

**LONG TERM CLOSURE OF AN AREA TO FISHERIES
AT THE FRISIAN FRONT (SE NORTH SEA):
EFFECTS ON THE BOTTOM FAUNA**

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Introductie

De directe effecten van boomkorvisserij op de bodemfauna in de zuidelijke Noordzee zijn duidelijk geworden uit diverse studies. Na een trek met een standaard commerciële boomkor werd een directe sterfte gemeten van gemiddeld 5 tot 40% van de initieel aanwezige groepen bodemdieren. Sterfte bij tweekleppige schelpensoorten varieerde van 20 tot 65%. Niet alleen veranderingen in de soortensamenstelling van bodemfauna, maar ook dichtheidsafname en het verdwijnen van kwetsbare soorten worden aan bodemvisserij toegeschreven. De in het spoor van de boomkor gedode dieren en het in zee teruggezette deel van de vangst (discards) komen na iedere vistrek beschikbaar voor aaseters en het verdere detritus voedselweb. Op jaarbasis is dit naar schatting 6 tot 13% van de jaarlijkse productie van bodemdieren. Introductie van deze voedselbron, die zonder visserij veel minder beschikbaar zou zijn, kan het voedselweb en de energiebanen binnen de bodemgemeenschap veranderen. De toegenomen productie van bijv. kreeftachtigen in de Noordzee over de laatste 30 jaar, kan echter ook een effect van de afgenomen predatiedruk door grote roofvissen zijn.

Lange termijn effecten van bodemvisserij in de Noordzee werden o.a. duidelijk door vergelijking van benthosgemeenschappen in beviste en onbeviste gebieden. Bevissing leidde tot een verlaagde biomassa van in en op de bodem levende soorten, dominantie van polychaete wormen en achteruitgang in aantallen tweekleppige schelpdieren en zeeëgels. Hoewel de globale structuur van het voedselweb onveranderd leek door deze verschuivingen in soortensamenstelling, is onderzoek vereist om effecten op soortniveau en het energietransport te traceren. Duidelijk is dat alle vormen van bodemvisserij met gesleepte tuigen de biogene structuur in en op de zeebodem beschadigen, en de habitatdiversiteit met de daaraan gekoppelde soortdiversiteit reduceren. Het is onbekend in hoeverre deze diversiteitsveranderingen het functioneren van het ecosysteem (mineralisatie, productie) beïnvloeden. Die kennis is wel van vitaal belang bij de beslissing of een benthisch systeem veerkrachtig genoeg is om de gevolgen van bodemvisserij te weerstaan.

De lange termijn effecten van bodemvisserij in de zuidelijke Noordzee staan nog steeds ter discussie. Pogingen om bestaande natuurlijke patronen in visserij intensiteit te correleren met diversiteit van benthosgemeenschappen leverden geen duidelijkheid, omdat natuurlijke gradiënten zowel de verspreiding van benthos en vis als ook van de daarop jagende visserij bepalen. Voor een dergelijk onderzoek zijn grote, homogene, langdurig onbeviste gebieden vereist, die in de zuidelijke Noordzee niet bestaan. Kleine onbeviste gebieden bestaan echter wel in de vorm van de voor bevissing gesloten, cirkelvormige, 500 m brede veiligheidszones rondom offshore installaties. In dit project is een kwantitatieve vergelijking gemaakt van de bodemfauna (infauna en epifauna) levend binnen en buiten de veiligheidszone rond een offshore installatie.

Doelstelling en methodiek

Dit project is uitgevoerd om de lange termijn effecten van de boomkorvisserij op de diversiteit en samenstelling van de bodemgemeenschap in de zuidelijke Noordzee te onderzoeken. De studie draagt bij aan de voorspelling of en hoe bodemgemeenschappen herstellen wanneer Marine Protected Areas zouden zijn geïmplementeerd in de zuidelijke Noordzee in het kader van (inter)nationale beheersplannen.

Als onderzoeksmethode is gekozen voor een kwantitatieve vergelijking van bodemfauna (infauna en epifauna) levend binnen en buiten een langdurig voor visserij gesloten gebied. Door het ontbreken van grote onbeviste gebieden op het Nederlands Continentale Plat, is als alternatief gekozen voor een vergelijking van de fauna binnen en buiten de 500 m brede veiligheidszone rond een gasproductieplatform. De selectie van een al lang functionerend platform werd beperkt door het gebruik en de lozing van Oil Based Mud tijdens de booractiviteiten in het verleden. Aangezien deze OBM lozingen ook na het lozingsverbod in 1993 langdurige effecten op bodemdieren hebben, juist in fijnzandige en faunarijke gebieden waar effecten van visserij meer geprononceerd kunnen zijn, beperkte de selectie zich tot platforms met gasreservoirs ooit geboord zonder OBM. Het betreffende platform L07A van TotalFinaElf is geselecteerd vanwege 1) de ligging in een fijnzandig, faunarijke gebied waardoor visserij effecten duidelijker waarneembaar zijn, 2) het ontbreken van OBM lozingen, 3) de lange periode dat het platform op locatie staat (~20 jaar), 4) de positie in een omgeving met een gemiddelde visserij intensiteit, en 5) de locatie in een gebied met homogene omgevingsfactoren en weinig natuurlijke verstoringen. De positie van het platform is 53° 35.976'N and 4° 04.932'E in het faunarijke Friese Front in de zuidoostelijke Noordzee.

Opzet en uitvoering

De bodemfauna in de veiligheidszone van platform L07A is in deze studie vergeleken met die in 4 normaal beviste referentiegebieden (ieder 2*2 km) op een afstand van 2.5 km ten zuiden, westen, noorden en oosten van het platform. In april 2004 is de bodemfauna in deze 5 deelgebieden bemonsterd. De Triple-D bodemschaaf werd ingezet om grotere en minder abundante soorten infauna en epifauna te bemonsteren. De vangsten (oppervlak 16 m², vangstdiepte 18 cm) werden gespoeld in een net met mazen van 7 x 7 mm en aan boord geanalyseerd. Boxcore monsters (bemonsteringsoppervlak 0.07 m², monsterdiepte 40 cm) werden gespoeld over een zeef met maaswijdte van 1 mm en, na conservering op 4% formaline, in het laboratorium op infaunasoorten gedetermineerd. Op ieder station werd een aparte boxcore genomen voor de analyse van het sediment.

De sedimentgegevens en de abundanties (dichtheden) van de faunasoorten werden geanalyseerd op verschillen tussen de onbeviste veiligheidszone en de normaal beviste referentiegebieden. Multivariate analyses, zoals cluster analyses gebaseerd op een Bray-Curtis similarity matrix, visualiseren de ruimtelijke verschillen in fauna. Met ANOSIM- en SIMPER analyses werden

* Voor referenties en illustraties: zie de Engelse tekst

verschillen tussen de groepsbemonsteringen van de deelgebieden getest en werden de bijdragen van diverse faunasoorten aan de gemiddelde ongelijkheid van de deelgebieden berekend. Verschillen in dichtheden van specifieke soorten tussen gebieden werden getest met een one-way Anova. Verschillen in mediane parameters tussen deelgebieden worden geïllustreerd met notched box-whisker plots. Als een maat voor diversiteit in de verschillende deelgebieden werden soortenrijkdom en dominantie berekend met de indices van Hurlbert en Hill.

Resultaten

Multivariate analyse van de Triple-D gegevens laat een significant verschil zien in bodemfauna van de onbeviste veiligheidszone en de omringende referentiegebieden. Opvallende verschillen zijn de hogere dichtheden in de veiligheidszone van kwetsbare tweekleppige schelpdieren (noordkromp *Arctica islandica*, bolle papierschelp *Thracia convexa*, gedoornde hartschelp *Cardium echinatum*, dichtgestreepte artemisschelp *Dosinia lupinus*, glanzende dunschaal *Abra nitida*, en sabelschede *Cultellus pellucidus*) en van de diep gravende kreeftjes *Callianassa subterranea* en *Upogebia deltaura*. Ook de soortenrijkdom en gelijkmatigheid van soortvoorkomen van de Triple-D fauna zijn hoger in de veiligheidszone. Multivariate analyse van de boxcore fauna laat daarentegen geen duidelijk significante verschillen zien tussen de 5 deelgebieden. Dit is het gevolg van het grote aandeel van kleine, kortlevende soorten (o.a. de hoefijzerworm *Phoronis*) in het totale aantal individuen in boxcore monsters. In het algemeen worden in de boxcore relatief weinig grotere en voor visserij kwetsbare soorten gevangen. Dichtheden van geselecteerde soorten die kwetsbaar bleken in de Triple-D analyse (o.a. de gravende kreeftjes) en van de fragiele slangster *Amphiura filiformis* zijn echter wel hoger in de boxcore monsters uit de veiligheidszone. Hoewel er geen statistisch significant verschil is in de diversiteit van de boxcore fauna in de 5 deelgebieden, is er wel sprake van een trend met de hoogste diversiteit in de veiligheidszone.

Deze resultaten zijn in lijn met de verwachtingen voor wat betreft de hogere soortenrijkdom en hogere dichtheid van langlevende grote schelpdieren in de voor visserij gesloten veiligheidszone. Opmerkelijk is echter, dat ondanks de grotere aantallen volwassen schelpdieren er toch geen aanwijzingen zijn gevonden voor een

toename in de vestiging en succesvolle overleving van jonge schelpdieren in dit deelgebied. Ook anderzijds zijn de resultaten nieuw, zoals de hoge aantallen diep gravende kreeftjes in de niet-beviste zone om het platform. Gezien de grote invloed die deze kreeftjes kunnen hebben op bodemstructuur, bodemchemie, mineralisatie en de verspreidingspatronen van andere soorten bodemdieren, reikt hun achteruitgang in beviste gebieden vermoedelijk veel verder dan een getalsmatig verlies in biodiversiteit.

Conclusies

Bodemfauna gevangen met de Triple-D in de voor visserij gesloten veiligheidszone rond het platform verschilt significant van de fauna in de beviste referentiegebieden. Opvallend waren de hogere dichtheden diep gravende kreeftjes (*Callianassa subterranea*, *Upogebia deltaura*) en kwetsbare schelpsoorten zowel langlevend (*Arctica islandica*, *Thracia convexa*, *Cardium echinatum*) als korter levend (*Abra nitida*, *Cultellus pellucidus*) in het gesloten gebied. Soortenrijkdom en gelijkmatigheid in dichtheid waren hier eveneens hoger.

Met de boxcore bemonstering kon een soortgelijk verschil in fauna tussen de deelgebieden niet worden aangetoond. Dit wordt toegeschreven aan de grote aantallen kleine, kortlevende soorten en de relatief lage aantallen grotere, kwetsbare soorten die gewoonlijk in een boxcore worden gevangen. De boxcore bemonstering bevestigde echter wel de hogere dichtheid van de gravende kreeftjes (*Callianassa subterranea*, *Upogebia deltaura*) in het voor visserij gesloten gebied, en toonde daar tevens een hogere dichtheid van de slangster *Amphiura filiformis* aan.

Een bevissingsdruk door boomkorvisserij die tot lagere dichtheden gravende kreeftjes leidt, zal implicaties voor bodemstructuur, bioturbatie en mineralisatie geven en kan daarmee grote gevolgen voor het functioneren van het ecosysteem hebben. Dit is een duidelijke aanwijzing dat deze vorm van visserij niet alleen leidt tot effecten op soortsniveau maar ook op ecosysteemniveau.

Ondanks het positieve effect van de niet-beviste zone rond het platform op de overleving van langlevende, grote en kwetsbare schelpdieren, werd er geen aanwijzing gevonden voor een toegenomen vestiging of overleving van jonge exemplaren in dit overigens relatief kleine gebied.

ABSTRACT

To determine the effects of areas closed for beam trawling on the composition and diversity of the macrofauna we compared the fauna in the 500 m exclusion zone around an offshore platform with the fauna in regularly fished subareas in the vicinity. The study was conducted in a silty-sand habitat in the southern North Sea (Frisian Front) near gas production platform L07A. Besides standard boxcorer samples, hauls were made with the Triple-D dredge in order to collect relatively rare and larger species. Multivariate analysis showed a distinct difference between the Triple-D samples from the fishery-closed area around the platform and those from the regularly trawled reference subareas. Conspicuous differences were higher abundances of mud shrimps (*Callinassa subterranea*, *Upogebia deltaura*) and sensitive bivalves (*Arctica islandica*, *Thracia convexa*, *Dosinia lupinus*, *Abra nitida*, *Cultellus pellucidus*) in the non-fished subarea near the platform. Species richness and evenness were higher as well. The boxcore samples did not clearly reveal the distinctness of the non-fished platform subarea. This is attributed to the large proportion of small, short-living species and the relatively low numbers of vulnerable larger species common to all boxcore samples. Nevertheless, boxcore samples did confirm the higher abundance of mud shrimps (*Callinassa subterranea*, *Upogebia deltaura*) in the non-fished platform subarea and demonstrated higher densities of the brittlestar *Amphiura filiformis*. The effect of beam trawling on the presence of long lived large bivalves as we found is in line with previous studies. Despite the positive effect of the fishery-exclusion zone on survival of their adults, however, no evidence was found for higher recruitment rates in this relative small area. Our observation that deep-living mud shrimps are affected by trawling may point to larger consequences for the functioning of the benthic ecosystem than solely loss of biodiversity.

INTRODUCTION

Direct impacts of beam trawling on the benthic community in the southern North Sea have been amply documented (see review Kaiser and de Groot, 2000). A single haul with a standard commercial beam trawl causes a direct mortality from 5 up to 40% of the initial densities of various groups of adult macrobenthos. Bivalve species show direct mortalities from 20 up to 65%. Vulnerability to trawling differs among the various taxa (Bergman and van Santbrink, 2000). Because of these differences, regular trawling of the benthic communities in the southern North Sea is expected to be responsible for observed species shifts and for scarcity or disappearance of certain species (Craeymeersch *et al.*, 2000). Together with the damaged individuals in the trawl path, fish and invertebrates discarded from the 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 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 *e.g.* crustaceans

increased in the North Sea over the last 30 years. Although this can be seen as an effect of the depletion of predatory demersal fish species, reducing the predation pressure, it might also have been generated by the enhanced food amount due to trawling mortality.

To perceive long term impacts of trawling Jennings *et al.* (2001) compared the benthic faunas in two areas in the central North Sea with different fishing intensity. They corroborated effects of trawling on epifauna as well as infauna such as the decrease in biomass, dominance of polychaetes and a scarcity of bivalves and spatangoids. The gross trophic structure of the communities, in contrast, did not seem to be altered by the species shifts. However, they point out that further study should be made of the trophic roles at the species level and of the ways energy is transferred through the community in the light of diminished biomass. Norse and Watling (1999) argued 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. Since this structural complexity is positively correlated with species diversity, trawling affects biodiversity by reducing structure-associated benthos species. Relationships between benthic biodiversity and ecosystem functioning (*e.g.* mineralization, production) are largely obscure. Yet this information is vital to assess in how far a benthic ecosystem is resilient to levels of trawling disturbance.

Despite the extensive dataset on direct trawling effects, there is still public debate on the long-term effects of beam-trawling on the benthic communities in the southern North Sea. Attempts to correlate patterns in fishing effort and benthos in order to distinguish long-term impacts have been largely unsuccessful (Bergman *et al.*, 1998; Craeymeersch *et al.*, 2000). One problem associated with these attempts is the fact that strong natural gradients exist in the southern North Sea governing distributions of benthos, fish and hence fishing effort (see Bergman *et al.*, 1998). These conditions hamper attempts to make within-community comparisons on long term effects of beam-trawling as for instance Jennings *et al.* (2002) did. An important requisite for a study on long term fishing effects *viz.* large homogeneous areas that are undisturbed for a sufficient length of time, do not exist 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. One drawback is that on many of the older and thus potentially interesting offshore sites, oil-based muds (OBM) have been discharged during past drilling operations. The negative effects of OBM's on benthic species are long-lasting and persist far beyond 1993 when the discharge of OBM's was prohibited on the Dutch Continental Sector (Kröncke *et al.*, 1992; Daan and Mulder, 1996). The site selection is further complicated by the fact that whereas trawling impact is assumed to be more evident in fine grained sediment where species diversity and biomass are high, right there OBM-sensitive species are present in relative high numbers (Bergman and Duineveld, 1990). The long term OBM effects forced us to select platforms that exploit wells drilled without OBM.

Here we report on a quantitative comparison between benthos (infauna and epifauna) living inside and outside the circular 500 m fishery-exclusion zone around gas production platform L07A in the southern North Sea (Fig. 1a, b). The ensuing data on species abundances are explored for differences between the exclusion zone and adjacent regularly trawled areas. We discuss our results in the light of in-

formation derived from earlier fishing impact studies and benthic studies in the area in an attempt to discriminate the long-term effect of closing an area to fisheries. This first study contributes to forecasting if and how communities recover once Marine Protected Areas have been implemented in the frame of (inter)national policies (IDON, 2005).

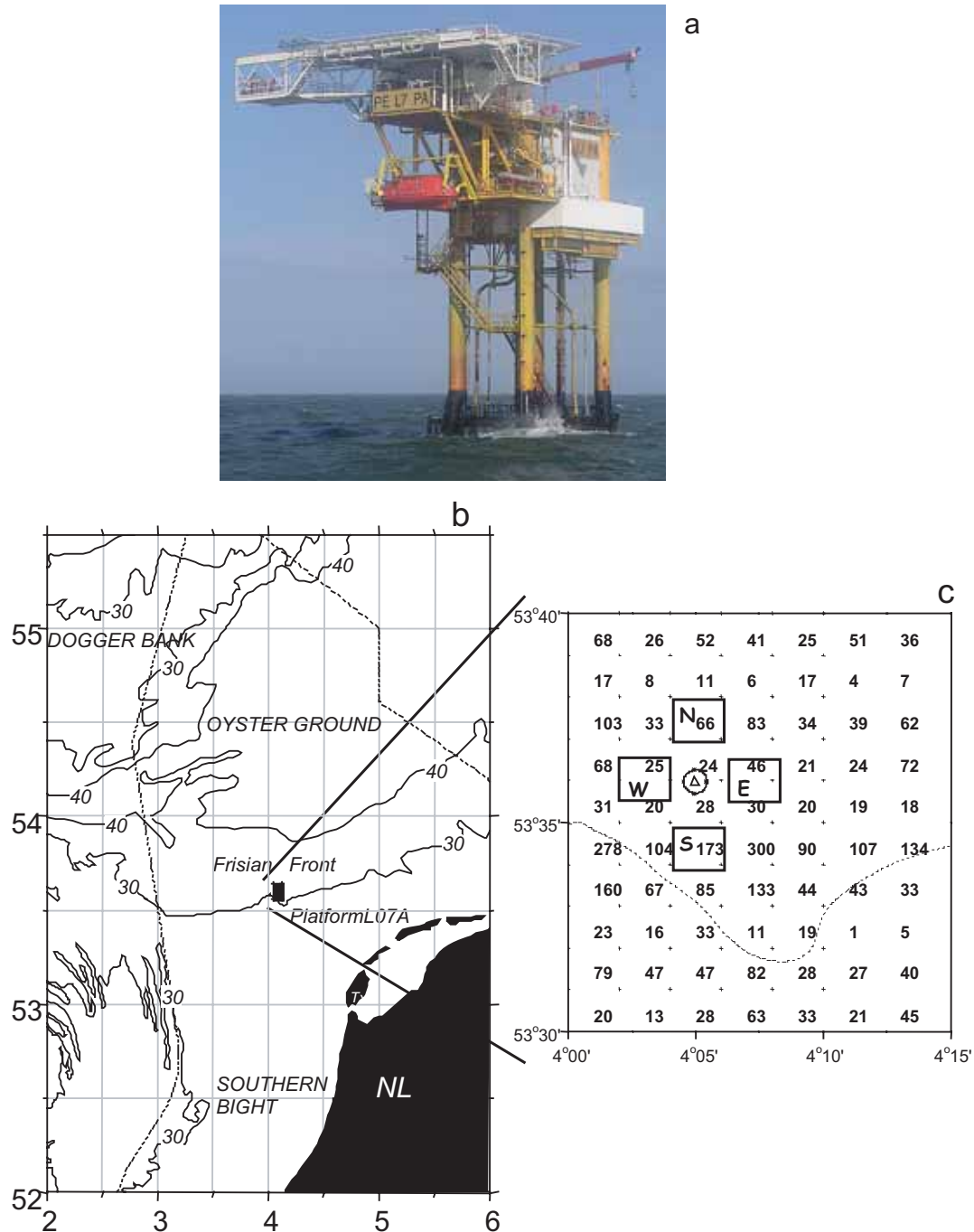


Figure 1. a) gas platform L07A (TotalFinaElf); b) position of the study site around platform L07A (53° 35.976'N and 4° 04.932'E) in the Frisian Front; c) detailed map of the study site showing the non-fished 500m exclusion area around the platform (circle) and the regularly trawled reference subareas N, S, W, E (squares). Numbers in map denote relative fishing frequencies based on satellite recordings of a selection of the Dutch beam trawlers in 1°x1° nautical miles quadrants totaled over 2000-2002 (RIVO data).

MATERIAL AND METHODS

Platform selection

The platform was chosen from a total of more than 200 potential platforms following the successive criteria: 1) situated in a fauna-rich area, 2) no OBM history, 3) exploitation phase during more than 10 years, 4) located in an area with representative trawling intensity, 5) homogeneous abiotic environment and low level of natural disturbance (see Kaiser and Spencer, 1996). Only a small number of platforms fulfilled these conditions and from those gas platform L07A owned by TotalFinaElf was selected (Fig. 1a). The platform is located at 53° 35.976'N and 4° 04.932'E in the fauna-rich Frisian Front (Fig. 1b). Some twenty years ago the well was drilled without the use of OBM. Since then its 500 m wide exclusion zone acts as a non-fished area.

Study site

The Frisian Front where the platform is located, is characterized by a gradient in environmental conditions *i.e.* current speed, depth and sediment grain size (de Gee et al., 1991). It also forms the convergence zone of different water masses giving rise to enhanced and prolonged primary production (Creutzberg, 1985). Due to the specific abiotic setting, the local benthic community has a high biomass, high biodiversity, and high level of activity (Cramer, 1990). On the basis of the benthic biodiversity, the Frisian Front has been proposed as candidate MPA (Lavaleye, 2000).

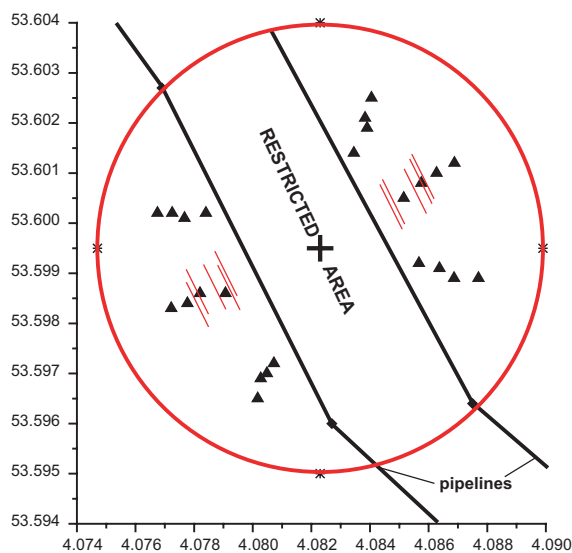


Figure 2. Non-fished 500 m exclusion zone (circle) around platform L07A (+) with intended sampling positions of boxcores (▲) and Triple D hauls (lines). Only data from 7 regularly dispersed boxcore samples have been used in this report. The elongated restricted area is closed for sampling activities in order to protect pipelines for the transport of gas embedded in the seabed in this corridor.

Data on beam trawl effort in the study area were supplied by the Netherlands Institute for Fisheries Research (RIVO). The data are based on satellite monitoring of a selected number of Dutch trawlers including some EURO trawlers (max. 300 Hp) during the interval 2000 to 2002 (Quirijns, RIVO, pers. comm.). Effort is expressed as the total number of satellite recordings of fishing Dutch beam trawlers per rectangular area of 1*1 nautical miles in this 3 years interval. Platform L07A is surrounded by an area with an average trawling effort (Fig. 1c).

Sampling procedures

Within the 500 m exclusion zone around the platform a corridor comprising under water pipelines was defined where sampling was prohibited. All samples in the platform subarea were taken outside this elongated corridor but within 400 m distance of the platform (Fig. 2). The outer 100m of the exclusion zone was not sampled to exclude interference by (accidental) fishing along the perimeters of the exclusion zone. The sampling design further encompassed 4 rectangular regularly trawled reference areas, each 1 x 1 nautical miles, situated at a distance of 1.5 nm north (Ref N), south (Ref S), east (Ref E) and west (Ref W) of the 500 m wide fishery-exclusion zone around the platform (Fig. 1c). We included four reference subareas in the study to ensure that any natural gradient in the study area could be accounted for.

Sampling for this study was carried out with the "Pelagia" (owned by Royal NIOZ) in the period 2-7 April 2004. Epifauna and larger infauna were collected with the Triple-D dredge (Fig. 3; Bergman and van Santbrink, 1994). The dredge excavates a strip of sediment about 80 m long, 20 cm wide and 18 cm deep (16 m²). The excavated sediment is washed through 7*7 mm netting. A total of 10 hauls were made in the 500 m exclusion area, whereas due to time limitations only 6 hauls were made regularly distributed in each reference subarea. Catches were sorted and the ani-



Figure 3. Triple-D dredge for sampling larger sized and lower abundant infauna and epifauna. Sampling area: a strip 80 m long and 20 cm wide (16 m²) to a depth of 18 cm. Meshsize of the netting 1.4 cm stretched (Bergman and van Santbrink, 1994).



Figure 4. Sorting and counting the specimens caught in the Triple-D hauls on board the Pelagia



Figure 5. Reineck boxcorer for sampling infauna. Sampling size 0.07 m^2 to a depth of 40 cm. Samples are washed over 1 mm sieves.

mals identified and measured on board of the ship (Fig. 4).

Infauna was collected with a NIOZ boxcorer (30 cm diameter, ~40 cm penetration into the seabed) which is equipped with a valve to prevent flushing and loss of the top layer (Fig. 5). In the platform subarea 7 samples were collected regularly dispersed along 6 radial transects (Fig. 2). In each of the reference subareas, 7 samples were taken at regularly dispersed positions. All boxcore samples were gently washed through a perforated 1 mm sieve on board and residues preserved in 4% formalin (Fig. 5). At every position a separate boxcore sample was taken that was preserved (4°C) for sediment grain-size analysis.

Analysis of data

The grain-size of sediment taken from a random selection of the boxcore stations *i.e.* from 4 stations in the fishery-exclusion zone and from 4 stations in each of the reference subareas was measured with a Coulter LS230 Laser Diffraction Particle Size Analyzer. On basis of the particle size distribution (range 0.04 – 2000 µm), median grain-size and percentage silt (<64 µm) were calculated. Differences between areas were tested using these two parameters. Homogeneity of variances was tested with Levene statistic. A subsequent one-way Anova and a Tukey HSD posthoc test were used to differentiate between subareas.

The boxcore samples were sorted in the laboratory and the animals identified to species level. Spatial differences in the fauna collected with boxcorer and Triple-D were assessed using the PRIMER™ 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 boxcore samples were visualized using Cluster Analysis on basis of a Bray-Curtis similarity matrix. Differences between density of least and most abundant species in the samples were usually more than 2 orders of magnitude. In order to down-weight the importance of dominant species but keep the importance of rare species in limits, we applied a square root transformation to the original data (see Clarke and Warwick, 2001). ANOSIM analyses were used to test the differences between groups of samples derived from the various subareas. By means of SIMPER analyses the contributions of particular species to the average dissimilarity were calculated.

Differences in density of specific species or of univariate diversity measures between subareas were formally tested with a one-way Anova followed by a posthoc-test. In case of unequal variances as determined by Levene's statistic, the Brown-Forsythe statistic was calculated to test for the equality of group means. This statistic is preferable to the F statistic when the assumption of equal variances does not hold. Further a Tamhane T2 test was used in a posthoc comparison instead of Tukey HSD (SPSS™ 11.5). Differences between median parameter values belonging to different subareas were depicted with notched box-whisker plots (McGill *et al.*, 1978).

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, since they put more weight on the common species. As diversity measures for the boxcore samples we used Hill's numbers (N_0 , N_1 , N_2 , N_{∞} ; see Hill, 1973). The successive numbers put a diminishing weight on rare species.

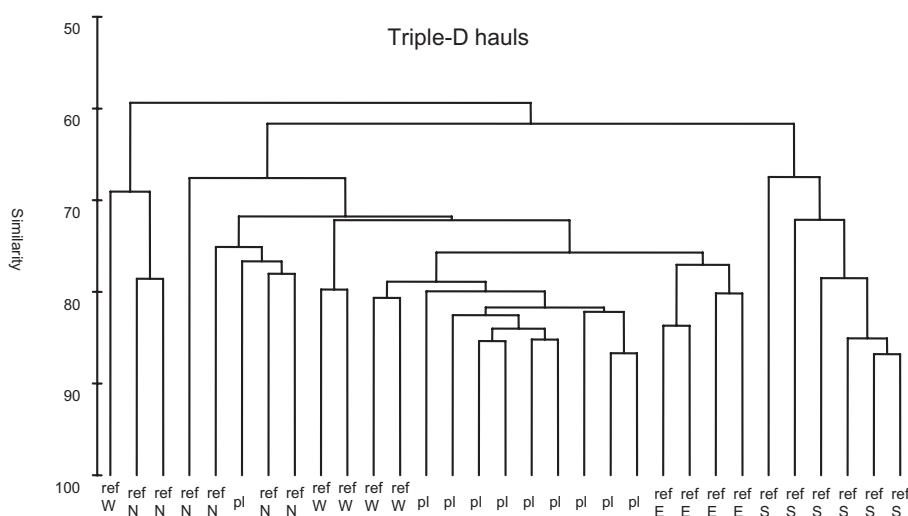


Figure 6. Dendrogram produced by cluster analysis of the Triple-D hauls in platform and reference areas. Reference areas (*ref*) have been coded as N(*orth*), S(*outh*), E(*ast*) and W(*est*). The raw data were $\sqrt{\cdot}$ -transformed before analysis.

RESULTS

Abiotic variables

The one-way Anova showed 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 posthoc test showed that the median grain-size in ref S was on average slightly higher than in the other subareas viz. 113 and 106 μm , respectively. There is also a subtle but significant gradient in the water depth of the study area. The Ref S area is shallowest (mean 35.9 m) and the Ref N deepest (mean 38.9 m) of the subareas.

Satellite data on fishing effort of a random selection of Dutch beam trawlers in 1 x 1 nautical miles rectangles showed that the trawling frequency within a distance of about 2 miles from the platform was patchy varying between 20 and 175 (one 300) recordings per 3-years interval (Fig. 1c). Notably the trawling intensity in the southern reference subarea was circa 3 to 7 times higher than in the other subareas.

Triple-D hauls

The results of a cluster analysis of the $\sqrt{\cdot}$ -transformed Triple-D data are shown by the dendrogram in Fig. 6. The integrity of the subareas is largely maintained with little mixing of the hauls derived from the individual subareas. Notably hauls taken in the southern reference subarea appear to be markedly different from the hauls in the other subareas (see Ref S in Fig. 6).

A global permutation test (ANOSIM) was performed on the dissimilarity matrix to check for differences between groups of hauls from various subareas. If groups do not differ then between-and within-group similarities would be equal and the ANOSIM R-statistic is zero. The resulting R-statistic ($R=0.638$, $p=0.001$) showed that significant differences exist between groups of hauls. A pairwise test of difference between subareas (Table 1) shows that hauls from the platform subarea and from Ref S are both significantly different from each other and all other subareas. Choice of a more severe ($\sqrt{\cdot}$) or no transformation does not alter this result.

	Platform	Ref S	Ref E	Ref W	Ref N
Platform	0				
Ref S	0.987	0			
Ref E	0.793	0.706	0		
Ref W	0.606	0.733	0.088	0	
Ref N	0.711	0.883	0.129	0.123	0

Table 1. R-values resulting from pairwise test (ANOSIM) between Triple-D hauls from different subareas. Data were $\sqrt{\cdot}$ -transformed before analysis. The **bold** values denote a significant difference between subareas ($p < 0.05$).

So on basis of the ANOSIM analysis three groups of hauls can be discerned: platform, Ref S and the pooled other reference subareas. The top ten species responsible for the average dissimilarity between the three groups (SIMPER analysis) have been summarized in Table 2. Briefly, Triple-D hauls in the platform subarea are different due to higher abundances of burrowing mud shrimps (*Upogebia deltaura*, *Callianassa subterranea*) and explicitly of large sized bivalves (*Thracia convexa*, *Arctica islandica*, *Cardium echinatum*,

a	Platform average abundance	Ref N, W, E average abundance	% contribution dissimilarity
species			
<i>Upogebia deltaura</i>	1061	382	11.0
<i>Ophiura albida</i>	3738	3425	8.0
<i>Callianassa subterranea</i>	635	225	6.5
<i>Echinocardium cordatum</i>	498	508	5.6
<i>Ophiura texturata</i>	123	62	3.1
<i>Thracia convexa</i>	63	23	2.4
<i>Dosinia lupinus</i>	13	2	1.4
<i>Chamelea gallina</i>	31	24	1.4
<i>Arctica islandica</i>	12	6	1.3
<i>Cardium echinatum</i>	11	3	1.2

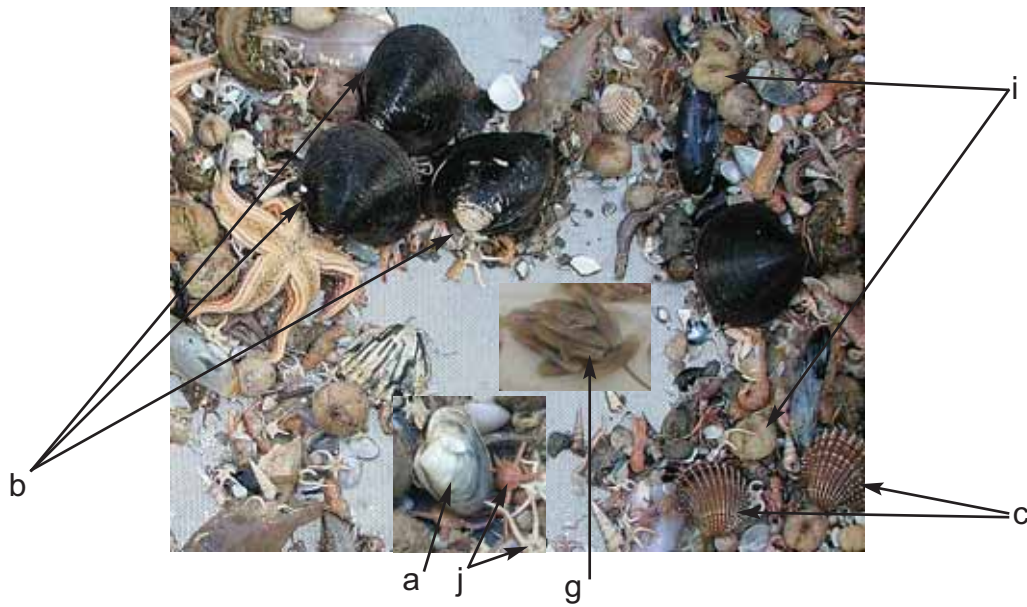
b	Platform average abundance	Ref S average abundance	% contribution dissimilarity
species			
<i>Corbula gibba</i>	305	6454	18.5
<i>Ophiura albida</i>	3738	12184	16.6
<i>Upogebia deltaura</i>	1061	8	10.0
<i>Callianassa subterranea</i>	635	54	6.3
<i>Echinocardium cordatum</i>	498	1339	4.6
<i>Ophiura texturata</i>	123	114	2.2
<i>Thracia convexa</i>	63	9	1.9
<i>Cultellus pellucidus</i>	72	27	1.3
<i>Abra nitida</i>	33	9	1.3
<i>Cucumaria elongata</i>	119	74	1.3

c	Ref N, W, E average abundance	Ref S average abundance	% contribution dissimilarity
species			
<i>Corbula gibba</i>	333	6455	20.7
<i>Ophiura albida</i>	3425	12184	19.5
<i>Echinocardium cordatum</i>	508	1339	6.8
<i>Upogebia deltaura</i>	382	9	4.4
<i>Callianassa subterranea</i>	226	55	3.4
<i>Ophiura texturata</i>	62	115	2.5
<i>Thracia convexa</i>	24	10	1.2
<i>Abra nitida</i>	20	10	1.2
<i>Upogebia stellata</i>	22	0	1.1
<i>Cultellus pellucidus</i>	44	27	1.0

Table 2a, b, c. Species contribution (%) to average dissimilarity resulting from SIMPER-analysis between three groups of Triple-D hauls viz. platform, Ref S and pooled Ref N, W and E. Data were $\sqrt{\cdot}$ -transformed prior to analysis. Average abundances of the species in the subareas (n per 100 m^2) are given.

Dosinia lupinus) (Table 2a; Fig. 7). In comparison to all other subareas (Table 2b, c), hauls in the subarea Ref S are characterized by relatively high abundances of the small bivalve *Corbula gibba*, the ophiuroid *Ophiura albida* and the heart urchin *Echinocardium cordatum* (Fig. 7) and, especially in contrast to the non-fished platform subarea, by low abundances of small sized bivalves (*Abra nitida*, *Cultellus pellucidus*) and burrowing mud shrimps (*Upogebia deltaura*, *Callianassa subterranea*).

As a measure for the diversity of the Triple-D hauls in the subareas we calculated species richness and dominance with the indices of Hurlbert (1971) and the N_2 index of Hill (1973), respectively. Results of a one-way Anova for Hurlbert's index ($F_{4,26}=11.304$, $P=0.000$) and Hill's N_2 ($F_{4,26}=3.690$, $P=0.017$) followed by a Posthoc test show that hauls taken in the platform subarea have on average significantly higher species richness and lower dominance (higher evenness). The reverse seems true for the Ref S subarea but the differences are not significant. Differences in diversity between subareas are illustrated by notched box-whisker plots showing confidence intervals for the medians by means of notches (Fig. 8).



e



f



Figure 7.
Macrofauna species found in high numbers in the Triple-D catches from the non-fished exclusion zone:

- a. *Thracia convexa*
 - b. *Arctica islandica*
 - c. *Cardium echinatum*
 - d. *Dosithea lupinus*
 - e. *Upogebia deltaura*
 - f. *Callinassa subterranea*
 - g. *Cultellus pellucidus*
- and in high numbers in the boxcore samples:
- h. *Amphiura filiformis*

Species found in high numbers in Triple-D catches from Ref S:

- i. *Echinocardium cordatum*
- j. *Ophiura albida*

d



h



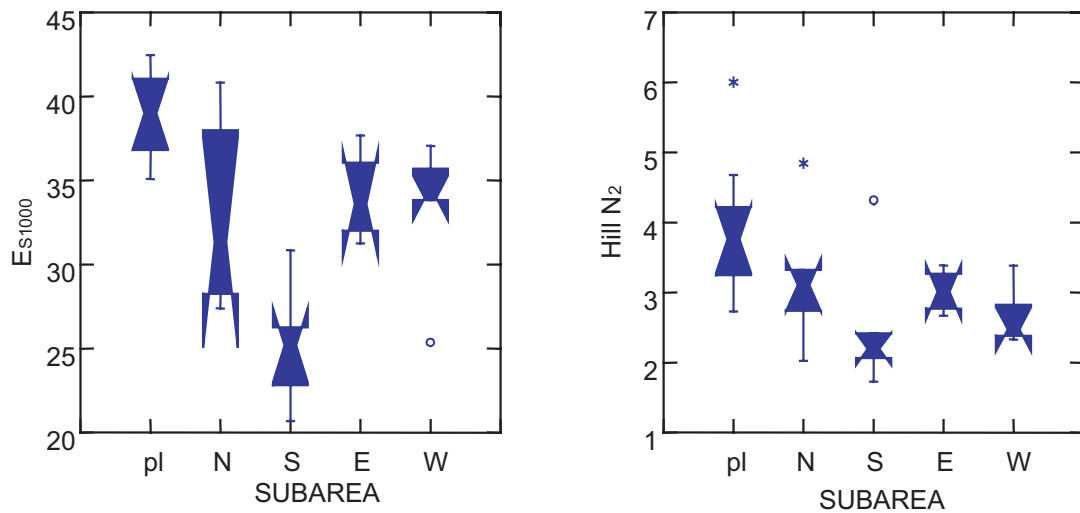


Figure 8. Boxplot comparing median species richness (Hurlbert's E_{S1000}) and the reciprocal of dominance (Hill N_2) of the Triple-D hauls in the platform subarea (pl) and the reference subareas (N, S, E and W). Non-overlapping notches denote a significant difference.

Boxcore samples

Prior to the analysis of the boxcore data, a square root transformation was applied. A cluster analysis of the $\sqrt{\cdot}$ -transformed boxcore data did not reproduce the subareas as accurately as was the case in the analysis of the Triple-D hauls (Fig. 9, cf. Fig. 6).

An ANOSIM test showed that differences exist between subareas ($R=0.146$, $p=0.003$) while the pairwise comparison demonstrated that boxcores from Ref S are significantly different from the groups of samples taken in other subareas. Further significant differences,

although marginally, exist between samples from Ref N and the platform subarea (Table 3). The species contributing to the contrast between Ref S on one hand and the pooled other subareas, including the non-fished platform subarea, on the other hand (SIMPER analysis) are listed in Table 4. Characteristic species in boxcores from Ref S were the ophiuroid *Ophiura albida* and the heart urchin *Echinocardium cordatum* whereas for instance the mud shrimp *Upogebia deltaura* and the polychaete *Polydora cf. guillyi* were more abundant in boxcores from the pooled other subareas.

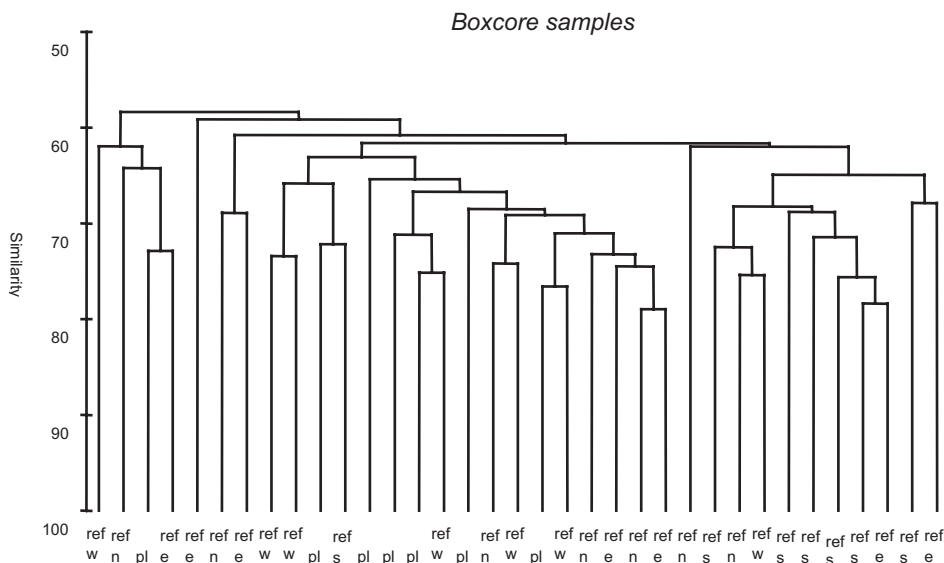


Figure 9. Dendrogram produced by cluster analysis of the boxcore samples in platform and reference areas. Reference areas (ref) have been coded as N(orth), S(outh), E(ast) and W(est). The raw data were $\sqrt{\cdot}$ -transformed before analysis.

	Platform	Ref S	Ref E	Ref W	Ref N
Platform	0				
Ref S	0.529	0			
Ref E	0.096	0.260	0		
Ref W	0.026	0.254	-0.021	0	
Ref N	0.186	0.448	0.015	-0.045	0

Table 3. R-values resulting from pairwise test (ANOSIM) between boxcore samples taken in different subareas. Data were $\sqrt{\cdot}$ -transformed prior to analysis. The **bold** values mark a significant difference between subareas ($p < 0.05$).

The ANOSIM result (Table 3) does not exclude that specific species found in the boxcore samples may have different densities in the pooled subareas. Species of interest in this context are for instance those that are discriminative in the separation of subareas in the Triple-D results (see Table 2). Because of the much smaller sample size of boxcores (0.07 m²) compared to Triple-D (16 m²), only few species listed in Table 2 had sufficient individuals in the boxcores to be tested i.e. the mudshrimps *Callianassa subterranea* and *Upogebia deltaura*. A one-way Anova with $\sqrt{\cdot}$ -trans-

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

Table 4. Species contribution to average dissimilarity resulting from SIMPER-analysis between the two groups of boxcore samples viz. pooled Ref N, W, E and platform vs. Ref S. Data were $\sqrt{\cdot}$ -transformed prior to analysis. Average abundances of the species (n per 0.07 m²) in the subareas are given.

	df	F	Sign.
<i>Callianassa subterranea</i>	4, 30	7.027	.000
<i>Upogebia deltaura</i>	4, 30	4.785	.004
<i>Amphiura filiformis</i>	4, 30	2.892	.039

Table 5. Results of a comparison (one-way Anova; $p < 0.05$) between abundances of selected species in boxcores collected in the different subareas. Homogeneity of variances was tested prior to analysis. Abundance data were $\sqrt{\cdot}$ -transformed.

formed abundances followed by Tamhane posthoc test showed that there were significant differences between subareas (Table 5) and that particularly the platform boxcores had higher abundances of mud shrimps than the reference areas N (notably only in case of *Callianassa subterranea*), E and S. These differences are illustrated by notched box-whisker plots (Fig. 10).

This is in line with the results of the Triple-D. Other relevant species are ones that are considered vulnerable to beam trawl damage (Bergman and van Santbrink 2000). A fragile and thus potentially vulnerable species occurring in sufficient numbers in the dataset is the brittlestar *Amphiura filiformis* (Fig. 7). 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. Differences in diversity between subareas were determined with a one-way Anova. As diversity measures we used Hill's numbers ($N_0, N_1, N_2, N_{\infty}$; see Hill, 1973). The successive numbers put a diminishing weight on rare species. There were no statistical differences between subareas with respect to diversity (Table 6) but there is nevertheless a tendency for the samples taken near the platform to have a lower degree of dominance (higher evenness) as measured by Hill N_2 . Differences in diversity between subareas were exemplified by notched box-whisker plots in Fig. 11.

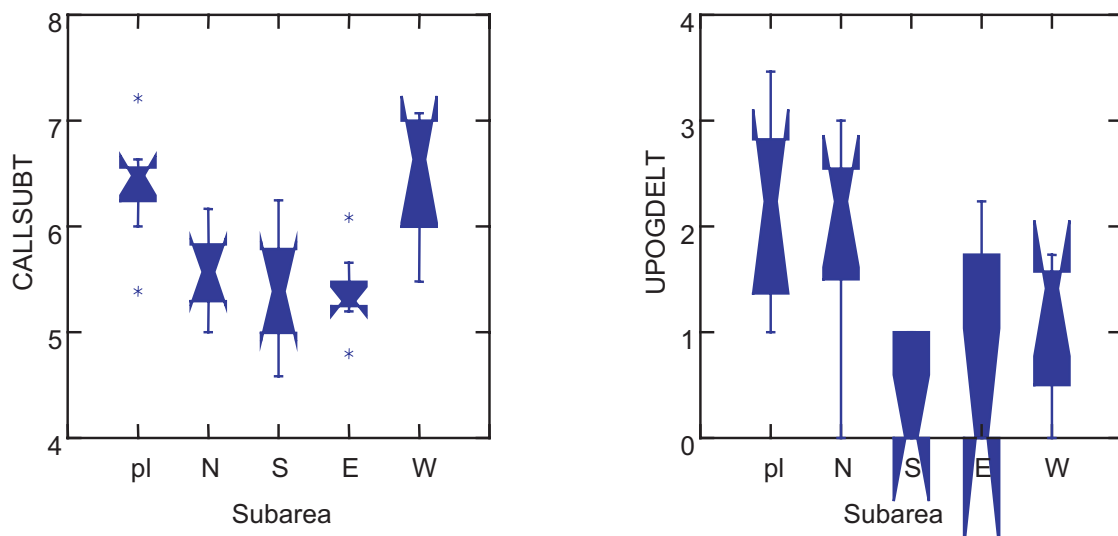


Figure 10. Comparison of densities ($\sqrt{\cdot}$ -transformed) of mud shrimps *Callianassa subterranea* and *Upogebia deltaura* in boxcore samples in the platform (pl) and reference subareas (N, S, E and W).

HILL	df	F	Sign.
N0	4, 30	1.595	.201
N1	4, 30	1.840	.147
N2	4, 30	2.338	.078
N _∞	4, 30	2.291	.083

Table 6. Results of a comparison (one-way Anova; $p < 0.05$) between diversity measures belonging to the boxcore samples in the subareas.

DISCUSSION

Results of this study especially those obtained with the Triple-D dredge point to a clear difference between the fauna in the fishery-closed area 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 catches more explicitly expose differences between non-fished and fished subareas than boxcore samples. Latter contain a suit (> 20) of small short lived species some of them in large numbers like in our case 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 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. However, regardless of the type of transformation, none of the boxcore 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 *Arctica islandica*, *Thracia convexa*, *Dosinia lupinus* and

Cardium echinatum (Table 2a). All are relatively large sized sensitive species living in reach of the beam 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 sized bivalves *Abra nitida* and *Cultellus pellucidus*. Both species had higher abundances in the non-fished subarea than in the heavily trawled Ref S. Bergman and van Santbrink (2000) reported for these species direct trawling mortalities of 18-38% and 27-29%, respectively, in the trawl path of a single beam trawl haul in silty sediments. Above results are in line with Jennings *et al.* (2001) who found an up to 6-fold reduction in abundance of bivalves and spatangoids in areas with trawling frequencies of 0.2 to 6.5 y^{-1} in the central North Sea. Abundance of infaunal polychaetes in contrast showed no relation with trawling frequency in the study by Jennings *et al.* (2001). The lack of clear patterns in our boxcore samples that are dominated by polychaetes (average 30% of the species and 40% of the individuals in a sample) is in accordance with above finding.

However, there are some unexpected results. One is the higher abundance of mud shrimps in the platform subarea or conversely their depressed abundance in the regularly trawled subareas. This was apparent in the Triple-D results (Table 2a, b) and was substantiated by the boxcore data when we tested this by Anova (Table 5). Because of the deeper penetration of the boxcoring latter is considered to yield more reliable estimates especially with respect to the smaller and deeper living *Callinassa subterranea*. The significant higher abundance of *C. subterranea* in boxcores from the platform subarea than in those from subareas Ref E, N and S (see Fig. 10) supports the results of the Triple-D analysis. Possibly Ref W did not differ from the platform because beam trawl effort was lowest of all reference subareas (Fig. 1c). In the case of *Upogebia deltaura*, however, significant differences between plat-

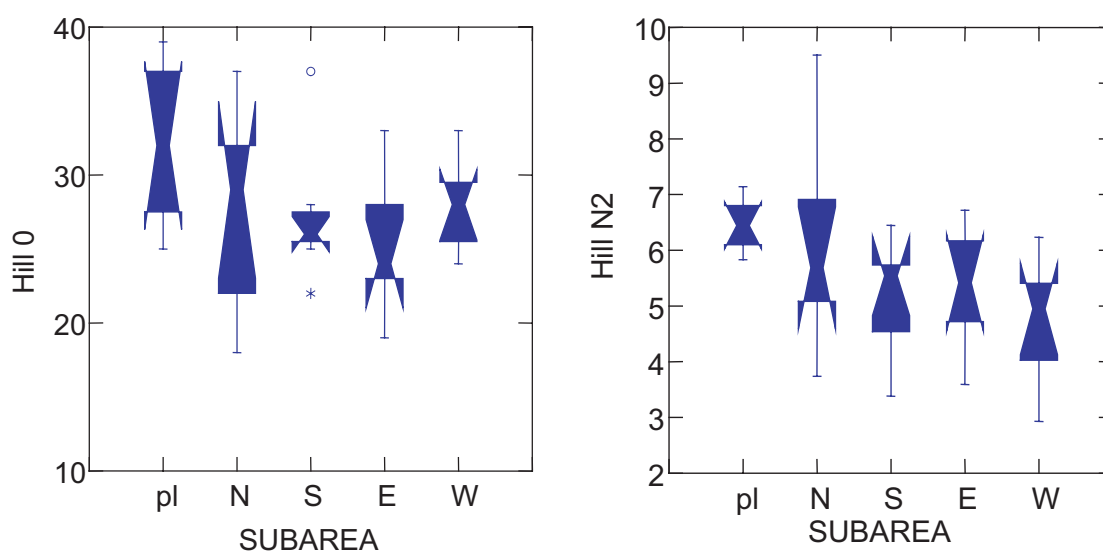


Figure 11. Hill's diversity N_0 (=Number of species) and N_2 (reciprocal of dominance) of boxcore samples in the platform (pl) and reference subareas (N, S, E and W).

form subarea on the one hand and reference areas on the other hand were found only for Ref E and S (Fig. 10). There is no obvious explanation for the fact that Ref N showed no significant difference.

Both mud shrimp species live permanently in tunnels extending down to 50 cm deep in the sediment (Fig. 12). The maximum penetration depth of beam trawls is only ~8 cm (Paschen *et al.*, 1999) implying that trawling will have little direct effect on mud shrimps. Support for this surmise comes from Bergman *et al.* (1998) who found no distinct relationship between the distributions of *Upogebia* spp. and beam trawl effort in the Oyster Ground. Decline of *Callianassa* in connection with fishing has so far only been reported from areas where Nephrops trawls are used designed to dig into the sediment (<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 regarded as not significant in the same document (http://www.marlin.ac.uk/biotopes/Bio_Sensexp_CMS.AfilEcor.htm). Yet, we think our data indicate that the effect of trawling in reducing *C. subterranea* densities, and presumably those of *Upogebia* as well, may not be insignificant at all. Because mud shrimps are considered to be engineering species with an important impact on sediment bioturbation, mineralization, and the erosion threshold of the seabed (Howe *et al.*, 2004; Rowden and Jones, 1993; Amaro *et al.*, 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 *Echinocardium cordatum* in Ref S being the subarea with highest fishing effort (Fig. 1c). 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 show that relatively high densities of *E. cordatum* are

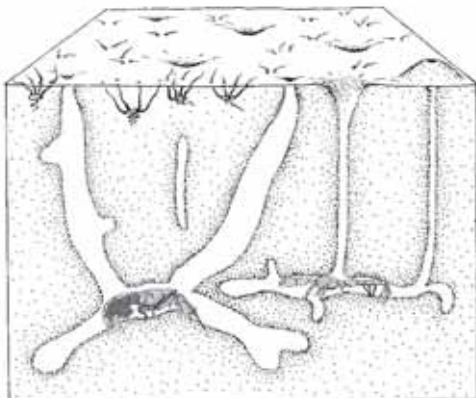


Figure 12. Sketch of the position of the brittle star *Amphiura filiformis* (upper layer), and the mud shrimps *Callianassa subterranea* (right) and *Upogebia deltaura* (left) in the sediment. Burrow outlines are based on resin casts. Horizontal and vertical scale is approx. 15*15 cm.

common along the southern edge of the Frisian Front (Creutzberg *et al.*, 1984; Duineveld and Daan, *unpubl.*), just south of our Ref S. What causes these bands 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. Latter is 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 food conditions and elevated survival and growth rates of the various species are important for the formation of the faunal bands. Alternatively bands could be due to enhanced deposition of pelagic larvae in relation to decreasing current speed or the pelagic front (Creutzberg, 1986; Lough and Manning, 2000). Since growth rates of *E. cordatum* at the Frisian Front are not enhanced (Duineveld and Jenness, 1984) and thus the critical period in which they live in the upper layers of the sediment in reach of the trawl is not shortened, the higher fishing mortality at Ref S most likely is compensated by enhanced larval supply.

The contrasting patterns of *Echinocardium cordatum* and for instance *Thracia convexa* i.e. both vulnerable species but the one more abundant in a heavily fished subarea 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 studies by Bergman *et al.* (1998) and Craeymeersch *et al.* (2000). Without adequate knowledge of 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 areas around the closed area (Fig. 1c) made it possible to test their homogeneity and for instance to show that Ref S was not representative as reference area in terms of fauna and abiotic characteristics (Tables 1 and 3).

It is further noteworthy that we did not find young stages of sensitive bivalves (*Thracia convexa*, *Arctica islandica*) in the platform exclusion zone. Earlier Witbaard and Bergman (2003) have noted the unimodal and skewed size distribution of the *A. islandica* stock in the Oyster Ground (Fig. 1b) where old specimens predominate and juveniles are rare. In more northern stocks (e.g. at Fladen Ground) in contrast, juveniles are much more abundant giving rise to a bimodal size distribution. They argue that beam trawling may be one of the factors responsible for the infrequent recruitment and skewed size distribution of *A. islandica* in the Oyster Ground. The lack of juvenile *A. islandica* in the closed platform subarea seems to suggest that direct trawling mortality among juveniles is presently not the main factor preventing successful recruitment. It is more likely that the adult density has so far declined that fertilization is hampered. The higher adult density in the exclusion zone does not generate higher local recruitment rates, most likely due to their relative long pelagic larval phase, which facilitates spatial dispersal. Import of larvae produced by adjacent stocks does not seem to occur regularly in the Oyster Ground. Recently, Holmes *et al.* (2003) found that all *Arctica* populations in the North Sea, including the one in the Oyster Ground, are genetically relatively isolated from each other.

CONCLUSIONS

Multivariate analysis showed that benthic fauna caught with the Triple-D dredge in the for fishery closed area around the platform differed distinctly from the fauna in the trawled reference subareas. Conspicuous were higher abundances of mud shrimps (*Callinassa subterranea*, *Upogebia deltaura*) and sensitive bivalves both long lived (*Arctica islandica*, *Thracia convexa*, *Cardium echinatum*) and shorter lived species (*Abra nitida*, *Cultellus pellucidus*) near the platform. Species richness and evenness were higher as well.

A similar analysis of the infauna collected with a boxcorer did not reveal a difference between of the fauna in the closed platform subarea and that in the trawled reference areas. This is attributed to the large share of small, short-living species common to all boxcores and the relatively low abundances of sensitive larger species. However, boxcore samples did confirm the higher abundance of mud shrimps (*Callinassa subterranea*, *Upogebia deltaura*) in the non-fished platform subarea, together with higher densities of *Amphiura filiformis*.

Beam trawl effort leading to lower densities of mud shrimps will have implications for the sediment structure, bioturbation and mineralization and may have

large consequences for the functioning of the benthic ecosystem. This is an indication that this type of fishery affects not only the species level but has impacts on ecosystem level as well.

Despite the positive effect of the non-fished platform subarea on survival of adults of sensitive bivalve species, no evidence was found for higher recruitment rates in this relative small subarea.

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REFERENCES

- Amaro, T., Bergman, M.J.N., Scheffer, M., and Duineveld, G.C.A. 2005. The consequences of the changes in the abundance of *Callianassa subterranea* and *Amphiura filiformis* on the sediment erosion (threshold) at the Frisian Front (SE North Sea). In The benthic shift of the Frisian Front (southern North Sea) ecosystem – possible mechanisms: 109-133. Ed. by T.P.F. Amaro. PhD Thesis, Wageningen University, Wageningen, the Netherlands.
- Bergman, M.J.N., and Duineveld, G.C.A. 1990. Verspreiding van OBM-gevoelige macrobenthossoorten in de Noordzee. NIOZ-Rapport, 1990-7: pp 29.
- Bergman, M.J.N., and Hup, M. 1992. Direct effects of beam trawling on macro-fauna in a sandy sediment in the southern North Sea. ICES Journal of Marine Science, 49: 5-11.
- Bergman, M.J.N., and Santbrink, J.W. van. 1994. A New Benthos Dredge (Triple-D) for Quantitative Sampling of Infauna Species of Low Abundance. Netherlands Journal of Sea Research, 33: 129-133.
- Bergman, M.J.N., and Santbrink, J.W. van. 2000. Fishing mortality of populations of megafauna in sandy sediments. In Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues, 49-69. Ed. by M.J. Kaiser and S.J. de Groot. Blackwell Science, Oxford.
- Bergman, M.J.N., Santbrink, J.W. van, Piet, G.J., and Rijnsdorp, A.D. 1998. Abundance and species composition of larger sized invertebrate species (megafauna) in relation to beam trawl effort. BEON Rapport, 98-2: 37-53.
- Clarke, K.R., and Gorley, R.N. 2001. Primer v5: User manual/Tutorial. Primer-E Ltd, Plymouth.
- Clarke, K.R., and Warwick, R.M. 2001. Change in marine communities - an approach to statistical analysis and interpretation. Primer-E Ltd, Plymouth.
- Coleman, F.C., and Williams, S.L. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution, 17: 40-44.
- Craeymeersch, J.A., Piet, G.J., Rijnsdorp, A.D., and Buijs, J. 2000. Distribution of macrofauna in relation to the micro-distribution of trawling effort. In Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues: 187-197. Ed. by M.J. Kaiser and S.J. de Groot. Blackwell Science, Oxford.
- Cramer, A. 1990. Seasonal variation in benthic metabolic activity in a frontal system in the North Sea. In Trophic relationships: 54-76. Ed. by M. Barnes and R.N. Gibson. Proceedings of the 24th European Marine Biology Symposium. Aberdeen Univ. Press.
- Creutzberg, F. 1985. A persistent chlorophyll-a maximum coinciding with an enriched benthic zone. In Proceedings of the 19th European Marine Biology Symposium: 97-108. Ed. by P.E. Gibbs. Plymouth. U.K. Cambridge Univ. Press.
- Creutzberg, F., 1986. Distribution patterns of two bivalve species (*Nucula turgida*, *Tellina fabula*) along a frontal system in the southern North Sea. Journal of Sea Research, 20: 305-311.
- Creutzberg, F., Wapenaar, P., Duineveld, G., and Lopez, N.L. 1984. Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions. Rapport et. Procès-verbaux des Réunions, Conseil international pour L'Exploration de la Mer, 183: 101-110.
- Daan, R., and Mulder, M. 1996. On the short-term and long-term impact of drilling activities in the Dutch sector of the North Sea. ICES Journal of Marine science, 53: 1036-1044.
- Duineveld, G.C.A., and Jenness, M.I. 1984. Differences in the growth rate of the sea urchin *Echinocardium cordatum* as estimated by the parameter w of the von Bertalanffy equation applied to skeletal rings. Marine Ecology Progress Series, 19: 65-72.
- Gee, A. de, Baars, M.A., and Veer, H.W. van der. 1991. De ecologie van het Friese Front. NIOZ Rapport, 1991-2, pp. 96.
- Groenewold, S. 2000. The effects of beam trawl fishery on the food consumption of scavenging epibenthic invertebrates and demersal fish in the southern North Sea. University Hamburg, pp. 146.
- Groenewold, S., and Fonds, M. 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam trawl fishery in the southern North Sea. ICES Journal of Marine Science, 57: 1395-1406.
- Heath, M.R. 2005. Changes in the structure and function of the North Sea foodweb, 1973-2000, and the impacts of fishing and climate. ICES Journal of Marine Science, 62: 847-868.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology, 54: 427-432.
- Holmes, S.P., Witbaard, R., and Meer, J van der. 2003. Phenotypic and genotypic population differentiation in the bivalve mollusc *Arctica islandica*: results from RAPD analysis. Marine Ecology Progress Series, 254: 163-176.
- Howe, R., Rees, A.P., and Widdicombe, S. 2004. The impact of two species of bioturbating shrimp (*Callianassa subterranea* and *Upogebia deltaura*) on sediment denitrification. Journal of the Marine Biological Association of the United Kingdom, 84: 629-632.
- Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology, 52: 577-586.
- IDON, 2005. Integraal Beheerplan Noordzee 2015. Interdepartementale Directeurenoverleg Noordzee, pp 130.
- Jennings, S., Nicholson, M.D., Dinmore, T.A., and Lancaster, J.E. 2002. Effect of chronic trawling disturbance on the production of infaunal

- communities. *Marine Ecology Progress Series*, 243: 251-260.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C., and Warr, K.J. 2001. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series*, 213: 127-142.
- Kaiser, M.J., and Groot, S.J. de. 2000. The effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell Science, Oxford, pp 399.
- Kaiser, M.J., and Spencer, B.E. 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal Animal Ecology*, 65: 348-358.
- Kroncke, I., Duineveld, G.C.A., Raak, S., Rachor, E., and Daan, R. 1992. Effects of a Former Discharge of Drill Cuttings on the Macrofauna Community. *Marine Ecology Progress Series*, 91: 277-287.
- Lavaleye, M.S.S. 2000. Karaktersitieke macrobenthos gemeenschappen van het NCP en een trendanalyse van de macrobenthos diversiteit van de Oestergronden en het Friese Front (1991-1998). NIOZ-Rapport, 2000-9: pp 25.
- Lough, R.G., and Manning, J.P. 2000. Tidal-front entrainment and retention of fish larvae on the southern flank of Georges Bank. *Deep-Sea Research II Topical studies*, 48: 631-644.
- McGill, R., Tuckey, J.W., and Larsen, W.A. 1978. Variation of box plots. *The American Statistician*, 32: 12-16.
- Norse, E.A., and Watling, L. 1999. Impacts of mobile fishing gear: the biodiversity perspective. *American Fisheries Society Symposium*, 22: 31-40.
- Paschen, M., Richter, U., Köpnick, W., Lorenzen, U., Zimmerman, M., Fonteyne, R., Marlen, B. van, Groot, S.J. de, Laban, C., and Klugt, P.C.M., van der. 1999. Trawl Penetration in the Seabed (TRAPESE). Draft Final Report EC-Study Contract No. 96-006.
- Rowden, A.A., and Jones, M.B. 1993. Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda Thalassinidae). *Journal of Experimental Marine Biology and Ecology*, 173: 265-272.
- Witbaard, R., and Bergman, M.J.N. 2003. The distribution and population structure of the bivalve *Arctica islandica* L. in the North Sea: what possible factors are involved. *Journal of Sea Research*, 50: 11-25.
- Witbaard, R., and Klein, R. 1994. Long term trends of the effects of the southern North Sea beam-trawl fishery on the bivalve mollusc *Artica islandica*. *ICES Journal of Marine Science*, 51: 99-105.