composition of the benthic fauna in the southern North Sea

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Duineveld, G. C. A., Bergman, M. J. N., and Lavaleye, M. S. S. 2007. Effects of an area closed to fisheries on the composition of the benthic fauna in the southern North Sea. – *ICES Journal of Marine Science*, 64: 899–908.

The effects of fishery exclusion on the composition of the macrofauna were determined by comparing the fishery-exclusion zone around a gas production platform in the southern North Sea (Frisian Front) with nearby regularly fished areas. A Triple-D dredge was used, in addition to a standard box corer, to collect the relatively rare and larger species. Multivariate analysis showed greater species richness, evenness, and abundance of mud shrimps (*Callinassa subterranea*, *Upogebia deltaura*) and fragile bivalves (*Arctica islandica*, *Thracia convexa*, *Dosinia lupinus*, *Abra nitida*, *Cultellus pellucidus*) in the Triple-D samples from the exclusion area. Although box cores did confirm the higher abundance of both mud shrimps in the exclusion zone and demonstrated greater densities of the brittlestar *Amphiura filiformis*, they did not clearly reveal the distinctness of the exclusion zone. This is attributed to the large proportion of small, short-living species in the samples and the relative scarcity of vulnerable larger species common to all the box core samples. There was no evidence of greater recruitment in the relative small exclusion zone, despite its positive effect on adult survival. The observation that the fishery affects deep-living mud shrimps may point to consequences for the functioning of the benthic ecosystem other than simple loss of biodiversity.

**Keywords:** benthos composition, epifauna, fishery-closed areas, infauna, long-term fishery impacts.

Received 30 November 2005; accepted 17 February 2007; advance access publication 16 May 2007.

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## Introduction

Direct impacts of beam trawling on the benthic community of the southern North Sea have been well documented (see review by Kaiser and de Groot, 2000). A single haul with a standard commercial beam trawl causes direct mortality of 5–40% of the initial densities of various adult macrobenthos species. Bivalve species are subjected to direct mortalities of 20–65% (Bergman and van Santbrink, 2000). Regular trawling of benthic communities in the southern North Sea is expected to be responsible for species shifts and for the scarcity or disappearance of certain species (Craeymeersch *et al.*, 2000). Together with the damaged individuals in the trawl path, fish and invertebrates discarded from trawlers become available to scavengers and to the detritus food chain. It is estimated that between 6% and 13% of the annual production of macrobenthos of the swept area suddenly becomes accessible after a single beam trawl (Groenewold and Fonds, 2000). This may generate changes in energy pathways and structure of the benthic community (Groenewold, 2000). Heath (2005) concluded that benthic production of, for instance, crustaceans has increased in the North Sea over the past 30 y. Although this could have been caused by a reduction in the numbers of predatory fish, it might also have been generated by an enhanced food supply attributable to trawling mortality.

To evaluate long-term impacts of trawling, Jennings *et al.* (2001) compared the benthic fauna in two areas of the central North Sea with different fishing intensities. They observed a decrease in biomass of epifauna and infauna, the dominance of

polychaetes, and the scarcity of bivalves and spatangoids. The gross trophic structure of the communities, in contrast, did not seem to be altered by species shifts. Norse and Watling (1999) argue that all mobile fishing methods easily damage the benthic structures on and in the seabed, including the biogenic structures that create a diversity of habitat patches. As this structural complexity is positively correlated with species diversity, trawling affects biodiversity by reducing structure-associated benthic species. Relationships between benthic biodiversity and ecosystem functioning (e.g. mineralization, production) are largely obscure, yet such information is vital in assessing how far a benthic ecosystem is resilient to levels of trawling disturbance.

Despite the extensive data set on direct trawling effects, there is still public debate on the long-term effects of beam trawling on the benthic communities of the southern North Sea. Attempts to correlate patterns in fishing effort and benthos to distinguish long-term impacts have been largely unsuccessful, because strong natural gradients exist in the southern North Sea that govern distributions of benthos and fish, and hence fishing effort (Bergman *et al.*, 1998; Craeymeersch *et al.*, 2000). Such conditions hamper within-community comparisons such as that of Jennings *et al.* (2002). Large, homogeneous, and permanent non-fished areas necessary for a study on long-term impact of trawling are not available in the heavily exploited southern North Sea. Nevertheless, relatively undisturbed, albeit small, areas do exist in the form of 500 m exclusion zones around offshore installations. The selection of any study site is complicated by the fact

that on many of the older and therefore potentially interesting platforms, toxic oil-based muds (OBMs) have been discharged during past drilling operations. The negative effects of OBMs on benthic species are long-lasting (Kröncke *et al.*, 1992), persisting long beyond 1993 when the discharge of OBMs was prohibited at the Dutch Continental Sector (Daan and Mulder, 1996; Daan *et al.*, 2006).

We report here on a quantitative comparison between benthos (infauna and epifauna) living inside and outside the circular 500 m fishery-exclusion zone around a gas production platform in the southern North Sea. We discuss our results in the light of earlier fishing impact studies and benthic studies in the North Sea in an attempt to discriminate the long-term effect of closing an area to fisheries, and to evaluate if and how communities recover once marine protected areas (MPA) have been implemented in the frame of (inter)national policies (IDON, 2005).

## Material and methods

### Study sites

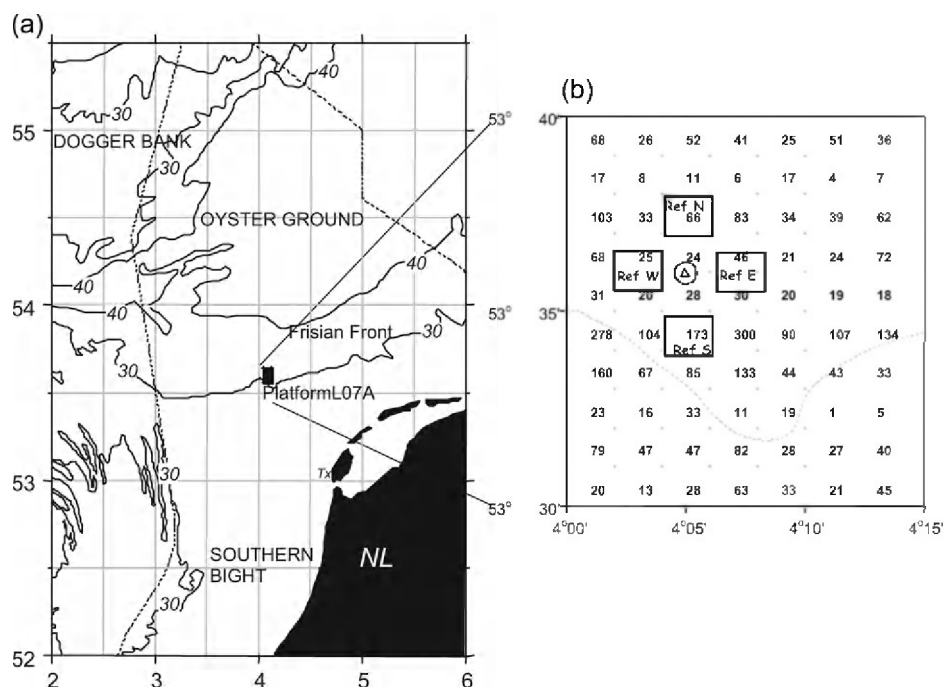
The exclusion zone around gas production platform L07A (owned by TotalFinaElf) was selected from a total of more than 200 potential platforms following the successive criteria: (i) situated in a fauna-rich area, (ii) no OBM history, (iii) exploitation phase lasting >10 y, (iv) located in an area with representative trawling intensity, (v) homogeneous abiotic environment, and (vi) low level of natural disturbance (Kaiser and Spencer, 1996). Some 20 y ago, the well was drilled without the use of OBM. Since then its 500 m wide exclusion zone has acted as a non-fished area. The platform is located at 53°35.97'N 4°04.93'E, near the southern border of the Oyster Ground in a fauna-rich area with fine muddy sand

called the Frisian Front (Figure 1a). This particular area is roughly delimited by the 30 and 40 m isobaths (53°30'N–53°55'N) and is part of a gradient in environmental conditions extending from the southern Bight into the Oyster Ground (de Gee *et al.*, 1991). In summer, the water column above the Oyster Ground becomes stratified, leading to a south-to-north gradient in bottom-water temperature across the Frisian Front. The Frisian Front forms the convergence zone of different water masses, giving rise to enhanced and prolonged primary production (Creutzberg, 1985). Because of its specific abiotic setting, the local benthic community has a large biomass, great biodiversity, and a high level of metabolic activity (Cramer, 1990). On the basis of its benthic biodiversity, the Frisian Front has been proposed as a candidate MPA (Lavaleye, 2000).

Data on beam trawl effort in the study area were supplied by the Netherlands Institute for Fisheries Research of Wageningen University (Wageningen IMARES). The data were based on satellite monitoring of a selected number of Dutch trawlers, including some EURO trawlers (maximum 300 hp), during the period 2000–2002 (F. J. Quirijns, Wageningen IMARES, pers. comm.). Effort is expressed as the total number of satellite recordings of Dutch beam trawlers operating per rectangular area of 1 × 1 nautical mile in this 3-y interval. The average trawling effort in a circular area with a diameter of 6 nautical miles surrounding platform L07A amounted to  $72.6 \pm 76.1$  s.d. over the 3 y (Figure 1b).

### Sampling

All samples in the platform subarea were taken within 400 m of the platform to exclude interference by (accidental) fishing along the



**Figure 1.** (a) The study site around gas platform L07A (TotalFinaElf) (53°35.976'N 4°04.932'E) in the Frisian Front. (b) Detailed map of the study site showing the 500 m exclusion subarea around the platform (circle) and the regularly trawled subareas Ref N, Ref S, Ref W, Ref E (squares). Numbers denote the relative fishing frequencies based on satellite recordings of a selection of the Dutch beam trawlers in 1 × 1 nautical mile quadrants totalled over the years 2000–2002 (Wageningen IMARES data).

perimeters of the exclusion zone. The sampling design further encompassed four rectangular reference areas, each  $1 \times 1$  nautical mile, situated 1.5 nautical mile north (Ref N), south (Ref S), east (Ref E), and west (Ref W) of the 500 m wide fishery-exclusion zone around the platform. The average trawling effort in the reference subareas amounted to  $74.1 \pm 68.4$  s.d. over the 3-y period, with a 3–7 times higher intensity in the southern subarea than in the other subareas (Figure 1b). We included four reference subareas in the study to ensure that any natural gradient in the study area could be accounted for.

Sampling was carried out on board the RV “Pelagia” (Royal NIOZ) in the period 2–7 April 2004. Epifauna and larger infauna were collected with a Triple-D dredge (Bergman and van Santbrink, 1994). The dredge excavated a strip of sediment about 80 m long, 20 cm wide, and 18 cm deep. The sediment that was excavated by the dredge moving forward was washed through a net about 6 m long with 7 mm mesh size attached to the dredge. Ten hauls were made in the platform subarea (500 m exclusion zone), and six hauls were made regularly distributed in each reference subarea. Catches were sorted, and the animals were identified and measured on board the ship.

Infauna was collected with a NIOZ box corer (30 cm diameter,  $\sim 40$  cm penetration into the seabed) equipped with a valve to prevent flushing and loss of the top layer. In each subarea, seven box cores were collected. Positions of the core samples were regularly dispersed in the reference subareas and as regularly as possible in the platform subarea, taking a closed corridor with pipelines into account. All box core samples were gently washed through a perforated 1 mm sieve on board, and the residues were preserved in 4% formalin. At every position, a separate box core was taken that was stored at  $4^\circ\text{C}$  for sediment grain size analysis.

## Analysis

The grain-size of sediment taken from a random selection of the box core stations, i.e. from four stations in the fishery-exclusion zone and from another four stations in each of the reference subareas, was measured with a Coulter LS230 Laser Diffraction Particle Size Analyser. On the basis of the particle size distribution (range  $0.04$ – $2000 \mu\text{m}$ ), the median grain size and the percentage silt ( $<64 \mu\text{m}$ ) were calculated. Differences between subareas were tested using these two parameters. Homogeneity of variances was verified with a Levene test. A subsequent one-way ANOVA and a Tukey HSD *post hoc* test were used to differentiate between subareas.

The box core samples were sorted in the laboratory and the animals identified to species level. Spatial differences in the fauna collected with the box corer and the Triple-D dredge were assessed using the PRIMER<sup>TM</sup> v5 package (Clarke and Gorley, 2001). In the analyses belonging to this package, there are no underlying assumptions about the statistical distribution of the data (e.g. normality, variance equality). Patterns among the Triple-D hauls and box core samples were visualized using cluster analysis on the basis of a Bray–Curtis similarity matrix. Differences between the density of the least and the most abundant species in the samples were usually more than two orders of magnitude. In order to weight the importance of dominant and rare species, we applied a square-root transformation to the original data (Clarke and Warwick, 2001). ANOSIM analyses were used to test the differences between groups of samples derived from the various subareas. SIMPER analyses were used

to calculate the contributions of particular species to the average dissimilarity.

As a measure for the diversity in the Triple-D hauls from the various subareas, we calculated species richness and dominance with the indices of Hurlbert (1971) and the  $N_2$  index of Hill (1973), respectively. These indices are suited for the slightly variable sample size of the Triple-D hauls, because they put more weight on the common species. As diversity measures for the box core samples, we used Hill's numbers ( $N_0$ ,  $N_1$ ,  $N_2$ ,  $N_\infty$ ; Hill, 1973). The successive numbers put a diminishing weight on rare species. Differences in density of specific species or of univariate diversity measures between subareas were formally tested with a one-way ANOVA, followed by either a Tukey HSD *post hoc* test (SPSS<sup>TM</sup> 11.5) or a Tamhane T2 test. In case of unequal variances determined by Levene's statistic, the Brown–Forsythe statistic was calculated to test for the equality of group means. In the latter case, a Tamhane T2 test was used in a *post hoc* comparison instead of a Tukey HSD. Differences between median parameter values belonging to different subareas were depicted with notched box and whisker plots (McGill *et al.*, 1978). An explanation of the symbols in the plots is given later, in the legend to Figure 2.

## Results

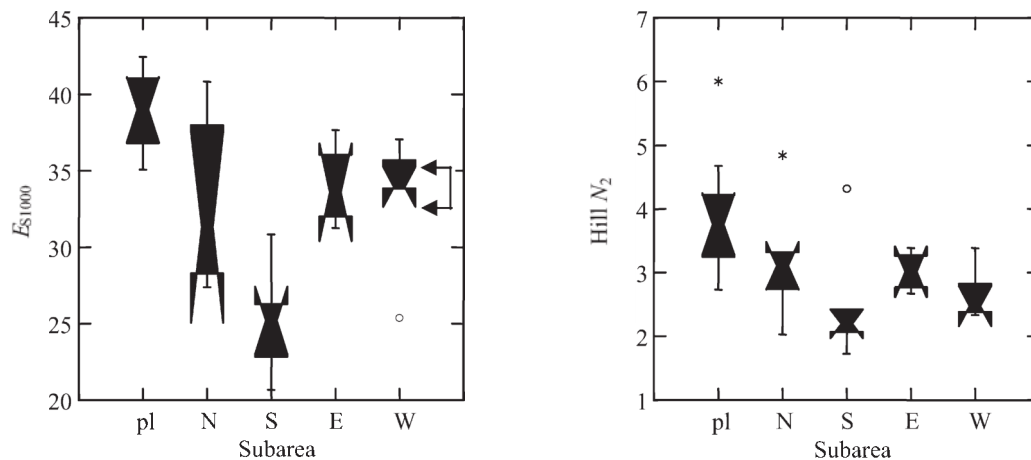
### Abiotic variables

The one-way ANOVA revealed that there were no differences between the subareas with regard to the percentage silt, although the subareas differed in terms of median grain size. A Tukey HSD *post hoc* test showed that the median grain size in Ref S was on average slightly higher than in the other subareas, namely  $113$  and  $106 \mu\text{m}$ , respectively. There was also a subtle but significant gradient in the water depth of the study area. The Ref S subarea was shallowest (mean  $35.9$  m) and the Ref N subarea the deepest (mean  $38.9$  m).

### Triple-D hauls

Cluster analysis of the square-root transformed Triple-D data indicated an integrity of the subareas, with little mixing of the hauls derived from the individual subareas (Figure 3). The hauls taken in the southern reference subarea were markedly different from the hauls in the other subareas. A global permutation test (ANOSIM) showed significant differences ( $R = 0.638$ ,  $p = 0.001$ ) between groups of hauls. A pairwise test of difference between subareas (Table 1) showed that hauls from the platform subarea and from Ref S were significantly different from each other and from all other subareas. Double square-root transformation ( $\sqrt{\sqrt{\cdot}}$ ) of the data or no transformation did not alter this result.

The ANOSIM analysis produced three groups of hauls: platform, Ref S, and pooled other reference subareas (Table 1). The top ten species contributing to the contrast between the three groups (SIMPER analysis) are listed in Table 2. The Triple-D hauls in the platform subarea were different from those in the pooled reference subareas because of greater abundances of burrowing mud shrimps (*U. deltaura*, *C. subterranea*) and particularly of large bivalves (*Thracia convexa*, *Arctica islandica*, *Cardium echinatum*, *Dosinia lupinus*) (Table 2). In comparison to all other subareas (Table 2), hauls in subarea Ref S were characterized by relatively high abundances of the small bivalve *Corbula gibba*, the ophiuroid *Ophiura albida*, and the heart urchin



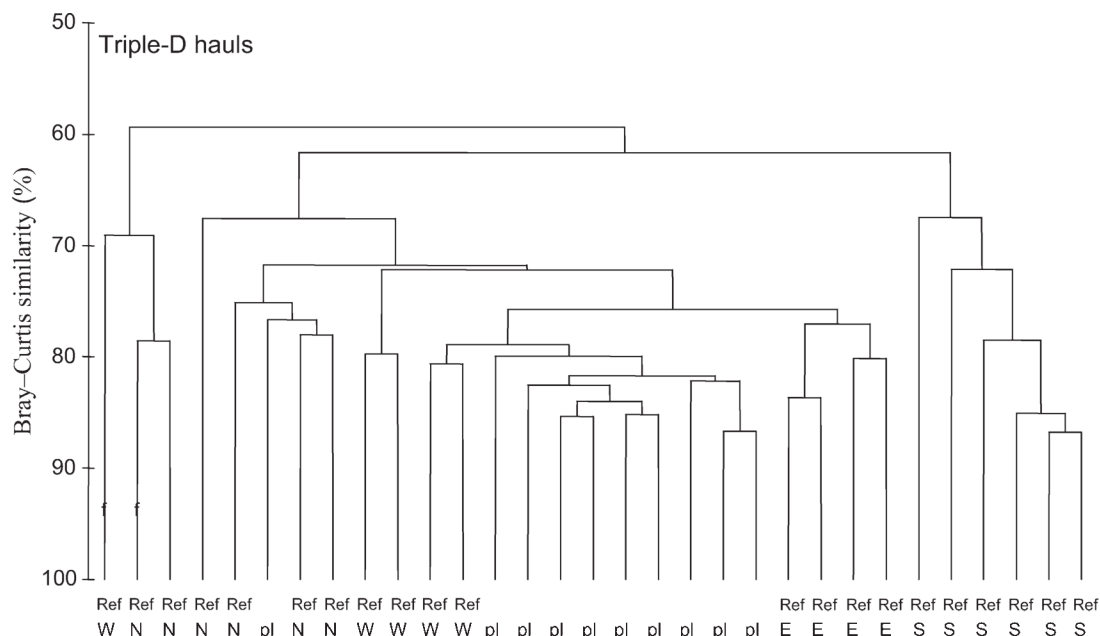
**Figure 2.** Notched box and whisker plots comparing median species richness (Hurlbert's  $E_{S1000}$ ) and the reciprocal of dominance (Hill  $N_2$ ) of the Triple-D hauls in the platform subarea (pl) and the reference subareas (N, S, E, and W). Non-overlapping notches denote a significant difference. The notch (narrow part) of the box to the right of the left panel is indicated by the two connected arrows that are drawn alongside. The notch represents the 95% simultaneous confidence interval of the median. Because the lower quartile in this case is greater than the lower confidence limit, the notch appears folded back on itself. The whiskers have a maximum length equal to 1.5 times the length of the box (the interquartile range, IR). If there are data outside this range, such points are marked as asterisks if the values fall within  $3 \times \text{IR}$  from the end of the box, or as circles if the values are outside this range.

*Echinocardium cordatum* and, especially in contrast to the non-fished platform subarea, by a scarcity of small bivalves (*Abra nitida*, *Cultellus pellucidus*) and burrowing mud shrimps (*U. deltaura*, *C. subterranea*).

Triple-D hauls taken in the platform subarea had on average significantly greater species richness (Hurlbert, 1971;  $F_{4,26} = 11.304$ ,  $p = 0.000$ ) and lower dominance (higher evenness,  $N_2$  index; Hill, 1973;  $F_{4,26} = 3.690$ ,  $p = 0.017$ ). The reverse seems to be true for the Ref S subarea, but the differences were not significant. Differences in diversity between subareas are illustrated by notched box and whisker plot confidence intervals for the medians by means of notches (Figure 2).

### Box core samples

A cluster analysis of the square-root-transformed box core data did not reproduce the subareas as accurately as did the Triple-D hauls (Figure 4, cf. Figure 3). The same held for the multidimensional scaling (MDS) plots (not shown) of both data sets. An ANOSIM test showed that differences existed between subareas ( $R = 0.146$ ,  $p = 0.003$ ), whereas the pairwise comparison demonstrated that box cores from Ref S were significantly different from the groups of samples taken in other subareas. Significant, albeit small, differences existed between samples from Ref N and the platform subarea (Table 3). The top ten species contributing to the contrast



**Figure 3.** Dendrogram produced by cluster analysis of the Triple-D hauls in the platform and reference subareas. Reference subareas (ref) have been coded as N(orth), S(outh), E(ast), and W(est). The raw data were square-root transformed before analysis.



**Table 1.** R-values resulting from pairwise tests (ANOSIM) between Triple-D hauls from different subareas.

	Platform	Ref S	Ref E	Ref W	Ref N
Platform	0	–	–	–	–
Ref S	<b>0.987</b>	0	–	–	–
Ref E	<b>0.793</b>	<b>0.706</b>	0	–	–
Ref W	<b>0.606</b>	<b>0.733</b>	0.088	0	–
Ref N	<b>0.711</b>	<b>0.883</b>	0.129	0.123	0

\*Data were square-root transformed before analysis. The emboldened values denote a significant difference between subareas ( $p < 0.05$ ).

(SIMPER analysis) between Ref S and the remaining pooled subareas, including the non-fished platform subarea, are listed in Table 4. Characteristic species in box cores from Ref S were the ophiuroid *O. albida* and the heart urchin *E. cordatum*, whereas the mud shrimp *U. deltaura* and the polychaete *Polydora* cf.

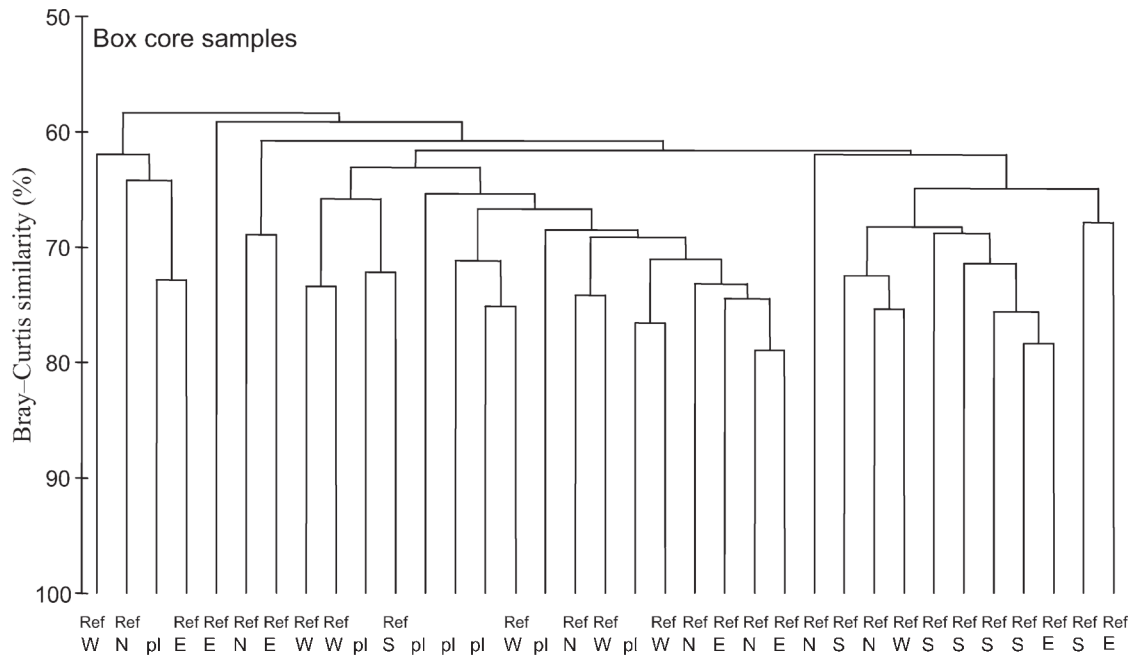
*guilly* were more abundant in box cores from the other pooled subareas. The bivalve *Corbula gibba*, which was highly discriminating for Ref S in the Triple-D samples (Table 2), was just outside the top ten list in Table 4. Nevertheless, as in the Triple-D samples, average *Corbula gibba* density in Ref S box cores was significantly ( $t$ -test,  $p = 0.03$ ) higher than in those from the remaining pooled subareas, i.e. 6.7 vs. 2.7 individuals  $m^{-2}$ .

This ANOSIM result does not exclude the possibility that certain species found in the box cores may have different densities in the pooled subareas. Species of interest in this context are those that discriminate in the separation of subareas in the Triple-D results (Tables 2 and 4). Because of the much smaller sample size of box cores (0.08  $m^2$ ) than the Triple-D dredge (16  $m^2$ ), only a few species listed in Table 2 had sufficient individuals in the box cores to be tested, the mud shrimps *C. subterranea* and *U. deltaura*. A one-way ANOVA with square-root transformed abundances revealed significant differences between subareas (*C. subterranea*  $F_{4,30} = 7.027$ ,  $p = 0.000$ ; *U. deltaura*  $F_{4,30} = 4.785$ ,

**Table 2.** Species contribution (%) to average dissimilarity resulting from SIMPER-analysis between three groups of Triple-D hauls, platform, Ref S, and pooled Ref N, Ref W, and Ref E.

Species	Platform average abundance	Ref N, W, E average abundance	% Contribution dissimilarity	Dissimilarity/s.d.
<i>Upogebia deltaura</i>	1 061	382	11.0	1.9
<i>Ophiura albida</i>	3 738	3 425	8.0	1.4
<i>Callianassa subterranea</i>	635	225	6.5	1.4
<i>Echinocardium cordatum</i>	498	508	5.6	1.8
<i>O. texturata</i>	123	62	3.1	1.2
<i>Thracia convexa</i>	63	23	2.4	1.4
<i>Dosinia lupinus</i>	13	2	1.4	1.4
<i>Chamelea gallina</i>	31	24	1.4	1.4
<i>Arctica islandica</i>	12	6	1.3	1.4
<i>Cardium echinatum</i>	11	3	1.2	1.3
	Platform average abundance	Ref S average abundance	% Contribution dissimilarity	Dissimilarity/s.d.
<i>Corbula gibba</i>	305	6 454	18.5	2.2
<i>O. albida</i>	3 738	12 184	16.6	2.2
<i>U. deltaura</i>	1 061	8	10.0	4.3
<i>C. subterranea</i>	635	54	6.3	2.7
<i>E. cordatum</i>	498	1 339	4.6	2.0
<i>O. texturata</i>	123	114	2.2	1.5
<i>T. convexa</i>	63	9	1.9	2.0
<i>Cultellus pellucidus</i>	72	27	1.3	1.3
<i>Abra nitida</i>	33	9	1.3	1.5
<i>Cucumaria elongata</i>	119	74	1.3	1.4
	Ref N, W, E average abundance	Ref S average abundance	% Contribution dissimilarity	Dissimilarity/s.d.
<i>Corbula gibba</i>	333	6 455	20.7	2.1
<i>O. albida</i>	3 425	12 184	19.5	1.9
<i>E. cordatum</i>	508	1 339	6.8	1.6
<i>U. deltaura</i>	382	9	4.4	1.0
<i>C. subterranea</i>	226	55	3.4	1.5
<i>O. texturata</i>	62	115	2.5	1.5
<i>T. convexa</i>	24	10	1.2	1.3
<i>Abra nitida</i>	20	10	1.2	1.3
<i>U. stellata</i>	22	0	1.1	0.9
<i>Cultellus pellucidus</i>	44	27	1.0	1.1

Data were square-root transformed prior to analysis. Average abundances of the species in the subareas (individuals  $100 m^{-2}$ ) are given. Columns show average abundances of the species, each species' contribution to dissimilarity between groups, and the ratio Dissimilarity/s.d. as a measure of the consistency of each species contribution.



**Figure 4.** Dendrogram produced by cluster analysis of the box core samples in platform and reference subareas. Reference subareas (ref) have been coded as N(orth), S(outh), E(ast), and W(est). The raw data were square-root transformed before analysis.

$p = 0.004$ ), whereas Tamhane's *post hoc* test showed that the platform box cores had greater abundances of mud shrimps than the reference subareas Ref N (notably so in the case of *C. subterranea*), Ref E, and Ref S. An illustration of the differences in abundance of mud shrimps in the different subareas is provided by notched box and whisker plots in Figure 5. This is in line with the results of the Triple-D sampling. Other relevant species are those that are considered vulnerable to beam trawl damage (Bergman and van Santbrink, 2000). A fragile and therefore potentially vulnerable species occurring in sufficient numbers in the box core data set is the brittlestar *Amphiura filiformis*. Comparing subareas with an ANOVA ( $F_{4,30} = 2.784$ ,  $p = 0.044$ ) revealed significant differences with relatively highest densities in the non-fished subarea near the platform.

There were no statistical differences in diversity between subareas, but there was nevertheless a tendency for samples taken near the platform to have a lower degree of dominance (higher evenness), as measured by a Hill  $N_2$  (Hill, 1973) and exemplified by the notched box and whisker plots in Figure 6.

## Discussion

Our results, especially those obtained with the Triple-D dredge, point to a clear difference between the fauna in the closed fishery subarea near the platform and the other regularly trawled subareas. Because the Triple-D dredge specifically targets the relatively less abundant large and long-living species such as bivalves, Triple-D samples more explicitly expose differences between non-fished and fished subareas than box core samples. The latter contain a suite ( $>20$ ) of small short-lived species, some of them in large numbers, e.g. the horseshoe worm *Phoronis*, the bivalve *Abra* spp., and various small polychaetes. Such species tend to weigh heavily in a multivariate analysis where they obscure the long-term effect of fishing as represented by changes in larger (older) and usually less abundant species. The effect of a

large number of rare species becomes stronger when the common species are downweighted by more severe transformations than we employed here. However, regardless of the type of transformation, none of the box core results replicated the distinct separation between subareas obtained with the Triple-D sampling.

Species that were more abundant in the Triple-D hauls near the platform included the bivalves *A. islandica*, *T. convexa*, *D. lupinus*, and *Cardium echinatum* (Table 2). All are relatively large fragile species in reach of the trawl that are known to be vulnerable to beam trawling (Bergman and Hup, 1992; Witbaard and Klein, 1994; Bergman and van Santbrink, 2000). The same holds for the fragile, but small, bivalves *Abra nitida* and *Cultellus pellucidus*. Both species were more abundant in the non-fished subarea than in the regularly trawled Ref S (Table 2). For these species, Bergman and van Santbrink (2000) reported direct trawling mortalities of 18–38% and 27–29%, respectively, in the trawl path of a single beam trawl haul in silty sediments. These Triple-D results are in accord with those of Jennings *et al.* (2001), who found an up to sixfold reduction in abundance of bivalves and spatangoids in areas with trawling frequencies of  $0.2\text{--}6.5\text{ y}^{-1}$  in the central North Sea. In contrast, the abundance of infaunal polychaetes

**Table 3.** *R*-values resulting from pairwise test (ANOSIM) between box core samples taken in different subareas.

	Platform	Ref S	Ref E	Ref W	Ref N
Platform	0	–	–	–	–
Ref S	<b>0.529</b>	0	–	–	–
Ref E	0.096	<b>0.260</b>	0	–	–
Ref W	0.026	<b>0.254</b>	–0.021	0	–
Ref N	<b>0.186</b>	<b>0.448</b>	0.015	–0.045	0

Data were square-root transformed prior to analysis. The emboldened values denote a significant difference between subareas ( $p < 0.05$ ).

**Table 4.** Species contribution to average dissimilarity resulting from SIMPER-analysis between the two groups of box core samples, pooled Ref N, W, E and platform vs. Ref S.

Species	Ref N, W, E, and platform average abundance	Ref S average abundance	% Contribution dissimilarity	Dissimilarity/s.d.
<i>Polydora cf. guilly</i>	6.1	0.0	3.8	1.4
<i>Ophiura albida</i>	0.3	2.1	3.0	1.7
<i>Echinocardium cordatum</i>	0.4	2.5	2.9	1.7
<i>Montacuta ferruginosa</i>	0.4	1.5	2.9	1.7
<i>Upogebia deltaura</i>	3.2	0.4	2.7	1.4
<i>Myriochele oculata</i>	2.9	0.5	2.5	1.1
<i>Prionospio cirrifera</i>	1.8	1.4	2.4	1.2
<i>Glycera rouxii</i>	1.0	1.4	2.2	1.1
<i>Ophiodromus flexuosus</i>	1.0	0.2	2.1	1.1
<i>Euspira poliana</i>	1.5	1.2	2.0	1.1
<i>Notomastus latericeus</i>	1.0	1.0	2.0	1.1
<i>Lepton squamosum</i>	1.0	0.4	2.0	1.0

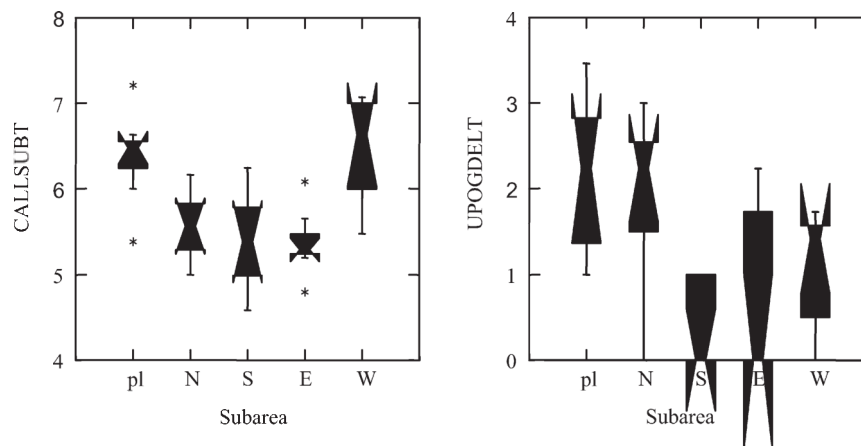
Species are ranked according to their decreasing contribution. Data were square-root transformed prior to analysis. Columns show average abundances of the species (number per 0.08 m<sup>2</sup>) in the subareas, each species' contribution to dissimilarity between groups, and the ratio dissimilarity/s.d. as a measure of the consistency of each species contribution. The average dissimilarity between the two groups is 40.7.

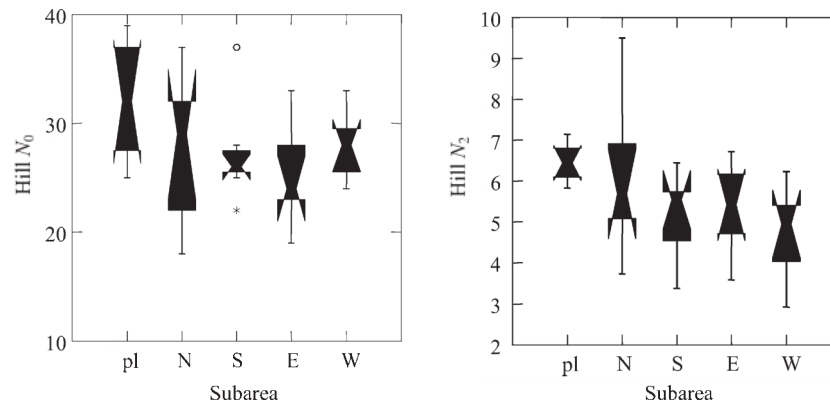
showed no relation to trawling frequency in the study of Jennings *et al.* (2001). The lack of clear patterns in our box core samples, which were dominated by polychaetes (average 30% of the species and 40% of the individuals in a sample), seems to support the earlier results.

However, there are some unexpected results. One is the greater abundance of mud shrimps in the platform subarea, or conversely their depressed abundance in the regularly trawled subareas. This was apparent from the Triple-D results (Table 2). Because of the deeper penetration of the box corer, it is considered to yield more reliable density estimates, especially of the smaller, deeper-living *C. subterranea*. The significantly greater abundance of *C. subterranea* in box cores from the platform subarea than in those from subareas Ref E, Ref N, and Ref S (tested by ANOVA; Figure 5) supports the results of the Triple-D analysis. It is possible that Ref W did not differ from the platform subarea, because beam

trawl effort there was least of all the reference subareas (Figure 1b). In the case of *Upogebia deltaura*, however, significant differences between platform subarea and reference subareas were found only for Ref E and Ref S (Figure 5). There is no obvious explanation for the fact that Ref N showed no significant difference from the platform subarea.

Both species of mud shrimp live permanently in tunnels extending down to 50 cm deep in the sediment. The maximum penetration depth of beam trawls is just ~8 cm (Paschen *et al.*, 2000), implying that trawling would have little direct effect on them. Support for this statement comes from the results of Bergman *et al.* (1998), who found no distinct relationship between the distributions of *Upogebia* spp. and beam trawl effort on the Oyster Ground. Decline of *Callinassa* in connection with fishing has so far only been reported from areas where *Nephrops* trawls designed to dig into the sediment are used

**Figure 5.** Comparison of densities (square-root transformed) of the mud shrimps *C. subterranea* (CALLSUBT) and *Upogebia deltaura* (UPOGDELT) in box core samples from the platform (pl) and reference (N, S, E, and W) subareas. Non-overlapping notches denote a significant difference. For explanation of symbols, see Figure 2.



**Figure 6.** Comparison of Hill's diversity  $N_0$  (number of species) and  $N_2$  (reciprocal of dominance) of box core samples from the platform (pl) and reference (N, S, E and W) subareas. For explanation of symbols, see Figure 2. The differences between subareas are statistically not significant at a level of  $p = 0.05$ .

(<http://www.jncc.gov.uk/page-2530>). Destruction of burrows by beam trawls leading to extra energetic costs for *C. subterranea* to reconstruct its tunnels has been mentioned, but is regarded as not significant in the same document ([http://www.marlin.ac.uk/biotopes/Bio\\_Sensexp\\_CMS.AfilEcor.htm](http://www.marlin.ac.uk/biotopes/Bio_Sensexp_CMS.AfilEcor.htm)). However, we think that our data indicate that the effect of trawling in reducing *C. subterranea* densities, and presumably those of *Upogebia* as well, may not be insignificant. Because mud shrimps are considered to be engineering species with an important impact on sediment bioturbation, mineralization, and the erosion threshold of the seabed (Rowden and Jones, 1993; Howe et al., 2004; Amaro, 2005), the ecosystem effect may be more far-reaching than a simple reduction in abundance (Coleman and Williams, 2002).

Also unexpected was the relatively high abundance of sea urchin *E. cordatum* in Ref S, the subarea with the greatest fishing effort (Figure 1b). Many studies have reported significant direct mortality of spatangoids such as *E. cordatum* after trawling, or declining numbers with increasing trawling frequency (e.g. Bergman and Hup, 1992; Bergman and van Santbrink, 2000; Jennings et al., 2001). Earlier data, however, show that relatively high densities of *E. cordatum* are common along the southern edge of the Frisian Front (Creutzberg et al., 1984) just south of our Ref S. What causes these bands of density is still unclear. Creutzberg et al. (1984) suggested that the marked south-to-north zonation of benthic fauna across the Frisian Front reflects the local gradient in organic enrichment, perhaps, the result of the decreasing current velocity allowing deposition of fine (in)organic particles just north of the sand–mud boundary. This hypothesis implies that favourable feeding conditions and elevated growth and hence survival rates of the various species are important for the formation of the faunal bands. Alternatively, bands could be the result of enhanced deposition of pelagic larvae in relation to decreasing current speed or the pelagic front (Creutzberg, 1986; Lough and Manning, 2000). The first hypothesis seems unlikely, because growth rates of *E. cordatum* at the Frisian Front are not enhanced over those in the southern North Sea (Duineveld and Jenness, 1984). Greater trawling mortality at Ref S must therefore be compensated by larval supply to create greater *E. cordatum* abundance.

The contrasting patterns of the similarly vulnerable *E. cordatum* and, for instance, *T. convexa*, one more abundant in the heavily fished subarea Ref S and the other in the fishery-closed subarea,

illustrates the pitfalls encountered when natural gradients co-occur with gradients in fishing effort, as in the studies of Bergman et al. (1998) and Craeymeersch et al. (2000). Without adequate knowledge of the natural processes leading to distribution patterns of the various species, the long-term impact of trawling will be hard to substantiate. Having in this study four regularly trawled reference subareas around the closed subarea (Figure 1b) made it possible to test their homogeneity and, for example, to show that Ref S was not representative as a reference subarea in terms of fauna and abiotic characteristics (Tables 1 and 3).

It is further worth recording that we did not find young stages of fragile bivalves (*T. convexa*, *A. islandica*) in the platform exclusion zone. Earlier, Witbaard and Bergman (2003) noted the unimodal and skewed size distribution of the *A. islandica* stock on the Oyster Ground (Figure 1a), where old animals dominate and juveniles are rare. In contrast, more northern stock (e.g. Fladen Ground) juveniles are much more abundant, giving rise to a bimodal size distribution. Witbaard and Bergman (2003) argue that beam trawling may be one of the factors responsible for the infrequent recruitment and skewed size distribution of *A. islandica* on the Oyster Ground. The scarcity of juvenile *A. islandica* in the closed platform subarea, however, suggests that direct trawling mortality among juveniles is likely not the main factor preventing successful recruitment. Because *A. islandica* has a long pelagic larval phase (up to 55 d; Witbaard and Bergman, 2003) and residual currents amount to several  $\text{cm s}^{-1}$ , recruitment of *A. islandica* in the study area, including the closed fishery subarea, must come from larvae produced by adjacent stocks. The absence of recruits in all subareas is possibly attributable to a low fertilization rate caused by the low adult density outside the study area (Witbaard and Bergman, 2003). Recently, Holmes et al. (2003) found that all *Arctica* populations in the North Sea, including those on the Oyster Ground, are genetically relatively isolated from each other, pointing to infrequent settlement of larvae derived from different sources.

This latter observation is of relevance in any discussion about establishing a MPA at the Frisian Front. In this context, long-living bivalves in general and *A. islandica* in particular are frequently mentioned as conservation targets. If the causes for their infrequent recruitment are not accounted for, the effect of a Frisian Front MPA on recovery of their depleted stocks will not be



predictable. Another significant outcome of our study is that a protected area as small as the 500 m exclusion zone around the platform in a heavily fished region holds a different, more diverse, macrofauna with a greater biomass and production (Bergman *et al.*, 2007). This implies that adverse direct effects of fishing, such as re-suspension in the surrounding fished area, do not seem to have much of an effect on a future MPA.

## Acknowledgements

We thank the captain and crew of RV "Pelagia" (Royal NIOZ) for their assistance during sampling, NAM for their assistance in selecting a suitable platform, and TotalFinaElf for giving permission to conduct the study near platform L07A. Ank Groenewold, Stefan Groenewold, and Steef Steeneke are thanked for their help on board, and P. W. van Leeuwen and A. Meijboom (Wageningen IMARES) for their contribution in sorting the box core samples. Finally, we thank F. J. Quirijns (Wageningen IMARES) for sharing data on trawling effort. The study was done in cooperation with and under contract Wageningen IMARES, commissioned and funded by the Ministry of LNV (Directorate Nature).

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doi:10.1093/icesjms/fsm029