An exploratory analysis of environmental conditions and trawling on species richness and benthic ecosystem structure in the Frisian Front and Central Oyster Grounds

Tobias van Kooten*, Daniel van Denderen*, Sander Glorius*, Jan Tjalling van der Wal*, Rob Witbaard^, Piet Ruardij^, Marc Lavaleye^, Diana Slijkerman*

*IMARES
^NIOZ

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Ministry of Economic Affairs
Wilmar Remmelts
PO box 20401
2500 EK The Hague
The Netherlands

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Nederlandse samenvatting

Deze studie gaat over de effecten van bodemvisserij op biodiversiteit in het Friese Front en de Centrale Oestergronden. De studie is uitgevoerd in het kader van de toekomstige sluiting van een deel van het Friese Front/Centrale Oestergronden voor bodemberoerende visserij, als onderdeel van het KRM maatregelenpakket. Het ministerie van I&M leidt het proces rondom de sluiting van de gebieden.

Doelen EU Kaderrichtlijn Mariene Strategie en Nederlandse Mariene Strategie
De Europese Kaderrichtlijn Mariene Strategie (2008) heeft als doel om het mariene ecosysteem integraal duurzaam te beheren. De richtlijn richt zich op 11 verschillende aspecten (descriptoren), waarvan ‘biodiversiteit’, ‘voedselweb’ en ‘bodemintegriteit’ in het kader van deze studie van belang zijn.
In de Nederlandse Mariene Strategie deel 1 (2013) zijn de concrete doelen beschreven om in de Nederlandse Noordzee een goede milieutoestand te bereiken. Het tussendoel voor 2020 is ‘*de trend van verslechtering van het mariene ecosysteem als gevolg van schade aan bodemhabitat en aan de biodiversiteit, om te buigen naar een ontwikkeling in de richting van herstel. Dit is een eerste stap naar een situatie waarin het mariene ecosysteem in het Nederlandse deel van de Noordzee op langere termijn (deels) kan herstellen. Het toekomstbeeld is een structuur waarbij relatieve verhoudingen van de ecosysteemcomponenten (habitats en soorten) in overeenstemming zijn met die welke behoren bij de heersende fysiografische, geografische en klimatologische omstandigheden*’. Er zijn verder subdoelen gesteld voor de verschillende onderdelen van het ecosysteem. Het subdoel voor benthos is *‘Verbetering omvang, conditie en verspreiding van populaties langlevende en/of kwetsbare (voor fysieke beroering gevoelige) benthos soorten’* Uitgangspunten zijn dat 10-15% van de zeebodem tegen bodemberoering beschermd wordt, en dat de visserij daarbij zoveel mogelijk wordt ontzien.

Kennisvragen en doel van de studie
Een van de kennisvragen die tijdens het stakeholderproces naar voren kwam, luidt: wat is de potentie voor herstel van het bodemleven na sluiting? Bescherming van gebieden met een hoge potentie is te prefereren boven gebieden met een lage potentie, is daarbij de gedachte. En is er binnen het zoekgebied Friese Front-Centrale Oestergronden variatie daarin? Dit is een lastige vraag, aangezien de huidige bodemfauna vooral bestaat uit soorten die de resultante zijn van langdurige visserijdruk. Om inzicht te krijgen in de potentie van een gebied is het dus belangrijk eerst inzicht te krijgen in het huidige effect van visserij op de structuur van het benthos.
Het doel van deze studie is om te achterhalen wat effecten zijn van visserij en omgevingsvariabelen, binnen het zoekgebied Friese Front/Centrale Oestergronden, op de functionele samenstelling, grootteverdeling en soortenrijkdom van de grotere bodemfauna. Het idee daarbij is dat de visserijdruk niet overal hetzelfde is, maar dat er specifieke ruimtelijke verschillen zijn die over langere tijd stand houden, met verschillen in benthossamenstelling als gevolg, los van effecten van omgevingsvariabelen.

Benthosdata en analyses
Voor de analyses is gebruik gemaakt van de benthosdataset van het NIOZ, verkregen met de bodemschaaf (Triple-D) in de jaren 2006-2012 in het zoekgebied Friese Front/Centrale Oestergronden. Gebruikte benthosdata van de bemonsterde 193 stations betreffen soortensamenstelling (139 taxa in totaal), biomassa- en dichtheid. Visserij-intensiteit is uitgedrukt als cumulatieve intensiteit per locatie 1.5 jaar voorafgaand aan de benthosbemonstering. Verder zijn data over primaire productie, waterdiepte en sedimentsamenstelling gebruikt.
Er zijn drie verschillende analyses uitgevoerd:

1. Effect bodemvissserij en omgevingvariabelen op functionele samenstelling van het benthos.

In deze analyse worden aan elk van de aanwezige soorten eigenschappen toegekend, zoals grootte, manier van voeden, positie in sediment, wel/niet gravend, mobiliteit, etc. Daarvoor is gebruik gemaakt van de “biological traits database” uit het EU project ‘BENTHIS’. Op deze manier kunnen verspreidingskaarten van ecologische functies worden gemaakt, zoals verspreiding van aaseters of riffenbouwers. Vervolgens is geanalyseerd hoe de ecologische functies samenhangen met de visserijdruk en omgevingsvariabelen. De verwachting is bijvoorbeeld dat bij toenemende visserijdruk er een verschuiving van filtreerders (zoals schelpdieren) naar aaseters (zoals zeesterren of krabben) te zien is. De potentie van sluiting van een gebied zou kunnen zijn dat bij afwezigheid van visserijdruk de filtreerders weer gaan toenemen.

1. Effect bodemvisserij en omgevingsvariabelen op groottestructuur van het benthos.
   In dit onderdeel onderzoeken we of, en voor welke soorten, binnen het zoekgebied Friese Front/Centrale Oestergronden, er verschillen zijn in populatie-grootteverdeling tussen zwaar-beviste en minder beviste gebieden. Een hypothese zou kunnen zijn dat in zwaar-beviste gebieden gemiddeld kleinere individuen voorkomen per soort en in gebieden met minder visserijdruk grotere individuen. De potentie van sluiting zou kunnen zijn dat er een herstel van de natuurlijk grootteverdeling optreedt.

2. Effect bodemvisserij en omgevingsvariabelen op soortenrijkdom.
   Met deze analyse worden de gezamenlijke effecten van visserijintensiteit en de omgevingsvariabelen op soortenrijkdom geanalyseerd (Technische benaming: Structural Equation Model). De verwachting is dat er bij hogere visserij-intensiteit minder soorten voorkomen. De potentie van sluiting zou kunnen zijn dat soorten weer terug kunnen keren.

Resultaten en conclusie

Op de Noordzee wordt al vele decennia met bodemberoerende tuigen gevist, en het benthische ecosysteem zal zich daaraan aangepast hebben. Op de langere termijn (decennia) zullen daarom veel grotere effecten van visserij te zien zijn dan hier zijn gevonden (1.5 jaar).

1. Effect bodemvissserij en omgevingvariabelen op functionele samenstelling van het benthos.
   Er zijn duidelijk benthos groepen met verschillende eigenschappen en functies zichtbaar die geografisch clusteren (aparte clusters voor FF en CO). Deze ruimtelijke verschillen in functionele eigenschappen tussen de benthosstations konden voor 18% worden verklaard door de gecombineerde voorspellende variabelen visserijdruk, korrelgrootte, diepte en primaire productie. Niet kon worden vastgesteld wat de specifieke bijdrage van visserijdruk ten opzichte van de andere factoren was. Vooral effecten van diepte en visserijdruk zijn moeilijk te onderscheiden, omdat visserijdruk met diepte correleert (hoe dieper hoe minder visserijdruk). Wel zijn de volgende functionele eigenschappen sterk gecorreleerd met visserijdruk:

Positief gecorreleerd met visserijdruk		Negatief gecorreleerd met visserijdruk	
ei ontwikkeling - broed	Bij hogere visserijdruk meer soorten met broedzorg (bv krabben die eieren met zich mee dragen)	*leefomgeving* – vrij levend	Bij hogere visserijdruk minder vrij levende soorten
bescherming - exoskelet	Bij hogere visserijdruk meer soorten met een exoskelet (bv krabben)	*bioturbatie* - diffusief mengen	Bij hogere visserijdruk minder bioturberende soorten (vertikaal/horizontaal bewegen van sediment of materiaal (bv gravende kreeftjes)

voedingswijze - predator	Bij hogere visserijdruk meer predator soorten (bv zeesterren)	*voedingswijze -* subsurface deposit	Bij hogere visserijdruk minder soorten die in bodem aanwezige deeltjes eten (bv wormen)
leefomgeving – graaft gangen	Bij hogere visserijdruk meer gangen gravende soorten (bv gravende kreeftjes)	*sediment positie -* 0-5cm	Bij hogere visserijdruk minder soorten die in toplaag (0-5 cm) zitten (bv bepaalde schelpdieren)
bioturbatie- oppervlakte depositie	Bij hogere visserijdruk meer soorten die sediment op oppervlak afzetten (bv bepaalde wormen)	*Ei ontwikkeling-* benthisch	Bij hogere visserijdruk minder soorten die eieren op bodem afzetten (bv wulk)

Biota die vrijlevend zijn of die gebruik maken van de bovenste 5 cm van het sediment, bevinden zich in de zone waar de verstoring door bodemvisserij het sterkst is, en zijn dan ook sterk negatief geassocieerd met bodemvisserij (zie tabel). Ook is er een lagere frequentie van soorten waarvan de eieren zich op de zeebodem ontwikkelen op locaties waar visserijdruk hoog is. De overige ‘top 5’ eigenschappen die sterk negatief met bodemvisserij zijn geassocieerd, zijn dat naar verwachting omdat zij sterk gecorreleerd zijn met omgevingsvariabelen die sturend zijn voor visserijdruk, of omdat zij gekoppeld zijn aan veelvoorkomende soorten die vanwege andere eigenschappen visserij-gevoelig zijn.

Positief met visserijintensiteit geassocieerde eigenschappen zijn een hard omhulsel, waardoor soorten beschermd worden, en waardoor ze logischerwijs resistent zijn tegen bevissing. Ook predatoren zijn talrijker, mogelijk als gevolg van het veel voorkomen van ‘gewonde’ individuen in gebieden met veel bodemvisserij, waardoor veel makkelijke prooien voorhanden zijn. Ook diepgravende biota in het sediment–zijn relatief talrijker in intensief beviste gebieden. Deze burchten zijn vaak zo diep dat de organismen die er in leven zich kunnen terugtrekken naar dieptes waar de bodemvisserij geen of bijna geen effect heeft.

2. Effect bodemvisserij en omgevingsvariabelen op <u>groottestructuur</u> van het benthos.
   Wat betreft de grootteverdeling laten enkele soorten zoals de gedoornde hartschelp (*Acanthocardia echinata*), hartegel (*Echinocardium cordatum*) en de dichtgestreepte artemisschelp (*Dosinia lupinus*) een zeer duidelijk verschil zien tussen licht en zwaar beviste gebieden. Voor een aantal andere soorten is er nauwelijks verschil, zoals voor diepgravende modderkreeftjes (*Callianassa subterranea* en *Upogebia deltaura*). Voor veel van de gevoeligste soorten is de verspreiding binnen het onderzochte gebied te beperkt om een effect met statistische significantie aan te tonen, hoewel wel een effect op de groottestructuur verwacht kon worden. De reden hiervoor is dat deze soorten in de zwaarst beviste gebieden überhaupt niet gevonden zijn, terwijl deze op basis van historische observaties, of de gebiedskenmerken wel verwacht zouden worden. Voor een aantal langlevende soorten zoals de afgeknotte gaper (*Mya truncata*) en de noordkromp (*Arctica islandica*) kan de vergelijking echter niet worden gemaakt, omdat ze in zwaar beviste gebieden niet zijn aangetroffen.

3. Effect bodemvisserij en omgevingsvariabelen op <u>soortenrijkdom.</u>
   De uitkomsten van het Structural Equation Model laten zien dat soortenrijkdom sterk wordt bepaald door primaire productiviteit, diepte, sedimenttype en biomassa. We vinden ook dat de mate van bodemvisserij met name wordt bepaald door diepte en primaire productiviteit.Een directe relatie tussen bodemvisserij en soortenrijkdom is in de gebruikte data niet gevonden. Zowel soortenrijkdom als de mate van bodemvisserij lijken dus vooral afhankelijk van

omgevingsvariabelen. In eerdere studies, op grotere ruimtelijke schaal en met een andere bemonsteringsmethode is wel een verband tussen bodemvisserij en soortenrijkdom aangetoond (van Denderen et al. 2014a).

Herstelpotentie van benthos na gebiedssluiting

Het uiteindelijke doel van deze studie was om te onderzoeken waar, binnen het zoekgebied Friese Front/Centrale Oestergronden, het effect van bodem-beroerende visserij in de huidige situatie het grootst is, en waar dus maximaal herstel kan worden verwacht na sluiting voor bodem-beroerende visserij.

Idealiter zouden we daarom kaarten willen laten zien van het zoekgebied met daarop verspreiding van herstelpotentie, en daaruit afleiden welke eigenschappen/ecosysteemfuncties, grootteverdelingen en soortenrijkdom we zouden verwachten bij sluiting voor de bodemberoerende visserij.

De visserijeffecten zijn echter sterk gerelateerd aan de effecten van andere omgevingsfactoren, waardoor zulke kaarten alleen het gecombineerde effect van visserij en de overige factoren (diepte, sedimenttype, productiviteit en biomassa) kunnen laten zien. Ze zijn dus van beperkte waarde voor het selecteren van gesloten gebieden.

Als we ervan uitgaan dat herstel optreedt bij afwezigheid van visserij, dan zijn er ecosysteemfuncties en eigenschappen die terug zouden kunnen keren na sluiting van gebieden: meer vrijlevende en meer ondiep ingegraven soorten zoals schelpdieren; meer soorten met benthische eieren, etc (zie tabel). De toename van die functies past bij een transitie naar een meer natuurlijk ecosysteem en dus als een verbetering van de zeebodemintegriteit. Er zijn ook functies en eigenschappen, zoals het hebben van een exoskelet en het zijn van een predator, die mogelijk zullen afnemen in gebieden waar niet langer wordt gevist. Deze afname past ook bij een transitie naar een meer natuurlijk ecosysteem.

Uit de analyse van de grootteverdeling bleek dat sommige soorten, waar ze wel verwacht werden, er niet meer waren bij hoge visintensiteit. Die gebieden hebben mogelijk een hoge potentie voor terugkeer van die soorten. Ook is er potentie voor een natuurlijker grootteverdeling voor de soorten die er nu nog wel zitten. Een potentie voor soortenrijkdom is niet te bepalen, omdat het aantal soorten vooral door de omgevingsvariabelen bepaald wordt. De potentie ligt meer in het verschuiven naar een natuurlijkere samenstelling van de soortengemeenschap.

Alternatief

Een alternatief, bij gebrek aan duidelijke kaarten met herstelpotentieel, is om te kiezen voor het maximale effect op het ecosysteem, en om daarom gebieden te sluiten over een breed scala van omgevingsvariabelen (diepte, productiviteit, sedimenttypen, primaire productie), functionele diversiteit en soortenrijkdom. Deze strategie zal de kans maximaliseren dat ten minste enkele van de beïnvloedde gebieden en bijbehorende soorten zich kunnen herstellen.

1 Introduction

1.1 Marine Strategy and need for measures

The EU Marine Strategy Framework Directive (2008) (MSFD) requires member status to come up with an national strategy for the management of their seas. In the Netherlands, the strategy is described in a series of 3 documents. The ‘Dutch Marine Strategy Part 1’ (I&M, 2013) describes the initial assessment, the good environmental status (GES) and the targets and indicators, Part 2 (2014) describes the MSFD monitoring programme. Part 3, the programme of measures, is still under development (deadline late 2015).

In the Marine Strategy Part 1, the main target for the structure of the Dutch marine ecosystem (encompassing the MSDF descriptors ‘biodiversity’, ‘foodwebs’ and ‘seafloor integrity’) is *to reverse the trend of degradation of the marine ecosystem due to damage to seabed habitat and to biodiversity towards a development of recovery* (IenM, 2013). This target implies an ecosystem structure in which the relative proportions of the ecosystem components (habitats and species) are in line with prevailing abiotic conditions (IenM, 2013). For benthos the subtarget is: *“Improvement of the size, quality and distribution of populations of long-living and/or vulnerable (i.e. sensitive to physical disturbance) benthic species”.*

The Dutch government has the ambition to safeguard 10-15% of the Netherlands part of the North Sea against seabed disturbance, while minimising the inconvenience for fisheries. This will be done by taking fisheries measures in the Natura 2000 areas and by creating additional protective measures (I&M, 2013). The Friese Front (Frisian Front) and Centrale Oestergronden (Central Oystergrounds) are considered "search" areas in this context. Situated in the central part of the Dutch Continental shelf (*Figure 1*) they are soft-bottom areas and biodiversity hotspots for benthos (Bos et al., 2011). Biodiversity is high and both areas host species that are long lived or grow large in size.

The Frisian Front area in particular has been recognised as a zone of high productivity due to its unique hydrographic conditions (it is a frontal area where different water masses meet, leading to a high productivity) and as such has an important role for higher trophic levels such as seabirds. The Frisian Front and Central Oyster Grounds are fished by several types of bottom trawlers, such as beam trawls (including pulse and sum wing) and several types of otter trawl. The intensity of fisheries in this area varies by type of fisheries, location, and in time.

Beam trawls target fish such as sole (*Solea solea*) and plaice (*Pleuronectus platessa*) (Rijnsdorp et al., 2008). This type of trawling induces physical disturbance on the seabed up to several centimetres into the sediment (Bergman & Hup 1992) and has a large impact on benthic organisms, benthic processes, and subsequently in the functioning of the (benthic) ecosystem (Jennings & Kaiser 1998; Kaiser et al., 2002). Recovery of these benthic ecosystems depends on the species involved, the community and habitat characteristics such as water depth and sediment type, and the species involved (Kaiser et al., 2006).

By the end of 2015 the programme of MSFD measures needs to be submitted to the EU. In preparation for this, the Dutch Ministries I&M leads a stakeholder process to delineate the areas that will be closed to bottom trawling. This report serves as input to that process.

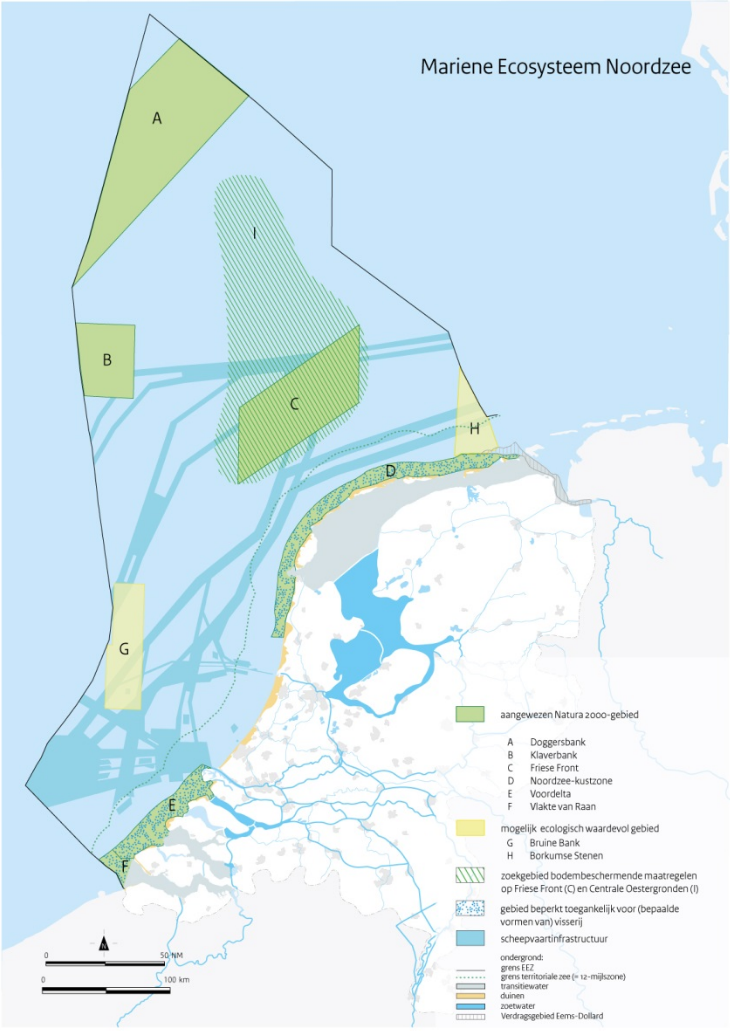

Figure 1 Search area (green striped zone) related to trawling cessation under MSFD (figure by IenM)).

1.2 This Study

In this study we analyse to what extent the current state of the search area has been altered by fisheries, in terms of ecosystem functions, species richness and size distributions. The results directly relate to MSFD indicators for biodiversity and seafloor integrity. Within the MSFD, species richness is an important element of biodiversity, and changes in seafloor integrity can be expected to lead to changes in biodiversity. Shifts in the functions of the species present at certain locations are also considered indicative of changed seafloor integrity, and some of the species traits we apply (e.g. longevity, protection), directly correspond to MSFD indicators for seafloor integrity. We also study changes in observed size distributions of individual species, which is a further measure of the degree of seafloor integrity.

This study consists of 3 parts:-

1. Biological traits analysis

The first part of this study assesses the effects of bottom trawling on species traits. Mortality from bottom trawling on benthic invertebrates is highly species-specific (Bergman and van Santbrink, 2000). Some species, such as large bivalves and large crustaceans suffer high mortality with long recovery times, whereas other species, such as some annelids, are almost unaffected (Kaiser et al., 2006). Trawling clearly selects against certain characteristics of organisms (traits) associated with vulnerability, and favours others which convey resistance. Hard-bodied and large benthic invertebrates are affected most by trawling activity. Chronic trawling therefore tends to induce a shift in the benthic community towards one with smaller and soft-bodied species (Engel et al., 1998, Kaiser et al 2000, Duineveld et al., 2007). Smaller species are also often associated with shorter generation times, which could lead to higher resilience after disturbances (Jennings et al., 2001). It is important to note that traits co-occur in species, and that this potentially has implications for the analysis. If a very common species is for example a predator living in the top layer of the sediment and is very sensitive to trawling, both ‘predator’ and ‘living in the top layer’ will turn up as traits that are affected by trawling, whereas in reality, the pattern may be driven only by ‘living in the top layer’, while the effect on ‘predator’ is caused by the prevalence of this particular species. This leads to a potentially highly complex trait response to trawling intensity, making it impossible to postulate *a priori* hypotheses about the trait-responses to bottom trawling. We therefore analyse the data using exploratory multivariate analysis.

We use a Biological Trait Analysis (BTA) to transform the species into their functional traits (see methods section), and quantify the effects of bottom trawling on the (spatial) distribution of these functional traits. Species traits may identify effects of fisheries on the structure of a benthic ecosystem and can thus be used to determine effects on ecosystem functioning (Tillin et al. 2006). Traits can elucidate effects of fishery even when no effect on biomass or species richness is found, for example when vulnerable species are replaced by less vulnerable competitors with different traits. These traits are potentially important indicators of ecosystem health, as they relate the benthic biomass to important functions such as food for higher trophic levels, filtering capacity and bioturbation. Furthermore, these traits relate to environmental targets set for the marine ecosystem. Targets defined in the Dutch Marine Strategy (IenM, 2013), include a sub-target for benthic species: *“Improvement of the size, quality and distribution of populations of long-living and/or vulnerable (i.e. sensitive to physical disturbance) benthic species”.* Species traits in this analysis such as “longevity”, “size”, and “protection” are thus directly related to MSFD targets.

2. Structural equation model for the effects of trawling on species richness

The second analysis focuses on the combined effects of trawl disturbance and environmental factors on benthic species richness in a subset of the benthic community. Many studies have examined the effect of either primary or secondary productivity or (trawl) disturbance on benthic richness in marine soft sediments (for example, Pearson & Rosenberg 1978; Collie et al., 2000; Hall et al., 2000; Huxham et al., 2000; Hiddink et al., 2006; Hinz et al., 2009; van Denderen et al., 2014). Van Denderen et al. (2014) showed that in the Dutch North Sea, the effect of trawling depended on abiotic characteristics such as sediment grain size and depth. In shallow areas with coarse sediments, no effect of bottom trawling was found on species richness, whereas in deeper areas with muddier sediments, trawling had a negative effect on species richness. The study of Van Denderen et al. (2014) emphasizes the importance of the right choice of spatial scale to assess the impact of trawl disturbance on the benthic community. Their study suggests that the choice of the right spatial scale largely depends on the patchiness of the habitat and the combined effects of trawl disturbance and productivity on the benthic community. Hence, they plead for a better understanding of processes and patterns associated with benthic richness and biomass in habitats, in order to facilitate conservation of these systems and the management of their exploitation.

The analysis of van Denderen et al. (2014) is applied in this study, focussing on the Frisian Front and Central Oyster Grounds MFSD search area exclusively (instead of whole NCP) and applies Triple D fauna data instead of boxcore data. The ultimate aim of this work is to elucidate where in these areas the most likely effect of bottom-trawling are found on biodiversity and biomass, taking the effects of abiotic conditions in account. This will allow us to point out locations within the area where the potential effects of closure to bottom trawling on benthic biomass and species richness will be greatest.

3. Effects of trawling on species size distributions

The final part focusses on the effects of trawling on species size distribution. The observed size distribution differs from ‘size’ as used in the biological traits analysis above. There, size is used to indicate the maximum body size that individuals of a species reach, here, body size refers to the actual sizes of individuals found in the samples. In this last analysis (the distribution), we go beyond species-level information, to the size distribution of individuals of particular species, in particular bivalves. Large bivalves are regarded as one of the best indicators for bottom disturbance by fishing gears. Many mollusc species are long lived, relatively immobile, and fishing mortality on the adult stages for some of these species is proven to be high (Bergman & Hup, 1992; Witbaard & Klein, 1994). For *Arctica islandica* it was demonstrated that 80% of shells caught in a beamtrawl were damaged to such an extent that they would die (*Witbaard & Klein, 1994*). Similar sensitivities can be estimated for the thinner shelled *Acanthocardia* and *Mya truncata*. This is reflected in the spatial distribution patterns of these sensitive species, which appears to be inversely linked to the distribution of the fishing fleet. Highest population densities for *Arctica islandica*, *Acanthocardia echinata* and *Chamelea striatula* were for instance found in the northern part of the Oystergrounds (Witbaard et al, 2013) where fishing intensity is lower than at the Frisian Front. Size frequency distributions of these species, which shows the demographic structure of the populations, may help with the interpretation of these observed spatial patterns.

2 Methods

2.1 Data

2.1.1 Data overview

The effects of trawl disturbance and productivity on benthic species richness were examined using data obtained in a NIOZ research program (2006-2012) which aimed to map the distribution of large and relatively less dense benthic species in the Dutch part of the North Sea (Witbaard et al., 2013). Trawl intensity was estimated from Vessel Monitoring by Satellite (VMS) data (Hintzen et al., 2010; Piet & Hintzen 2012). We used primary productivity, calculated from the ecosystem model ERSEM (Baretta et al., 1995) and used as an approximation for benthic food availability.

We also include biomass in our analysis, because it is an important determinant of species richness (Gough et al., 1994), and total biomass of benthic organisms can also be a consideration in protecting benthic communities. Finally, our analysis included both sediment grain size and water depth, which are seen as important factors to predict benthic richness in soft-bottom marine systems (Gray 2002) and hence help to prevent confounding effects. Primary production is the basis for benthic productivity. Total primary production thus gives an indication for potential available food for benthos. This is however dependent of depth. An overview of the data characteristics is provided in *Table 1*.

Table 1 Data characteristics

Nr	**Parameter**	**Remark**	**Property**	**Unit**
1	Depth	-	Continuous	meter
2	Grain size	RWS 2010, median grain size d50 of sand fraction (63-2000 µm)	Continuous (strictly positive)	µm
3	Primary production	Average period 2000 – 2007	Continuous (strictly positive)	gr C/m2/y
4	Trawl intensity	Swept area, cumulative of 1.5 year prior sampling	Continuous (strictly positive)	Portion of grid cell (0.057 km^2)
5	Biomass	Selection of benthic species (ML) & exl. fish species	Continuous (strictly positive)	Ash free dry weight (gram)
6	Richness	Selection of benthic species (ML) & exl. fish species	Counts (strictly positive)	species

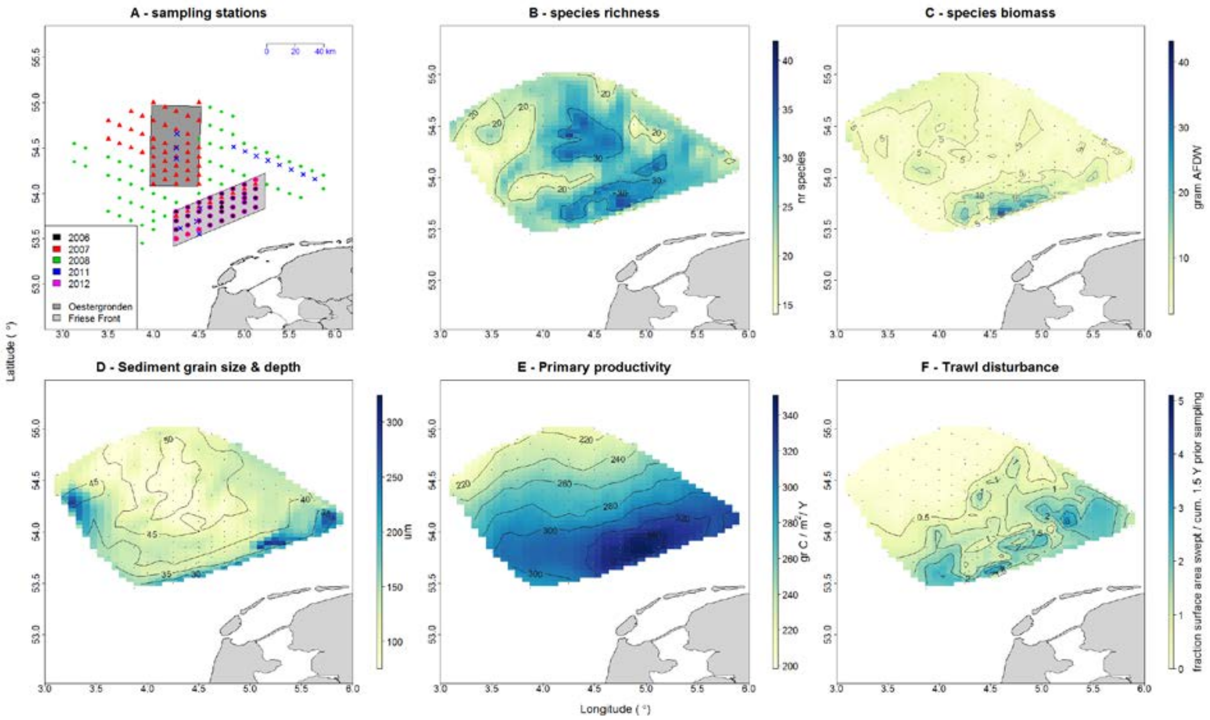

Figure 2 Maps of macrozoobenthos stations (by NIOZ) and the variables studied. A Macrozoobenthos stations sampled between 2006 and 2012 in the Dutch EEZ (all points). Panels B–F are created using point interpolation of the average of all years per station for species richness (B, color scale; number), species biomass (C, color scale; gram AFDW/sample), sediment grain size with depth contours (in meters) (D, color scale; lm), primary productivity (E, color scale; gr C/m2/y), and trawl disturbance (F, color scale; fraction of surface area trawled within 1.5 year prior sampling) (Color figure online).

2.1.2 Benthic Sampling

The benthic sampling effort within the selected area is not equally distributed over space, years and seasons, as can be seen in *Table 2*. Sampling effort was relative high in the years 2007 and 2008. In both years 2007 and 2008 sampling took place in winter/spring, while sampling in 2006 and 2012 took place in autumn and in 2011 in summer.

Table 2. Sampling effort (number of stations) per year, month and area.

Year	Month	Frisian Front	Central Oyster Grounds	Outside FF / COG
2006	10	30		
2007	2	11	25	
2007	3	1		
2007	4		9	12
2008	4		1	55
2011	6	4	3	8
2012	11	34		

Year	Sampling effort
2006	30
2007	58
2008	56
2011	15
2012	34

Species with poor sampling efficiency, such as pelagic species or very small benthic species were excluded from the analysis. Furthermore, all fish species were excluded as this group was not the focus of our study. In Appendix A an overview is given of the species that were in- or excluded.

Nine benthic species which contributed individually for more than 50% the total biomass in some of the samples, as can be seen in *Table 3*. Especially *Echinocardium cordatum* (sea urchin) and *Upogebia deltaura* (mud lobster) dominate the biomass of some samples (>80%).

Table 3. Species that singly contributed for more than 50% of the biomass in some samples.

	Mean contribution	**Max contribution**	**Occasions (in %) that species contribute for >xx% of the total-biomass**					
Latin	**(%)**	**(%)**	**>30**	**>40**	**>50**	**>60**	**>70**	**>80**
Echinocardium cordatum	9.3	88.8	3.6	2.6	1.0	0.5	0.5	0.5
Upogebia deltaura	12.6	82.1	18.7	13.0	6.7	3.6	1.0	0.5
Ophiura albida	5.8	69.3	3.6	1.6	0.5	0.5	0	0
Liocarcinus holsatus	4.8	61.4	1.0	0.5	0.5	0.5	0	0
Asterias rubens	3.9	60.9	3.1	1.0	0.5	0.5	0	0
Corystes cassivelaunus	10.0	58.3	5.2	2.6	0.5	0	0	0
Brissopsis lyrifera	5.4	58.0	6.2	2.1	1.0	0	0	0
Turritella communis	7.9	57.9	2.1	0.5	0.5	0	0	0
Pagurus bernhardus	6.7	50.2	5.7	2.6	0.5	0	0	0

All sampling was carried out using the "Triple D" (Deep Digging Dredge; Bergman and van Santbrink, 1994, Witbaard et al., 2013, photo see appendix E). The Triple-D consists of a steel cage fitted within a strong and pressure resistant frame. At the back of the steel cage a 6 m long fine meshed net (mesh size 7*7 mm) is fitted. The dredge runs over the seafloor on flat runners like a sledge. The dimensions of the dredge cage are 2.7 meter wide, 2.4 meter long and 1.6 meter high. Its empty weight is about 1.5 tons. The effective part of the dredge is a hinged bottom plate with a cutting blade underneath the steel cage.

The dredge has an actively controlled mechanism for opening and closing of the cutting blade which is powered by compressed air and triggered by an odometer which is integrated in the pneumatic circuit. The cutting blade is 20 cm wide and penetrates the bottom 20 cm. The haul length is set at 100 meter. This results in a sampled surface of 20 m^2 or a sediment volume of 4 m^3. The catch is collected in a fine meshed net (7 × 7 mm). Because of the length of a haul, spatial heterogeneities in faunal density are integrated. Catch of each haul is sorted and weighted on board. Later densities and biomass are calculated on basis of the number of caught animals. Wet weights are transferred to Ash Free dry weights on basis of published relationships. The data used in this study have been collected between 2006 and 2012.

2.1.3 Primary productivity

Primary productivity was obtained through predictions from GETM-ERSEM (General Estuarine Transport Model—European Regional Seas Ecosystem Model) (Baretta and others 1995). GETM-

ERSEM describes the temporal and spatial patterns of the biogeochemistry of the water column and sediment using two coupled hydrodynamic models. These models predicted total production of new phytoplankton biomass for each year (g C/m²/y) per sampled macrobenthic station on a 10*10 km spatial scale. Total production was estimated for each area over a period of one year prior to the sampling date. These modeled productivities are an approximation of primary productivity, which correspond well to field measurements (Ebenhoh and others 1997). The distribution of primary productivity is provided in Figure 2E.

Primary productivity fluctuates per year and location. The model estimates show that there is a clear spatial gradient in primary production with higher production at the Frisian Front. The spatial gradient in primary production is relatively constant over the years, and no time trend was observed for the period 2000-2007 (see appendix B). As a result, we have used the average primary productivity over the entire period for all analyses.

2.1.4 Trawl Disturbance

Trawl disturbance at the sampled locations was estimated from the VMS (Vessel Monitoring System) data. VMS data provides information for each fishing vessel on its position, speed, and heading approximately every 2 h. The VMS data were linked per fishing trip to vessel logbook data with information on vessel and gear characteristics (Hintzen et al., 2012). VMS data from beam trawl, otter trawl and twin trawls were included in the analysis. These gears sum up to more than 95% of all bottom trawling gears in the area. From this selected dataset, trawl disturbance was estimated on a fine spatial grid, approximating an area of 110 by 70 meter (VMS: 1 ping/2 hours), to have the best approximation of disturbance at each of the dredge sampling stations using the method described in Hintzen et al. (2010) and Piet and Hintzen (2012).

Trawl disturbance was aggregated temporally by week. For each station, we selected the 78 weeks (1.5 years) preceding the date that the benthic fauna was sampled. This choice reflects the period of time for which high quality VMS data was available preceding the collection of the oldest samples. This potentially introduced bias in the relationship between the benthic community and the trawling intensity, because not all samples were taken in the same season, and there is seasonality in the distribution of trawling disturbance over the year (van Denderen et al., 2014b). However, we considered the maximal use of available data more important than the effects of this potential bias.

Trawl disturbance is essentially the average frequency with which the area is disturbed by bottom trawl gear per unit time (total surface disturbed divided by area surface). To obtain this frequency, we sum the effect of beam trawl gear, and part of the effects of otter trawl gear. An otter trawl consists of two heavy ‘doors’ to keep the net open. These doors penetrate the seabed. The ground-rope in between these doors penetrates the bottom to a much lesser extent than the tickler chains of a beamtrawl. We have used only the effect of the doors in this analysis. Hence, our estimate of trawl disturbance is limited to that part of the disturbance that penetrates into the seabed. This method allows us to sum the effects of more than one gear type, and is in agreement with methodology used in the EU project BENTHIS (www.benthis.eu). Figure 2F shows a map of the trawl disturbance.

2.1.5 Sediment grain size

Median sediment grain size (of sand fraction = 63-2000 µm) for each benthic station was obtained from a map constructed by Deltares in 2010 and published by Ministry of Infrastructure and the Environment.

Water depth for each station was determined by extracting this information from a bathymetric map produced by Deltares in 2011. The bathymetric map was based on data provided by the Netherlands Hydrographic Office of the Royal Netherlands Navy (Dutch Ministry of Defence) and Rijkswaterstaat Directorate North Sea (Dutch Ministry of Infra-structure and the Environment). Further details on the methodology is available in Van Dijk *et al.* (2011).

2.2 Effects of trawling and environmental conditions on species traits

2.2.1 Trait classification

The taxonomical genera of data collected at all sampling stations were coupled to the BENTHIS infaunal trait dataset, which is available from www.benthis.eu and first described by Bolam et al. (2014). This data matrix comprises of 12 different traits (*Table 4*). Each trait is subdivided into multiple modalities (categories) and in appendix D, all modalities of the 12 traits classes and corresponding codes are provided.

The trait dataset essentially consists of a large list of genera, with a column added for each trait modality. Each of these modalities is then assigned a numerical value, representing to what extent the modality occurs in each genus. These values can be zero, or a fraction.
The trait information is first combined with the sample data by adding to each species corresponding traits for its genus, and subsequently multiplying each entry in these columns by the biomass of the species in the sample. In a second step, the information in all trait modalities is summed for each sample. This yields the final ‘trait by sample’ matrix, which describes each sample as a distribution of biomass over modalities. This matrix is the basis for further analysis.

The trait dataset also contains trait classifications for higher taxonomic levels. This was used when trait information for a specific genus was missing. In total 139 different taxonomic units were present in the dataset. Determinations at levels above genus were made for 17 taxonomic units (6 Family, 5 Order and 6 Class levels). The remaining 122 are Genus or species level determinations. The trait set “bed forming or reef building” proved not to be relevant for the benthic species found in the sampling stations as most species were classified as “none/neither”.

2.2.2 Redundancy Analysis

Effects of trawling, grain size, productivity and depth on the occurrence of the various trait modalities in the data were analysed using redundancy analysis (RDA). Redundancy analysis (RDA) is a method to extract and summarise variation in a set of response variables that can be explained by a set of explanatory variables.

In this study, we calculate two such synthetic variables, which are a linear combination of factors in one dataset (trawling, grain size, productivity and depth per sample). These variables are constructed in such a way that they explain as much of the variation as possible in the dataset of response variables (biomass in modalities per sample). This allows us to study the sensitivity of the biomass in each modality to changes in trawling, grain size, productivity and depth. We also conducted a partial redundancy analysis, which compares the explained variance in the full model with that excluding single factors. This yields an estimate of the contribution of each individual factor (trawling, grain size, productivity and depth) to the total variance explained.

RDA assumes that there is a linear effect between the predictor variable and its response. Hence, trawl disturbance was log-transformed. Whether trawl disturbance, in combination with depth, sediment grain size and primary productivity, had a significant effect on community composition for each area was tested using a permutation test. All multivariate analyses were done using the package vegan in R (Oksanen et al. 2013).

Table 4 Traits and definitions, slightly adapted from BENTHIS and Bolam et al. (2014).

Traits	Trait Definition and functional significance
Size (mm)	Relates to organic matter transfer in ecosystem. Large organisms hold organic matter (low turnover) within the system relative to small-bodied species (high turnover) (Pearson and Rosenberg, 1978). Furthermore, is catchability size dependent. Furthermore, if a species is larger, and thus heavier, it will be less prone to the bow wave of the gear.
Morphology	Relates to species sensitivity. External characteristics of the taxon.
Longevity (years)	Maximum reported life span of the adult stage. A proxy for relative r- and k-strategy of the species (Pearson and Rosenberg, 1978)
Larval development	Indicates the potential for dispersal of the larval stage. Affects ability to recover from disturbance with planktonic recruitment affording potentially faster recolonisation than direct development (Thrush and Whitlatch, 2001).
Egg development	Indicates dispersal via the egg stage and the potential susceptibility of eggs to damage from fishing. Benthic eggs are generally more concentrated over smaller areas. Asexual reproduction allows the potential to increase numbers rapidly, particularly following disturbance.
Living habitat	Indicates potential for the adult stage to evade, or to be exposed to, physical disturbance.
Sediment position	Typical living position in sediment profile. Organisms occupying shallower positions in the sediment are more likely to contact trawl gear than those living deeper. Sediment position also has implications for the effect of the organism to affect sediment-water nutrient and/or oxygen exchange.
Feeding type	Feeding mode has important implications for the potential for transfer of carbon between the sediment and water and within the sediment matrix. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg, 1995).
Mobility	Mobility affects the ability for adult recolonisation of disturbed areas.
Bioturbation	Describes the ability of the organism to rework the sediments. Can either be upward, downward, onto the sediment or mixing of the sedimentary matrix. Bioturbation mode has important implications for sediment-water exchange and sediment biogeochemical properties.
Protection	Describes the capacity to withstand physical disturbance and thus the potential for the adult population to remain viable following acute fishing.
Bed/reef formers	Important factor for affecting a number of ecological functions such as biodiversity, productivity and sediment stability

2.3 Effects of trawling and environmental conditions on species richness

In this study the Structural equation modelling method used in Van Denderen et al. (2014) was followed. A structural equation model (SEM) is a multivariate analysis of networks of causal relationships (Grace 2006). This was used to examine the combined effects of productivity, disturbance, biomass, sediment grain size and depth on species richness. The construction of the initial model was based on the study by Van Denderen et al. (2014), who investigated effects of beam trawl disturbance on infaunal benthic richness over the entire Dutch part of the North Sea.

Following Van Denderen et al. (2014), the initial model (results section- *Figure 7*, left panel) had pathways between depth and both primary productivity and sediment grain size and it was expected that all three explained variation in species richness in the study area (Frisian Front, Oystergrounds). The model connected depth, primary productivity and grain size with biomass and primary productivity, grain size, trawl disturbance and biomass with species richness. The initial model did not include a pathway between trawl disturbance and biomass (as this was not found by Van Denderen et al. 2014), but whether such a relationship existed, was verified using the SEM.

The constructed SEM had two degrees of freedom. Richness, biomass and grain size were log-transformed to improve distributional properties of model residuals. The final model was tested for overall model fit using a Chi square test. SEM analyses were performed using the package Lavaan in R (Rosseel 2012).

2.4 Effects of trawling and environmental conditions on species size of distributions

We performed an analysis in which the mean and maximum body sizes of individuals in the samples were related to the fishing intensity. This analysis was done for each species and for the entire area for which enough observations were available. Selection of species was furthermore based on their abundance in both the Frisian Front and the Oystergrounds. Another prerequisite for selection was that catchability of the species in the triple D dredge was high. Because of the co-variation of factors like "Depth", "Primary production", and "grain size" multiple linear regression was applied. On the basis of these results, effects of bottom trawling, apart from the effects of the other factors were identified.

3 Results

3.1 Effects of trawling and environmental conditions on species traits

Redundancy analysis (RDA) was used to explore the effects of trawling in combination with primary productivity, median grain size and depth on trait composition. The analysis is based on fractions of biomass per modality.

All four predictor variables have a significant effect on trait composition (all p-values < 0.01) and explain together 18% of the variation in trait modalities between the different stations. The effect of trawling intensity and the other environmental variables in the RDA point in roughly the same, or opposite directions (*Figure 3*). This means that trends in trait occurrence cannot be linked to a single environmental variable, but are related to several simultaneously. The interrelationship between trawling and the other environmental factors is not strong enough that the validity of the analysis is reduced by collinearity between the different abiotic factors and trawling, as all pairwise correlation coefficients (*Table 5*) are below 0.6, the commonly accepted threshold value above which collinearity is considered problematic.

The redundancy analysis furthermore shows that the multivariate axes, which are constructed to maximize the explained variation in trait composition, also separate into clusters of geographical location (Frisian Front and Oystergrounds,

*Figure 3*b), which suggests that the benthic community in the different areas differs in its trait composition. Trawling generally occurs at locations with a relatively high productivity, coarse sediment and low depth. Within the search area, these characteristics are mostly associated with the Frisian Front area (see *Figure 2*).

The results of the RDA show that trawling is most positively correlated with

- egg development location – brooded
- protection - exoskeleton
- feeding mode – predator
- living habitat - burrow dwelling
- bioturbation- surface deposition

and most negatively correlated with

- living habitat - free living
- bioturbation - diffusive mixing
- feeding type - subsurface deposit
- sediment position - 0-5cm
- benthic egg development

The relationships between trawling intensity and total biomass per sampling station of these modalities are shown in *Figure 4*. This figure shows that the strong association with trawling, found in the RDA for these modalities, is not true when other factors (grain size, depth, primary productivity) are not corrected for.

Since trawl effects were difficult to disentangle from the other predictor variables, we further attempted to disentangle its effect on trait composition with a partial redundancy analysis. Such an analysis attempts to correct for the abiotic conditions and can test the effects of each factor in isolation. Unfortunately, this yielded no useful additional insights (results not shown). This is most likely due to certain combinations of environmental factors and trawling (for example, stations that are very deep, yet intensely trawled) not being present in the data.

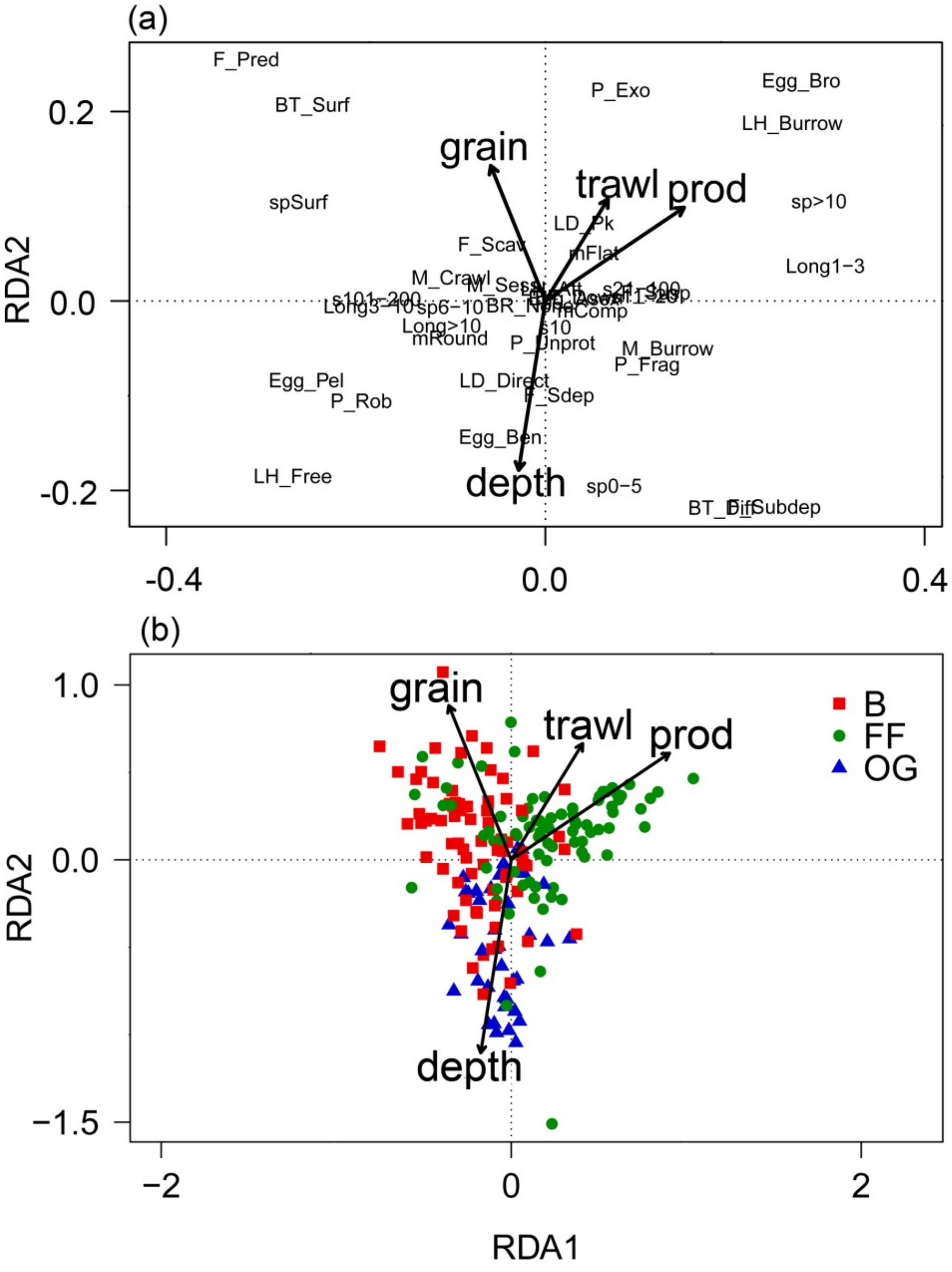

Figure 3 Outcome of the redundancy analysis for both trait modalities (a) and sampling stations (b). The four predictor variables (depth, sediment grain size, trawling intensity and primary productivity) all had a significant effect on community composition (all p-values<0.01). The analysis is based on fractions of biomass per modality (codes shown in plot are listed in Appendix D) for all stations. The four predictor variables explain 18% of the variation. The length of the arrows show the relative importance of the four variables. Colours indicate the area B = search area, but not IN FF or CO, FF = Frisian Front, OG = Oystergrounds

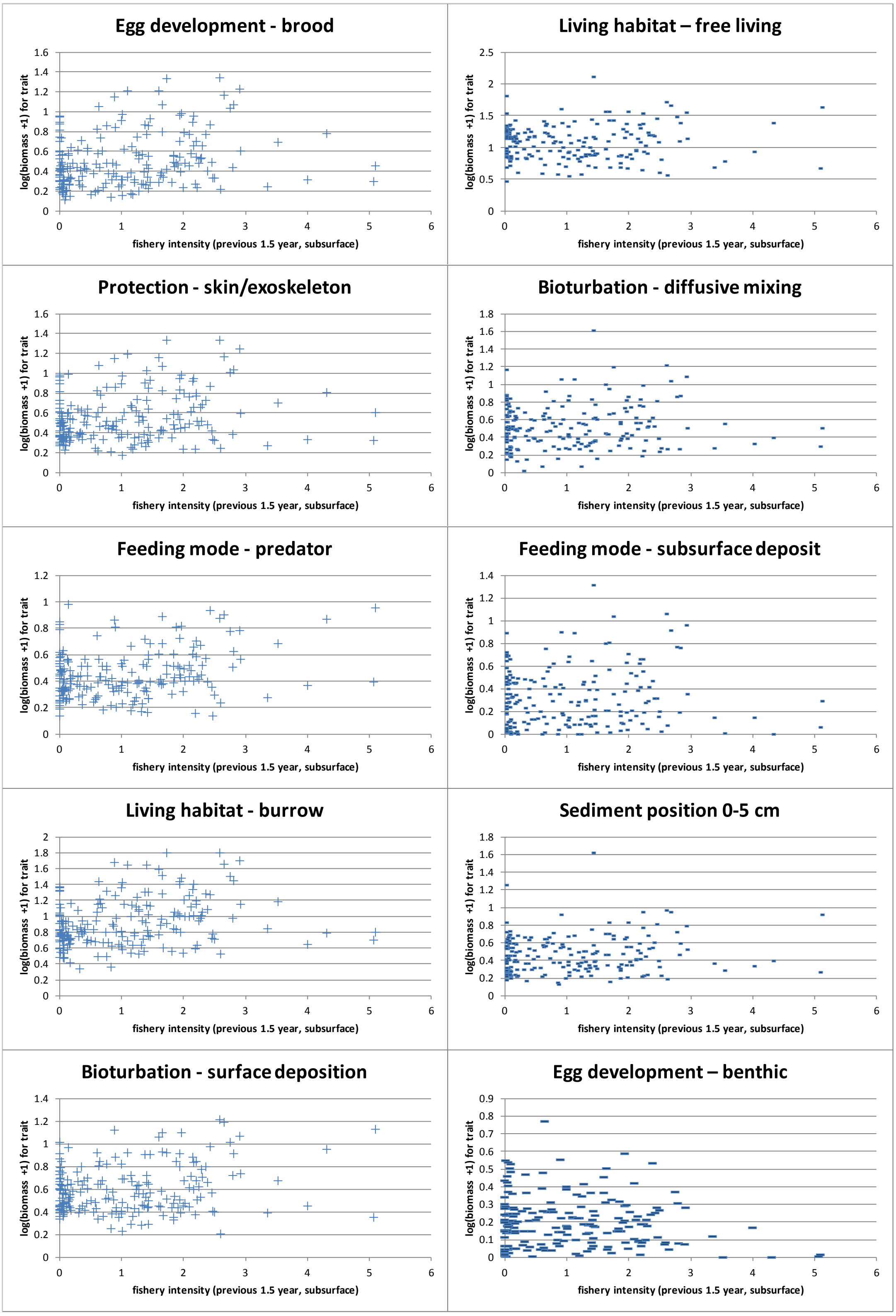

Figure 4 Bivariate scatterplots of biomass of traits versus trawling intensity for traits for which the RDA analysis (Fig. 3a) shows they are most strongly associated with trawling intensity. Left panels: positive association, right panels: negative association. See the main text for further explanation.

3.2 Effects of trawling and environmental conditions on species richness

Correlations

As a first exploration of patterns in the data, bivariate plots and pairwise correlations show that most variables strongly correlate with each other, except species richness vs. trawl disturbance, depth vs. species richness and grain size vs. species biomass (see *Figure 5*, *Figure 6*, *Table 5*, and plots in Appendix C).

Pairwise correlations between species richness and primary productivity (Figure 5B, r2 = 0.158), and biomass (Figure 5C, r2 = 0.117) are positive, while sediment grain size (Figure 5D, r2 = 0.0278) correlates negatively with species richness. Trawl disturbance and species richness do not correlate (Figure 5A, r2=0.0124), while trawl disturbance and biomass are positively correlated (Table 5, r2=0.26).

Whether these correlations observed for richness are direct effects of the predictor variables (grain size, depth, etc), or indirect effects governed by relationships between various predictor variables is examined with a Structural Equation Model (SEM), which allows us to study the relative strengths of the different factors in combination. Using this approach it is possible that pairwise correlations which are present in the preliminary analysis (*Figure 5*, *Figure 6*, *Table 5*), disappear because the SEM shows that they are caused by interdependence between the various predictor variables (for example between depth and sediment grain size).

We started with a model identical to that used in van Denderen et al. (2014). In this model, water depth is the exogenous parameter, meaning that depth is not influenced by any other factor. As the initial model has 2 degrees of freedom, a model fit can be calculated. This resulted in a significant difference (p=0.026) between the observed covariance matrix (solely based on the data) and the implied covariance matrix (based on data in combination with model structure). The significant difference implies that the model structure does not describe the data correctly.

Exploration of alternative model structures revealed that the pathway between depth and species richness is significant. The inclusion of this pathway leads to a model structure that fits the data (X^2=0.11, p=0.74 and dg=1), while the SEM contains no effect of trawl disturbance on benthic biomass (which was present in the pairwise correlations). In this model, there are four non-significant pathways (depth – biomass, grain size – trawl disturbance, trawl disturbance – richness and the double arrow between grain size and primary productivity, representing a joint factor not included in the analysis, see van Denderen et al. 2014). These pathways may be removed in the model structure without causing large effects on model fit. Since the trawl disturbance – richness relationship is an important focus of this study, we only removed the three other non-significant pathways. This resulted in our final model structure which had a X^2=0.49, p=0.97 and dg=4.

Interestingly, we found a significant pairwise correlation between trawling intensity and biomass, but the effect of trawling on biomass is not significant in the SEM (*Figure 7*). Consideration of the final SEM shows clearly that the pairwise correlation is spurious, and is caused by the fact that both trawling intensity and biomass are to a large extent determined by primary productivity. This result highlights the importance of looking beyond pairwise correlations (as is done in a SEM analysis), and to consider a number of factors in parallel.

Based on the final model structure we obtained the following results (*Figure 7*– right):

(1) Richness is best described (mean r2 = 0.40) by the combined effects of depth (positively correlated), primary productivity (positively correlated), grain size (negatively correlated) and biomass (positively correlated).
(2) Biomass is explained by primary production and grain size (mean r2= 0.13)
(3) Primary production has a positive effect on richness, biomass and trawling disturbance;
(4) The SEM model structure fits the data better if no direct relationship between trawl disturbance on richness and biomass is incorporated;
(5) Variation in trawl disturbance is largely explained by depth and primary productivity (mean r2 = 0.37).

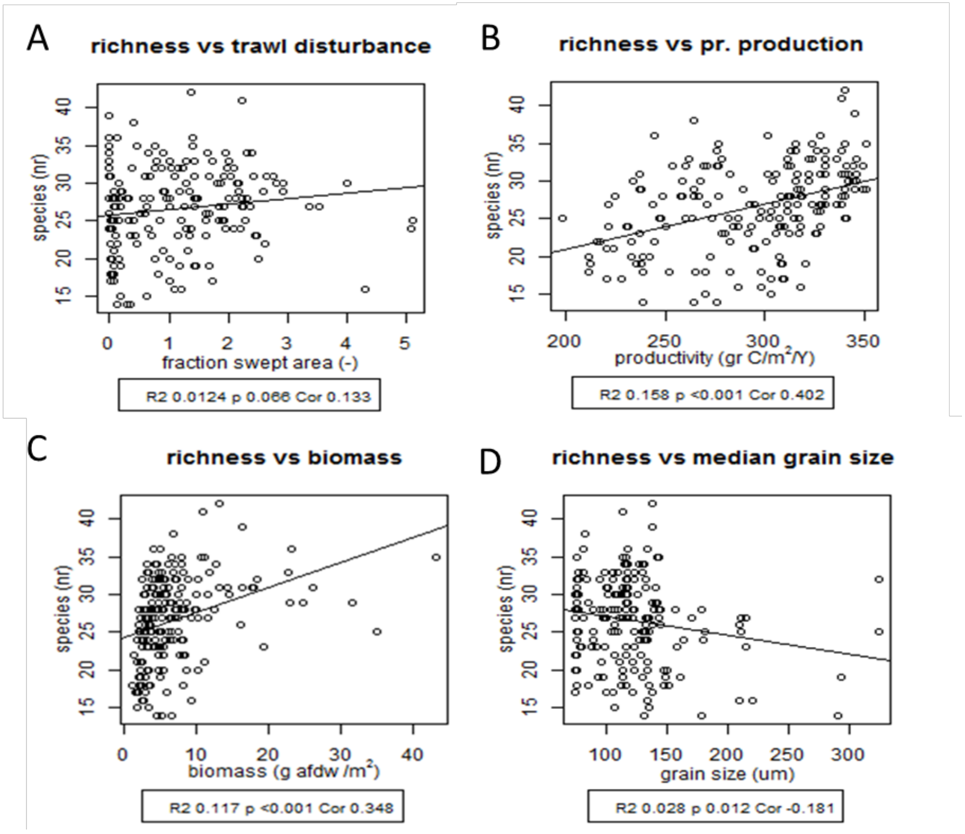

Figure 5 Bivariate correlations between species richness and trawl disturbance (A), primary productivity (B), species biomass (C), and sediment grain size (D). See Table 5 for correlation coefficient and significance values. The lines in the bivariate plots were constructed using linear regression.

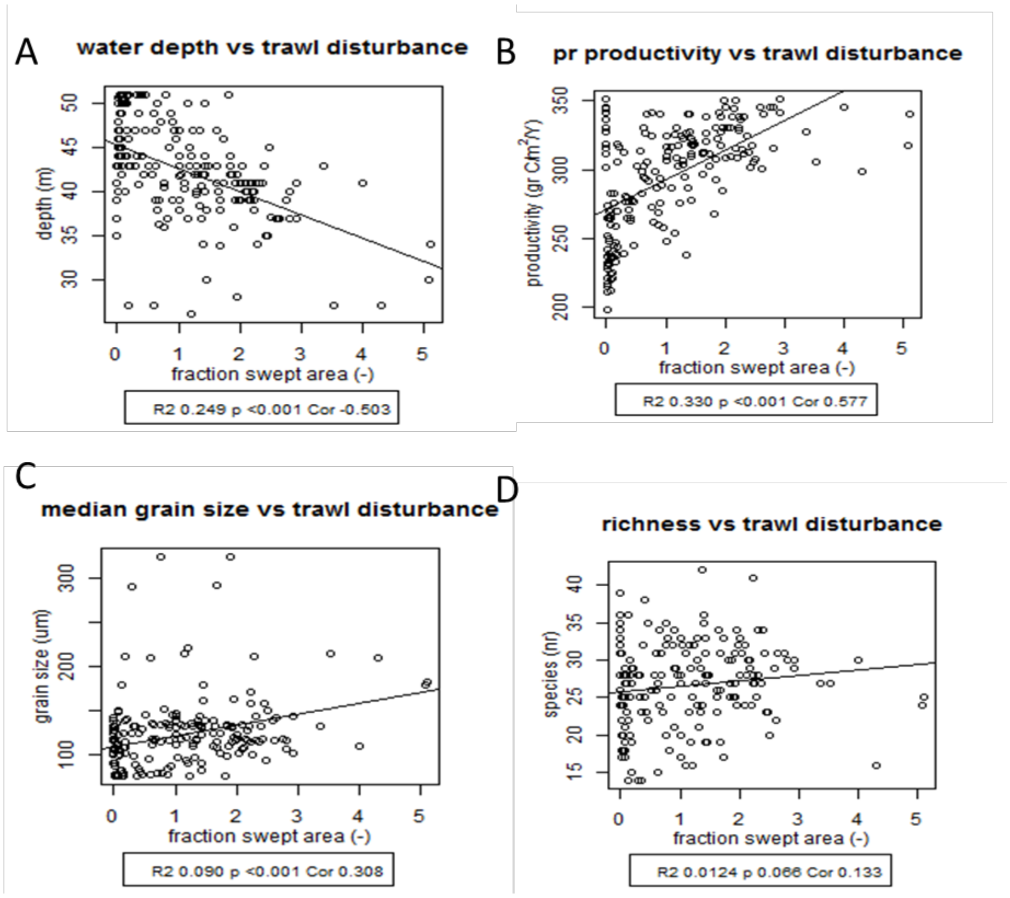

Figure 6 Bivariate correlations between trawl disturbance and water depth (A), primary productivity (B), grain size (C), and species richness (D). See Table 5 for correlation coefficient and significance values. The lines in the bivariate plots were constructed using linear regression.

Table 5 Bivariate Correlation Coefficient Matrix for All Variables Studied.

	Biomass		Richness		Grain size		Depth		Primary production	
	Corr.	*P*	Corr.	*P*	Corr.	*P*	Corr.	*P*	Corr.	*P*
Richness	0.35	**<0.001**								
Grain size	0.04	0.572	-0.181	**0.012**						
Depth	-0.25	**<0.001**	0.03	0.660	-0.63	**<0.001**				
Primary production	0.35	**<0.001**	0.40	**<0.001**	0.33	**<0.001**	-0.59	**<0.001**		
Trawl disturbance	0.26	**<0.001**	0.13	0.066	0.31	**<0.001**	-0.50	**<0.001**	0.58	**<0.001**

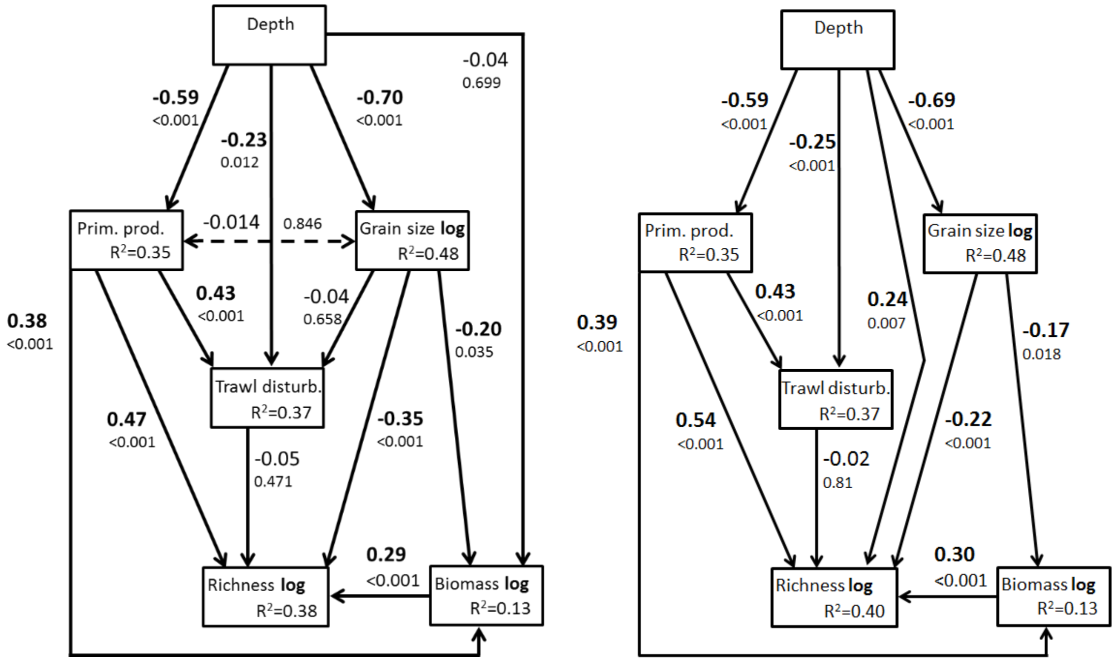

Figure 7 Left, output structural equation model (SEM) according to Denderen et al., 2014, (df=2, p=0.026, AIC = 136.4). Right, final SEM model (df=4, p=0.97, X2=0.49). Boxes represent our variables, the R2 values in each box show the fraction of the variation in that variable which is explained by the model. The numbers next to the arrows are the mean standardized coefficients and the P value. The dashed line with arrows on both sides shows strong correlation but direction is unknown. Model selection procedure and data transformations are explained in the main text.

3.3 Species size distributions

Many of the species used in above analyses have distinct distribution patterns within the NCP and are exclusively found in the Oystergrounds and Frisian Front. The observed peak abundance of molluscs (Witbaard et al, 2013) at the Frisian Front is related to the high densities of small species such as *Nucula nitidosa*[1] and *Turritella communis* and *Corbula gibba*. The observed abundance maximum in the northern part of the Oystergrounds is related to high densities of *Arctica islandica* (~1/m2), *Acanthocardia echinatum*, *Mysia undata* and *Chamelea striatula*. Density estimates for these species suggest an inverse relationship with trawling disturbance.

On basis of the constructed database we compared size distributions of species in heavily and lightly fished areas. The size frequency data for the various species show that they are in line with the expectations on basis of the trait analyses as depicted in Figure 6.

Surface dwelling large and fragile animals tend to have smaller sizes in heavily fished areas, while for deeply burrowing organisms no difference could be detected. Small thick shelled bivalves neither show differences in their size distributions. Examples are given in *Figure 8*. *Acanthocardia echinatum* a free living large bivalve mollusc which shows a distinct difference in its size distribution between heavily fished and lightly fished areas.

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[1] Species names are translated in appendix F

Dosinia lupinus is a relatively small mollusc which lives burried in the top cms of the seabed. The size distribution of this species in lightly fished areas is bimodal and shows, that younger and smaller animals are found next to big and older animals in areas which are lightly fished. In the heavily fished areas the maximum size is smaller than in lightly fished areas.

Echinocardium cordatum is a fragile echinoderm which lives buried in the top few cm of the sediment. Heavily fished areas are inhabited by smaller animals.

Some other species do not show differences in their size frequency distributions. Two of these species refer to deep burrowing crustaceans (*Callianassa subterranea* and *Upogebia deltaura*). The small brittle bivalve *Phaxas pellucides* neither shows a marked difference in size frequency distributions between lightly and heavily fished areas.

For some of the larger and older growing bivalves such as *Arctica islandica* and *Mya truncata* similar comparisons could not be made because they were not found in the heavily fished areas. For *Arctica* a few young specimens were however exclusively found in lightly fished areas.
The observed differences in the size distributions of these example species support the findings of the RDA trait analyses (*Figure 3*). Deep burrowing species show no difference, while free living, fragile and relatively long lived species do show a difference.

We tested the size differences between heavily fished and lightly fished areas numerically with linear multiple regression. The covariates used to explain the maximum observed sizes were the same as used in the RDA analyses, i.e. Depth, Primary Production, Median grainsize and Fishing intensity. This analyses showed that the effect of fishing on the size distribution of *Acanthocardia* was the only significant relationship. The negative effects of fishing on this species indeed have been documented in previous field studies. *Acanthocardia* suffers from increased mortality when caught or left in the trawl track (Impact-Reduce; van Marlen et al, 2001; van Marlen et al, 2005). For the other species the significance of fishing intensity on the observed differences in size frequency distribution could not be demonstrated, despite the observed inverse relationship between fishing intensity and size. For these species the other factors (Primary production, Depth, Median Grain size) overshadowed such a potential effect or the detection of statistical significant differences (*Arctica, Mya*, *Dosinia*) was impossible due to their absence in the most heavily fished areas. This in itself suggests that these species are sensitive for bottom fishing, which for *Arctica islandica* has been documented by Witbaard & Klein (1994).

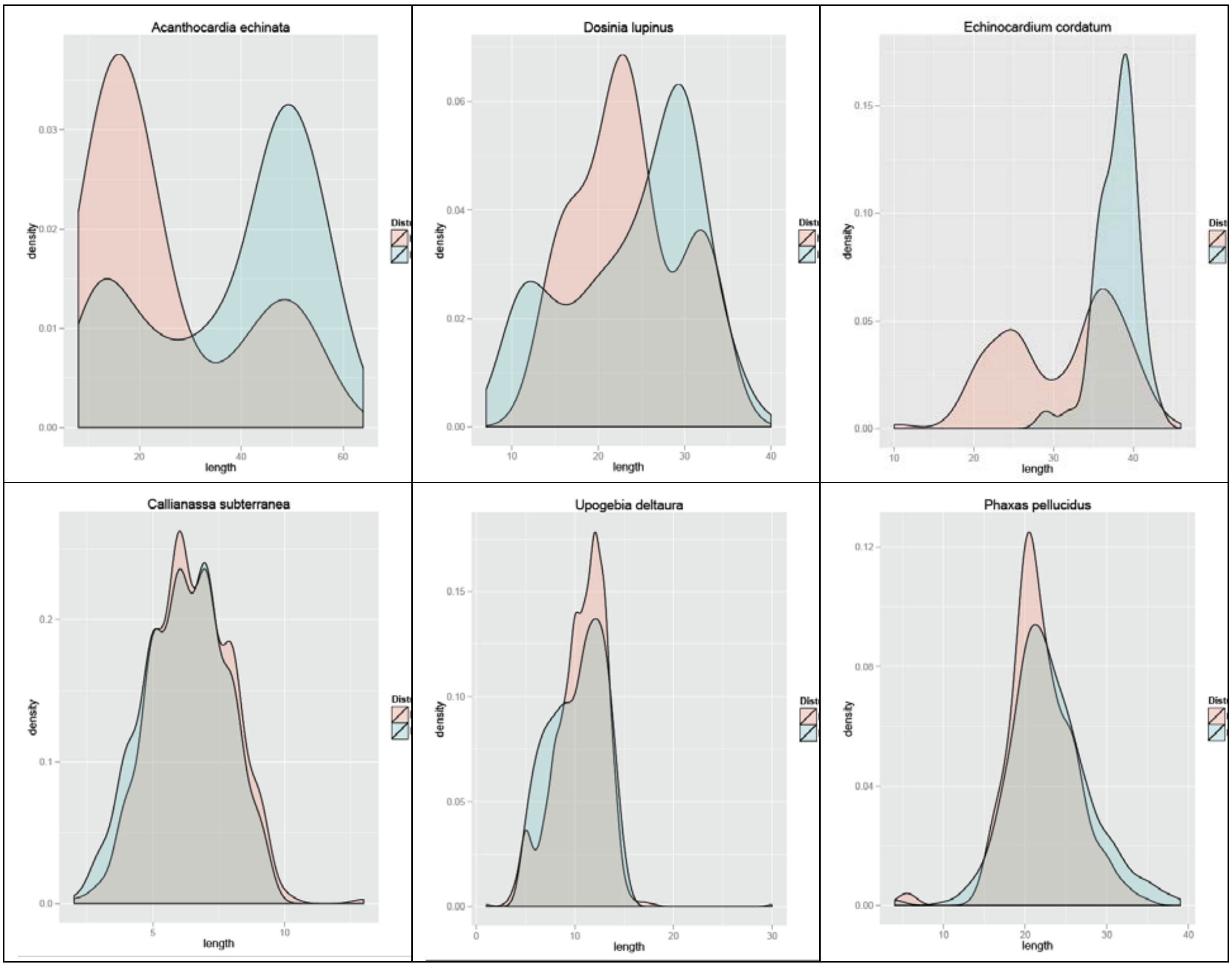

Figure 8 Examples of the comparison of the size distribution in heavily fished and lightly fished areas of the Frisian Front and Oystergrounds. Pinkish colour represents size frequency in heavily fished areas, blue colour represent size frequency in lightly fished areas.

4 Discussion and conclusions

In this study the effects of bottom disturbance by beam trawl fishery and environmental conditions on biological traits, species richness and the species size distributions of the benthic community were explored. The ultimate aim of the study was to elucidate where in the area of the Frisian Front and Central Oystergrounds the highest likely effects of bottom trawling on biodiversity, species biomass, and species traits could be found, taking into account the effects of abiotic conditions. This analysis would allow us to point out locations within the area where the potential effects of a ban on bottom trawling benthic species would be greatest. However, effects of trawling turned out to be highly related to effects of other environmental factors. This means that maps of trawling impact on traits or richness can only show the combined effect of trawling and the other factors (depth, sediment grain size, productivity). This means that such maps are of limited value for the purpose of selecting closed areas for maximum effect because the predicted potential effects at each location may be related to fishing intensity, depth, sediment grain size, or any combination of these factors.

Effects of trawling on species traits

The analysis of effects of trawling on species traits indicates that total variation in traits between the sampling stations is significantly explained for 18% by the combination of the factors trawling, primary productivity, median grain size and depth. Further separation of the effects of trawling from those of primary productivity, sediment grain size and depth was attempted using partial RDA, but was unsuccessful due to lack of independent occurrence of certain combinations of these factors.

The effects of depth and trawling intensity are particularly difficult to separate, because almost all lightly trawled locations are in the deeper parts of the area, while intensely trawled samples all come from the shallowest parts of the Frisian Front and Oystergrounds.
Despite the strong interrelationship between the various factors in terms of their explanatory power of the trait composition, there are a number of modalities for which a true effect of fishing is likely (Table 6). In particular, the modalities ‘exoskeleton’ and ‘predator’ are more abundant in fished areas, possibly representing a shift towards more mobile scavenger/predators, which has also been observed by Tillin et al. (2006). We also observe an increase in the relative abundance of ‘burrow dwelling’ taxa, which together with ‘exoskeleton’ points towards mud shrimps such as *Calianassa*. These are often buried deeply in the sediment, where they are largely immune to disturbance of the top sediment layer.

Other trait modalities are strongly negatively related to fishing intensity. The most obvious fishery effect in this list (Table 6) is the decline of infaunal biomass inhabiting the top 0-5 cm of the sediment. The fact that species occur in the top 5 cm of the sediment means that they are inevitably affected by the physical disturbance of the trawl gear. Furthermore, these are often bivalves, which are generally sensitive to bottom trawling (Tillin, 2006). Of these traits (Table 6) some strongly relate to MSFD criteria for biodiversity and seafloor integrity, such as maximum size, sediment position, bioturbation and living habitat.

Table 6 Selection of traits strongly associated with fishing (see Table 4 and appendix D for more details on traits)

Positive	**Negative**
egg development – brooded	living habitat - free living
protection - exoskeleton	bioturbation - diffusive mixing
feeding mode – predator	feeding type - subsurface deposit
living habitat - burrow dwelling	sediment position - 0-5cm
bioturbation- surface deposition	egg development- benthic

Effects of trawling on species size distributions

The analyses of effects of trawling on species size distributions showed that the factor fishing intensity is only a weak estimator for mean and maximum size. Body sizes of the species found in the sampling stations show strongest significant relationships with primary production, water depth and grain size. The data however suggest that for some species body size tends to be smaller in heavily fished areas. A negative relationship between size and fishing intensity could however only be proven with statistical significance for the large bivalve *Acanthocardia echinatum*. This result supports previous field studies which showed a high impact of trawling on this species. For the other large bivalve species such as *Mya truncata* and *Arctica islandica* statistical significant trends could not be identified because the numbers of caught specimens in the various levels of fishing intensity were too small.

The low densities of the fragile species is not unexpected and are most likely due to additional mortality due to fishing. It has been demonstrated that especially *Arctica islandica* is vulnerable for bottom trawling (Witbaard & Klein, 1994). Its almost absence from the most heavily fished areas illustrates the long term effect of bottom disturbance on this species.

Already in 2003, Witbaard and Bergman (2003) discussed bottom trawling as possible cause of the skewed size distribution and relatively low densities of *Arctica islandica* in the SE North Sea. In 2007, estimates from a population model, and using measured fishing mortality, predicted that by 2017 *Arctica* would be virtually extinct in the Frisian Front and have densities of less then 10/ha (Witbaard, 2007). The abundance and distribution data derived from the present Triple D data now support this earlier prediction and illustrates why trends between heavily fished and lightly fished areas for this species cannot be detected, i.e. its absence from the heavily fished areas. It seems reasonable to assume that similar absence mask the effect on other large species as well, like *Mya truncata* or *Dosinia lupinus.*

Effects of trawling on species richness

Although the samples in our data clearly differ in richness, these differences are best explained by a combination of depth, grain size, primary productivity and biomass, and not by trawling intensity directly. Variation in trawling intensity is explained by water depth and primary productivity. In other words, environmental factors affect both trawling intensity and species richness, whereas trawling intensity does not, in our data, affect richness. The highest species richness is found in fine sediments in areas with a high primary productivity and high total biomass. Depth affects species richness both directly and indirectly, as it is strongly correlated with both grain size and primary productivity. The highest trawling intensity is found in relatively shallow areas with high primary productivity.

This result may point to that trawling is not important in determining species richness, but can also be caused by data limitations. The SEM and the pairwise correlations contain some indications pointing towards such limitations. In particular, the different sign of the effects of depth on trawling intensity and species richness implies that the most species rich samples come from deeper water, while deeper water is also less intensively trawled. Inspection of the pairwise correlation plots shows that the majority of species-rich samples are from larger depths, but there are no heavily trawled samples from deep water. This means that the data contain an implicit bias against finding a direct effect of trawling on richness, due to absence of certain combinations of factors. This is a common limitation when working with empirical rather than experimental data: there are no 'controls' with low fishing in shallow, or high fishing in deep areas. The presence of these limitations in the data means that based on this data set, we cannot conclude whether or not trawling has an effect on species richness.

Trawling intensity could only be determined up to 1.5 years before sampling took place, due to the limited availability of VMS data of fishing vessels. The likely history of long-term trawling in this area may have led to a benthic community which is relatively resistant to trawling already, which could mean that there is limited scope for further 'short term' effects of trawling. Furthermore, the dataset used, only contained a subset of all species present. There may be effects on unsampled parts of the benthic community, which we have missed in this analysis (van Denderen et al, 2014). It is also important to note that this analysis is limited to species richness, with no consideration for species composition.

The relationships between variables in the SEM found here largely correspond to those found in van Denderen et al. (2014). The general correspondence (and lack of contradicting results) of the direction and significance of the effects strengthens the generality of the pattern found, namely that species richness is most strongly determined by environmental factors. The main difference between these studies is the absence of certain effects in the current analysis, which were identified in van Denderen et al. (2014) when analysing boxcore data and VMS data over the entire Dutch continental shelf. The most notable difference is the absence of a significant effect of trawling intensity on biomass, which van Denderen et al. did find.

There are two potential considerations which both may explain this difference. First, the faunal data used in this study are collected with a different sampling gear and consist of a different species selection due to the gear specific selection. The gear used in this study is designed to sample large and sparsely distributed species and as a consequence often small, relatively short lived biota are not well sampled (Witbaard et al, 2013). It may be this fraction of the biota which explains the biomass-trawling intensity pattern in van Denderen et al. (2014), which we have not found here.

Another reason could be the smaller range of abiotic conditions over which this analysis is done, compared to the study of Van Denderen et al (2014). The range of sediment types, depths, primary production and fishing intensity over the Oystergrounds and Frisian Front is much smaller than the range over the entire Dutch Continental Shelf, considered in van Denderen et al. (2014). Only a limited number of benthic samples was taken in areas with very high trawling intensity (Fig. 4). It may be that the biomass-trawling relationship in van Denderen et al. (2014) depends on samples with very high trawling intensity and very low biomass, which simply do not occur in our data set, and that this prevents us from finding a statistical relationship. Van Denderen et al. (2014) showed, based on boxcore samples of the entire Dutch Continental Shelf, a location-dependent effect of trawling on benthic species richness. An effect of trawling was confined to deeper areas with smaller grain sizes. In shallower areas, and more sandy sediments, an effect of trawling was not observed (Van Denderen et al., 2014). In this study, we find a positive correlation between primary productivity and species richness, which was not present in the analysis of Van Denderen et al. (2014). We can only speculate regarding the cause of this difference, which can be either due to the sampling gear, the area selected, or some more fundamental difference between the analysed benthic ecosystems.

Implications for measures: Closing areas for fisheries

The ultimate aim of this work was to elucidate where in these areas the most likely effect of bottom-trawling are found on species traits, biodiversity and size distributions, taking the effects of abiotic conditions into account. This analysis would allow us to point out locations within the area where the potential effects of closure to bottom trawling on the benthic ecosystem would be greatest. However, effects of trawling turned out to be highly related to effects of other environmental factors. This means that maps of trawling impact on traits or richness can only show the combined effect of trawling and the other factors (depth, sediment grain size, productivity), and such maps are be of limited value for the purpose of selecting closed areas for maximum effect because the predicted potential effects at each location may be related to fishing intensity, depth, sediment grain size, or any combination of these factors.

We do find clear effects of fisheries on the occurrence of specific functions and properties (traits) of benthic organisms, and it is likely that a number of these traits will increase in prevalence after cessation of trawling. On the other hand, there are also functions and properties which occur more frequently in heavily trawled areas, and it is very well possible that these will decline in areas which are no longer fished.

We find that species richness is determined by depth, sediment grain size, total benthic biomass and primary productivity, while trawling intensity is determined by depth and primary productivity. As a consequence of limitations in the data, we cannot answer whether or not there is an effect of trawling intensity on species richness. We find that for a selection of species, the size distribution in samples from highly trawled areas is truncated, indicative of high mortality from trawling. Many other species for which such a trawling effect is expected do not occur in the highly trawled areas, so that a comparison of the size distribution cannot be made, but the absence in itself can be interpreted as an indication of their sensitivity to trawling.

Because both trawling intensity and species traits and richness are strongly determined by environmental factors, the safest option for preserving ecosystem function and diversity is to close areas representing the full range of environmental conditions. This strategy would maximize both (1) the range of trait modalities which is protected from trawling, and (2) the chance that at least some of the areas which may be impacted by trawling will have a chance to recover.

5 Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 124296-2012-AQ-NLD-RvA). This certificate is valid until 15 December 2015. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Fish Division has NEN-EN-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 1th of April 2017 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

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Justification

Report number : C037/15
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The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department of IMARES.

Approved: Drs. P. de Vries
Researcher

Signature:

Date: 20th of November 2015

Approved: Dr. ir. L.J.W. van Hoof
Head of Department Fish

Signature:

Date: 20th of November 2015

Appendix A. In- and exclusion of benthic species

Table 1. Species included in SEM analysis

Phylum	**Class**	**Latin name**	**Included species**
Annelida	Polychaeta	*Aphrodita aculeata*	incl.
Annelida	Polychaeta	*Lanice conchilega*	incl.
Annelida	Polychaeta	*Pectinaria auricoma*	incl.
Annelida	Polychaeta	*Pectinaria belgica*	incl.
Annelida	Polychaeta	*Pectinaria koreni*	incl.
Annelida	Polychaeta	*Pectinaria spec.*	incl.
Annelida	Polychaeta	*Sabella spec.*	incl.
Annelida	Polychaeta	*Sabellaria spec.*	incl.
Arthropoda	Crustacea	*Callianassa subterranea*	incl.
Arthropoda	Crustacea	*Carcinus maenas*	incl.
Arthropoda	Crustacea	*Cirolana cranchi*	incl.
Arthropoda	Crustacea	*Corystes cassivelaunus*	incl.
Arthropoda	Crustacea	*Crangon allmanni*	incl.
Arthropoda	Crustacea	*Crangon crangon*	incl.
Arthropoda	Crustacea	*Ebalia cranchii*	incl.
Arthropoda	Crustacea	*Ebalia spec.*	incl.
Arthropoda	Crustacea	*Ebalia tumefacta*	incl.
Arthropoda	Crustacea	*Goneplax rhomboides*	incl.
Arthropoda	Crustacea	*Liocarcinus depurator*	incl.
Arthropoda	Crustacea	*Liocarcinus holsatus*	incl.
Arthropoda	Crustacea	*Liocarcinus marmoreus*	incl.
Arthropoda	Crustacea	*Liocarcinus navigator*	incl.
Arthropoda	Crustacea	*Liocarcinus spec.*	incl.
Arthropoda	Crustacea	*Macropodia spec.*	incl.
Arthropoda	Crustacea	*Natatolana borealis*	incl.
Arthropoda	Crustacea	*Necora puber*	incl.
Arthropoda	Crustacea	*Nephrops norvegicus*	incl.
Arthropoda	Crustacea	*Pagurus bernhardus*	incl.
Arthropoda	Crustacea	*Pestarella tyrrhena*	incl.
Arthropoda	Crustacea	*Processa spec.*	incl.
Arthropoda	Crustacea	*Rissoides desmaresti*	incl.
Arthropoda	Crustacea	*Thia scutellata*	incl.
Arthropoda	Crustacea	*Thysanocardia procera*	incl.
Arthropoda	Crustacea	*Upogebia deltaura*	incl.
Arthropoda	Crustacea	*Upogebia stellata*	incl.
Arthropoda	Malacostraca	*Philocheras trispinosus*	incl.
Bryozoa		*Bryozoa*	incl.
Bryozoa	Gymnolaemata	*Alcyonidium diaphanum*	incl.
Bryozoa	Gymnolaemata	*Flustra foliacea*	incl.

Phylum	**Class**	**Latin name**	**Included species**
Chordata	Tunicata	*Ascidia virginea*	incl.
Chordata	Tunicata	*Ascidiacea*	incl.
Chordata	Tunicata	*Pelonaia corrugata*	incl.
Chordata	Tunicata	*Tunicata*	incl.
Cnidaria	Anthozoa	*Actiniaria*	incl.
Cnidaria	Anthozoa	*Calliactis parasitica*	incl.
Cnidaria	Anthozoa	*Cerianthus lloydii*	incl.
Cnidaria	Anthozoa	*Metridium senile*	incl.
Cnidaria	Anthozoa	*Sagartia troglodytes*	incl.
Cnidaria	Anthozoa	*Sagartiogeton undatus*	incl.
Cnidaria	Hydrozoa	*Hydrozoa*	incl.
Cnidaria	Hydrozoa	*Tubularia*	incl.
Cnidaria	Hydrozoa	*Tubularia indivisa*	incl.
Echinodermata	Asteroidea	*Asterias rubens*	incl.
Echinodermata	Asteroidea	*Astropecten irregularis*	incl.
Echinodermata	Asteroidea	*Luidia sarsi*	incl.
Echinodermata	Asteroidea	*Luidia spec.*	incl.
Echinodermata	Echinoidea	*Brissopsis lyrifera*	incl.
Echinodermata	Echinoidea	*Echinocardium cordatum*	incl.
Echinodermata	Echinoidea	*Echinocardium flavescens*	incl.
Echinodermata	Echinoidea	*Psammechinus miliaris*	incl.
Echinodermata	Holothuroidea	*Holothuroidea*	incl.
Echinodermata	Holothuroidea	*Leptopentacta elongata*	incl.
Echinodermata	Holothuroidea	*Leptosynapta inhaerens*	incl.
Echinodermata	Holothuroidea	*Oestergrenia digitata*	incl.
Echinodermata	Ophiuroidea	*Acrocnida brachiata*	incl.
Echinodermata	Ophiuroidea	*Amphiura filiformis*	incl.
Echinodermata	Ophiuroidea	*Ophiothrix fragilis*	incl.
Echinodermata	Ophiuroidea	*Ophiura albida*	incl.
Echinodermata	Ophiuroidea	*Ophiura ophiura*	incl.
Echiura	Echiuroidea	*Echiurus echiurus*	incl.
Echiura		*Priapulida or Echiura*	incl.
Mollusca	Bivalvia	*Abra alba*	incl.
Mollusca	Bivalvia	*Abra nitida*	incl.
Mollusca	Bivalvia	*Abra prismatica*	incl.
Mollusca	Bivalvia	*Acanthocardia echinata*	incl.
Mollusca	Bivalvia	*Angulus fabula*	incl.
Mollusca	Bivalvia	*Aquipecten opercularis*	incl.
Mollusca	Bivalvia	*Arctica islandica*	incl.
Mollusca	Bivalvia	*Chamelea striatula*	incl.
Mollusca	Bivalvia	*Corbula gibba*	incl.
Mollusca	Bivalvia	*Dosinia exoleta*	incl.
Mollusca	Bivalvia	*Dosinia lupinus*	incl.

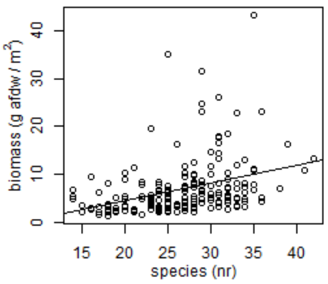
Phylum	Class	Latin name	Included species
Mollusca	Bivalvia	*Ensis ensis*	incl.
Mollusca	Bivalvia	*Ensis magnus*	incl.
Mollusca	Bivalvia	*Ensis siliqua*	incl.
Mollusca	Bivalvia	*Ensis spec.*	incl.
Mollusca	Bivalvia	*Gari fervensis*	incl.
Mollusca	Bivalvia	*Hiatella arctica*	incl.
Mollusca	Bivalvia	*Lepton squamosum*	incl.
Mollusca	Bivalvia	*Lutraria lutraria*	incl.
Mollusca	Bivalvia	*Mactra stultorum*	incl.
Mollusca	Bivalvia	*Modiolus or Musculus*	incl.
Mollusca	Bivalvia	*Mya truncata*	incl.
Mollusca	Bivalvia	*Mysia undata*	incl.
Mollusca	Bivalvia	*Nucula nitidosa*	incl.
Mollusca	Bivalvia	*Phaxas pellucidus*	incl.
Mollusca	Bivalvia	*Spisula subtruncata*	incl.
Mollusca	Bivalvia	*Thracia convexa*	incl.
Mollusca	Bivalvia	*Thracia phaseolina*	incl.
Mollusca	Cephalopoda	*Alloteuthis subulata*	incl.
Mollusca	Cephalopoda	*Sepiola atlantica*	incl.
Mollusca	Gastropoda	*Acteon tornatilis*	incl.
Mollusca	Gastropoda	*Aporrhais pespelecani*	incl.
Mollusca	Gastropoda	*Buccinum undatum*	incl.
Mollusca	Gastropoda	*Epitonium clathrus*	incl.
Mollusca	Gastropoda	*Gastropoda*	incl.
Mollusca	Gastropoda	*Lunatia catena*	incl.
Mollusca	Gastropoda	*Lunatia pulchella*	incl.
Mollusca	Gastropoda	*Lunatia spec.*	incl.
Mollusca	Gastropoda	*Neptunea antiqua*	incl.
Mollusca	Gastropoda	*Turridae*	incl.
Mollusca	Gastropoda	*Turritella communis*	incl.
Nemertea	Anopla	*Cerebratulus marginatus*	incl.
Nemertea		*Nemertea*	incl.
Sipuncula	Sipunculidea	*Golfingia (lang)*	incl.
Sipuncula	Sipunculidea	*Golfingia elongata*	incl.
Sipuncula	Sipunculidea	*Golfingia vulgaris*	incl.

Table 2. Species excluded from analysis.

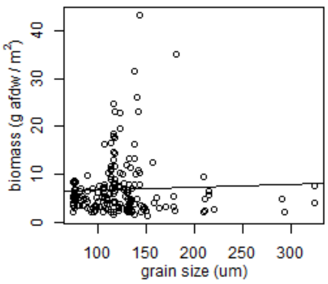
Phylum	**Class**	***Latin name***	**Excluded**
Annelida	Polychaeta	*Chaetopterus variopedatus*	excl.
Annelida	Polychaeta	*Eunereis longissima*	excl.
Annelida	Polychaeta	*Gattyana cirrhosa*	excl.
Annelida	Polychaeta	*Glycera spec.*	excl.
Annelida	Polychaeta	*Harmothoe spec.*	excl.
Annelida	Polychaeta	*Nephtys hombergii*	excl.
Annelida	Polychaeta	*Nephtys spec.*	excl.
Annelida	Polychaeta	*Nereidae*	excl.
Annelida	Polychaeta	*Opheliidae*	excl.
Annelida	Polychaeta	*Orbinia spec.*	excl.
Annelida	Polychaeta	*Owenia fusiformis*	excl.
Annelida	Polychaeta	*Polychaeta*	excl.
Arthropoda	Crustacea	*Amphipoda*	excl.
Arthropoda	Crustacea	*Pinnotheres pisum*	excl.
Arthropoda	Crustacea	*Pisidia longicornis*	excl.
Arthropoda	Crustacea	*Sacculina carcini*	excl.
Chordata	Pisces	*Agonus cataphractus*	excl.
Chordata	Pisces	*Ammodytes tobianus*	excl.
Chordata	Pisces	*Arnoglossus laterna*	excl.
Chordata	Pisces	*Buglossidium luteum*	excl.
Chordata	Pisces	*Callionymus lyra*	excl.
Chordata	Pisces	*Callionymus reticulatus*	excl.
Chordata	Pisces	*Callionymus spec.*	excl.
Chordata	Pisces	*Chelidonichtys cuculus*	excl.
Chordata	Pisces	*Clupea harengus*	excl.
Chordata	Pisces	*Enchelyopus cimbrius*	excl.
Chordata	Pisces	*Engraulis encrasicolus*	excl.
Chordata	Pisces	*Entelurus aequoreus*	excl.
Chordata	Pisces	*Entelurus or Syngnathus*	excl.
Chordata	Pisces	*Eutrigla gurnardus*	excl.
Chordata	Pisces	*Gadus morhua*	excl.
Chordata	Pisces	*Gobiidae*	excl.
Chordata	Pisces	*Hippoglossoides platessoides*	excl.
Chordata	Pisces	*Hyperoplus lanceolatus*	excl.
Chordata	Pisces	*Lepidorhombus whiffiagonis*	excl.
Chordata	Pisces	*Limanda limanda*	excl.
Chordata	Pisces	*Merlangius merlangus*	excl.
Chordata	Pisces	*Microstomus kitt*	excl.
Chordata	Pisces	*Mullus surmuletus*	excl.

Phylum	**Class**	***Latin name***	**Excluded**
Chordata	Pisces	*Pleuronectes platessa*	excl.
Chordata	Pisces	*Pomatoschistus lozanoi*	excl.
Chordata	Pisces	*Solea solea*	excl.
Chordata	Pisces	*Sprattus sprattus*	excl.
Chordata	Pisces	*Syngnathus acus*	excl.
Chordata	Pisces	*Syngnathus rostellatus*	excl.
Mollusca	Cephalopoda	*Loligo spec.*	excl.
Mollusca	Cephalopoda	*Sepia officinalis*	excl.
Platyhelminthes	Turbellaria	*Turbellaria*	excl.

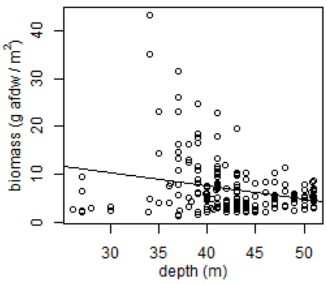
Appendix B. All bivariate correlation figures


biomass vs species richness

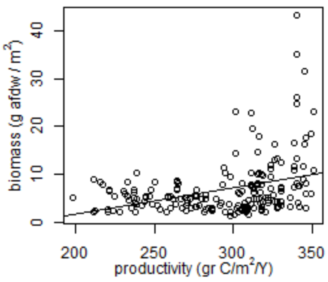
R2 0.117 p <0.001 Cor 0.348


biomass vs median grain size

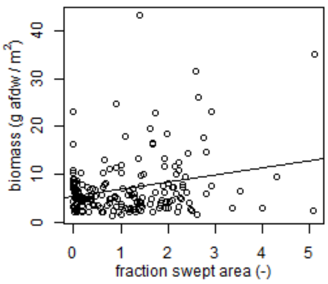
R2 0.000 p 0.572 Cor 0.041


biomass vs water depth

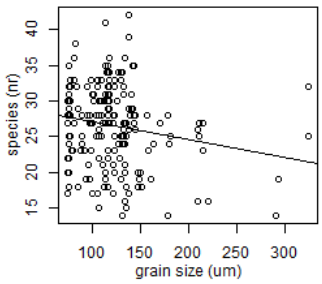
R2 0.055 p <0.001 Cor -0.246


biomass vs pr. productivity

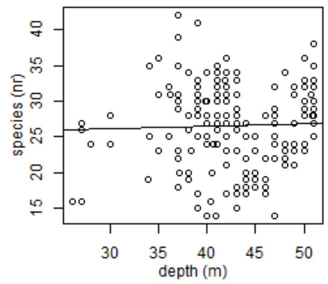
R2 0.117 p <0.001 Cor 0.348


biomass vs trawl disturbance

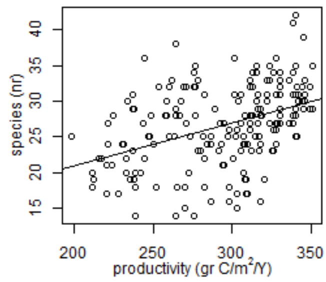
R2 0.065 p <0.001 Cor 0.263


richness vs median grain size

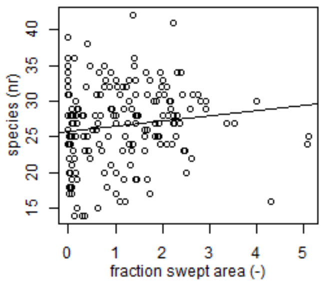
R2 0.028 p 0.012 Cor -0.181


richness vs water depth

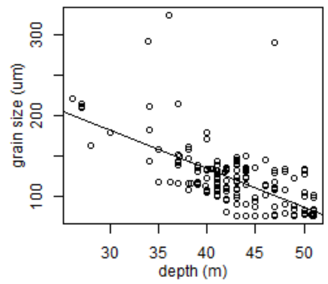
R2 0.000 p 0.660 Cor 0.032


richness vs pr. production

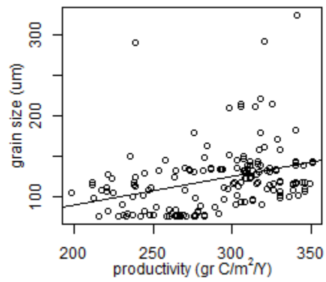
R2 0.158 p <0.001 Cor 0.402


richness vs trawl disturbance

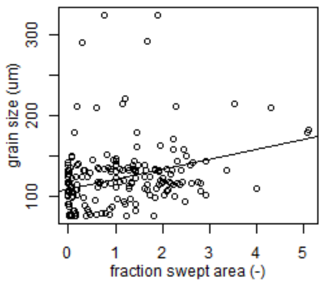
R2 0.0124 p 0.066 Cor 0.133


median grain size vs water depth

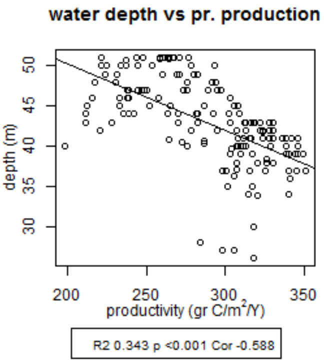
R2 0.397 p <0.001 Cor -0.633

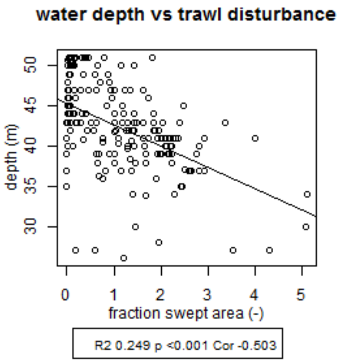

median grain size vs pr. production

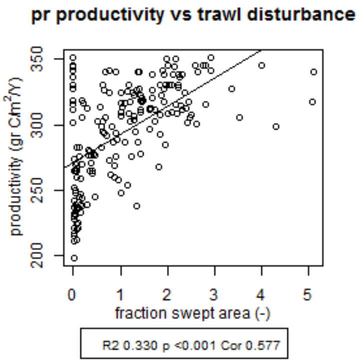
R2 0.105 p <0.001 Cor 0.331


median grain size vs trawl disturbance

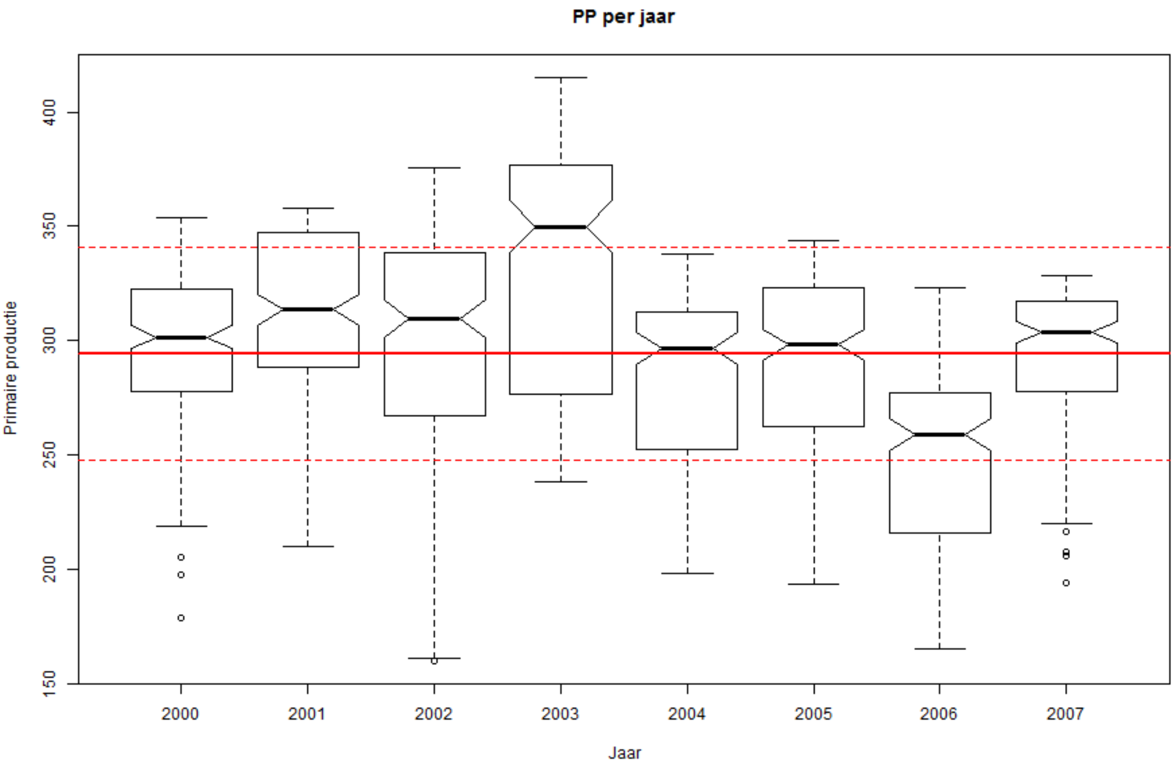
R2 0.090 p <0.001 Cor 0.308


water depth vs pr. production
depth (m)
30
35
40
45
50
200
250
300
350
productivity (gr C/m²/Y)
R2 0.343 p <0.001 Cor -0.588


water depth vs trawl disturbance
depth (m)
30
35
40
45
50
0
1
2
3
4
5
fraction swept area (-)
R2 0.249 p <0.001 Cor -0.503


pr productivity vs trawl disturbance
productivity (gr C/m²/Y)
200
250
300
350
0
1
2
3
4
5
fraction swept area (-)
R2 0.330 p <0.001 Cor 0.577

Appendix C. Variation in primary production



Appendix D. Traits and categories

Traits and trait categories. The labelling of each trait category during numerical analyses and for presentation within figures and tables (see results) is given in brackets. All modalities signed with three asterisks (***) had a mean proportion of biomass that was less than 0.01 for all stations. These modalities were not included in the redundancy analysis.

Trait + code	Epifaunal categories (RDA)	Trait Definition and functional significance
Size range (s)	≤ 10 (s10) 11 – 20 (s11-20) 21 – 100 (s21-100) 101 – 200 (s101-200) 200-500 (s200-500) *** >500 (s>500) ***	In mm. Maximum recorded size of adult (as individuals or colonies). Implications for the movement of organic matter within the benthic system as large organisms hold organic matter (low turnover) within the system relative to small-bodied species (high turnover) (Pearson and Rosenberg, 1978).
Morphology (m)	Flat/encrusting (mFlat) Round-bodied (mRound) Stalked/pen-shaped (mPen) *** Stalked/fan-shaped (mFan) *** Stalked/complex (mComp)	External characteristics of the taxon.
Longevity (Long)	<1 (Long<1) *** 1 – 3 (Long1-3) 4 – 10 (Long3-10) >10 (Long>10)	Maximum reported life span of the adult stage. Indicates the relative investment of energy in somatic rather than reproductive growth and the relative age of sexual maturity, i.e. a proxy for relative r- and k- strategy (Pearson and Rosenberg, 1978)
Larval development strategy (LD)	Planktotrophic (LD_Pk) Lecithotrophic (LD_Lc) *** Direct (LD_Direct)	Indicates the potential for dispersal of the larval stage prior to settlement from direct (no larval stage), lecithotrophic (larvae with yolk sac, pelagic for short periods) to planktotrophic (larvae feed and grow in water column, generally pelagic for several weeks). Affects ability to recover from disturbance with planktonic recruitment affording potentially faster recolonisation than lecithotrophic and direct development (Thrush and Whitlatch, 2001).
Egg development location (Egg)	Asexual/fragmentation (Egg_asex) Eggs – pelagic (Egg_Pel) Eggs – benthic (Egg_Ben) Eggs – brooded (Egg_Bro)	Indicates dispersal via the egg stage and the potential susceptibility of eggs to damage from fishing. Benthic eggs are generally more concentrated over smaller areas. Asexual reproduction allows the potential to increase numbers rapidly, particularly following disturbance.
Living habit (LH)	Tube-dwelling (LH_Tube) *** Burrow-dwelling (LH_Burrow) Free living (LH_Free) Crevice/under stone (LH_Crev) *** Epi/endo zoic/phytic (LH_Epi)	Indicates potential for the adult stage to evade, or to be exposed to, physical disturbance.

Trait + code	Epifaunal categories (RDA)	Trait Definition and functional significance
	*** Attached to bed (LH_Att)	
Sediment position (SP)	Surface (spSurf) 0 – 5 cm (sp0-5) 5 – 10 cm (sp6-10) >10 cm (sp>10)	Typical living position in sediment profile. Organisms occupying shallower positions in the sediment are more likely to contact trawl gear than those living deeper. Sediment position also has implications for the effect of the organism to affect sediment-water nutrient and/or oxygen exchange.
Feeding mode (F)	Suspension (F_Susp) Surface deposit (F_Sdep) Subsurface deposit (F_Subdep) Scavenger (F_Scav) Predator (F_pred)	Feeding mode has important implications for the potential for transfer of carbon between the sediment and water and within the sediment matrix. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg, 1995).
Mobility (M)	Sessile (M_Sess) Swim (M_Swim) *** Burrow (M_Burrow) Crawl (M_Crawl)	Adults of faster moving species are more likely to evade capture by trawl gear than slow-moving or sessile individuals. Mobility also affects the ability for adult recolonisation of disturbed areas.
Bioturbation (BT)	Diffusive mixer (BT_Diff) Surface deposition (BT_Surf) Upward conveyor (BT_Up) *** Downw. conv.(BT_Down) None (BT_None) ***	Describes the ability of the organism to rework the sediments. Can either be upward, downward, onto the sediment or mixing of the sedimentary matrix. Bioturbation mode has important implications for sediment-water exchange and sediment biogeochemical properties.
Protection (P)	Fragile (P_Frag) Unprotected (P_Unprot) Protected (skin/exoskeleton) (P_Exo) Protect (robust shell) (P_Rob)	Describes the capacity to withstand physical disturbance and thus the potential for the adult population to remain viable following acute fishing.
Bed/reef formers (BR)	None (BR_None) Reef-builder (BR_Reef) *** Bed-former (BR_Bed) ***	Important for affecting a number of ecological functions such as biodiversity, productivity and sediment stability.

Appendix E. Triple Dredge

Appendix F. Species list Scientific – Dutch

Scientific name	Nederlandse naam	Phylum
Acanthocardia echinata	Gedoornde hartschelp	Mollusca
Amphiura filiformis	Draadarmige Slangster	Echinodermata
Arctica islandica	Noordkromp	Mollusca
Brissopsis lyrifera	-	Echinodermata
Callianassa subterranea	Modder garnaal	Crustacea
Chamelea striatula	Gestreepte venusschelp	Mollusca
corbula gibba	Korfschelp	Mollusca
Corystes cassivelaunus	Helmkrab	Crustacea
Dosinia lupinus	Dicht gestreepte artemisschelp	Mollusca
Echinocardium cordatum	Hartegel	Echinodermata
Goneplax rhomboides	trapeziumkrab	Crustacea
Mya truncata	Afgeknotte strandgaper	Mollusca
Mysia undata	Zandschelp	Mollusca
Nepthys incisa	-	Polychaeta
nucula nitidoda	Parelmoerneut	Mollusca
Phaxas pellucides	Sabelschede	Mollusca
Pleuronectus platessa	Schol	Pisces
Solea solea	Tong	Pisces
Thracia convexa	Bolle papierschelp	Mollusca
Turristella communis	Penhoren	Mollusca
Upogebia deltaura	Harige molkreeft	Crustacea
Upogebia stellata	Gestippelde molkreeft ?	Crustacea