University of Groningen

Seafloor communities and habitat disturbances in the North Sea

van der Reijden, Karin J.

DOI:
[10.33612/diss.178510795](https://doi.org/10.33612/diss.178510795)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2021

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):
van der Reijden, K. J. (2021). *Seafloor communities and habitat disturbances in the North Sea*. [Thesis fully internal (DIV), University of Groningen]. University of Groningen. <https://doi.org/10.33612/diss.178510795>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Seafloor communities and habitat disturbances in the North Sea

Karin J. van der Reijden

This thesis should be cited as:

van der Reijden, KJ (2021): Seafloor communities and habitat disturbances in the North Sea. PhD thesis, University of Groningen, Groningen, The Netherlands.

The research presented in this thesis was performed at the Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, The Netherlands according to the requirements of the Graduate School of Science (Faculty of Mathematics and Natural Sciences, University of Groningen).

This research is part of the DISCLOSE project, financed by the Gieskes-Strijbis-Fund.

Cover and lay-out: Karin J. van der Reijden
Photographs: Ben Stiefelhagen (p196),
Carlos Minguell / OCEANA (p179 top and bottomleft, p183 topright and bottom),
Danielle Prins-de Jonge (p94, p179 middle, p183 topleft),
Ecomare / Oscar Bos (p178 bottom),
Jip Vrooman (p134),
Juan Cuetos / OCEANA (p26, p178 middle),
Karin van der Reijden (all other photos),
Karline Soetaert (p44),
Ming Tsang Lin (p178 top),
Nadia Hijner (p152, p200)
Printing: Ridderprint | www.ridderprint.nl

Copyright © 2021 by K.J. van der Reijden.

All rights reserved. No part of this thesis may be reproduced, stored or transmitted in any form or by any means without prior written permission of the author.

**rijksuniversiteit
 groningen**

Seafloor communities and habitat disturbances in the North Sea

Proefschrift

ter verkrijging van de graad van doctor aan de
Rijksuniversiteit Groningen
op gezag van de
rector magnificus prof. dr. C. Wijmenga
en volgens besluit van het College voor Promoties.

De openbare verdediging zal plaatsvinden op

vrijdag 17 september 2021 om 16.15 uur

door

Karin Johanna van der Reijden

geboren op 11 mei 1990
te Schiedam

Promotores

Prof. dr. H. Olff

Prof. dr. A. D. Rijnsdorp

Copromotor

Dr. L. L. Govers

Beoordelingscommissie

Prof. dr. B. D. H. K. Eriksson

Prof. dr. J. G. Hiddink

Prof. dr. D. van der Wal

Paranimfen

E. R. Veldhuis

E. C. van der Reijden

Table of contents

Samenvatting

Chapter 1	General introduction
Chapter 2	North Sea demersal fisheries prefer specific benthic habitats
Chapter 3	Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front
Chapter 4	Connecting the dots: a multi-scale, multi-resolution approach to marine habitat mapping
Chapter 5	Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples
Chapter 6	Linking the morphology and ecology of subtidal soft-bottom marine benthic habitats: A novel multiscale approach
Chapter 7	Seafloor classification in a sand wave environment on the Dutch Continental Shelf using multibeam echosounder backscatter data
Chapter 8	Discovery of Sabellaria spinulosa reefs in an intensively fished area of the Dutch Continental Shelf, North Sea
Chapter 9	Conservation implications of Sabellaria spinulosa reef patches in a dynamic sandy-bottom environment
Chapter 10	Synthesis
Appendices	Acknowledgements Biography List of publications

Samenvatting

Bodemleefgemeenschappen

Kustzeeën kennen een grote diversiteit van diersoorten die in, op of vlak boven de zeebodem leven. Deze bodemdieren spelen een essentiële rol in het ecosysteem. Zo zetten bodemdieren organisch materiaal om in belangrijke voedingsstoffen, leggen ze het onderliggende sediment vast en bewerken de zeebodem wat leidt tot een verhoogt zuurstofgehalte in de zeebodem. Daarnaast dienen bodemdieren als een belangrijke voedselbron voor zowel mensen als commercieel belangrijke vissoorten. Bodemdieren zijn ingedeeld in leefgemeenschappen, waarbij de soorten die in een leefgemeenschap voorkomen voornamelijk wordt bepaald door de leefomgeving. Factoren zoals getijstromingen, zoutgehalte en bodemtype bepalen bijvoorbeeld of een soort op een bepaalde plek kan overleven. Op een kleinere schaal kunnen ook biologische processen een rol spelen. Zo bestaan er soorten die hun omgeving zodanig veranderen dat andere soorten hiervan profiteren, doordat bijvoorbeeld schuilplekken zijn ontstaan, er een geschikte ondergrond wordt gevormd om op te vestigen, of omdat het voedselaanbod plaatselijk wordt vergroot. Dergelijke soorten heten ecosystemeingenieurs of biobouwers. Bekende voorbeelden zijn koraalriffen, zeegrasvelden en mosselbanken. Ten slotte worden bodemleefgemeenschappen ook beïnvloed door menselijke activiteiten, waarbij bodemberoerende visserij de activiteit is die het meeste voorkomt. Bodemberoerende visserij omvat alle visserijen die gericht vissen op vissen die op of vlak boven de zeebodem leven, en waarbij het vistuig fysiek de zeebodem raakt. Deze visserijen beïnvloeden de bodemleefgemeenschappen onder andere door het wegvangen van zowel gewilde als (ongewenste) bijvangst soorten, en door het beschadigen van structuren op de zeebodem.

Elke leefgemeenschap reageert anders op verstoringen, afhankelijk van zijn veerkracht. Deze veerkracht hangt af van de weerbaarheid van de gemeenschap en zijn vermogen tot herstel. Zeer weerbare leefgemeenschappen kunnen veel verstoringen verdragen zonder in samenstelling of hoeveelheid te worden aangetast. Leefgemeenschappen met een lage veerkracht hebben een lage weerbaarheid en een lange hersteltijd. Leefgemeenschappen die van nature veel verstoord worden door golfslag en stromingen zijn aangepast aan deze omstandigheden en hebben gemiddeld een hoge veerkracht. Van nature hebben de leefgemeenschappen in dieper water vaak een lage veerkracht omdat deze minder vaak verstoord worden. Juist hier kan menselijke verstoring, bijvoorbeeld door bodemberoerende visserij, resulteren in een andere leefgemeenschap. Soorten die een grotere veerkracht hebben kunnen vaker voorkomen, terwijl leefgemeenschappen met een lage veerkracht verdwijnen.

Om het voortbestaan van alle verschillende bodemleefgemeenschappen te waarborgen moeten de kustzeeën duurzaam beheerd worden. Dit betekent dat er een goede balans is tussen de sociale, economische en ecologische belangen. Een dergelijk beleid vereist goed inzicht in de ruimtelijke verspreiding van zowel bodemleefgemeenschappen als menselijke activiteiten, en hun relatie tot de omgeving. Daarnaast moeten de gevolgen van menselijke activiteiten op de bodemleefgemeenschappen nauwkeurig kunnen worden ingeschat, waarbij rekening wordt gehouden dat de gevolgen afhangen van de soort en locatie van de activiteit. Om de kennis van (kwetsbare) leefgemeenschappen in de Noordzee te vergroten en daarmee duurzaam beheer te stimuleren werd het onderzoeksproject DISCLOSE opgericht. Deze samenwerking van de Technische Universiteit Delft, de Rijksuniversiteit Groningen, het Koninklijk Nederlands Instituut voor Onderzoek der Zee en Stichting de Noordzee had als doel om de verspreiding, structuur en functioneren van (kwetsbare) bodemleefgemeenschappen in de Noordzee te onderzoeken door verschillende onderzoeksmethodes te combineren. Als onderdeel van dit DISCLOSE project heb ik in mijn proefschrift de ruimtelijke verspreiding en samenhang van omgevingsfactoren, bodemberoerende visserij en bodemleefgemeenschappen onderzocht in de zeer dynamische en veelgebruikte Noordzee.

Bodemberoerende visserij

De bodemberoerende visserij staat bekend om zijn negatieve invloed op het bodemleven. In hoofdstuk 3 gaan we hier dieper op in en bestuderen we de korte-termijn effecten van de boomkorvisserij. Dit deden we door met verschillende methodes de bodem te onderzoeken voor en na het vissen. Bodemonsters onthulden welke dieren er in de bodem leven; videobeelden welke dieren die op de bodem leven en een speciale fotocamera bracht het bodemprofiel (de bovenste ~15 cm) in kaart. Op deze manier kregen we een goed en compleet beeld van de zeebodem voor en na het vissen. De videobeelden voorafgaand aan het vissen toonden grote hoeveelheden kleine gaatjes in de bodem, wat de openingen zijn van ondergrondse holletjes van dieren die in de bodem leven. Deze aantallen waren direct na het vissen veel lager. Bovendien toonden bodemprofielfoto's dat er na het vissen een licht gekleurd laagje van fijn sediment boven op de bodem lag. Beide resultaten laten zien dat de boomkorvisserij de bodem egaliseert, waarbij ondergrondse holletjes worden dichtgemaakt. Enkele dagen na het vissen zat de bodem weer bijna net zo vol met gaatjes al voor het vissen. Uit de videobeelden en bodemonsters bleek dat het aantal dieren op en in de bodem sterk verminderd was na het vissen, en dat dit ook niet herstelde binnen enkele dagen. Daarnaast zagen we op de videobeelden dat er na het vissen veel minder dieren op de zeebodem rondliepen. Deze afname betrof voornamelijk de dieren op de bodem, en de kleine (jonge) dieren die vlak onder het bodemoppervlak leven. Er was nauwelijks een afname van de grotere dieren die dieper in de zeebodem leven en die met name verantwoordelijk zijn voor de gaatjes in de bodem. De invloed van de boomkorvisserij verschilt dus per diersoort en levensfase, waarbij sommige soorten beter bestand zijn tegen het vissen dan anderen.

De studie in hoofdstuk 3 laat het belang zien van gedetailleerde, ruimtelijke informatie over visserijmethodes en bodemleefgemeenschappen om de gevolgen van visserij op het bodemleven te kunnen inschatten. Daarom onderzochten we in hoofdstuk 2 de ruimtelijke verspreiding van 1) de boomkorvisserij op tong, 2) de boomkorvisserij op schol, en 3) de bordenvisserij op Noorse kreeft en platvis. De positie van vissersschepen wordt met satellieten geregistreerd, en het gebruikte vistuig wordt door de vissers geregistreerd in een logboek. De Nederlandse gegevens hebben wij vervolgens gebruikt om, voor de drie visserijtypen apart, zogenoemde visserij-hotspots te identificeren. Dit zijn locaties die voor 7 of 8 jaar binnen de 8-jarige studieperiode tot de top 1% meest beviste gebieden behoorden. Met andere woorden, deze hotspots zijn locaties die langdurig zeer intensief worden bevestigd. Daarnaast bepaalden we voor de gehele Noordzee de lokale omgevingsomstandigheden, zoals waterdiepte, gemiddelde bodemtemperatuur en zeebodemstructuur. Door deze te koppelen aan de locaties van de visserij-hotspots konden we vaststellen dat de omgeving van invloed was op de vislocaties. De visserijtypen bleken voorkeur te hebben voor bepaalde omstandigheden. Zo lagen de hotspots van de boomkorvisserij op tong voornamelijk in de zuidelijke Noordzee, specifiek in de dalen van grote zandbanken. Voor de boomkorvisserij op schol werden minder hotspots vastgesteld en kwam een minder duidelijk patroon in omstandigheden naar voren wat er op wijst dat deze visserij minder gebonden is aan specifieke omstandigheden. De hotspots van de bordenvisserij op Noorse kreeft en platvis lagen juist op plekken met modderige bodems in dieper water. De voorkeuren van visserijen voor specifieke omstandigheden zorgt ervoor dat visserij activiteit niet evenredig over de Noordzee verdeeld is. Hierdoor worden sommige omgevingen amper bevestigd, terwijl andere, geprefereerde omgevingen juist veel bevestigd worden. Omdat bodemleefgemeenschappen ook afhangen van omgevingsomstandigheden betekent dit dat ook de leefgemeenschappen een onevenredige visserijdruk kennen. Dit hoofdstuk laat zien dat het visserijbeleid de ruimtelijke verspreiding van visserij in acht moet nemen om te waarborgen dat leefgemeenschappen niet volledig worden bevestigd.

In hoofdstuk 4 gaan we dieper in op de ruimtelijke patronen van bodemleefgemeenschappen en visserij activiteiten. Hier definieerden we de bodemleefgemeenschap op drie functionele niveaus: vissen die op of vlak boven de bodem leven (bodemvis), ongewervelden die op de bodem leven (epifauna) en organismen die in de bodem leven (endobenthos). Voor elk functioneel niveau

zijn wetenschappelijke metingen beschikbaar die inzicht geven in de soortsaamenstelling op losse meetpunten verspreid over de Noordzee. Voor de bodemvissen werden bijvoorbeeld de gegevens van een monitoringsproject gebruikt dat een boomkor als onderzoeksmethode heeft. Meetpunten met overeenkomstige soortsaamenstellingen werden vervolgens gegroepeerd en geclassificeerd als dezelfde leefgemeenschap. Door de verschillende leefgemeenschappen te koppelen aan de plaatselijke omgevingsvariabelen kunnen we de ruimtelijke verspreiding van de leefgemeenschappen modelleren. Dit leverde ons drie gedetailleerde habitatkaarten op die de verspreiding van leefgemeenschappen voor bodemvis, epifauna en endobenthos over de gehele Noordzee laten zien. Daarnaast maakten we ook fysiotopenkaarten, die alleen gebaseerd zijn op gelijkenissen in omgevingsvariabelen. De ruimtelijke verdeling van de fysiotopen verschilt met die van de habitatkaarten en laat zien dat fysiotopenkaarten geen goede indicators zijn van bodemleefgemeenschappen. Ook hebben we de drie habitatkaarten vergeleken met de ruimtelijke verspreiding van internationale visserijactiviteit, windparken en natuurgebieden (Natura2000-gebieden). Hieruit blijkt dat menselijke activiteiten verschillen per habitat, en dat voornamelijk windparken en natuurgebieden vaak in dezelfde habitats liggen. De gepresenteerde habitatkaarten uit hoofdstuk 4 vergroten onze kennis over de ruimtelijke verspreiding van het bodemleven. Ook zijn de gevolgen van menselijke activiteiten op het lokale bodemleven beter in te schatten met deze kaarten, wat ten gunste komt aan een duurzaam beheer van de Noordzee.

Zandkokerwormriffen

Tijdens een van onze eerste expedities hebben we per toeval zandkokerwormriffen ontdekt op de Bruine Bank in de Nederlandse Noordzee (hoofdstuk 8). Zandkokerwormen zijn kleine wormen die van speeksel en zand een hard kokertje om zich heen bouwen ter bescherming. Als meerdere kokertjes tegen elkaar aan worden gebouwd ontstaat een rif. Andere soorten vinden een schuilplaats in dit rif, of kunnen zich vestigen op de harde kokertjes. Zandkokerwormen zijn dus biobouwers. Vergelijkingen van videobeelden op en naast de riffen lieten zien dat er op de riffen meer soorten leven, waaronder ook enkele soorten die bekend staan om hun voorkeur voor harde ondergronden.

In een vervolgstudie lieten we zien dat deze riffen weinig invloed lijken te hebben op soorten die in de bodem leven (hoofdstuk 9). Daarentegen lijkt het mobiele grotere leven op de zeebodem, zoals krabben en hondshaaien, te worden aangetrokken tot de riffen. We zagen rond de riffen een verhoogde soortenrijkdom en -dichtheid. Onze ontdekking van de riffen was extra verassend omdat er op de Bruine Bank ook veel gevestigd wordt met bodemberoerende technieken zoals de boomkor. Van de vier bezochte plekken lag het grootste rif op de plek met de laagste visserij inspanning (hoofdstuk 8). Dit suggereert dat bodemberoerende visserij schadelijk is voor de (vorming van de) riffen. Het is daarom waarschijnlijk dat de grotere riffen op delen van de zeebodem staan die 'per ongeluk' worden gemist bij het vissen. De videobeelden van de Bruine Bank lieten verder zien dat de zandkokerwormriffen vaak een fragmentarische verspreiding hebben. Kleine stukken rif werden afgewisseld met kale zandvlaktes. Hierbij leek het er meerdere keren op dat de riffen wat dieper lagen dan de kale zandbodem.

Bodemstructuren

De zeebodem van het Bruine Bank gebied is verre van vlak. Onder invloed van getijdestroming en golven zijn hier verschillende ritmische structuren ontstaan op de zeebodem. Het gebied is vernoemd naar de hoogste zandbank; de Bruine Bank. De zandbanken hebben een hoogte van 10-25 meter, en een onderlinge afstand van 5-10 kilometer. Daarnaast komen er in het gebied ook zandgolven en megaribbels voor. Zandgolven zijn 2-4 meter hoog en liggen 100-300 meter uit elkaar. Megaribbels hebben een hoogte van 0.5-1 meter en liggen 10-30 meter uit elkaar. Zandgolven en megaribbels zijn asymmetrisch, waarbij de ene helling lang en vlak is (loefzijde) en de andere helling kort en steil (lijzijde). Dergelijke structuren komen niet alleen voor in de Bruine Bank, maar vrijwel

overal ter wereld in zeeën met een zandbodem tot een diepte van 30-40 meter. Voor de Noordzee komt dit neer op het gehele zuidelijke deel en voor de kust boven de Waddeneilanden. In meerdere expedities hebben we aandacht besteed aan de effecten van dergelijke bodemstructuren op de bodemleefgemeenschappen.

Zo laten we met twee videotransecten zien dat zandgolven uit de kust bij Texel een behoorlijke invloed hebben op het bodemleven (hoofdstuk 5). Beide videotransecten gaan over een zandgolf heen, waardoor we een vergelijking konden maken tussen het dal en de top van de zandgolven. De videobeelden lieten zien dat er in het dal meer organismen op en in de bodem leven, waarbij we het aantal gaatjes in de zeebodem als maat nemen voor het aantal dieren in de bodem. Daarnaast toonden we aan dat er op de top zeer regelmatige zandribbels liggen, terwijl die in de dalen juist heel onregelmatig zijn of geheel ontbreken. Deze zandribbels zijn een goede indicator van de lokale bodemschuifspanning: de kracht waarmee de waterstroming aan de zeebodem 'trekt'. Onze videobeelden bewezen dus dat de bodemschuifspanning varieert over een zandgolf. Deze informatie kan vervolgens worden gebruikt om zandgolf-modellen te verbeteren, welke momenteel nog aannemen dat de bodemschuifspanning overal gelijk is. Zulke modellen worden veel gebruikt bij bouwprojecten in de kustzone, zoals bijvoorbeeld voor de aanleg van windparken.

In hoofdstuk 6 gaan we dieper in op de effecten van zeebodemstructuren op het bodemleven. In het Bruine Bank gebied verzamelden we akoestische gegevens met een multibeam, videotransecten, bodemprofielfoto's en bodemonsters. Hieruit werd duidelijk dat de zandbank kan worden opgedeeld in de drie sub-habitats 'top', 'helling' en 'dal'. De video's en bodemprofielen lieten grote verschillen zien tussen de top en de beide dalen van de zandbank. Op de top waren bijna geen organismen zichtbaar, en bestond de bodem eigenlijk alleen uit zand, terwijl er in de dalen veel meer organismen en (lege) schelpen zichtbaar waren. Ook bodemonsters van de drie sub-habitats toonden verschillende bodemleefgemeenschappen. Door de bodemonsters te linken aan de gedetailleerde dieptekaarten van de multibeam werd een ruimere interpretatie van de bodemonsters mogelijk. Zo werden bijvoorbeeld verschillen zichtbaar tussen de dalen en toppen van de veel kleinere zandgolven (2-4 meter hoog), vergelijkbaar met de grotere zandbank (10-25 meter hoog). Deze studie laat zien dat bodemstructuren, zelfs op zeer kleine schaal, bepalend kunnen zijn voor bodemgemeenschappen en dat het combineren van verschillende methoden zorgt voor een betere interpretatie van de bodemonsters.

Naast gedetailleerde dieptekaarten kan een multibeam ook inzicht geven in het type sediment op de zeebodem, door te kijken naar de backscatter: de intensiteit van de teruggekaatste geluidsgolven. In hoofdstuk 7 beschrijven we hoe we ruimtelijke patronen in de backscatter onderzoeken, en laten we zien dat die overeenkomen met megaribbels (0.5-1 meter hoog). In de dalen lag grover sediment, de toppen en de hellingen aan loefzijde bestonden uit fijner sediment en de steile hellingen aan lijzijde waren juist een mix van grof en fijn sediment. Bovendien bleek dat het akoestische signaal van grove sedimenten mogelijk ook samen hing met de aanwezigheid van zandkokerwormriffen. Deze data laten zien dat de bodemstructuur (megaribbels) het sedimenttype beïnvloed op een schaal van ongeveer 20-30 meter, iets waar tijdens het nemen van bodemonsters geen rekening mee wordt gehouden.

Zowel de akoestische gegevens als de videobeelden suggereerden dat de zandkokerwormriffen voornamelijk in de dalen van de megaribbels (0.5-1 meter hoog) voorkomen. In hoofdstuk 9 hebben we deze observatie in meer detail onderzocht en inderdaad, veel zandkokerwormriffen liggen in de dalen van de megaribbels. Waarom ze specifiek daar liggen is nog steeds onbekend, al geven we in hoofdstuk 8 een mogelijke verklaring. De structuur van de megaribbels zou mogelijk bescherming kunnen bieden tegen visserij. De megaribbels hebben een oost-west oriëntatie. De meeste vissersschepen in het gebied vissen juist loodrecht op de megaribbels, waardoor het zou kunnen dat de visnetten de bodem niet of minder sterk raken in de dalen met een grotere overlevingskans als gevolg.

Conclusies, implicaties en aanbevelingen

In dit proefschrift onderzoek ik hoe bodemleefgemeenschappen in de Noordzee beïnvloed worden door zowel natuurlijke als menselijke verstoringen. De bevinding dat relatief kleine bodemstructuren zoals megaribbels en zandgolven een grote invloed hebben op het bodemleven heeft een aantal belangrijke consequenties. Niet alleen is het in acht nemen van bodemstructuren van belang voor goede monitoring en beheer van bodemleefgemeenschappen. Het laat ook zien dat gevolgen van bodemberoerende visserij op een dergelijke kleine schaal moet worden bestudeerd. Hiervoor is het noodzakelijk om zeer nauwkeurig en met een hoge dekkinggraad te kunnen bemonsteren. Echter beperken de hoge kosten het aantal metingen, en daarmee ook de ruimtelijke schaal. Bovendien hebben veel bemonstermethodes een onzekerheid in hun exacte locatie, omdat bemonstering veelal gebeurt door het meetapparaat op zee overboord te zetten. De exacte locatie op de bodem kan hierdoor beïnvloed worden door aanwezige stroming. Het was voor ons bijvoorbeeld onmogelijk om de exacte locatie van de beelden van onze sleepcamera te bepalen en direct te koppelen aan gedetailleerde dieptekaarten. Terwijl juist het combineren van verschillende meettechnieken een veel completer beeld geeft van het bestudeerde gebied. In de discussie (hoofdstuk 10) doe ik daarom enkele aanbevelingen die de huidige monitoring programma's kunnen verbeteren. Daarnaast beschrijf ik daar de implicaties van dit proefschrift voor duurzaam visserijbeheer. Ik beargumenteer dat de huidige inschattingmethoden voor de gevolgen van bodemberoerende visserij kunnen worden verbeterd door visserijactiviteit en bodemleven op een fijnere schaal aan elkaar te koppelen, en door kennis van de lokale bodemleefgemeenschap mee te nemen.

Chapter 1

General introduction

Benthic communities

The seafloor is home to a large diversity of organisms. All organisms that live within, on top, or close to the seafloor are called benthic organisms. This is often further divided into the endobenthos (invertebrates within the seafloor), epifauna (invertebrates on top of the seafloor), and demersal fish (fish living near the seafloor)¹. These organisms are spatially structured in benthic communities, with their boundaries mostly determined by environmental conditions like sediment type and water depth^{2–5}.

Water depth is an important variable that structures benthic communities, as it affects a range of other environmental variables^{1,6}. Deep waters often provide a stable habitat for species, because the seafloor is hardly affected by wind-driven surface waves and tidal currents. Such waters are often stratified and allow small, dissolved particles to settle, resulting in a seafloor with fine sediments and high organic content^{7–10}. Hence, a gradient from fine, muddy particles to coarser sand grains is observed from deeper to shallower waters. Rocky and gravelly substrates, on the other hand, generally have a geological origin independent of the water depth¹⁰. More environmental variables are important in explaining species distributions, such as salinity and temperature ranges^{1,11,12}. Freshwater inflow from rivers results in less saline conditions near the coasts. These coastal waters are also more affected by terrestrial temperatures. The sun heats surface waters but does not reach water at greater depths. The resulting stratification leads to a rather constant temperature¹¹, and also affects food availability for the benthic organisms. In stratified areas, primary productivity is restricted to the upper layer, limiting food availability for the benthic community⁹.

At smaller-scales, the presence of specific organisms may structure the prevailing benthic community as well. So-called ecosystem engineers are organisms that modify their environment to such an extent that environmental conditions and/or resources are altered for other species¹³. A key marine example of an ecosystem engineer is seagrass^{14,15}, which beds provide shelter against predation and currents¹⁶, attenuate waves¹⁷, trap sediments¹⁸, and provide additional food sources¹⁹. Species that construct biogenic reefs are also considered ecosystem engineers, as these reefs stabilize the sediment²⁰, offer refuge to currents and predators^{21,22}, and provide suitable (hard) substrate for settlement²³. Leading examples of these marine biogenic reef builders are coral reefs²², however, numerous reef-building species can be found in temperate waters such as cold water corals²⁴, rhodoliths²⁵, various shellfishes^{26–28}, and tubeworms^{29,30}.

Disturbance regimes

The interplay of water depth, sediment type, tidal currents, and wind-driven waves define the natural disturbance regime of a habitat, which represents the frequency of natural seafloor disturbances. Wind-driven waves do not reach the seafloor in waters deeper than about 30 m on average. Prevailing tidal currents are similarly dampened in deeper waters, as the same volume of water is distributed over a larger area. Hence, shallow waters generally have a higher natural disturbance regime^{7,8}.

In the current Anthropocene, humans are influencing marine ecosystems to such an extent that very few unimpacted areas are remaining³¹, especially on the continental shelves. Hence, most benthic communities are subjected to different anthropogenic disturbances, in addition to their natural disturbance regime. Such anthropogenic disturbance gradients range from single events to continuous disturbances, depending on the frequency, intensity and extent of anthropogenic activities. Dominant source of anthropogenic disturbance is demersal fishing^{31,32}, which impacts benthic communities in various ways. Targeted species are extracted from the ecosystem, while undersized target species, species with low commercial value, and benthic invertebrates are discarded^{33–35}. Discards generally have low survival probability estimates^{36–38}. All demersal fisheries encompass gears that are actively trawled over the seafloor, causing physical damage to benthic

communities^{39–42}, with especially large impact for emergent structures such as biogenic reefs^{34,43}. Frequent fishing activity results in a homogenization of the seafloor⁴⁴, while sediment types are indirectly altered due to displacement and resuspension processes⁴¹. Locations subjected to frequent bottom trawling activity can hence be classified as areas with high anthropogenic disturbance regimes.

Dredging, sediment extraction and sand nourishments are also anthropogenic activities with large effects on seafloor communities^{45,46}. Dredging and extraction activities completely remove the upper layer of the seafloor and all its inhabitants from an area. Sand nourishments, on the other hand, deposits a layer of sand on top of the seafloor, smothering all prevailing life. They are probably best described as intense, but local disturbances⁴⁷ as they are thought to be limited to the area directly impacted^{45,48,49}. For artificial offshore structures, such as oil and gas stations and offshore wind farms, it is more difficult to apply this anthropogenic disturbance gradient. Apart from ecosystem effects caused by the permanent hard-substrate structures they introduce into the ecosystem^{50–53}, physical disturbance is thought to be limited to the construction phase⁵⁴. In fact, demersal fisheries are excluded from offshore wind farms⁵⁵, which potentially result in a lower anthropogenic disturbance regime^{50,56}.

Resilience: resistance and recovery

Each benthic community responds differently to disturbances, based on its resilience. The exact definition of resilience is currently still debated^{57,58}, but is generally related to community resistance and its capability to recover (Fig. 1)⁵⁹. Typically, disturbances impact benthic communities by the reduction of (certain) species or species richness in either abundance or biomass^{60–62}. In this, resistance describes the ability of the community to withstand disturbances without being impacted⁵⁹. One could see this as a threshold of disturbance needed to (negatively) affect the community, for which more resistant communities have a higher threshold. Recovery is the subsequent process in which an impacted community returns to the pre-impacted state^{61,63,64}. In this thesis, the resistance and recovery potential of a community determine its resilience, with the less resilient communities being those that have a low resistance and a long recovery (Fig. 1).

Figure 1. Different responses of a benthic community to a disturbing event (dashed line) for a) a high-resistant community (red), b) a low-resistant, fast-recovering community (blue) and c) a low-resistant, long-recovering community (green).

In high natural disturbance regimes, benthic communities have developed various traits to survive the frequent natural disturbances^{60,65–67}. When stable rocky substrates are available, species prevent dislodging by firm attachment to the substrate, whereas high mobility capacities allow species to escape disturbances in soft-substrate environments, either by swimming or burrowing^{6,12,68}. The high disturbance regime also requires species to be opportunistic in their food intake, stimulating both predatory and scavenging species⁶⁷. Traits supporting a fast reproduction enable species to quickly recover after disturbances, like short life spans, early maturation and smaller body sizes^{60,69,70}. In low natural disturbance habitats, species have developed completely different traits. Sessile, filter-feeding, or surface deposit-feeding species with slow reproduction systems are more common. These species generally have longer life spans, late maturation and larger body sizes^{6,60,67,69,70}. Biogenic reef building organisms, however, may pose an exemption to this contradistinction. Several biogenic reef building species can establish in areas with high natural disturbance regimes, due to their engineering effects that alter local conditions. However, even species adjusted to such high disturbance regime are generally low-resistant to physical disturbances, due to their emergent structures^{34,43,65,70}. Together with the generally long time required for constructing a reef (recovery), this makes them highly vulnerable to anthropogenic disturbances^{70–72}.

In most cases, however, the disturbance impact is similar for natural and anthropogenic disturbances⁶⁰. Therefore, large impacts are expected when high anthropogenic disturbances regimes are imposed in areas with low natural disturbance regimes^{61,69,73}. Because demersal fisheries are so widespread, they are the main cause of such high anthropogenic disturbance regimes in areas with low natural disturbance regimes^{72,73}. As a result, high-resilient species can dominate communities that naturally would consist of low-resilient species, while its original low-resilient species disappear completely^{74,75} (Fig. 2). A good spatial management of anthropogenic disturbances is therefore essential to ensure persistence of low-resilient habitats^{72,73}.

Figure 2. Low-resilient communities (red) dominate in low disturbance regimes, as high-resilient communities (black) require disturbances to maintain. Under a high disturbance regime, high-resilient communities thrive while low-resilient communities degrade and ultimately disappear.

Marine spatial planning

Marine Spatial Planning (MSP) comprises all spatial management of marine ecosystems. Good MSP balances different societal interests such as nature protection, transport, and the exploitation of various resources (wind, oil & gas, sediment, food). Sustainable use ensures that marine resources are not depleted, while overall ecosystem health and functioning is safeguarded^{76–79}. Under the European Marine Strategy Framework Directive (MSFD), for instance, nations are obliged to ensure a ‘good status’ of their marine habitats and resources. This ecological status is assessed based on eleven descriptors, which describe the desired ecological functioning of the system and levels of anthropogenic influences^{80–82}. Ecological functioning is dominantly described by descriptors 1, 4, and 6, which state that biodiversity of both resources and habitats should be maintained (descriptor 1); all elements of the food web should be kept at levels that enable long-term abundance and reproduction of the species (descriptor 4); and seafloor integrity levels should safeguard the structure and functioning of benthic ecosystems (descriptor 6).

To enable good MSP, a detailed spatial overview and alignment of anthropogenic activities and benthic communities is required^{3,76,78}. Moreover, a good assessment of the vulnerability of different communities to anthropogenic activities is needed^{83–85}. Both requirements are challenged by two main factors. Making a fair balance between different societal interests is difficult due to the differences in units of value. For example, biodiversity is often seen as an intrinsic, non-monetary value, whereas commercial exploitation yields is more easily economically valued⁷⁶. This is now often solved by the elaboration and analyses of several scenarios, which can function as guidelines for management^{86–88}. Such scenarios can for instance differ in their balance between nature conservation and economic profit, enabling a cost-benefit analysis of the different interests. Secondly, knowledge on both the spatial distribution and the functioning of benthic communities is limited. It is costly to gather seafloor data at open seas, due to operation costs of larger vessels and technical difficulties of sampling under water^{89–91}. The spatial distribution of environmental variables obtained by modelling, acoustic methods or remote sensing are therefore often used as proxies of benthic community distribution^{3,5,92}.

The North Sea

In this thesis, I focus on the southern North Sea, a coastal sea on the European Continental Shelf, enclosed by Norway, Denmark, Germany, the Netherlands, Belgium, France, and Great Britain (Fig. 3). It is connected to the Atlantic Ocean through the English Channel in the south, and in the north to the Norwegian Sea. The North Sea is a shallow shelf sea, that is often classified into 2 sections based on depth: shallow (<50 m), and deep (>50 m)^{1,6}. Centrally located between Denmark and Great Britain, lies the Dogger Bank; the largest sandbank in the North Sea. This sandbank forms the border between the deep parts in the northwest, and the shallow parts in the southeast.

In the deep part, Atlantic water inflow has two main directions; one east of the Shetland Islands along the deep Norwegian Trench, and the other west of the Shetland Islands along the East Scottish coast⁹³. Based on these major currents, the deep part can be subdivided in a shallower (50–100 m) and a deeper part (>100 m) in the west and east respectively. Atlantic inflow of the shallow part is coming through the English Channel. Due to the relatively narrow passage of the Dover Straits and the shallow depth, strong tidal currents are created^{7,8}. Because of this high natural disturbance regime, the sandy bottom is shaped into multiple morphological bedforms, of which the large-scale sandbanks can easily be observed on the bathymetry map^{94,95}. Such sandbanks have amplitudes of ~10–20 meters, and a wavelength of 5–10 km. Multiple types of smaller sand waves are present as well^{96,97}. Sand waves, for instance, are usually ~200 m apart and have height differences of several meters. The smaller megaripples have wavelengths of ~10 m and amplitudes of ~0.5–1 m. The shallow part further covers the German Bight, the Central Oyster Grounds and the Dogger Bank. The waters between the Dogger Bank and the German and Dutch borders are called the German

Bight. This includes an area often referred to as the Central Oyster Grounds, which indicate the relatively deep, stable, and muddy area east of the Dogger Bank. They are named after the large oyster beds that used to be here⁹⁸.

Figure 3. The Greater North Sea, as defined by the International Council for the Exploitation of the Sea (ICES). The map shows overall bathymetry, two-letter codes represent surrounding countries, and some areas of interest are highlighted. Hatched lines represent the borders of the national waters.

The North Sea is intensively used as multiple anthropogenic activities are taking place. Some of the worlds' largest ports are located around the North Sea, resulting in busy shipping lanes⁹⁹. It houses many offshore installations for oil and gas harvesting¹⁰⁰ and under the current energy transition, plans are being developed for vast offshore wind farms¹⁰¹. Still, demersal fisheries is the most wide-spread anthropogenic activity that affects the seafloor, with high concentrations in the shallow, southern part of the North Sea and the Kattegat and Skagerrak¹⁰². The Habitats¹⁰³ and Bird¹⁰⁴ Directives have resulted in the designation of multiple Natura 2000 areas. These specific areas aim to protect specific bird species (for instance the common guillemot in the Frisian Front area) or habitat types (e.g., habitat type H1110 'Submerged sandbanks' in the Dogger Bank area). In addition, the European MSFD requires a good status of all benthic habitats and communities. Hence, a careful balance between the various societal interests should be made.

Objective and thesis outline

To enable a balance in societal interests in the North Sea, this thesis aims to improve the spatial understanding of the interaction between habitat disturbance regimes and benthic communities in the North Sea. It therefore focuses on the relationships between natural and anthropogenic disturbance regimes and benthic communities.

Firstly, the spatial distribution of demersal fisheries and their impact on the benthic community were studied. In **Chapter 2**, we investigated the structuring effects of abiotic variables on the spatial distribution of demersal fisheries. For this, environmental conditions were compared between satellite-derived hotspots of three distinct types of Dutch demersal fisheries. **Chapter 3** studies the short-term effects of a single trawl event on the benthic community. Multiple measuring techniques were combined, enabling a comprehensive assessment. Then, based on the relation between environmental conditions and observed benthic communities, full-scale, high-resolution habitat maps were produced for the North Sea endobenthos, epifauna and demersal fish communities in **Chapter 4**.

Sandy-bottom habitats with high dynamic regimes are known to shape seabed morphologies at multiple scales. In the southern North Sea, tidal currents have resulted in tidal ridges and sand waves. However, the impact of these morphologies on benthic communities is sparsely documented. Using video-transects only, the spatial distribution of benthic communities over sand waves was investigated in **Chapter 5**. A more comprehensive approach is presented in **Chapter 6**, in which acoustic data, video transects and boxcore data were combined to investigate how both the functional and taxonomic composition of benthic communities are affected by both tidal ridges and sand waves. Morphological structures are shaped under the natural disturbance regime, but they potentially also affect some of the local abiotic variables. **Chapter 7** describes the effects of small-scale megaripple structures on prevailing sediment and benthic community, based on acoustic remote sensing.

Biogenic reef structures of *Sabellaria spinulosa* were encountered in an area with a high natural disturbance regime. Observations indicated that the multi-scale seafloor morphology as studied in **Chapters 5-7** played a crucial role in the persistence of these *Sabellaria* reefs. The discovery of these reefs and the hypothesized facilitating effects of the morphological structures within the area are described in **Chapter 8**. **Chapter 9** elaborated on this interplay between morphological structures and *Sabellaria* reefs, and presented a more thorough investigation on the conservation value of the patchy distribution of the reefs.

Finally, in **Chapter 10**, I elaborate on the coherence of the main findings as presented in the previous chapters. I further discuss methodological challenges experienced during this thesis and make recommendations to improve future benthic monitoring. Finally, I conclude with the conservation implications, including my personal point of view on marine management.

Box 1. The DISCLOSE project

The research presented in this thesis is part of the DISCLOSE-project. DISCLOSE is an acronym for “**D**istribution, **S**truCture and functioning of **L**ow-resilience benthic communities and habitats of the Dutch North **S**ea” and is a research collaboration between Delft University of Technology (TU), the University of Groningen (UG), the Royal Netherlands Institute for Sea Research (NIOZ) and the North Sea Foundation (NSF). Its main aim is to map the habitats of the North Sea, with special attention to the dispersal, structure and functioning of vulnerable seafloor communities. A combination of spatially hierarchical methods is applied, from large-scale remote acoustic sensing (TU), to middle-scale video techniques (UG), and to small-scale functional trait analyses of benthic communities (NIOZ) (Fig. B1.1). The North Sea Foundation safeguards the societal relevance of research questions during the project, and disseminates resulting research output to policymakers, NGO’s and other stakeholders of the North Sea. With this multidisciplinary approach, DISCLOSE intends to extrapolate the detailed findings of community functioning at the small-scale to full-scale habitat maps, based on the knowledge gathered at the middle and large scales. Within DISCLOSE the UG aims to improve knowledge about the spatial distribution of the various benthic habitats in the North Sea and their spatial cohesion.

Figure B1.1. Schematic drawing of the DISCLOSE approach, with a) large-scale remote acoustic sensing, b) mid-scale video techniques and c) small-scale functional trait analysis of benthic communities.

References

1. Reiss, H. *et al.* Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* **67**, 278–293 (2010).
2. Vasquez, M. *et al.* Broad-scale mapping of seafloor habitats in the north-east Atlantic using existing environmental data. *J. Sea Res.* **100**, 120–132 (2015).
3. Andersen, J. H. *et al.* European broad-scale seabed habitat maps support implementation of ecosystem-based management. *Open J. Ecol.* **08**, 86–103 (2018).
4. Davies, C. E., Moss, D. & Hill, M. O. *EUNIS Habitat Classification Revised 2004*. European Environment Agency. European Topic Centre on Nature Protection and Biodiversity (2004).
5. McArthur, M. A. *et al.* On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuar. Coast. Shelf Sci.* **88**, 21–32 (2010).
6. Callaway, R. *et al.* Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES J. Mar. Sci.* **59**, 1199–1214 (2002).
7. Aldridge, J. N., Parker, E. R., Bricheno, L. M., Green, S. L. & van der Molen, J. Assessment of the physical disturbance of the northern European Continental Shelf seabed by waves and currents. *Cont. Shelf Res.* **108**, 121–140 (2015).
8. Bricheno, L. M., Wolf, J. & Aldridge, J. Distribution of natural disturbance due to wave and tidal bed currents around the UK. *Cont. Shelf Res.* **109**, 67–77 (2015).
9. van Leeuwen, S., Tett, P., Mills, D. & van der Molen, J. Stratified and nonstratified areas in the North Sea: Long-term variability and biological and policy implications. *J. Geophys. Res. Ocean.* **120**, 4670–4686 (2015).
10. Stephens, D. & Diesing, M. Towards quantitative spatial models of seabed sediment composition. *PLoS One* **10**, (2015).
11. Jones, N. S. Marine bottom communities. *Biol. Rev.* **25**, 283–313 (1950).
12. Künitzer, A. *et al.* The benthic infauna of the North Sea: Species distribution and assemblages. *ICES J. Mar. Sci.* **49**, 127–143 (1992).
13. Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
14. van der Heide, T. *et al.* Ecosystem engineering by seagrasses interacts with grazing to shape an intertidal landscape. *PLoS One* **7**, 14–16 (2012).
15. Maxwell, P. S. *et al.* The fundamental role of ecological feedback mechanisms in seagrass ecosystems - A review. *Biol. Rev.* (2016).
16. Lannin, R. & Hovel, K. Variable prey density modifies the effects of seagrass habitat structure on predator-prey interactions. *Mar. Ecol. Prog. Ser.* **442**, 59–70 (2011).
17. Paul, M., Bouma, T. J. & Amos, C. L. Wave attenuation by submerged vegetation: Combining the effect of organism traits and tidal current. *Mar. Ecol. Prog. Ser.* **444**, 31–41 (2012).
18. van der Heide, T., van Nes, E. H., van Katwijk, M. M., Olff, H. & Smolders, A. J. P. Positive feedbacks in seagrass ecosystems - Evidence from large-scale empirical data. *PLoS One* **6**, e16504 (2011).
19. van der Zee, E. M. *et al.* How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proc. R. Soc. B.* **283**, 20152326 (2016).
20. Callaway, R. *et al.* Ephemeral bio-engineers or reef-building polychaetes: How stable are aggregations of the tube worm *Lanice conchilega* (Pallas, 1766)? *Integr. Comp. Biol.* **50**, 237–250 (2010).
21. Coni, E. O. C. *et al.* An evaluation of the use of branching fire-corals (*Millepora spp.*) as refuge by reef fish in the Abrolhos Bank, eastern Brazil. *Environ. Biol. Fishes* **96**, 45–55 (2012).
22. Ferrario, F. *et al.* The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat. Commun.* **5**, 3794 (2014).
23. Coolen, J. W. P. *et al.* Reefs, sand and reef-like sand: A comparison of the benthic biodiversity of habitats in the Dutch Borkum Reef Grounds. *J. Sea Res.* **103**, 84–92 (2015).
24. Biber, M. F. *et al.* Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. *Deep. Res. Part II Top. Stud. Oceanogr.* **99**, 134–145 (2014).
25. Chimienti, G. *et al.* Rhodolith beds heterogeneity along the Apulian Continental Shelf (Mediterranean sea). *J. Mar. Sci. Eng.* **8**, 1–20 (2020).
26. van der Zee, E. M. *et al.* Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. *Ecosystems* **15**, 664–673 (2012).
27. Lenihan, H. S. Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecol. Monogr.* **69**, 251–275 (1999).
28. Rees, E. I. S., Sanderson, W. G., Mackie, A. S. Y. & Holt, R. H. F. Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea: III. Crevice, sediment infauna and epifauna from targeted cores. *J. Mar. Biol. Assoc. UK* **88**, 151–156 (2008).
29. Rabaut, M., Vincx, M. & Degraer, S. Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. *Helgol. Mar. Res.* **63**, 37–46 (2009).
30. Hendrick, V. J. & Foster-Smith, R. L. *Sabellaria spinulosa* reef: a scoring system for evaluating 'reefiness' in the context of the Habitats Directive. *J. Mar. Biol. Assoc. UK* **86**, 665–677 (2006).
31. Halpern, B. S. *et al.* A global map of human impact on marine ecosystems. *Science*. **319**, 948–953 (2008).
32. Amoroso, R. O. *et al.* Bottom trawl fishing footprints on the world's continental shelves. *Proc. Natl. Acad. Sci.* **115**, 201802379 (2018).
33. Catchpole, T. L., Frid, C. L. J. & Gray, T. S. Discards in North Sea fisheries: Causes, consequences and solutions. *Mar. Policy* **29**, 421–430 (2005).
34. de Groot, S. J. The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Manag.* **9**, 177–190 (1984).
35. Heath, M. R. & Cook, R. M. Hind-casting the quantity and composition of discards by mixed demersal fisheries in the North Sea. *PLoS One* **10**, 1–35 (2015).
36. Depestele, J., Desender, M., Benoît, H. P., Polet, H. & Vincx, M. Short-term survival of discarded target fish and non-target invertebrate species in the 'eurocutter' beam trawl fishery of the southern North Sea. *Fish. Res.* **154**, 82–92

- (2014).
37. Kaiser, M. J. & Spencer, B. E. Survival of by-catch from a beam trawl. *Mar. Ecol. Prog. Ser.* **126**, 31–38 (1995).
 38. van der Reijden, K. J. *et al.* Survival of undersized plaice (*Pleuronectes platessa*), sole (*Solea solea*), and dab (*Limanda limanda*) in North Sea pulse-trawl fisheries. *ICES J. Mar. Sci.* **74**, 1672–1680 (2017).
 39. Depestele, J. *et al.* Measuring and assessing the physical impact of beam trawling. *ICES J. Mar. Sci.* **73**, 15–26 (2015).
 40. Eigaard, O. R. *et al.* Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J. Mar. Sci.* **73**, 27–43 (2015).
 41. O'Neill, F. G. & Ivanovic, A. The physical impact of towed demersal fishing gears on soft sediments. *ICES J. Mar. Sci.* **73**, i5–i14 (2016).
 42. Hiddink, J. G. *et al.* Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can. J. Fish. Aquat. Sci.* **63**, 721–736 (2006).
 43. Jennings, S. & Kaiser, M. J. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* **34**, 201–352 (1998).
 44. Handley, S. J. *et al.* The importance of benchmarking habitat structure and composition for understanding the extent of fishing impacts in soft sediment ecosystems. *J. Sea Res.* **86**, 58–68 (2014).
 45. de Jong, M. F., Baptist, M. J., Lindeboom, H. J. & Hoekstra, P. Short-term impact of deep sand extraction and ecosystem-based landscaping on macrozoobenthos and sediment characteristics. *Mar. Pollut. Bull.* **97**, 294–308 (2015).
 46. de Boer, W. P., Roos, P. C., Hulscher, S. J. M. H. & Stolk, A. Impact of mega-scale sand extraction on tidal dynamics in semi-enclosed basins. An idealized model study with application to the southern North Sea. *Coast. Eng.* **58**, 678–689 (2011).
 47. de Jong, M. F. The ecological effects of deep sand extraction on the Dutch Continental Shelf. Implications for future sand extraction. PhD Thesis. (Wageningen University & Research, 2016).
 48. de Jong, M. F. *et al.* Ecosystem-based design rules for marine sand extraction sites. *Ecol. Eng.* **87**, 271–280 (2016).
 49. van Dalfsen, J. A. *et al.* Differential response of macrozoobenthos to marine sand extraction in the North Sea and the Western Mediterranean. *ICES J. Mar. Sci.* **57**, 1439–1445 (2000).
 50. Lindeboom, H. J. *et al.* Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. *Environ. Res. Lett.* **6**, 1–13 (2011).
 51. Stenberg, C. *et al.* Long-term effects of an offshore wind farm in the North Sea on fish communities. *Mar. Ecol. Prog. Ser.* **528**, 257–265 (2015).
 52. Coolen, J. North Sea Reefs. Benthic biodiversity of artificial and rocky reefs in the southern North Sea. PhD Thesis. (Wageningen University and Research, 2017).
 53. Coates, D. A., Deschutter, Y., Vincx, M. & Vanaverbeke, J. Enrichment and shifts in macrobenthic assemblages in an offshore wind farm area in the Belgian part of the North Sea. *Mar. Environ. Res.* **95**, 1–12 (2014).
 54. Coates, D. A., van Hoey, G., Colson, L., Vincx, M. & Vanaverbeke, J. Rapid macrobenthic recovery after dredging activities in an offshore wind farm in the Belgian part of the North Sea. *Hydrobiologia* **756**, 3–18 (2015).
 55. Bergman, M. J. N., Ubels, S. M., Duineveld, G. C. A. & Meesters, E. W. G. Effects of a 5-year trawling ban on the local benthic community in a wind farm in the Dutch coastal zone. *ICES J. Mar. Sci.* **72**, 962–972 (2015).
 56. Kamermans, P. *et al.* Offshore wind farms as potential locations for flat oyster (*Ostrea edulis*) restoration in the Dutch North Sea. *Sustainability* **10**, (2018).
 57. Levin, S. A. & Lubchenco, J. Resilience, robustness, and marine ecosystem-based management. *BioScience* vol. 58 27–32 (2008).
 58. Gunderson, L. H. Ecological Resilience—In Theory and Application. *Annu. Rev. Ecol. Syst.* **31**, 425–439 (2000).
 59. Grimm, V. & Wissel, C. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* **109**, 323–334 (1997).
 60. van Denderen, P. D. *et al.* Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar. Ecol. Prog. Ser.* **541**, 31–43 (2015).
 61. Hiddink, J. G. *et al.* Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci.* 1–6 (2017).
 62. Kaiser, M. J. *et al.* Global analysis of response and recovery of benthic biota to fishing. *Mar. Ecol. Prog. Ser.* **311**, 1–14 (2006).
 63. Dernie, K. M., Kaiser, M. J., Richardson, E. A. & Warwick, R. M. Recovery of soft sediment communities and habitats following physical disturbance. *J. Exp. Mar. Bio. Ecol.* **285–286**, 415–434 (2003).
 64. Lambert, G. I., Jennings, S., Kaiser, M. J., Davies, T. W. & Hiddink, J. G. Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. *J. Appl. Ecol.* **51**, 1326–1336 (2014).
 65. Hiddink, J. G., Jennings, S. & Kaiser, M. J. Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. *J. Appl. Ecol.* **44**, 405–413 (2007).
 66. Szostek, C. L., Murray, L. G., Bell, E., Rayner, G. & Kaiser, M. J. Natural vs. fishing disturbance: drivers of community composition on traditional king scallop, *Pecten maximus*, fishing grounds. *ICES J. Mar. Sci.* **73**, 70–83 (2016).
 67. Bolam, S. G. *et al.* Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar. Environ. Res.* **126**, 1–13 (2017).
 68. Heip, C. H. R. *et al.* The benthic communities of the North Sea: a summary of the results of the North Sea benthos survey. *ICES Coop. Res. Report.* **190**, 148–175 (1992).
 69. Rijnsdorp, A. D. *et al.* Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol. Appl.* **28**, 1302–1312 (2018).
 70. Kaiser, M. J., Hormbrey, S., Booth, J. R., Hinz, H. & Hiddink, J. G. Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. *J. Appl. Ecol.* **55**, 1060–1070 (2018).
 71. Fariñas-Franco, J. M. *et al.* Marine Strategy Framework Directive Indicators for Biogenic Reefs formed by *Modiolus modiolus*, *Mytilus edulis* and *Sabellaria spinulosa*. Part 1: Defining and validating the indicators. *JNCC Report* vol. 523 (2014).
 72. Clark, M. R. *et al.* The impacts of deep-sea fisheries on benthic communities: A review. *ICES J. Mar. Sci.* **73**, 51–69 (2016).
 73. Watling, L. & Norse, E. A. Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conserv. Biol.* **12**, 1180–1197 (1998).
 74. Kaiser, M. J., Ramsay, K., Richardson, C. A., Spence, F. E. & Brand, A. R. Chronic fishing disturbance has changed shelf sea

- benthic community structure. *J. Anim. Ecol.* **69**, 494–503 (2000).
75. Tillin, H. M., Hiddink, J. G., Jennings, S. & Kaiser, M. J. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar. Ecol. Prog. Ser.* **318**, 31–45 (2006).
 76. White, C., Halpern, B. S. & Kappel, C. V. Ecosystem service tradeoff analysis reveals the value of marine spatial planning for multiple ocean uses. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 4696–4701 (2012).
 77. Douvère, F. & Ehler, C. N. New perspectives on sea use management: Initial findings from European experience with marine spatial planning. *J. Environ. Manage.* **90**, 77–88 (2009).
 78. Schiele, K. S., Darr, A. & Zettler, M. L. Verifying a biotope classification using benthic communities - An analysis towards the implementation of the European Marine Strategy Framework Directive. *Mar. Pollut. Bull.* **78**, 181–189 (2014).
 79. Gilbert, A. J. *et al.* Marine spatial planning and good environmental status: a perspective on spatial and temporal dimensions. *Ecol. Soc.* **20**, 64 (2015).
 80. Gilbert, A. J., McQuatters-Gollop, A., Langmead, O., Mee, L. & Vermaat, J. Visions for the North Sea: The societal dilemma behind specifying good environmental status. *Ambio* **44**, 142–153 (2015).
 81. Borja, Á., Elliott, M., Carstensen, J., Heiskanen, A. S. & van de Bund, W. Marine management - Towards an integrated implementation of the European marine strategy framework and the water framework directives. *Mar. Pollut. Bull.* **60**, 2175–2186 (2010).
 82. European Commission. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Official Journal of the European Union* vol. 164 19–40 (2008).
 83. Pitcher, C. R. *et al.* Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. *Methods Ecol. Evol.* **8**, 472–480 (2017).
 84. Rijsdorp, A. D. *et al.* Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. *ICES J. Mar. Sci.* **73**, 127–138 (2015).
 85. Kaiser, M. J. *et al.* Prioritization of knowledge-needs to achieve best practices for bottom trawling in relation to seabed habitats. *Fish Fish.* 1–27 (2015).
 86. Jongbloed, R. H., van der Wal, J. T. & Lindeboom, H. J. Identifying space for offshore wind energy in the North Sea. Consequences of scenario calculations for interactions with other marine uses. *Energy Policy* **68**, 320–333 (2014).
 87. Gusatu, L. F., Yamu, C., Zuidema, C. & Faaij, A. A spatial analysis of the potentials for offshore wind farm locations in the North Sea region: Challenges and opportunities. *ISPRS Int. J. Geo-Information* **9**, (2020).
 88. Matthias, V. *et al.* The impact of shipping emissions on air pollution in the greater North Sea region - Part 2: Scenarios for 2030. *Atmos. Chem. Phys.* **16**, 759–776 (2016).
 89. Ware, S. & Downie, A. L. Challenges of habitat mapping to inform marine protected area (MPA) designation and monitoring: An operational perspective. *Mar. Policy* **111**, 103717 (2020).
 90. Brown, C. J., Smith, S. J., Lawton, P. & Anderson, J. T. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast. Shelf Sci.* **92**, 502–520 (2011).
 91. van Rein, H. B., Brown, C., Quinn, R. & Breen, J. A review of sublittoral monitoring methods in temperate waters: A focus on scale. *Underw. Technol.* **28**, 99–113 (2009).
 92. Pitcher, C. R. *et al.* Exploring the role of environmental variables in shaping patterns of seabed biodiversity composition in regional-scale ecosystems. *J. Appl. Ecol.* **49**, 670–679 (2012).
 93. Turrell, W. R. New hypotheses concerning the circulation of the northern north sea and its relation to north sea fish stock recruitment. *ICES J. Mar. Sci.* **49**, 107–123 (1992).
 94. Knaapen, M. A. F. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo-Marine Lett.* **29**, 17–24 (2009).
 95. van Dijk, T. A. G. P. *et al.* Benthic habitat variations over tidal ridges, North Sea, The Netherlands. In *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
 96. Knaapen, M. A. F., Hulscher, S. J. M. H., De Vriend, H. J. & Stolk, A. A new type of sea bed waves. *Geophys. Res. Lett.* **28**, 1323–1326 (2001).
 97. Terwindt, J. H. J. Sand waves in the southern bight of the North Sea. *Mar. Geol.* **10**, 51–67 (1971).
 98. Olsen, O. T. *The Piscatorial Atlas of the North Sea, English and St. Georges Channels.* (Taylor and Francis, Red Lion Court, Fleet Street EC., 1883).
 99. Aulinger, A. *et al.* The impact of shipping emissions on air pollution in the greater North Sea region - Part 1: Current emissions and concentrations. *Atmos. Chem. Phys.* **16**, 739–758 (2016).
 100. OSPAR. Update of the inventory of oil and gas offshore installations in the OSPAR maritime area. *Offshore Industry Series* (2015).
 101. Breton, S. P. & Moe, G. Status, plans and technologies for offshore wind turbines in Europe and North America. *Renew. Energy* **34**, 646–654 (2009).
 102. Eigaard, O. R. *et al.* The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865 (2017).
 103. European Commission. Council Directive 92/43/ECC on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union* vol. 94 40–52 (1992).
 104. European commission. Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. *Official Journal of the European Union* (2009).

Chapter 2

North Sea demersal fisheries prefer specific benthic habitats

Karin J. van der Reijden

Niels T. Hintzen

Laura L. Govers

Adriaan D. Rijnsdorp

Han Olf

Published as

van der Reijden KJ, Hintzen NT, Govers LL, Rijnsdorp AD, Olf H. (2018) North Sea demersal fisheries prefer specific benthic habitats. PLoS ONE, 13(12), e0208338.

Abstract

Introduction: The future protection of marine biodiversity through good conservation planning requires both the identification of key habitats with unique ecological characteristics and detailed knowledge of their human utilization through fisheries. Demersal fisheries are important disturbers of benthic habitats. They often have a heterogeneous spatial distribution, pressurizing particular habitats with high abundances of target species. For the North Sea, we quantified the commonness/rarity of habitats in relation to the environmental determinants of so-called fishing hotspots, to support better-informed conservation planning of benthic habitats in this intensively used continental shelf.

Methods: We first distinguished 9 main seascapes in the study area based on seabed morphology. Secondly, we determined average fishing intensity and fishing hotspots using VMS-data for the three dominant Dutch fisheries from 2008 to 2015: beam-trawlers targeting sole *Solea solea* (Beam-Sole), beam-trawlers targeting plaice *Pleuronectes platessa* (Beam-Plaice), and otter-trawlers targeting Norway lobster *Nephrops norvegicus* and demersal fish (Otter-Mix). Within the seascapes subjected to >80% of the fishing activity, nineteen environmental factors (summarized by PCA) were used to ecologically characterize fishing hotspot locations using MaxEnt response modelling.

Results: We found that all three fisheries target highly specific, uncommon habitats. Beam-Sole fishers targeted warmer, shallow, dynamic, nearshore habitats, and within these specifically the depressions between sand ridges. Beam-Plaice fishers mainly targeted the exposed, non-muddy flanks of the Dogger Bank and similar large-scale elevations (50-75 km) where especially the ridges of smaller sand banks are used. Otter-Mix fisheries concentrated in areas with low bed shear stress, located in muddy, relatively deeper areas.

Implications: This study is the first to provide insight in benthic habitat types that are frequently targeted by fishers in the North Sea. We demonstrated unequal exploitation pressure between seabed habitats, with the majority of hotspots in the less common habitats. Our results hence contribute to a more effective, ecologically informed planning for the protection and monitoring of all seabed habitats and biodiversity of the North Sea.

Introduction

Marine conservation planning generally aims at protecting key and unique habitats and biodiversity, characterized by specific combinations of environmental conditions. To establish successful conservation measures such as novel marine protected areas, it is important to know both where these sites of special conservation interest are located, and how such locations are presently affected by anthropogenic impacts¹. Benthic habitats can be subject to multiple human impacts, with demersal fisheries as one of the dominant stressors with long-term impacts on community structure and biodiversity^{2,3}. On continental shelves, bottom trawling affects habitats not only through removal of the target species, but also by both causing mortality of unintended bycatch species and through their physical impact on the seafloor^{4–7}. The contact of gear components as trawl doors and tickler chains with the seafloor causes direct damage to benthic organisms⁸, resuspension of sediments^{9,10} and the destruction of bioengineered epi- and endobenthic structures such as reefs and burrows¹¹. The physical impact varies between different types of sediment¹², while the impact on benthic communities depends on the resilience of the community itself as well^{4,13}. Good understanding of both the spatial distribution and the environmental drivers of demersal fisheries and benthic habitats is therefore necessary to find adequate management measures that minimize fisheries impacts on marine benthic communities and habitats. This helps answering the important question which habitats are now strongly impacted by human activities throughout their entire geographic range and which habitats also persist under conditions of low human impact.

It is known that demersal fishers target quite specific fishing grounds instead of homogeneously distributing their fishing effort^{3,14–16}. Previous studies have linked these fishing grounds to fish aggregation patterns^{17–20}, primary production²¹, seabed morphology³, unsuitability of particular fishing gears for specific substrates³, and legislator restrictions, as marine protected areas²². Nevertheless, a complete overview of physical and ecological characteristics of North Sea fishing grounds is lacking. Therefore, we do not know which combinations of environmental conditions (habitats) are currently most impacted by different types of fisheries, and which habitats are less affected. Since 2002, more detailed analyses of fisheries distributions are becoming possible, as all fishing vessels above a threshold (>24 m since 2002, >15 m since 2006, and >12 since 2012) are required to participate in the European Vessel Monitor System (VMS)²³, in addition to the obliged daily logbook registrations^{24,25}. For the North Sea, a recent analysis of international VMS-data revealed that, over the three-year study period, trawling occurred in 93% of the 1 x 1 minute longitude and latitude grid cells. However, 90% of the fishing activity was concentrated in 45.4% of the area³, showing the highly heterogeneous distribution of fishing activities. Within the set of grid cells of concentrated fishing effort, locations with yearly recurring high fishing activity can be observed, the so-called ‘hotspots’. The exact locations of these hotspots, however, are yet unknown.

Moreover, the key environmental factors that are associated with the stable fishing hotspots are not well understood³, requiring an analysis at an even higher spatial resolution and with the inclusion of a large set of environmental predictors. We hypothesize that these stable hotspots are structured by small-scale variations in environmental conditions. This habitat heterogeneity could be created by oceanographic structures, such as depressions or elevations relative to the surrounding seabed, but also by the presence of smaller patches of specific sediment types, or particular hydrodynamic conditions. These conditions could then directly²⁶ or indirectly^{27–29} result in stable aggregations of target species, attracting specific fisheries. Most likely, these stable species aggregations underlying the stable fishing hotspot locations are fisheries-specific, as each fishery is targeting different species. We therefore hypothesize that each fishery targets specific environmental conditions, resulting in unique, fisheries-specific sets of environmental conditions at the various stable hotspots.

In this study, we performed a detailed analysis of the environmental characteristics of the demersal fisheries hotspots in the Southern and Central North Sea by comparing prevailing conditions within and between fishing hotspots, but also with environmental conditions at non-hotspot locations. We identified seascapes, based on seabed morphology, and selected those subject to >80% of the fishing activity as main fishing ground. Within these fishing grounds, we determined the relevant multifactor environmental gradients with Principal Component Analysis (PCA), using 19 environmental variables. Maximum Entropy (MaxEnt) species distribution models were then applied to both stable fishing hotspot locations, based on VMS data for all Dutch vessels in the area from 2008 to 2015, and the environmental gradients³⁰. Additionally, we quantified if the targeted environmental ranges reflect rare or common benthic habitats. We discuss how the yielded information can improve current management of marine resources.

Materials and methods

Study area and seascape determination

We focus our study on the demersal fisheries by the Dutch fleet in the Southern and Central North Sea, defined as the combination of subdivisions IVb and IVc according to the International Council for the Exploration of the Sea (ICES; Fig. 1). We subdivided this region in areas with similar seabed morphological characteristics, which we call seascapes. We determined seabed morphology using Bathymetry Positioning Indices (BPI), which depict the depth of a location (pixel) relative to the depth of its surrounding. This allows for the identification of underwater sand ridges, troughs, and relative flat areas. Using bathymetry data from the European Marine Observation and Data Network (EMODnet; www.emodnet.eu/bathymetry) with a resolution of $\pm 178\text{m}$, we calculated the relative depth of every pixel as the difference between the average depth of all pixels within a certain radius and its absolute depth³¹. The relative depth was classified into 5 classes; strong depression ($< -10\text{m}$), weak depression (-10m to -1m), flat (-1m to $+1\text{m}$), weak elevation ($+1\text{m}$ to $+10\text{m}$), strong elevation ($> +10\text{m}$). Main seabed morphology was then determined as the weighted summation of the classified BPI with radii of 5, 10, 30, 50, and 75 km, giving reduced weight to BPI's with smaller radii as shown in formula 1. This methodology was chosen as it emphasizes the large-scale seabed morphology, which is expected to have the largest impact on benthic communities³². The aforementioned seascapes were manually delineated in ArcGIS based on the main seabed morphology.

$$(1) \quad BPI_{75km} + 0.9 * BPI_{50km} + 0.8 * BPI_{30km} + 0.7 * BPI_{10km} + 0.6 * BPI_{5km}$$

Main fishing grounds and fisheries hotspots

VMS and logbook data, covering all Dutch demersal fishing vessels >15m, were available from 2008 to 2015. VMS-data recordings comprise a satellite-based registration of the location, speeding and heading of the vessel, and the date and time, which are recorded with an interval of ± 2 hours. Logbook data additionally include information on the vessel and the gear used. These datasets are coupled for each unique combination of vessel and day within the fishing trip. Based on gear type, engine power, and mesh size, distinct fisheries were defined, which typically have a specific (set of) target species. Then, based on speed and gear, VMS pings are categorized as either 'fishing', 'steaming' or 'floating'^{24,33}. To correct for heaving and shooting during fishing activity, 'floating' pings in between 'fishing' pings are reclassified to 'fishing'³⁴. We calculated the swept area for each ping, as the product of speed (km/h), fishing time (h), and the width of the gear (km)³⁵. At a grid of 1 km^2 , total swept surface was aggregated to calculate annual fishing intensity for each fishing gear. Taking the mean of the fishing intensities of each grid cell over the study period resulted in the average fishing distribution (average of the yearly swept area ratio ($\text{km}^2 \text{ year}^{-1}$)). In this study, we restrict ourselves to the three types of fisheries that are internationally dominated by Dutch fishers and who have their main fishing grounds offshore. (1) Beam-Sole: beam-trawlers deploying

Figure 1. The study area with 9 seascapes. The seascapes comprise 8 (numbered) offshore seascapes and multiple coastal seascapes (not numbered). Brown values show elevated areas, while blue values show local depressions. The Plaice Box and the National Territorial Waters (12 nautical miles from the shore line) are shown as grey shaded areas with dotted contour, while the Exclusive Economic Zones are depicted with grey lines. Current Natura 2000 areas are displayed, with red lines showing protected areas under the Bird Directive, pink lines showing protected areas under the Habitat Directive. Purple lines outline protected areas under both the Bird and Habitat Directive.

nets with mesh sizes of 70-99mm, targeting sole *Solea solea*³⁶. (2) Beam-Plaice: beam-trawlers with mesh sizes of 100mm or larger, mainly targeting plaice *Pleuronectes platessa*³⁷. And (3) Otter-Mix: otter-trawlers with mesh sizes of 70-99mm, fishing for both demersal flatfish and Norway lobster³⁸. To enable a complete overview of the Dutch demersal fishing activity distribution, however, we calculated the average fishing activity for the remaining demersal gears together as well.

For each seascape, the average fishing effort was calculated based on this average fishing distribution (Table 1). Fisheries-specific main fishing grounds were then determined as those seascapes in which the majority (>80 %) of the fishing effort took place. Stable fishing hotspots, on the other hand, were defined as those individual grid cells (1x1 km) that belonged to the annual top 1% most fished grid cells in at least 7 out of the 8 year study period. Therefore, hotspots depict the stable areas with the highest fishing intensities (in yearly swept area (km²year⁻¹). These hotspots corresponded to 12.1 - 13.8% (Beam-Sole), 1.7 - 4.8% (Beam-Plaice), and 29.9 - 56.5% (Otter-Mix) of the total annual fishing activity per fishery.

Table 1. Fishing activity per seascape for the Beam-Sole, Beam-Plaice, and Otter-Mix fishing categories.

Seascape	1	2	3	4	5	6	7	8	9
Surface (km ²)	47341	52420	26114	36584	25214	55420	10266	58253	15259
Beam-Sole									
Fishing effort (kW)	0	273	1	1758	463	18135	3058	44763	78
Fishing effort (%)	-	0.4	0.0	2.6	0.7	26.5	4.5	65.3	0.1
Hotspots present	0	0	0	0	0	7	7	2632	6
Beam-Plaice									
Fishing effort (kW)	0	30	99	1067	3159	353	23	240	26
Fishing effort (%)	-	0.6	2.0	21.4	63.2	7.1	0.5	4.8	0.5
Hotspots present	0	0	0	68	91	1	0	0	0
Otter-Mix									
Fishing effort (kW)	2	585	3	572	75	15329	6817	1035	356
Fishing effort (%)	0.0	2.4	0.0	2.3	0.3	61.9	27.5	4.2	1.4
Hotspots present	0	0	0	12	0	2062	786	6	1

Squares displayed in bold indicate seascapes that define the fisheries-specific study sites used in the MaxEnt models.

Environmental data

Nineteen environmental variables were used, from different data sources (Fig. 2). Bathymetry data for the entire North Sea is available from the EMODnet project (<http://portal.emodnet-bathymetry.eu/>) at a resolution of $\pm 178 \times 178$ m (Fig. S1). These data formed the basis for the BPI calculations (Fig. S2-S6). GeoTIFFs for gravel, mud and sand content of the sediment were obtained from Stephens (2015; Fig. S7-S9). Tidal bed shear stress (BSS; the force exerted on the seabed by tidal currents in N/m²) was obtained from a hydrodynamic model by John Aldridge (CEFAS) as used in^{4,39} (Fig. S10). The daily significant wave height for 2015 was obtained from the North-West European Shelf Wave Analysis and Forecast system by MetOffice, at the European website Copernicus (<http://marine.copernicus.eu/>). Herewith, the maximum significant wave height and the average wave height were determined (Fig. S11 and S12). The same Copernicus website was used to simultaneously obtain monthly average modelled bottom salinity and temperature estimates of the seawater for 2008-2013 from the ocean physics reanalysis by MetOffice (Fig. S13). We used temperature data to determine average temperature (mean of all monthly temperatures), and the average annual minimum and maximum temperature (by first determining the minimum and maximum temperature within a year and averaging these over the study period). Additionally, the difference between average minimum and maximum temperature was calculated, as a measure for temperature variation (Fig. S14-S17). Finally, the shortest distance to a surrounding coastal line (Fig. S18) and a Dutch harbour with auction (Fig. S19) were calculated for all locations within the study area. The environmental variables were all obtained as raster-files, with varying resolution, extent and projection. Re-projection to the same ETRS89/UTM31 projection (EPSG: 25831) and a bilinear interpolation method were then applied to create a consistent set of environmental factor raster files, with similar characteristics as the abiotic factor with the highest resolution (depth; $\pm 178 \times 178$ m).

Figure 2. Overview of all environmental factors taken into consideration in this study. For the Bathymetric Position Indices (BPIs), a brown (relative elevation) to blue gradient (relative depression) is used to show seabed morphology. Bathymetry has a gradient of blue (deep waters) to green to brown (shallow). Higher sediment contents are depicted with darker brown colours, while Bed Shear Stress and wave action are shown from blue (low stress/action) to red (high stress/action). Higher salinity values show darker blue. Distance to nearest coast and port, as well as largest temperature difference range from small distance/difference (white) to large distance/difference (red). The bottom temperatures are depicted with blue representing the coolest temperatures towards the highest temperatures in red. All figures are individually included in the Supplementary Materials, including the range and associated legend.

Data analysis

Ordination of environmental factors

Fishermen have practical considerations in choosing their fishing ground, with a trade-off between travelling (fuel) costs and expected yield^{33,40}. To ensure that we only include relevant ranges of environmental factors in the analysis, we restricted our analysis to the conditions prevailing at the main fishing grounds (seascapes with >80% of the fishing activity; Table 1)⁴¹. This also enables the potential identification of preferences for minor deviating habitats, which would be overshadowed by the distance-to-shore gradient otherwise. For each fishing ground, we extracted the environmental gradient values at the midpoints of all enclosed grid cells. Any potential prejudice in importance (weight) of specific environmental factors was excluded by the separate inclusion of all environmental factors. The values were then scaled and centered, and a Principal Component Analysis (PCA) was performed. This reduced the number of dimensions, and yielded an ecological relevant interpretation of the different sets of correlated environmental factors important within

that specific fishing ground. Components with eigenvalues >1 were kept⁴², representing sets of correlated factors here-after referred to as environmental gradients. For each environmental gradient, a frequency distribution of grid cell values was calculated to determine range distribution over the main fishing ground. This can be interpreted as the rarity of a specific gradient value within its range for the area.

Spatial autocorrelation

The likelihood that two points are similar depends on the distance between them, with more similar points located closer together. To ensure that our analysis was not affected by such spatial auto-correlation, we tested for spatial auto-correlation by applying a variogram (package “gstat”) to the midpoints of the grid cells⁴³. A variogram calculates the correlation between the points and plots these, sorted for the distance between the points. Herewith, the minimum distance between two points to have no auto-correlation (range) can be determined. We set the upper limits of our variograms to a distance of <20 km, as others¹⁵ found less than 5% similarity between fishing locations with this distance. The best fitted variogram-model was selected, and its range determined. This range was then used as minimum distance in a resampling of the hotspot locations.

Species distribution models

The relation of fishing hotspots with environmental gradients was determined using a MaxEnt species distribution model^{30,43}, one of the various ecological niche modelling methods currently available for presence-only data (MaxEnt version 3.3.3k). Combining species presences and background locations with a set of (uncorrelated) environmental predictors, a relative occurrence rate (ROR) is calculated. By applying a logistic output to this ROR and by assuming random spatial sampling for species presence, species presence probability can be estimated⁴¹. Moreover, the model calculates the correlation between environmental predictors and the species distribution, allowing for complex, nonlinear responses. We specifically applied a MaxEnt model for this ability, because these curves provide a realistic correlation between fishing hotspot location and their environmental conditions, although they can be hard to interpret⁴¹.

Here, we compared conditions at fishing hotspots (presences) with the overall environment, by randomly creating background locations among all non-hotspot grid-cells within the main fishing ground. These background locations had a similar minimum distance and exceeded the number of presence locations by a factor 5⁴³. Environmental gradient values were extracted for the midpoints of the grid cells defined as hotspot or background and supplied to the MaxEnt model. With these, the model constructed the most optimal response curves in a single run, allowing for linear, quadratic, threshold and hinge features⁴¹. Product features, which are comparable to interactive functions between separate environmental gradients, were set to not-allowed.

Results

Seascapes

Based on the similarity of seabed morphology features (as determined by the weighted summation of five bathymetry position indices (equation 1)), we determined nine seascapes in the study area (Fig. 1). Seascapes 1 and 3 show elevated areas, whereas seascape 2 is relatively lower compared to its surroundings. Seascape 1 is characterized by strong relief at the 5-10 km scale; seascape 3 has little of such relief. Seascape 4 is separated in the north from seascape 3 and from seascape 6 (Central Oyster Grounds) in the west by a depression. Seascape 5, which comprises the Dogger Bank area, is strongly elevated compared to its surroundings, whereas seascape 7 (the Cleaver Bank) is characterized by some very low areas. Seascape 8 shows high, well-structured relief at the small-scale (5-10km), which is caused by tidal ridges. Seascape 9 is the only seascape comprising multiple separate areas, but all located near the coast and characterized by locally elevated areas.

Figure 3. Average fishing intensity of A) Beam-Sole, B) Beam-Plaice, C) Otter-Mix, and D) the remaining demersal gears in the Dutch fleet over the time period 2008-2015. For the three gear types of interest, the stable fishing hotspots are depicted in E. Fishing intensity is calculated as the averaged fished area in km^2 per year. Stable fishing hotspots are those grid cells of 1km^2 that belong to the annual 1% most intense used grid cells at least 7 times over the study period (no unit). Black solid lines represent the seascapes, the dashed line shows National Territorial Waters (12 nm). The Plaice Box is displayed by the dotted line. Fishing intensity of 0 means that no fishing activity has been observed during the study period, or that the average fishing activity was based on < 3 separate VMS-recordings, of which the activity cannot be shown due to privacy laws. Current Natura 2000 areas are displayed, with red lines showing protected areas under de Bird Directive, pink lines showing protected areas under the Habitat Directive. Purple lines outline protected areas under both the Bird and Habitat Directive.

Main fishing grounds and fisheries hotspots

Fishing effort was quantified in the different seascapes (Fig. 3A-D), showing a clear separation of the main fishing grounds for each fishing gear (Table 1). Beam-Sole was mainly concentrated in seascapes 8 (Southern North Sea; 65%) and 6 (Central Oyster Grounds; 27%), while Beam-Plaice showed a preference for seascapes 5 (Dogger Bank; 63%) and 4 (Coastal Denmark; 21%). Otter-Mix had three clearly separated fishing locations, all located within seascapes 6 (Central Oyster Grounds; 62%) and 7 (Cleaver Bank; 28%). All other Dutch demersal fisheries were strongly concentrated in the coastal zone, with some additional locations in seascapes 4 and 7, showing that the three selected fisheries represented the main Dutch fisheries on the open North Sea (Fig. 3D). When calculating the fisheries hotspots, we found that their spatial distribution generally captured the overall patterns of fishing activity (Fig. 3E, Table 1). Beam-Plaice showed less hotspots compared with Beam-Sole and Otter-Mix, caused by yearly differences in the location of the 1% most intense fished grid cells, resulting in only a few grid cells belonging >6 years to the top 1%.

Environmental factors

In the main fishing ground of Beam-Sole (seascapes 6 and 8), five environmental gradients from the PCA had an eigenvalue larger than 1 and were used for the further analysis (Table 2). The most important environmental gradient (PC1) in this area represents bottom temperature, depth, wave height, BSS, and distance to harbours and the nearest coastline (Fig. S20). High values reflect relative shallow, warm waters near the shore (and harbours), with high BSS and low wave action. The second environmental gradient (PC2) mostly reflects BPI at different scales, where higher values are relative elevations of the seafloor.

For the Beam-Plaice main fishing ground (seascapes 4 and 5), the PCA distinguished six independent main environmental gradients (Table 2). The first environmental gradient (PC1) reflects wave action and mid-scale BPI (30 and 50km), with higher values representing areas with elevations at the mid-scale and higher wave action (Fig. S21). The second environmental gradient (PC2) captures water temperature and absolute depth, with low values corresponding with deeper and colder waters.

For the Otter-Mix main fishing ground (seascapes 6 and 7), the PCA identified 5 environmental gradients (Table 2), of which the most important one (PC1) reflects salinity, depth, bottom temperature and harbour distance. This gradient ranges from saline, deep, and cold waters offshore (low values) to less saline, shallow, warmer waters nearshore (high values; Fig. S22). The second environmental gradient (PC2) represents seabed morphology, with high values indicating local depressions.

MaxEnt distribution model

Our fisheries-specific MaxEnt distribution models yielded response curves of fishing hotspot presence to all relevant environmental gradients (Tables S1-S3) and determined the importance of each gradient. These response curves show preferences of the fishers, which were combined with estimates of gradient value commonness and rarity. This is assessed through the frequency distribution of environmental gradient values of the main fishing area. The plots therefore indicate the commonness or rarity of the preferred environmental conditions by the different fisheries. The values of these plots are also given in supplementary materials (Tables S4-S6). The MaxEnt model for Beam-Sole (training AUC = 0.842; Fig. S23) showed that hotspot location was mainly explained by PC1 (55%), the gradient of depth, bottom temperature, BSS, wave action and distance to the coast and harbours. A preference was shown for shallow, nearshore waters characterized by higher bottom temperatures, high BSS, and low wave action (Fig. 4). Within this area, the Beam-Sole targeted relative depressions (5-10 km) while avoiding gravelly sediments. These preferred environmental ranges were, except for gravel content, relatively rare in the main fishing ground.

Table 2. Loadings for the relevant principal component (eigenvalue >1) from a principal component analysis of the full set of variables for the main fishing grounds of the three fisheries.

Principal component	Beam-Sole					Beam-Plaice					Otter-Mix					
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC6	PC1	PC2	PC3	PC4	PC5
Total variance explained (%)	32.3	23.5	16.6	10.7	6.3	28.4	25.0	14.6	8.5	8.1	5.9	33.5	24.8	15.2	9.0	5.6
Component loadings																
Salinity (PSU)	-0.066	0.059	0.413	0.181	0.342	0.237	-0.267	-0.156	0.138	0.004	0.357	-0.323	-0.110	-0.066	-0.271	-0.267
Gravel content (%)	0.085	0.057	0.259	-0.548	-0.085	0.095	0.060	-0.021	0.552	-0.124	-0.104	-0.015	-0.032	-0.201	-0.035	-0.255
Mud content (%)	-0.192	-0.048	-0.252	-0.288	0.444	-0.248	-0.075	0.095	0.311	0.490	0.099	0.108	0.217	0.225	-0.549	0.113
Sand content (%)	0.072	-0.010	-0.025	0.654	-0.256	0.206	0.050	-0.086	-0.524	-0.432	-0.056	-0.108	-0.217	-0.216	0.554	-0.100
BPI 5km	-0.086	-0.368	0.091	-0.013	-0.340	-0.167	-0.004	-0.421	0.164	-0.274	-0.065	-0.098	0.306	0.093	0.245	-0.332
BPI 10km	-0.099	-0.396	0.092	-0.017	-0.308	-0.209	0.005	-0.441	0.174	-0.257	-0.034	-0.124	0.364	0.100	0.224	-0.255
BPI 30km	-0.107	-0.429	0.089	-0.049	-0.099	-0.308	0.021	-0.342	0.067	-0.114	0.008	-0.152	0.398	0.064	0.099	-0.041
BPI 50km	-0.108	-0.430	0.074	-0.030	0.077	-0.346	-0.003	-0.271	-0.135	0.104	-0.002	-0.152	0.401	0.017	0.057	0.051
BPI 75km	-0.109	-0.409	0.035	0.015	0.238	-0.289	-0.020	-0.217	-0.304	0.305	0.018	-0.135	0.402	-0.035	0.034	0.148
Depth (m)	0.305	-0.110	0.222	-0.044	0.081	0.227	0.357	0.037	0.049	-0.034	0.200	0.305	-0.233	-0.062	0.062	-0.207
BSS	0.311	0.204	-0.014	-0.093	-0.322	0.204	0.178	-0.174	-0.071	0.269	-0.573	0.177	0.138	-0.367	0.193	0.424
Maximum temperature difference (°C)	0.182	-0.133	-0.449	-0.072	-0.055	-0.161	0.403	0.097	0.017	-0.059	0.187	0.357	0.080	0.182	0.099	-0.145
Average bottom temperature (°C)	0.359	-0.145	-0.050	0.104	0.198	0.095	0.416	-0.102	0.117	-0.011	0.145	0.338	0.130	-0.148	-0.070	-0.200
Maximum bottom temperature (°C)	0.298	-0.166	-0.296	0.031	0.120	-0.094	0.424	0.058	0.078	-0.070	0.212	0.367	0.099	0.096	0.027	-0.180
Minimum bottom temperature (°C)	0.202	-0.056	0.344	0.232	0.354	0.298	-0.247	-0.218	0.080	0.155	-0.095	-0.253	0.005	-0.365	-0.275	-0.014
Average significant wave height (m)	-0.345	0.053	-0.239	0.113	0.083	-0.301	-0.218	0.251	-0.097	-0.137	0.157	-0.084	-0.155	0.529	0.015	-0.012
Maximum significant wave height (m)	-0.324	0.039	-0.216	0.052	0.038	-0.335	-0.079	0.319	-0.051	-0.155	-0.099	-0.044	-0.114	0.429	0.239	0.409
Distance to closest coastal line (m)	-0.348	0.114	0.051	0.198	0.001	0.182	-0.214	-0.221	-0.112	0.067	0.557	-0.283	-0.175	0.183	0.011	-0.348
Distance to closest Dutch harbour (m)	-0.261	0.151	0.318	-0.128	-0.174	0.008	-0.284	0.181	0.273	-0.383	-0.139	-0.360	-0.109	-0.036	0.051	0.186
Loadings larger than 0.3 are given in bold

Figure 4. Response curves of the environmental gradients in the MaxEnt model for Beam-Sole, in relation to the abundance of the specific environmental condition. Each figure shows the representative range of a principal component (x-axis), the probability of fishing hotspot presence within that range (red line), and the abundance frequency of that range on the main fishing ground (histogram). The figures are ordered in decreasing importance for model explanation, which can be found between brackets underneath the x-axis. Only curves that explain >5% of the model are included.

The fishing hotspots of Beam-Plaice (training AUC = 0.865; Fig. S23) were mostly explained by PC3 (43%), reflecting small-scale (5-10 km) seabed morphology and wave action, with higher probability in areas with high wave action and areas that elevate of the seabed (Fig. 5). The two environmental gradients most dominant in the area (PC1 and PC2) were also important (with 24% and 26% respectively). They represented a gradient in depth, bottom temperature and temperature variability (PC2) and a gradient in wave action and large-scale morphology (PC1). For the two most important gradients (PC3 and PC2), the preferred locations were more rare habitats. Especially for the most important gradient (PC3), small-scale elevated areas with high wave action were targeted, which are a relatively rare habitat in the main fishing ground.

The Otter-Mix hotspot locations (training AUC = 0.843; Fig. S23) were mostly explained by seabed morphology (47%), with an increase in probability at relative depressions (Fig. 6). In addition, Otter-Mix showed a preference for areas with low bed shear stress, low minimum temperatures and high wave actions (36%). The presence of these hotspots was somewhat affected by sediment type (8%), with a preference towards muddy sediments. Within the Otter-Mix fishing ground, the preferred areas with these conditions were relatively rare.

Figure 5. Response curves of the environmental gradients in the MaxEnt model for Beam-Plaice, in relation to the abundance of the specific environmental condition. Each figure shows the representative range of a principal component (x-axis), the probability of fishing hotspot presence within that range (red line), and the abundance frequency of that range on the main fishing ground (histogram). The figures are ordered in decreasing importance for model explanation, which can be found between brackets underneath the x-axis. Only curves that explain >5% of the model are included (Ls: Large-scale, Ss: Small-scale).

Discussion

We confirmed our hypothesis that stable fishing hotspot locations are associated by highly specific environmental conditions, showing that fishers have a clear preference for particular seabed habitats. The majority of these targeted habitats are uncommon in their fishing grounds. Beam-Sole hotspots were primarily targeting depressions within shallow, nearshore waters, with high bottom temperatures, high BSS values, and low wave action. Beam-Plaice was concentrated at small-scale ridges (5-10km) subjected to high wave action, which were located on top of large-scale

Figure 6. Response curves of the environmental gradients in the MaxEnt model for Otter-Mix, in relation to the abundance of the specific environmental condition. Each figure shows the representative range of a principal component (x-axis), the probability of fishing hotspot presence within that range (red line), and the abundance frequency of that range on the main fishing ground (histogram). The figures are ordered in decreasing importance for model explanation, which can be found between brackets underneath the x-axis. Only curves that explain >5% of the model are included (Ls: Large-scale, Ss: Small-scale).

elevations around a depth of -35 meters. Otter-Mix targeted relative depressions with low values of BSS, low minimum temperatures, high wave action and high mud content. Our results emphasize that, from a conservation perspective, calculations of fishing efforts (annual % of the area fished) should be performed for each specific habitat separately, instead of for the whole North Sea. We show that particular habitats are subjected to much higher fishing efforts than others, while knowledge on the ecological potential of the highly preferred areas remains limited. Remarkably, part of the stable fishing hotspots is located within Natura 2000 areas, which represent the present habitat protection measures.

Fishing vessels are satellite-tracked by both the Vessel Monitoring System and the Automatic Identification System (AIS), and both data sources can be used to study fishing distributions⁴⁴. Whereas VMS yields information on a 2-hour interval, the AIS-data has a much higher temporal resolution⁴⁵. Complete implementation of AIS, however, is only well developed since 2012, limiting the ability to study long-term stable patterns. As the temporal resolution required for this analysis was well met by VMS data, we identified the stable fishing hotspots with VMS data solely. Our methodology of stable fishing hotspots identification comes with some other limitations as well, but we assume that our analysis is indicative of general patterns. For example, fisheries are not entirely restricted to these hotspots, with the majority of the fishing activity actually taking place outside the fisheries hotspots in most years. Especially Beam-Plaice hotspots represent only a minority of the average fishing activity, because the spatial distribution of the most intense fished areas is very variable between years. This indicates that plaice fisheries patterns are spatially different between years, potentially because plaice is relatively evenly distributed over a larger area and multiple habitats, or is characterised by opportunistic behaviour where habitat preference varies from year to year. Secondly, due to our strict definition of stable fisheries hotspots, such temporal and transient hotspots are most likely not included. Likewise, recent shifts in distribution of the sole fisheries due to the introduction of the pulse fishing technique that affect the catch efficiency and selectivity are not taken into account^{46–48}. However, the hotspot definition used in this study provides a very robust estimate of stable locations subjected to the highest fishing intensities per unit area. Our MaxEnt predicted maps and the average fishing activity patterns are very similar, strengthening the assumption that results presented in this study may be interpreted as general patterns within the distinct fisheries.

Our study assumes that the fishing hotspots reflect high abundances of the different target species, potentially reflecting an idea free distribution of predators competing for an aggregated prey⁴⁹. We found that all three fisheries prefer areas with conditions that are similar to preferred habitats of their target species. Beam-Sole fishers target warmer dynamic and sandy habitats, conditions that sole seems to prefer as well^{50–53}. We show that, within these waters, Beam-Sole targets depressions. These troughs are associated with higher benthic species abundance^{28,29}, which may attract sole^{54,55}. Beam-Plaice hotspots coincide with the Tail End of the Dogger Bank (the narrowest part at the Northeast of the Dogger Bank), a key topographical feature in plaice distribution⁵⁶. This area mainly consist of sandy substrates, which seem preferred by plaice^{53,57–59}. Moreover, the targeted area in general has higher abundances of other species⁵⁸, including some high-value by-catch species (like turbot (*Scophthalmus maxima*), brill (*Scophthalmus rhombus*) and lemon sole (*Microstomus kitt*)) in the plaice fisheries^{37,38,60}. Hotspots of Otter-Mix are located in deep, muddy areas; conditions preferred by Norway lobster^{26,61}. The good correspondence between hotspots and knowledge on habitat preferences of the target species make it likely that the observed fishing hotspots reflect high local densities of the specific target species.

These fisheries hotspots may be favourable for more species than the target species only, promoting rich benthic communities. The environmental variables studied here are known to strongly determine the species composition of benthic communities³². The troughs in between relatively stable sand ridges⁶² targeted by Beam-Sole, for instance, show higher benthic species abundance and richness in the troughs than on the crests²⁹, possibly due to local differences in sediment content²⁸. Similarly, the hotspot locations of Otter-Mix are located in the Central Oyster Grounds and Frisian Front, which score high for various benthos biodiversity metrics⁶³. Both observations suggest that the conditions prevailing at the hotspot locations support rich benthic communities. Moreover, the fact that there are only a few locations with these conditions in the North Sea indicates that the species depending on these conditions probably are relatively uncommon.

Our findings that stable fishing hotspots are highly structured by environmental conditions is important for sustainable fisheries management. Bottom trawling is among the most disturbing factors of the seabed worldwide⁸, but current management is dominantly directed on the limitation

2 of both Total Allowable Catch (TACs) and average fishing effort (days-at-sea)⁶⁴. Despite separate legislations to protect benthic habitats (the Natura 2000 network as part of the Habitat⁶⁵ and Bird⁶⁶ Directive and the Marine Strategy Framework Directive⁶⁷, for instance), hardly any regulation exist for the spatial distribution of fishing effort. Currently implied habitat protecting measures, like the Natura 2000 areas, account to some extent for habitat variability. However, the discussion on the allowed fishing practices within these areas is far from settled. We show that part of the stable fishing hotspots is located within the Natura 2000 areas, areas designated for demersal habitat protection. Hence, present fisheries management ignores that bottom trawling is highly aggregated³ and impacts habitats differently⁴. We show that the North Sea comprises a strong, relatively fine-scale variety of demersal habitats. Moreover, we demonstrate that fishers are aware of these conditions and target very specific habitats which are uncommon within their main fishing grounds. These results prove that, in addition to the variability of physical impact, the aggregated structure of demersal fisheries affects benthic habitats and associated communities unequally. We show that rare habitats and communities are subjected to high exploitation rates, while the more common habitats and communities receive relatively little fishing activity. These observations emphasize that sustainable management of benthic habitats can only be achieved if the spatial distribution of both the benthic habitats and their users are incorporated in fisheries management.

This study therefore can provide scientific underpinnings for stable fisheries hotspot distributions, and enables managers and policy makers to improve monitoring and conservation planning. Moreover, our results may be used in risk assessments of anthropogenic disturbances to specific benthic habitats and communities in the North Sea. Based on the three dominant Dutch demersal fisheries, our results emphasize that marine policy should include the heterogeneity of the North Sea and the aggregated patterns of its users to enable sustainable exploitation and sufficient nature protection.

Acknowledgements

We would like to thank the Dutch ministry of Agriculture, Nature and Food Quality and Wageningen Marine Research for providing the Dutch VMS-data. We thank Leo Koop, Lucas Krüger and three anonymous reviewers for valuable comments on the manuscript.

Supplementary materials

Supplementary materials can be found online at <https://doi.org/10.1371/journal.pone.0208338>.

Figure S1. Absolute water depth of the study area.

Figure S2. Bathymetry Position Index with a radius of 5 km.

Figure S3. Bathymetry Position Index with a radius of 10 km.

Figure S4. Bathymetry Position Index with a radius of 30 km.

Figure S5. Bathymetry Position Index with a radius of 50 km.

Figure S6. Bathymetry Position Index with a radius of 75 km.

Figure S7. Percentage of the gravel content in the sediment.

Figure S8. Percentage of the mud content in the sediment.

Figure S9. Percentage of the sand content in the sediment.

Figure S10. Tidal component of the Bed Shear Stress.

Figure S11. Maximum modelled annual wave height.

Figure S12. Average modelled wave height.

Figure S13. Averaged modelled bottom salinity.

Figure S14. Averaged modelled bottom temperature.

Figure S15. Maximum modelled bottom temperature.

Figure S16. Minimum modelled bottom temperature.

Figure S17. Maximum difference in modelled bottom temperature.

Figure S18. Distance to the nearest coastal line.

Figure S19. Distance to the nearest Dutch harbour with auction.

Figure S20. Visual interpretation of the relevant principal components (eigenvalue >1) on the Beam-Sole main fishing grounds.

Figure S21. Visual interpretation of the relevant principal components (eigenvalue >1) on the Beam-Plaice main fishing grounds.

Figure S22. Visual interpretation of the relevant principal components (eigenvalue >1) on the Otter-Mix main fishing grounds.

Figure S23. ROC-curves for the MaxEnt models for (a) Beam-Sole, (b) Beam-Plaice, and (c) Otter-Mix.

Table S1. Contribution and importance of each relevant Principal Component to the Beam-Sole MaxEnt model.

Table S2. Contribution and importance of each relevant Principal Component to the Beam-Plaice MaxEnt model.

Table S3. Contribution and importance of each relevant Principal Component to the Otter-Mix MaxEnt model.

Table S4. Response curves of the environmental gradients in the MaxEnt model for Beam-Sole, in relation to the abundance of the specific environmental condition.

Table S5. Response curves of the environmental gradients in the MaxEnt model for Beam-Plaice, in relation to the abundance of the specific environmental condition.

Table S6. Response curves of the environmental gradients in the MaxEnt model for Otter-Mix, in relation to the abundance of the specific environmental condition.

References

- Schwartz, M. W. *et al.* Decision support frameworks and tools for conservation. *Conserv. Lett.* **11**, 1–12 (2018).
- Halpern, B. S. *et al.* A global map of human impact on marine ecosystems. *Science*. **319**, 948–953 (2008).
- Eigaard, O. R. *et al.* The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865 (2017).
- Hiddink, J. G. *et al.* Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can. J. Fish. Aquat. Sci.* **63**, 721–736 (2006).
- Jennings, S. & Kaiser, M. J. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* **34**, 201–352 (1998).
- van der Reijden, K. J. *et al.* Survival of undersized plaice (*Pleuronectes platessa*), sole (*Solea solea*), and dab (*Limanda limanda*) in North Sea pulse-trawl fisheries. *ICES J. Mar. Sci.* **74**, 1672–1680 (2017).
- Kelleher, K. Discards in the world's marine fisheries. An update. *FAO Fish. Tech. Pap.* **470**, (2005).
- Hiddink, J. G. *et al.* Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci.* 1–6 (2017).
- Jones, J. B. Environmental impact of trawling on the seabed: A review. *New Zeal. J. Mar. Freshw. Res.* **26**, 59–67 (1992).
- O'Neill, F. G. & Ivanovic, A. The physical impact of towed demersal fishing gears on soft sediments. *ICES J. Mar. Sci.* **73**, i5–i14 (2016).
- Kaiser, M. J., Ramsay, K., Richardson, C. A., Spence, F. E. & Brand, A. R. Chronic fishing disturbance has changed shelf sea benthic community structure. *J. Anim. Ecol.* **69**, 494–503 (2000).
- Eigaard, O. R. *et al.* Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J. Mar. Sci.* **73**, 27–43 (2015).
- Hiddink, J. G., Hutton, T., Jennings, S. & Kaiser, M. J. Predicting the effects of area closures and fishing effort restrictions on the production, biomass, and species richness of benthic invertebrate communities. *ICES J. Mar. Sci.* **63**, 822–830 (2006).
- Rijnsdorp, A. D., Buys, A. M., Storbeck, F. & Visser, E. G. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES J. Mar. Sci.* **55**, 403–419 (1998).
- Ellis, N., Pantus, F. & Pitcher, C. R. Scaling up experimental trawl impact results to fishery management scales — a modelling approach for a “hot time”. *Can. J. Fish. Aquat. Sci.* **71**, 733–746 (2014).
- Poos, J. J. & Rijnsdorp, A. D. The dynamics of small-scale patchiness of plaice and sole as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the fleet dynamics. *J. Sea Res.* **58**, 100–112 (2007).
- Rijnsdorp, A. D. & Pastoors, M. A. Modelling the spatial dynamics and fisheries of North Sea plaice (*Pleuronectes platessa* L.) based on tagging data. *ICES J. Mar. Sci.* **52**, 963–980 (1995).
- Rijnsdorp, A. D., Poos, J. J. & Quirijns, F. J. Spatial dimension and exploitation dynamics of local fishing grounds by fishers targeting several flatfish species. *Can. J. Fish. Aquat. Sci.* **68**, 1064–1076 (2011).
- Sampson, D. B. Fishing tactics and fish abundance, and their influence on catch rates. *ICES J. Mar. Sci.* **48**, 291–301 (1991).
- Temming, A., Floeter, J. & Ehrich, S. Predation hot spots: Large scale impact of local aggregations. *Ecosystems* **10**, 865–876 (2007).
- van Denderen, P. D., Hintzen, N. T., Rijnsdorp, A. D., Ruurdij, P. & van Kooten, T. Habitat-specific effects of fishing disturbance on benthic species richness in marine soft sediments. *Ecosystems* **17**, 1216–1226 (2014).
- Murawski, S. A., Wigley, S. E., Fogarty, M. J., Rago, P. J. & Mountain, D. G. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES J. Mar. Sci.* **62**, 1150–1167 (2005).
- European commission. Commission Regulation (EC) No 2244/2003 of 18 December 2003 laying down detailed provisions regarding satellite-based Vessel Monitoring Systems. *Official Journal of the European Union* vol. L333, 17–27 (2003).
- Hintzen, N. T. *et al.* VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fish. Res.* **115–116**, 31–43 (2012).
- Jennings, S. & Lee, J. Defining fishing grounds with vessel monitoring system data. *ICES J. Mar. Sci.* **69**, 51–63 (2011).
- Johnson, M. P., Lordan, C. & Power, A. M. Habitat and ecology of *Nephrops norvegicus*. *Adv. Mar. Biol.* **64**, 27–63 (2013).
- de Jong, M. F., Baptist, M. J., Lindeboom, H. J. & Hoekstra, P. Relationships between macrozoobenthos and habitat characteristics in an intensively used area of the Dutch coastal zone. *ICES J. Mar. Sci.* **72**, 2409–2422 (2015).
- Baptist, M. J., van Dalfsen, J., Weber, A., Passchier, S. & van Heteren, S. The distribution of macrozoobenthos in the southern North Sea in relation to meso-scale bedforms. *Estuar. Coast. Shelf Sci.* **68**, 538–546 (2006).
- van Dijk, T. A. G. P. *et al.* Benthic habitat variations over tidal ridges, North Sea, The Netherlands. in *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
- Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**, 231–259 (2006).
- Verfaillie, E., Doornenbal, P., Mitchell, A. J., White, J. & van Lancker, V. The bathymetric position index (BPI) as a support tool for habitat mapping. *Worked example for the MESH Final Guidance* (2007).
- Reiss, H. *et al.* Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* **67**, 278–293 (2010).
- Poos, J. J., Turenhout, M. N. J., van Oostenbrugge, H. A. E. & Rijnsdorp, A. D. Adaptive response of beam trawl fishers to rising fuel cost. *ICES J. Mar. Sci.* **70**, 675–684 (2013).
- van Denderen, P. D., Hintzen, N. T., van Kooten, T. & Rijnsdorp, A. D. Temporal aggregation of bottom trawling and its implication for the impact on the benthic ecosystem. *ICES J. Mar. Sci.* **72**, 952–961 (2015).
- Piet, G. J. & Hintzen, N. T. Indicators of fishing pressure and seafloor integrity. *ICES J. Mar. Sci.* **69**, 1850–1858 (2012).
- Rijnsdorp, A. D., van Overzee, H. M. J. & Poos, J. J. Ecological and economic trade-offs in the management of mixed fisheries: A case study of spawning closures in flatfish fisheries. *Mar. Ecol. Prog. Ser.* **447**, 179–194 (2012).
- van der Reijden, K. J. *et al.* Discard self-sampling of Dutch bottom-trawl and seine fisheries in 2013. *CVO Report 14.007*. (2014).

38. Catchpole, T. L., Frid, C. L. J. & Gray, T. S. Resolving the discard problem-A case study of the English Nephrops fishery. *Mar. Policy* **30**, 821–831 (2006).
39. van Denderen, P. D. *et al.* Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar. Ecol. Prog. Ser.* **541**, 31–43 (2015).
40. Bastardie, F., Nielsen, J. R., Andersen, B. S. & Eigaard, O. R. Effects of fishing effort allocation scenarios on energy efficiency and profitability: An individual-based model applied to Danish fisheries. *Fish. Res.* **106**, 501–516 (2010).
41. Merow, C., Smith, M. J. & Silander, J. A. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography (Cop.)* **36**, 1058–1069 (2013).
42. Verfaillie, E., Degraer, S., Schelfaut, K., Willems, W. & van Lancker, V. A protocol for classifying ecologically relevant marine zones, a statistical approach. *Estuar. Coast. Shelf Sci.* **83**, 175–185 (2009).
43. Fortin, M.-J. & Dale, M. Spatial analysis. A guide for ecologists. (Cambridge University Press, 2008).
44. Shepperson, J. L. *et al.* A comparison of VMS and AIS data: The effect of data coverage and vessel position recording frequency on estimates of fishing footprints. *ICES J. Mar. Sci.* **75**, 988–998 (2018).
45. Natale, F., Gibin, M., Alessandrini, A., Vespe, M. & Paulrud, A. Mapping fishing effort through AIS data. *PLoS One* **10**, e0130746 (2015).
46. Haasnoot, T., Kraan, M. & Bush, S. R. Fishing gear transitions: lessons from the Dutch flatfish pulse trawl. *ICES J. Mar. Sci.* **73**, 1235–1243 (2014).
47. van Marlen, B., Wiegerinck, J. A. M., van Os-Koomen, E. & van Barneveld, E. Catch comparison of flatfish pulse trawls and a tickler chain beam trawl. *Fish. Res.* **151**, 57–69 (2014).
48. Sys, K., Poos, J. J., van Meensel, J., Polet, H. & Buysse, J. Competitive interactions between two fishing fleets in the North Sea. *ICES J. Mar. Sci.* **73**, 1485–1493 (2016).
49. Sutherland, W. J. Aggregation and the 'Ideal Free' Distribution. *J. Anim. Ecol.* **52**, 821–828 (1983).
50. Teal, L. R., van Hal, R., van Kooten, T., Ruurdij, P. & Rijnsdorp, A. D. Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. *Glob. Chang. Biol.* **18**, 3291–3305 (2012).
51. van Hal, R., van Kooten, T. & Rijnsdorp, A. D. Temperature induced changes in size dependent distributions of two boreal and three Lusitanian flatfish species: A comparative study. *J. Sea Res.* **107**, 14–22 (2016).
52. Maxwell, D. L., Stelzenmüller, V., Eastwood, P. D. & Rogers, S. I. Modelling the spatial distribution of plaice (*Pleuronectes platessa*), sole (*Solea solea*) and thornback ray (*Raja clavata*) in UK waters for marine management and planning. *J. Sea Res.* **61**, 258–267 (2009).
53. Amezcua, F. & Nash, R. D. M. Distribution of the order pleuronectiformes in relation to the sediment type in the North Irish Sea. *J. Sea Res.* **45**, 293–301 (2001).
54. Tableau, A., Brind'Amour, A., Woillez, M. & Le Bris, H. Influence of food availability on the spatial distribution of juvenile fish within soft sediment nursery habitats. *J. Sea Res.* **111**, 76–87 (2016).
55. Nicolas, D. *et al.* Relationships between benthic macrofauna and habitat suitability for juvenile common sole (*Solea solea*, L.) in the Vilaine estuary (Bay of Biscay, France) nursery ground. *Estuar. Coast. Shelf Sci.* **73**, 639–650 (2007).
56. Hunter, E. *et al.* Migration route and spawning area fidelity by North Sea plaice. *Proc. R. Soc. B* **270**, 2097–2103 (2003).
57. Wieking, G. & Kröncke, I. Is benthic trophic structure affected by food quality? The Dogger Bank example. *Mar. Biol.* **146**, 387–400 (2005).
58. Sell, A. F. & Kröncke, I. Correlations between benthic habitats and demersal fish assemblages - A case study on the Dogger Bank (North Sea). *J. Sea Res.* **80**, 12–24 (2013).
59. Lauria, V., Vaz, S., Martin, C. S., MacKinson, S. & Carpentier, A. What influences European plaice (*Pleuronectes platessa*) distribution in the eastern English Channel? Using habitat modelling and GIS to predict habitat utilization. *ICES J. Mar. Sci.* **68**, 1500–1510 (2011).
60. Gillis, D. M., Rijnsdorp, A. D. & Poos, J. J. Behavioral inferences from the statistical distribution of commercial catch: patterns of targeting in the landings of the Dutch beam trawler fleet. *Can. J. Fish. Aquat. Sci.* **65**, 27–37 (2008).
61. Aldridge, J. N., Parker, E. R., Briceno, L. M., Green, S. L. & van der Molen, J. Assessment of the physical disturbance of the northern European Continental Shelf seabed by waves and currents. *Cont. Shelf Res.* **108**, 121–140 (2015).
62. Knaapen, M. A. F. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo-Marine Lett.* **29**, 17–24 (2009).
63. Bos, O. G. *et al.* Biodiversity hotspots on the Dutch Continental Shelf. *IMARES report C071/11*. (2011).
64. European Commission. Regulation (EU) No 1380/201308 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy. *Official Journal of the European Union* vol. 354 22–61 (2013).
65. European Commission. Council Directive 92/43/ECC on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union* vol. 94 40–52 (1992).
66. European commission. Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. *Official Journal of the European Union* (2009).
67. European Commission. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Official Journal of the European Union* vol. 164 19–40 (2008).

Chapter 3

Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front

Justin C. Tiano

Karin J. van der Reijden

Sarah O'Flynn

Olivier Beauchard

Sietse van der Ree

Jelmer van der Wees

Tom Ysebaert

Karline Soetaert

Published as

Tiano JC, van der Reijden KJ, O'Flynn S, Beauchard O, van der Ree S, van der Wees J, Ysebaert T, Soetaert K. (2020). Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front. *Marine Environmental Research*, 159, 104964.

Abstract

In this study, we analysed the benthic effects of two *in situ* fisheries disturbance experiments using a combination of side-scan sonar, high-definition underwater video, sediment profile imagery, and box core sampling techniques after conventional beam trawling and box core sampling after electric pulse trawling in a southern North Sea habitat. Acoustic and optical methods visualised the morphological changes induced by experimental beam trawling, showing the flattening and homogenisation of surface sediments. Video transects found a 94% decrease in epibenthos in beam trawled sediments compared to an untrawled control site and a 74% decrease in untrawled sediments of the same transect. Box core samples taken 5.5 h, 29 h and 75 h after trawling detected a downward trend in infaunal densities and species richness that continued after the initial impact with small-bodied and juvenile taxa being especially prone to depletion. Data from shallow sediment samples showed trawl resilience in large mud shrimps and evidence of their upward movement towards the sediment surface after disturbance. Both trawl gears induced significant changes to infaunal communities, with no differential effect between the two gears. Our results suggest that in the Frisian Front, trawling may favour the survival of deep burrowers while removing surficial macrofauna.

Introduction

Bottom fishing has been a controversial practice since its origins in the thirteenth century¹. Historical records of the North Sea show maps of biogenic reefs and harder substrates which were present before the arrival of extensive bottom trawling². It is also believed that soft sediment habitats and macrobenthic communities in the southern North Sea have been shaped by anthropogenic processes including beam trawling^{3,4}. The exact causes of these changes, however, can be difficult to pinpoint and are location specific. Furthermore, fishermen argue that their methods are comparable to farming on land which creates similar if not greater effects to terrestrial habitats. In order to better manage and mitigate bottom trawling effects on benthic ecosystems, it is essential to gain a detailed understanding of their biotic and abiotic impacts on marine habitats.

Beam trawling removes benthic organisms^{5,6} and can affect the stability of a system through cascading food web modifications^{7,8}. Studies have shown increased vulnerability for large-bodied invertebrate epifauna to bottom trawl disturbance, while burrowing fauna may show more resilience^{9–11}. Trawling can also expose previously buried benthos leaving them at a higher risk for predation^{12–14}. Several methods are available to evaluate the effects of bottom trawl disturbance on benthic communities.

The majority of trawl assessment studies base their findings on the physical collection of benthos from benthic grab and core samplers and/or bottom trawls/dredges. Compared with single point benthic samplers, towed video imagery allows greater spatial coverage of the seafloor, it has the potential to record changes to seabed morphology and benthic communities, and has also been suggested as an alternative to trawl surveys^{15–18}. Acoustic techniques, such as side-scan sonar, provide an even broader perspective of seabed bathymetry and have been used extensively in trawl impact studies¹⁹. The use of sediment profile imagery (SPI) for impact assessments allows the observation of subsurface redox conditions and can be used to derive indices describing benthic habitat quality^{20–22}. Each of the aforementioned techniques has its advantages and limitations; however, the use of these methods in conjunction with each other may help gain a more complete assessment of anthropogenic disturbance²².

The primary objective of this study is to combine acoustic, optical, and sediment extraction methods, to provide a comprehensive assessment of bottom trawl disturbance in the Frisian Front. In the same study site, Tiano *et al.* reported differences in benthic biogeochemical effects created from electric pulse trawl and tickler chain beam trawling²³. While beam trawls regularly use chains to physically dig flatfish out of the sediment, pulse trawls use electric stimulation to perform the same task leading to lower gear penetration depths²⁴. The secondary objective of this study is to follow up on Tiano *et al.* by comparing differences in macrobenthos composition before and after an experimental disturbance by beam and pulse trawls²³.

Materials and methods

Study area: Frisian front

All sampling and experimental trawling was conducted in the area of the North Sea known as the Frisian Front between 53.6861°N, 4.4414°E and 53.6814°N, 4.4719°E, at a water depth of ~ 34 m (Fig. 1). The experimental area exhibited muddy sand with a median grain size averaging 92.6 μm and an organic matter percentage of 0.35 %²³. This relatively homogenous sedimentary environment hosts diverse and abundant benthic faunal assemblages^{25–27}. The high productivity in the Frisian Front arises as water currents from the north and south converge and decelerate, allowing the deposition of organic matter^{28,29}. Evidence suggests that this area has undergone a phase shift in recent decades, from a habitat dominated by the shallow burrowing brittlestar *Amphiura filiformis* to one which now supports high individual densities of the deep burrowing mud shrimp *Callinassa subterranea*^{4,30}. Although bottom trawl activities occur regularly in the Frisian Front, vessel monitoring system (VMS) analysis from Tiano et al. (2019) which was used to estimate fishing intensity, suggested that the probability of trawling in the experimental area within the prior year was minimal.

Experimental design

Experimental trawling was conducted in June 2017, with one vessel equipped with traditional tickler-chain beam trawls and the other with electric PulseWing trawls (Table 1). The vessels carried out beam trawling (BT) and pulse trawling (PT) treatments by making 7 parallel trawled passes through designated BT and PT plots (Fig. 1). More details about the gear configuration and experimental trawling procedure can be found in Tiano et al.²³.

Figure 1. Location of field experiment and data collection in the North Sea (left). Sample locations and experimental fishing areas: beam trawl (BT) plot, PulseWing trawl (PT) plot (right). For video transects and sediment profile imagery (SPI) data collection, the PT plot was used as an untrawled reference area prior to the fishing disturbance. Three additional reference deep core locations, situated outside the experimental fishing areas, are also indicated.

A before-after-control-impact (BACI) design experiment was originally planned for both fishing methods. However, logistic constraints (pre-BT sampling was limited by a late vessel replacement and early arrival of BT fishers) and inclement weather (a storm occurring shortly after PT) prevented this. As a result, a control-impact design was used for SPI and video transect data using BT impacted sediments, compared with untrawled sediments in and around the PT plot (prior to PT disturbance; Table 1). For macrofauna collection, a before-after design was used to collect most of the data for both BT and PT in their designated plots (Table 1). As a proper before-after comparison was lacking for certain BT impacted samples (see section: 2.3.4 for “deep cores” reference treatment) additional untrawled sediments were collected adjacent to BT and PT plots for comparison (control-impact design; Table 1). All experimental equipment was deployed from the RV “Pelagia” (Royal NIOZ).

Table 1. Information collected for the beam trawling (BT) and pulse trawling (PT) experiments.

Beam trawling (1 June 2017, 8:30 – 11:30)					
		Date	Start Time	Location	Impact
Side-Scan Sonar					
<i>Sonar Survey</i>		2 June 2017	10:27	BT Plot	<i>Trawled</i>
<i>Sonar Survey</i>		3 June 2017	20:59	BT Plot	<i>Trawled</i>
High Definition Hopper Camera					
<i>Video Transects</i>		2 June 2017	14:42	BT Plot	<i>Trawled</i>
<i>Video Transects</i>		3 June 2017	16:21	PT Plot*	<i>Untrawled</i>
<i>Video Transects</i>		4 June 2017	16:41	BT Plot	<i>Trawled</i>
Sediment profile imagery (SPI)					
<i>SPI images</i>		1 June 2017	13:44	BT Plot	<i>Trawled</i>
<i>SPI images</i>		4 June 2017	9:00	PT Plot*	<i>Untrawled</i>
Macrofauna collection (box corer)					
<i>T0</i>	<i>3 shallow cores</i>	1 June 2017	8:08	BT Plot	<i>Untrawled</i>
<i>T1</i>	<i>3 shallow cores</i>	1 June 2017	17:02	BT Plot	<i>Trawled</i>
	<i>2 deep cores</i>				
<i>T2</i>	<i>2 shallow cores</i>	2 June 2017	16:38	BT Plot	<i>Trawled</i>
<i>T3</i>	<i>3 shallow cores</i>	4 June 2017	14:27	BT Plot	<i>Trawled</i>
<i>Ref</i>	<i>3 deep cores</i>	4 June 2017	15:01	Surroundings	<i>Untrawled</i>
Pulse trawling (6 June 2017, 7:30 – 10:00)					
		Date	Start Time	Location	Impact
Macrofauna collection (box corer)					
<i>P0</i>	<i>3 shallow cores</i>	3 June 2017	10:16	PT Plot	<i>Untrawled</i>
	<i>5 deep cores</i>				
<i>P1</i>	<i>7 shallow cores</i>	6 June 2017	11:36	PT Plot	<i>Trawled</i>
	<i>4 deep cores</i>				

* Samples were collected before trawling

Data collection

Side-scan sonar

A Kongsberg PULSAR high resolution side scan-sonar (Kongsberg, Norway) was used to provide a qualitative assessment of the disturbance created after BT. The towfish was deployed from the stern of the RV Pelagia and was towed at 5 m over the seabed at a speed of 3.5 km h⁻¹. Side-scan sonar surveys were performed over beam trawled sediments ~26 h and ~62 h after BT (Table 1).

HD Video transects

Video footage of the seabed was collected using the downward facing HD NIOZ (Netherlands Institute for Sea Research, Texel) hopper camera, as described in Damveld *et al.*¹⁷. The frame comprised a HD video camera, a light, and 2 lasers that were placed 30 cm apart for scaling. Its height above the seabed was kept constant by adjusting the length of the towing cable, based on video live-view. During video operations, the vessel had a speed of ± 0.1 m/s. Video transects were carried out ~27 h and ~50 h after BT (Table 1). At the BT plot, these transects covered both trawled and untrawled sections (Fig. 1). Transects over sediments in the PT plot prior to trawling disturbance were used as an untrawled reference area. For the three treatments (untrawled, ~27 h, ~50 h), 2 transects of ± 200 m were performed. Video stills were automatically created for every second. For analysis, subsequent stills were selected with a 15 s interval to prevent spatial overlap. If a still was not usable, the previous or following still was selected. All still-analyses were performed by two independently working observers, to minimize potential observer-bias. For each selected still, the observed surface was determined from the laser points in ImageJ version 1.52a^{31,32}, any epibenthos present was identified to the lowest taxonomic level possible and epibenthos density (number of organisms per m²) was calculated. Further analysis was restricted to the area in between the laser points (Fig. 2e). All epifauna burrow entrances (holes) in the seabed were marked, and total surface area was determined to calculate hole density (number holes per m²), average hole size, and hole coverage (% hole surface relative to seabed surface). Location of each still was determined by an interpolation of the vessels' GPS position, which was recorded every 30 seconds. Subsequently, for individual transects in the BT plot, all stills were classified as "trawled" or "non-trawled" depending on its GPS position in relation to the trawled sediments inside and the untrawled areas directly outside the plot (Fig. 1). Comparisons were made between stills in the untrawled reference transects (all of which were "non-trawled") and "trawled" stills from ~27 h and ~50 h time steps. For further analysis of post-trawled sediments (~27 h and ~50 h), "non-trawled" stills were compared with the "trawled" stills for the individual transects at the BT plot.

For each parameter of interest (hole density, hole size, hole coverage, epibenthos density), six linear mixed effect models were created using the *lmer*-function in the lme4-package³³ from the open source software R³⁴. Model 1a and 1b were based on data from observer 1, whereas model 2a and 2b were based on data from observer 2. Model 3a and 3b were based on all values, and included 'observer' as a random explanatory variable. Models 'a' contained the full model, in which the parameter was tested against the time step (fixed) and transect (random). Models 'b' only contained the random parameter transect. For each set of models, the a-model was tested against the b-model with a one-way ANOVA to test for significance. When the average model (3a) was significant, the estimated marginal means were calculated for the time step factor with the *emmeans*-function from the emmeans R-package³⁵ and the three time steps were compared. Comparisons of trawled and non-trawled stills between time steps were performed by a similar methodology.

Figure 2. Side-scan sonar (a – d; scale bar = 10 m) and high-definition underwater video imagery (e; scale bar = 0.1 m). Sinusoidal waveforms on the seabed adjacent to flattened beam trawled sediment (a). Several furrows in beam trawled sediment after multiple trawl passes (b). Two parallel trawl tracks showing evidence of a single beam trawl pass (c). Evidence of old trawl tracks running diagonally and intersecting north of newly created experimental tracks which are located on the bottom of the image (d). A video still produced from the HD hopper camera with encircled depressions in the sediment created by infaunal burrow entrances. Only information in the area between the two laser points were processed (e).

Sediment Profile Imagery (SPI)

The subsurface structure of the seabed was studied using a Sediment Profile Imagery (SPI) camera (Ocean Imaging Systems, North Falmouth, MA, USA) made available by the Flanders Marine Institute (VLIZ), which was deployed ~ 2 h after BT in the trawled area and in an untrawled reference area (Table 1). The SPI camera consists of a galvanized frame that is lowered to the seabed. There, a prism protrudes in the seafloor, enabling the built-in camera to photograph a vertical section of the seabed (see Rhoads and Cande for the principle of the SPI³⁶). For all images, the Benthic Habitat Quality index (BHQi) was determined, based on surficial structures, sub-surficial structures, and average Redox Potential Discontinuity (aRPD) depth^{37,38}. In addition, penetration depth was measured, as well as the thickness of the fine-sediment layer at the top of the seabed. All photos were analysed in ImageJ^{31,32}, using the dimensions of the prism frame (14 x 25 cm) as scale. Differences in BHQi, RPD-depth and fine-sediment layer thickness before and after trawling were determined with Wilcoxon signed-rank tests.

Macrofauna collection

A round NIOZ box corer with a height of 55 cm and an internal diameter of 30 cm was used to collect benthic sediment samples both inside and outside experimentally trawled plots (Fig. 1). Twenty-three cores (14 cm diameter x 30 cm height) were subsampled from box cores and incubated to derive oxygen and nutrient fluxes for a biogeochemical focused study²³ (Table 1). After the incubations, the cores were sieved and processed for the analysis of species communities. An additional fourteen intact box cores were taken and sieved specifically for macrofaunal collection (Table 1).

We hereafter refer to the incubation cores as “shallow cores” and the intact box cores as “deep cores” to reflect the infaunal communities found in the samples. For the BT treatments, box core samples were taken 0.5 h before (T0; 4 shallow cores), 5.5 h after (T1; 4 shallow cores, 2 deep cores), 29 h after (T2; 2 shallow cores), and 75 h after (T3, 3 shallow cores) trawl disturbance. For the PT treatments, the box corer was deployed 3 days before (P0; 3 shallow cores, 5 deep cores) and 3.5 h after (P1; 7 shallow cores, 4 deep cores) trawling. Deep cores were only taken for T1, P0, and P1 treatments due to logistic and time constraints limiting the number of data collection methods

available (see section 2.2). To facilitate further comparisons with undisturbed samples, deep cores were taken at adjacent locations to serve as an additional untrawled “reference” treatment (Ref; 3 deep cores; Fig. 1, Table 1).

Both the deep core and shallow core samples were rinsed on a 1 mm mesh sieve before preserving faunal samples in 4% formalin seawater on board the RV Pelagia. Macrofauna were sorted and identified to the lowest possible taxon before individuals were counted and weighed (blotted wet weights) for abundance and biomass measurements.

Macrofauna found in the box cores were grouped amongst five biological traits: burrowing depth, body length, body mass, fragility, and motility. Each trait was subdivided into modalities describing trait-based characteristics. Twenty-one different modalities were identified among the five selected traits (Table S1). Infaunal densities and biomasses were compared between different treatments (T0, T1, T2, T3, P0, P1, Ref).

Univariate ecological characteristics and biological traits were analysed using a one-way ANOVA. Shapiro-Wilk and Levene’s tests were conducted to determine if data met the parametric assumptions of normal distributions and/or homogeneity of variances. If the assumptions were not met, a *log* transformation was performed to normalize the data prior to analysis. Pairwise Tukey HSD post hoc tests were applied upon detection of significant differences by the ANOVA. Effects on community composition were explored and tested by means of Between Class Analysis (BCA) on *log*-transformed organism densities³⁹ from the “ade4” package⁴⁰. Monte-Carlo tests with 999 permutations were carried out to see if trawling significantly affected benthic faunal assemblages⁴¹.

All statistical analysis and data visualization were performed using the R software³⁴.

Results

Sonar

Images from side-scan sonar revealed a visible bathymetrical disturbance in the BT plot (Fig. 2). BT impacted sediments were flattened compared to adjacent untrawled areas. In addition, noticeable furrows were observed in the trawled areas (Fig. 2b, 2c). Sinusoidal waveforms created from water movement were detected in the untrawled sediments adjacent to the BT plot, though the surrounding seabed did not show drastic differences in water depth (33.8 ± 0.6 m). Although analysis of VMS data suggested little to no bottom trawling within a year prior to the experimental trawling in the specified sites²³, old trawl tracks were observed intersecting the experimentally trawled sediments within 0.5 km of some sampling locations (Fig. 2d).

Video Transects

Compared with information from the side-scan sonar, the trawl marks and furrows were less conspicuous in the downward facing video images. Biogenic mounds produced from bioturbating macroinvertebrates were visible in all sediments though the seabed was noticeably flatter within the trawled area. Six video transects were performed, resulting in 1178 stills which were analysed by two independent observers. Data differed slightly between the two observers but was consistent among all stills and did not affect patterns observed between transects (Fig. 3). A drastic difference in epibenthos density was detected between trawled sediments from video transects covering the BT plot (0.6 ± 1.4 ind m^{-2} after 27 h, $p < 0.001$; 1.7 ± 3.1 ind m^{-2} after 50 h, $p < 0.001$) and transects covering the untrawled reference location (10.8 ± 8.9 ind m^{-2} ; Fig. 3c). Burrow holes present in trawled sediments were smaller and hence, covered significantly less area (Fig. 3b, 3d). Individual transects conducted over the BT plot also yielded significant differences between ‘trawled’ and ‘non-trawled’ video stills for all parameters (epibenthos, hole density, % hole coverage, hole size) 27 h after trawling and for epibenthos and % hole coverage 50 h after trawling (Table S2).

Figure 3. The effects of beam trawling on burrow hole density per m^2 (a), burrow hole size (b), epibenthos density per m^2 (c), and burrow hole coverage (d) from an untrawled control area, and areas covered twenty-seven (~27 h) and fifty (~50 h) hours after trawling. Only trawled stills are included for ~27 h and ~50 h time steps (See text). n.s. = not significant; . = p-value below 0.1; * = p-value below 0.05; ** = p-value below 0.01; *** = p-value below 0.001.

Figure 4. Fine sediment layer thickness (a), average Redox Potential Discontinuity (b) and Benthic Habitat Quality index score (c) for the untrawled control and areas beam trawled within 2 hours (~2 h), based on sediment profile imagery (SPI). n.s. = not significant; * = p -value below 0.05; ** = p -value below 0.01.

SPI Camera

A total of 59 SPI photos were taken. Of these, 13 photos were classified invalid, due to the seabed surface being invisible as the prism had protruded too deep. The SPI photos that were retained had a penetration depth of 17.2 ± 2.88 cm (mean $\pm$ SD). Infauna was observed in 72% of beam trawled images and 61% of untrawled images. SPI images from the BT impacted area displayed mechanically stirred sediments, showing a layer of lighter coloured fine sediment on a flattened surface (Fig. S1). In contrast, images from the untrawled area showed a non-uniform sediment surface consisting of biogenic mounds and/or sand ripples. Compared with the BT impacted images, the untrawled reference images showed a significantly thinner layer of fine sediments ($p < 0.01$) and a significantly deeper aRPD ($p < 0.05$; Fig. 4). BHQI did not differ significantly between beam trawled and untrawled areas ($p > 0.05$).

Macrofauna

In total, 121 taxa were identified in the shallow cores and deep core sediment samples used in this study. Both shallow cores and deep cores were dominated numerically by juvenile white furrow shell *Abra alba*, juvenile Ophiuroidea, and adult brittle star *Amphiura filiformis* individuals. In particular, the aforementioned juveniles were present (in relatively large quantities) in all samples except for T3 shallow cores (Table S3). In total, juveniles contributed to 54% and 55% of macrofauna in shallow and deep cores respectively.

Average densities of the burrowing mud shrimps, *Callinassa subterranea* and *Upogebia deltaura*, were noticeably higher in the deep cores (126.2 m^{-2}) compared to shallow cores (48.0 m^{-2}). As this indicated a fundamental difference between the taxa found between the two sampling methods, shallow cores and deep cores were analysed separately. When scaled to m^2 , organismal densities and biomass in the two core types fell within the same range (Fig. 5), however, direct comparisons between shallow and deep cores should be interpreted with caution given the disparity in deep (>15 cm depth) dwelling taxa.

Figure 5. Univariate ecological data collected in shallow cores (a, c, d) and deep cores (b, d, e). Dashed lines indicate the experimental fishing occurrences. Organism densities (individuals per m^2 ; a, b), infaunal biomass (grams wet weight per m^2 ; c, d) and species richness (number of taxa per sample; d, e) are compared between untrawled (T0, P0, Ref) and trawled (T1, T2, T3, P1) fishing treatments. Orange points show values from individual samples. T = Beam trawling. P = Pulse trawling.

Figure 6. Between-class analysis (BCA) of trawling effects on benthic community structure for shallow cores (top) and deep cores (bottom) including taxon projections (b, d) and associated eigenvalue diagrams (a and c bottom left). The first and second axes account for 73 % of BCA inertia in a, and 72 % in c. For clarity, only the most contributing taxa were labelled (b, d) with juvenile taxa highlighted in red. Classes are grouped per treatment; T = Beam trawling, P = Pulse trawling. “d” represents the grid scale.

Effects on general community descriptors

Macrofaunal individual densities (mean $\pm$ standard deviation) in shallow cores declined from before (T0: 7698 ± 4760 ind m^{-2} ; P0: 8207 ± 4760 ind m^{-2}) to immediately after trawling (T1: 3963 ± 1876 ind m^{-2} ; P1: 3721 ± 593 ind m^{-2}) for both gears but were only significantly lower between T0 and T3 (1213 ± 1090 ind m^{-2}) treatments ($p < 0.01$, Fig. 5). In deep cores, average densities decreased from P0 (5645 ± 2210 ind m^{-2}) to P1 (2805 ± 707 ind m^{-2}) but this was not significant ($p > 0.05$, Fig. 5). Reference (6842 ± 2278 ind m^{-2}) and T1 (6218 ± 2991 ind m^{-2}) deep cores showed very little difference in macrofaunal densities (Fig. 5).

Species richness in the shallow cores was significantly higher for T0 (22.7 taxa per sample) compared to T2 (12.5 taxa per sample, $p < 0.05$) and T3 (7.3 taxa per sample, $p < 0.001$) samples for the BT treatment (Fig. 5). Deep cores displayed a significantly higher biomass after PT in P1 (373.2 ± 111.3 g wet weight per m^2) compared to P0 (127.3 ± 32.1 g wet weight per m^2) samples ($p < 0.01$), though values between trawled and untrawled samples were similar for other univariate parameters ($p > 0.05$, Fig. 5).

Wet weight (mean $\pm$ sd) of individual organisms found in shallow cores showed variable results, increasing from T0 (5.66 ± 8.39 g ind^{-1}) to T1 (13.98 ± 12.91 g ind^{-1}), decreasing to T2 (3.28 ± 0.27 g ind^{-1}) and increasing again to T3 (13.23 ± 7.61 g ind^{-1}) for BT samples. Individual weights from PT shallow cores decreased from P0 (10.91 ± 17.19 g ind^{-1}) to P1 (8.52 ± 11.38 g ind^{-1}). Mean individual weights were notably lower in deep cores compared to shallow cores due to the higher amounts of small organisms collected in the deep samples. These showed increases from untrawled P0 (0.94 ± 0.76 g ind^{-1}) and Ref (0.99 ± 0.64 g ind^{-1}) samples compared to trawled P1 (2.10 ± 0.99 g ind^{-1}) and T1 (1.59 ± 1.51 g ind^{-1}) samples, though differences between treatments remained insignificant ($p > 0.05$).

Figure 7. Densities of taxa (individuals per m^2) representing biological traits (burrowing depth, body length, body mass, fragility and mobility) from shallow cores (a – e) and deep cores (f – j). Open symbols represent the pulse trawl treatment while closed symbols represent the beam trawl treatment. Densities are plotted against trait modalities and fishing treatments: P0, P1, T0, T1, T2, T3 for shallow cores; P0, P1, Ref, T1, for deep cores. Plots are scaled individually to emphasize within trait variation. T = Beam trawling. P = Pulse trawling.

Effects on community structure

BCA on shallow and deep cores revealed prominent trawling effects (Fig. 6). On shallow cores, the effect accounted for 43 % of compositional community variation ($p < 0.001$). Most of the trawling effect was expressed on axis 1, with a gradual ordination of both T and P temporal treatments (Fig. 6a), characterised by a persistence of *C. subterranea*, in trawled sediments opposed to most other taxon responses (Fig. 6b). Axis 2 represented differences in treatments T1 and P1, characterised by *Phoronida*, and juvenile *Spatangoida* for the former, and *Amphiura filiformis*, *Lumbrineris cyngulata*, *Oxydromus flexuosus*, *Nucula nitidosa*, and adult *Abra alba* for the latter. On deep cores, the trawling effect accounted for 33.5 % of compositional community variation ($p < 0.01$). Axis 1 mainly separated P1 with the other treatments, while axis 2 slightly isolated P0 from the other treatments (Fig. 6c). P0 was characterised by strong covariances between juvenile *A. alba* and the polychaetes *Diplocirrus glaucus* and *Scalibregma inflatum*, whereas the reference and T1 samples were more characterised by juveniles of Ophiuroidea and Echinoidea, *Eudorella truncatula*, and *Kurtiella bidentata*. Only three taxa were characteristic of the P1 treatment: *Mediomastus fragilis*, *Atherospio* and *Parexogone hebes* (Fig. 6d). Table S4 shows the taxa with the highest and lowest ordination scores for axes 1 and 2 from the BCA analysis for the shallow cores and deep cores.

Treatment effects on biological traits

For shallow burrowing organisms (residing in the top 0-5 cm in the sediment), significantly lower individual densities were detected in BT samples from the shallow cores (T0-T3, $p > 0.001$) and PT samples from deep cores (P0-P1, $p > 0.05$; Fig. 7). Shallow cores displayed a general decreasing trend in individual densities from T0 to T3 and P0 to P1 amongst almost all modalities. However, this effect was more pronounced for shallow burrowers (0-5 cm) and taxa belonging to smaller sizes in modalities representing 'body length' and 'body mass' traits. A similar decreasing pattern was observed from P0 to P1 samples collected via deep cores but not between untrawled reference and T1 deep core samples (the latter only being represented by two samples). The full dataset containing macrofaunal densities per sample can be found in Tables S5 and S6.

Discussion

It is important to note that the 'untrawled' areas in this study are not necessarily indicative of a pristine marine ecosystem. Hundreds of years of intensive bottom trawling and other types of anthropogenic disturbance in the North Sea make it virtually impossible to find habitats reflecting historical conditions unaffected by human activity^{2,42}. The findings of this study are, therefore, conservative and the effects of bottom trawling are potentially much greater in pristine habitats⁴³.

This study achieved our primary objective by using a multi-faceted approach to gain detailed information of bottom trawl effects in the Frisian Front. In spite of uncontrollable logistic constraints which did not allow the use of sonar, SPI, and video after the PT experiment, we were able to assess the trawling impact on infaunal communities from both fishing methods, which was sufficient for our secondary objective. Better meteorological conditions led to a more comprehensive assessment of BT disturbance. Our results suggest that trawling simplifies the benthic food web by reducing the number of epifaunal organisms and shallow burrowers, in line with the postulated notion of trawl-induced regime shifts occurring in the southern North Sea^{3,4}. The following discusses the results on physical, biological and biogeochemical parameters as interpreted through optical, acoustic and traditional approaches to bottom trawl assessment.

Effect on sediment morphology

The combination of acoustic and optical methods allows the observation of trawl-induced physical changes on different spatial scales. The broad perspective achieved from the side-scan sonar is used to observe the greater extent of trawling impacts^{13,18,44,45}. In our study, the sonar information

suggested the flattening and homogenisation of the seafloor, and trawl-induced furrows and other three-dimensional features were clearly visible in the sonar images. On the other hand, the downward facing video data, gave a higher level of spatial resolution which was vital for assessing biological features¹⁷. SPI information confirmed the flattening effect shown in the sonar analysis by providing details on the surface and subsurface sediment characteristics. Our SPI data differs slightly from Depestele *et al.* who conducted a trawl experiment in a nearby site in that our images featured a distinct layer of fines on the surface of BT impacted sediments (Fig. S1)²⁴. This is likely due to the shorter time interval between trawling and SPI data collection in our study (~ 2 h) as the longer time frame (~ 12 h) seen in Depestele *et al.* may have allowed the removal of the deposited fine material by tidal currents²⁴.

Effect on benthic macrofaunal communities

It was decided to keep juvenile taxa in the analysis as they contributed to a substantial proportion of all collected samples (Table S3). When conducting our BCA without juveniles, the trawling effect accounted for 7.6% less inertia in shallow cores and 1.3% less inertia in deep cores compared to the full dataset. As trawling only disturbs the surficial sediment layers^{23,24,46,47}, its effect on the macrofauna community was more visible in shallow versus deep samples. In particular, the T1 deep core samples showed no strong evidence of trawl disturbance. This may be due to limited representation (2 samples), possibly sampling in areas missed by the BT gear (in the space between the two gears), a dilution effect from having a deeper sample with more unaffected taxa or a combination of these factors (Fig. 6c).

Nevertheless, we found lower macrofaunal densities and diversity in 5 out of 6 trawled treatments (T1, T2, T3, P1 shallow cores; P1 deep cores) confirming a pattern seen in numerous trawl impact studies using macrofaunal collection methods^{6,48–50}. Video technology in trawl impact studies have documented similar decreases in observed epibenthos^{9,11,13,18,51–54}. We observed a prominent (94 %) reduction in epibenthos between trawled sediments and an untrawled transect 500 m away. Perhaps more telling was the 74% decrease in epibenthos found between trawled and untrawled areas of the same transect. Fauna found in these areas, however, may have been subject to trawl-induced sediment deposition as evidenced by our SPI camera images (Fig. S1). Nevertheless, to our knowledge, this is the first study to record trawl-induced decreases of this magnitude using underwater video. This effect was supported by the reduction of infaunal species densities found in the sediment samples.

Species residing on or near the sediment surface, such as newly settled juvenile infauna, are particularly vulnerable to trawl disturbances. The BCA for both the shallow and the deep cores, linked juvenile *A. alba* and juvenile Ophiuroidea within the top three taxa most affected by trawl disturbance (Fig. 6, Table S4). The presence or absence of trawling during important breeding seasons can have significant effects on juvenile survival⁵⁵. The idea of a regime shift induced by trawling in the Frisian Front from epifauna to burrowing infauna^{30,56} is supported by this study; particularly if the trawling disturbed juvenile settlement during a critical recruitment period.

On the other end of the spectrum, it is generally accepted that older and larger invertebrates show higher vulnerability to trawl disturbance^{9,10}. This, however, appears contradictory to our findings of increased bottom trawl resilience in certain large macrofauna. High densities of mud shrimps *C. subterranea* and *U. deltaura* in the Frisian Front help explain this phenomenon. These species could have evaded the direct trawl impact in their deeper burrows. Increases in the average weight of individuals from trawled vs. untrawled samples, suggest that smaller taxa were displaced (leaving behind the larger deeper dwelling organisms) and were thus more heavily affected by trawling at our experimental location.

Larger-sized taxa can dilute trawl-induced impacts on community biomass⁵⁷ and likely led to the inconsistent patterns in biomass found between treatments in this study. *C. subterranea*, was

observed in higher densities in trawled shallow cores where it significantly contributed to the community biomass, (Fig. 6). This increase may have been caused from the upward movement of the mud shrimps towards the sediment water interface in order to rebuild collapsed burrow entrances. Evidence from our video transect data supports this hypothesis. After an initial trawl-induced reduction in burrow hole density, the subsequent increase from 27 to 50 h after trawling implies the reconstruction of macrofaunal burrow entrances by surviving taxa.

This study did not find evidence of recovery for total macrofaunal densities and species richness in BT impacted sediments in the time frame of the investigation. After the initial BT impact (T1), values continued to decline up to 75 h (T3) after disturbance (Fig. 5a, 5e). This prolonged decrease might be explained by increased predation as trawling can create an exploitable food source for benthivores by unearthing damaged macrobenthos^{14,49,58}. Likewise, benthos found in T1 samples may have already been dead upon collection owing their continued depletion from the area by tidal currents.

Biogeochemical effects

While the effects of trawling on biogeochemistry in these sediments were assessed in Tiano et al.²³, the present study is able to add new information to this discussion. Tiano et al. found decreased sediment oxygen demand in trawled sediments²³. Based on the same samples, the present study did not detect significant patterns for community biomass between treatments and sometimes recorded a higher biomass in trawled sediment samples (Fig. 5). This suggests that the changed sediment oxygen dynamics in this location may be governed more from microbial patterns than from macrofaunal respiration.

Oxygen penetration and sediment mixing from faunal or anthropogenic sources are factors which influence benthic redox conditions²⁰. The vertical colour change (from light to dark) indicating the aRPD depth, is used as a proxy for sediment oxidation depth⁵⁹. Impact assessment studies have linked shallower aRPD depths to increased sediment oxygen demand as this will limit the oxidation of the sediment by reducing the O₂ penetration depth^{21,60,61}. The trawl-induced reduction of the aRPD found in this study, thus, appeared in contradiction with the increased thickness of the oxic layer and decreased benthic oxygen demand, found in Tiano et al.²³. Whereas oxygen profiles readjust quickly to altered oxygen consumption rates, it is likely that the aRPD needed a prolonged period in order to re-establish itself to new oxic conditions after disturbance. This is supported in Depestele et al. where trawled sediments needed over 48 hours to establish a visible oxidised layer comparable to pre-trawled conditions²⁴.

Implications

Although hampered by logistic constraints, this study allowed some comparison between the impact of two bottom gears (BT and PT) on benthic infauna. Tiano et al. found a smaller impact from PT compared to BT on sediment chlorophyll a concentrations and benthic oxygen consumption²³. On the same samples, we recorded significant effects from both bottom gears on infaunal community composition. Nonetheless, we were not able to properly distinguish whether one method had a larger impact than the other. Bergman and Meesters found a lower impact for PT compared to BT when sampling benthic megafauna⁶². Our study, however, focused mostly on smaller as well as deeper dwelling infauna, thereby observing trawl effects on a different species community. Although PT gears have been linked with lower mechanical disturbance^{23,24,63} and bycatch rates^{64,65} compared to BT gears, our results show that their direct impact on benthic infaunal communities can be comparable to that of BT in soft sediment ecosystems.

The use of multiple techniques presented a variety of perspectives on which to measure the impact of bottom trawling gears. Sonar and video transect data coupled with more detailed SPI and box core information showed that BT flattens the top layer of sediment while significantly displacing

epibenthos and smaller shallow burrowing species. Densities and biomass of deep burrowing taxa seemed relatively unaffected, although some species were probably impacted indirectly. Our study provides evidence of trawl induced behavioural changes prompting burrowing organisms to move closer to the sediment water interface potentially increasing their vulnerability to predation. Collapsed burrow entrances likely hinder burrow ventilation⁶⁶ and add an increased energetic cost upon the reconstruction of these structures⁶⁷. The loss of juvenile infauna after both BT and PT fishing may have implications for the recruitment success of benthic invertebrates.

In light of these findings, we can speculate that trawling in the Frisian Front favoured the proliferation of deep burrowing species while limiting the recruitment and abundances of macrofauna at or closer to the sediment surface. This possibility was mentioned as a potential trigger behind the shift from an *A. filiformis* to a *C. subterranea* dominated benthic community in the Frisian Front^{4,30}. Here we provide experimental results supporting this proposed mechanism, adding details on how human activities can affect benthic ecosystems.

Acknowledgements

We express our gratitude to Matt Parsons, Maria Balcelar Martinez from FUGRO and Loran Kleine Schaars, Bianka Rasch, Choo Min Yi, and Loh Ling Sheng from the NIOZ benthos lab for processing and identifying the infauna used in this study. We also thank the Flanders Marine Institute (VLIZ) for providing the SPI camera, the fishermen of the UK 227 and HD 29 for their involvement in this study and the crew of the RV Pelagia for making it possible to collect this data, even in difficult weather conditions. This research was made possible by the European Maritime and Fisheries Fund (EMFF) and the Netherlands Ministry of Agriculture Nature and Food Quality (LNV) for the Impact Assessment Pulstrawl Fishery (IAPF) project. K.J. van der Reijden, S. O'Flynn, O. Beauchard and T. Ysebaert received financial support from the Gieskes-Strijbis fund within the DISCLOSE project.

Supplementary materials

Supplementary materials can be found online at <https://doi.org/10.1016/j.marenvres.2020.104964>.

Figure S1. An assortment of sediment profile images (SPI) displaying beam trawled sediment (top) compared with images from an untrawled reference area (bottom).

Table S1. Biological traits and modalities.

Table S2. Trawled vs. untrawled comparisons of epibenthos density (individuals m⁻²), burrow hole density (holes m⁻²), burrow hole size (cm²), and burrow hole coverage (%) from video transects covering beam trawled sediments (27 h and 50 h after disturbance).

Table S3. Mean individual densities of juvenile *Abra alba* and *Ophiuroidea* per sample per m².

Table S4. Top five highest and lowest ordination scores for taxa for Axis 1 (x-axis) and Axis 2 (y-axis) from the Between-Class Analysis (BCA) from shallow subcore and deep boxcores.

Table S5. Macrofauna individual densities found in shallow cores.

Table S6. Macrofauna individual densities found in deep cores.

References

- de Groot, S. J. The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Manag.* **9**, 177–190 (1984).
- Coolen, J. W. P. North Sea Reefs. Benthic biodiversity of artificial and rocky reefs in the southern North Sea. (Wageningen University and Research, Wageningen, 2017).
- Capuzzo, E., Stephens, D., Silva, T., Barry, J. & Forster, R. M. Decrease in water clarity of the southern and central North Sea during the 20th century. *Glob. Chang. Biol.* **21**, 2206–2214 (2015).
- van Nes, E. H., Amaro, T., Scheffer, M. & Duineveld, G. C. A. Possible mechanisms for a marine benthic regime shift in the North Sea. *Mar. Ecol. Prog. Ser.* **330**, 39–47 (2007).
- Hiddink, J. G. *et al.* Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci.* 1–6 (2017).
- Sciberras, M. *et al.* Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish.* **19**, 698–715 (2018).
- Shephard, S., Brophy, D. & Reid, D. G. Can bottom trawling indirectly diminish carrying capacity in a marine ecosystem? *Mar. Biol.* **157**, 2375–2381 (2010).
- Shephard, S. *et al.* Scavenging on trawled seabeds can modify trophic size structure of bottom-dwelling fish. *ICES J. Mar. Sci.* **71**, 398–405 (2014).
- Thrush, S. F. *et al.* Disturbance of the marine benthic habitat by commercial fishing: Impacts at the scale of the fishery. *Ecol. Appl.* **8**, 866–879 (1998).
- Tillin, H. M., Hiddink, J. G., Jennings, S. & Kaiser, M. J. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar. Ecol. Prog. Ser.* **318**, 31–45 (2006).
- O'Neill, F. G., Robertson, M., Summerbell, K., Breen, M. & Robinson, L. A. The mobilisation of sediment and benthic infauna by scallop dredges. *Mar. Environ. Res.* **90**, 104–112 (2013).
- Kaiser, M. J. & Spencer, B. E. Fish scavenging behaviour in recently trawled areas. *Mar. Ecol. Prog. Ser.* **112**, 41–50 (1994).
- Schwinghamer, P. *et al.* Effects of experimental otter trawling on surficial sediment properties of a sandy-bottom ecosystem on the Grand Banks of Newfoundland. *Conserv. Biol.* **12**, 1215–1222 (2010).
- Groenewold, S. & Fonds, M. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. *ICES J. Mar. Sci.* **57**, 1395–1406 (2000).
- McIntyre, F. D., Neat, F., Collie, N., Stewart, M. & Fernandes, P. G. Visual surveys can reveal rather different 'pictures' of fish densities: Comparison of trawl and video camera surveys in the Rockall Bank, NE Atlantic Ocean. *Deep. Res. Part I Oceanogr. Res. Pap.* **95**, 67–74 (2015).
- Ayma, A. *et al.* Comparison between ROV video and Agassiz trawl methods for sampling deep water fauna of submarine canyons in the Northwestern Mediterranean Sea with observations on behavioural reactions of target species. *Deep. Res. Part I Oceanogr. Res. Pap.* **114**, 149–159 (2016).
- Damveld, J. H. *et al.* Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophys. Res. Lett.* **45**, (2018).
- Smith, C. J., Banks, A. C. & Papadopoulos, K.-N. Improving the quantitative estimation of trawling impacts from sidescan-sonar and underwater-video imagery. *ICES J. Mar. Sci.* **64**, 1692–1701 (2007).
- Graham, N., Jones, E. G. & Reid, D. G. Review of technological advances for the study of fish behaviour in relation to demersal fishing trawls. *ICES J. Mar. Sci.* **61**, 1036–1043 (2004).
- Teal, L., Parker, E. & Solan, M. Sediment mixed layer as a proxy for benthic ecosystem process and function. *Mar. Ecol. Prog. Ser.* **414**, 27–40 (2010).
- Mulsow, S., Krieger, Y. & Kennedy, R. Sediment profile imaging (SPI) and micro-electrode technologies in impact assessment studies: Example from two fjords in Southern Chile used for fish farming. *J. Mar. Syst.* **62**, 152–163 (2006).
- Birchenough, S. N. R. *et al.* Lights, camera and acoustics: Assessing macrobenthic communities at a dredged material disposal site off the North East coast of the UK. *J. Mar. Syst.* **62**, 204–216 (2006).
- Tiano, J. C. *et al.* Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling. *ICES J. Mar. Sci.* (2019).
- Depestele, J. *et al.* Comparison of mechanical disturbance in soft sediments due to tickler-chain SumWing trawl versus electro-fitted PulseWing trawl. *ICES J. Mar. Sci.* (2018).
- Dauwe, B., Herman, P. M. J. & Heip, C. H. R. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Mar. Ecol. Prog. Ser.* **173**, 67–83 (1998).
- Dewicke, A., Rottiers, V., Mees, J. & Vincx, M. Evidence for an enriched hyperbenthic fauna in the Frisian front (North Sea). *J. Sea Res.* **47**, 121–139 (2002).
- Duineveld, G. C. A. & Boon, A. R. Short-term variations in the fluxes and composition of seston in near-bottom traps in the southern North Sea. *Helgol. Mar. Res.* **56**, 140–148 (2002).
- Otto, L. *et al.* Review of the physical oceanography of the North Sea. *Netherlands J. Sea Res.* **26**, 161 (1990).
- Boon, A. & Duineveld, G. Chlorophyll *a* as a marker for bioturbation and carbon flux in southern and central North Sea sediments. *Mar. Ecol. Prog. Ser.* **162**, 33–43 (1998).
- Amaro, T. The benthic shift of the Frisian front ecosystem - possible mechanisms. PhD Thesis. (Wageningen University and Research, 2005).
- Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* vol. 9 671–675 (2012).
- Schindelin, J. *et al.* Fiji: An open-source platform for biological-image analysis. *Nature Methods* vol. 9 676–682 (2012).
- Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
- R Development Core Team, X. R: A language and environment for statistical computing. (2014).
- Lenth, R. Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.2-1. (2020).
- Rhoads, D. C. & Cande, S. Sediment profile camera for in situ study of organism-sediment relations. *Limnol. Oceanogr.* **16**, 110–114 (1971).
- Nilsson, H. C. & Rosenberg, R. Benthic habitat quality assessment of an oxygen stressed fjord by surface and sediment

- profile images. *J. Mar. Syst.* **11**, 249–264 (1997).
38. Shumchenia, E. J. & King, J. W. Comparison of methods for integrating biological and physical data for marine habitat mapping and classification. *Cont. Shelf Res.* **30**, 1717–1729 (2010).
 39. Doledec, S. & Chessel, D. Seasonal successions and spatial variables in freshwater environments. I. Description of a complete two-way layout by projection of variables. *Acta Oecologica/Oecologia Gen.* **8**, 403–426 (1987).
 40. Dray, S., Dufour, A. & Ade4: Analysis of Ecological Data. *Explor. Euclidean Methods Environ. Sci.* **22**, (2007).
 41. Heo, M. & Gabriel, K. R. A permutation test of association between configurations by means of the RV coefficient. *Commun. Stat. Part B Simul. Comput.* **27**, 843–856 (1998).
 42. Robinson, L. A. & Frid, C. L. J. Historical Marine Ecology: Examining the Role of Fisheries in Changes in North Sea Benthos. *AMBIO A J. Hum. Environ.* **37**, 362–372 (2008).
 43. Jones, J. B. Environmental impact of trawling on the seabed: A review. *New Zeal. J. Mar. Freshw. Res.* **26**, 59–67 (1992).
 44. Lucchetti, A. & Sala, A. Impact and performance of Mediterranean fishing gear by side-scan sonar technology. *Can. J. Fish. Aquat. Sci.* **69**, 1806–1816 (2012).
 45. Humborstad, O.-B., Nøttestad, L., Løkkeborg, S. & Rapp, H. T. RoxAnn bottom classification system, sidescan sonar and video-sledge: spatial resolution and their use in assessing trawling impacts. *ICES J. Mar. Sci.* **61**, 53–63 (2004).
 46. Palanques, A., Puig, P., Guillén, J., Demestre, M. & Martín, J. Effects of bottom trawling on the Ebro continental shelf sedimentary system (NW Mediterranean). *Cont. Shelf Res.* **72**, 83–98 (2014).
 47. Mengual, B. *et al.* Influence of bottom trawling on sediment resuspension in the “Grande-Vasière” area (Bay of Biscay, France). *Ocean Dyn.* **66**, 1181–1207 (2016).
 48. Fariñas-Franco, J. M., Allcock, A. L. & Roberts, D. Protection alone may not promote natural recovery of biogenic habitats of high biodiversity damaged by mobile fishing gears. *Mar. Environ. Res.* **135**, 18–28 (2018).
 49. Mangano, M. C. *et al.* The effectiveness of fish feeding behaviour in mirroring trawling-induced patterns. *Mar. Environ. Res.* **131**, 195–204 (2017).
 50. Pranovi, F., Raicevich, S., Franceschini, G., Farrace, M. & Giovanardi, O. Rapido trawling in the northern Adriatic Sea: effects on benthic communities in an experimental area. *ICES J. Mar. Sci.* **57**, 517–524 (2000).
 51. Buhl-Mortensen, L., Ellingsen, K. E., Buhl-Mortensen, P., Skaar, K. L. & Gonzalez-Mirelis, G. Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on density, diversity, and composition. *ICES J. Mar. Sci.* **73**, i98–i114 (2016).
 52. Smith, C. J., Papadopoulou, K. N. & Diliberto, S. Impact of otter trawling on an eastern Mediterranean commercial trawl fishing ground. *ICES J. Mar. Sci.* **57**, 1340–1351 (2000).
 53. Engel, J. & Kvitek, R. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. *Conserv. Biol.* **12**, 1204–1214 (1998).
 54. Collie, J., Escanero, G. A. & Valentine, P. C. Photographic evaluation of the impacts of bottom fishing on benthic epifauna. *ICES J. Mar. Sci.* **57**, 987–1001 (2000).
 55. Abdul Jaleel, K. U. *et al.* Evaluation of changes in macrobenthic standing stock and polychaete community structure along the south eastern Arabian Sea shelf during the monsoon trawl-ban. *Cont. Shelf Res.* **102**, 9–18 (2015).
 56. van Nes, E., Amaro, T., Scheffer, M. & Duineveld, G. Possible mechanisms for a marine benthic regime shift in the North Sea. *Mar. Ecol. Prog. Ser.* **330**, 39–47 (2007).
 57. Hinz, H., Prieto, V. & Kaiser, M. J. Trawl disturbance on benthic communities: chronic effects and experimental predictions. *Ecol. Appl.* **19**, 761–773 (2009).
 58. van Denderen, P. D., van Kooten, T. & Rijnsdorp, A. D. When does fishing lead to more fish? Community consequences of bottom trawl fisheries in demersal food webs. *Proc. R. Soc. B* **280**, 20131883 (2013).
 59. Rhoads, D. C. & Cande, S. Sediment Profile Camera for in Situ Study of Organism-Sediment Relations. *Limnol. Oceanogr.* **16**, 110–114 (1971).
 60. Wildish, D. J., Hargrave, B. T., MacLeod, C. & Crawford, C. Detection of organic enrichment near finfish net-pens by sediment profile imaging at SCUBA-accessible depths. in *Journal of Experimental Marine Biology and Ecology* vols 285–286 403–413 (2003).
 61. Badino, G., Bona, F., Maffiotti, A., Giovanardi, O. & Pranovi, F. Impact of mechanical clam harvesting on a benthic habitat: evaluation by means of sediment profile imaging. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **14**, S59–S67 (2004).
 62. Bergman, M. J. N. & Meesters, E. H. First indications for reduced mortality of non-target invertebrate benthic megafauna after pulse beam trawling. *ICES J. Mar. Sci.* **77**, 846–857 (2020).
 63. Depestele, J. *et al.* Measuring and assessing the physical impact of beam trawling. *ICES J. Mar. Sci.* **73**, 15–26 (2015).
 64. van Marlen, B., Wiegerinck, J. A. M., van Os-Koomen, E. & van Barneveld, E. Catch comparison of flatfish pulse trawls and a tickler chain beam trawl. *Fish. Res.* **151**, 57–69 (2014).
 65. van der Reijden, K. J. *et al.* Survival of undersized plaice (*Pleuronectes platessa*), sole (*Solea solea*), and dab (*Limanda limanda*) in North Sea pulse-trawl fisheries. *ICES J. Mar. Sci.* 1–9 (2017).
 66. Witbaard, R. & Duineveld, G. C. A. Some aspects of the biology and ecology of the burrowing shrimp *Callinassa subterranea* (Montagu; Thalassinidea) from the southern north sea. *Sarsia* **74**, 209–219 (1989).
 67. Rowden, A. A. & Jones, M. B. The burrow structure of the mud shrimp *Callinassa subterranea* (Decapoda: Thalassinidea) from the north sea. *J. Nat. Hist.* **29**, 1155–1165 (1995).

Chapter 4

Connecting the dots: a multi-scale, multi-resolution approach to marine habitat mapping

Karin J. van der Reijden

Laura L. Govers

Leo Koop

Johan H. Damveld

Peter M. J. Herman

Sebastiaan Mestdagh

Gerjan Piet

Adriaan D. Rijnsdorp

Grete E. Dinesen

Mirjam Snellen

Han Olff

Published as

van der Reijden KJ, Govers LL, Koop L, Damveld JH, Herman PMJ, Mestdagh S, Piet G, Rijnsdorp AD, Dinesen GE, Snellen M, Olff H (2021) Beyond connecting the dots: A multi-scale, multi-resolution approach to marine habitat mapping. *Ecological Indicators* 128, [107849]

Abstract

Conflicts of interests between economic and nature conservation stakeholders are increasingly common in coastal seas, inducing a growing need for evidence-based marine spatial planning. This requires accurate, high-resolution habitat maps showing the spatial distribution of benthic assemblages and enabling intersections of habitats and anthropogenic activities. However, such detailed maps are often not available because relevant biological data are scarce or poorly integrated. Instead, physiotope maps, solely based on abiotic variables, are now often used in marine spatial planning. Here, we investigated how pointwise, relatively sparse biological data can be integrated with gridded, high-resolution environmental data into informative habitat maps, using the intensively used southern North Sea as a case-study. We first conducted hierarchical clustering to identify discrete biological assemblages for three faunal groups: demersal fish, epifauna, and endobenthos. Using Random Forest models with high-resolution abiotic predictors, we then interpolated the distribution of these assemblages to high resolution grids. Finally, we quantified different anthropogenic pressures for each habitat. Habitat maps comprised a different number of habitats between faunal groups (6, 13, and 10 for demersal fish, epifauna, and endobenthos respectively) but showed similar spatial patterns for each group. Several of these 'fauna-inclusive' habitats resembled physiotores, but substantial differences were also observed, especially when few (6; demersal fish) or most (13; epifauna) physiotores were delineated. Demersal fishing and offshore wind farms (OWFs) were clearly associated with specific habitats, resulting in unequal anthropogenic pressure between different habitats. Natura-2000 areas were not specifically associated with demersal fishing, but OWFs were situated mostly inside these protected areas. We thus conclude that habitat maps derived from biological datasets that cover relevant faunal groups should be included more in ecology-inclusive marine spatial planning, instead of only using physiotope maps based on abiotic variables. This allows better balancing of nature conservation and socio-economic interests in continental shelf seas.

Introduction

Continental shelf seas are subject to increasing anthropogenic activities, such as shipping¹, sediment extraction², offshore wind farms³ (OWFs), and industrial fishing⁴. Meanwhile, calls for effective marine conservation are increasing⁵, for example, in demanding the establishment of no-use marine protected areas⁶. Ecology-inclusive marine spatial planning that balances the socio-economic and ecological interests can help to resolve current spatial conflicts of interest^{7,8}. At present, anthropogenic activities are predominantly located in areas where they are most profitable³. However, to improve the balance between both socio-economic and conservation interests, ecological knowledge on, for instance, species abundance and diversity, community sensitivity, and ecosystem resilience should also be included in spatial zonation of anthropogenic activities. This requires accurate high-resolution maps that capture the spatial heterogeneity, extent, and biological characteristics of different marine habitats^{8,9}. These can be translated into maps representing the uniqueness, diversity, vulnerability and resilience of local demersal assemblages and their relation to anthropogenic pressures^{8,10}.

Biological sampling (through research-based trawls, cores, grabs, etc.) provides information on the spatial distribution of benthic assemblages. However, such sampling is very labour intensive and expensive. It furthermore is prone to methodological limitations in capture efficiency, site accessibility, and sampling of all biological strata^{11,12}, and to observer bias in taxonomic identification¹³. In addition, biological samples are by nature 'station-based' point samples and thus need interpolation to obtain full-coverage predictions of benthic assemblage distributions. Accuracy increases with better interpolation techniques¹⁴ and higher sampling resolution^{10,15}.

Due to these difficulties of collecting and analysing biological data, high-resolution environmental ('abiotic') variables are often typically used instead. Variables as water temperature, bathymetric depth, salinity and sediment type are typically derived through combinations of remote sensing, modelling and point measurements, and often form the basis for habitat mapping processes. This includes the currently most commonly used habitat mapping approach: hierarchical classification schemes¹⁶. These maps are structured in multiple (stacked) hierarchical 'levels'. Lower levels delineate broad habitat types based only on environmental factors, often combinations of bathymetry and sediment composition categories. The more detailed, higher levels subsequently divide these into more specific habitat types, based on additional environmental factors and/or station-based biological information^{16–18}. However, usage of these maps is often limited to the broad, low-level habitat types, so based on environmental variables only^{17,19,20}.

Here, we define maps that are exclusively based on environmental variables as 'physiotope maps', which are often seen as surrogates for benthic assemblage distributions^{21–24}. However, although benthic communities are strongly affected by environmental conditions, they typically are not defined by static environmental conditions alone^{17,25}. Communities and environmental conditions can be heavily affected by biological processes like predation, competition, or ecosystem engineering effects^{26,27}, and can change under anthropogenic pressures, such as frequent bottom trawling²⁸. Moreover, the relevance of different environmental factors varies greatly between spatial scales^{29,30}, differs between faunal groups (e.g. demersal fish versus endobenthos³¹), and not all relevant environmental variables may be included in physiotope maps. Therefore, physiotope maps at best represent the required biological reality only partially.

Using the North Sea as a case-study, we here explore a novel approach to derive high-resolution habitat maps that combine low resolution, point-based biological data of three faunal groups with higher resolution key environmental variables. The resulting habitat maps were compared with physiotope maps to visualize the contribution of biological input data. In this, the role of fishing intensity as an anthropogenic environmental variable was studied and spatial associations of anthropogenic uses (fisheries, OWFs, Natura-2000 areas) with the identified habitats were

quantified. We conclude with a discussion on our findings can improve ecology-inclusive marine spatial planning in coastal seas.

Methods

In our study we compare habitat maps based on biological samples, spatially interpolated using high-resolution environmental gradients with physiotope maps that are solely based on the same environmental gradients (Fig. 1). Sampled species abundances of three faunal groupings were separately clustered into assemblages with a hierarchical clustering. Environmental gradients were determined by reducing 21 environmental variables (Table 1) to less dimensions (main environmental gradients) using Principal Component Analysis (PCA). The point-wise assemblages were interpolated based on these main environmental gradients into full-coverage habitat maps. The resulting habitat maps were then compared to physiotope maps, which resulted from a clustering of the main environmental gradients exclusively, to investigate the added value of biological information in the habitat mapping exercise. We additionally studied the potential of fishing intensity as an explanatory, anthropogenic variable by performing the whole analysis twice: first with the 21 environmental variables, and then with the 21 environmental variables in combination with fishing intensity.

Figure 1. Schematic overview of the methodology presented in this paper to create the final habitat (green boxes) and physiotope (yellow boxes) maps. Grey boxes depict input data. Purple letters refer to appendices where additional information can be found regarding the selection procedure of endobenthos data (A), the environmental variables used (B), the characteristics of resulting habitat maps (C), a comparison in clustering methodology (D), a comparison of interpolation methodology (E), the characteristics of resulting physiotores (F), and the added value of fishing intensity as explanatory variable (G).

Study area

In this study, we focused on the offshore Central and Southern North Sea, defined by the International Council for the Exploration of the Sea (ICES) as subdivisions IVb and IVc (Fig. 2). To avoid any near-coastal effects of modelled parameters, the national territorial waters (12 nautical miles from shoreline) are excluded from the analysis.

Figure 2. Bathymetry of the southern North Sea, including names of important subareas. The study area is delineated with a black solid line. Grey hatched areas depict Natura-2000 areas and offshore wind farms, and two-letter codes reflect surrounding countries. Black dotted lines represent Exclusive Economic Zones (EEZ).

Biotic data

Demersal fish

We obtained demersal fish abundances from the annual North Sea Beam Trawl Survey (BTS). This survey samples demersal fishes with a beam trawl (8 m width, 4 cm mesh size), at relatively fixed stations throughout the North Sea (Fig. 3A) by performing 30-min hauls at 5 knots (covering ~ 0.037 km²). All caught individuals were identified and counted (see ICES for detailed methodology³²). We obtained all BTS-data from the DATRAS website for the years 2008-2015³³. Only valid hauls with species recordings, a maximum distance of 10 km covered, and located within the study area were included. Species with missing abundances were removed, as were all non-fish species and species

with recordings in <5 hauls. For each haul, we determined species density (in number per m²), using swept area (m²) as the product of beam width and track distance.

Epifauna

For epifauna, we used the data collected in 2003 and 2004 by the internationally harmonized MAFCONS project (Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity) that sampled epifauna with a small beam trawl (2m width, 5 mm mesh size). Five-min hauls were performed at 1 knot (covering ~ 300 m²) at 283 stations (Fig. 3B). All caught organisms were determined to the lowest possible taxonomic level (see detailed methodology in Callaway *et al.*³⁴). A checked and cleaned version of the dataset was used here, comprising a list of species abundances (in total number or weight per m², depending on the species) per station (Robinson, Unpublished data). We removed stations outside our study area, species that were not epifauna, species that appeared in <5 stations, and species without any weight or number recordings. Registrations with some unquantified presences were given the species-specific minimum observed weight/number per m².

Figure 3. Sampling locations for demersal fish (A), epifauna (B), and endobenthos (C) within the study areas. Grey hatched areas depict Natura-2000 areas and offshore wind farms. Black dotted lines represent Exclusive Economic Zones (EEZ).

Endobenthos

For infauna, we used the data sampled with a boxcore or grab (covering ~ 0.071 m²) in the internationally harmonized North Sea Benthos Survey (NSBS) in 1986³⁵. The stations were regularly distributed across the entire North Sea (Fig. 3C). Samples were sieved over a 1 mm sieve and all organisms were subsequently identified to the lowest level possible, resulting in a dataset of species densities (see Heip *et al.*, for detailed methodology³⁶). This dataset was obtained from the EMODnet Biology data portal³⁷. Subsequent endobenthos surveys have been performed since the NSBS, but these could unfortunately not be merged in a single, sufficiently uniform dataset (results shown in Appendix A). To increase replicability of our study, we decided to only use the well-tested NSBS dataset, despite its age. Sampling stations outside our study area were removed, as were species that appeared in <5 stations, and species without any recorded densities.

Biological clustering

Each biological dataset was analysed separately. We determined Bray-Curtis dissimilarities in community composition between sampling stations based on the fourth root of species densities¹³. Hierarchical clustering was then done using an average linkage sorting^{13,38}, adopting a Flexible

Dissimilarity Height (FDH-) approach. Based on visual inspection of the dendrograms, we performed a first cut-off at 0.50. Stations that were then in clusters with ≤ 5 stations were subsequently merged with larger clusters, as long as the dissimilarity height did not exceed 0.60. Remaining clusters with ≤ 5 stations were then removed as outliers. In appendix D, we test the robustness of this approach by comparing it to a Fixed Number (FN-) approach, which identified a fixed number of clusters (here: 5, 10, 15) without considering dissimilarity height or cluster size.

Physiotopes

A total of 21 environmental variables were included in the physiotope clustering (Table 1; see Appendix B for detailed descriptions and figures of each individual variable). We additionally investigated the added value of fishing intensity as an explanatory, anthropogenic variable, which is further described in Appendix G.

All environmental variables were bilinearly interpolated to the highest resolution available ($\sim 180 \times 180$ m). Physiotope classification followed the methodology described in Verfaillie *et al.*⁴⁴. To avoid collinearity, all variables were summarized with a Principal Component Analysis (PCA) into environmental gradients. The first seven principal components (eigenvalue > 1) were kept, which together explained 77.5% of the observed variation. A hierarchical cluster analysis was performed on all grid cells, based on these seven main environmental gradients, using Wards method in the 'Rclusterpp' package⁴⁵. Subsequent K-means partitioning used the hierarchical tree as starting points and were set to yield equal numbers of clusters as defined for biological assemblages, to facilitate the comparison between physiotopes and habitat maps.

Modelling habitat distributions

Habitat distributions were determined by applying Random Forest machine learning algorithm to the identified biological assemblages for the three faunal groups separately⁴⁶. The Random Forest classifier calculated the probability for a grid cell to belong to each assemblage, based on the main environmental gradients. This avoided collinearity of individual environmental variables and provided equal weight to the different gradients. Each model encompassed 500 internal runs. This resulted in three habitat maps with a resolution of $\sim 180 \times 180$ m. Model accuracy was interpreted from 'Out-of-Bag' (OOB)-estimates and the median kappa value obtained from a cross-validation based on 100 iterations with half of the input data, using the 'rfUtilities' package⁴⁷. We also determined spatial accuracy patterns. For this, a cross-validation was performed on five cluster-stratified folds after which the Shannon diversity index was determined for each grid cell. This index is 0 when grid cells were assigned to the same habitat (cluster) in all 5 predicted maps (so high accuracy), and increases to 1.6 when the cell was assigned to a different cluster in all 5 maps. The more different habitats a cell was assigned to in the 5 maps, and the more equal the proportional abundances of the five habitats were in the 5 runs, the more difficult it is to correctly predict which habitat the cell would be assigned to the next run. The Shannon entropy therefore quantifies the uncertainty (entropy or degree of surprise) associated with this prediction.

In Appendix E, the added value of environmental knowledge in the interpolation step is investigated. For this, we created alternative full-coverage habitat maps, using the Nearest Neighbour method (NN-approach). This method applies *Voronoi* tessellation^{48,49} on the point-wise biological clusters.

Table 1. Environmental variables used in this study, and the anthropogenic variable fishing intensity as used in appendix G.

Environmental variable	Explanation	Source
Depth	Absolute water depth	³⁹
BPI-5	Depth relative to its surrounding, using a 5 km-radius	Derived from the bathymetry data
BPI-50	Depth relative to its surrounding, using a 50 km-radius	Derived from the bathymetry data
BPI-500	Depth relative to its surrounding, using a 500 km-radius	Derived from the bathymetry data
Slope	Angle of the seabed compared to a flat seabed	Derived from the bathymetry data
Northness	Cosine of the compass direction of the seabed slope	Derived from the bathymetry data
Eastness	Sine of the compass direction of the seabed slope	Derived from the bathymetry data
Mean temperature	Average of the monthly temperature at the seabed over 2008-2017	Atlantic-European North West Shelf – Ocean Physics Analysis and Forecast Model by MetOffice ⁴⁰
Maximum temperature	Average of the annual maximum monthly temperature at the seabed over 2008-2017	Derived from the temperature data
Minimum temperature	Average of the annual minimum monthly temperature at the seabed over 2008-2017	Derived from the temperature data
Temperature variability	Average of the annual differences in maximum and minimum monthly temperatures at the seabed over 2008-2017	Derived from the temperature data
Mean salinity	Average of the monthly salinity at the seabed over 2008-2017	Atlantic-European North West Shelf – Ocean Physics Analysis and Forecast Model by MetOffice ⁴⁰
Salinity variability	Average of the annual differences in maximum and minimum monthly salinity at the seabed over 2008-2017	Derived from the salinity data
Mean mixed layer depth	Average of the annual monthly mixed layer depth over 2008-2017	Atlantic-European North West Shelf – Ocean Physics Analysis and Forecast Model by MetOffice ⁴⁰
Mixtures	Average number of months per year that the water column is completely mixed	Derived from the bathymetry and mixed layer depth data
Average wind-driven BSS	Annual average of daily wind-driven bed shear stress, determined from modelled wave height and peak period values combined with bathymetry data over 2015-2017	Atlantic-European North West Shelf – Ocean Wave Analysis and Forecast Model by MetOffice ⁴⁰
Maximum wind-driven BSS	Average of annual maximum daily wind-driven bed shear stress, determined from modelled wave height and peak period values combined with bathymetry data over 2015-2017	Derived from the wave and bathymetry data
Tidal-driven BSS	Modelled estimates of tidal bed shear stress	Obtained from a hydrodynamic model by John Aldridge
Mud	The modelled fraction of mud	(CEFAS), as used in ^{41,42}
Sand	The modelled fraction of sand	⁴³
Gravel	The modelled fraction of gravel	⁴³

Anthropogenic variable

Fishing intensity* The average annual international fishing intensity over 2010-2012

* The usage of this variable as an explanatory variable is further described in Appendix G.

Anthropogenic pressures

We studied habitat associations of anthropogenic pressures by comparing the spatial distributions of habitats and anthropogenic activities. As anthropogenic variables we used international demersal fishing intensity, given as the average annual swept area ratio (SAR; year⁻¹) over 2010-2012⁴, and rasterized shapefiles of OWFs⁵⁰ and Natura-2000 areas⁵¹. Grid cells with a SAR >1 were classified as 'fished', and average fishing intensity of the fished cells was calculated. In addition, habitat-specific extents were determined for the presence of OWFs and Natura-2000 areas. Finally, we compared fishing pressure and OWF presence in- and outside of Natura-2000 areas.

Results

Habitat maps

The datasets used for demersal fish, epifauna, and endobenthos included 1501, 192, and 149 stations and 73, 147, and 200 species, respectively. Hierarchical clustering resulted in 6, 13, and 10 assemblages for demersal fish, epifauna, and endobenthos, respectively, that were interpolated to full-scale habitat maps (Fig. 4; Table 2; see Appendix C for detailed descriptions of the habitats and their characteristic species and environmental conditions). Herein, the FDH-approach was favoured over the FN-approach to determine the assemblages because it corrected for deviating stations that were unique clusters in the FN-approach (Appendix D). Secondly, the Random Forest models were favoured over the NN-approach (Appendix E) as their results matched better with our independent knowledge of the heterogeneity of the North Sea. Moreover, fishing intensity was not included as an explanatory variable as it did not alter the habitat distributions (Appendix G).

The spatial extent of different habitat varied between faunal groups (DF: 0-53%; EF: 3-16%; EB: 3-23%; Table 2). However, general patterns could be observed among the three faunal groups (Fig. 4). Although the deeper waters northwest of the Dogger Bank were typified as one large demersal fish habitat (DF-1), they contained multiple epifauna and endobenthos habitats. These were located near the Norwegian trench (EF-2&3, EB-9), the Devil's Hole (EF-7, EB-3), the western coast (EF-1, EB-1&2) and the central North Sea (EF-4&8, EB-4) (Fig. 4). The shallower waters southeast of the Dogger Bank showed a similar pattern. Habitat DF-2 for demersal fish covered the entire area, whereas distinct epifauna and endobenthos habitats separated between the Brown Bank region (EF-11, EB-6), the Central Oyster Grounds (EF-10, EB-10), around the Dogger Bank (EF-5, 12&13, EB-5 & 7), and the eastern coast (EF-9, EB-8). Interestingly, the two demersal fish habitats identified very locally near the outer Wash (DF-4, DF-5) did not have equivalent distinct epifauna or endobenthos habitats.

The demersal fish Random Forest model had an overall Kappa of 0.82 and an OOB-estimate of 8%, showing a reliable prediction of the habitats (Table 2). Prediction accuracy was lowest for the smallest habitats (<0.01% coverage) DF-3 and DF-6, whereas the slightly larger sized (<1%) habitats DF-4 and DF-5 already showed accuracies of >74% (Table 2). For epifauna and endobenthos, models showed reasonable, but lower overall Kappa values (0.59 and 0.58 respectively) and higher OOB-estimates (37% and 35% respectively; Table 2). Habitat extent, number of observations within the cluster, and habitat-specific accuracy were not clearly related (Table 2). Spatial patterns in accuracy differed between the three models (Fig. 5.) Uncertainty in demersal fish habitats was dominantly restricted to the Central Oyster Grounds and south of the Dogger Bank (Fig. 5A). For epifauna and endobenthos, higher Shannon diversity values were more common and widespread over the study area, representing lowered model consistency between the five cross-validations. Whereas the classifications of epifauna habitats were most consistent in the eastern and southern North Sea (Fig. 5B), endobenthos habitats were classified more consistently at the Dogger Bank, Central Oyster Grounds and the Brown Ridge Region (Fig. 5C).

Figure 4. The spatial distribution of demersal fish (A), epifauna (C), and endobenthos (E) habitats, and the corresponding maps with comparable numbers of physiotypes (B:6, D:13, F:10). Grey hatched areas depict Natura-2000 areas and offshore wind farms. Black dotted lines represent national economic exclusive zones.

Table 2. Model accuracy*, habitat details, and anthropogenic pressures*** for demersal fish, epifauna, and endobenthos habitat maps.**

Habitat	Model accuracy details					Habitat details		Anthropogenic usage						
	Nr. Stations	Class. Error	User acc	Pred acc	Overall Kappa	OOB-estimate (%)	Coverage (%)	Extent (x 10,000 km ²)	% Fished	Fishing intensity (mean ± SD)	% Offshore wind farm	% Natura 2000 area	% Fished in Natura 2000 area	% OWF in Natura 2000 area
Demersal fish	DF-1	402	0.080	92.2	93.2		44.87	12.67	32.13	4.36 ± 3.87	0.66	3.69	42.66	0.08
	DF-2	1007	0.041	96.1	92.9		53.48	15.10	48.07	3.20 ± 2.83	5.86	36.85	43.96	10.64
	DF-3	28	1.000	0.0	0.0	0.824	0.01		61.15	2.62 ± 1.30	0.42	23.14	19.27	1.83
	DF-4	21	0.238	79.4	80.7	8.36	0.79	0.22	8.79	3.53 ± 3.45	11.09	41.43	17.32	8.90
	DF-5	31	0.323	70.9	74.4		0.85	0.24	27.41	5.42 ± 4.46	9.62	48.16	26.39	10.08
	DF-6	10	1.000	0.0	NA		0.00	0.00	32.62	4.93 ± 3.66	1.07	100	32.62	1.07
Epifauna	EF-1	10	0.600	40.4	40.4		9.25	2.61	29.25	4.14 ± 3.29	3.41	9.30	35.72	1.87
	EF-2	7	1.000	82.4	79.0		3.26	0.92	33.09	4.84 ± 3.90	0.00	0.31	7.02	0.00
	EF-3	11	0.182	64.5	73.7		8.78	2.48	38.28	5.08 ± 4.18	0.29	1.43	47.59	0.01
	EF-4	8	0.500	40.0	44.9		5.76	1.63	14.77	3.43 ± 2.93	0.01	0.28	21.09	0.00
	EF-5	7	0.571	20.9	17.9		3.14	0.89	54.83	2.80 ± 2.42	0.45	2.84	50.38	6.06
	EF-6	9	0.667	0.0	NA		4.34	1.23	25.14	3.81 ± 3.12	3.50	31.25	26.61	6.37
	EF-7	11	0.091	81.7	61.9	37.18	7.66	2.16	32.68	6.21 ± 4.84	0.23	1.17	56.78	0.01
	EF-8	6	0.333	50.1	38.9		3.30	0.93	23.72	2.15 ± 1.67	0.00	0.52	65.24	0.00
	EF-9	44	0.091	42.9	59.8		16.29	4.60	45.85	3.63 ± 3.06	2.43	22.92	30.76	1.36
	EF-10	9	0.222	33.6	36.7		6.25	1.77	45.01	2.38 ± 1.96	0.81	14.52	40.12	1.16
	EF-11	9	0.444	90.6	90.3		11.15	3.15	45	3.73 ± 3.12	10.94	58.56	34.48	14.59
	EF-12	15	0.533	77.0	56.9		14.29	4.03	53.07	3.00 ± 2.75	8.05	46.62	61.99	13.45
	EF-13	10	0.800	92.0	90.5		6.54	1.85	52.83	2.53 ± 2.39	3.89	26.12	47.02	8.86
Endobenthos	EB-1	6	1.000	11.2	20.0		2.82	0.80	30.12	4.21 ± 3.52	8.64	14.16	31.43	2.16
	EB-2	9	0.556	91.9	75.5		7.75	2.19	29.69	4.12 ± 3.16	1.58	10.99	33.14	0.00
	EB-3	8	0.375	48.5	47.6		5.90	1.67	38.67	6.70 ± 4.93	0.00	1.25	54.92	0.00
	EB-4	21	0.048	56.4	67.5		19.53	5.51	19.11	3.11 ± 2.81	0.01	1.06	34.12	0.00
	EB-5	22	0.409	90.9	67.7	35.29	22.74	6.42	47.88	3.42 ± 3.18	8.31	46.61	50.01	12.56
	EB-6	8	0.250	55.8	56.4	0.580	9.10	2.57	54.47	3.80 ± 3.12	10.36	53.88	39.01	15.36
	EB-7	22	0.273	75.0	75.6		15.58	4.40	50.45	2.80 ± 2.52	0.94	8.17	46.65	2.24
	EB-8	8	0.875	70.1	68.5		7.56	2.13	46.41	3.93 ± 3.26	2.58	34.87	28.22	1.33
	EB-9	6	0.400	22.3	35.0		3.36	0.95	45.68	5.57 ± 4.2	0.00	0.70	79.46	0.00
	EB-10	10	0.100	50.6	100.0		5.66	1.60	44.51	2.47 ± 2.07	0.96	20.13	39.18	1.16
Overall study area						100.00	28.24	40.43	3.63 ± 3.30	3.60	22.10	43.14	9.81	

* Model accuracy details comprise the number of stations within an identified habitat (Nr. Stations), habitat-specific classification error (Class. Error) of the full model, and user (User acc) and prediction (Pred acc) accuracy estimates for the cross-validations. Overall Kappa and OOB-estimates are shown per model.

** Habitat details comprise the spatial coverage (%) and extent (in km²).

*** Anthropogenic pressures are displayed as the % of area that is fished (intensity >1 year⁻¹), used for offshore wind farms, and designated as Natura-2000 area. Mean ($\pm$ SD) fishing intensity (year⁻¹) is given for the fished (intensity > 1 year⁻¹) area. In addition, the habitat-specific percentage of Natura-2000 areas covered by the spatial extent of fishing activity and OWFs is given.

Figure 5. Spatial accuracy of the Random Forest model for demersal fish (A), epifauna (B), and endobenthos (C). Accuracy is determined as the Shannon diversity index of the model predictions for five cross-validations. Higher values represent a lower consistency of assigned habitats for a grid cell, as indicated with the letters in the legend.

Physiotopes

We applied hierarchical and K-means clustering on all grid cells, based on their score on the seven main environmental gradients resulting in high-resolution physiotope maps with 6, 13, and 10 clusters (P6, P10, P13; Fig. 4; see Appendix F for detailed environmental information of the physiotopes). To facilitate the comparison with the habitat maps, we visually matched the naming of individual physiotopes and habitats based on approximately shared locations. All three physiotope maps showed large ranges in spatial extent between physiotopes (P6: 1-41%; P10: 0-37%; P13: 0-23%; Table 3).

All physiotope maps showed a distinction between the deep waters northwest of the Dogger Bank and the shallow waters to its southeast (Fig. 4). The P6-map (Fig. 4B) distinguished 5 physiotopes in the southeast: Brown Bank region (P6-3), eastern coast (P6-6), central North Sea (P6-2), outer Wash (P6-4), and a combination of the shallowest part of the Dogger Bank with a strip along the southern Danish coast (P6-5). These physiotopes largely remain the same in the P10- and P13-maps, although some physiotopes become divided into smaller ones (Fig. 4D&F). A relatively large (9%) physiotope was associated with the Central Oyster Grounds (P10-10, P13-10), while several relatively small (<5%) physiotopes were identified as well. These comprised the edge of the Norwegian Trench (P10-9, P13-3), sand ridge troughs in the Brown Bank region (P10-1, P13-6), and the deep trenches of Devil's Hole (P10-3, P13-13; Fig. 4; Table 3). The northwest waters remained a singly physiotope when 6 and 10 physiotopes were delineated. Only when 13 physiotopes were defined, this area was divided into multiple physiotopes (P13-1, P13-4, P13-7).

Comparison physiotopes and habitats

All physiotope and habitat maps separated the deep waters northwest from the shallower waters southeast (Fig. 4). When taking the P13-map as the leading physiotope map, physiotopes P13-7, P13-9, P13-10, and P13-11 showed a reasonable match with habitat distributions (Fig. 4). For instance, the Brown Bank region (P13-11) was spatially very comparable to habitats EF-11 and EB-6. Similarly, distinct physiotopes at the Central Oyster Grounds (P13-10) and along the eastern coast (P13-9) were also represented as habitats (EF-10, EB-10 and EF-9, EB-8 respectively).

Table 3. Physiotope details as percentage spatial coverage, extent (in km²), and anthropogenic pressures*.

Physiotope		Coverage (%)	Extent (x 10.000 km ²)	% Fished	Fishing intensity (mean ± SD)	% Offshore wind farm	% Natura-2000 area
6 Physiotoypes	P6-1	41.25	11.65	27.84	4.58 ± 3.97	1.07	4.77
	P6-2	32.92	9.29	50.32	2.69 ± 2.40	4.70	27.43
	P6-3	10.45	2.95	50.56	3.77 ± 3.10	10.35	58.28
	P6-4	1.25	0.35	11.73	3.73 ± 3.28	10.51	39.09
	P6-5	3.36	0.95	54.91	3.85 ± 3.36	4.00	71.84
	P6-6	10.78	3.04	47.39	4.26 ± 3.54	2.41	19.66
13 Physiotoypes	P13-1	19.94	5.63	29.14	3.64 ± 3.09	2.36	9.87
	P13-2	2.83	0.80	54.02	3.96 ± 3.44	1.88	70.59
	P13-3	2.82	0.80	78.76	6.88 ± 4.46	0.00	3.60
	P13-4	17.91	5.06	18.46	3.53 ± 3.16	0.00	1.44
	P13-5	0.58	0.16	6.96	2.85 ± 2.30	11.61	30.66
	P13-6	1.46	0.41	36.68	4.42 ± 3.65	7.11	46.01
	P13-7	2.56	0.72	60.51	7.41 ± 5.01	0.22	2.49
	P13-8	1.44	0.41	16.05	4.53 ± 4.02	8.57	47.65
	P13-9	9.23	2.61	44.23	3.89 ± 3.17	2.54	20.67
	P13-10	9.64	2.72	46.98	2.46 ± 1.94	1.26	11.65
	P13-11	8.18	2.31	57.43	3.79 ± 3.09	11.21	57.62
	P13-12	23.17	6.54	50.79	2.69 ± 2.43	6.43	36.20
	P13-13	0.24	0.07	52.96	7.40 ± 4.62	4.09	19.81
10 Physiotoypes	P10-1	1.66	0.47	36.22	4.51 ± 3.74	7.46	43.14
	P10-2	1.21	0.34	11.03	3.72 ± 3.19	10.61	38.95
	P10-3	0.41	0.12	55.76	6.87 ± 4.59	3.05	18.56
	P10-4	37.08	10.47	23.76	3.94 ± 3.52	1.02	4.75
	P10-5	25.93	7.32	50.34	2.76 ± 2.51	6.05	33.86
	P10-6	8.73	2.47	54.52	3.80 ± 3.12	10.97	57.98
	P10-7	3.00	0.85	54.25	3.91 ± 3.41	2.33	70.61
	P10-8	9.82	2.77	44.18	3.83 ± 3.14	2.38	19.54
	P10-9	3.15	0.89	78.49	6.78 ± 4.44	0.03	3.33
	P10-10	9.00	2.54	48.91	2.99 ± 2.91	1.33	12.12
Overall study area		100.00	28.24	40.43	3.63 ± 3.30	3.60	22.10

* Anthropogenic pressures are displayed as the % of area that is fished (intensity >1 year⁻¹), used for offshore wind farms, and designated as Natura-2000 area. Mean (± SD) fishing intensity (year⁻¹) is given for the fished (intensity > 1 year⁻¹) area.

Despite this overall similarity, the physiotope map showed several discrepancies with the habitat maps. In figure 6 we show how much area (in %) of a habitat overlaps with each physiotope, as an addition to visual comparison. When all habitats and physiotopes perfectly match, a strict declining diagonal should emerge, which is not the case (Fig. 6). This is mainly caused by habitats that cover multiple physiotopes or vice versa. The demersal fish habitat DF-2, for instance, comprised almost all physiotopes, except for P6-1 (Fig. 6A). Contrary, the physiotope P10-4 covered endobenthos habitats EB-2, 3, 4, & 9 (Fig. 6C; Fig. 4) and the physiotopes P13-1 and P13-12 were unable to detect environmental differences between epifauna habitats EF-1, 3, 5, 6, & 8 and EF-5, 9, 11, 12 & 13 respectively (Fig. 6B; Fig. 4). Interestingly, all three physiotope maps consistently delineate a physiotope (P6-5, P13-2, P10-7) that covered part of the eastern coast with an additional location at the Dogger Bank (Fig. 4) without an equivalent habitat in any faunal group.

Figure 6. Comparisons between physiotopes and habitats for demersal fish (A), epifauna (B) and endobenthos (C). For each physiotope (Y-axis), the spatial overlap (in % of the physiotope extent) with each biological habitat (X-axis) is displayed.

Habitat-specific anthropogenic pressures

All habitats were subjected to demersal fishing and/or offshore wind farms (Table 2). The fished extent (in %) of each habitat varied between 9–65 % (Table 2), showing strong associations of demersal fishing with specific habitats. Preferred habitats (>40 % fished extent) were dominantly located in the shallow waters southeast. Habitats with large OWF (>5 %) and Natura-2000 area (>40 %) extents were mostly located in the Brown Bank region and at the Dogger Bank. It should be noted, however, that especially the calculation of fished extent is probably less accurate for smaller habitats.

Strong positive correlations were found (analysis on all DF, EF, and EB habitats >5 %) between the habitat-specific extents of OWFs and fished area, and the spatial extent of Natura-2000 area within that habitat (fished: $R^2=0.464$, $p<0.001$; OWF: $R^2=0.884$, $p<0.0001$; Table 2). This analysis, however, does not determine the spatial overlap of the different activities within a habitat. When habitat-specific extents of fisheries and OWFs were determined within Natura-2000 areas, a more nuanced pattern is observed (Table 2), especially when small habitats (<5 %) and habitats with little Natura-2000 area (<5 %) were excluded. For demersal fisheries, the overall fished extent (40 %) did not differ much from within Natura-2000 sites (43 %; Table 2). However, a larger fished extent inside Natura-2000 areas was observed in Dogger Bank habitat EF-12 (61 % compared to 52 %), while smaller extents were shown for habitats in the Brown Bank region (EF-11: 35 % versus 45 %; and EB-6: 39 % versus 54 %; Table 2) and near the Danish coast (EF-9: 30 % versus 46 %; and EB-8: 28 % versus 46 %; Table 2). OWFs, on the other hand, were generally three times larger within Natura-2000 areas (9 %) compared to the overall study area (3 %; Table 2). Especially in the habitats EF-12 and EB-5, which are located at the Dogger Bank, and habitats EF-11 and EB-6 which cover the Brown Bank region, large parts (>10 %) of OWFs were constructed within Natura-2000 areas (Table 2).

Discussion

Creating accurate, high-resolution marine habitat maps is challenging¹⁴, but essential for ecology-inclusive marine spatial planning⁷. Here, we developed a novel method that combines point-wise biological data with grid-based environmental variables to create full coverage, high resolution habitat maps. We expand earlier work in the spatial modelling of species assemblages (see e.g.^{52–54} by (i) the modelling of both physiotopes and observed assemblages for different faunal

groups, (ii) our explorations in the usage of environmental gradients based on environmental and anthropogenic variables (Appendix G), and (iii) the direct comparison between habitat types and anthropogenic activities. As a result, our final habitat maps represent benthic assemblage distributions, congruent to spatial patterns in benthic assemblages as previously described by station-based studies^{13,55}. Although several habitats showed close resemblance to physiotopes delineated from environmental variables, some essential differences were observed. Several physiotopes did not distinguish between multiple identified habitats, and one physiotope had no equivalent habitat, suggesting that important environmental variables or ecological processes might not have been captured in the delineation of physiotopes and habitats. Furthermore, we showed that separating maps for three faunal groups – demersal fish, epifauna, and endobenthos – yielded substantially different habitat maps, as expected based on their differences in ecology and mobility. By spatially comparing the habitats identified herein with anthropogenic pressures such as demersal fishing and OWFs, we confirmed that these activities have spatial associations with specific habitats^{3,56}. Hence, to sustainably manage anthropogenic pressures, habitat-specific impact assessments should be undertaken for the main faunal groups of benthic assemblages. Our findings provide an important new approach to marine habitat mapping, which will enable improvement of habitat-specific impact assessments for ecology-inclusive marine spatial planning.

The presented methodology enabled the inclusion of distinct environmental variables which were relevant to specific communities and faunal groups^{29,31} and avoided subjective choices regarding included variables and exact classification boundaries. As a consequence, the resulting habitat maps predicted a substantially different spatial distribution of benthic assemblages compared to physiotopes maps, including the ones currently used for marine management and spatial planning^{20,54,57}. The Broad Habitat Types under the Marine Strategy Framework Directive (MSFD) are an example of such a currently used habitat map for management of the North Sea. The MSFD aims to achieve Good Environmental Status (GES) in all marine EU waters, for instance by the conservation of seafloor integrity⁵⁸. Seafloor integrity is assessed by habitat-specific analyses of fishing pressures and sensitivity^{20,59}. This assessment uses the MSFD Broad Habitat Types (MSFD-BHT¹), which are dominantly based on water depth and sediment type^{20,60}. However, these MSFD-BHT show different habitat distributions compared to our maps, with higher habitat complexity than the demersal fish level, but lower complexity for both epifauna and endobenthos. Most remarkably, the clear distinction between the deeper northwest and shallower waters southeast of the Dogger Bank, which was dominant in all three presented habitat maps, is not captured by the MSFD-BHT map. Some resulting discrepancies between expected benthic assemblages and MSFD-BHT were already recognized during the assessment⁵⁹, and more of such mismatches are likely given our results. These mismatches probably affect the required estimate of habitat sensitivity, which is parameterized by both habitat- and gear-specific depletion and recovery rates after a bottom trawl pass^{61–63}. Especially habitat-specific recovery rates, based on longevity estimates of local endobenthos abundances will probably change if the boundaries of endobenthos habitats are adjusted^{20,61}. In addition, a similar or integrated analysis for epifauna and demersal fish assemblages would allow for an assessment of the overall demersal ecosystem. Hence, our case-study showed that the current assessments of fishing impact on seafloor integrity probably fail to capture the true ecological status of benthic and demersal assemblages. Similar discrepancies between benthic assemblages and physiotopes have been observed in other areas than the North Sea as well^{54,57}.

Our methodology relies on the interpolation of biological assemblages with environmental variables, and its reliability is thus related to the quality of input data and the ability to apply a correct interpolation. Our input data, especially the endobenthos dataset, showed a spatiotemporal mismatch with the environmental data, increasing the uncertainty of the habitat maps¹⁴. Environmental data is often surveyed at or modelled to higher spatial and temporal resolution than what is available for biological data, which are generally snapshots in time. This can result in temporal mismatches, both in actual timing and represented time period. As a consequence,

the correlations between benthic clusters and environmental gradients used for the interpolation have lower certainty. This can be observed in figure 5A, where the demersal fish Random Forest model shows high consistency between all cross-validations, probably because the input data has no spatiotemporal mismatch. The presented endobenthos habitat map has much lower certainty, caused by a large spatiotemporal mismatch in the input data in combination with (anthropogenic) changes in the North Sea since the initial sampling. Recent efforts to merge available endobenthos data for EMODnet demonstrated that the NSBS86 survey is still the leading survey in several regions of the North Sea (Herman, pers. comm.), with limited sampling stations in the northern part of our study area⁶⁴. And although a comparison of endobenthos composition in 1986 and 2000 showed relatively little difference in the large-scale community distributions⁵⁵, we strongly recommend for a new North Sea Benthos Survey that is internationally harmonized and covers the entire North Sea. Nevertheless, data availability will always dictate what can be used as input data, and therefore spatiotemporal problems will remain. International harmonization of national sampling surveys is therefore required to reduce spatiotemporal mismatches in marine habitat mapping (Appendix A).

Conclusions

We demonstrate a new approach to derive high-resolution, full-coverage habitat maps representing benthic assemblages for different faunal groups. The detailed spatial information on benthic assemblages captured by our habitat maps are a first step to true ecology-inclusive marine spatial planning^{7,8,54,57}. Nonetheless, we find that the quality of the input data is key for accurate output, which demands international harmonization of existing sampling surveys. Our detailed overview in spatial distribution of both habitats and anthropogenic pressures identifies potential areas of conflicting interests and facilitate discussions on a fair balance between economic and ecological values. Assembly-specific knowledge based on species traits and species-environment feedbacks, leading to assessments of resilience, sensitivity, and longevity, can now further improve habitat-specific impact assessments and subsequent management.

Acknowledgements

We would like to thank the Centre for Information Technology of the University of Groningen for their support and for providing access to the Peregrine high-performance computing cluster. We also thank Raphaël Scherrer for his assistance with MatLab calculations, Olivier Beauchard for his help in the compilation of the endobenthos dataset, and Alireza Amiri-Simkooei for his valuable comments on earlier versions of the manuscript. This work was funded by the Gieskes-Strijbis Fonds, The Netherlands. LG was funded by NWO grant 016.Veni.181.087. The funders had no involvement in the execution of the study.

Supplementary materials

Supplementary materials can be found online at <https://doi.org/10.1016/j.ecolind.2021.107849>.

Appendix A. Endobenthos data and clustering

Appendix B. Environmental data

Appendix C. Biological habitats and their characteristic species and environmental conditions

Appendix D. Clustering methodology

Appendix E. Random Forest versus Nearest Neighbour

Appendix F. Physiotope characteristics

Appendix G. Fishing intensity as an explanatory, environmental variable

References

- Sardain, A., Sardain, E. & Leung, B. Global forecasts of shipping traffic and biological invasions to 2050. *Nat. Sustain.* **2**, (2019).
- de Boer, W. P., Roos, P. C., Hulscher, S. J. M. H. & Stolk, A. Impact of mega-scale sand extraction on tidal dynamics in semi-enclosed basins. An idealized model study with application to the southern North Sea. *Coast. Eng.* **58**, 678–689 (2011).
- Grothe, O. & Schnieders, J. Spatial dependence in wind and optimal wind power allocation: A copula-based analysis. *Energy Policy* **39**, 4742–4754 (2011).
- Eigaard, O. R. *et al.* The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865 (2017).
- Johnson, C. N. *et al.* Biodiversity losses and conservation responses in the Anthropocene. *Science (80-.)*. **356**, 270–275 (2017).
- Costello, M. J. & Ballantine, B. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends Ecol. Evol.* **30**, 507–509 (2015).
- White, C., Halpern, B. S. & Kappel, C. V. Ecosystem service tradeoff analysis reveals the value of marine spatial planning for multiple ocean uses. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 4696–4701 (2012).
- Kaiser, M. J. *et al.* Prioritization of knowledge-needs to achieve best practices for bottom trawling in relation to seabed habitats. *Fish Fish.* 1–27 (2015) doi:10.1111/faf.12134.
- Reiss, H. *et al.* Benthos distribution modelling and its relevance for marine ecosystem management. *ICES J. Mar. Sci.* **72**, 297–315 (2015).
- Cooper, K. M., Bolam, S. G., Downie, A. L. & Barry, J. Biological-based habitat classification approaches promote cost-efficient monitoring: An example using seabed assemblages. *J. Appl. Ecol.* **56**, 1085–1098 (2019).
- Beisiegel, K., Darr, A., Gogina, M. & Zettler, M. L. Benefits and shortcomings of non-destructive benthic imagery for monitoring hard-bottom habitats. *Mar. Pollut. Bull.* **121**, 5–15 (2017).
- Jørgensen, L. L., Renaud, P. E. & Cochran, S. K. J. Improving benthic monitoring by combining trawl and grab surveys. *Mar. Pollut. Bull.* **62**, 1183–1190 (2011).
- Reiss, H. *et al.* Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* **67**, 278–293 (2010).
- ICES. *Working Group on Marine Habitat Mapping (WGMHM)*. *ICES Scientific Reports* vol. 1 (2019).
- Compton, T. J. *et al.* Distinctly variable mudscapes: Distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *J. Sea Res.* **82**, 103–116 (2013).
- Strong, J. A. *et al.* A review of the influence of marine habitat classification schemes on mapping studies: Inherent assumptions, influence on end products, and suggestions for future developments. *ICES J. Mar. Sci.* **76**, 10–22 (2019).
- Galparsoro, I. *et al.* Using EUNIS habitat classification for benthic mapping in European seas: Present concerns and future needs. *Mar. Pollut. Bull.* **64**, 2630–2638 (2012).
- Schiele, K. S., Darr, A. & Zettler, M. L. Verifying a biotope classification using benthic communities - An analysis towards the implementation of the European Marine Strategy Framework Directive. *Mar. Pollut. Bull.* **78**, 181–189 (2014).
- Andersen, J. H. *et al.* European broad-scale seabed habitat maps support implementation of ecosystem-based management. *Open J. Ecol.* **08**, 86–103 (2018).
- ICES. *Working Group on Fisheries Benthic Impact and Trade-Offs (WGFBIT; outputs from 2019 meeting)*. *ICES Scientific Reports*. vol. 2 <http://doi.org/10.17895/ices.pub.5955> (2020).
- Huang, Z., Brooke, B. P. & Harris, P. T. A new approach to mapping marine benthic habitats using physical environmental data. *Cont. Shelf Res.* **31**, S4–S16 (2011).
- Pitcher, C. R. *et al.* Exploring the role of environmental variables in shaping patterns of seabed biodiversity composition in regional-scale ecosystems. *J. Appl. Ecol.* **49**, 670–679 (2012).
- Vasquez, M. *et al.* Broad-scale mapping of seafloor habitats in the north-east Atlantic using existing environmental data. *J. Sea Res.* **100**, 120–132 (2015).
- McArthur, M. A. *et al.* On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuar. Coast. Shelf Sci.* **88**, 21–32 (2010).
- Stevens, T. & Connolly, R. M. Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management. *Biol. Conserv.* **119**, 351–362 (2004).
- Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
- Menge, B. A. & Sutherland, J. P. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. *Am. Nat.* **110**, 351–369 (1976).
- Kaiser, M. J., Ramsay, K., Richardson, C. A., Spence, F. E. & Brand, A. R. Chronic fishing disturbance has changed shelf sea benthic community structure. *J. Anim. Ecol.* **69**, 494–503 (2000).
- Lecours, V. *et al.* Spatial scale and geographic context in benthic habitat mapping: Review and future directions. *Mar. Ecol. Prog. Ser.* **535**, 259–284 (2015).
- Damveld, J. H. *et al.* Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophys. Res. Lett.* **45**, (2018).
- Hewitt, J. E., Wang, D., Francis, M., Lundquist, C. & Duffy, C. Evaluating demersal fish richness as a surrogate for epibenthic richness in management and conservation. *Divers. Distrib.* **21**, 901–912 (2015).
- ICES. *Manual for the offshore Beam Trawl Surveys, Revision 1.2, June 2009, Working Group on Beam Trawl Surveys*. http://ices.dk/marine-data/Documents/DATRAS Manuals/WGBEAM_Manual.pdf (2009).
- Millar, C., Large, S. & Magnusson, A. icesDatras: DATRAS trawl survey database web services. (2019).
- Callaway, R. *et al.* Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES J. Mar. Sci.* **59**, 1199–1214 (2002).
- Künitzer, A. *et al.* The benthic infauna of the North Sea: Species distribution and assemblages. *ICES J. Mar. Sci.* **49**, 127–143 (1992).
- Heip, C. H. R. *et al.* The benthic communities of the North Sea: a summary of the results of the North Sea benthos survey. *ICES Coop. Res. Report*. **190**, 148–175 (1992).

37. EMODnet Biology, Q. European Marine Observation Data Network Biology project, funded by the European Commission's Directorate - General for Maritime Affairs and Fisheries (DG Mare). www.emodnet-biology.eu (2018).
38. Oksanen, J. *et al.* Vegan: Community ecology package. R package version 2.5-6. (2019).
39. EMODnet. EMODnet Bathymetry. www.emodnet.eu/bathymetry (2019).
40. Copernicus. Marine Copernicus. <http://marine.copernicus.eu/> (2019).
41. Hiddink, J. G. *et al.* Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can. J. Fish. Aquat. Sci.* **63**, 721–736 (2006).
42. van Denderen, P. D. *et al.* Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar. Ecol. Prog. Ser.* **541**, 31–43 (2015).
43. Stephens, D. & Diesing, M. Towards quantitative spatial models of seabed sediment composition. *PLoS One* **10**, (2015).
44. Verfaillie, E., Degraer, S., Schelfaut, K., Willems, W. & van Lancker, V. A protocol for classifying ecologically relevant marine zones, a statistical approach. *Estuar. Coast. Shelf Sci.* **83**, 175–185 (2009).
45. Linderman, M. Rclusterpp: Linkable C++ clustering. R package version 0.2.3. (2013).
46. Breiman, L. Random forests. *Mach. Learn.* **45**, 5–32 (2001).
47. Evans, J. & Murphy, M. rUtilities. (2018).
48. Hijmans, R. J., Phillips, S., Leathwick, J. & Elith, J. Dismo: Species distribution modelling. (2017).
49. Turner, R. Delaunay Triangulation and Dirichlet (Voronoi) Tessellation. (2019).
50. EMODnet. EMODnet HumanActivities. <https://www.emodnet-humanactivities.eu/> (2019).
51. EEA. EEA. <https://www.eea.europa.eu/data-and-maps/data/natura-10#tab-gis-data> (2018).
52. Smoliński, S. & Radtke, K. Spatial prediction of demersal fish diversity in the Baltic Sea: Comparison of machine learning and regression-based techniques. *ICES J. Mar. Sci.* **74**, 102–111 (2017).
53. Ferrier, S. & Guisan, A. Spatial modelling of biodiversity at the community level. *J. Appl. Ecol.* **43**, 393–404 (2006).
54. Rubidge, E. M., Gale, K. S. P. & Curtis, J. M. R. Community ecological modelling as an alternative to physiographic classifications for marine conservation planning. *Biodivers. Conserv.* **25**, 1899–1920 (2016).
55. Kröncke, I. *et al.* Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. *Estuar. Coast. Shelf Sci.* **94**, 1–15 (2011).
56. van der Reijden, K. J., Hintzen, N. T., Govers, L. L., Rijnsdorp, A. D. & Olff, H. North Sea demersal fisheries prefer specific benthic habitats. *PLoS One* **13**, 1–21 (2018).
57. Ferrari, R. *et al.* Integrating distribution models and habitat classification maps into marine protected area planning. *Estuar. Coast. Shelf Sci.* **212**, 40–50 (2018).
58. European Commission. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Official Journal of the European Union* vol. 164 19–40 (2008).
59. ICES. Interim Report of the Working Group on Fisheries Benthic Impact and Trade-offs (WGFBIT), 12-16 November 2018, ICES Headquarters, Copenhagen, Denmark. (2019).
60. EMODnet. EUSeaMap: A broad-scale seabed habitat map for European Seas. https://www.emodnet-seabedhabitats.eu/media/1530/20180508eu_seamap_exec-summary-report_low.pdf (2018).
61. Rijnsdorp, A. D. *et al.* Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol. Appl.* **28**, 1302–1312 (2018).
62. Hiddink, J. G. *et al.* Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J. Appl. Ecol.* **56**, 1075–1084 (2019).
63. Hiddink, J. G. *et al.* Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci.* **114**, 8301–8306 (2017).
64. Rees, H. L., Eggleton, J. D., Rachor, E. & Vanden Berghe, E. *Structure and dynamics of the North Sea benthos*. (ICES Cooperative Research Report No. 288, 2007).

Chapter 5

Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples

Karin J. van der Reijden*

Johan H. Damveld*

Chiu Cheng

Leo Koop

Lisa Rose Haaksma

Cameron A. J. Walsh

Karline Soetaert

Bas W. Borsje

Laura L. Govers

Pieter C. Roos

Han Olf

Suzanne J. M. H. Hulscher

* These authors contributed equally to this work.

Published as

Damveld JH, van der Reijden KJ, Cheng C, Koop L, Haaksma LR, Walsh CAJ, Soetaert K, Borsje BW, Govers LL, Roos PC, Olf H, Hulscher SJMH. (2018) Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophysical Research Letters*, 45(21), 11837-11846.

Abstract

The sandy seabed of shallow coastal shelf seas displays morphological patterns of various dimensions. The seabed also harbors a rich ecosystem. Increasing pressure from human-induced disturbances necessitates further study on drivers of benthic community distributions over morphological patterns. Moreover, a greater understanding of the sand ripple distribution over tidal sand waves may improve morphological model predictions. Here, we analyzed the biotic abundance and ripple morphology in sand wave troughs and crests using video transects. We found that both the epi- and endobenthos are significantly more abundant in sand wave troughs, where ripples are less abundant and more irregularly-shaped. Finally, we show that camera systems are relatively quick and effective tools to study biotic spatial patterns in relation to seabed morphology.

Introduction

Worldwide, coastal seas are extensively used for numerous human activities. Fisheries, shipping, sand extraction, land reclamation, wind farms, oil and gas production and recreation are putting an increasing pressure on the coastal environment. Sustainable use of available resources requires information on the environmental impact of these activities^{1,2}. In this respect, knowledge concerning the distribution of benthic communities in these areas is crucial. It is well known that benthic community composition is related to various abiotic variables, such as sediment type, grain size, temperature and chlorophyll- α content³⁻⁵. However, less is known about how macrobenthic species relate to both large and small-scale morphological bed patterns.

Bed patterns are common features in sandy coastal shelf seas and estuaries, shaped by the interplay of tides, currents, waves, and biology. Various types of offshore bed forms can be found, for instance sand banks⁶, long bed waves⁷, tidal sand waves⁸, mega ripples⁶ and sand ripples⁹. Of all the described bed forms, sand waves are the most relevant to study as their dynamic behavior can pose a threat to offshore civil engineering constructions, such as pipelines¹⁰ and cables to wind farms¹¹. Sand wave crests are perpendicular to the tidal current¹², with heights up to ten meters, wavelengths of 100-1000 meters, and migration rates of several meters per year^{13,14}. They are formed at time scales of 1-10 years¹⁵. The smallest morphological bed patterns are mega ripples and sand ripples, which are usually superimposed on sand waves¹⁶. Their wavelengths are of the order of meters to centimeters, respectively, and they are highly mobile, migrating up to several meters per day¹⁷. Both may serve as roughness indicators in morphological models¹⁸. Sand waves commonly occur in many areas around the world, but are primarily observed in coastal, semi-shallow areas (20 to 40 m water depth) with strong tidal currents¹⁹, for instance in the Taiwan Strait²⁰, the Bahia Blanca estuary²¹, the Bisanseto Sea²² and in the North Sea²³.

The coastal seabed is inhabited by rich benthic communities²⁴. Benthic species may influence near-bed processes on a large spatial and temporal scale²⁵⁻²⁷. By their burrowing activity, sea urchins (*Echinocardium cordatum*) reduce seabed stability²⁷. Dense aggregations of the tube-building polychaete sand mason worm (*Lanice conchilega*), on the other hand, decrease near-bed flow velocities, and stabilize the seabed^{25,28,29}. Process-based modelling studies have shown that such activities can significantly influence sand wave dimensions³⁰. Contrarily, coastal bed forms are reported to drive the spatial distribution of benthic communities. The crests of large-scale tidal sandbanks in the North Sea were shown to harbor a less dense and less diverse community, compared with the troughs³¹. Baptist *et al.* studied sand wave effects on benthos spatial distribution³². For two out of four seasons, they found different species compositions between the troughs and crests. However, they only studied endobenthos with a limited spatial resolution, due to their employed methodology (boxcores). Moreover, knowledge on benthos distribution in relation to small-scale morphology could not be acquired. No clear relationship has yet been delineated between seabed morphology and benthic communities of sand waves.

Both coastal engineering projects and ecological maintenance policies heavily rely on monitoring in order to assess the feasibility of engineering projects and the status quo of benthic communities, respectively. Morphological and ecological models complement these data as they allow for predicting the evolution of bed patterns and communities. Several existing models deal with sand wave evolution. Hulscher was the first to use a process-based model to study the initial growth phase³³, after which many additions were made (e.g., Campmans *et al.*, and references therein³⁴). Also, more complex models are available which describe equilibrium amplitudes^{35,36}. Until now, these morphological models lack interaction with spatially varying small-scale biological processes. In order to construct and validate such models, more information is required about the spatial relationships among benthic habitats, (mega) ripples and sand waves.

Studies on the distribution of benthic assemblages can be very time consuming and the spatial resolution is often limited. Common methods like grabs, boxcores and multicores are point measurements, which only give an indication of the endobenthic community in the area³⁷. Larger, mobile species living on and within the seabed are easily missed. In order to study the spatial distribution of such species, sledges and trawls are commonly used^{24,38}. However, with these techniques, it remains difficult to capture the complex spatial structure of benthic communities: trawls and sledges provide species densities integrated over the total sampled area, losing information on variance within the track. Alternatively, camera systems can be used to increase the spatial resolution of species density information^{39,40}. Using camera systems, observations on species composition and environmental characteristics can be done simultaneously. Another major advantage of a camera system is that it does not alter the bed structure, and thus enables data collection of small-scale bed features such as ripples.

The main goal of this paper is (1) to investigate the spatial distribution of benthic assemblages over sand waves. Secondary objectives are (2) to relate sand wave patterns to the spatial distribution of small-scale morphology and (3) to present the use of a camera system as a method to simultaneously study benthic species abundance and small-scale morphology.

Materials and Methods

Study site

Our study site is representative of sand waves occurring in the Dutch, Belgian and English Continental Shelf in the North Sea. We selected an area of approximately 3.4 km², located 12 nautical miles (~22.2 km) off the coast of Texel, the Netherlands (N 53° 11.241'; E 4° 28.628'; Fig. 1). It is characterized by sand waves, oriented in a northwest direction perpendicular to the coast. At an average depth of 30 m, the sand waves have an amplitude of around 3 meters, a wavelength of around 200 meters, and are covered by small sand ripples. The study site is located in a narrow stretch between two busy traffic lanes, and therefore subjected to extremely low demersal fishing activity.

Bathymetric data

A bathymetric survey was conducted in June 2017 using the RV Pelagia's hull-mounted Kongsberg EM302 Swath Multibeam Echosounder (MBES). MBES-data was processed to a 1 m grid resolution. Two sand waves in the area were selected based on the accessibility of the area, and their crests and troughs were subsequently identified from the MBES-data. This yielded four different study locations: the troughs (T1, T2), and crests (C1, C2) of sand wave 1 and 2, respectively (Fig. 1).

Hopper camera system

The NIOZ hopper camera that was used consisted of a custom-made drop-frame with a downward facing HD-video camera⁴¹, an underwater light source (100 W), and two parallel green lasers (30 cm apart) for scaling. The camera system was lowered to 0.5 m above the seabed, tethered to the vessel by a Kevlar cable with glass fiber core allowing real-time video transfer. Positioning of the hopper camera above the seabed was manually controlled by adjusting the cable length from the winch, based on a live video feed. A sailing speed of ~0.3 knots (~0.56 km/h) with respect to the stationary seabed was maintained.

Figure 1. The study area. Its exact location in the North Sea, indicated with a red dot in (a). Detailed bathymetry of the complete area and the location of both video transects in (b). Enlarged versions of the video transects including the locations of the trough (T) and crest (C) in (c, d).

Video analysis

We performed two video transects within a 2-hour timeframe from each other, around slack tide (after high water), and under relatively calm weather conditions. Both transects started on the sand wave crest and were oriented roughly perpendicular to the sand waves, crossing the adjacent trough and crest (Fig. 1). The camera recorded the seabed continuously, and video stills were automatically created from this footage for every second (Fig. 2). In addition, the exact location of the vessel was recorded every 30 seconds and subsequently linked to video stills by time-matching. This enabled the plotting of video results in ArcGIS (ArcMAP 10.3, ESRI), although a small offset was probably present due to a mismatch between the exact positions of the camera and the vessel. This geo-referenced information was used to select video stills to include in the analysis. Both the first and last video still in each study location (T1, T2, C1, C2) were identified. The first and all subsequent

Figure 2. Video stills from the hopper camera for trough (top) and crest (bottom), classified for sand ripple regularity as class A (no ripples), B (irregular ripples), C (some irregularity), and D (regular ripples). Red and blue lines represent the ripple length measurements of both observers, the green laser dots indicate a distance of 30 cm.

video stills were selected with a fixed interval, until the registered time of the last video still within the study area was reached. To prevent overlap of consecutive video stills, a 10-second interval was used. If a selected video still comprised an invalid image (due to dust clouds or movement blur), the next video still was selected instead.

All selected video stills were visually analyzed with ImageJ 1.51n⁴² by two independently working observers. For each selected still, biotic abundance, sand ripple morphology and surface area were determined, using the laser dots as reference. If epibenthic organisms were present, they were identified to the lowest taxonomic level possible, sometimes with the additional use of the continuous footage. Moreover, the number of holes in the seabed was counted as a proxy for endobenthos abundance. All counts were transformed into surface densities ($\# \text{ m}^{-2}$). For sand ripple morphology, both observers independently chose three random sand ripples and measured their crest-to-crest length (Fig. 2). Additionally, a visual judgement of the sand ripple pattern regularity was made. Regularity was classified in 4 classes: no sand ripples (A), no regular sand ripple pattern (B), some regular sand ripple pattern (C), and a strong, regular sand ripple pattern (D).

Statistical analysis

A total of 232 video stills, distributed unequally over the four study locations (T1: 37, T2: 61, C1: 91, C2: 43) were analyzed, which were nested within the two video transects. Ripple length (cm), regularity class, epibenthos abundance ($\# \text{ m}^{-2}$) and hole density ($\# \text{ m}^{-2}$) were available for each video still from both observers. The statistical analysis of this dataset was performed in R (R Core Team, 2018).

We used Linear Mixed Models (LMM) from the “nlme”-package⁴³ to study the effects of location (trough versus crest) on epibenthos density, hole density, and average sand ripple length. Each model included location (trough/crest) as a fixed factor and transect and study location (T1, T2,

C1, C2) as random factors. The latter was included to minimize any spatial autocorrelation of observations within a trough or crest. Missing values were omitted. To elucidate potential observer-bias, we performed each LMM model three times, on different datasets. The first two models were performed for the two observers separately. Subsequently, the third model was fitted on the averaged values of the two observers. Next, likelihood Ratio Tests between the third model and a model without the explanatory variable (but with random factors included) were performed to assess the effect of the explanatory variable.

We analyzed the effects of the location on the regularity of the sand ripples using a Generalized Linear Mixed Model (GLMM) of the “binomial” family in the “lme4”-package⁴⁴. We needed a different model as using an LMM is limited to independent data. With more observations of a certain regularity class, the less observations of a different class could be made at that study location. To deal with this relation we transformed the data into ‘successes’ and ‘failures’, with ‘successes’ being the observations and ‘failures’ being all other observations in that study location. Next, the number of ‘successes’ was modelled using the explanatory variables location (trough versus crest), interaction of location and regularity class (A, B, C, D), and random effects of transect and study location (T1, T2, C1, C2). The GLMM was performed on three distinct datasets: for both observers separately and one on the averaged values. Finally, a Likelihood Ratio Test between the averaged model and a similar model, but without the interaction of regularity class and location, was performed to assess the effect of regularity class per location.

Results

Bathymetric data

Nearly complete coverage of the study area was achieved in the bathymetric survey, with a resolution of 1 m (Fig. 1a-b). The study area comprised a total of twelve sand waves, having an average amplitude height difference of 3.0 m between trough and crest and an average wavelength of 207 m. The sand waves were asymmetrical in their cross-section: the northeast-facing slope being steeper than the southwest-facing slope. The two selected sand waves for the video transects had their crests at -28.0 m and the troughs at -31.7 m depth with respect to mean sea level (Fig. 1c-d).

Video analysis: Biota

Hole density was on average 30 times higher in the troughs than on the crests (LMM; $\chi^2(1)=7.18$, $p=0.0074$), indicating that endobenthic species abundance was significantly higher in troughs than on the crests (Table 1; Fig. 3a). In line with this, we found four times more epibenthic organisms (LMM; $\chi^2(1)=4.06$, $p=0.044$) in the troughs than on the crests (Table 1; Fig. 3b). The two non-averaged, observer-specific models for both hole density and epibenthos abundance yielded similar results (Table 1). Only a limited number of epibenthos species were observed in the video. The common star fish (*Asterias rubens*) was most frequently observed, followed by sand stars (*Ophiura* spp.), and the common hermit crab (*Pagurus bernhardus*). Tubes of the sand mason worm (*Lanice conchilega*) were frequently observed as well. However, it was impossible to determine from the video stills and footage whether the tubes were inhabited by live specimens. Other observations included anemones (*Sagartia* spp., but also *Metridium dianthus*), gobies (Gobiidae), brown crab (*Cancer pagurus*), bryozoans, and some flatfishes (Pleuronectidae).

Video analysis: Sand ripples

Sand ripple length was shorter in the sand wave troughs compared with the crests (LMM; $\chi^2(1)=13.55$, $p=0.00023$). In the troughs, sand ripple length was 11.2 cm on average, while on the crests, the ripples had an average length of 16.7 cm (Table 1; Fig. 3c). Observer-specific models yielded similar results as the final model based on the averaged data. In addition to the shorter sand ripple length, ripples were often absent in the sand wave troughs, or showed an irregularly-shaped pattern. The relative proportions of classes A (no ripples) and B (irregular ripples) were much higher in the troughs than on the crests (Fig. 3d). On the crests, sand ripples were classified more often as classes C (some regularity) and D (regular ripples). The GLMM supported that the location (trough versus crest) affected the chance of an observation in a certain class significantly (GLMM; $\chi^2(6)=112.09$, $p<0.001$), with increased observations for classes C and D on the crests compared to observations of class A on the crests (Table 1).

Figure 3. Hole density (a) epibenthos density (b), ripple length (c) and regularity class abundance (d) in the crests and on troughs of sand waves. Class A: no sand ripples, B: irregular ripples, C: some irregularity, D: regular ripples.

Table 1. Results of the Linear Mixed Models for hole density, epibenthos abundance, and sand ripple length, as well as the results for the Generalized Linear Mixed Model for sand ripple regularity class. Standard deviations (SD) of the random effects represent the variation explained by that factor. The coefficient of 'location' shows the effect and direction of this fixed effect, with positive values representing positive effects for the troughs compared to the crests. The fourth models are only included to show the exact model formula for the model used in the likelihood ratio test. Observers are indicated by (obs1) and (obs2). The values displayed in class A-D represent the slopes for that class in that location, in relation to the abundance of class A on the crest. Class A: no sand ripples; B: irregular ripples; C: some irregularity; D: regular ripples.

Hole density (HD)									
Model		SD ϵ (Transect)	SD ϵ (Location)	SD residuals	Coefficient location				
1	HD (obs1) ~ Location + ϵ (Transect) + ϵ (Location)	2.79x10 ⁻⁶	8.35	10.98	35.64				
2	HD (obs2) ~ Location + ϵ (Transect) + ϵ (Location)	0	5.54	11.10	29.48				
3	HD (Average) ~ Location + ϵ (Transect) + ϵ (Location)	2.72x10 ⁻⁸	6.98	10.50	32.57				
4	HD (Average) ~ ϵ (Transect) + ϵ (Location)	1.68x10 ⁻⁶	17.79	10.50	-				
Epibenthos abundance (EBA)									
Model		SD ϵ (Transect)	SD ϵ (Location)	SD residuals	Coefficient location				
1	EBA (obs1) ~ Location + ϵ (Transect) + ϵ (Location)	2.35x10 ⁻⁷	1.59	2.42	4.60				
2	EBA (obs2) ~ Location + ϵ (Transect) + ϵ (Location)	0	1.56	2.37	4.11				
3	EBA (Average) ~ Location + ϵ (Transect) + ϵ (Location)	0	1.58	2.33	4.36				
4	EBA (Average) ~ ϵ (Transect) + ϵ (Location)	1.12x10 ⁻⁷	2.70	2.33	-				
Sand ripple length (SRL)									
Model		SD ϵ (Transect)	SD ϵ (Location)	SD residuals	Coefficient location				
1	SRL (obs1) ~ Location + ϵ (Transect) + ϵ (Location)	0.00	2.19x10 ⁻³	0.04	-0.055				
2	SRL (obs2) ~ Location + ϵ (Transect) + ϵ (Location)	0	0	0.03	-0.056				
3	SRL (Average) ~ Location + ϵ (Transect) + ϵ (Location)	1.82x10 ⁻¹⁰	8.844x10 ⁻¹¹	0.03	-0.056				
4	SRL (Average) ~ ϵ (Transect) + ϵ (Location)	0	0.02641	0.04	-				
Sand ripple regularity (SRR)									
Model		Class A		Class B		Class C		Class D	
		Crest	Trough	Crest	Trough	Crest	Trough	Crest	Trough
1	SRR (obs1) ~ Location:Class + Location + ϵ (Transect) + ϵ (Location)	-	2.77	1.96	0.11	3.3	-0.24	2.89	-2.21
2	SRR (obs2) ~ Location:Class + Location + ϵ (Transect) + ϵ (Location)	-	2.15	1.01	0.21	2.60	-0.77	2.10	-2.33
3	SRR (Average) ~ Location:Class + Location + ϵ (Transect) + ϵ (Location)	-	2.40	1.43	0.16	2.87	-0.49	2.44	-2.27
4	SRR (Average) ~ Location + ϵ (Transect) + ϵ (Location)	-	-	-	-	-	-	-	-

Discussion

This study reveals for the first time that both epi- and endobenthos abundance is significantly higher in sand wave troughs compared to the crests. Our results are similar to patterns in larger-scale offshore bed forms, such as sand banks³¹ and with observed differences in endobenthic community clusters over sand waves³². In addition, our results demonstrate that in sand wave troughs, sand ripples are generally less abundant than on sand wave crests, and if present, sand ripples have a less regularly-shaped pattern. Finally, we have shown for the first time that using a camera system enables directly-coupled observations of both small-scale seabed morphology and benthic community composition at high spatial resolution.

In this study, we used holes as an indicator for endobenthos abundance. This is based on the fact that, among others, sediment-inhabiting bivalve species use their siphon to access seawater for food and oxygen, resulting in a small hole at the seabed surface⁴⁵. The majority of the encountered holes were small, with a diameter of several millimeters. It remains difficult, however, to pinpoint the exact species that produces these holes. Moreover, the abundance of species that do not produce surficial structures cannot be determined by merely using cameras. In order to provide this information, additional point measurements like boxcores could be used to establish a relationship between hole density and total endobenthos abundance. Nevertheless, we feel confident that the number of holes can be used as an indicator for endobenthos density.

Higher epi- and endobenthos densities in the sand wave troughs could be explained by differences in abiotic conditions between the troughs and crests. Median grain size, for instance, is generally lower in the troughs of sand waves^{32,46}, resulting from an interplay of both hydro- and sediment dynamics^{47,48}. Whereas sand wave crests are more exposed to both strong tidal currents and surface gravity waves, sand wave troughs are somewhat sheltered, resulting in the sedimentation of smaller grains. Similarly, this process could also favor the deposition of dead organic matter in the troughs, which could serve as a food source for benthic species. Altogether, these processes likely lead to more favorable habitat conditions for benthic species in sand wave troughs.

We observed sand ripples less abundantly and less regularly-shaped in the sand wave troughs. This is potentially caused by the result of the aforementioned interplay of hydro- and sediment dynamics, with the sheltered conditions in the troughs resulting in irregular or absent ripples. Alternatively, as the presence and activity of biota may affect ripple formation^{49,50}, the observed variations in ripple morphology could thus also be related to the spatial distribution of benthic organisms. Other complex processes (e.g. local turbulence) interact at the seabed-water interface as well, hindering quantification of the exact causality of the interaction between biota and small-scale morphology. Nevertheless, sand ripples are an important source of seabed roughness⁵¹ and the observed absence of sand ripples in the sand wave troughs clearly indicates that seabed roughness varies over sand waves.

Due to their migration rates, sand waves may pose risks to offshore human infrastructure on the seabed¹⁰. Sand wave models provide information on various sand wave properties, such as migration rates and equilibrium heights, which is necessary for the planning of offshore engineering activities. Apart from some theoretical explorations^{30,52,53}, most sand wave models solely include hydro- and sediment dynamics, without taking biotic effects into account. Moreover, they assume a uniform distribution of seabed roughness (e.g. ^{36,54}). Here, we demonstrated that both endo- and epibenthos are not evenly distributed over sand waves, with higher species densities in troughs. In addition, the troughs show irregularly-shaped or a complete lack of sand ripples. By including this detailed spatial knowledge, the accuracy of biogeomorphological models, which predict both sand wave dynamics and benthic habitat distributions, is likely to improve. In turn, this may expedite licensing procedures and project realization for future offshore engineering activities⁵⁵. Future monitoring of sand waves, along with model validation studies, should therefore aim to include

phase-related spatial patterns of both benthic biota and small-scale seabed morphology.

Cameras are increasingly applied in marine habitat mapping^{56–58}, and multiple guidelines exist for their on-board operation and subsequent footage analysis^{59–62}. Video footage was analyzed by two independently-working observers⁶⁰, and despite small absolute differences between observers, both observer-specific models and models based on the averaged data yielded similar results, showing that our methodology is robust. Due to the small offset between the GPS positions of the vessel and the camera system, we opted to be conservative in only distinguishing between sand wave crests and troughs (rather than studying a continuous elevation profile). In order to study both benthic organisms and small-scale morphology over sand waves in higher spatial detail, for instance on the slopes, future studies would benefit from including a more accurate positioning system. Nevertheless, we demonstrate that video transects may provide valuable insight into phase-related biological and morphological spatial patterns within sand waves, which combined with boxcores, could be a relatively fast and comprehensive method that yields high-resolution spatial information about benthic communities.

Conclusions

For two sand waves on the Dutch Continental Shelf, video transects were performed to count both visible epibenthic species and seabed holes, used as proxies for endobenthos abundance. Both show significantly higher abundance in the sand wave troughs compared to the crests. Thus, this study shows that sand waves affect the distribution of benthic communities.

The video transects also revealed that sand wave troughs are typified by a highly-irregular ripple pattern with shorter wavelengths than those in sand wave crests. Finally, this study showed that video transects are an efficient method to collect data on both benthic communities and small-scale morphology with relevant spatial resolution.

Acknowledgements

This study was a joint effort by the SANDBOX and DISCLOSE research programs, funded by NWO and Royal Boskalis Westminster NV, and by the Gieskes-Strijbis Fund, respectively. The authors also acknowledge Royal Netherlands Institute for Sea Research (NIOZ) for partly financing the Pelagia research vessel and providing the hopper camera. Data available from dataverse: <https://dataverse.nl/dataset.xhtml?persistentId=hdl:10411/4OARYB>

References

1. Eigaard, O. R. *et al.* The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865 (2017).
2. Halpern, B. S. *et al.* A global map of human impact on marine ecosystems. *Science*. **319**, 948–953 (2008).
3. Künitzer, A. *et al.* The benthic infauna of the North Sea: Species distribution and assemblages. *ICES J. Mar. Sci.* **49**, 127–143 (1992).
4. Heip, C. H. R. *et al.* The benthic communities of the North Sea: a summary of the results of the North Sea benthos survey. *ICES Coop. Res. Report*. **190**, 148–175 (1992).
5. Reiss, H. *et al.* Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* **67**, 278–293 (2010).
6. Stride, A. Offshore Tidal Sands. (Chapmann & Hall, 1982).
7. Knaapen, M. A. F., Hulscher, S. J. M. H., De Vriend, H. J. & Stolk, A. A new type of sea bed waves. *Geophys. Res. Lett.* **28**, 1323–1326 (2001).
8. Van Veen, J. Sand waves in the North Sea. *Hydrographic review, Vol. XII, No. 1* (1935).
9. Allen, J. Sedimentary structures. (Elsevier, 1984).
10. Nemeth, A., Hulscher, S. J. M. H. & Vriend, H. J. de. Offshore sand wave dynamics, engineering problems and future solutions. *Pipeline gas J.* **230**, 67–69 (2003).
11. Roetert, T., Raaijmakers, T. & Borsje, B. W. Cable route optimization for offshore wind farms in morphodynamic areas. In *27th International Ocean and Polar Engineering Conference* (2017).
12. Huntley, D. A. *et al.* Hydrodynamics and sediment dynamics of North Sea sand waves and sand banks. *Philos. Trans. R. Soc. London. Ser. A Phys. Eng. Sci.* **343**, 461–474 (1993).
13. van Dijk, T. A. G. P. & Kleinhans, M. G. Processes controlling the dynamics of compound sand waves in the North Sea, Netherlands. *J. Geophys. Res.* **110**, 1–15 (2005).
14. Damen, J. M., van Dijk, T. A. G. P. & Hulscher, S. J. M. H. Spatially varying environmental properties controlling observed sand wave morphology. *J. Geophys. Res. Earth Surf.* **123**, 262–280 (2018).
15. Knaapen, M. A. F. & Hulscher, S. J. M. H. Regeneration of sand waves after dredging. *Coast. Eng.* **46**, 277–289 (2002).
16. van Santen, R. B., de Swart, H. E. & van Dijk, T. A. G. P. Sensitivity of tidal sand wavelength to environmental parameters: A combined data analysis and modelling approach. *Cont. Shelf Res.* **31**, 966–978 (2011).
17. Idier, D., Ehrhold, A. & Garlan, T. Morphodynamique d'une dune sous-marine du détroit du pas de Calais. *Comptes Rendus Geosci.* **334**, 1079–1085 (2002).
18. Idier, D., Astruc, D. & Hulscher, S. J. M. H. Influence of bed roughness on dune and megaripple generation. *Geophys. Res. Lett.* **31**, n/a–n/a (2004).
19. Fredsøe, J. & Deigaard, R. Mechanics of coastal sediment transport. (Advanced Series on Ocean Engineering: Volume 3, 1992).
20. Boggs, S. Sand-Wave Fields in Taiwan Strait. *Geology* **2**, 251–253 (1974).
21. Aliotta, S. & Perolli, G. M. E. A Sand Wave Field in the Entrance To Bahia Blanca. *Mar. Geol.* **76**, 1–14. (1987).
22. Katoh, K., Kume, H., Kuroki, K. & Hasegawa, J. Development of sand waves and the maintenance of navigation channels in the Bisanseto Sea. *Proc. Coast. Eng. Conf.* **3**, 3490–3502 (1998).
23. McGave, N. Sand waves in the North Sea off the coast of Holland. *Mar. Geol.* **10**, 199–225 (1971).
24. Callaway, R. *et al.* Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES J. Mar. Sci.* **59**, 1199–1214 (2002).
25. Rabaut, M., Guilini, K., van Hoey, G., Vincx, M. & Degraer, S. A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuar. Coast. Shelf Sci.* **75**, 525–536 (2007).
26. Widdows, J. & Brinsley, M. Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. *J. Sea Res.* **48**, 143–156 (2002).
27. Lohrer, A. M., Thrush, S. F., Hunt, L., Hancock, N. & Lundquist, C. Rapid reworking of subtidal sediments by burrowing spatangoid urchins. *J. Exp. Mar. Bio. Ecol.* **321**, 155–169 (2005).
28. Eckman, J. E., Nowell, A. R. M. & Jumars, P. A. Sediment destabilization by animal tubes. *J. Mar. Res.* **39**, 361–374 (1981).
29. Borsje, B. W., Bouma, T. J., Rabaut, M., Herman, P. M. J. & Hulscher, S. J. M. H. Formation and erosion of biogeomorphological structures: A model study on the tube-building polychaete *Lanice conchilega*. *Limnol. Oceanogr.* **59**, 1297–1309 (2014).
30. Borsje, B. W. *et al.* Modeling bio-geomorphological influences for offshore sandwaves. *Cont. Shelf Res.* **29**, 1289–1301 (2009).
31. van Dijk, T. A. G. P. *et al.* Benthic habitat variations over tidal ridges, North Sea, The Netherlands. in *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
32. Baptist, M. J., van Dalfsen, J., Weber, A., Passchier, S. & van Heteren, S. The distribution of macrozoobenthos in the southern North Sea in relation to meso-scale bedforms. *Estuar. Coast. Shelf Sci.* **68**, 538–546 (2006).
33. Hulscher, S. J. M. H. Tidal-induced large-scale regular bed form patterns in a three-dimensional shallow water model. *J. Geophys. Res. C Ocean.* **101**, 20727–20744 (1996).
34. Campmans, G. H. P., Roos, P. C., de Vriend, H. J. & Hulscher, S. J. M. H. Modeling the influence of storms on sand wave formation: A linear stability approach. *Cont. Shelf Res.* **137**, 103–116 (2017).
35. Campmans, G. H. P., Roos, P. C., Vriend, H. J. & Hulscher, S. J. M. H. The influence of storms on sand wave evolution: A nonlinear idealized modeling approach. *J. Geophys. Res. Earth Surf.* **123**, 2070–2086 (2018).
36. van Gerwen, W., Borsje, B. W., Damveld, J. H. & Hulscher, S. J. M. H. Modelling the effect of suspended load transport and tidal asymmetry on the equilibrium tidal sand wave height. *Coast. Eng.* **136**, 56–64 (2018).
37. Rees, H. L., Eggleston, J. D. & Rachor, E. Structure and dynamics of the North Sea benthos. (ICES Cooperative Research Report No. 288, 2007).
38. Witbaard, R., Lavaleye, M. S. S., Duineveld, G. C. A. & Bergman, M. J. N. Atlas of the megabenthos (incl. small fish) on the Dutch continental shelf of the North Sea. *NIOZ report 2013-4*. (2013).

39. Spencer, M. L., Stoner, A. W., Ryer, C. H. & Munk, J. E. A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: Comparison with beam trawls and divers. *Estuar. Coast. Shelf Sci.* **64**, 497–503 (2005).
40. Sheehan, E. V., Stevens, T. F. & Attrill, M. J. A quantitative, non-destructive methodology for habitat characterisation and benthic monitoring at offshore renewable energy developments. *PLoS One* **5**, e14461 (2010).
41. Biber, M. F. *et al.* Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. *Deep. Res. Part II Top. Stud. Oceanogr.* **99**, 134–145 (2014).
42. Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* vol. 9 671–675 (2012).
43. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team, X. nlme: Linear and nonlinear mixed effects models. (2020).
44. Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
45. Zwarts, L. & Wanink, J. Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. *Mar. Biol.* **100**, 227–240 (1989).
46. van Lancker, V. & Jacobs, P. The dynamical behaviour of shallow marine dunes. In *International Workshop on Marine Sandwave Dynamics* (2000).
47. Van Oyen, T., Blondeaux, P. & Van den Eynde, D. Sediment sorting along tidal sand waves: A comparison between field observations and theoretical predictions. *Cont. Shelf Res.* **63**, 23–33 (2013).
48. Roos, P. C. *et al.* Grain size sorting over offshore sandwaves: Observations and modelling. In *RCEM 2007, 5th IAHR symposium on river, coastal and estuarine morphodynamics* (2007).
49. Featherstone, R. P. & Risk, M. J. Effect of tube-building polychaetes on intertidal sediments on the Minas Basin, Bay of Fundy. *J. Sediment. Res.* **47**, 446–450 (1977).
50. Friedrichs, M., Leippe, T., Peine, F. & Graf, G. Impact of macrozoobenthic structures on near-bed sediment fluxes. *J. Mar. Syst.* **75**, 336–347 (2009).
51. Soulsby, R. L. The bottom boundary layer of shelf seas. *Elsevier Oceanogr. Ser.* **35**, 189–266 (1983).
52. Borsje, B. W., Hulscher, S. J. M. H., Herman, P. M. J. & De Vries, M. B. On the parameterization of biological influences on offshore sand wave dynamics. *Ocean Dyn.* **59**, 659–670 (2009).
53. Borsje, B. W. *et al.* On the modeling of bio-physical influences on seasonal variation in sandwave dynamics. *J. Coast. Res.* **56**, 698–702 (2010).
54. Blondeaux, P. & Vittori, G. A model to predict the migration of sand waves in shallow tidal seas. *Cont. Shelf Res.* **112**, 31–45 (2016).
55. Damveld, J. H., Borsje, B. W., Roos, P. C. & Hulscher, S. J. M. H. Smart and sustainable design for offshore operations in a sandy seabed - The SANDBOX programme. In *MARID V. Fifth International Conference on Marine and River Dune Dynamics*. (2016).
56. Kendall, M. S. *et al.* Benthic mapping using sonar, video transects, and an innovative approach to accuracy assessment: A characterization of bottom features in the Georgia Bight. *J. Coast. Res.* **21**, 1154–1165 (2005).
57. Stoner, A. W., Spencer, M. L. & Ryer, C. H. Flatfish-habitat associations in Alaska nursery grounds: Use of continuous video records for multi-scale spatial analysis. *J. Sea Res.* **57**, 137–150 (2007).
58. Guinan, J., Grehan, A., Dolan, M. & Brown, C. Quantifying relationships between video observations of cold-water coral cover and seafloor features in Rockall Trough, west of Ireland. *Mar. Ecol. Prog. Ser.* **375**, 125–138 (2009).
59. Coggan, R., Mitchell, A., White, J. & Golding, N. Recommended operating guidelines (ROG) for underwater video and photographic imaging techniques. MESH report (2007).
60. Hitchin, R., Turner, J. A. & Verling, E. Epibiota remote monitoring from digital imagery: Operational guidelines. JNCC report (2015).
61. Sheehan, E. V. *et al.* An experimental comparison of three towed underwater video systems using species metrics, benthic impact and performance. *Methods Ecol. Evol.* (2016).
62. White, J., Mitchell, A., Coggan, R. A., Southern, I. & Golding, N. Seafloor video mapping: Collection, analysis and interpretation of seafloor video footage for the purpose of habitat classification and mapping. MESH report (2007).

Chapter 6

Linking the morphology and ecology of subtidal soft-bottom marine benthic habitats: a novel multiscale approach

Sebastiaan Mestdagh

Alireza Amiri-Simkooei

Karin J. van der Reijden

Leo Koop

Sarah O'Flynn

Mirjam Snellen

Christiaan Van Sluis

Laura L. Govers

Dick G. Simons

Peter M. J. Herman

Han Olff

Tom Ysebaert

Published as

Mestdagh S, Amiri-Simkooei A, van der Reijden KJ, Koop L, O'Flynn S, Snellen M, van Sluis C, Govers LL, Simons DG, Herman PMJ, Olff H, Ysebaert T. (2020) Linking the morphology and ecology of subtidal soft-bottom marine benthic habitats: a novel multiscale approach. *Estuarine, Coastal and Shelf Science*, 238, 106687.

Abstract

High-resolution surveying techniques of subtidal soft-bottom seafloor habitats show higher small-scale variation in topography and sediment type than previously thought, but the ecological relevance of this variation remains unclear. In addition, high-resolution surveys of benthic fauna show a large spatial variability in community composition, but this has yet poorly been linked to seafloor morphology and sediment composition. For instance, on soft-bottom coastal shelves, hydrodynamic forces from winds and tidal currents can cause nested multiscale morphological features ranging from metre-scale (mega)ripples, to sand waves and kilometre-scale linear sandbanks. This multiscale habitat heterogeneity is generally disregarded in the ecological assessments of benthic habitats. We therefore developed and tested a novel multiscale assessment toolbox that combines standard bathymetry, multibeam backscatter classification, video surveying of epibenthos and box core samples of sediment and macrobenthos. In a study on the Brown Bank, a sandbank in the southern North Sea, we found that these methods are greatly complementary and allow for more detail in the interpretation of benthic surveys. Acoustic and video data characterised the seafloor surface and subsurface, and macrobenthos communities were found to be structured by both sandbank and sand wave topography. We found indications that acoustic techniques can be used to determine the location of epibenthic reefs. The multiscale assessment toolbox furthermore allows formulating recommendations for conservation management related to the impact of sea floor disturbances through dredging and trawling.

Introduction

Subtidal soft-sediment beds form the most widespread benthic habitat type on earth and result from the interplay of geological, physical and biological drivers^{1,2}. When occurring within the depth range affected by hydrodynamic activity from wind and currents (e.g. < 50 m deep on coastal shelves), these sediment beds form clear, multiscale nested structures, such as sandbanks, sand waves, or (mega)ripples^{3,4}. Consequently, heterogeneous seafloor landscapes are created, in which topographic features shape soft-sediment habitat diversity with respect to sediment type and hydrodynamic exposure. This impact of topography on habitat heterogeneity is additionally complemented by variations in the physico-chemical composition of the sediment. In a sandbank system, for example, a clear sediment distribution can be distinguished, with generally finer and carbonate-poorer sediments in the troughs than on the crest^{5,6}. Habitat variation resulting from this physico-chemical heterogeneity of the seafloor creates important variation in habitat conditions for benthic fauna. Spatial heterogeneity therefore influences important ecosystem features at various scales, including species diversity, density and biomass, community composition, and several ecosystem processes^{7,8}. Classic ecology theory states that more heterogeneous habitats support more species per unit area^{9,10}. In marine ecosystems, for example, macrobenthic communities tend to be richer, denser, and different in species composition in troughs than on crests of sandbanks¹¹, but also of sand waves¹² and small-scale ripples¹³.

In terms of biodiversity, underlying gradients in the physical habitat template can be greatly amplified by biological mechanisms, especially where organisms modifying their physical habitat ('ecosystem engineers' *sensu* Jones et al. 1994) play a decisive role. Such abrupt biogenic landscape boundaries are well known from coral reefs, but also from intertidal habitats where several autogenic ecosystem engineers form complex three-dimensional structures, e.g. at the boundary of vegetated and non-vegetated tidal flats or seagrass meadows^{15,16}, or in the vicinity of oyster reefs and other bivalve beds^{17,18}. Through density-dependent feedbacks, ecosystem engineers can buffer the impact of physical forces, although their occurrence is generally limited where these physical forces exceed critical thresholds. In heavily trawled subtidal soft-sediment areas with high substrate mobility, such as sand wave-dominated sediments, their presence seems limited but not absent¹⁹. Some reef-forming organisms, such as tube worms, may occur in sandbank troughs, where food and suspended sediment needed to build their tubes are sufficiently present^{20,21}. The presence of these reefs induces high local biodiversity, sustained by increased local habitat heterogeneity, physical shelter and better food supply^{22–24}.

Anthropogenic physical disturbance, e.g. bottom trawl fisheries, tends to homogenise soft-bottom sediments by removing smaller-scale habitat heterogeneity in subtidal soft sediments, jeopardising their structure, function and biodiversity^{25,26}. Epibenthos is particularly vulnerable to this influence^{20,27}, but infaunal organisms are also affected, resulting in a shift of benthic communities towards a dominance of shorter-lived species^{28,29}. Given the high prevalence and intensity of demersal fisheries in shallow coastal seas such as the North Sea^{30–32}, benthic surveys may not be sufficiently able to reveal the biodiversity potential of many benthic (sub)habitats created by the interplay between hydrodynamic and biological forces. An approach that resolves the underlying physical gradients and evaluates both the potential of this template for biogenic self-reinforcing biodiversity development, and vulnerability/sensitivity to disturbance, is therefore needed.

The most important constraint for biodiversity-oriented benthic surveys is the trade-off between extent and 'grain' (resolution in space and time, and in terms of variables estimated) of the different observational methods. As sampling is often costly and time-consuming, and areas needing coverage are large, a balance between extent and resolution needs to be found^{33,34}. With respect to the identification of the physical habitat template, a very promising approach is the use of multibeam echo-sounding (MBES). Especially when the full information in the returning acoustic signals (including backscatter intensity) is used, this acoustic technique allows for a detailed

characterisation of the seafloor bathymetry, but can also give information about the sediment type variation of the seafloor^{35,36}. However, the method does not give direct information on the species composition of benthic assemblages³⁷. *In situ* sampling remains necessary to link topography to seafloor ecology. To map seafloor communities, multibeam data can be combined with camera surveying, such as video transects, photos of the seafloor by landing frames or sediment profile imaging³⁸ (SPI camera), or by box core samples. Between these techniques, there is also a trade-off between the area covered per unit effort, and taxonomic resolution of the biodiversity surveys. An optimal combination of several techniques is likely the best compromise between these approaches.

In this study, we combined MBES, video, photographic (SPI) and box core sampling of the seafloor macrobenthos communities in a dynamic area in the southern North Sea. We tested how the combination of these techniques can be used to accurately link biodiversity to seafloor morphology and explored if it enables us to upscale locally sampled biodiversity patterns to the wider seafloor landscape. Since different seafloor morphologies can offer different substrate characteristics and varying food availability to the benthic fauna, we also explored the relationships between benthic macrofauna abundance and biodiversity, and sediment grain size and organic matter quantity and biochemical composition. The aim of this study is to quantify the correlation between the outcomes of the different approaches and to generalise this information in the design of optimal survey approaches for larger areas of the North Sea.

Material and methods

Study area

This study focused on the Brown Bank, a large sandbank with a height difference of about 26 m between crest and trough, belonging to the north-south oriented Dutch Banks in the southern North Sea (Fig. 1). The sandbank is located nearly halfway between the Netherlands and the United Kingdom, at about 85 km from the Dutch coast. The seafloor in this region additionally forms smaller-scale sand waves that are roughly east-west oriented, with wavelengths of about 200 m and heights of 5 m, and smaller megaripples, with wavelengths and heights of about 10 m and 0.1 m, respectively. Both sand waves and megaripples migrate over the seafloor, at rates in the order of several metres per year for sand waves and within weeks or even hours for megaripples^{39–41}. The area is heavily fished by bottom trawlers, especially the troughs between the large sandbanks³¹. The sampling took place from 26 October till 5 November 2017, during a campaign on board *RV Pelagia*.

Multibeam echo sounding

A hull-mounted Kongsberg EM302 MBES (Kongsberg Maritime, Kongsberg, Norway) with a central frequency of 30 kHz was deployed during the sampling campaign. The MBES operated with 432 beams, a swath opening angle of 130 degrees, and across and along track beam opening angles of two and one degrees, respectively. Bathymetry and backscatter were logged using the Kongsberg Seafloor Information System software.

The data were cleaned in Qimera, exported using Qinsy (Quality Positioning Services, Zeist, the Netherlands), and further processed in MatLab 2018b (Mathworks, 2018). Steep seafloor slopes were corrected and a Bayesian classification method was performed on the backscatter data, yielding four acoustic classes for the survey area^{40,42–44}. From the backscatter data, sediment median grain size M_z , surface roughness w_z and volume scattering σ_z were calculated, whereby the latter two variables describe the backscatter signal caused by seafloor surface roughness and by heterogeneities underneath the sediment surface, respectively^{45–47}. Bathymetry was used to calculate slope and the Bathymetric Position Index (BPI) for each pixel, which represents the average height difference between that pixel and its surroundings within a pre-defined radius. We

Figure 1. Location of the 22 sampling stations on and around the Brown Bank, with background colour indicating (a) bathymetry, (b) backscatter-based acoustic classes, (c) volume scattering (σ_2) and (d) surface roughness (w_2). The inset (e) shows the location of the Brown Bank in the southern North Sea.

used BPI-2000 (with a 2000 m radius) as a measure for sandbank topography, BPI-200 for sand waves and BPI-10 for megaripples.

Box core samples

After inspection of the seafloor bathymetry based on the MBES, 22 stations on and around the Brown Bank were selected for sampling. Along three transects (north, middle, south), stations were chosen on the sandbank crest and flanks, in the troughs and beyond the troughs in sand wave-dominated areas that form gentle slopes of the next sandbanks. Based on a real-time observed deviating pattern in the acoustic data, an additional transitional station (station 22) was sampled, at the western edge of the western trough (Fig. 1). The sampled stations were classified according to their topographic position: 'Crest', 'Flank', 'Trough', 'Transitional' and 'Beyond', the last of which refers to the sand wave-dominated area beyond the troughs of the Brown Bank. At each station, three replicate box core samples were taken with a box corer (30 cm internal diameter). Beyond the eastern trough of the Brown Bank, two stations were located in a sand wave trough (stations 10 and 15) and one (station 5) on a crest, whereas two stations were located on a stoss-side flank (stations 6 and 11) and one (station 1) in a trough of a sand wave beyond the western trough of the sandbank.

From each box core sample, sediment subsamples were taken with a 50 ml syringe and immediately stored at -20 °C before processing. After at least four days of freeze drying, these subsamples were analysed for granulometry, chlorophyll *a* concentration, total organic carbon (TOC) and total nitrogen (TN). Granulometry was determined by sieving the samples over a 4 mm, 2 mm and 1 mm mesh and analysing the smallest fraction by laser diffraction with a Malvern Mastersizer 2000 (Malvern Instruments, Worcestershire, UK). The larger sediment fractions were weighed, and mass percentages were calculated for each separate fraction. However, since these mass percentages were negligible (less than 2 % of the total mass in most samples), the coarser fractions were discarded for further analysis. After extraction in a bullet blender with 90 % acetone, chlorophyll *a* was analysed using a Specord 210 spectrophotometer (Analytik Jena, Jena, Germany). TOC and TN were analysed according to the Dumas method⁴⁸, using a Thermo Flash 2000 Element Analyser (Thermo Fisher Scientific, Waltham, Massachusetts, USA).

The remaining sediment was sieved over a 0.5 mm mesh to extract the macrobenthos. Animals were fixed in 4-6 % formalin and transported to the laboratory, where they were counted and identified to the lowest possible taxonomic level. For each sample, densities, species richness (*S*) and Pielou's evenness (*J'*) were calculated. Furthermore, functional groups were defined based on combinations of sediment reworking mode (E: epifauna, S: surficial modifiers, C: conveyor-belt feeders, B: biodiffusors, R: regenerators), and motility in the sediment (A: in a fixed tube; B: sessile, but not in a tube; C: slow movement through the sediment; D: free movement through a burrow system)^{49,50}.

Sediment Profile Imaging

A Sediment Image Profiler (SPI) was used to determine the subsurface seabed structure. The SPI consists of a galvanized frame with a camera-comprising prism, which protrudes the seafloor when lowered onto the seabed⁵¹. The SPI was lowered three times at each, except the transitional, station. At each drop, two pictures were taken, resulting in 6 pictures per station. The penetration depth was measured, the presence of shell fragments was classified (0: no shell fragments; 1: few shell fragments; 2: medium shell fragments; 3: many shell fragments), and the dominant sediment type was identified (Sand or Mud).

Video transects

Videos of the seabed were collected using a towed video camera frame, as described in Koop et al. (2019). This aluminium frame was equipped with a remotely operated video camera (Kongsberg OE14-522A-0009 Colour HD Pan), lights (Fisheye FIX NEO 1000DX SW II LED), and lasers (Z-Bolt, SCUBA-II green) for scaling. Its approximate height above the seabed was constantly checked using live view from the camera. The length of the towing cable was adjusted to maintain the desired height if needed. During video operations, the vessel had a speed of ± 0.1 m/s, with the camera towed at approximately 0.5 m above the seafloor.

Video transects were performed at 10 stations, in the crest and both troughs, and the transitional station (see Supplement Fig. 1). Two transects were performed for each except the transitional station. Validity and superficial landscape type were deduced from the video footage, as well as shifts between landscape types and the number of observed organisms. The observed species were identified to the lowest taxonomic level possible. The horizontal geographic position of the camera was deduced from a time match with interpolated GPS positions of the vessel, which were recorded every 30 s. For each transect, the surveyed area was determined as the summed surface of grid cells with camera presence in a 0.50×0.50 m grid. The number of individuals of each species could hence be converted to densities (m^{-2}) per transect. The number of switches in landscape type was determined as an indicator of small-scale habitat heterogeneity. For this, the number of landscape switches was divided by the length of the transect, which was determined as the sum of distances between valid recordings.

Statistical analysis

All variables concerning macrobenthos density and diversity, and sediment properties were analysed through a Kruskal-Wallis test, using the topographic position (TP) on or around the sandbank as the predictor with five levels ('Crest', 'Flank', 'Trough', 'Transitional', 'Beyond'), followed by a Dunn test for pairwise contrasts. In the 'Beyond' TP, a Mann Whitney U Test was conducted with the same properties, to discern between sand wave flanks/crests and troughs. The composition of macrobenthos communities in the different TPs was analysed with a one-factor PERMANOVA on species densities and functional group densities, using the function *adonis()* in the R package *vegan*⁵². Homogeneity of dispersions was tested with function *betadisper()* in the same package. For 'Trough', 'Flank' and 'Beyond', one-factor PERMANOVA analyses were conducted to reveal differences between the eastern and western side of the Brown Bank. The data were further explored through Non-metric MultiDimensional Scaling (NMDS), on which the topographic position, orientation and location of sand waves were indicated. SIMPER analyses were performed to reveal the most discriminating species or functional groups between the TPs.

The penetration depth for the SPI pictures was tested using a linear mixed model (LMM), with topographic position as explanatory and station as random variable. Log likelihood ratio was determined between this model and a null model with only the random effect of station included. For both the organism density and the small-scale heterogeneity based on video data, a similar approach was taken.

Acoustic data derived from the MBES and other environmental data were linked to macrobenthos community data via redundancy analysis (RDA). Both species densities and functional group densities were tested. A backward stepwise selection was performed to select significant variables from the full set of MBES data (M_z , w_z , σ_z , slope, backscatter, bathymetry, BPI2000, BPI200, BPI10), as well as TOC, TN and chlorophyll *a* content for the RDA model.

All analyses were performed in the open source statistical software R⁵³. Values are represented as mean $\pm$ standard deviation.

Results

Acoustic characterisation of the seafloor

Bathymetric mapping clearly indicated the presence of the sandbank, flanked east and west by troughs, and a sand wave-dominated region beyond the troughs. The bathymetric features can also be distinguished when using backscatter classes or either surface roughness w_2 or volume scattering σ_2 for mapping, with generally higher backscatter values in the troughs and lower on the crests. Backscatter shows similar patterns as σ_2 , while w_2 gives an inverse pattern, with lower values in the troughs and higher on the crest (Fig. 1).

Abiotic properties of the sandbank sediments

The median grain size and mud content of the sediment were found to differ significantly between different TPs, with the 'Transitional' differing most from the other TPs (Table 1). While grain sizes and mud content in the 'Transitional' reached values of $43.33 \pm 25.93 \mu\text{m}$ and $60.13 \pm 15.48 \%$, respectively, median grain size in the other TPs ranged from $294.65 \pm 12.97 \mu\text{m}$ ('Flank') to $314.65 \pm 16.24 \mu\text{m}$ ('Crest'), and mud content from $0 \pm 0 \%$ ('Crest' and 'Flank') to 1.63 ± 3.31 ('Trough').

TOC differed significantly between nearly all TPs. Only the 'Flank' and 'Beyond', and the 'Trough' and 'Transitional' were similar. TOC was highest in the 'Transitional' ($0.59 \pm 0.19 \%$) and lowest on the 'Crest' ($1.17 \pm 0.32 \times 10^{-2} \%$). TN values were significantly different between the 'Transitional' and other TPs, and between the 'Trough' and other TPs, but not between 'Transitional' and 'Trough'. Values were lowest on the 'Crest' ($4.67 \pm 3.16 \times 10^{-3} \%$) and highest in the 'Transitional' ($6.12 \pm 1.36 \times 10^{-2} \%$). Chlorophyll *a* content showed significant and similar patterns, with highest values in the 'Trough' ($0.51 \pm 0.27 \mu\text{g g}^{-1}$) and lowest on the 'Crest' ($0.08 \pm 0.02 \mu\text{g g}^{-1}$). Of the sediment properties, only chlorophyll *a* content was found significantly different between the flanks and troughs of sand waves within the 'Beyond', with higher values in the troughs than on the flanks (Table 1).

Table 1. Kruskal-Wallis and Dunn tests for significant differences of abiotic (median grain size, mud content, TOC: Total Organic Carbon, TN: Total Nitrogen, chlorophyll *a* content) and biotic variables (*S*: Species richness, *J'*: Pielou's evenness) between the various Brown Bank topographic positions, and *p*-values of the Mann-Whitney U test (MWU) to discern between sand wave flanks and troughs. Bey: Beyond; Cre: Crest; Fla: Flank; Tra: Transitional; Tro: Trough.

Variable	Kruskal-Wallis Test		Significant pairwise contrasts ($\alpha = 0.05$)	MWU
	χ^2	<i>p</i>		
Median grain size	16.60	< 0.001	Bey-Fla, Bey-Tra, Cre-Fla, Cre-Tra, Fla-Tra, Tra-Tro	0.387
Mud content	31.10	< 0.001	Bey-Tra, Cre-Tra, Fla-Tra, Fla-Tro, Tra-Tro	0.374
TOC	45.90	< 0.001	Bey-Cre, Bey-Tra, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.058
TN	27.38	< 0.001	Bey-Tra, Bey-Tro, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.627
Chlorophyll <i>a</i>	42.22	< 0.001	Bey-Cre, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	< 0.001
<i>S</i>	25.78	< 0.001	Bey-Cre, Bey-Tra, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.033
<i>J'</i>	2.86	0.580	-	0.114
Total density	23.31	< 0.001	Bey-Cre, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.667

Subsurface seabed structure

At two stations, only four usable pictures were obtained due to malfunctioning of the SPI. The average penetration depth was 6.3 ± 2.9 cm, with 39 pictures having a penetration depth of < 5 cm. Penetration depth was much larger on the crest (11.5 ± 2.9 cm) than at the other locations (5.6 ± 2.1 cm) (log likelihood ratio of LMM: -6.8). The amount of shell fragments was higher in the troughs compared to the crest locations, as crest pictures were all classified as no shell fragments (class 0), while the trough pictures showed the highest percentages of class 1 and 2 (medium and many shell fragments, respectively).

Video transects

A total of 1813 individuals of 16 species were observed, over a total observed area of 1358 m². The most recorded species was the starfish *Asterias rubens* (1378 individuals), followed by Ophiuroidea brittle stars (256 ind.) and the hermit crab *Pagurus bernhardus* (65 ind.). Compared to the crest (0.128 ± 0.057), the troughs (East: 3.079 ± 4.502 ; West: 0.770 ± 0.298) had higher densities of organisms (log likelihood ratio LMM: -4.9). Moreover, the troughs (East: 3.463 ± 2.876 ; West: 5.315 ± 3.183) showed 3 to 5 habitat type changes per 100 m transect, while the crest showed none (log likelihood ratio LMM: -4.9). Crest transects only showed sandy sediment with hardly any shell fragments, while all other stations alternated between sandy sediments with shell fragments and sandy sediments with shell fragments and incidental large stones (see Supplement Fig. 1). Sandy sediments with shell fragments, incidental stones and *Sabellaria* reef fragments (*Sabellaria* landscape) were observed in the northern station in the eastern trough (station 4) and the middle station in the western trough (station 7). Moreover, the transitional station (station 22) showed some *Sabellaria* habitat, but also the unique “sand with clay” and “sand with clay and incidental stones” habitats.

Macrobenthos communities in the different topographic positions

A total of 129 different taxa, divided over 9 phyla, was observed (see Supplement Table 1). Overall, communities were mostly dominated by mobile hooded shrimp (cumaceans) and amphipods, whereas less mobile species, among which phoronids, sessile polychaetes and bivalves, reached higher densities in the ‘Trough’ and the ‘Transitional’ (see Supplement Table 2). Here, individuals of the reef-building Ross worm (*Sabellaria spinulosa*) were also found. Community composition was determined by the TPs within the Brown Bank environment, as indicated by the PERMANOVA test (Table 2). Significant differences between habitats were found for all pairwise contrasts, except between the ‘Flank’ and the ‘Beyond’ and between the ‘Trough’ and the ‘Transitional’. Significant differences between the eastern and western side were found within the ‘Beyond’ and between the two flanks of the Brown Bank. Fourteen different functional groups of macrobenthos, based on sediment reworking mode and motility, were identified in our dataset (see Supplement Table 1). Functional group composition also differed significantly among TPs (Table 2). While surficial modifiers that slowly move through the sediment (SC) were the dominant functional group in all TPs, biodiffusors (BC) reached similar densities in the sandbank troughs and on the flanks. Functional community compositions in the ‘Trough’ and ‘Flank’ were found significantly different from the other TPs, except from the ‘Beyond’. However, the northernmost station of the eastern trough (station 4) was located far outside the point cloud on the NMDS plot, and after removal of this point, no significant effect of sandbank region was found in the PERMANOVA test (Table 2). The NMDS plot with the taxonomical community compositions show that within the ‘Beyond’, both functional and taxonomical community composition from the troughs and crests of sand waves share relative similarities with the sandbank trough and crest communities, respectively (Fig. 2).

Table 2. PERMANOVA results, testing taxonomical and functional macrofauna community composition for significant differences between topographic positions (TP), and testing between eastern and western troughs, flanks and beyond troughs. *P*: p-value for the PERMANOVA test; *P* (*disp*): p-value for the multivariate dispersion of variances. The asterisk (*) represents the results of the test after removal of the outlying station 4.

Sandbank TP	Pseudo-F	P	P (<i>disp</i>)
Taxonomical	4.54	< 0.001	0.096
Functional	3.76	< 0.001	0.287
Functional*	1.77	0.055	0.363
East-West			
Trough	1.68	0.095	0.099
Flank	3.76	< 0.001	0.720
Beyond	2.96	0.002	0.913

Figure 2. NMDS plots based on (a) taxonomical composition of the macrobenthic communities, with indication of the species that contributed more than 5 % to the dissimilarity between topographic positions (TP) in the SIMPER analysis (Bel: *Bathyporeia elegans*; Csu: *Callianassa subterranea*; Kbi: *Kurtiella bidentata*; Mag: *Megaluropus agilis*; Mgi: *Monopseudocuma gilsoni*; Mjo: *Magelona johnstoni*; N: *Nemertea*; Nri: *Nephasoma rimicola*; P: *Phoronis* sp.; Plo: *Pseudocuma longicorne*; Ssp: *Sabellaria spinulosa*; Ssq: *Scolecopsis squamata*; Ubr: *Urothoe brevicornis*) and (b) functional composition of the macrobenthos communities, with functional groups based on sediment reworking mode (E: epifauna, S: surficial modifiers, C: conveyor-belt feeders, B: biodiffusors, R: regenerators), and motility in the sediment (A: in a fixed tube; B: sessile, but not in a tube; C: slow movement through the sediment; D: free movement through a burrow system).

The species richness was lowest with 9.44 ± 3.50 species per sample on the 'Crest' and highest with 28 ± 9.54 species in the 'Transitional', and showed significant differences between all TPs, except between the 'Flank' and 'Beyond' and between the 'Trough' and the 'Transitional'. Pielou's evenness ranged from 0.79 ± 0.08 in the 'Trough' to 0.84 ± 0.09 on the 'Crest' and did not differ significantly among TPs (Table 1). In the 'Beyond', species richness, but not Pielou's evenness, was found significantly different between sand wave crests and troughs. Total densities were lowest on the 'Crest' (380.40 ± 224.52 individuals/m²) and highest in the 'Trough' and 'Transitional' (2092.99 ± 2834.49 and 1872.13 ± 1092.39 individuals/m², respectively). Densities on the 'Crest' were significantly lower than all other TPs and densities in the 'Trough' significantly higher than all others except the 'Transitional'.

The SIMPER analysis revealed that the most discriminating species between TPs were hooded shrimp (*Monopseudocuma gilsoni*), horseshoe worms (*Phoronis* sp.) and Ross worms (*Sabellaria spinulosa*) (see Supplement Table 3). *M. gilsoni* was the most discriminating species when comparing most TPs with each other. *Phoronis* sp. was the most important discriminator between 'Beyond' and 'Transitional', 'Crest' and 'Transitional' and 'Flank' and 'Transitional', while *S. spinulosa* was the most discriminating species between the 'Trough' and 'Transitional'. The most discriminating functional group for most pairs of TPs was the group of the surficial modifiers that slowly move through the sediment (SC), a group that encompasses the abundant *M. gilsoni*. Of the significantly different TPs, we found that this group was also the most important discriminator between the 'Trough' and 'Flank', but sessile surficial modifiers (CB) between the 'Crest' and 'Flank' and surficial modifiers in a fixed tube (SA) between the 'Flank' and 'Transitional'.

Integration of the different methods

The video, SPI footage and MBES data show similar features, with the more topographically diverse seafloor habitats outside the sandbank crest corresponding with a higher backscatter signal. For the RDA model linking acoustic and macrobenthos data, the stepwise selection procedure selected TOC, σ_2 and bathymetry as contributing significantly to the variation in macrobenthos (taxonomic) community structure based on densities. The model explained 46.7 % of the total variation in the data, with the first two ordination axes explaining 28.6 % and 11.9 %, respectively. Bathymetry mostly separated the macrobenthos communities in the different topographic positions from each other, as well as sand wave flanks/crests from the sand wave troughs in the 'Beyond' TP. TOC and σ_2 mostly separated the majority of the stations from the 'Transitional' station and the 'Trough' station where video footage showed a high *Sabellaria* presence (Fig. 3a). For the RDA model based on functional groups, σ_2 and backscatter were selected as significant contributors to the variation in community structure, mostly separating the 'Trough' and 'Transitional' stations, as well as 'Beyond' stations in sand wave troughs, from the others (Fig. 3b). This model explained 31.1 % of the total variation in the data, with the first two ordination axes explaining 23.7 % and 7.3 %, respectively.

Discussion

Linking data from multiscale sampling methods

The observation of stones and shell fragments in the troughs from both video and SPI footage and the MBES data, corresponds to earlier findings at the Brown Bank and other sandbanks in the southern North Sea^{40,54}. Houziaux *et al.* argued that intensive bottom trawling in the twentieth century probably covered these coarse materials by and mixed them with sand⁵⁵. The resulting mixed sediment beds explain the higher volume scattering observed in the sandbank troughs. The relatively low surface roughness on the other hand, suggests a smoother sediment surface in the troughs than elsewhere, possibly due to a relative lack of sand ripples caused by lower hydrodynamic conditions⁴⁷.

Figure 3. RDA plots based on (a) taxonomical and (b) functional composition of the macrobenthos communities, with indication of the environmental variables that contribute significantly to the variation and species/functional groups as in Fig. 2. TOC: Total Organic Carbon; Backscatter: Backscatter intensity; σ_2 : Volume scattering.

Macrobenthic community compositions appear to be largely determined by topographic position (as determined by hydrodynamics), with higher biodiversity in the sandbank troughs than on the crest, confirming earlier research^{11,56}. Although our communities beyond the Brown Bank troughs were also separated according to their location within sand waves, this smaller-scale separation between communities was not significant. On the other hand, differences between the eastern and western 'Beyond' TP may have been caused by different locations on the sand waves. Note, however, that sand waves were mainly abundant beyond the Brown Bank and its troughs and were therefore only sampled in a small subset of all stations. Moreover, sand wave samples outside troughs were not always taken exactly on a crest, but often on stoss-side flanks, which are affected by the currents, just like crests. Yet, the separation of communities according to their occurrence in either the trough of a sand wave or on its flank, and their relative similarities to those of the corresponding sandbank TPs, indicates that the processes shaping benthic communities operate similarly on different spatial scales. The higher biodiversity in troughs of different scales has been associated with a higher organic matter or mud content^{11–13}. However, our communities from the sand wave-dominated areas were hardly separated based on their organic matter content (TOC), and we could only find this distinction in sediment properties for the large-scale sandbank. We therefore suggest that – next to sediment properties – physical stress caused by the dynamics of water and sediment is an important factor in determining which species will dominate communities in sand wave environments.

Sabellaria reefs and the impact of bottom trawling

Our findings supported earlier observations of *Sabellaria spinulosa* reef fragments in the troughs around the Brown Bank²⁰. However, analysis of the video and box core data did not always lead to the same conclusions. At the transitional station, high abundances of individual *Sabellaria* worms were found in the box cores, whereas the video showed only few reef fragments. Likewise, in the northernmost station in the western trough one box core sample contained *Sabellaria* worms, but no reef fragments were observed in the video transects. For the northernmost station in the eastern trough and the central station in the western trough, video observations of *Sabellaria* reef

fragments did not automatically coincide with frequent presence of *Sabellaria* worms in the box core samples. This indicates that this species has a larger distribution area, but forms reefs solely in specific locations, and its patchy distribution demands a sampling approach covering multiple scales. Our samples suggest that the presence of both *Sabellaria* reefs and individuals stimulates the establishment of diverse and – both taxonomically and functionally – distinct macrobenthos communities. Earlier studies have emphasised the ecological importance of reef-forming benthic species, especially through promoting habitat heterogeneity and organic matter entrapment^{23,24,57}. Interestingly, we show that high abundances of *Sabellaria* individuals might have the same effect. Furthermore, the specific locations where reef fragments were observed appeared to occur in areas characterised by high acoustic volume scattering, suggesting that this parameter can be used to identify potential *Sabellaria* reef locations.

The presence of *Sabellaria* reefs and more diverse and dense macrobenthos communities in the Brown Bank troughs can promote a higher local fish diversity, since several species of demersal fish are known to feed near these reefs⁵⁸. Van der Reijden *et al.* showed that beam trawl fisheries strongly prefer the Brown Bank troughs, resulting in intense local fishing³¹. Beam trawling is known to destroy epibenthic structures such as reefs and disrupt endobenthic communities by dragging heavy gear over the seafloor^{59,60}. This intense trawling is therefore a likely reason why only sparse reefs are known around the Brown Bank, whereas higher amounts of reefs still occur in British waters, where they have enjoyed a longer protection^{20,61}. The macrobenthos communities of the Brown Bank troughs are probably adapted to high disturbance, as the region has already been trawled since the thirteenth, and more intensively since halfway the twentieth century^{62,63}. As the communities are either influenced by anthropogenic disturbance (bottom trawling in the troughs and lower flanks) or by a higher physical stress (high hydrodynamic regime on the crests and higher parts of the sandbank), their current functional composition lacks a clear distinction. Only where trawling is – probably by chance – relatively limited, for example in topographic “safe sites”, both a functionally distinct community and a (small) biogenic reef can form, as observed in the northernmost station of the eastern trough.

Implications for monitoring

By combining different sampling methods, we obtained a more detailed image of the seafloor than would otherwise be possible. Traditional designs that merely focus on grab or box core samples do not take small-scale heterogeneity of the seafloor into account and extrapolate the findings of sampling points to their direct surroundings. Great care should therefore be taken in the spatial interpolation between samples. Although macrobenthos communities largely corresponded with the Brown Bank morphology, we showed that additional techniques are useful to obtain information about smaller-scale variability. Acoustic data were crucial to identify sand waves, allowing us to compare patterns in community structure on the sandbank and the sand wave scale. Furthermore, video footage revealed that the *Sabellaria* found in the box core samples formed (fragmented) reefs, which occurred only in areas with high volume scattering. Not only can we therefore use these techniques to add detail to our interpretation of seafloor heterogeneity, they may also be useful to delineate regions where biogenic structures can be present, and therefore potentially serve as an important tool in conservation management. The box core samples, in contrast with the other survey techniques, allowed inferring the correlation structure between the occurrence of all species of macrobenthos. This is needed in order to properly evaluate the community effects of features like *Sabellaria* reefs.

Conclusion

The combined use of multiple sampling techniques for seafloor and benthos characterisation allowed us to make a detailed interpretation of our findings. As standard sampling schemes tend to inadvertently ‘homogenise’ the studied region when spatially extrapolating data, we recommend the complementary use of MBES and video footage. This allows for a greater detail of the surveys, allowing us to make predictions about the interlaying seafloor that can potentially serve for conservation management.

Acknowledgments

No conflicts of interest are declared. The authors would like to thank Karline Soetaert (NIOZ) for organising the cruise and acknowledge Rob Witbaard (NIOZ) for his role as chief scientist during the cruise. The crew of *RV Pelagia* is also acknowledged for their practical assistance on board. Peter van Breugel is thanked for performing the particle size analysis in the NIOZ lab, and Matthew Parsons and Maria Bacelar Martinez for processing of the macrobenthos samples. Finally, the authors acknowledge the Gieskes-Strijbis Fonds for financial support of the DISCLOSE project, within which this research took place.

Supplementary materials

Supplementary materials can be found online at <https://doi.org/10.1016/j.ecss.2020.106687>.

Figure S1. A: Landscapes observed in the different video transects, with indication of transect locations. B: Number of landscape switches per topographic position. C: Abundance of species observed on video footage per m² in each topographic position. D: Abundance of organisms observed on video footage per m² in each topographic position.

Table S1. List of macrobenthos taxa observed in the box core sampling of the Brown Bank, with indication of sediment reworking mode (R; E = epifauna, S = surficial modifiers, C = conveyor-belt feeders, B = biodiffusors, R = regenerators) and motility (M; A = in a fixed tube; B = sessile, but not in a tube; C = slow movement through the sediment; D = free movement through a burrow system).

Table S2. Species per sampling station (St) that comprise at least 5 % of the total density of macrobenthos, and the percentage of the total density each species comprises.

Table S3. Results of the SIMPER analyses for the most discriminating species and functional groups between the different topographic positions. Only the five most important discriminators are shown. Functional groups are combinations of sediment reworking mode (E = epifauna, S = surficial modifiers, C = conveyor-belt feeders, B = biodiffusors, R = regenerators) and motility (A = in a fixed tube; B = sessile, but not in a tube; C = slow movement through the sediment; D = free movement through a burrow system).

References

1. Snelgrove, P. V. R. Getting to the bottom of marine biodiversity: Sedimentary habitats. *Bioscience* **49**, 130–153 (1999).
2. Zeiler, M., Schwarzer, K. & Ricklefs, K. Seabed morphology and sediment dynamics. *Die Küste* **74**, 31–44 (2008).
3. Passchier, S. & Kleinhans, M. G. Observations of sand waves, megaripples, and hummocks in the Dutch coastal area and their relation to currents and combined flow conditions. *J. Geophys. Res.* **110**, F04S15 (2005).
4. Mazières, A. *et al.* Dynamics of inner-shelf, multi-scale bedforms off the south Aquitaine coast over three decades (Southeast Bay of Biscay, France). *Cont. Shelf Res.* **92**, 23–36 (2015).
5. Heathershaw, A. D. & Codd, J. M. Depth-controlled changes in grain size and carbonate content on a shelf-edge sand bank. *Mar. Geol.* **72**, 211–224 (1986).
6. Trentesaux, A., Stolk, A., Tessier, B. & Chamley, G. Surficial sedimentology of the Middelkerke Bank (southern North Sea). *Mar. Geol.* **121**, 43–55 (1994).
7. García-Charton, J. A. *et al.* Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Mar. Biol.* **144**, 161–182 (2004).
8. Lovett, G. M., Jones, C. G., Turner, M. G. & Weathers, K. C. Ecosystem function in heterogeneous landscapes (Springer, 2006).
9. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography*. (Princeton University Press, 1967).
10. Tilman, D. Resource competition and community structure. (Princeton University Press, 1982).
11. van Dijk, T. A. G. P. *et al.* Benthic habitat variations over tidal ridges, North Sea, The Netherlands. in *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
12. Damveld, J. H. *et al.* Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophys. Res. Lett.* **45**, (2018).
13. Ramey, P. A., Grassle, J. P., Grassle, J. F. & Petrecca, R. F. Small-scale, patchy distributions of infauna in hydrodynamically mobile continental shelf sands: Do ripple crests and troughs support different communities? *Cont. Shelf Res.* **29**, 2222–2233 (2009).
14. Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
15. Temmerman, S. *et al.* Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh. *J. Geophys. Res. Earth Surf.* **110**, 1–18 (2005).
16. Koch, E. W., Ackerman, J. D., Verduin, J. & van Keulen, M. Fluid dynamics in seagrass ecology - from molecules to ecosystems. In *Seagrasses: Biology, Ecology and Conservation* 193–225 (Springer, 2006).
17. van der Zee, E. M. *et al.* Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. *Ecosystems* **15**, 664–673 (2012).
18. Walles, B., Salvador de Paiva, J., van Prooijen, B. C., Ysebaert, T. & Smaal, A. C. The ecosystem engineer *Crassostrea gigas* affects tidal flat morphology beyond the boundary of their reef structures. *Estuaries and Coasts* **38**, 941–950 (2015).
19. Houziaux, J.-S., Kerckhof, F., Degrendele, K., Roche, M. & Norro, A. *The Hinder Banks: yet an important area for the Belgian marine biodiversity?* (2008).
20. van der Reijden, K. J. *et al.* Discovery of Sabellaria spinulosa reefs in an intensively fished area of the Dutch Continental Shelf, North Sea. *J. Sea Res.* **144**, 85–94 (2019).
21. van Lancker, V. *et al.* Fine-scale geomorphological mapping of sandbank environments for the prediction of macrobenthic occurrences, Belgian part of the North Sea. In *Seafloor Geomorphology as Benthic Habitat* 251–260 (Elsevier Inc., 2012).
22. Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M. & Degraer, S. A bio-engineered soft-bottom environment: The impact of *Janice conchilega* on the benthic species-specific densities and community structure. *Estuar. Coast. Shelf Sci.* **75**, 525–536 (2007).
23. Dubois, S., Retière, C. & Olivier, F. Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs: effects of human disturbances. *J. Mar. Biol. Assoc. UK* **82**, 817–826 (2002).
24. Gravina, M. F. *et al.* *Sabellaria spinulosa* (Polychaeta, Annelida) reefs in the Mediterranean Sea: Habitat mapping, dynamics and associated fauna for conservation management. *Estuar. Coast. Shelf Sci.* **200**, 248–257 (2018).
25. McConnaughey, R. A., Mier, K. L. & Dew, C. B. An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. *ICES J. Mar. Sci.* **57**, 1377–1388 (2000).
26. Thrush, S. F. & Dayton, P. K. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Annu. Rev. Ecol. Syst.* **33**, 449–473 (2002).
27. Jenkins, C. *et al.* North Norfolk Sandbank and Saturn Reef cSAC/SCI management investigation report. JNCC/CEFAS Partnership Report Series (2015).
28. Rijnsdorp, A. D. *et al.* Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol. Appl.* **28**, 1302–1312 (2018).
29. Sciberras, M. *et al.* Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish.* **19**, 698–715 (2018).
30. Amoroso, R. O. *et al.* Bottom trawl fishing footprints on the world's continental shelves. *Proc. Natl. Acad. Sci. U. S. A.* **115**, E10275–E10282 (2018).
31. van der Reijden, K. J., Hintzen, N. T., Govers, L. L., Rijnsdorp, A. D. & Olff, H. North Sea demersal fisheries prefer specific benthic habitats. *PLoS One* **13**, 1–21 (2018).
32. Eigaard, O. R. *et al.* The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865 (2017).
33. Bennett, J. R. *et al.* Optimizing taxonomic resolution and sampling effort to design cost-effective ecological models for environmental assessment. *J. Appl. Ecol.* **51**, 1722–1732 (2014).
34. Bates, C. R., Scott, G., Tobin, M. & Thompson, R. Weighing the costs and benefits of reduced sampling resolution in biomonitoring studies: Perspectives from the temperate rocky intertidal. *Biol. Conserv.* **137**, 617–625 (2007).
35. De Moustier, C. & Matsumoto, H. Seafloor acoustic remote sensing with multibeam and bathymetric sidescan sonar systems. *Mar. Geophys. Res.* **15**, 27–42 (1993).
36. Hellequin, L., Boucher, J.-M. & Lurton, X. Processing of high-frequency multibeam echo sounder data for seafloor

- characterization. *IEEE J. Ocean. Eng.* **28**, 1–11 (2003).
37. Brown, C. J., Smith, S. J., Lawton, P. & Anderson, J. T. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast. Shelf Sci.* **92**, 502–520 (2011).
 38. Rhoads, D. C. & Cande, S. Sediment profile camera for in situ study of organism-sediment relations. *Limnol. Oceanogr.* **16**, 110–114 (1971).
 39. Knaapen, M. A. F. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo-Marine Lett.* **29**, 17–24 (2009).
 40. Koop, L. *et al.* Seafloor classification in a sand wave environment on the Dutch continental shelf using multibeam echosounder backscatter data. *Geosciences* **9**, 142 (2019).
 41. Knaapen, M. A. F. Sandwave migration predictor based on shape information. *J. Geophys. Res. Earth Surf.* **110**, 1–9 (2005).
 42. Amiri-Simkooei, A., Snellen, M. & Simons, D. G. Riverbed sediment classification using multi-beam echo-sounder backscatter data. *J. Acoust. Soc. Am.* **126**, 1724–1738 (2009).
 43. Alevizos, E., Snellen, M., Simons, D. G., Siemes, K. & Greinert, J. Acoustic discrimination of relatively homogeneous fine sediments using Bayesian classification on MBES data. *Mar. Geol.* **370**, 31–42 (2015).
 44. Simons, D. G. & Snellen, M. A Bayesian approach to seafloor classification using multi-beam echo-sounder backscatter data. *Appl. Acoust.* **70**, 1258–1268 (2009).
 45. Jackson, D. R. & Briggs, K. B. High-frequency bottom backscattering: Roughness versus sediment volume scattering. *J. Acoust. Soc. Am.* **92**, 962–977 (1992).
 46. Collier, J. S. & Brown, C. J. Correlation of sidescan backscatter with grain size distribution of surficial seabed sediments. *Mar. Geol.* **214**, 431–449 (2005).
 47. Amiri-Simkooei, A. R., Koop, L., van der Reijden, K. J., Snellen, M. & Simons, D. G. Seafloor characterization using multibeam echosounder backscatter data: Methodology and results in the north sea. *Geosci.* **9**, (2019).
 48. Nieuwenhuize, J., Maas, Y. E. M. & Middelburg, J. J. Rapid analysis of organic carbon and nitrogen in particulate materials. *Mar. Chem.* **45**, 217–224 (1994).
 49. Queirós, A. M. *et al.* A bioturbation classification of European marine infaunal invertebrates. *Ecol. Evol.* **3**, 3958–3985 (2013).
 50. Solan, M. *et al.* Extinction and ecosystem function in the marine benthos. *Science*. **306**, 1177–1180 (2004).
 51. Rhoads, D. C. & Cande, S. Sediment profile camera for in situ study of organism-sediment relations. *Limnol. Oceanogr.* **16**, 110–114 (1971).
 52. Oksanen, J. *et al.* Vegan: Community ecology package. R package version 2.5-6. (2019).
 53. R Development Core Team, X. R: A language and environment for statistical computing. (2014).
 54. Bellec, V. K., van Lancker, V., Degrendele, K., Roche, M. & Le Bot, S. Geo-environmental characterization of the Kwinte Bank. *J. Coast. Res. Special Is*, 63–76 (2010).
 55. Houziaux, J. S., Fettweis, M., Francken, F. & van Lancker, V. Historic (1900) seafloor composition in the Belgian-Dutch part of the North Sea: A reconstruction based on calibrated visual sediment descriptions. *Cont. Shelf Res.* **31**, 1043–1056 (2011).
 56. Ellis, J. R., Maxwell, T., Schratzberger, M. & Rogers, S. I. The benthos and fish of offshore sandbank habitats in the southern North Sea. *J. Mar. Biol. Assoc. United Kingdom* **91**, 1319–1335 (2011).
 57. Godet, L., Fournier, J., Jaffré, M. & Desroy, N. Influence of stability and fragmentation of a worm-reef on benthic macrofauna. *Estuar. Coast. Shelf Sci.* **92**, 472–479 (2011).
 58. Pearce, B. The ecology of *Sabellaria spinulosa* reefs. PhD Thesis. (University of Plymouth, 2014).
 59. Jones, J. B. Environmental impact of trawling on the seabed: A review. *New Zeal. J. Mar. Freshw. Res.* **26**, 59–67 (1992).
 60. Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M. & Stephens, D. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. *J. Sea Res.* **85**, 162–177 (2014).
 61. Gibb, N., Tillin, H., Pearce, B. & Tyler-Walters, H. Assessing the sensitivity of *Sabellaria spinulosa* reef biotopes to pressures associated with marine activities. *JNCC Report No. 504* (2014).
 62. de Groot, S. J. The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Manag.* **9**, 177–190 (1984).
 63. Frid, C. L. J., Harwood, K. G., Hall, S. J. & Hall, J. A. Long-term changes in the benthic communities on North Sea fishing grounds. *ICES J. Mar. Sci.* **57**, 1303–1309 (2000).

Chapter 7

Seafloor classification in a sand wave environment on the Dutch Continental Shelf using multibeam echosounder backscatter data

Leo Koop

Alireza Amiri-Simkooei

Karin J. van der Reijden

Sarah O'Flynn

Mirjam Snellen

Dick G. Simons

Published as

Koop L, Amiri-Simkooei A, van der Reijden KJ, O'Flynn S, Snellen M, Simons DG. (2019) Seafloor classification in a sand wave environment on the Dutch Continental Shelf using multibeam echosounder backscatter data. *Geosciences*, 9(3), 142.

Abstract

High resolution maps of sandy seafloors are valuable to understand seafloor dynamics, plan engineering projects, and create detailed benthic habitat maps. This paper presents multibeam echosounder backscatter classification results of the Brown Bank area of the North Sea. We apply the Bayesian classification method in a megaripple and sand wave area with significant slopes. Prior to the classification, corrections are implemented to account for the slopes. This includes corrections on the backscatter value and its corresponding incident angle. A trade-off in classification resolutions is found. A higher geo-acoustic resolution is obtained at the price of losing spatial resolution, however, the Bayesian classification method remains robust with respect to these trade-off decisions. The classification results are compared to grab sample particle size analysis and classified video footage. In non-distinctive sedimentary environments, the acoustic classes are not attributed to only the mean grain size of the grab samples but to the full spectrum of the grain sizes. Finally, we show the Bayesian classification results can be used to characterize the sedimentary composition of megaripples. Coarser sediments were found in the troughs and on the crests, finer sediments on the stoss slopes and a mixture of sediments on the lee slopes.

Introduction

In recent years, increasing use has been made of multibeam echosounder (MBES) systems to characterize the seafloor by acoustic remote sensing. Use has been made of the bathymetric data derived from MBES systems (or single beam echo sounders (SBES)), correlated with grab samples to determine the variations in sediment over sand waves in the North Sea¹⁻⁴. In addition to bathymetry data, MBES systems also provide backscatter (BS) data which can be utilized more directly to characterize seafloor sediments⁵. There are a variety of approaches in use for the classification of the seafloor using MBES backscatter data. These range from image-based segmentation approaches^{6,7}, classification based on backscatter angular response curves^{8,9}, as well as, principal component analysis of both bathymetry and backscatter data¹⁰⁻¹², among others.

We employ the Bayesian classification method, which was first developed in¹³. One of the key components of the method is that it considers the BS data per beam angle. This method can discriminate between relatively homogeneous sediments¹⁴, can be used as a reliable tool for long-term environmental monitoring¹¹, and was previously applied to river beds where significant slopes needed to be accounted for¹⁵.

The Brown Bank area of the North Sea (Fig. 1a) exhibits sand waves of various sizes, namely, sand banks (Fig. 1b), sand waves (Fig. 1c), and megaripples (Fig. 1d) (see Section 2.1 for definitions). Although the main sediment is sand, there is a variation of muddy sediments mixed with gravel and shell fragments in the deep troughs and well sorted medium sand on the crest¹⁶. Also, infauna species diversity and abundance are much higher in the troughs than on the crest¹⁶. A high-resolution classification map of seafloor sediments in a sand wave area provides valuable information for both marine biologists, who study the spatial variability of seabed habitats and benthic communities, and modelers of seafloor dynamics.

The goal of this paper is four-fold. We first apply the Bayesian classification method to a sand wave area where there exist significant and rapidly changing slopes in small areas. The second goal is to investigate to what extent different acoustic classes can be distinguished. A comparison with grabs is carried out to investigate what sediment properties drive the acoustic discrimination in an area with relatively homogenous sediments. The third goal is to examine the trade-off between the geo-acoustic (Geo-acoustic resolution: the scale at which different types of sediments can be resolved using a certain acoustic classification/characterization technique¹⁴) versus spatial resolution of classification results. The final goal is to determine the patterns of sediments on different parts of the megaripple cycle using the acoustic classification results.

Study Area, Materials, and Methods

Study area

The Brown Bank is located 85 km off the coast of the Netherlands, in the middle between the UK and the Netherlands, due west of Egmond aan Zee (52°32'59.994" N, 3°18'36.400" E; Fig. 1). This area was visited in 2017 with the Royal Netherlands Institute for Sea Research (NIOZ) vessel, the *Pelagia*, from 27 October to 3 November (Cruise number/name: 64PE428disclose). Tidal currents in this area oscillate between a north eastern and south western flow direction with current flow rates exceeding 1 km/h. The average water current is in the north eastern direction¹⁸. The annual mean significant wave height is 2 m¹⁹. The main seabed substrate in this part of the North Sea is sand, with sand waves of various sizes clearly visible in the bathymetry. The dominant bathymetric features of the research area are sand banks (Fig. 1b), which can be tens of meters high and have a length of 5 - 10 km²⁰. In the study area there is mainly one sand bank, i.e., the most dominant one in the North Sea²⁰, which is called the Brown Bank. The Brown Bank runs from north to south, with a water depth on the top of the bank of ~19 m, and a water depth in the troughs on either

Figure 1. (a) Location of Brown Bank area in North Sea (source: ESRI¹⁷); (b) Bathymetry of Brown Bank; arrows indicate sand banks; (c) Survey area; red circles and yellow triangles are ground truthing locations, survey lines are in red, and arrows point to sand wave structures (spatial resolution 1 m x 1 m); (d) Megaripple bed forms, indicated by arrows (spatial resolution is 1 m x 1 m, all depths are given in meters (m)).

side being ~45 m.

In addition to the sand banks, there are two other periodic bed forms that are defined in this paper as sand waves (Fig. 1c) and megaripples (Fig. 1d)²¹, respectively. Sand waves occur with a wavelength of around 200 m, with the occasional wavelength as short as 100 m and others as long as 300 m. In Knaapen et al., it was found that sand waves migrate at a rate of several meters per year²², and that the migration speed is strongly correlated with the sand wave shape. Superimposed on the sand waves are megaripples²¹, which have a wavelength of 15 m, where some wavelengths are as short as 10 m and others as long as 25 m. The megaripples move faster than the sand waves, in the scale of weeks^{21,23} or even hours²⁴. The troughs of the Brown Bank consist of muddy sediments mixed with gravel and shell fragments and the crests contain well sorted medium sand¹⁶.

Multibeam echosounder data

Multibeam echosounder settings

The acoustic survey was performed with a hull-mounted Kongsberg EM 302 multibeam echosounder (MBES). The EM 302 has a central frequency of 30 kHz and has 2° and 1° beam opening angles in the across and along track directions respectively. Four transmit sectors were used during the survey, each using a slightly different frequency of 26.5 kHz, 30.5 kHz, 33.5 kHz, and 28.5 kHz for sectors 1 to 4. The beam coverage of the 432 beams was set to equidistant (vs. equiangular). A swath opening angle of 130° was used, with port and starboard coverage both being 65°. The pulse length was 750 µs for the entire survey. The EM 302 has a sensitivity resolution of 0.1 dB. Bathymetry, backscatter, and water column data were recorded using Kongsberg's native seafloor information system (SIS) software. A Seapath global positioning system (GPS) and motion reference unit (MRU) provided position and motion correction information. GPS information was fed into the MBES processing, therefore eliminating the need to perform tide corrections. The MBES data were corrected for roll, heave, and yaw.

The data from the Pelagia were cleaned using the following steps. Firstly, the data was imported into the QPS Qimera software, and a spline filter was used to flag data points that were depth outliers. Subsequently, the cleaned data from Qimera were imported into Qinsy to convert them into an ASCII tabular format. Further processing was then carried out in Matlab. Aeration artifacts were filtered out if the average backscatter over 15 adjacent pings was more than 1.5 dB lower than the average backscatter over the nearest 700 pings

Backscatter corrections for seafloor slopes

Because the survey area is dominated by sand waves and megaripples, with seafloor slopes as steep as 20 degrees, a slope-corrected grazing angle is needed. If not corrected, the significant slopes of the seafloor can in principle degrade the classification results. This is thus an essential pre-processing step because the Bayesian classification method uses the backscatter data at a specific grazing angle. We closely follow the pre-processing steps proposed by Amiri-Simkooei et al.¹⁵. Fig. 2 shows the across-track cross section of the signal footprint for three different environments, i.e., a shallow water, a deep water and a non-flat seafloor.

A three-step algorithm is employed to estimate and hence apply the corrections required due to the local slopes. The steps are as follows: (1) Estimating the along- and across-track seafloor slopes; (2) Correction of the true beam grazing angle; and (3) Correcting the backscatter data. These steps require the along- and across-track slopes in the time-varying coordinate system of the vessel. The details of the above steps are as follows.

Step 1: Estimation of local slopes

The least-squares method is employed to estimate the local slopes using the bathymetry data. The slopes are computed in the time-varying coordinate system of the vessel. The bathymetry data of a

given MBES line was gridded to a grid size of 2 m $\times$ 2 m. Such a regular surface patch includes a few pings and beams around the central beam angle. For the discrete points within the surface patch, we then have $z_i = f(x_i, y_i)$, $i = 1, \dots, n$, n indicating the number of bathymetry data within the surface patch. Here x_i and y_i refer to the along and across-track coordinates in relation to the vessel for point i . The surface patch is assumed to be a plane, with the form

$$(1) \quad f(x, y) = a_0 + a_x x + a_y y$$

consisting of three unknown coefficients a_0 , a_x and a_y . The model of observation equations is of the form $z = Aa$, where $z = [z_1, \dots, z_n]^T$ is the n -vector of observations containing the bathymetry data within the 2 m $\times$ 2 m surface patch, $a = [a_0 \ a_x \ a_y]^T$ is the vector of unknown parameters, and A is the $n \times 3$ design matrix for which its i^{th} row is $A_i = [1 \ x_i \ y_i]$. Assuming the observations are independent and have identical variances, the least squares estimate of the parameters is $\hat{a} = (A^T A)^{-1}$. A procedure called 'data snooping' can also be used to test for the presence of outliers in the bathymetry data^{25,26}. This will then leave out some outlying depth measurements when computing the local slopes.

Having estimated the parameters of the above surface patch $f(x, y)$, one can obtain the local slopes $f_x(x, y) = a_x$ and $f_y(x, y) = a_y$ where a_x and a_y are the ratios of the vertical to horizontal changes in the along and across-track directions respectively. Fig. 3 shows one typical area in which the along and across-track slopes have been estimated. The signature of the megaripples is clearly visible from the computed slopes.

Figure 2. Across-track cross section (y-z) plane for the signal footprint of an oblique beam for three environments: shallow water (a), non-flat bottom (b), and deep water (c), (figure after Amiri-Simkooei et al.¹⁵)

Figure 3. (a) Bathymetry data on a crest of a sand wave, (b) across track slopes and (c) along track slopes ; depths are given in meters, slopes are in degrees (d).

Step 2: Grazing angle correction

After estimating the local surface, the local slopes a_x and a_y of the plane are known (Eq. 1). The normal vector to the plane is the gradient of the surface, expressed as $\vec{n} = [a_x \ a_y \ -1]^T$. The nominal receiving-beam direction based on the flat surface in the z-y plane is provided as $\vec{m} = [0 \ -\sin \theta \ \cos \theta]^T$, where θ is the nominal incident angle. The angle between the two vectors $\vec{n}$ and $\vec{m}$ is the true incident angle, given as

$$(2) \quad \theta_t = \frac{\sin \varphi + a_y \cos \varphi}{\sqrt{1 + a_x^2 + a_y^2}}$$

where $\varphi = \frac{\pi}{2} - \theta$ is the nominal grazing angle. Therefore, the nominal incident angle θ should be corrected to the true incident angle θ_t . This is an essential step because the classification method uses the backscatter data at a specific angle.

Step 3: backscatter correction

The local slopes also affect the backscatter data. This is because the received backscatter refers to a flat signal footprint $A_f'^{15}$. In the presence of local slopes, the signal footprint will change and hence the corresponding backscatter values need to be corrected for the actual ensonified area A_f using the along and across-track slope angles $\alpha_x = \arctan a_x$ and $\alpha_y = \arctan a_y^{15}$ (Fig. 2). The correction C of the backscatter for the actual ensonified area, expressed in decibels (dB) is given as

$$(3) \quad C = 10 \log \left(\frac{\sin(\theta - \alpha_y) \cos \alpha_x}{\sin \theta} \right)$$

The corrected data is then supplied to the Bayesian classification method.

Bayesian classification method

This section provides an overview of the essential steps to generate the acoustic classification maps from the backscatter (BS) data. The central limit theorem expresses that the BS follows a Gaussian distribution for one sediment type, if sufficient independent measurements are considered for determining the BS values. For a given frequency and angle, the backscatter strength depends on the seabed properties. If the survey area contains m sediment types, the BS histogram of the backscatter data for a specific incident angle is then represented by a linear combination of m Gaussian distributions as

$$(4) \quad f(y_j | x) = \sum_{k=1}^m c_k \exp \left(-\frac{(y_j - \bar{y}_k)^2}{2\sigma_{y_k}^2} \right)$$

where y_j is the BS value at bin $(y_j, y_j + \Delta)$ of the BS histogram, with $j = 1, \dots, M$ and M being the total number of bins. The bin size Δ is set by the sensitivity resolution of the MBES. The vector x contains the unknown parameters of the Gaussian distribution: $x = (\bar{y}_1, \dots, \bar{y}_m, \sigma_{y_1}, \dots, \sigma_{y_m}, c_1, \dots, c_m)$, where the triple $(\bar{y}_k, \sigma_{y_k}, \text{and } c_k)$ indicates the mean, standard deviation and contribution of each Gaussian distribution for $k = 1, \dots, m$. The curve fitting procedure is performed in an iterative manner for increasing m . The error in the fitting is tested by the χ^2 goodness of fit test, which is of the form

$$(5) \quad \chi^2 = \sum_{j=1}^M \frac{(n_j - f(y_j | x))^2}{\sigma_j^2}$$

where n_j denotes the number of backscatter measurements per bin j in the BS histogram. For a Poisson-distribution is postulated, indicating that the variance σ_j^2 is equal to n_j . The goodness of fit statistic has a chi-squared distribution with $v = M - 3m$ degrees of freedom. The goodness-of-fit criterion is then defined as the reduced chi-squared statistic, given by

$$(6) \quad \chi_v^2 = \frac{\chi^2}{v}$$

which has a value close to 1 for a good fit, indicating that the difference between modelled and

measured histograms fall within the uncertainties of the BS data. The value of m for which no significant improvement on the reduced chi-squared statistic is obtained, or when it has a value close to 1, can be considered to be the optimal value of m based on the backscatter data.

The final classification step uses the Bayes decision rule. The above m Gaussians introduce m hypotheses as $H_k, k = 1, \dots, m$ which correspond to the m seafloor sediment types. It is assumed that the hypotheses are equally likely and the Bayesian decision rule for multiple hypotheses then indicates to accept H_k if $\max_i \{f(y_j|H_i)\} = f(y_j|H_k)$. Given the observation y , the hypothesis that maximizes the likelihood $f(y|H)$ gets accepted. Thus, in principle, the intersections of the m Gaussians result in m non-overlapping acceptance regions A_k , corresponding to m acoustic classes (ACs).

Two levels of data averaging

To ensure that the central limit theorem is satisfied, namely the backscatter strength per angle and sediment type is Gaussian distributed, the backscatter values used should be the result of a sufficient number of independent measurements. The backscatter per beam is an average value, i.e., the result of N_s measurements, with N_s representing the number of signal footprints (or scatter pixels) within the beam footprint, see Fig. 2. Sometimes the number of scatter pixels in a beam is small. Then the backscatter values are averaged over a certain number of neighboring beams and consecutive pings. This, though reducing the spatial resolution, ensures that each BS value is representative of a sufficient number of scatter pixels. In addition, a larger number of scatter pixels per backscatter strength value provides narrower Gaussian distributions per sediment type, i.e., increased geo-acoustic resolution. For beams away from nadir, the ensonified area A_F is (much) smaller than the beam footprint. Therefore many scatter pixels fall within the footprint of the receiving beam. The number of scatter pixels

$$(7) \quad N_s(\theta, \alpha_y) = \frac{\left(\frac{R\Omega_y}{\cos(\theta - \alpha_y)} \right) m}{\left(\frac{cT}{2 \sin(\theta - \alpha_y)} \right)}$$

where Ω_y is the beam aperture in the across-track direction, c is the average water sound speed, T the length of the transmitted pulse, and $R = H / \cos \theta$, where H is the water depth. Eq. 7 only holds for the beams sufficiently away from nadir. For beams closer to nadir the ensonified area is limited by the beam aperture and not the projected pulse duration. Thus, the nadir beams have only one scatter pixel.

To investigate the trade-off between the spatial and geo-acoustic resolution, two levels of data averaging were performed. In the first averaging scheme, no averaging was done as long as a data point was based on 20 or more scatter pixels, which was the case for the outer beams. If a data point had less than 20 scatter pixels, it was averaged with the geographically nearest neighbors until it was representative of at least 20 scatter pixels.

For the second scheme the data of a given MBES line was gridded to a grid size of $2 \text{ m} \times 2 \text{ m}$. The average backscatter and the average depth of all the points in a grid cell are used to form a single data point for that grid cell. It was further required that a grid cell contained at least 10 data points, otherwise the data within that grid cell was discarded. The advantage of this method is that the averaging of the backscatter increases, and hence it reduces noise in the classification results. The disadvantage is that it decreases the number of data points used in the classification, and thereby decreases the spatial resolution of the classification.

Megaripple partitioning

To investigate the distribution of sediments over megaripples, thirty-two areas with a size of $\sim 100 \text{ m} \times 100 \text{ m}$, where a clear megaripple pattern was present, were selected for further study. Using the orientation of the megaripples and the values of the absolute slopes, a direction specific slope was computed such that positive slopes would be on the stoss side (the side that receives dominant tidal current, also the less steep side) and the negative slopes would be on the lee side

of the megaripple (Fig. 4). The polarity of the computed slopes thus separated the area into the different sides of a megaripple. Further subareas were created by defining the crests and troughs of the megaripples. This was done by fitting a plane $Z = f(E, N) = a_0 + a_1E + a_2N$ to the bathymetric data using the least squares method. Here E and N refer to the easting and northing coordinates of the bathymetry data in a UTM (Universal Transverse Mercator) coordinate system. The points above the fitted plane are classified to be on the crest, and those below the plane, in the trough of the megaripple. The area was then binned based on the directional slope, ranging from -20 to 20 degrees with a bin size of 5 degrees (Fig. 4). The bin centers are then at -17.5, -12.5, ..., 17.5 degrees. The mean and mode occurrences of acoustic classes was calculated per bin and per trough and crest area for each of the 32 selected areas and used for determining sediment patterns over megaripples.

Figure 4. Schematic structure of a megaripple; wavelength is 10 m and depth variation is ~1 m. Also indicated are crest versus trough area and stoss versus lee sides. Slopes of the megaripple are presented with a bin size of 5 degrees.

Video data

Videos of the seabed were collected along 150 m transects at 10 stations (Fig. 1c) with a towed video camera system. This system was inspired by the one used in Sheehan et al.²⁷. The aluminum frame houses a remotely controlled forward-facing video camera (Kongsberg OE14-522A-0009 Colour HD Pan), a downward facing DSRL camera (NIKON D750), eight lights (Fisheye FIX NEO 1000DX SW II LED), and two sets of lasers (Z-Bolt, SCUBA-II green) with a fixed separation distance. The video camera was set to view the seabed just in front of the frame. Moreover, the frame was equipped with multiple floats, resulting in a small positive buoyancy. Two drag chains underneath the frame cause for negative buoyancy. The varying length of the part of the drag chain which touches the seabed stabilizes the frame's height above the seabed. Three towing cables were attached to the frame at different points, which were combined after 6.5 m into one towing cable. A drop weight of 55 kg was attached to this merging point, which reduced the vertically oriented towing forces of the vessel on the frame. The video camera was connected to a computer on-board with a video data "umbilical cord", which was held in place separate from the towing cable. Using the live stream from the video camera, the length of the towing cable was adjusted to maintain seabed view during transects. During video operations, the vessel had a speed of ~0.1 m/s.

The collected video footage was analyzed and the superficial seabed type determined. The time of every observed change in seabed type was recorded. All recordings in which the seabed was not (clearly) visible, due to particle clouds or motion, or in which at least one of the lasers was not visible were defined as invalid. The position of the camera was estimated based on a time-match with the position of the vessel, which was saved by the vessel's logging system every 30 seconds. As the distance between the camera and vessel varies, depending on the prevailing depth and current, the exact position of the camera cannot be determined. However, because the camera was deployed on the starboard side of the vessel, with as little towing cable as possible, we assume the positioning error to be >10 m but <100 m.

Grab sample data

Twenty-two grab sample locations were selected, with twenty-one of these falling on a regular grid. That includes seven vertically oriented parallel lines each with three locations; in the eastern most border of the survey area, in the troughs on both sides, on the slopes on either side, and on the crest of the Brown Bank, and in the western most border of the survey area (Fig. 1). At each sampling location three replicate samples were taken resulting in a total of 66 grab samples. The grab samples were acquired with a 30 cm Box Core. Subsamples were taken for particle size analysis (PSA). Between the time that the samples were gathered until they were processed in the lab, they were stored at -20°C. Prior to PSA the samples were freeze-dried. For the particle size analysis, the contents of the sample were successively sieved over 4, 2, and 1 mm sieves and the weights of these fractions were measured. The particles that were larger than 2 mm were separated to determine the gravel fraction. The grain size distribution of the portion smaller than 1 mm was determined by means of laser diffraction with a Malvern Mastersizer 2000 (Malvern Instruments, Worcestershire, UK). The sieving and laser diffraction results were combined by scaling the results from the Malvern by the mass proportion of the sample that was smaller than 1 mm. This combined dataset was then used for further analysis.

The results of the grab sample sieving process were converted into the phi grain size units by using $\phi = -\log_2 d$, where d is the representative diameter of the grains in millimeters. Two measures are often used to describe the sediment grain size of a grab sample, that is, the median or the mean grain size. The median corresponds to the 50th percentile on the cumulative curve of which half the particles by weight are larger and half are smaller than the median. It is therefore of the form $M_z = \phi_{50}$. The mean is the average grain-size for which several formulas are used in the literature. The most commonly used formula is that given by Folk and Ward²⁸

$$(8) \quad M_z = \frac{\phi_{16} + \phi_{50} + \phi_{84}}{3}$$

where ϕ_{16} , ϕ_{50} and ϕ_{84} represent the size at the 16th, 50th, and 84th percentiles of the sample by weight. For the work presented here the mean grain size is used; but similar results are obtained using the median grain size.

In addition to the mean grain size, provided by Eq. 8, statistics for sorting σ (Eq. 9), skewness s (Eq. 10), and kurtosis k (Eq. 11) of the grain size distribution were also calculated²⁸.

$$(9) \quad \sigma = \frac{\phi_{84} - \phi_{16}}{4} + \frac{\phi_{95} - \phi_5}{6.6}$$

$$(10) \quad s = \frac{\phi_{16} + \phi_{84} - 2\phi_{50}}{2(\phi_{84} - \phi_{16})} + \frac{\phi_5 + \phi_{95} - 2\phi_{50}}{2(\phi_{95} - \phi_5)}$$

$$(11) \quad k = \frac{\phi_{95} - \phi_5}{2.44(\phi_{75} - \phi_{25})}$$

These were used to create a feature matrix $\gamma = [M_z \sigma s k]$. Principal component analysis of this matrix, which is of size 66×4 , was performed and the most informative principal components (PCs) were selected. These are then used to determine the correlation between the acoustic classification results and the full grain size spectrum of the grab samples.

Folk classification of the grab samples is also used. According to this classification method, sediments are given a descriptive label based on the proportions of Mud, Sand, and Gravel. Gravel particles are those larger than 2 mm, Sand those between 2 mm and 0.0625 mm, and Mud what is less than 0.0625 mm. A 0.01 % boundary was used between a “no gravel” content and a “slightly gravelly” label.

Results and Discussion

Acoustic classification results

The Bayesian Classification Method is now applied to the backscatter (BS) data that was cleaned and pre-processed. That is, the correct grazing angles are known and the backscatter data has been corrected for the change in the ensonified area induced by the seafloor slopes.

In the first step, the number of sea bottom types, distinguishable in the acoustic data, is determined. This is achieved by increasing the number of Gaussians to well describe the histogram of the BS values at a given grazing angle. The number of seafloor types, m , was found to be 4 (Fig. 5). The beam angles used to create the histograms and to perform the Gaussian fitting procedure were the 30° , 28° , and 26° grazing angles, for both the port and starboard sides. The error bars in Fig. 5 give the standard deviation of the χ^2_ν statistic, $\sqrt{2/\nu}$. Because the backscatter data from the EM 302 multibeam is recorded at a resolution of 0.1 dB the number of bins M per histogram tended to be well above 100. The variable ν gets larger with larger M and therefore the standard deviations of the χ^2_ν statistic, represented by the error bars in Fig. 5, become small.

Fig. 6 shows the BS histograms along with their best fit for the grazing angles 30° , 28° , and 26° . The intersecting points of the corresponding probability density functions (PDFs) are used to form the acceptance regions of the four classes. The percentages of the histogram at these reference angles that fall into a specific class were then recorded and used to divide, and thereby classify, the histograms for the grazing angles from 65° to 25° .

The acoustic classification results are presented in Fig. 7. The broad scale classification results fall into the following patterns. For water depths shallower than 25 m, on the crest of the Brown Bank, mainly acoustic classes 1 and 2 occur. Lower classes (1 and 2) generally correlate with smaller grain sizes¹¹. In the troughs on either side of the Brown Bank, for water depths deeper than 35 m, the classes are higher, mainly classes 3 and 4. In the remainder of the area the classes tend to be a mixture of classes 2 and 3.

Figure 5. Reduced chi-square as a function of number of Gaussians. Error bars, which were multiplied by a factor of 2 for distinction, indicate standard deviation of reduced chi-square test statistics.

Ground truth data

In total there were 16,594 classified, and geo-referenced, seconds of valid video footage (video frames, Table 1). In all areas where video data was collected “Sand with a ripple structure” was found (Fig. 8). The presence of shell fragments (Fig. 8b), smaller and larger stones (or Granules and Pebbles according to the Udden-Wentworth grain size classification scheme²⁹) (Fig. 8c), and Sabel-laria fragments (Fig. 8d) varied from one area to the next. Fig. 9 represents the video classification results overlaid on the acoustic classes. The class “Sand with hardly any shell fragments” was only found on the crest of the Brown Bank, see Fig. 9 (upper right). The remaining 3 classes were all found in the troughs on either side of the Brown Bank.

Figure 6. Measured histograms for grazing angles 30°, 28°, and 26° for both port and starboard sides, in gray; sum of number of Gaussians, in red (see: Eq. 4), individual Gaussians are in black. Error bars (in blue) were multiplied by a factor of 3 for distinction.

Table 1. Classification of video data with numbers and percentages of total frames per class.

Classification	Number of Frames	% of Total Frames
Sand with hardly any shell fragments	4495	27.1 %
Sand with some shell fragments	8651	52.1 %
Sand with Sabellaria fragments and incidental larger stones	1257	7.6 %
Sand with small stones and incidental larger stones	2191	13.2 %
Total	16,594	100 %

Figure 7. Acoustic classification map of Brown Bank obtained from backscatter data for beams between 25° and 65°. Also shown are grab Folk classes with their station numbers. Depth contours (solid black lines) are presented at 5 m intervals.

At Station 2 (Fig. 9, upper left), alternating video classes of “sand with some shell fragments” and “sand with small stones and incidental larger stones” are seen. The alternation matches with the wavelength of the megaripples in this area. The acoustic classification also alternates on this spatial scale, between class 4, as the highest class, and class 3 or 2 for the lower classes. The video data at Station 8, containing “Sand with hardly any shell fragments”, have mainly lower acoustic classes 1 and 2. At Stations 9 and 14 (lower parts of Fig. 9) the video is classified as mostly “Sand with some shell fragments”. However, some frames are classified as also having either “Small stones and incidental larger stones” at Station 14, or “Sabellaria fragments and incidental larger stones” at Station 9. Their locations match with areas of higher acoustic classes (Fig. 9).

To further investigate the relation between the video data and the acoustic classification results, the two datasets were geographically matched, and the occurrences of the acoustic and video classifications were counted. The mode of the acoustic class within a one-meter radius was used. If there were no acoustic classes within this radius then the video data point was discarded. The results are presented in Fig. 10. In areas where the video recordings indicate “sand with no shell fragments” the occurrence of acoustic class 1 is dominant. There are no instances of acoustic class 4 in these areas. In areas where the video data indicate the presence of “sand with some shell fragments” the occurrence of acoustic classes 2 and 3 is highest at 32 % and 49 %. For “Sand with Sabellaria fragments and incidental larger stones” and “Sand with small stones and incidental larger stones” the distribution of acoustic class occurrences is very similar, with higher percentages for the higher acoustic classes. There were hardly instances of acoustic class 1 in these areas.

Figure 8. Sample video frames classified as (a) Sand with hardly any shell fragments, (b) Sand with some shell fragments, (c) Sand with small stones and incidental larger stones, and (d) Sand with *Sabellaria* fragments and incidental larger stones.

As for the grab samples, the majority have a mean grain size ranging from $M_z = 1.50\phi$ to $M_z = 1.75\phi$. The standard deviation of the mean grain sizes from the three samples taken at each station was at the same level as the size range of all the samples i.e., $\sigma_{M_z} = 0.25\phi$. There was one triple of grab samples (from Station 23) with a smaller mean grain size, $M_z = 4.04 \pm 1.18$, than the rest of the grab samples. The grab at this station was composed of very fine particles that were compacted and stuck together. For most grab samples, clumps of particles that were stuck together could be brushed lightly in order for them to be sieved. The grab samples from Station 23, however, had to be crushed through the various sieve sizes with force. After doing this, the particle size analysis (PSA) indicated small grain sizes for this grab sample.

Often, backscatter-based acoustic classes are compared to the mean grain sizes to create sediment maps^{10,30,31}. Fig. 11a shows the results of such a comparison. It can be seen that the acoustic classification results are not correlated with mean grain size values. This observation not only holds when the mean grain size is compared with the acoustic classes, but also when the mean grain size of a grab sample is compared to its Folk classification (Fig. 11b). Thus, a grab sample with different Folk class can have the same mean grain size.

When using Folk classes, the sediments “sandy mud” (sM), “sand” (S), “slightly gravelly sand” ((g)S), and “gravelly sand” (gS) were encountered. Out of the 22 grab sample positions there is 1 location that is classified as sM. There were 5, 15, and 1 locations that were classified as S, (g)S and gS, respectively. Thus, the dominant sediment type in the surveyed area is either sand or slightly gravelly sand again indicating an almost non-distinctive sedimentary environment.

The number of matches between the Folk class and acoustic class at the grab sample locations shows a general trend of coarser sediments for higher acoustic classes (Fig. 12). Sand corresponds mainly to acoustic classes 1 and 2. Slightly gravelly sand is matched dominantly with acoustic classes 2 and 3, and gravelly sand with acoustic class 3. However, the finest sediment sM correlates with acoustic class 4. This is likely due to the compactness of the sediment for this grab sample,

Figure 9. Video classification results at four stations. Per station, indicated location and class of video frame in colored dots and MBES classification results as background.

Figure 10. Percentages of occurrence of acoustic classes within one-meter radius of video data points, classified as follows: “Sand with hardly any shell fragments” (No S.F.), “Sand with some shell fragments” (Some S.F.), “Sand with Sabellaria fragments and incidental larger stones” (Sab. & L.S.), or “Sand with small stones and incidental larger stones” (S.S. & L.S.).

as was described earlier. We may assume that (g)S of the grab samples corresponds to “Sand with some shell fragments” in the video data. This correspondence is also observed when comparing the grab samples and acoustic classes in Fig. 12 with the video data and acoustic classes in Fig. 10.

Figure 11. Averaged mean grain sizes and standard deviations versus acoustic class numbers (a) and Folk classification (b) for 21 of the grab samples with M_z from 1.50 to 1.74 ϕ .

Full spectrum of grain size distribution for classification

Based on the mean grain size of the grab samples, the survey area is very homogeneous. However, both the Folk classes of grab samples and the acoustic data indicate four sediment types. This indicates that the acoustic classes are to be attributed to the full spectrum of the grain size distribution and not just the mean grain size.

This hypothesis is now investigated by using the variables M_z , σ , s , and k from Eq. 8-11 and performing PCA on these. The first PC, representing 53 % of the feature variabilities, is not far from being just the sign-corrected average of the above four features with the dominant contributions from σ , M_z , and s . This PC is thus considered to be the most informative feature and hence will be used for comparison. Fig. 13 shows this PC versus the acoustic classification results. A positive correlation is observed. This verifies that the full spectrum of the grain size distribution should be used when comparing grab samples with the acoustic classes and not just the mean grain size.

From the literature, it is expected that higher backscatter values would correspond to larger grain sizes. As indicated in Fig. 11 there is no correlation with higher acoustic classes (which correspond to higher backscatter values) for larger mean grain sizes, because the mean grain size does not vary much over the grab samples. To check what influence larger grains have on backscatter values, the backscatter values from the beam angles ranging from 25 to 65 degrees were averaged over a few pings around each grab sample. These averaged backscatter values were compared to the percentage of the grab sample with a grain size greater than 0.5 mm (Fig. 14). This showed that larger percentages of large grain sediments correspond to higher backscatter values (the linear correlation coefficient is 0.51). This finding is in agreement with the results presented by Simons et al. who found a positive correlation between backscatter levels and shell or gravel percentage of grab samples³². It can therefore be concluded that the areas of high backscatter values (classes 3 and 4) correspond to slightly gravelly sand and lower backscatter values (classes 1 and 2) correspond to sand. Further investigation would be needed to quantify the influence of other factors affecting backscatter strength, such as surface roughness and volume scattering³³.

Figure 12. Correlation between sediment type and acoustic class at grab sample locations. Size of dots and numbers indicate number of matches between sediment types and acoustic classes.

Figure 13. Acoustic class numbers versus first principal component obtained from grain size statistics given by Folk and Ward²⁸.

Figure 14. Mean backscatter value of angular response curve (excluded data around nadir) versus percentage of grab contents with grain sizes greater than 0.5 mm.

7 Geo-acoustic versus spatial resolution

The classification of sediments in the Brown Bank area brings to the forefront a dilemma of resolutions. On the one hand sediments may vary from crest to trough of some of the smallest sand waves, i.e., megaripples, which have a wavelength of a few tens of meters. It would be desirable to accurately classify sediments over these features at a high spatial resolution. On the other hand, a high geo-acoustic resolution is needed to account for small changes in sediment composition from the crest to the trough of the megaripple. When applying the Bayesian classification method, the geo-acoustic resolution is increased when the data points are representative of a higher number of scatter pixels due to the standard deviation of the Gaussians being less. The theoretical standard deviation of the Gaussians is $\sigma_y = 5.57 / \sqrt{N_s}$, where N_s is the number of scatter pixels¹³. An approach to increasing the number of scatter pixels per data point is to average the backscatter (BS) data over several beams in the across track direction, and several pings in the along track direction as employed by Amiri-Simkooei et al.¹⁵. Performing such an averaging procedure has the added benefit of averaging out much of the ping-to-ping variability of backscatter data that is not dependent on the seafloor properties. While such averaging increases the geo-acoustic resolution, it directly decreases the spatial resolution of the classification.

For determining a good trade-off, the acoustic data were preprocessed with different levels of averaging. Fig. 15 shows the fits of a Gaussian PDF to the BS histogram at the 26° starboard grazing angle for both approaches. A few observations are highlighted:

- The above averaging procedure can in principle reduce the noise of the backscatter data. This may, however, not decrease the standard deviation proportionally to the square root of the number of scatter pixels represented. This is because this rule is valid only for independent and identically distributed data. This cannot be the case for the backscatter data averaged over a small surface patch, because the variation and uncertainty in the BS data has independent and dependent components. The independent component is known as noise, which can be averaged out. This however does not hold for the dependent component, which is intrinsic to acoustic sediment properties and its heterogeneity. The fact that the two histograms in Fig. 15 look similar also verifies the above reasoning; otherwise the second data set would have a significantly narrower histogram due to the averaging procedure.
- There is a trade-off between the spatial and geo-acoustic resolutions. While heavier averaging increases the geo-acoustic resolution of the classification, it directly decreases its spatial resolution. Narrower and relatively more separated Gaussians as well as chi-squared values closer to 1, obtained for the averaged data set (Fig. 15 bottom subplots), indicate a better geo-acoustic resolution.

Figure 15. Comparison of Gaussian curve fitting to histogram of backscatter under two levels of averaging; limited averaging (top), heavier averaging (bottom); indicated in plots are Gaussian curve fitting (a,c), and chi-square test statistics (b,d). Fitting was done on grazing angle 26 degrees starboard.

- The results obtained in Fig. 15 show that the means and standard deviations of the Gaussians are characteristic of the acoustic properties of the sediment types. Given that the mean grain sizes of the grab samples suggested a homogeneous seabed in this survey area, it might be thought that if the parameters of the Gaussian were given a significant range within which they could vary, only one (or a few) Gaussians would be fitted to the entire histogram. The results show that this is not the case. For both datasets, the bounds for the standard deviation were set to a range of 0.5-2 dB but for neither dataset were the lower or upper bounds used after the curve fitting was implemented. This indicates that the Bayesian classification results are not significantly affected by the averaging procedure.

Classifying sediments over megaripples

Now we investigate to what extent MBES backscatter data can be used to classify the sediments over megaripples. This is of particular interest for detailed habitat mapping³⁴, engineering projects such as offshore wind farms or pipe laying²², and for modelers of sand waves who study the morphology, hydrodynamics, and sand transport at the seafloor^{1,24}. In the previous sections it is found that higher acoustic classes correspond to sediments with a larger proportion of coarse sediments in this study area. These terms will thus be used interchangeably in the following paragraphs.

Thirty-two areas where megaripples were present were selected and partitioned; see Fig. 16 for two examples. Fig. 17 shows the histogram of the maximum slopes computed for the above-mentioned areas. For these areas the occurrences of acoustic classes per location on the megaripples were counted. These classification results for the slope bin centers are presented in Fig. 18. At the lowest point of the stoss side of the trough, i.e., bin center (BC) = 2.5°, the dominant AC is 3 (Fig. 18, right). From the trough moving towards the crest, this gradually changes from higher classes to lower classes. The finest sediments (class 1) are found on the stoss side at BC = 17.5°, for both the trough and crest areas. Continuing towards the crest, the sediments are classified as either class 2 or class 3. At the highest point on the lee side of the crest, BC = -2.5°, the dominant acoustic class is again 3. This tends to become coarser when continuing down the crest towards the trough on the lee side. At BC = -17.5°, the steepest point on the lee side, on the boundary between the crest and trough areas (specified by rectangles in Fig. 18), a mixture of acoustic classes, ranging from fine to coarse (class 1 to 4), is observed. This is also clearly visible in the two typical areas (out of the 32) in Fig. 19. An important characteristic of this part of the megaripples, is that the coarsest sediments appear only here (see also Fig. 19, left). In the remaining parts of the trough, at BC = -12.5°, -7.5°, and -2.5°, the sediments are again classified as coarse-grained.

To create a generalized acoustic class per position on the megaripple structure a weighted average of the dominant acoustic class was calculated for each slope bin, side of the megaripple, and trough or crest area. This can be considered a combining of the classification results presented in Fig. 18. The result is shown in Fig. 20. The alternating green and red line on the steepest part of the lee side slope indicates that the entire range of acoustic classes was found on this part of the megaripple. We hypothesize that this is a result of megaripple migration.

Megaripples migrate towards the lee side, known based on bathymetry comparisons with older data. This is also the average flow direction. We hypothesize that fine suspended sediments are deposited on the lee side of the megaripple. Then low acoustic classes are expected. At times of high tidal currents, the combination of the steep slope and a downward current causes an avalanche of the fine sediment deposition²⁴, leaving only the coarse sediments exposed. For that area high acoustic classes are then expected. This is why such a range of acoustic classes are encountered on the steepest leeward slopes of the megaripples.

Figure 16. Maximum slopes (in degrees), representing megaripple structures, in two typical examples in Brown Bank area.

Figure 17. Histogram of maximum slopes computed in 32 typical areas with megaripple structures.

Figure 18. Acoustic classification results of 32 typical areas with megaripple structure given for bin centers ranging from -17.5 to 17.5 degrees; crest (left), trough (right).

Figure 19. Acoustic classification results in two typical areas of Fig. 16. Black dots indicate steep slopes of $<-10^\circ$ on the lee side of megaripples

Summary and Conclusions

The Bayesian classification method was applied to MBES backscatter data gathered in the Brown Bank area of the North Sea. To obtain reliable classification results, steep and rapidly changing slopes over tens of meters had to be corrected for. Acoustic classification results were then compared with video and grab sample data.

Based on the results of the sediment grain size analysis it was found that the seafloor sediments of the Brown Bank area are very homogeneous. The variance in the mean grain size over the entire area was at the level of the variance within the triplicate grab samples from individual sampling stations. However, Folk classification of grab samples, as well as, the acoustic classification results were more discriminative. A further analysis showed that for areas like the Brown Bank, the full grain size distribution should be used when classifying the grab samples and when relating this ground truth data to the acoustic classification results. This should be taken into account for any future sediment studies in homogeneous sandy environments.

For acoustic classification of sediments in relatively homogeneous environments, especially over megaripple structures, high spatial and geoacoustic resolutions are required. There is, however, a trade off in these resolutions. Therefore, depending on the aim of a classification application, either of these resolutions can be optimized for. It was found that the Bayesian classification method remains statistically sound when optimizing for the spatial resolution, as long as the number of scatter pixels used in the averaging satisfies the central limit theorem requirements. This is a pivotal result that underscores the validity of our acoustic classification results over megaripples.

The results revealed that there was a significant sorting of sediments over megaripples. Higher acoustic classes, and therefore coarser sediments, were found in the troughs and on the crests. Low acoustic classes were consistently found to be on the steepest part of the stoss side of a megaripple. On the, even steeper, lee side slope of the megaripple a mixture of all acoustic classes was found. These detailed results have a number of implications. First, for detailed habitat maps, the size of the megaripple and not that of the sand wave should define the resolution scale of the map. Next, researchers gathering ground truth data, such as grab samples and video data, should strive to geo-reference the point measured on the seafloor with an accuracy well below the wavelength of megaripples to avoid ambiguities in measurement. Finally, it confirms that the classification of

backscatter data from MBES systems is a powerful method to further study and display the spatial distribution of sediments over megaripple bed forms. As such, it can provide valuable information for habitat mapping, engineering projects such as offshore wind farms or pipe laying, or to serve as field validation data for sand wave modelers.

Figure 20. Schematic sedimentary composition of megaripple migrating to right; wavelength is 10 m and depth variation is ± 1 m. Colors represent interpolated classes among class numbers 1, 2, 3, and 4; dashed green-red lines indicate all variants of sediment types (from fine to coarse).

Acknowledgements

The authors would like to thank Rob Witbaard for being the chief scientist during the data gathering cruise and the crew of the NIOZ vessel the Pelagia for all of their assistance during the acquisition of the data. Karline Soetaert of NIOZ is acknowledged for her role in organizing the cruise, as well as Tom Ysebaert, who also coordinated the particle size analysis of the grab samples. Peter van Breugel was key in performing the particle size analysis in the NIOZ lab. Laura Govers and Han Olf of the University of Groningen are acknowledged for their valuable comments to earlier versions of this manuscript. We also thank Leendert Dorst and Daniëlle van Kuijk of the Hydrographic Service within the Royal Netherlands Navy for making full coverage bathymetry data of the Brown Bank area available. We acknowledge the Gieskes-Strijbis Fonds for the financial support of the DIS-CLOSE project, within which this research took place.

References

1. Roos, P. C., Wemmenhove, R., Hulscher, S. J. M. H., Hoeijmakers, H. W. M. & Kruyt, N. P. Modeling the effect of nonuniform sediment on the dynamics of offshore tidal sandbanks. *J. Geophys. Res. Earth Surf.* 112, (2007).
2. Stolk, A. Variation of sedimentary structures and grain size over sandwaves. In *Proceedings of Marine Sandwave Dynamics International Workshop* 193–197 (2000).
3. Svenson, C., Ernsten, V., Winter, C., Bartholomä, A. & Hebbeln, D. Tide-driven sediment variations on a large compound dune in the Jade tidal inlet channel, Southeastern North Sea. *Journal of Coastal Research* vol. 1 (2009).
4. van Lancker, V. & Jacobs, P. The dynamical behaviour of shallow marine dunes. In *International Workshop on Marine Sandwave Dynamics* (2000).
5. Brown, C. J., Smith, S. J., Lawton, P. & Anderson, J. T. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast. Shelf Sci.* 92, 502–520 (2011).
6. Marsh, I. & Brown, C. Neural network classification of multibeam backscatter and bathymetry data from Stanton Bank (Area IV). *Appl. Acoust.* 70, 1269–1276 (2009).
7. Ojeda, G. Y., Gayes, P. T., Van Dolah, R. F. & Schwab, W. C. Spatially quantitative seafloor habitat mapping: Example from the northern South Carolina inner continental shelf. *Estuar. Coast. Shelf Sci.* 59, 399–416 (2004).
8. Clarke, J. H., Danforth, B. & Valentine, P. Areal seabed classification using backscatter angular response at 95kHz. In *High Frequency Seafloor Acoustics (SACLANTCEN Conference Proceedings CP-45)* 243–250 (1997).
9. Lamarche, G., Lurton, X., Verdier, A. L. & Augustin, J. M. Quantitative characterisation of seafloor substrate and bedforms using advanced processing of multibeam backscatter-Application to Cook Strait, New Zealand. *Cont. Shelf Res.* 31, (2011).
10. Eleftherakis, D., Amiri-Simkooei, A., Snellen, M. & Simons, D. G. Improving riverbed sediment classification using backscatter and depth residual features of multi-beam echo-sounder systems. *J. Acoust. Soc. Am.* 131, 3710–3725 (2012).
11. Snellen, M., Gaida, T. C., Koop, L., Alevizos, E. & Simons, D. G. Performance of multibeam echosounder backscatter-based classification for monitoring sediment distributions using multitemporal large-scale ocean data sets. *IEEE J. Ocean. Eng.* 44, 142–155 (2019).
12. Brown, C. J., Todd, B. J., Kostylev, V. E. & Pickrill, R. A. Image-based classification of multibeam sonar backscatter data for objective surficial sediment mapping of Georges Bank, Canada. *Cont. Shelf Res.* 31, (2011).
13. Simons, D. G. & Snellen, M. A Bayesian approach to seafloor classification using multi-beam echo-sounder backscatter data. *Appl. Acoust.* 70, 1258–1268 (2009).
14. Alevizos, E., Snellen, M., Simons, D. G., Siemes, K. & Greinert, J. Acoustic discrimination of relatively homogeneous fine sediments using Bayesian classification on MBES data. *Mar. Geol.* 370, 31–42 (2015).
15. Amiri-Simkooei, A., Snellen, M. & Simons, D. G. Riverbed sediment classification using multi-beam echo-sounder backscatter data. *J. Acoust. Soc. Am.* 126, 1724–1738 (2009).
16. van Dijk, T. A. G. P. et al. Benthic habitat variations over tidal ridges, North Sea, The Netherlands. In *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
17. ESRI. World Topographic Map. Online Baselayer Database. 2012
18. Herman, P. M. J., Beauchard, O. & van Duren, L. A. De staat van de Noordzee. In *De Noordzeedagen 2014* (2014).
19. MetOcean Online Database. MSL SWAN Annual Mean Significant Wave Height.
20. Knaapen, M. A. F. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo-Marine Lett.* 29, 17–24 (2009).
21. Lindenberg, R. C., van Dijk, T. A. G. P. & Egberts, P. J. P. Separating bedforms of different scales in echo sounding data. In *Coastal Dynamics 2005* 1–14 (American Society of Civil Engineers, 2006).
22. Knaapen, M. A. F. Sandwave migration predictor based on shape information. *J. Geophys. Res. Earth Surf.* 110, 1–9 (2005).
23. Nemeth, A. Modelling offshore sand waves. PhD Thesis. (University of Twente, 2003).
24. Idier, D., Ehrhold, A. & Garlan, T. Morphodynamique d'une dune sous-marine du détroit du pas de Calais. *Comptes Rendus Geosci.* 334, 1079–1085 (2002).
25. Teunissen, P. Testing theory: an introduction. Series on Mathematical Geodesy and Positioning. (VSSD Press, 2006).
26. Teunissen, P., Simons, D. J. & Tiberius, C. Probability and Observation Theory. (Delft University of Technology, 2004).
27. Sheehan, E. V., Stevens, T. F. & Attrill, M. J. A quantitative, non-destructive methodology for habitat characterisation and benthic monitoring at offshore renewable energy developments. *PLoS One* 5, e14461 (2010).
28. Folk, R. L. & Ward, W. C. Brazos River bar [Texas]; a study in the significance of grain size parameters. *J. Sediment. Res.* 27, 3–26 (1957).
29. Wentworth, C. K. A scale of grade and class terms for clastic sediments. *J. Geol.* 30, 377–392 (1922).
30. Collier, J. S. & Brown, C. J. Correlation of sidescan backscatter with grain size distribution of surficial seabed sediments. *Mar. Geol.* 214, 431–449 (2005).
31. Eleftherakis, D., Snellen, M., Amiri-Simkooei, A., Simons, D. G. & Siemes, K. Observations regarding coarse sediment classification based on multi-beam echo-sounder's backscatter strength and depth residuals in Dutch rivers. *J. Acoust. Soc. Am.* 135, 3305–3315 (2014).
32. Simons, D. G., Snellen, M. & Ainslie, M. A. A multivariate correlation analysis of high-frequency bottom backscattering strength measurements with geotechnical parameters. *IEEE J. Ocean. Eng.* 32, 640–650 (2007).
33. Jackson, D., Baird, A. M., Crisp, J. J. & Thomson, P. A. G. High-frequency bottom backscatter measurements in shallow water. *J. Acoust. Soc. Am.* 80, 1188–1199 (1986).
34. van der Reijden, K. J. et al. Discovery of Sabellaria spinulosa reefs in an intensively fished area of the Dutch Continental Shelf, North Sea. *J. Sea Res.* 144, 85–94 (2019).

Chapter 8

Discovery of *Sabellaria spinulosa* reefs in an intensively fished area of the Dutch Continental Shelf, North Sea

Karin J. van der Reijden

Leo Koop

Sarah O'Flynn

Silvia Garcia

Oscar Bos

Christiaan van Sluis

David J. Maaholm

Peter M.J. Herman

Dick G. Simons

Han Olf

Tom Ysebaert

Mirjam Snellen

Laura L. Govers

Adriaan D. Rijnsdorp

Ricardo Aguilar

Published as

van der Reijden KJ, Koop L, O'Flynn S, Garcia S, Bos O, van der Sluis C, Maaholm DJ, Herman PMJ, Simons DG, Olf H, Ysebaert T, Snellen M, Govers LL, Rijnsdorp AD, Aguilar R (2019). Discovery of *Sabellaria spinulosa* reefs in an intensively fished area of the Dutch Continental Shelf, North Sea. *Journal of Sea Research*, 144, 85-94.

Abstract

The tube-building polychaete *Sabellaria spinulosa* (Ross worm) can form conspicuous biogenic reefs that stabilize the seabed and increase biodiversity by providing a habitat for a multitude of other species. These reefs, however, are assumed to be vulnerable to human-induced physical disturbances of the seabed. In the Greater North Sea, *S. spinulosa* reefs are recognized to be under threat and worthy of protection. In August 2017, three *S. spinulosa* reefs with a minimum extent of 1016 m² were discovered in the Dutch Brown Bank area. This area comprises a large-scale sandbank and adjacent troughs. The reefs were found within the sandbank troughs, which have proven to be subject to high demersal fishing intensities (fished >5 times a year). Detailed bathymetry measurements showed that *S. spinulosa* reefs were mainly located within valleys of smaller-scaled sand waves, which have a perpendicular orientation compared to the large-scale sandbank structure of the Brown Bank. We hypothesize that the valleys in between sand waves offer suitable substrate for settlement and refuge from abrasion by fishing activities, enabling the *S. spinulosa* reefs to persist despite high fishing intensities. ROV footage of the reefs showed higher estimates of species abundances on the reefs compared with adjacent habitats, with some species present that are typical for hard substrate (rock gunnel, *Pholis gunnellus*; edible crab, *Cancer pagurus*; and velvet swimming crab, *Necora puber*). The information presented could be used for drafting management policies to protect these reefs, as Contracting Parties of the OSPAR Convention are committed to take measures and protect biodiversity.

Introduction

Biogenic reefs are formed by ecosystem engineers, and are known to promote biodiversity of otherwise soft sediment bottoms by increasing habitat complexity and adjusting prevailing environmental conditions^{1,2}. The best known biogenic reefs are built by corals, but in temperate waters multiple species with similar reef-building properties can be found. For instance, some sponges are known to increase habitat complexity³, while oysters, mussels, and sand mason worms form beds that act as biogenic reefs^{4–6}. Habitat complexity provides refuge possibilities and suitable substrate for settlement⁷ as well as food provisioning for multiple, higher-trophic species⁸. Biogenic reefs also stabilize sediments and reduce current and wave speeds^{5,9}, enabling the settlement of species requiring conditions of low hydrodynamic stress¹⁰. However, biogenic reefs are disappearing on a worldwide-scale due to anthropogenic pressures^{11,12}. Where coral reefs are mainly affected by global warming and acidification¹², sediment disturbing practices, such as demersal fisheries, are thought to have a high negative impact on temperate biogenic reefs^{13,14}.

The sedentary polychaete *Sabellaria spinulosa* is capable of forming such biogenic reefs, by creating aggregations of thousands of individual tubes from sand particles^{15,16}. The polychaete has a wide distribution, with recordings in the Atlantic, the North Sea, the Mediterranean Sea and the English Channel^{17–20}. However, in most of its geographical range *S. spinulosa* is encountered as low numbers of individual worms encrusting available substrate, shells, and kelp holdfasts^{16,21,22}. The occasions in which *S. spinulosa* acts as an ecosystem engineer, by the formation of biogenic reefs that are significantly elevated from the seabed, is thought to be rare, with the majority of the reefs established near the British coast^{17,18,21,22}. The areas around the North Norfolk coast and the Wash are particularly important for *S. spinulosa* establishment²¹. Reefs are less well known from elsewhere in the North Sea. Extensive, intertidal reefs have been present in the German Wadden Sea, but they have been completely lost^{22–24}. On the Dutch Continental Shelf, solitary observations have been made during dredge sampling²⁵, diving expeditions (Stichting Duik de Noordzee Schoon, Bureau Waardenburg BV), and scientific ROV surveys (OCEANA North Sea Expedition 2016). Recordings of extensive *S. spinulosa* reefs, however, could not be found in either international or national databases^{17,26,27}. Moreover, after consultation with multiple Dutch North Sea scientists, researchers, policy makers and environmental agencies, we conclude that, currently, no *S. spinulosa* reefs are known on the Dutch Continental Shelf.

Based primarily on the reported decline of *S. spinulosa* reefs in the German Wadden Sea²², the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR convention) has recognised that *S. spinulosa* reefs are threatened and in decline in the Greater North Sea²². The largest threat to *S. spinulosa* reefs is thought to be abrasion by physical disturbance²². Sand extraction and demersal fisheries impose a particularly high risk, as these activities damage the tubes and remove (parts of the) reef²¹. Multiple studies conclude that fisheries are the most likely explanation of reef destruction^{22,28,29}. Other studies show clear trawl scars and other signs of trawling damage in *S. spinulosa* reefs^{19,30}.

In this study, however, we report on the discovery of three separate *S. spinulosa* reefs in an intensively fished area on the Dutch Continental Shelf. In August 2017, the reefs were unexpectedly observed in the Brown Bank area during an expedition of OCEANA. This expedition aimed to strengthen the networks of Marine Protected Areas in the North Sea, by documenting habitats and species in 16 areas. Acoustic and videographic data and sediment samples were collected serendipitously within and around these reefs. In addition, surrounding patterns of demersal fishing activity were determined from Vessel Monitoring System (VMS) data.

Materials and Methods

Study area

In August 2017, the research vessel ‘Neptune’ was used to investigate benthic habitats and communities in the Brown Bank area (52° 32′ 59.994″ North, 3° 18′ 36.400″ East; Fig. 1a). The Brown Bank area is characterized by a large, north-south oriented sandbank. The water depth at the top of the bank is 19 m; deep troughs with a water depth of 45 m are found on both sides of the crest (Fig. 1b). Similarly oriented but less elevated sandbanks dominate the surroundings³¹. Formed by the (stable) north-south oriented tidal currents, these sandbanks are kilometres long, tens of meters high and around 5-10 km apart from each other³¹. Sandbank crests, slopes, and troughs are comprised of contrasting sediments and fauna. Van Dijk *et al.* described the fauna as a function of the geomorphology and found well-sorted, medium sand at the crests and muddy sediments

Figure 1. The location of the Brown Bank area within the Southern North Sea (a) and a high-resolution bathymetry map of the Brown Bank area depicting the locations of the sediment samples (1-8) and ROV-transects (dots) (b). Location of acoustic data collected in this survey is depicted in black lines. *S. spinulosa* presence, including reef condition (reef structure versus low abundances), are shown for the separate ROV-locations with *S. spinulosa* present (1c – 1e).

mixed with gravel and shell fragments in the troughs³². Infauna species diversity and abundance was much higher in the troughs than on the crests. The slopes were a mix of these two extremes³². According to van Dijk *et al.* sand waves and mega ripples are present on the crests of the sandbanks, with a perpendicular orientation. The sand waves are symmetrical in cross-sectional shape, with an average wavelength and height of 190 m and 2.6 m respectively³².

Video footage

Video footage was collected with a Remotely Operated Vehicle (ROV), Saab Seaeye Falcon DR (Saab Seaeye Ltd, Saab North America Inc), equipped with two forward-facing video cameras: (1) a high-definition camera with 1920x1080 px resolution, 1/2.9" Exmor R CMOS Sensor, minimum scene illumination of 3-11 Lux, and a 4-48 mm, f/1.8-3.4 zoom lens; and (2) a low-definition camera with a resolution of 540 TVL, 1/2" interline transfer CCD sensor, sensitivity of 0.35 Lux, and a 1/2" aspherical, wide-angle, fixed-focus lens. The high-definition camera could be repositioned remotely by the operators (both pilot and scientists) and was used to shoot selective high-quality photos and video-fragments. Moreover, a continuous video of lower quality was separately recorded by the camera. The second camera was mounted on top of the ROV and looked forward with an oblique angle to the seabed. This camera recorded continuously. So for each ROV track, we had two continuous videos (with differing viewing angles) and several high-quality video-fragments. The track of the ROV was constantly recorded by a TrackLink 1500 system (LinkQuest Inc., San Diego, USA) that registered the exact location of the ROV in relation to the vessels' location. The course of the ROV depended on the prevailing currents and decisions of the operators.

Five ROV dives were made in total, of which four were at a random location within the Brown Bank area. The fifth dive was taken at the same reef as discovered during the first dive. The video footage was not collected according to scientific operational guidelines^{33,34} as this was intended as an exploratory characterisation survey, disallowing for the application of a standard scientific video analysis method. Hence, we developed an appropriate protocol to analyse the videos, based loosely on the standard video analysis guidelines¹⁶. All five videos were analysed twice, by two independent observers. Results shown are the averages of both observations. For each video, the total time at the seabed was determined, presence of *S. spinulosa* was recorded, and reef structure was assessed. In line with the OSPAR recommendations²², we classified *S. spinulosa* as a reef if its structure had a general elevation of >5 cm above the seabed and a local coverage of >30% of the seabed. All other recordings of *S. spinulosa* were scored as 'low abundance'. The continuous video enabled us to identify and count organisms larger than 5 cm. From the high-quality video fragments, however, we could frequently identify smaller organisms as well. All species observations were registered per habitat type: *S. spinulosa* reef, *S. spinulosa* in low abundance, or adjacent area.

The TrackLink system yielded GPS positions of the ROV for every second. Based on the time registration, we could link GPS positions to the video analysis. This resulted in the exact route of the ROV near the seabed and GPS positions of *S. spinulosa* observations. Due to the meandering course and varying depth and speed of the ROV, the observed surface of the seabed differed during the ROV-track. Therefore, we plotted the ROV positions over a 1 m² grid. The total observed surface covered in a video was then estimated as the total number of grid cells with ROV positions, while the ROV was at the seabed. We similarly estimated the area with *S. spinulosa* present and the total reef extent for the ROV surveyed area. Unfortunately, the TrackLink system log-system crashed after a few minutes during the second dive, resulting in missing GPS-positions for the rest of this video. In the low-quality video however, the GPS-positions are displayed on the screen as well. From this video, we have registered the GPS-position for every 15 seconds of the dive. Plotting both the logged and video-based GPS-positions showed four outliers, which were located >100m apart from the other GPS-locations. These outliers were most likely caused by errors in the TrackLink system. We removed the four outliers and subsequently analysed the remaining ROV-positions as described.

Acoustics

Acoustic surveys of the seabed were performed with a hull-mounted Reson Seabat 7125 multi-beam echo-sounder (MBES). The MBES operated at 200 kHz and had 2° and 1° beam opening angles in the along and across track directions respectively. The beam coverage of the 256 beams was set to equidistant (vs. equiangular) with a maximum ping rate of 50 Hz and a pulse length of 300 μ s. Both bathymetry and backscatter data were recorded using Qinsy. A Kongsberg Seatex DPS 200 global positioning system (GPS) provided position information and the MBES data was motion corrected by use of a Seatronics POS MV 320 motion reference unit (MRU).

The MBES data collected was very noisy, perhaps because the MBES was approaching its service cycle. The data noise was cleaned in a three-step process. First, extreme depth outliers were removed in Qinsy using the 3D-editing tool. Second, Qinsy's automated cleaning tool 'Qloud' was applied to eliminate the majority of the faulty depth soundings. As a last step, all the data was again reviewed in the 3D-editing tool to remove aeration spikes and other small defects not corrected by 'Qloud'. A roll offset that was noticed in post processing was also corrected for.

After cleaning, the acoustic data was exported in custom ASCII format. In MatLab, the acoustic backscatter data was classified with the Bayes algorithm^{35–39}. Due to the steep slopes on the sand waves, a slope correction step was performed to eliminate grazing angle effects on the classification results. This slope correction was performed by first gridding the data into square grid cells containing ten data points per grid cell on average. Size of the grid cells varied between survey lines, but was restricted between 0.25 x 0.25 m and 5 x 5m, with most grid cells having a size between 0.75 x 0.75 m and 1.25 x 1.25 m. A digital terrain model was created by taking the mode depth of all points in the grid cells, which was then used to calculate the slope per grid cell by applying the average maximum technique⁴⁰ to the eight neighbouring grid cells. The true grazing angle was calculated as the angle between the vector from a given data point d to the source (transducer) s and the vector from d to a point n . Where n is on the plane p , passing through d having the same slope as calculated for the grid cell within which d lies, and the line m perpendicular to p passing through s .

Sediment samples

Sediment sample locations were selected following assessment of preliminary acoustic data and at random locations within the area of interest. Sampling was conducted with a 12 L van Veen grab, with a surface area of around 880 cm². Representative subsamples acquired for particle size analysis were immediately stored in plastic bags at -20 °C until processed. The samples were freeze dried for 4 days, homogenized, and subsampled for the determination of sediment grain size, total organic carbon and nitrogen content. To determine sediment grain size, subsamples were sieved over a 1 mm mesh sieve and analysed by means of a laser diffraction technique using a Malvern Mastersizer 2000 (Malvern Instruments, Worcestershire, UK). The >1 mm fraction was not included in the analysis. Results were verified using two internal control samples, in accordance with the UK National Marine Biological Quality Control Scheme (NMBAQC).

Organic carbon and total nitrogen content were analysed according to the Dumas method⁴¹, using a Thermo Flash 2000 Element Analyser (Thermo Scientific). Freeze-dried subsamples were measured and subsequently oxidized at high temperature (1020°C) with excessive oxygen supply and oxidation catalysts. This produced CO₂ and nitrous oxides (NO_x), of which the latter were reduced to N₂ over copper grains at 650°C. Both gasses were separated using gas chromatography and total amounts were determined by thermal conductivity. Samples containing inorganic carbon were acidified before analysis to remove the inorganic carbon.

Fisheries

Satellite data of Dutch demersal fisheries (all vessels >12 m) were obtained from the Dutch Ministry of Agriculture, Nature and Food Quality for the years 2008-2015. These data comprised satellite recordings of date, time, position, heading, and speed of the vessel, with an interval of around two hours. In addition, daily logbook information was available, which included the date, general position, and fishing gear of the vessel. Satellite positional data was merged with daily logbook information, coupling the unique combination of date and vessel within a fishing trip⁴². This yielded one dataset, comprising both spatial and fisheries-technical data. Based on the speed and fishing gear, each satellite recording was identified as 'steaming', 'floating', or 'fishing'. If a recording was determined as 'floating' in between two 'fishing' recordings, the floating recording was re-identified to 'fishing' to correct for setting and heaving of the fishing gear⁴³. Then, for each 'fishing' ping, the swept area was calculated, as the product of speed (km/h), fishing time (h), and the width of the gear (km)⁴⁴. At a resolution of 1 x 1 km, total annual swept area was aggregated for all demersal fisheries and divided by the surface of the grid cell (1 km²). This fishing intensity (yearly swept area) was then averaged for the 8 years of the study period, resulting in an average fishing intensity distribution. For the main fishing method present in the area (beam-trawlers with a mesh size between 70-99 mm), the heading during fishing was determined for all VMS-pings classified as 'fishing' in three depth classes.

Results

Video footage

S. spinulosa was observed in four of the five video transects, located at three separate locations within the troughs of the Brown Bank area (Fig. 1a-b). Altogether, the videos had a total seabed recording time of 164 minutes and 3 seconds (45:14, 26:08, 25:23, 46:44, 20:34 [minutes:seconds]), a total transect length of around 7.5 km (3124 m, 1665 m, 885 m, 1344 m, 523 m), and an observed area of 1995 m² (1063¹ m², 86 m², 399 m², 447 m²). An area of 1603 m² was observed with *S. spinulosa* present, which is 80% of the total surveyed area. Based on the OSPAR recommendations (>30 % coverage and >5 cm elevation from the seabed), an area of 1023 m² (51%) was classified as *S. spinulosa* reef (Fig. 2). Of the four observed locations, the most northern location identified mainly *S. spinulosa* in low abundances (Fig. 1c). From the 344 m² with *S. spinulosa* present, only 72 m² was classified as reef (21%). At the middle location, the ROV did not reveal the presence of any *S. spinulosa*. The two southern locations comprised *S. spinulosa* observations, including extensive reef structures (Fig. 1d-e). At the eastern location, 44% was classified as reef (165 m² out of 376 m²). The western location showed the highest percentage of reef structures present (89%, 786 m² out of the 883 m²). For all three locations with *S. spinulosa* reefs, the video footage suggested that the *S. spinulosa* reefs were dominantly located in local depressions of the seabed, as the seabed became elevated at the border of *S. spinulosa* reefs, comprising a sandy plateau with sand ripples.

Thirty different organisms were identified from the continuous video and the high-quality video fragments (Table 1). Some of the organisms could only be identified to order level such as anemones (Actiniaria) and sea squirts (Ascidiacea). For all other species, the enumerated individuals were translated to abundance classes of the SACFOR scale², using the calculated extent of the observed surface. Hermit crab (*Pagurus bernhardus*), common starfish (*Asterias rubens*), dragonet (*Callionymus* spp.), and swimming crab (*Liocarcinus* spp.) were present at all locations, with a slightly higher density in the *S. spinulosa* reefs compared to adjacent areas. Other species, like the small-spotted catshark (*Scyliorhinus canicula*), rock gunnel (*Pholis gunnellus*), edible crab (*Cancer pagurus*) and the velvet crab (*Necora puber*) were less abundant or absent at some of the locations. Moreover, these species were almost exclusively observed in areas of *S. spinulosa*

¹ This is the summation of video 1 and 5, as they partly covered the same location.

² Marine Nature Conservation Review (MNCR) SACFOR abundance scale <http://jncc.defra.gov.uk/page-2684>.

Figure 2. Pictures of the *S. spinulosa* reefs in low abundance (a,b) and reef structure (c,d), with associated species (a: Common starfish (*Asterias rubens*); b: Common starfish (*A. rubens*) and dragonets (*Callionymus* spp.); c: Edible crab (*Cancer pagurus*); d: Small-spotted catshark (*Scyliorhinus canicula*)).

reefs. The long-clawed porcelain crab (*Pisidia longicornis*) was too small to be observed from the continuous footage, but several high-quality video fragments showed that this species was massively abundant between the *S. spinulosa* tubes within the reefs. Drifting algae and bivalves on top of the seabed were excluded, as they were not attached or probably dead.

Acoustics

The acoustic survey consisted of two main lines perpendicular to the Brown Bank, extending 7 km west and 9 km east of the Brown Bank, and one east-west line of 6.22 km covering only the Brown Bank and the troughs on either side of the Brown Bank (Fig. 3a). In addition to the east-west lines, there are five sets of three crosslines that intersect with the east-west lines and have a length of 1.6 km each. The sets of crosslines are in the troughs on either side of the Brown Bank, on the Brown Bank crest, on the eastern slope of the eastern trough, and on the sand wave plateau to the east of the Brown Bank. The acoustic lines cover the two most southern locations with *S. spinulosa* present. No acoustic data of sufficient quality was recorded for the other two ROV locations.

The collected bathymetry data has a high-resolution (0.5 m) and confirms the presence of both large scale sandbank-structures and the smaller, perpendicular sand waves. Moreover, in addition to the described sand waves on the large-scale sandbank crests, our bathymetry data showed the presence of even smaller sand waves in the large-scale sandbank troughs. The multibeam data did not show any trawl marks, nor the presence of *S. spinulosa* reef structures.

The most western location with *S. spinulosa* reefs observed was characterized as an area of around 39-43 m depth with east-west oriented sand waves (Fig. 3b). These small-scale sand waves were generally around 13 m apart from each other and had a height difference of around 30 cm (Fig. 3d). The most eastern location with *S. spinulosa* reefs observed was a little deeper, around 43-45 m of water depth (Fig. 3c). The small-scale sand wave pattern was present here as well, but oriented

Table 1. Video observed organisms, with species abundance estimates for the three observed habitat types (*S. spinulosa* reefs (SR), Low abundances of *S. spinulosa* (LA), and adjacent areas with sandy sediments (Aa)). The location of the video is given in parentheses, referring to Figure 1. Species abundances are presented in SACFOR abundance classes with (S) 1-9 individuals per 0.1 m², (A) 1-9 individuals per 1 m², (C) 1-9 individuals per 10 m², (F) 1-9 individuals per 100 m², (O) 1-9 individuals per 1000 m², (R) <1 individuals per 1000 m². If no abundance estimate could be determined, but the species is observed in the transect, presence (P) of that species is registered.

Common name	Scientific name	Video 1 (1d)			Video 2 (not shown)			Video 3 (1c)			Video 4 (1e)			Video 5 (1d)		
		SR	LA	Aa	SR	LA	Aa	SR	LA	Aa	SR	LA	Aa	SR	LA	Aa
Small-spotted catshark	<i>Scyllorhinus canicula</i>	O	F	O	-	-	-	-	-	-	-	-	-	F	F	-
Dragonet	<i>Callionymus</i> spp.	F	C	O	-	-	C	F	F	F	C	C	F	F	F	-
Hooknose	<i>Agonus cataphractus</i>	-	-	-	-	-	-	O	O	-	O	-	-	-	-	-
Rock gunnel	<i>Pholis gunnellus</i>	-	-	-	-	-	-	-	-	-	F	-	-	-	-	-
Gobies	Gobiidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Greater pipefish	<i>Syngnathus acus</i>	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Snake pipefish	<i>Entelurus aequoreus</i>	-	-	-	-	-	-	-	-	-	O	-	-	-	-	-
-	<i>Trisopterus</i> sp.	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lesser weever	<i>Echiichthys vipera</i>	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-
Flatfishes*	Pleuronectiformes*	O	F	O	-	-	C	F	O	-	F	F	O	-	-	F
Solenette	<i>Buglossidium luteum</i>	P	-	-	-	-	P	-	-	-	-	P	P	-	-	-
Scaldfish	<i>Arnoglossus laterna</i>	-	-	-	-	-	-	P	P	-	-	P	-	-	-	-
Lemon sole	<i>Microstomus kitt</i>	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-
Dab	<i>Limanda limanda</i>	P	P	P	-	-	P	-	P	-	P	P	P	P	-	P
Dover sole	<i>Solea solea</i>	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-
Common starfish	<i>Asterias rubens</i>	C	A	C	-	-	C	C	C	F	A	A	C	A	C	C
Serpent star	<i>Ophiura</i> spp.	O	-	F	-	-	C	-	O	F	F	C	C	F	F	C
Hermit crab	<i>Pagurus bernhardus</i>	F	C	-	-	-	F	-	F	-	F	F	F	C	F	F
Swimming crab	<i>Liocarcinus</i> spp.	F	C	-	-	-	F	C	C	F	C	F	F	F	F	-
Edible crab	<i>Cancer pagurus</i>	F	F	-	-	-	-	O	-	-	F	O	O	-	-	-
Velvet crab	<i>Necora puber</i>	F	F	-	-	-	-	F	-	-	C	F	-	F	-	-
-	<i>Atelecyclus undecimdentatus</i>	-	-	-	-	-	-	-	P	-	F	-	-	-	-	-
Long-legged spider crab	<i>Macropodia</i> spp.	F	-	-	-	-	F	-	-	-	F	-	F	O	-	-
Long-clawed porcelain crab	<i>Pisidia longicornis</i>	P	P	-	-	-	-	P	P	-	P	P	-	P	P	-
Ghost shrimp	<i>Caprella</i> sp.	P	-	-	-	-	-	P	-	-	P	P	-	P	-	-
Shrimp	<i>Eualus</i> spp.	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-
Anemones	<i>Sagartia</i> spp.	P	P	-	-	-	-	P	P	-	P	P	-	P	P	-
Sea squirts	Ascidacea	P	-	-	-	-	-	-	-	-	P	-	-	P	-	-
Common flower-head	<i>Ectopleura larynx</i>	P	-	-	-	-	-	P	P	-	P	P	P	P	-	-
Sand mason worm	<i>Lanice conchilega</i>	-	-	P	-	-	P	-	P	P	-	P	P	P	P	P
Snailfur	<i>Hydractinia echinata</i>	P	P	P	-	-	P	-	P	-	P	P	P	P	P	P
Sea beard	<i>Nemertesia antennina</i>	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sickle hydroid	<i>Hydrallmania falcata</i>	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-

* Pleuronectiformes comprise all flatfish species. No abundance estimate is given for single species, as not all flatfish species could be identified to species level. Those that have been identified to species level are classified as present (P).

Figure 3. Acoustic data collected at the Brown Bank in the vicinity of the two most southern ROV locations. In (a), an overview of the data is presented, with the performed acoustic transects depicted with black lines, and white dots representing the mean centre of the ROV-track. The two sections of interest are highlighted in pink (a) and enlarged (b, c), showing the high-resolution bathymetry, including the video-based *S. spinulosa* reefs (pink dots). The depth profile along the two transects depicted with brown lines in (b) and (c) is given in (d) and (e) respectively, with the length of the transect (m) on the x-axis and the depth (m) on the y-axis. Habitat classification results of the acoustic data of (b) and (c) are respectively shown in (f) and (g). Both also include the *S. spinulosa* reef observations (pink dots) and the depth-profile transects (brown line).

in a slightly northeast-southwest direction. Moreover, the sand waves seemed smaller, both in wavelength (around 10 m) and in height difference (15-20 cm) (Fig. 3e). At both locations, the *S. spinulosa* reefs were dominantly located within the valleys between the sand waves (Fig. 3b-c).

The Bayes algorithm identified 4 distinct classes in backscatter, with class 1 showing lower reflectivity than class 4. Acoustic reflectivity is an indicator for sediment composition, with higher reflectivity being related to coarse sediments or sediments with high roughness. Acoustic signatures of biogenic reef structures can therefore show increased reflectivity⁴⁵. A more detailed examination of the acoustic classification of the two southern *S. spinulosa* locations showed that the areas overall are classified as acoustic class 2 (Fig. 3f-g). The crests or slopes of sand waves appeared almost solely the less reflective class 1, while the sand wave valleys were categorized as the higher reflective classes 3 and 4. This suggests that the sand wave valleys probably comprise *S. spinulosa* reefs and coarser sediments than the slopes and crests.

Sediment samples

A total of eight sediment samples were analysed (Fig. 1a). Sampled sediments were dominated by medium sand (250-500 μm ; Table 2). However, some differences between the crest (stations 1, 4, 5) and trough (stations 2, 3, 6, 7, 8) could be observed. Proportions of fine sand (125-250 μm) were in general higher at the crests [Trough: $25.7\% \pm 15.5\%$. Crest: $45.0\% \pm 3.4\%$. (Mean $\pm$ SD)]. The coarse particles (500-1000 μm) showed an opposite pattern, with higher fractions in the troughs [Trough: $12.7\% \pm 8.4\%$. Crest: $0.6\% \pm 0.1\%$]. The stations in the troughs congruently had a slightly higher median grain size [Trough: 319.27 ± 45.09 . Crest: 258.84 ± 6.52] and higher 90% quantile [Trough: 524.51 ± 104.58 . Crest: 374.18 ± 2.12]. The large variation in particle grain size between the trough stations was caused by station 6, which had a relative high fraction of very fine (62.5-125 μm) particles (Table 2). Organic and chemical content did not vary considerably between the stations (Table 2).

Table 2. Granulometric, organic and chemical composition of the sediment samples. The columns "all" represent the mean and SD for that location (Crest or Trough).

Parameters	Location Station	Crest				Trough				
		1	4	5	All	2	3	6	7	8 All
Median grain size (μm)		260.04	264.68	251.80	258.84 ± 6.52	344.89	319.88	242.80	357.89	319.27 ± 45.09
Median grain size (ϕ)		1.94	1.92	1.99	1.95 ± 0.04	1.54	1.64	2.04	1.48	1.66 ± 0.22
Modus grain size (μm)		259.83	264.58	251.76	258.72 ± 6.48	352.69	324.94	242.69	356.91	319.84 ± 45.92
0.1 quantile (μm)		181.76	185.82	170.15	179.24 ± 8.13	189.63	198.38	157.95	249.45	193.30 ± 35.12
0.9 quantile (μm)		372.52	376.57	373.45	374.18 ± 2.12	595.27	492.48	373.74	514.55	524.51 ± 104.58
Sediment fractions (%)										
Coarse (500-1000 μm)		0.54	0.56	0.71	0.60 ± 0.09	19.80	9.18	0.85	11.99	12.70 ± 8.43
Medium (250-500 μm)		54.91	57.43	50.20	54.18 ± 3.67	56.13	66.15	45.81	77.87	59.01 ± 13.12
Fine (125-250 μm)		44.45	41.92	48.62	45.00 ± 3.38	20.57	21.26	51.71	10.15	25.73 ± 15.53
Very fine (62.5-125 μm)		0.10	0.09	0.48	0.22 ± 0.22	0.13	0.00	1.63	0.00	0.47 ± 0.69
Silt (<63 μm)		0.00	0.00	0.00	0.00 ± 0.00	3.38	3.4	0.00	0.00	2.11 ± 1.93
Organic and chemical composition										
Organic carbon (%)		6.53	4.92	12.31	7.92 ± 3.89	8.00	8.35	8.09	3.86	7.24 ± 1.90
Total Nitrogen (%)		1.14	0.99	2.07	1.40 ± 0.59	1.40	1.32	1.45	0.95	1.25 ± 0.21
Ratio C:N		6.69	5.80	6.95	6.48 ± 0.60	6.65	7.37	6.52	4.76	6.70 ± 1.27

Fisheries

The Brown Bank area was intensively fished in the period 2008-2015 by Dutch demersal fisheries (Fig. 4a-b). Fisheries were concentrated in the large-scale sandbank troughs, with an average fishing intensity of more than 5 times per year. Fishing intensity on the large-scale sandbank crests was on average lower than 2 times per year. Fishing intensity differed at the four observed locations. At the most northern location of observed *S. spinulosa*, fishing intensity was highest (>10 times per year; Fig. 4a-b). The other locations were subject to lower fishing intensities; the location in the western trough had a fishing intensity of 1-2 times per year, while both locations in the eastern trough showed an intensity of 5-10 times per year. The majority of all fishing activity (93%) was comprised of beam-trawlers with a mesh size between 70-99 mm, with limited activity of flyshooters (5%), beam-trawlers with a different mesh size (1%), and otter-trawlers (1%; data not shown). The main fishing direction depended on the water depth, with equal percentages of west-, east- and southwards headed pings for water depths above 30 m (Fig. 4c). For the deeper waters in the large-scale sandbank troughs (40-50 m), however, north and south oriented pings were dominant.

Figure 4. Overview of fisheries data, showing the average fishing intensity (total yearly swept area (km²) per 1x1 km grid cell) in the Brown Bank area, without (a) and with (b) exact satellite locations of all Dutch demersal fisheries in the period 2008-2015. Sediment sample locations are indicated, as well as the ROV locations. A density plot of the vessels' heading for all fishing VMS-pings for the dominant fisheries (beam-trawl with 70-99mm mesh size) is given in (c), separated for the active fishing depth classes.

Discussion

Three extensive *S. spinulosa* reefs were discovered serendipitously at three separate locations within the large-scale sandbank troughs of the intensively fished Brown Bank area of the Dutch continental shelf. *S. spinulosa* reefs are restricted to areas with sufficient suspended sand grains, as the polychaetes require these for the building of their tubes. Hence, the reefs are located in turbid areas with a constant supply of sand grains⁴⁶. Apparently, the troughs of such large-scale sandbanks provide a suitable habitat for *S. spinulosa*, which is congruent with the observations of *S. spinulosa* reefs in the troughs of the North Norfolk Sandbanks in UK waters⁴⁷. The two southern locations

comprised aggregated structures that generally met the OSPAR recommendations for *S. spinulosa* reef classification (>30% cover and >5 cm elevation from the seabed), whereas the observed *S. spinulosa* in the northern location was predominantly classified as low abundance.

The discovery of these *S. spinulosa* reefs is remarkable as biogenic reefs are assumed to be vulnerable to physical disturbances^{21,22}, and the observed reefs are located in an intensively fished area. This raises questions about the impact of demersal fisheries on *S. spinulosa* reefs. Using Dutch VMS data, we showed that beam trawlers are very active in this area, with the total fishing intensity potentially even higher as foreign vessels are also allowed to fish in this area. However, considering our minimal estimation of the experienced fishing intensity experienced by the reefs, the question remains how they can persist under this pressure. The location with the most extensive *S. spinulosa* reefs had the lowest fishing intensity. The three other locations, including the one without *S. spinulosa* observed, were subject to higher fishing intensities. This suggests that the reefs are negatively affected by demersal fisheries, but that they nevertheless are able to persist in the presence of this pressure, even when the pressure is high (>10).

The only 'experimental' study of fisheries impacts on *S. spinulosa* reefs to date was performed by Vorberg, who measured the load-bearing capacity until fracture of preserved reef fragments and compared those with calculated forces exerted on the seabed by shrimp fishing gears⁴⁸. He concluded that shrimp fisheries are not likely to significantly damage *S. spinulosa* reefs⁴⁸. Beam-trawlers, the dominant fishing gear used in this area, however, are larger and much heavier than shrimp fishing gear^{49,50}. Moreover, Vorberg made his conclusions based on one passing of the fishing gear on a *Sabellaria alveolata* reef⁴⁸. These reefs have a honeycomb structure, whereas *S. spinulosa* reefs have a highly patchy and irregular structure¹⁹, making *S. spinulosa* reefs probably more vulnerable to fishing impacts. In addition, some locations within the large-scale sandbank troughs of the Brown Bank area are subjected to trawling intensities of more than 10 times per year. We therefore conclude that the *S. spinulosa* reefs are likely to be negatively impacted by demersal fishing activities in the Brown Bank area.

The persistence of the observed *S. spinulosa* reefs in this area with high fishing intensities might be explained by the exact location of the reefs in the landscape. In the Belgian Hinder banks area, it was observed that sand wave structures created refuge areas for branching organisms like sponges⁵¹. Due to the combination of the rigid structure and towing speed of the fishing gear and the sand wave dimensions, the fishing gears did not physically impact the sand wave valleys. Instead, the demersal fishing gears "jumped" from each sand wave top to the next top. This led to refuge areas with high biodiversity in the sand wave valleys⁵¹. Our video and acoustic bathymetry data showed that most of the *S. spinulosa* reefs were located in small-scale sand wave valleys, within the larger scale troughs. We hypothesize that a similar mechanism protects the valleys between the sand waves of the Brown Bank, enabling the formation and persistence of *S. spinulosa* reefs under fishing pressures that otherwise would destroy *S. spinulosa* reefs (Fig. 5).

The refuge hypothesis is supported by both acoustic classification and fisheries data. The acoustic data shows that sand wave valleys in general have a relatively higher acoustic reflection than the crests. The higher reflectivity is likely caused by biogenic reef presence, as these reefs are harder than the surrounding substrate and increase seabed roughness⁴⁵. It could also indicate that the sand wave valleys comprise relatively harder substrates than the sand wave crests, which may favour the settlement of *S. spinulosa*. The fisheries data suggests that the extent of the reefs may be negatively impacted by fishing activity, with the greatest reef extent being observed under the lowest fishing pressure. The dominant fishing gears deployed in the area are beam trawlers with a mesh size of 70-99 mm, targeting sole (*Solea solea*) and plaice (*Pleuronectes platessa*)⁵². Their gears consist of two nets towed alongside the vessel with a towing speed of around 6 knots⁵³. Each net is 12 m wide, held open by a solid construction (the beam or a so-called sumwing), fitted with tickler chains or electrodes stimulating fish to enter the nets^{50,54-56}. Based on the registered heading of all

VMS pings classified as ‘fishing’, we showed that the majority of the fishing activity in the large-scale sandbank troughs (>40 m water depth) is in a direction perpendicular to the small-scale sand waves (north to south), potentially ‘skipping’ the sand wave valleys (Fig. 5).

Figure 5. Sketch of seabed topography in relation to fishing activities, which enables the formation of refuge areas. The top view (a) shows a beam trawl net (blue). The small-scale sand waves (shown by a light top and dark valley) are perpendicular to the main fishing direction. The side view (b) shows a cross-section of the seabed with the sand waves and the potential refuge areas (black ovals).

Our data show that *S. spinulosa* is not restricted to the created refuge areas. For instance, the most western located reef showed *S. spinulosa* reef both in and outside sand wave valleys. This location also had the lowest fishing intensity, of 1-2 times per year. With higher fishing intensities, the reef was less extensive, and dominantly located within sand wave valleys. These observations suggest that the large-scale sandbank troughs of the Brown Bank area create favourable conditions for *S. spinulosa* reefs, but that the reefs are restricted to refuge areas under high fishing pressures. As *S. spinulosa* larvae prefer to settle on cement secretions of their own species⁵⁷, the persistence of *S. spinulosa* reefs in refuge areas may enable for a fast recovery of fragmented reefs if fishing pressure decreases.

We discovered the described *S. spinulosa* reefs in the Brown Bank area by chance, but it is very likely that more *S. spinulosa* reefs exist in the surrounding area. Accidental discoveries might be made during the obligatory monitoring prior to constructions of wind farms and pipelines and the extraction of marine aggregates⁵⁸. However, our data suggests that dedicated surveys should focus on sand bank trough areas with low fishing pressures and an average grain size of 350 μm . In particular, efforts should be focussed on the small-scale refuge areas located in sand waves valleys, which unfortunately cannot be predicted by fishing intensity maps alone. Areas prohibited for fisheries, like safety zones around oil platforms and offshore wind farms could also form a useful focus for future studies. With remote acoustic scanning methods like side scan sonar, the chosen areas can then easily be scanned for reef-like structures⁵⁸. Ground-truthing should be performed to verify *S. spinulosa* presence and reef extent²². This ground-truthing does not necessarily have to be done with expensive ROVs as used here; towed video and drop-down camera systems may give similar results¹⁶.

S. spinulosa reefs are known to locally increase biodiversity, providing shelter and substrate for other species within their 3D-structure^{22,58}. Our video footage supports this. Reef structures with a height up to 50 cm were observed, showing species sheltering in between reef fragments. Epifauna species abundance was notably higher within the reefs than in adjacent areas. Some observations within the reefs included species that are known for their association with hard substrates, for example the rock gunnel, the velvet crab, and the edible crab^{59–61}. We showed that the long-clawed porcelain crab is massively abundant between the tubes of the *S. spinulosa* reefs, which is a very important prey item for many associated fish species⁶². Moreover, the small-spotted catshark was observed to rest in between *S. spinulosa* reefs. These observations emphasize the importance of the *S. spinulosa* reefs for the ecosystem, and may also explain why fishermen are very active in the area.

Our discovery of significant *S. spinulosa* reefs on the Dutch Continental Shelf could have important implications. Biogenic reefs, including *S. spinulosa* reefs, are classified as natural habitat type “Reefs” (H1170) in Annex I of the Habitats Directive. Moreover, the OSPAR Convention has listed *S. spinulosa* reefs in the Greater North Sea on the OSPAR list of threatened and or declining species and habitats⁶³. As one of the Contracting Parties of the OSPAR Convention, the Netherlands is committed to protect listed species and habitats, including *S. spinulosa* reefs in accordance with Annex V of the OSPAR Convention. As such, the Netherlands have obliged themselves to collect more information about the extent and structure of these reefs, and to ensure sustainable management of human activities based on the ecological requirements of the reefs.

Acknowledgements

We would like to thank the Dutch Postcode Lottery for their generous funding of the OCEANA project ‘Protecting the North Sea 2017: Biodiversity Hotspots and recovering fish stocks’. We are grateful to the crew of both OCEANA and the Neptune for their help in the field. The Dutch ministry of Agriculture, Nature and Food Quality and Wageningen Marine Research are acknowledged for the provisioning of the Dutch VMS-data. We also thank Leendert Dorst and Daniëlle van Kuijk of the Hydrographic Service within the Royal Netherlands Navy for making the high-resolution bathymetry data of the Brown Bank area available to us. K.J. van der Reijden, L. Koop, S. O’Flynn, C. van Sluis, P.M.J. Herman, D. Simons, H. Olff, T. Ysebaert, M. Snellen and L.L. Govers received financial support from the Gieskes-Strijbis fund.

References

1. Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
2. Connell, J. H. Diversity in tropical rain forests and coral reefs. *Science*. **199**, 1302–1310 (1978).
3. Ryer, C. H., Stoner, A. W. & Titgen, R. H. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar. Ecol. Prog. Ser.* **268**, 231–243 (2004).
4. Rabaut, M., Vincx, M. & Degraer, S. Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. *Helgol. Mar. Res.* **63**, 37–46 (2009).
5. Lenihan, H. S. Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecol. Monogr.* **69**, 251–275 (1999).
6. van der Zee, E. M. *et al.* Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. *Ecosystems* **15**, 664–673 (2012).
7. Gratwicke, B. & Speight, M. R. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J. Fish Biol.* **66**, 650–667 (2005).
8. van der Zee, E. M. *et al.* How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proc. R. Soc. B.* **283**, 20152326 (2016).
9. Ferrario, F. *et al.* The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat. Commun.* **5**, 3794 (2014).
10. Donadi, S. *et al.* Cross-habitat interactions among bivalve species control community structure on intertidal flats. *Ecology* **94**, 489–498 (2013).
11. Airoldi, L. & Beck, M. W. Loss, Status and Trends for Coastal Marine Habitats of Europe. Oceanography and Marine Biology: An Annual Review vol. 45 (CRC Press-Taylor & Francis group, 2007).
12. Hoegh-Guldberg, O. *et al.* Coral reefs under rapid climate change and ocean acidification. *Science*. **318**, 1737–1742 (2008).
13. Hiddink, J. G. *et al.* Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci.* 1–6 (2017).
14. Bordehore, C., Ramos-Esplá, A. A. & Riosmena-Rodríguez, R. Comparative study of two maerl beds with different otter trawling history, southeast Iberian Peninsula. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **13**, S43–S54 (2003).
15. Lisco, S. *et al.* Sedimentological features of *Sabellaria spinulosa* bioconstructions. *Mar. Pet. Geol.* **87**, 203–212 (2017).
16. Hendrick, V. J. & Foster-Smith, R. L. *Sabellaria spinulosa* reef: a scoring system for evaluating ‘reefiness’ in the context of the Habitats Directive. *J. Mar. Biol. Assoc. UK* **86**, 665–677 (2006).
17. The National Biodiversity Network (NBN) Atlas.
18. The Marine Life Information Network (MarLIN).
19. Pearce, B. The ecology of *Sabellaria spinulosa* reefs. PhD Thesis. (University of Plymouth, 2014).
20. Gravina, M. F. *et al.* *Sabellaria spinulosa* (Polychaeta, Annelida) reefs in the Mediterranean Sea: Habitat mapping, dynamics and associated fauna for conservation management. *Estuar. Coast. Shelf Sci.* **200**, 248–257 (2018).
21. Gibb, N., Tillin, H., Pearce, B. & Tyler-Walters, H. Assessing the sensitivity of *Sabellaria spinulosa* reef biotopes to pressures associated with marine activities. *JNCC Report No. 504* (2014).
22. OSPAR Commission. Background document on *Sabellaria spinulosa* reefs.
23. Reise, K. Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: Are polychaetes about to take over? *Netherlands J. Sea Res.* **16**, 29–36 (1982).
24. OSPAR Commission. Quality Status Report 2010. (2010).
25. Witbaard, R., Lavaleye, M. S. S., Duineveld, G. C. A. & Bergman, M. J. N. Atlas of the megabenthos (incl. small fish) on the Dutch continental shelf of the North Sea. *NIOZ report 2013-4*. (2013).
26. Ocean Biogeographic Information System (OBIS).
27. Marine Information and Data Centre.
28. Reise, K. & Schubert, A. Macrobenthic turnover in the subtidal Wadden Sea: the Norderaue revisited after 60 years. *Helgoländer Meeresuntersuchungen* **41**, 69–82 (1987).
29. Collins, K. Dorset marine habitat surveys: Maerl, worm reefs, bream nests, sea fans and brittlestars. Dorset Wildlife Trust and English Nature report (2003).
30. Limpenny, D. S. *et al.* Best methods for identifying and evaluating *Sabellaria spinulosa* and cobble reef. *Natural England report, ALSF Ref No. MAL0008* (2010).
31. Knaapen, M. A. F. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo-Marine Lett.* **29**, 17–24 (2009).
32. van Dijk, T. A. G. P. *et al.* Benthic habitat variations over tidal ridges, North Sea, The Netherlands. In *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
33. Coggan, R., Mitchell, A., White, J. & Golding, N. Recommended operating guidelines (ROG) for underwater video and photographic imaging techniques. *MESH report* (2007).
34. Hitchin, R., Turner, J. A. & Verling, E. Epibiota remote monitoring from digital imagery: Operational guidelines. *JNCC report* (2015).
35. Snellen, M., Gaida, T., Koop, L., Alevizos, E. & Simons, D. G. Performance of multi-beam echo-sounder backscatter based classification for monitoring sediment distributions using multi-temporal large-scale ocean data sets. *J. Ocean. Eng.* **44**, 142–155 (2019).
36. Simons, D. G. & Snellen, M. A Bayesian approach to seafloor classification using multi-beam echo-sounder backscatter data. *Appl. Acoust.* **70**, 1258–1268 (2009).
37. Alevizos, E., Snellen, M., Simons, D. G., Siemes, K. & Greinert, J. Acoustic discrimination of relatively homogeneous fine sediments using Bayesian classification on MBES data. *Mar. Geol.* **370**, 31–42 (2015).
38. Eleftherakis, D., Amiri-Simkooei, A., Snellen, M. & Simons, D. G. Improving riverbed sediment classification using backscatter and depth residual features of multi-beam echo-sounder systems. *J. Acoust. Soc. Am.* **131**, 3710–3725 (2012).
39. Eleftherakis, D., Snellen, M., Amiri-Simkooei, A., Simons, D. G. & Siemes, K. Observations regarding coarse sediment

- classification based on multi-beam echo-sounder's backscatter strength and depth residuals in Dutch rivers. *J. Acoust. Soc. Am.* **135**, 3305–3315 (2014).
40. Burrough, P. A. & McDonnell, R. Principles of Geographical Information Systems. (Oxford University Press, 1998).
 41. Nieuwenhuize, J., Maas, Y. E. M. & Middelburg, J. J. Rapid analysis of organic carbon and nitrogen in particulate materials. *Mar. Chem.* **45**, 217–224 (1994).
 42. Hintzen, N. T. *et al.* VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fish. Res.* **115–116**, 31–43 (2012).
 43. van Denderen, P. D. *et al.* Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar. Ecol. Prog. Ser.* **541**, 31–43 (2015).
 44. Piet, G. J. & Hintzen, N. T. Indicators of fishing pressure and seafloor integrity. *ICES J. Mar. Sci.* **69**, 1850–1858 (2012).
 45. Manik, H. M. Acoustical measurement and biot model for coral reef detection and quantification. *Adv. Acoust. Vib.* (2016).
 46. Jones, L. A., Hiscock, K. & Connor, D. W. Marine habitat reviews. A summary of ecological requirements and sensitivity characteristics for the conservation and management of marine SACs. Joint Nature Conservation Committee, UK Marine SACs Project report (2000).
 47. Jenkins, C. *et al.* North Norfolk Sandbank and Saturn Reef cSAC/SCI management investigation report. JNCC/CEFAS Partnership Report Series, Report No. 7 (2015).
 48. Vorberg, R. Effects of shrimp fisheries on reefs of *Sabellaria spinulosa* (Polychaeta). *ICES J. Mar. Sci.* **57**, 1416–1420 (2000).
 49. Eigaard, O. R. *et al.* The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865 (2017).
 50. Eigaard, O. R. *et al.* Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J. Mar. Sci.* **73**, 27–43 (2015).
 51. Houziaux, J.-S., Kerckhof, F., Degrendele, K., Roche, M. & Norro, A. The Hinder Banks: yet an important area for the Belgian marine biodiversity? (2008).
 52. van der Reijden, K. J. *et al.* Discard self-sampling of Dutch bottom-trawl and seine fisheries in 2013. *CVO Report 14.007*. (2014).
 53. Rijnsdorp, A. D., Buys, A. M., Storbeck, F. & Visser, E. G. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES J. Mar. Sci.* **55**, 403–419 (1998).
 54. Poos, J. J. & Rijnsdorp, A. D. The dynamics of small-scale patchiness of plaice and sole as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the fleet dynamics. *J. Sea Res.* **58**, 100–112 (2007).
 55. Haasnoot, T., Kraan, M. & Bush, S. R. Fishing gear transitions: lessons from the Dutch flatfish pulse trawl. *ICES J. Mar. Sci.* **73**, 1235–1243 (2014).
 56. Soetaert, M., Decostere, A., Polet, H., Verschueren, B. & Chiers, K. Electrotrawling: A promising alternative fishing technique warranting further exploration. *Fish Fish.* **16**, 104–124 (2015).
 57. Wilson, D. P. The larvae of *Sabellaria spinulosa* and their settlement behaviour. *J. Mar. Biol. Assoc. UK* **50**, 33–52 (1970).
 58. Pearce, B., Fariñas-franco, J. M., Wilson, C., Pitts, J. & Somer, P. J. Repeated mapping of reefs constructed by *Sabellaria spinulosa* Leuckart 1849 at an offshore wind farm site. *Cont. Shelf Res.* **83**, 3–13 (2014).
 59. Shorty, J. T. & Gannon, D. P. Habitat Selection by the Rock Gunnel, *Pholis gunnellus* L. (Pholidae). *Northeast. Nat.* **20**, 155–170 (2013).
 60. Hayward, P. & Ryland, J. The marine fauna of the British Isles and North-West Europe. (Clarendon Press, 1990).
 61. Krone, R., Gutow, L., Brey, T., Dannheim, J. & Schröder, A. Mobile demersal megafauna at artificial structures in the German Bight - Likely effects of offshore wind farm development. *Estuar. Coast. Shelf Sci.* **125**, 1–9 (2013).
 62. Pearce, B. *et al.* *Sabellaria spinulosa* reef ecology and ecosystem services. Marine Research Report. (The Crown Estate, 2013).
 63. OSPAR Commission. Case reports for the OSPAR list of threatened and/or declining species and habitats. (2008).

Chapter 9

Conservation implications of Sabellaria spinulosa reef patches in a dynamic sandy-bottom environment

Karin J. van der Reijden

Leo Koop

Sebastiaan Mestdagh

Mirjam Snellen

Peter M.J. Herman

Han Olf

Laura L. Govers

Published as

van der Reijden KJ, Koop L, Mestdagh S, Snellen M, Herman PMJ, Olf H, Govers LL (2021): Conservation implications of Sabellaria spinulosa reef patches in a dynamic sandy-bottom environment. *Frontiers in Marine Science* 8, [642659]

Abstract

Biogenic reefs form biodiversity hotspots and are key components of marine ecosystems, making them priority habitats for nature conservation. However, the conservation status of biogenic reefs generally depends on their size and stability. Dynamic, patchy reefs may therefore be excluded from protection. Here, we studied epibenthos and epifauna density, richness, and community composition of patchy, dynamic *Sabellaria spinulosa* (ross worm) reefs in the North Sea. This study was conducted by comparing boxcore (endobenthos) and video transect (epifauna) data from two research campaigns in 2017 and 2019 to the Brown Bank area on the Dutch Continental Shelf, where *S. spinulosa* reefs were first discovered in 2017. The Brown Bank area is characterized by dynamic, migratory bedforms at multiple scales which potentially affect biogenic reef stability. We showed that *S. spinulosa* habitats had a patchy distribution and alternated with habitats comprised of plain sand. Average *S. spinulosa* habitat patch size was 5.57 ± 0.99 m and 3.94 ± 0.22 m in 2017 and 2019 respectively (mean $\pm$ SE), which especially in 2019 closely resembled the small-scale megaripple bedforms. Contrary to the endobenthos communities that were unaffected by *S. spinulosa*, epifauna density and species richness were at least two times higher in *S. spinulosa* habitats compared to sandy habitats, resulting in different community compositions between the two habitat types. We showed that *S. spinulosa* persisted in the area for almost 2 years. Although the stability of individual patches remained unclear, we demonstrated that even patchy biogenic reefs may promote density and local biodiversity of mobile, epibenthic species, very likely as a result of increased habitat heterogeneity provided by reef habitat patches. This indicates that patchy biogenic reefs that occur in dynamic environments may also have high ecological value and their conservation status should be (re)considered to ensure their protection.

Introduction

Biogenic reefs are physical benthic structures formed by ecosystem engineering species. Key examples are coral reefs^{1–3} and oyster beds^{4–6}. By their physical presence, biogenic reefs modify their surroundings to such an extent that resource availability for other species is positively altered⁷. They engineer a new habitat that can provide suitable settlement substrate⁸, increase refuge possibilities⁹ and food sources⁶ for associated species, and decrease turbidity due to attenuation of waves and currents^{4,10}. Such effects of biogenic reefs can stretch well beyond the actual physical extent of these organisms^{5,6}. As a result, biogenic reefs often form biodiversity hotspots and can be considered key components of marine ecosystems^{3,11,12}. Unfortunately, biogenic reefs are generally assumed to be vulnerable to (external) physical disturbances, due to their emergent structures^{13,14} and the time required for these reef structures to recover¹⁵. Biogenic reefs are therefore prioritized in nature conservation. Various legislative bodies exist to protect biogenic reefs, for instance by the designation of protected areas that locally restrict anthropogenic use and thus prevent any anthropogenic disturbance^{16–18}. However, there is no real consensus as to what characteristics are required for biogenic reefs in order to become protected. Within the European Habitats Directive¹⁹, for instance, these characteristics are limited to the general statement that reefs 1) arise from the seafloor and 2) support a zonation of benthic communities²⁰. As a result, the more stable reefs with persistent associated communities are generally favoured for conservation²¹.

The ross worm (*Sabellaria spinulosa*) is a biogenic reef builder in soft-sediment environments^{22,23}. This polychaete builds strong, cohesive tubes by cementing sand particles, which can form biogenic reefs when they aggregate in high densities^{21,24}. *S. spinulosa* has a widespread distribution, with observations in the northeast Atlantic, the greater North Sea including the Skagerrak, Kattegat and English Channel, the Mediterranean, and the Indian Ocean^{25,26}. Reef structures are dominantly formed in areas with a continuous supply of suspended sand particles and nutrients²⁴. In the North Sea, most reefs are located near the British coast^{22,26,27}. They are often encountered on rocky substrates²⁶, but are also observed on sandy bottoms^{28,29}. The worms excrete fecal matter that may increase local food availability²⁶, while the reefs increase habitat complexity and provide refugia and settlement substrate^{21,30,31}. The long-clawed porcelain crab (*Pisidia longicornis*), for instance, is well-known to hide between the individual tubes of *S. spinulosa* reefs^{22,26,30}. The reefs form biodiversity hotspots²⁵, with locally distinct endobenthos and epifauna communities²². As such, *S. spinulosa* reefs are included as priority habitats under both the Habitats Directive¹⁹ and the OSPAR convention²³. Hendrick and Foster-Smith (2006) introduced a scoring system to evaluate the 'reefiness' of *S. spinulosa* reefs under the Habitats Directive²¹. They propose to assess a reef on physical, biological and temporal characteristics, such as elevation, biodiversity, and stability, respectively, on a continuous scale from low to high. In addition, they state that some threshold values could be set in place for specific characteristics, like a minimal total extent. However, multiple characteristics are difficult to assess as they require detailed information over a longer time period, resulting in the need for multiple surveys with advanced sampling techniques. Whereas several advanced methods have been developed to study intertidal or shallow subtidal reefs at the required spatiotemporal scales^{32,33}, the application of these methods is less suitable in deep or turbid waters.

In 2017, *S. spinulosa* reefs were discovered for the first time on the Dutch Continental Shelf, in the Brown Bank area³⁰. This area is characterized by large-scale (5–10 km) tidal ridges, superimposed with dynamic, migrating bedforms at smaller scales: sand waves with wavelengths of ~200 m, and megaripples with wavelengths of ~10 m^{34–36}. In addition, the area is fished at least once a year by demersal fisheries^{30,37}. The multi-scale seafloor morphology potentially offers *S. spinulosa* small-scale safe sites to these fisheries, allowing them to persist and form reef patches in this area³⁰. At the same time, the highly dynamic environment is likely to limit reef stability and therewith promote patchy reef formation. As a result, the protection status of these reefs may also be limited.

In this study, we aimed to determine the ecological relevance of these patchy, dynamic *S. spinulosa* reefs and the implications for the conservation of such reefs. During two research campaigns in autumn 2017 and May 2019, we investigated *S. spinulosa* reef patches in the dynamic Brown Bank area on the Dutch Continental Shelf. By means of acoustic, videographic and boxcore data, we assessed their spatial extent and associated endobenthic and epifaunal assemblages. We subsequently discuss the implications of our observations for reef conservation policy.

Materials & Methods

Study area

This study focused on the Brown Bank area within the Dutch sector of the North Sea (52°36'09.461" N, 3°18'54.884" E; Fig. 1A). This region is characterized by stable north-south oriented tidal ridges, with amplitudes ranging from 7.5 m to 29 m for the Brown Bank tidal ridge^{35,36}. Sand waves are superimposed on these ridges, with average wave lengths of ~200 m, amplitudes of several meters and orientated in a northwest to southeast direction. Smaller scaled megaripples are found

Figure 1. The study area. (A) An overview of the Brown Bank area including bathymetry, sampling locations for the MWTL- survey (squares) and the locations of more intensively studied areas displayed in other panels. Inset shows the location of the study area within the North Sea. (B) An overview of data gathered in the research campaign of 2017, showing bathymetry data (background), boxcores (black circles) and video transect locations (pink lines) and the locations of panels C and D (dotted lines). (C-E) Close-up of the three survey areas in the 2019 campaign, showing bathymetry data, boxcore and video transect locations. Note the differences in bathymetry color scales used for panels A-B and C-E.

superimposed on the sand waves. These megaripples have wavelengths of ~10 m, amplitudes of ~0.5 m, and an east-west orientation³⁴. Both sand waves and megaripples are known to migrate. Sand waves migrate several meters a year^{38,39}, whereas the migration speed of megaripples is not entirely clear but assumed to be site-specific with speeds up to 1 m h⁻¹ reported for megaripples in the Dover Straits⁴⁰.

Research campaigns

For this study, two research campaigns were conducted on board of the *RV Pelagia*; one in October–November 2017 and one in May 2019. The 2017 campaign aimed to study the spatial effects of the large-scale tidal ridge on benthic communities. It covered a study area of 5x10 km with sampling positions determined by the structure of the tidal ridge (Fig. 1B). Only the stations located in the troughs have been included for this particular study, as the *S. spinulosa* reefs have been observed in the troughs exclusively⁴¹. The 2019 campaign was a dedicated survey aimed to study the ecological relevance of the *S. spinulosa* reefs discovered in 2017. For this, 3 smaller, separate survey areas were selected, in which the locations of videographic and boxcore samples were determined based on a preliminary analysis of freshly acquired acoustic data (Fig. 1C–E). In addition, the sampling design was furthermore focused to have minimal impact on the reefs, by minimizing the number of boxcores and using a drop camera that hovered above the seafloor. To summarize, acoustic, videographic and boxcore data were gathered during both campaigns, but with slightly different methods. These will therefore be described separately for both years.

Acoustics

Data collection

During both campaigns acoustic data were gathered with a hull-mounted Kongsberg EM 302 multibeam echosounder (MBES), which was operated at 30 kHz. In the 2019 campaign, acoustic data was also collected using the multi-spectral R2Sonic MBES, operating at 90, 200 and 400 kHz. This second MBES was mounted on a pole on the vessels' portside. Because the R2Sonic was newly-installed, a patch test was performed prior to survey operations, using a shipwreck as a ground object. This patch test validated that the MBES was correctly installed by acquiring validation data while sailing a standard set of survey lines designed for such a test⁴². Location data was provided by a Kongsberg Seapath 360 global positioning system and motion reference unit. The 2017 acoustic data was cleaned and processed as described in Koop *et al.*³⁴, while more details on cleaning and processing of the R2Sonic data can be found in Koop *et al.*⁴³.

Data processing

The acoustic surveys yielded nearly 60 km² of surveyed seabed (2017: 41.18 km²; 2019: 17.23 km²), with a resolution of ~1 x 1 m for 2017 and 0.75 x 0.75 m in 2019. Small-scale (10 m) Bathymetric Position Indices (BPIs) were then derived from the bathymetry, using the Benthic Terrain Modeler toolbox add-in for ArcGIS^{1 44,45}. These BPIs represent the local depth relative to the average depth of the surroundings and is therefore a suitable method to identify the positioning of morphological structures. We classified our BPI in 3 classes that represented the crests, slopes and troughs of megaripples, by applying visually verified cut-off values of -10 and 10 cm. This means that all pixels ≥10 cm below the average surrounding depth were classified as a trough and all pixels ≥10 cm above were defined as a crest. Pixels between these values are considered to be on a slope. To determine BPI-habitat patch sizes along the video transects, we computed straight line segments at the video locations. These line segments were determined by performing a linear regression on the camera coordinates, with a similar direction as applied in the video transect. Cross-sections of BPI-habitats along these straight video lines were then made, which enabled the calculation of the observed patch sizes.

Videographic data

Video transects were conducted on both campaigns. During the video transects, vessel speed was kept at $\sim 0.1 \text{ m s}^{-1}$ with respect to the seabed. The towed camera frames were attached to the starboard side winch, which was located centrally on the vessel. Both systems comprised of a full HD-camera, a set of scaled lasers, and underwater lights attached to a frame. Main differences between the video devices were caused by the differences in the positioning of the camera and the construction of towing cables (Fig. 2).

Figure 2. The different camera frames used in this study, showing the towed video frame (A) and the drop camera (B). Note the differences in towing construction and camera set-up. The towed video frame (A) has three (yellow) towing cables on the front of the frame, and a forward-facing camera. For the drop camera (B), the towing cable is attached to the top of the frame, and has a downward-facing camera. Photo credits to Danielle Prins-de Jonge (A) and Jip Vrooman (B).

2017 Campaign

A video sledge was used in the 2017 campaign. The frame was designed to float in the water, at a stable height above the seafloor. This was achieved as a result of two specific construction aspects^{46,47}. Firstly, three towing cables were attached to the front of the frame at the left and right side of the bottom, and in the middle on top (Fig. 2A). After 6.5 m, these were combined into one towing cable, which was connected to the winch. At the conjunction point, a drop weight (55 kg) was added to ensure the horizontal position of the three towing cables. A live-view enabled manual adjustments of the towing cable length if needed. Secondly, the camera frame itself had a slightly positive buoyancy which was neutralized by two drag chains attached to both sides of the frame. The ends of these drag chains touched the seafloor, and stabilized the frame at a specific height. The video sledge is described in more detail in Koop *et al.* and Mestdagh *et al.*^{34,41} During the $\sim 200 \text{ m}$ long video transects, the video sledge hovered around $0.5 - 1 \text{ m}$ above the seafloor, with the camera set to view an area of $\sim 0.25 \text{ m}^2$ just in front of the frame. At both the eastern and western trough, two replicate video transects were performed at three different latitudes (Fig. 1B. Top: $52^{\circ}37'22.897'' \text{ N}$, middle: $52^{\circ}36'11.210'' \text{ N}$, bottom: $52^{\circ}34'55.329'' \text{ N}$). In addition to these 6 stations, three extra stations were picked based on observations within the acoustic data, at which a total of 4 video transects were conducted.

2019 Campaign

In the 2019 campaign, a hopper camera was used to perform the video transects. A Kevlar cable was centrally attached on top of the frame, which resulted in a vertical drop of the camera from the winch (Fig. 2B). Height above the seabed was manually controlled based on a live-view, and was estimated to be around 1.5 - 2 m. The downward facing camera recorded an area of $\sim 1 \text{ m}^2$. More details on the camera specifics can be found in Damveld *et al.*⁴⁸. A total of 19 video transects was conducted. The location of each transect was chosen based on a preliminary analysis of acoustic data.

Data processing

All footage with unclear visibility of the seabed was classified as invalid. Analysis of all valid footage comprised the recording of observed organisms and prevailing habitats. Specimens were identified to the lowest taxonomic level possible. Habitats were defined by their sediment features, resulting in three different habitats: (1) Sand, (2) Rubble, and (3) Sabellaria (Fig. 3). Sand habitats classified all seafloors that were comprised of plain sand without any deviating features apart from some small shell fragments. Rubble and Sabellaria habitats were comprised of seafloor habitats that both contained a sandy seafloor, with coarser material like small stones and/or many shell fragments (Rubble) or Sabellaria reef fragments (Sabellaria). As a consequence, Sabellaria habitats do not necessarily have a 100% coverage of *S. spinulosa* reefs. For both research campaigns, an example screenshot of each habitat is shown in figure 3.

Figure 3. Habitat types observed in video transects. (A) Sand habitat in 2017. (B) Rubble habitat in 2017. (C) Sabellaria habitat in 2017, with several *S. spinulosa* reef fragments, two starfish (*Asteras rubens*) and a dragonet (*Callionymidae*). (D) Sand habitat in 2019, showing a hermit crab (*Pagurus bernhardus*). (E) Rubble habitat in 2019. (F) Sabellaria habitat in 2019, showing several *S. spinulosa* reef fragments, and three starfish (*A. rubens*). Green dots are lasers, set to a distance of 35 cm and 30 cm for 2017 (A-C) and 2019 (D-F) respectively.

The camera location was derived from the vessels' GPS logging system, which registered the vessels' location every 30 seconds. These locations were linearly interpolated to obtain a GPS position for every second. The interpolated vessel positions were then time-matched to camera locations. Depending on the prevailing depth, currents and waves, the distance between the camera and the vessel varied, causing for a positioning error of the camera. Because both cameras were deployed approximately in the middle of the vessel, not far from the GPS receivers, and with as little towing cable as possible, we expect this positioning error to be >10 m and <100 m. Moreover, we assume this error to be larger in 2017 compared to 2019 (but still within the given range), due to the horizontal component of the towed camera sledge used in 2017 that the drop camera does not have.

We determined the surveyed area by matching all camera positions to a grid. The grid resolution was 0.5×0.5 m in 2017, and 1×1 m in 2019, corresponding to the average area observed by the camera. We then summed the number of unique grid cells per habitat type per transect, and calculated the total observed area per habitat type. Habitat patch size was determined as the physical distance between the camera location at the first and last recording of each habitat patch. Large interruptions (>10 s) of the video transects, due to invalidity of footage, were included as patch boundaries.

Boxcores

Data collection

Endobenthos samples were collected with a boxcorer (30 cm diameter) during both cruises. During the 2017 campaign, triplicate samples were taken at 7 sampling stations. In 2019, 31 single boxcores were taken at each station. All samples were sieved over a 0.5 mm sieve in 2017 and a 1 mm sieve in 2019, after which the organisms were stored in 4–6% formaldehyde. Subsequently, organisms were counted and identified to the lowest taxonomic level possible in the laboratory.

We additionally used boxcore data collected by the Directorate General for Public Works and Water Management of the Dutch Ministry of Infrastructure and Water Management for their MWTL-program ('Monitoring Waterstaatkundige Toestand des Lands'). This monitoring program samples endobenthos over the entire Dutch Continental Shelf with a similar methodology as applied in the 2019 research campaign. For this study, we selected the stations within 15 km of the Brown Bank Area, sampled in the summer of 2018. This yielded 11 stations (Fig. 1A). Endobenthos densities ($N\ m^{-2}$) and species richness ($N\ m^{-2}$) were determined and compared to the data gathered at the 2019 research campaign.

Data processing

Boxcore stations for the 2017 and 2019 research campaigns were spatially linked to video observations. For this, boxcore areas were created by extending the station location with a radius of 50 m. All valid video footage within these boxcore areas were then assigned to that specific boxcore station. Stations without any assigned video observations were removed from the dataset. Remaining boxcores were classified as "*Sabellaria*" or "*no-Sabellaria*", depending on whether any *Sabellaria* habitat was assigned to that station.

Species nomenclature was checked against the World Register of Marine Species (WoRMS) to ensure validity and similarity of taxonomic names⁴⁹. Then, a taxonomic levelling exercise was performed to increase similarity of species' taxonomic levels. With this levelling, we specifically wanted to 1) exclude single observations at higher taxonomic levels while the majority of similar specimens was identified to lower taxonomic levels, and to 2) account for the higher taxonomic precision of only a small subset of related observations. An example of the first event is the recording of two amphipods at order level, while all other amphipods were identified to species or genus level. The levelling removed the two registrations at the order level. The second event comprised, for example, the merging of *Ensis ensis* recordings with the recordings of *Ensis sp.* as the majority of the observations were made on a genus level. For this levelling exercise, we determined the

number of observations for all species, genera, families and orders observed. We then calculated the percentage of observations at each lower taxonomic level with respect to the total number of observations at the corresponding higher taxonomic levels. Within this taxonomic ranking, lower taxonomic levels were merged with a higher taxonomic level if that higher level contributed to more than 50 % of the observations. Higher taxonomic records were removed if they contributed to less than 15 % of the total observations within the associated ranking. After this species leveling, species richness ($N\ m^{-2}$) was determined for all stations, in which the triplicates of 2017 were merged and divided by the total sampled area.

Data analysis

All data processing and analysis was performed in R, version 3.6.2.⁵⁰

Epifauna

The video analysis yielded registrations of organism observations and their associated habitat type. For each transect separately, we determined both the habitat-specific epifauna densities ($N\ m^{-2}$) and the overall density ($N\ m^{-2}$). Epifauna densities represent the observed species densities, determined by the total number of observations for each species within a certain habitat, divided by the total observed surface of that habitat. Overall density represents the total number of organisms per square meter of observed habitat. This resulted in two datasets that represent the epifauna and overall density for each combination of habitat type and transect. A non-Metric Multi-Dimensional Scaling (nMDS) was applied in order to visually determine differences in community composition between habitats separately for both research campaigns. Bray-Curtis dissimilarities were determined based on the epifauna densities and were used as input for this nMDS.

Differences in overall density between habitats were tested for with linear mixed models (LMM) from the lme4-package⁵¹, taking the transects as separate sampling locations. These models included 'habitat type' as fixed effects, and one of either random factors 'station' (2017) or 'survey area' (2019) to limit spatial autocorrelation. Pairwise comparisons between habitat types were determined using an a post-hoc Tukey test from the emmeans-package⁵². Model assumptions of homogeneity of variance and normality were visually checked by plotting the model residuals.

We also determined differences in species richness between habitats. However, the three habitat types differed in their total observed area, and their ratios were also unequally distributed over the transects. We had to correct for this in our calculations of species richness. Hence, we determined the number of species and the observed area (m^2) for each individual habitat patch encountered in the video transects. We then modelled species-area curves using the *specaccum*-function in the vegan package⁵³. These curves represent the total number of species observed over an increasing sampling effort. The presented species-area curves are based on 1000 permutations comprising random resampling of the different patches, in which each patch was weighted for their sampled surface.

Endobenthos

Both research campaigns were analyzed separately, because the different methods used impacted the results. Community composition was compared between the MWTl survey and the 2019 campaign, for which similar sampling methods were used. For this, Bray-Curtis dissimilarities were determined on fourth root transformed endobenthos densities at the stations sampled in both the MWTl-survey and the 2019 campaign⁵⁴. A nMDS was subsequently applied in order to assess distinctions between the MWTl-stations and the *Sabellaria* and *no-Sabellaria* stations of the 2019 campaign. A similar analysis was performed for the 2017 campaign. A pairwise PERMANOVA, based on Bray-Curtis dissimilarities, was used to test for significant differences in community composition between stations. Both the nMDS and the PERMANOVA used the vegan-package⁵³.

In addition, total species richness was compared between habitat types. Differences in richness

were tested with an ANOVA and a subsequent post-hoc Tukey test. Model assumptions were visually checked.

Results

Habitat patchiness

The 35 video transects covered a total area of 6295.75 m² (2017: 1050.75 m²; 2019: 5245 m²), with three types of habitat: Sand (4674.25 m²), Rubble (767 m²), and Sabellaria (854.50 m²). For 2017, 73% was comprised of Sand habitat, with the remaining area being ascribed to 9 % Sabellaria (95.50 m²) and 18 % Rubble (190 m²) habitat. In 2019, a similar percentage of Sand habitat was observed (75 %), but slightly more Sabellaria habitat was observed, with 14 % (759 m²) and 11 % (577 m²) for Sabellaria and Rubble habitat respectively.

Video transects revealed a patchy distribution of the different habitats, with alternating patterns. In 2017, Sand habitats often alternated with Rubble habitats (Fig. 4A). The limited Sabellaria habitat observed in 2017 (24 patches) showed a similar alternating pattern with Sand habitat, but consisted generally of larger patches than the Rubble habitat (Fig. 4B). Habitat patches were 5.57 ± 0.99 m (mean $\pm$ SE) for Sabellaria, 4.13 ± 0.35 m for Rubble, and 9.13 ± 0.81 m for Sand habitat. In 2019, a similar alternating habitat pattern was observed (Fig. 4D-E). Patch sizes of the Sabellaria and Rubble habitats, however, were smaller than in 2017 (Sabellaria: 3.94 ± 0.22 m, Rubble: 3.58 ± 0.29 m, Sand: 11.12 ± 1.10 m).

The seabed was shown to have multiple morphological structures, at various scales (Fig. 1). The seafloor structure, created by the small-scale megaripples, closely resembled the observed alternating habitat pattern (Fig. 4A-B, D-E). The troughs of these megaripples had a mean size of 3.69 ± 0.33 m and 2.98 ± 0.12 m in 2017 and 2019 respectively. The histograms in figures 4C and F show a strong similarity in Sabellaria patch sizes and megaripple trough sizes. For 2017, this pattern showed less similarities, probably as a result of the low number of Sabellaria habitat patches encountered, their slightly larger sizes (2017: 5.57 ± 0.99 m; 2019: 3.94 ± 0.22 m), and the lower resolution of the bathymetry data (Fig. 4C). A similar size comparison could also be made for Sabellaria patches and megaripple crests, as the latter had a comparable mean size (2017: 3.76 ± 0.21 m; 2019: 2.75 ± 0.10 m). However, at multiple occasions during the video analysis, we observed that the seafloor dropped directly before a Sabellaria habitat patch started, indicating *S. spinulosa* reef presence in the troughs rather than on crests.

Endobenthos

A total of 105 and 121 species were observed in the 2017 and 2019 research campaigns respectively, which amounted to the observation of 176 species in total. In contrast, only 50 species were observed in the MWTL-survey, of which 10 were exclusively observed in this dataset. Most abundant species in all three datasets were ribbon worms (Nemertea), sand-dwelling amphipods (*Bathyporeia elegans*, *Bathyporeia guilamsoniana*, and *Nototropis swammerdamei*), the white catworm (*Nephtys cirrosa*), and a bristleworm (*Ophelia borealis*) (Table S1). The endobenthos community composition did not differ significantly between boxcores classified as *Sabellaria* and *no-Sabellaria* for 2019 (Fig. 5A). In 2017, the limited number of samples prohibits any firm conclusion on community composition differences (Fig. 5B). However, there was a difference in community composition at the landscape-scale (Fig. 5A). Community compositions of the small survey areas of the 2019 campaign were shown to deviate from the community composition found in the MWTL survey, representing the wider surrounding area of the Brown Bank (PERMANOVA, $p=0.041$). The subsequent pairwise PERMANOVA demonstrated a significant difference between the MWTL survey and the boxcores in the south eastern trough (pair-wise PERMANOVA, $p=0.024$).

Figure 4. Habitat patch distributions and their link to seafloor morphology for 2017 (A-C) and 2019 (D-F). (A) Detailed maps showing the bathymetry and BPI-subhabitats surrounding the video-observed habitat patches (*Sabellaria* in blue, Sand in green, and Rubble in Orange) for two representative video transects gathered in 2017 in the western trough. Black lines represent the line segments used to determine BPI-subhabitat sizes. Similar maps of bathymetry and BPI-subhabitat overlaid with video-observed habitats are shown for (B) 2017, eastern trough, (D) 2019, western trough, and (E) 2019, eastern trough. Histograms show the absolute frequency of the sizes for the video-observed *Sabellaria* habitat patches and BPI-subhabitats 'trough' for 2017 (C) and 2019 (F).

In addition, some interesting observations could be made with regard to species richness of the samples (Fig. 5C). For 2017, a significant higher species richness was observed in *Sabellaria*, compared to *no-Sabellaria* (*Sabellaria*: 50 ± 3.5 ; *no-Sabellaria*: 30 ± 3.7 ; ANOVA: $p=0.038$). Such a significant difference was not observed for the 2019 campaign (*Sabellaria*: 20.9 ± 1.9 ; *no-Sabellaria*: 25.5 ± 2.4 ; Tukey emmeans: $p=0.305$). A significant twofold of species richness compared to the MWTL survey was observed for *no-Sabellaria* in 2019 (Tukey emmeans: $p=0.004$), while a trend toward higher species richness was observed for *Sabellaria* (Tukey emmeans: $p=0.065$). Species richness in 2017 should not be compared to species richness of 2019 and MWTL samples, as different methods were used (smaller sieve and larger sampled surface).

Epifauna

A total of 4947 epibenthic organisms were observed, comprising 21 species. Dominant species was the common star fish (*Asterias rubens*). The hermit crab (*Pagurus bernhardus*) and several demersal fish species were also frequently observed (Table S2). Different community compositions were observed between Sand and Sabellaria habitat types (Fig. 6A-B). Moreover, overall density was at least twice as high within the Sabellaria habitat compared to the Sand habitat (Fig. 6C. LMM 2017

Figure 5. Comparison of endobenthos data between both research campaigns and the MWTL survey. (A) NMDS of endobenthos data gathered in the joint MWTL survey and the 2019 campaign, and for (B) the 2017 campaign. Samples with video-based observed Sabellaria habitat within a 50 m distance are blue; samples without Sabellaria habitat are green. Circles show the western trough, triangles the eastern trough south, and diamonds the eastern trough north. (C) Species richness (m^{-2}) is shown per habitat for the MWTL survey and 2019 campaign combined, and separately for the 2017 campaign. n represents the number of boxcores included. Significant differences are represented by different letters. Note that the 2017 campaign data are analyzed separately from the MWTL survey and 2019 campaign data.

& 2019: $p < 0.0001$). In 2019, *Sabellaria* and Rubble habitats had a similar community composition (Fig. 6A) and overall density (Fig. 6C). An opposite pattern was observed in 2017. Then, *Sabellaria* and Rubble habitats differed in community composition (Fig. 6B). Rubble habitat strongly resembled Sand habitat, with lower overall densities than in the *Sabellaria* habitat (Fig. 6C). The species-area curves of both campaigns show that species richness of the *Sabellaria* habitat was higher than the Sand and Rubble habitats (Fig. 6D).

Figure 6. Differences in community composition between the different habitat types *Sabellaria* (blue), Sand (green), and Rubble (orange). (A) NMDS of epifauna data gathered in the 2019 campaign and (B) in the 2017 campaign. Each habitat type observed within a transect is displayed separately, with the different symbols representing the video transects. (C) Overall density (# m⁻²) and species richness (m⁻²) per habitat type for 2019 and (D) for 2017. n represents the number of different transects with this habitat type. Significant differences are represented by different letters.

Discussion

We here studied the effects of *S. spinulosa* habitat patches on associated endo- and epibenthic communities in the dynamic Brown Bank area in the North Sea. We showed that within this area, *S. spinulosa* reef habitats have a highly patchy distribution that may be linked to seafloor megaripple morphology. These migratory bedforms are commonly abundant in dynamic sand-bottom environments^{34,36}. The patchy Sabellaria habitats had similar endobenthic community compositions compared to surrounding habitats and showed slightly higher species richness in 2017, but not in 2019. In contrast, species richness and overall density of mobile epifauna was higher near *S. spinulosa* reefs, suggesting that especially the mobile, epifauna community is positively affected by the presence of *S. spinulosa* reef patches. Our study demonstrates that patchy biogenic reefs have a relevant positive impact on benthic biodiversity even in morphologically dynamic sandy-bottom environments.

Compared with the surrounding Sand habitat, *S. spinulosa* patches showed 2 and 12 times higher epifauna densities for 2019 and 2017 respectively. Moreover, species richness of mobile, epifaunal organisms was higher. Similar patterns have been observed in *S. spinulosa* reefs elsewhere, showing higher local species densities than in surrounding habitats^{22,26,31}. We did not observe clear effects of the *S. spinulosa* patches on endobenthic organisms, contrary to observations described in literature. They show that biogenic reefs can locally exclude soft-sediment endobenthic species due to their physical structure, and promote higher endobenthic densities in their direct surroundings as a consequence of altered hydrodynamics or fecal output^{5,6,55}. Potentially, the investigated *S. spinulosa* patches were too small to produce such effects. It may however also demonstrate the methodological challenge to adequately sample a patchy reef feature. Contrary to our intentions, no boxcore samples were taken within *S. spinulosa* reef patches themselves, but in their surroundings. This underlines that –when small-scale habitat heterogeneity is expected– more precise sampling methods should be deployed, such as scuba-diving or ROV-directed sampling^{8,55,56}. The results also demonstrated that it is necessary to apply multiple sampling methods that target different ecological components and different spatial scales. Only the combination of these techniques provides a comprehensive overview of, in this case, the ecological relevance of *S. spinulosa* reefs⁵⁷. In addition, our multi-scale design of acoustics, video transects, and boxcores enabled the integration of prevailing habitat heterogeneity in the interpretation of local observations.

The importance of this small-scale habitat heterogeneity was further investigated at a landscape-scale. Slightly different endobenthos communities were observed between boxcore samples taken in the wider surroundings and boxcores gathered in the 2019 campaign. These differences could have resulted from the large-scale morphological seabed structure alone^{35,41}. However, it is very likely that the *S. spinulosa* reef patches contributed to this difference in endobenthos communities. The reef patches produce a high level of small-scale habitat heterogeneity, which has proven important for overall biodiversity^{58,59}. We demonstrated that *S. spinulosa* patch size is very likely related to small-scale heterogeneity created by dynamic, morphological bedforms, as the mean patch size of Sabellaria habitat matches the average size of megaripple troughs^{30,34,39}. Similarly, in Dorset (SW England), a *S. spinulosa* reef appeared to be constrained by mobile sand waves, which periodically overwhelmed the reef⁶⁰. Most likely, sand wave migration has limited effect on our *S. spinulosa* reefs, as sand waves were almost absent in the tidal sand bank troughs^{34,38}. Megaripple migration, however, could considerably affect *S. spinulosa* reef patchiness and stability. Migration patterns are thought to be site-specific³⁹ and affected by morphological bedforms at larger scales⁶¹. Intertidal megaripples with similar amplitude and wavelength as encountered in the Brown Bank area were shown to migrate around 1 m week⁻¹⁶². Together with the high burial tolerance of *S. spinulosa*⁶³, this migration speed might pose a tolerable stress for the reefs. However, it does not explain the observed patchy distribution of Sabellaria habitats. Another possibility is that megaripple migration opposingly is altered by reef presence since biogenic reefs are known for their sediment stabilization effects^{64,65}. Modelling studies show that artificial tubes mimicking the sand

mason worm (*Lanice conchilega*) affect near-bed flow velocities, which result in sediment trapping⁶⁶ and affect sand wave morphology^{67,68}. A preliminary model run showed that the presence of tube-worm patches can decrease sand wave migration speed⁶⁹. Hence, *S. spinulosa* reef patches might be able to reduce megaripple dynamics to levels they can cope with, enabling them to persist. To test these hypotheses, detailed studies on the mechanistic link between *S. spinulosa* reefs and megaripples should be conducted. Such a study would also provide insights in the stability of the studied *S. spinulosa* reef patches.

Our observations, however, pose an interesting case with respect to marine habitat conservation. Despite the patchiness and dynamics of the observed *S. spinulosa* reefs, their persistence in the area has been demonstrated over a time period of almost two years. The preference of *S. spinulosa* larvae to settle on conspecifics^{22,70}, especially in combination with the hypothesized small-scale refugia created by the megaripples³⁰, can potentially explain this persistence. The reef patches increased both local diversity and density of mobile epifauna. We therefore argue that the observed *S. spinulosa* reef patches definitely have conservation value. Many other biogenic reefs are characterized by patchy distributions or small-scale variation of sub-habitats as well. Aggregations of the sand mason worm (*Lanice conchilega*) for example, form patchy mounts that are elevated from the seabed^{64,71}. Similarly, horse mussels (*Modiolus modiolus*) can form distinct beds that are typified by ridges of mussels with muddy patches in between⁵⁵. The positive impact on biodiversity and ecosystem functioning has been demonstrated for both examples of patchy biogenic reefs^{8,59,71,72}. Together with our observations, we therefore argue that conservation status of patchy, dynamic reefs should be reconsidered to ensure their protection.

The assessment of biogenic reef habitats, for instance under the European Habitats Directive, should hence include dynamic and patchy reefs that currently have low conservation status. Often, it is stated that communities in dynamic environments are less vulnerable to anthropogenic disturbances, like demersal fisheries, than those in stable environments^{14,73,74}. However, migrating bedforms and high hydrodynamics pose a different stress on the reef fragments than the physical disturbance of demersal fishing gears. For *S. spinulosa*, multiple studies indicate that demersal fisheries pose a threat to the reefs, which could result in reef damage, fragmentation and ultimately disappearance^{22,27,30}. In addition, a sliding scale is introduced when anthropogenic activities cause reef fragmentation, which in turn results in patchy reef habitats with little conservation status⁷². Assessments of reef conservation value should therefore focusing dominantly on the contribution of reef structures to ecosystem functioning in addition to the physical dimensions of these structures^{21,75}. Moreover, the physical dimensions assessed should be considered at the right scale and with respect to the entire landscape. For a patchy reef like the one described here, dimensions of individual reef fragments or habitat patches contain little information. It is the extent of the area in which the reef habitat patches are found that is of importance for the ecosystem, including the non-reef habitats⁷⁵. The subsequent conservation of such patchy, dynamic reef habitats should allow a continuity of natural dynamic processes, without anthropogenic disturbances at the seafloor, at scales relevant to the dynamics of both reef patches and morphological bedforms.

Acknowledgments

We would like to thank the crew of RV *Pelagia* for their assistance during the fieldwork campaigns, and Rob Witbaard and Jip Vrooman for their role as cruise leaders. Joël Cuperus of the Directorate General for Public Works and Water Management of the Dutch Ministry of Infrastructure and Water Management was so kind to share the MWTL- survey dataset. We further thank Loran Kleine Schaars and his colleagues from the NIOZ benthos laboratory for the processing of endobenthos samples of the 2019 campaign, and Matthew Parsons and Maria Bacelar Martinez for processing the endobenthos samples from the 2017 campaign. We also would like to thank two anonymous reviewers that substantially improved the manuscript with their comments.

Supplementary materials

Supplementary materials can be found online at <https://doi.org/10.3389/fmars.2021.642659>.

Table S1. Endobenthos density (m^{-2}) per habitat classification type for the research campaigns in 2017 and 2019 and for the MWTL-survey.

Table S2. Epifauna density (m^{-2}) per habitat for 2017 and 2019 separately.

References

- Ferrario, F. *et al.* The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat. Commun.* **5**, 3794 (2014).
- Plaisance, L., Caley, M. J., Brainard, R. E. & Knowlton, N. The diversity of coral reefs: What are we missing? *PLoS One* **6**, (2011).
- Roberts, C. M. *et al.* Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* (80-.). **295**, 1280–1284 (2002).
- Lenihan, H. S. Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecol. Monogr.* **69**, 251–275 (1999).
- Donadi, S. *et al.* Cross-habitat interactions among bivalve species control community structure on intertidal flats. *Ecology* **94**, 489–498 (2013).
- van der Zee, E. M. *et al.* Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. *Ecosystems* **15**, 664–673 (2012).
- Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
- Coolen, J. W. P. *et al.* Reefs, sand and reef-like sand: A comparison of the benthic biodiversity of habitats in the Dutch Borkum Reef Grounds. *J. Sea Res.* **103**, 84–92 (2015).
- Ryer, C. H., Stoner, A. W. & Titgen, R. H. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar. Ecol. Prog. Ser.* **268**, 231–243 (2004).
- van der Heide, T., van Nes, E. H., van Katwijk, M. M., Olff, H. & Smolders, A. J. P. Positive feedbacks in seagrass ecosystems - Evidence from large-scale empirical data. *PLoS One* **6**, e16504 (2011).
- van der Zee, E. M. *et al.* How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proc. R. Soc. B.* **283**, 20152326 (2016).
- Christianen, M. J. A. *et al.* Biodiversity and food web indicators of community recovery in intertidal shellfish reefs. *Biol. Conserv.* **213**, (2016).
- Sciberras, M. *et al.* Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish.* **19**, 698–715 (2018).
- Collie, J. S., Hall, S. J., Kaiser, M. J. & Poiner, I. A. N. R. A quantitative analysis of fishing impacts on shelf-sea benthos. *J. Anim. Ecol.* **69**, 785–798 (2000).
- Hiddink, J. G. *et al.* Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J. Appl. Ecol.* **56**, 1075–1084 (2019).
- Fariñas-Franco, J. M., Allcock, A. L. & Roberts, D. Protection alone may not promote natural recovery of biogenic habitats of high biodiversity damaged by mobile fishing gears. *Mar. Environ. Res.* **135**, 18–28 (2018).
- Costello, M. J. & Ballantine, B. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends Ecol. Evol.* **30**, 507–509 (2015).
- Boonzaier, L. & Pauly, D. Marine protection targets: An updated assessment of global progress. *Oryx* **50**, 27–35 (2016).
- European Commission. Council Directive 92/43/ECC on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union* **94**, 40–52 (1992).
- European Commission. Interpretation Manual of European Union Habitats. EU28. (2013).
- Hendrick, V. J. & Foster-Smith, R. L. *Sabellaria spinulosa* reef: a scoring system for evaluating 'reefiness' in the context of the Habitats Directive. *J. Mar. Biol. Assoc. UK* **86**, 665–677 (2006).
- Fariñas-Franco, J. M. *et al.* Marine Strategy Framework Directive Indicators for Biogenic Reefs formed by *Modiolus modiolus*, *Mytilus edulis* and *Sabellaria spinulosa*. Part 1: Defining and validating the indicators. *JNCC Report* **523**, (2014).
- OSPAR Commission. Background document on *Sabellaria spinulosa* reefs. (2013).
- Lisco, S. *et al.* Sedimentological features of *Sabellaria spinulosa* bioconstructions. *Mar. Pet. Geol.* **87**, 203–212 (2017).
- Gravina, M. F. *et al.* *Sabellaria spinulosa* (Polychaeta, Annelida) reefs in the Mediterranean Sea: Habitat mapping, dynamics and associated fauna for conservation management. *Estuar. Coast. Shelf Sci.* **200**, 248–257 (2018).
- Pearce, B. The Ecology of *Sabellaria spinulosa* Reefs. (University of Plymouth, 2014).
- Gibb, N., Tillin, H., Pearce, B. & Tyler-Walters, H. Assessing the sensitivity of *Sabellaria spinulosa* reef biotopes to pressures associated with marine activities. *JNCC Report No.* 504 (2014).
- Pearce, B., Fariñas-franco, J. M., Wilson, C., Pitts, J. & Somer, P. J. Repeated mapping of reefs constructed by *Sabellaria spinulosa* Leuckart 1849 at an offshore wind farm site. *Cont. Shelf Res.* **83**, 3–13 (2014).
- Jenkins, C., Eggleton, J., Barry, J. & O'Connor, J. Advances in assessing *Sabellaria spinulosa* reefs for ongoing monitoring. *Ecol. Evol.* **8**, 7673–7687 (2018).
- van der Reijden, K. J. *et al.* Discovery of *Sabellaria spinulosa* reefs in an intensively fished area of the Dutch Continental Shelf, North Sea. *J. Sea Res.* **144**, 85–94 (2019).
- Pearce, B. *et al.* *Sabellaria spinulosa* reef ecology and ecosystem services. (The Crown Estate, 2013). doi:10.13140/2.1.4856.0644
- Collin, A., Dubois, S., James, D. & Houet, T. Improving intertidal reef mapping using UAV surface, red edge, and near-infrared data. *Drones* **3**, 67 (2019).
- Ventura, D. *et al.* Integration of close-range underwater photogrammetry with inspection and mesh processing software: a novel approach for quantifying ecological dynamics of temperate biogenic reefs. *Remote Sens. Ecol. Conserv.* **rse2.178** (2020). doi:10.1002/rse2.178
- Koop, L. *et al.* Seafloor classification in a sand wave environment on the Dutch continental shelf using multibeam echosounder backscatter data. *Geosci.* **9**, 1–24 (2019).
- van Dijk, T. A. G. P. *et al.* Benthic habitat variations over tidal ridges, North Sea, The Netherlands. in *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
- Knaapen, M. A. F. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo-Marine Lett.* **29**, 17–24 (2009).
- van der Reijden, K. J., Hintzen, N. T., Govers, L. L., Rijnsdorp, A. D. & Olff, H. North Sea demersal fisheries prefer specific benthic habitats. *PLoS One* **13**, 1–21 (2018).

38. Knaapen, M. A. F. Sandwave migration predictor based on shape information. *J. Geophys. Res. Earth Surf.* **110**, 1–9 (2005).
39. Knaapen, M. A., van Bergen Henegouw, C. N. & Hu, Y. Y. Quantifying bedform migration using multi-beam sonar. *Geo-Marine Lett.* **25**, 306–314 (2005).
40. Idier, D., Ehrhold, A. & Garlan, T. Morphodynamique d'une dune sous-marine du détroit du pas de Calais. *Comptes Rendus Geosci.* **334**, 1079–1085 (2002).
41. Mestdag, S. *et al.* Linking the morphology and ecology of subtidal soft-bottom marine benthic habitats: A novel multi-scale approach. *Estuar. Coast. Shelf Sci.* **238**, 106687 (2020).
42. R2Sonic LLC, X. *Operational Manual V6.3.* (2017).
43. Koop, L. *et al.* Measuring centimeter scale sand ripples using multibeam echosounder backscatter data on the Brown Bank of the Dutch Continental Shelf. *Geosciences* **10**, (2020).
44. Walbridge, S., Slocum, N., Pobuda, M. & Wright, D. J. Unified geomorphological analysis workflows with Benthic Terrain Modeler. *Geosciences* **8**, (2018).
45. ESRI. ArcGIS. (2018).
46. Sheehan, E. V., Stevens, T. F. & Attrill, M. J. A quantitative, non-destructive methodology for habitat characterisation and benthic monitoring at offshore renewable energy developments. *PLoS One* **5**, e14461 (2010).
47. Barker, B. A. J. *et al.* A vessel-towed camera platform for surveying seafloor habitats of the Continental Shelf. *Cont. Shelf Res.* **19**, 1161–1170 (1999).
48. Damveld, J. H. *et al.* Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophys. Res. Lett.* **45**, (2018).
49. Holstein, J. Worms: Retriving Aphia Information from World Register of Marine Species. R package version 0.2.2. (2018).
50. R Development Core Team, X. R: A language and environment for statistical computing. (2014).
51. Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
52. Lenth, R. Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.2-1. (2020).
53. Oksanen, J. *et al.* Vegan: Community ecology package. R package version 2.5-6. (2019).
54. Reiss, H. *et al.* Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* **67**, 278–293 (2010).
55. Rees, E. I. S., Sanderson, W. G., Mackie, A. S. Y. & Holt, R. H. F. Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea: III. Crevice, sediment infauna and epifauna from targeted cores. *J. Mar. Biol. Assoc. UK* **88**, 151–156 (2008).
56. Parry, D. M., Kendall, M. A., Pilgrim, D. A. & Jones, M. B. Identification of patch structure within marine benthic landscapes using a remotely operated vehicle. *J. Exp. Mar. Bio. Ecol.* **285–286**, 497–511 (2003).
57. Tiano, J. C. *et al.* Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front. *Mar. Environ. Res.* **159**, 104964 (2020).
58. Hewitt, J. E., Thrush, S. F., Halliday, J. & Duffy, C. The importance of small-scale habitat structure for maintaining beta diversity. *Ecology* **86**, 1619–1626 (2005).
59. Sanderson, W. G. *et al.* Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. II. Epifauna recorded by divers and cameras. *J. Mar. Biol. Assoc. United Kingdom* **88**, 143–149 (2008).
60. Collins, K. *Dorset marine habitat surveys: Maerl, worm reefs, bream nests, sea fans and brittlestars.* (2003).
61. Leenders, S. *et al.* Numerical modelling of the migration direction of tidal sand waves over sand banks. *Coast. Eng.* **163**, 103790 (2021).
62. van der Wal, D., Ysebaert, T. & Herman, P. M. J. Response of intertidal benthic macrofauna to migrating megaripples and hydrodynamics. *Mar. Ecol. Prog. Ser.* **585**, 17–30 (2017).
63. Hendrick, V. J., Hutchison, Z. L. & Last, K. S. Sediment burial intolerance of marine macroinvertebrates. *PLoS One* **11**, (2016).
64. Rabaut, M., Vincx, M. & Degraer, S. Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. *Helgol. Mar. Res.* **63**, 37–46 (2009).
65. Paul, M., Bouma, T. J. & Amos, C. L. Wave attenuation by submerged vegetation: Combining the effect of organism traits and tidal current. *Mar. Ecol. Prog. Ser.* **444**, 31–41 (2012).
66. Borsje, B. W., Bouma, T. J., Rabaut, M., Herman, P. M. J. & Hulscher, S. J. M. H. Formation and erosion of biogeomorphological structures: A model study on the tube-building polychaete *Lanice conchilega*. *Limnol. Oceanogr.* **59**, 1297–1309 (2014).
67. Damveld, J. H., Borsje, B. W., Roos, P. C. & Hulscher, S. J. M. H. Biogeomorphology in the marine landscape: Modelling the feedbacks between patches of the polychaete worm *Lanice conchilega* and tidal sand waves. *Earth Surf. Process. Landforms* **45**, 2572–2587 (2020).
68. Damveld, J. H., Roos, P. C., Borsje, B. W. & Hulscher, S. J. M. H. Modelling the two-way coupling of tidal sand waves and benthic organisms: a linear stability approach. *Environ. Fluid Mech.* **19**, 1073–1103 (2019).
69. Damveld, J. H. The feedbacks among tidal sand waves, benthic organisms and sediment sorting processes. (University of Twente, 2020). doi:10.3990/1.9789036550000
70. Wilson, D. P. The larvae of *Sabellaria spinulosa* and their settlement behaviour. *J. Mar. Biol. Assoc. UK* **50**, 33–52 (1970).
71. van Hoey, G., Guilini, K., Rabaut, M., Vincx, M. & Degraer, S. Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems. *Mar. Biol.* **154**, 1009–1019 (2008).
72. Cook, R. *et al.* The Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A Dilemma for Evidence-Based Conservation. *PLoS One* **8**, e69904 (2013).
73. van Denderen, P. D. *et al.* Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar. Ecol. Prog. Ser.* **541**, 31–43 (2015).
74. Hiddink, J. G. *et al.* Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can. J. Fish. Aquat. Sci.* **63**, 721–736 (2006).
75. Sheehan, E. V. *et al.* Drawing lines at the sand: Evidence for functional vs. visual reef boundaries in temperate Marine Protected Areas. *Mar. Pollut. Bull.* **76**, 194–202 (2013).

Chapter 10

Synthesis

The aim of this thesis was to improve our spatial understanding of the interaction between habitat disturbance regimes and benthic communities in the North Sea. Humans are increasingly impacting coastal seas¹. At the same time, the call to make our activities sustainable is also slowly growing^{2,3}. As a consequence, ecosystem-based management approaches are more frequently applied, which require a thorough understanding of ecosystem structure and functioning. This includes an accurate overview of the spatial distribution of both anthropogenic activities and benthic habitats and communities, including their functioning and vulnerability. Therefore, I studied the spatial distribution of benthic communities in relation to environmental variables and demersal fisheries as an anthropogenic disturbance. In addition, I investigated the effect of environmental conditions on the distribution of anthropogenic activities, as well as bioengineering effects of communities on the local environmental conditions and demersal fishing activity. My research covered a variety of spatial scales (Fig. 1), ranging from the North Sea wide mapping of fishing activity (**Chapter 2**) and benthic habitats (**Chapter 4**), to local, small scale studies on fishing impact (**Chapter 3**), seafloor bedforms (**Chapters 5-9**), and biogenic *Sabellaria spinulosa* reefs (**Chapters 7-9**). In this synthesis chapter, I will first elaborate on the coherence of all findings from previous chapters, by the introduction of a “realized dynamics regime” concept. Secondly, I discuss several methodological challenges that I experienced during this thesis work, with a special focus on underwater video techniques. I finish with conservation implications and my personal view on marine management.

Realized disturbance regime

Benthic communities are affected in much the same way by both natural and anthropogenic disturbances⁴. Communities subjected to chronic demersal fishing pressure have been shown to shift towards more resistant ones, consisting of small, highly mobile species^{5,6} or larger-bodied species that live deeply burrowed in the seafloor (**Chapter 3**). The same type of species dominate under high natural disturbance regimes⁷. Benthic communities are thus structured by the combination of prevailing natural and anthropogenic disturbances, which I here defined as the realized disturbance regime. In the Dutch North Sea, the current realized disturbance regime is dominantly determined by strong tidal currents, waves, and demersal fisheries⁸⁻¹⁰. The southern part is characterized by high natural disturbances and demersal fishing activity, whereas the northern part has relatively little natural disturbances and is subjected to varying intensities of demersal fishing (**Chapters 2 & 4**). Hence, realized disturbance regimes are high in the southern part, and vary with fishing intensities in the northern part.

We hypothesized that these realized disturbance regimes largely determine the spatial distributions of benthic communities^{11,12}. Northern communities are species rich and generally have higher species densities and biomass than southern communities, and comprise more sessile species¹³⁻¹⁵. In addition, experimental bottom trawling corroborated that species responded differently to this type of disturbance^{16,17} (**Chapter 3**). In an area with relatively little natural disturbances (Fig. 1B), a beam trawl passage resulted in large, short-term decreases of epifauna species and superficial (juvenile) endobenthos, while larger, deep-burrowing endobenthos could survive⁷. Hence, chronic demersal fishing in areas with low natural disturbance regimes can result in the disappearance of more sensitive communities, comprised of larger-bodied sessile epifauna species.

During this PhD-project, I showed that that dynamic seafloor bedforms significantly affected benthic community distributions and could locally alter the realized disturbance regime. The high natural disturbance regime in the southern North Sea determined the formation of various bedforms at multiple scales that are often found superimposed on each other in multi-scale patterns (Table 1). Tidal ridges and sand waves affected benthic communities, with different communities inhabiting the troughs compared to the crests^{18,19} (**Chapters 5 & 6**). The smaller megaripples were shown to affect sediment sorting (**Chapter 7**), and were correlated to the presence of ross worm (*Sabellaria spinulosa*) biogenic reef patches (**Chapters 7-9**). These patches themselves attracted mobile epifauna, which locally resulted in higher species densities and richness²⁰⁻²².

The seafloor bedforms were also shown to affect the realized disturbance regime. In the southern North Sea, demersal fisheries concentrated their fishing activity in the troughs of the large-scale tidal ridges²⁹ (**Chapter 2**). Fishermen are unlikely to steer on the scale of sand waves here, and are certainly not able to do so on the scale of megaripples. Combined with their physical characteristics, these middle to small-scale seafloor bedforms may hence create local safe-sites from demersal fisheries and thus locally alter the realized disturbance regime³⁰ (**Chapter 8**).

Figure 1. Location overview of the studies presented in this thesis, showing the spatial scale and prevailing bathymetric characteristics. (A) The North Sea wide research in Chapters 2 and 4 are focused on the area depicted by the pink line. Borders of national waters are represented by grey hatched lines. (B) The three small plots in the Frisian Front area to study bottom trawling impact (Chapter 3). (C) The sand wave field near the coast of Texel investigated in chapter 5. (D) The characteristic tidal ridge, sand waves, (E) and megaripples of the Brown Bank area, studied in chapters 6-9.

Figure 2. Schematic overview of this PhD-project, and the positioning of the chapters in relation to this framework.

To summarize, in this thesis I unravel how benthic communities are structured by the realized disturbance regime, which is the combination of the natural and anthropogenic disturbance regimes, with respect to any moderating effects of local seafloor bedforms (Fig. 2).

Structuring effects of dynamic seafloor bedforms

In the southern North Sea, various dynamic, offshore bedforms are formed by the strong tidal currents and waves^{23,31–33} (**Chapters 4, 6, 7**). Although their characteristics allow them all to be classified as ‘underwater dunes’³⁴, we defined the offshore bedforms observed within this thesis as tidal ridges, sand waves, megaripples and sand ripples. Migration speed of these bedforms increases with smaller wavelength (Table 1). Whereas large-scale tidal ridges hardly migrate, the very small-scale sand ripples were shown to change shape and direction every tidal cycle²⁸. But in addition to the dimensions, migration speed within each bedform is also highly dependent on the local conditions. As such, a wide variety of different megaripple migration speeds have been observed. Megaripples in the Dover Straits (10–20 m wavelength, 2 m amplitude) were shown to migrate with maximum speeds of 1 m per hour²⁷. In the Western Scheldt, much lower speeds between 0.05 – 0.14 m per day were observed for intertidal megaripples (10–16 m wavelength, 0.16–0.24 m amplitude)²⁶. And even lower migration speeds of 40 m per year (0.003 m day^{–1}) were measured for megaripples in the North Sea (11 m wavelength, 0.09 m amplitude)²⁵. It is therefore likely that the migration speed of megaripples in the Brown Bank area is somewhere in between the presented range. Despite their migration, the multi-scale seafloor bedforms create a structured landscape in the otherwise flat, sandy area.

Table 1. Offshore seafloor bedforms in the southern North Sea with their characteristics.

	Amplitude (m)	Wavelength (m)	Migration speed	References
Tidal ridge	10-20	5000-10.000	1 m year ⁻¹	19,23,24
Sand wave	2-4	200	2-6 m year ⁻¹	19,25 Chapter 6
Megaripple	0.5-2	10-20	1 m h ⁻¹ to 40 m year ⁻¹	25–27 Chapters 6, 8
Sand ripple	0.01	0.10-0.20	Every tidal cycle (6h)	28 Chapter 6

This habitat heterogeneity also structures the prevailing benthic communities. In general, organisms seemed to concentrate within the troughs of tidal ridges, sand waves and megaripples, potentially because the troughs have reduced hydrodynamics, which can provide for shelter and increased food availability^{18,19} (**Chapters 6-8**). These benthic communities, on the other hand, may also affect the dynamics of the bedforms. However, disentangling the mechanistic effects within the interaction between benthic communities and bedforms has proven difficult. Multiple modeling studies tried to include biological components in sand wave models^{35–38}. Benthic sediment-stabilizing diatoms affected suspended sediment concentrations for instance³⁷. Emergent structures created by biogenic reef building organisms such as the sand mason worm (*Lanice conchilega*), on the other hand, altered the near-bed water velocity, especially under high densities^{38,39}. As a result, mounts can be created³⁹ which affect both epifauna distributions^{40,41} and sand wave formation^{35,38}. The models further predicted that, congruent to field observations, the sand mason worm would dominantly settle in sand wave troughs³⁵. The interaction between megaripples and benthic communities has been much less studied, as their small scale requires data at higher resolutions than commonly available.

In our studies, we observed *S. spinulosa* reef patches dominantly within megaripple troughs (**Chapters 7-9**). Multiple hypotheses can be drafted to explain this observation, as many aspects of both *S. spinulosa* reef patches and megaripple dynamics are unknown. As shown in modeling studies for sand waves³⁵, hydrodynamics are likely to be locally reduced in megaripple troughs. These mitigated hydrodynamics could stimulate the settlement and subsequent survival of (*Sabellaria*) larvae that would otherwise wash away, which would result in higher abundances of these organisms in the megaripple troughs. However, hydrodynamic changes due to megaripple presence are likely to be smaller than hydrodynamic effects of sand waves due to their smaller sizes (Table 1). This does not explain the persistence of the *S. spinulosa* reefs within an area of migrating megaripples. Potentially, the reefs can survive temporal burial by migrating megaripples when burial periods are short⁴². It is also possible that *S. spinulosa* reefs could be formed everywhere in the area, but are limited by migrating megaripples similar to a process observed in Dorset (south England). Here, the *S. spinulosa* reef was restricted by migrating sand waves, which periodically smothered the reef⁴³. As megaripples have generally higher migration speeds, such limitation by megaripples is less likely. However, sediment stabilization effects of reef patches that alter, preclude or delay megaripple migration, analogue to effects of sand mason worm on sand waves^{35,44}, could affect such fragmentation processes. Our knowledge is inconclusive in this matter at present and will require follow up studies. Apart from any migration-effects, megaripples could create natural, small-scale safe-sites against bottom trawling (**Chapter 8**). The observed reef patches are then the remnants of larger reefs subjected to bottom trawling, also explaining the presence of larger patches. However, despite local high fishing intensities of >10 times a year (**Chapters 2, 8**), the observed small-scale reef patchiness is unlikely to solely result from demersal fishing activity as trawling-induced damages can often be observed on the reef^{45,46}. A combination of aforementioned hypotheses can therefore most likely best explain the interaction between megaripples and *S. spinulosa* reefs.

Dynamic bedforms, and sand waves and megaripples in particular, are very common in sandy coastal areas down to depths of ~40 m and subjected to strong tidal currents⁴⁷. They occur worldwide, from the North Sea^{23,31,33} to the Taiwan Strait⁴⁸ between China and Taiwan, and from the Bisanseto Sea⁴⁹ near Japan to the entrance of the Bahia Blanca estuary⁵⁰ in Argentina. Coastal waters are also subjected to the highest demersal fishing intensities^{1,51,52}. As such, the hypothesis that dynamic seafloor bedforms can create small-scale refugia against demersal fisheries would have major implications for fishing impact assessments worldwide. These refugia may allow less-resilient organisms to persist in areas subjected to frequent anthropogenic disturbances. Conversely, human engineering activities that level these bedforms might result in the disappearance of such small-scale refugia. Several studies have already emphasized that fishing impact assessments should be performed on a high spatial^{53,54} and temporal⁵⁵ scale, taking into account habitat-specific vulnerability^{12,56,57}. The existence of the small-scale refugia and their potential mitigation of fishing impacts underline once again the need for detailed impact assessments.

Seafloor sampling methods

Such detailed impact assessments depend on accurate and comprehensive knowledge of the seafloor communities, which requires high-resolution sampling of the seafloor. However, precise sampling of the seafloor is much more difficult than for terrestrial bottoms, due to the obvious seawater coverage. Expensive vessels and remotely operated sampling devices are needed, which limit the number of samples collected. Over time, a wide variety of sampling methods has been developed, ranging from the remote gathering of large-scale information of the seafloor with acoustics, to the physical collection of small-scale seafloor samples such as grabs, cores and trawls (Box 2). The DISCLOSE project, in which this PhD was a partner, aimed to improve the integration of multiple sampling methods to investigate benthic habitats and communities. Herein, three measuring techniques with various scales were combined: large-scale acoustic remote sensing, middle-scale video techniques, and small-scale bottom samples (see Box 1 on page 22).

I conclude that the integration of multiple sampling methods contributes to a more thorough understanding of the benthic communities^{28,58} (**Chapters 3, 4, 6, 7, 9**). In general, a trade-off between scale and detail is observed in sampling. Large-scale methods such as acoustic remote sensing gather high-resolution information about the prevailing water depth and the main sediment type. However, it lacks any information about the benthic community. Small-scale sampling, such as box cores, on the other hand, provides detailed information about the benthic community and sediment composition, but the relationship of the sample to the wider environment is unknown. Therefore, DISCLOSE aimed to integrate multiple techniques that collect data at different spatial scales, which would allow the extrapolation of detailed community data to larger spatial scales. When few physical samples in combination with acoustic methods could provide a comprehensive picture of the benthic communities and their functioning, this could ultimately also reduce the costs for structural benthic monitoring.

Sampling resolution and scale of interest

Due to the high costs of obtaining seafloor samples, the total number of samples collected is restricted. As a consequence, the spatial resolution of these samples is very low. For instance; in the Netherlands, marine endobenthos is structurally monitored within the governmental monitoring program 'Monitoring Waterstaatkundige Toestand des Lands (MWTL)'. This program comprises 103 stations that are sampled once every three years⁵⁹. It covers the entire Dutch Continental Shelf, an area roughly 58.000 km². This means that each station, sampled with a box core (~0.071 m²), represents an area of ~563 km². That is similar to sampling 60 locations on the entire Dutch mainland. The low resolution observed in the MWTL-survey is widespread in marine sampling. The international bottom trawl survey (IBTS) for stock assessments of various groundfish, for example, covers the North Sea annually with two hauls (~1.2 km²) per ICES statistical rectangle, which have a

Figure 3. Sketch of the positional error for a box corer (white) and a towed video frame (blue) in relation to seafloor megaripples (brown background) and biogenic reef patches (orange). In addition, two camera transects are displayed, represented in dark-green.

surface between 2991 km² and 3884 km² depending on the exact location⁶⁰.

As a consequence of this low sampling resolution, only large-scale patterns and variations in benthic communities can be observed^{13,14}. We have demonstrated that benthic communities are locally affected by seafloor bedforms at various scales (**Chapters 5-7**) (Fig. 1). Even the largest scaled bedforms, sandbanks with wavelengths of 5-10 km (Fig. 1D), are insufficiently sampled in the standard monitoring programs, so that differences in benthic community compositions between sandbank-associated habitats (crests, slopes, troughs) cannot be observed. Hence, the even smaller scaled changes in sediment sorting and habitat heterogeneity due to megaripples or biogenic reef structures (**Chapters 7-9**) can definitely not be taken into account within the large monitoring programs.

Sampling precision and habitat heterogeneity

In fact, we experienced that most sampling techniques that we used were not accurate enough to capture the small-scale patterns created by megaripples, because the error in the determination of their position exceeded the scale of interest (Fig. 3). Heavy devices, like a box corer, go almost straight down from the winch to the seafloor. Depending on depth, currents, and waves, they may slightly deviate, which results in a positional error restricted to a small area underneath the winch. The positional error of a towed video system is much larger, especially for one with a horizontal component in the towing cable.

Besides positional errors related to small scale patterns, we experienced also difficulty in the analysis of samples acquired within areas with small-scale habitat heterogeneity. In fig. 3, biogenic reefs are patchily distributed within the troughs of megaripples (**Chapters 7-9**). The two video transects depicted have an identical observed area, but differ in their amounts of observed biogenic reef.

The collection of box cores would result in similar differences, in which the box core can either 'hit' or 'miss' a biogenic reef patch. Such differences are levelled out when enough samples are obtained within the area. However, the low resolutions of monitoring programs do not allow for such levelling, which could result in the wrong interpretation of samples. Another alternative to avoid such sampling bias is to stratify the sampling with respect to the small-scale habitats, for instance by deploying divers or remotely operated vehicles (ROVs)^{41,61,62}

Spatial extrapolation

The aforementioned challenges with respect to sampling resolution and precision, scale of interest, and habitat heterogeneity underline the difficulty in the interpretation of samples. To enable such an extrapolation of samples, information about the wider landscape should be available. Within the DISCLOSE project, an integrative approach was applied, which linked small-scale observations to large-scale bathymetry and videographic data. For this, the new towed video system 'BRUCE' was developed (Fig. 4; Box 3).

This integrative approach yielded promising results, congruent to other studies applying multiple techniques with different scales^{63–66}. A comprehensive picture was obtained for the effects of bottom trawling on benthic communities by the combination of multiple methods that each dealt with a different aspect of bottom trawling impact (**Chapter 3**). Boxcores and video footage corroborated each other in the reduction of endobenthos and epifauna organisms respectively, while side scan sonar and sediment profile images showed physical changes of the seabed after a bottom trawling event. In **Chapter 6**, we showed that the direct linkage of videographic and box core-based observations with acoustically derived habitat classes provided for large-scale, acoustic indicators of local community types. In addition, video observations of patchily distributed biogenic reefs demonstrated that mobile epifauna and demersal fish were unequally distributed over the small-scale habitat patches, a pattern that was not found in endobenthos sampling with box cores (**Chapter 9**).

Advantages of integrating multi-scale information could also improve standard monitoring programs, such as the MWTl or IBTS. The current low resolution of these monitoring programs will probably not be resolved quickly, as financial support is not planned to increase soon. However, small adjustments are likely to improve the monitoring programs. Based on the experiences gained during this thesis work, I recommend to:

- Increase harmonization of the various national surveys with regard to sampling technique and species identification, to ensure a similar coverage over the entire North Sea and to enable fair comparisons between all regions.
- Equip sampling devices with acoustic positioning devices, which minimize the position error of the sampling device.
- Equip sampling devices with underwater cameras, to enable the determination of the sampled (sub)habitat. These cameras preferably provide a somewhat wider overview of the prevailing habitat heterogeneity.
- Evaluate and redesign sampling locations with respect to current (acoustic) information about small-scale habitat heterogeneity, to ensure that areas with high habitat heterogeneity are sampled with higher resolutions.
- Gather acoustic data (high-resolution bathymetry and backscatter) every time a research/governmental vessel is at sea and make these data freely available to science.

Sustainable fisheries management

In various chapters of this thesis, implications of the findings for sustainable marine management are discussed. My main overall conclusion is that spatial management of anthropogenic activities should include detailed (high-resolution) knowledge of prevailing benthic habitats and distributions, whether that is the case for general management of demersal fisheries (**Chapter 2**), or specific conservation of patchy biogenic reefs (**Chapter 10**).

Fishing impact assessment

Demersal fisheries, the dominant source of anthropogenic disturbance, have already been subject to many impact assessment studies and proposals of sustainable management strategies, in which habitat is accounted for in various ways^{12,56,67–73}. Whereas this thesis demonstrates that benthic communities and fisheries are structured by multiple environmental variables and at various spatial scales, these studies all defined habitats by combinations of sediment type and water depth (e.g. deep and muddy; shallow rocks). While most studies are about accurate impact assessments, two studies propose new types of fisheries management to manage the fishing impact at the habitat level. They propose credit systems as a method to encourage fishermen to adopt sustainable fishing practices^{72,73}. Although such systems have not been implemented (yet), they provide an interesting point of view on sustainability of fishing impact and potential management solutions. The simplest credit system is based on the establishment of habitat credits, of which each fisherman receives a certain amount. These credits must then be used to ‘buy access’ to the habitats fished, where sensitive habitats will cost more credit than resilient habitats⁷². Under such systems, no areas are pertinently closed to fisheries, but the high costs of fishing within such areas will strongly reduce the profitability of these areas. As a result, fishing activity will concentrate at specific, resilient, fishing grounds, with reduced fishing activity in the more sensitive habitats. There is general consensus that such aggregation will benefit the overall ecosystem^{72,74–76}. Contrary to this consensus, however, we showed that fishing hotspots often coincide with unique environmental conditions and that specific habitat types were subjected to much higher fishing intensities than other habitats (**Chapter 2**). In addition, we demonstrated that benthic communities had deviating distributions than physiotopes based on environmental variables solely (**Chapter 4**). A thorough assessment of habitat resilience and overall habitat impact should hence form the basis of such a credit system, in which habitats are defined by the combination of prevailing benthic organisms and environmental conditions. The detailed habitat information for the North Sea provided in this thesis could contribute to this.

Habitat-specific fishing impact assessments are important. Recent studies focus on the usage of the average maximum life duration (longevity) of prevailing organisms as an estimate for their resilience to fishing impacts^{12,56,68,77}. A North Sea wide map of average longevity has been modelled, by extrapolating observations of community longevity with bed shear stress, sediment type, and gear-specific fishing intensities⁷⁷. This longevity composition is subsequently used to estimate community-specific recovery rates, defined as the time required by the community to reach a certain percentage of the carrying capacity, assuming longevity-dependent logistic growth rates^{12,17,56}. The reduction of biomass due to the fishing disturbance on the other hand is depending on the penetration depth of the fishing gear and sediment type^{7,10,16,78}. These studies demonstrate that impacts are generally largest for heavy, deep-penetrating gears^{10,17,79}, and when low-resilient species and habitats are fished^{12,16,68}. Our observations after a single beam trawl event explain these conclusions, as it demonstrated that deep-burrowing species survived the trawl pass while abundances of superficial living species were substantially reduced (**Chapter 3**). Fishing gears that penetrate deeper in the sediment, dredges for instance, would also affect the now spared deep-burrowing species.

Box 2. Sampling methods

The multibeam echosounder (MBES) is an acoustic device, often attached to the bottom of the vessel. It emits sound waves and records their echoes. Based on the time elapsed before an echo is received, the exact water depth is determined. In addition, the intensity of the echoes is indicative of the sediment type and seafloor structures. The swath width varies with water depth, but is around ~120 m.

The Side-Scan Sonar (SSS) is a torpedo-shaped acoustic device that is towed behind the vessel, at a certain height above the seafloor. It emits its sound waves sideways to the seafloor, where they reflect off the first structure they hit. This creates detailed image of the structure of the seafloor, based on reflective objects and non-reflective areas ('shades'). Swath width of the SSS is about ~150 m to either side, depending on the water depth and its height above the seafloor.

The beam trawl is a fishing net that is actively towed behind a vessel, to target demersal species like shrimp or flatfish. The net is kept open by a horizontal beam, and so-called shoes at either side of the beam. Tickler chains are usually placed in front of the net opening to stimulate buried organisms into the nets. Net opening and mesh size vary with target species. However, the Dutch maximum allowed beam length is 12m, resulting in a maximum swath width of 24 m.

Towed underwater video systems enable the recording of the seafloor along transects. There is a wide variety of video systems, but here the advanced Remotely Operated Vehicle used for chapter 6 is shown. More information about the custom-developed DISCLOSE system can be found in box 3. Video footage allows for the observation of larger epifauna and demersal fish species, and a direct link to the prevailing habitat. In general, video transects were ~200 m long, with the camera overseeing an area of ~0.25 m².

The Sediment Profile Image (SPI) is a device that takes pictures of the soil profile. The device is lowered to the seafloor. There, the camera system penetrates the seafloor. Through the glass window, it can take pictures of the enclosed sediments, showing the soil profile of the enclosed sediments. The picture has a surface of around 20 x 15 cm.

Grabs (left) and box cores collect seafloor samples by retaining a grab or core from the seafloor. This is brought on deck, where it can be processed further. Such samples are generally used for sediment collection and macrofauna analysis. Sampled surface varies with the dimensions of the device, but usually is ~0.1 m².

Regarding habitat-specific fishing activities, we determined in **Chapter 2** the spatial distribution of otter and beam trawlers targeting (a mixture of) Norway lobster (*Nephrops norvegicus*) and demersal fish, which are the dominant types of fisheries in the Netherlands. The most recent fishing impact study demonstrates that these fishing gears also have the highest overall impact in the North Sea⁷⁷. This assessment is based on a global review of depletion and subsequently longevity-specific recovery estimates of trawling impact studies^{16,17}, longevity estimates derived from endobenthos communities collected at 401 stations⁶⁸, and international gear-specific fishing intensities⁷⁵. Longevity compositions were modelled against prevailing sediment type, fishing intensity, and bed shear stress to derive estimations of a median longevity under non-fished conditions. These estimates can be greatly improved by the inclusion of epifauna species and demersal fish species, as they generally have higher longevities than endobenthos^{7,68,80} and different spatial patterns in both species richness^{13,14} and community distributions (**Chapter 4**). As a consequence, habitats that are assessed to be resilient at the endobenthos level, might be essential to low-resilient epifauna or fish species. Epifauna and demersal fish, however, generally have a greater mobility than endobenthos, which makes realistic estimations of local longevity compositions difficult, especially for demersal fish. Also, actual depletion rates may change due to this higher mobility, as highly mobile (fish) species might be able to escape the fishing gear. As demersal fish communities are more uniformly spread over the North Sea than epifauna and endobenthos communities (**Chapter 4**), priority should be given to include epifauna longevity in fishing impact assessments. When epifauna is included in overall longevity estimates for fishing impact assessments, special attention should be given to ecosystem engineers. The constructions of biogenic structures alter the local benthic communities²⁰ (**Chapters 8, 9**), and can last longer than the lifespan of individual species²¹. Unfortunately, they are more vulnerable to fishing activities^{57,69,81,82} and require longer recovery times than the individual species^{11,20,82}. Hence, both depletion and (longevity-based) recovery rates of ecosystem engineer species should be determined on the level of the biogenic reef structure and not at species level.

Baseline

I defined resilience of a habitat or community as the combination of its resistance to impacts and its capability to subsequently recover from them^{17,83}. This definition implicitly defines a reference state or baseline as the state the impacted habitat/community should recover to, generally the unimpacted state. However, the determination of such a baseline is difficult because most coastal seas have been subjected to human impacts for centuries^{6,84}. Beam trawlers have been active in the North Sea for centuries, with their introduction somewhere in the thirteenth century^{69,85}. Since 1850, their impact strongly increased with the transition from wind-driven to engine-driven propagation, which allowed fishing with much heavier gear in much deeper water⁸⁵. As such, the benthic communities have been altered significantly, with (large) replacements of low-resilient species by resistant ones^{5,6,84}. Only little information exists about the state of the different North Sea communities at the start of bottom trawling. Remarkably, the first documentation of bottom trawling worldwide is a request made to the English King Edward III in 1376 to ban this new and destructive gear⁸⁵. The description stated that bottom trawling “...destroys the flowers of the land below water there, and also the spat of oysters, mussels, and other fish upon which the great fish are accustomed to be fed and nourished.”^{85,86}, and also emphasized the large proportion of (juvenile) bycatch not suitable for human consumption. They state furthermore that trawlers caught high quantities of so-called ‘scruff’ (benthic invertebrates and seaweeds, which most likely represent both macroalgae and plant-like animals such as hydrozoans), that ceased after several visits to the same area^{85,87,88}. Historical records indicate that most fish species that are abundant today were already abundant in the 16th century⁸⁹. This comprises for instance the pelagic herring (*Clupea harengus*) and haddock (*Melanogrammus aeglefinus*), and the demersal plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*). Several low-resilient species such as cod (*Gadus morhua*) and various ray and shark species were also described as abundant in the 16th century, but they are currently less abundant⁸⁹. These species were already less abundant around 1906, with their

declines likely being related to fisheries⁹⁰.

Especially for benthic communities, the first trawl passage is (much) more destructive than repeated ones^{72,91}. It is therefore likely that the seafloor in many parts of the North Sea once was covered by a thick layer of epibenthic life, that has been removed over time. Such a well-established benthic community would significantly stabilize and consolidate the underlying sediment, which would affect turbidity, bed shear stress, and substrate availability^{85,87,92}. In addition to all the anthropogenic activities that have impacted the North Sea since the first trawling event, the North Sea has also been exposed to the effects of global warming. This makes it impossible to establish a “pristine” baseline for the North Sea, either from recently gathered data or from historical literature. Yet, baselines are required for proper impact assessments and subsequent management. This resulted in the estimation of unfished baselines by modelling⁶⁸ and in the definition of new baselines^{7,93,94}. It is important to realize that both approaches represent a (set of) subjective choice(s), and have a high risk of viewing the degraded situation as the “new normal”; so a shifting baseline⁹².

Personal view on management

Defining a baseline will always be a subjective choice, and dependent on the geographic and historic setting. I am convinced that the present ecosystem is a degraded version of the one present before bottom trawling occurred⁸⁵. As such, my preferred North Sea would be in the situation as before significant anthropogenic impacts took place. However, that does not mean that we should or can strive for North Sea wide recovery to that baseline. Firstly, we don't know what exactly the communities were comprised of and how they would have reacted to global warming effects. Secondly, recovery to pristine conditions implies that all anthropogenic activities should be banned in the North Sea, which is not realistic. However, even if we would like to allow for more pristine conditions in certain areas, this may not be possible by natural recovery only⁹⁵. We have potentially degraded the ecosystem to such a level that natural recovery might not be possible, as the system has shifted to an alternative stable state⁹⁶. Active restoration is then required to cross thresholds⁹⁷. In addition to the shift towards more resilient species compositions^{5,6}, chronic bottom trawling has systematically homogenized the seafloor⁹⁸ and altered prevailing sediment types^{99,100}. Active restoration, for instance the re-establishment of suitable settlement substrates¹⁰¹ or the reintroduction of a start population¹⁰², are then necessary to create pristine-like conditions⁹⁵. Hence, I fully support current initiatives that aim to restore biogenic reefs of amongst others the European oyster (*Ostrea edulis*) in the North Sea.

I furthermore think we should strive to reduce the impact of human activities as much as possible, with a realistic evaluation of societal and ecological constraints. In this, anthropogenic impact is assessed against a baseline defined by the currently undisturbed habitats, as this will prevent the present ecosystems to deteriorate further. However, the precautionary approach is applied when interpreting the assessment results, based on the fact that the baselines represent degraded ecosystems with respect to the pre-impacted state of the North Sea. The anthropogenic activities that are allowed should be spatially managed to leave protected areas within all habitat types. The establishments of such protected areas are supported by the great uncertainty of a pre-impacted baseline in the North Sea, and could be seen as major scientific experiments which potentially can provide insight in the composition and functioning of long-term unimpacted communities. We should furthermore closely monitor the status of benthic communities in impacted areas. For this, national monitoring programs have to be harmonized at regional levels and increased in both temporal and spatial resolution, such that all national programs combined allow for detailed, North Sea wide assessments of the benthic communities.

Box 3. BRUCE

Design

The design of BRUCE is based on the flying video array used by the University of Plymouth¹⁰³, which in turn simplified the towed automatically compensating observations system concept proposed in 1999¹⁰⁴. Contrary to the common video sledges^{105,106} and dropcameras^{107,108}, these video systems are based on the principle that the video frame is self-stabilizing at a certain height above the seafloor. This is achieved by the introduction of a horizontal component in the towing design, achieved by a dropweight and drag chains (Fig. B3.1). Three sprout cables are attached to the frontside of the camera frame at the top center, bottom left, and bottom right so that the frame is pulled straight forward. After 4.5 m, these sprout cables fuse into 1 towing cable. At this merging point, a drop weight of 55 kg is attached that determines the height to the seafloor. The video frame itself has a slightly positive buoyancy, which is canceled by the drag chains attached to the bottom of the frame on both sides. These chains slide over the bottom during the transects, and stabilize the height of the frame above the seafloor with the amount of chain on the bottom. An umbilical cord, connecting the camera with the on-board computer, is kept separate from the towing cable except for the last part. It is loosely connected to the top sprout cable along with some buoys to prevent it from getting caught at the seafloor. This horizontal component in the towing construction proved very effective in stabilizing the video frame above the seafloor, even in relatively rough weather conditions of wind force 6-7.

Figure B3.1. Schematic drawing of the towing construction of the video frame BRUCE, showing the three sprout cables that merge into one towing cable (black), with the dropweight at the junction. The umbilical cord (blue) set-up is also shown.

The aluminum frame contains a remotely controllable HD-camera (Kongsberg OE14-522A-0009 Colour HD Pan) and a downward facing DSRL camera (NIKON D750), each with 4 underwater lights (Fisheye FIX NEO 1000DX SWII LED) and a pair of lasers for scaling (Z-Bolt, SCUBA-II green) (Fig. B3.2).

Figure B3.2. The towed video system 'BRUCE' in frontal (A) and ventral (B) view, showing the main, forward looking HD video camera (a), the downward facing Nikon DSLR-photo camera (b), underwater lights (c), lasers for scaling (d), floaters (e), drag chains (f), and the attachment positions of the three towing cables (g).

An umbilical cord connects the HD-camera to a custom-made computer on deck, showing a live-feed and allowing manual control of the HD-camera (Fig. B3.3).

Figure B3.3. The custom-made computer with a live-view of the camera footage and allowing manual control of the camera.

Box 3. BRUCE

Pros and cons

The deployment of BRUCE resulted in multiple publications²⁸ (Chapters 6, 7, 9). Together with the experiences gained with other underwater video systems (Chapters 3, 5, 8), this enabled me to provide an overview with the pros and cons of video systems in practice (Table B3.1).

Table B3.1. The pros and cons of underwater video systems, including some rationale of why I think the advantage is important, and recommendations to deal with any drawbacks.

	Statement	Rationale
Pros	- Visualization of the seafloor	- Envisioning the study area improves the interpretation of the results.
	- Identification of demersal fish and larger epifauna over large areas	- These organisms are not sampled adequately by box cores and grabs, although dredges and trawls can provide similar data.
	- Direct linking of organisms to their habitats	- This is crucial information for a thorough knowledge of the distribution, structure and functioning of benthic habitats.
	- Small morphological structures, like sand ripples, can be observed	- Video observations are the only method that allow for such observations ²⁸ .
	- Less destructive than bottom sampling techniques like trawls and box cores	- This is especially relevant when sampling vulnerable systems, like (biogenic) reef structures ^{64,103,106,107} .
	- Most systems are relatively easily deployed from a variety of vessels	- The dimensions of BRUCE allow its deployment from many different vessels.
	- Deployable in areas where trawls and box cores are difficult/impossible	- For instance, in areas with stones or near anthropogenic structures such as oil platforms.
	Statement	Recommendations
Cons	- Video deployment and subsequent analysis is time-consuming	- Fast developments in the field of computer-automated identification may enable automatic species identification that could help reduce analysis time ¹⁰⁹ .
	- Species identification is often difficult due to: <ul style="list-style-type: none"> o Turbidity o Speed over the seafloor o Inability to alter point of view o Animal behavior (hiding, fleeing) 	- High-resolution of video footage is important, as it enables zooming in.
	- Relatively large positional error, especially when the towing construction has a horizontal component	- Speed over the bottom should be kept constant at low speeds.
	- Standardization of especially the video analysis is difficult	- An acoustic positioning system could solve this problem.
		- Transparency on design, assumptions, choices, methods and deviations thereof is key to perform robust analyses. Also, literature on video studies provide examples of validated analyzing methods.

References

- Halpern, B. S. *et al.* A global map of human impact on marine ecosystems. *Science*. **319**, 948–953 (2008).
- Johnson, C. N. *et al.* Biodiversity losses and conservation responses in the Anthropocene. *Science*. **356**, 270–275 (2017).
- Costello, M. J. & Ballantine, B. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends Ecol. Evol.* **30**, 507–509 (2015).
- van Denderen, P. D. *et al.* Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar. Ecol. Prog. Ser.* **541**, 31–43 (2015).
- Tillin, H. M., Hiddink, J. G., Jennings, S. & Kaiser, M. J. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar. Ecol. Prog. Ser.* **318**, 31–45 (2006).
- Kaiser, M. J., Ramsay, K., Richardson, C. A., Spence, F. E. & Brand, A. R. Chronic fishing disturbance has changed shelf sea benthic community structure. *J. Anim. Ecol.* **69**, 494–503 (2000).
- Bolam, S. G. *et al.* Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar. Environ. Res.* **126**, 1–13 (2017).
- Bricheno, L. M., Wolf, J. & Aldridge, J. Distribution of natural disturbance due to wave and tidal bed currents around the UK. *Cont. Shelf Res.* **109**, 67–77 (2015).
- Aldridge, J. N., Parker, E. R., Bricheno, L. M., Green, S. L. & van der Molen, J. Assessment of the physical disturbance of the northern European Continental Shelf seabed by waves and currents. *Cont. Shelf Res.* **108**, 121–140 (2015).
- Eigaard, O. R. *et al.* Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J. Mar. Sci.* **73**, 27–43 (2015).
- Clark, M. R. *et al.* The impacts of deep-sea fisheries on benthic communities: A review. *ICES J. Mar. Sci.* **73**, 51–69 (2016).
- Hiddink, J. G. *et al.* Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J. Appl. Ecol.* **56**, 1075–1084 (2019).
- Reiss, H. *et al.* Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES J. Mar. Sci.* **67**, 278–293 (2010).
- Callaway, R. *et al.* Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES J. Mar. Sci.* **59**, 1199–1214 (2002).
- Künitzer, A. *et al.* The benthic infauna of the North Sea: Species distribution and assemblages. *ICES J. Mar. Sci.* **49**, 127–143 (1992).
- Sciberras, M. *et al.* Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish.* **19**, 698–715 (2018).
- Hiddink, J. G. *et al.* Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci.* **114**, 8301–8306 (2017).
- Baptist, M. J., van Dalfsen, J., Weber, A., Passchier, S. & van Heteren, S. The distribution of macrozoobenthos in the southern North Sea in relation to meso-scale bedforms. *Estuar. Coast. Shelf Sci.* **68**, 538–546 (2006).
- van Dijk, T. A. G. P. *et al.* Benthic habitat variations over tidal ridges, North Sea, The Netherlands. In *Seafloor Geomorphology as Benthic Habitat* 241–249 (Elsevier Inc., 2012).
- Fariñas-Franco, J. M. *et al.* Marine Strategy Framework Directive Indicators for Biogenic Reefs formed by *Modiolus modiolus*, *Mytilus edulis* and *Sabellaria spinulosa*. Part 1: Defining and validating the indicators. *JNCC Report* vol. 523 (2014).
- Hendrick, V. J. & Foster-Smith, R. L. *Sabellaria spinulosa* reef: a scoring system for evaluating ‘reefiness’ in the context of the Habitats Directive. *J. Mar. Biol. Assoc. UK* **86**, 665–677 (2006).
- Gravina, M. F. *et al.* *Sabellaria spinulosa* (Polychaeta, Annelida) reefs in the Mediterranean Sea: Habitat mapping, dynamics and associated fauna for conservation management. *Estuar. Coast. Shelf Sci.* **200**, 248–257 (2018).
- Knaapen, M. A. F. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo-Marine Lett.* **29**, 17–24 (2009).
- Knaapen, M. A. F. Sandwave migration predictor based on shape information. *J. Geophys. Res. Earth Surf.* **110**, 1–9 (2005).
- Knaapen, M. A., van Bergen Henegouw, C. N. & Hu, Y. Y. Quantifying bedform migration using multi-beam sonar. *Geo-Marine Lett.* **25**, 306–314 (2005).
- van der Wal, D., Ysebaert, T. & Herman, P. M. J. Response of intertidal benthic macrofauna to migrating megaripples and hydrodynamics. *Mar. Ecol. Prog. Ser.* **585**, 17–30 (2017).
- Idier, D., Ehrhold, A. & Garlan, T. Morphodynamique d’une dune sous-marine du détroit du pas de Calais. *Comptes Rendus Geosci.* **334**, 1079–1085 (2002).
- Koop, L. *et al.* Measuring centimeter scale sand ripples using multibeam echosounder backscatter data on the Brown Bank of the Dutch Continental Shelf. *Geosciences* **10**, (2020).
- Hintzen, N. T., Aarts, G. & Rijnsdorp, A. D. Persistence in the fine-scale distribution and spatial aggregation of fishing. *ICES J. Mar. Sci.* **76**, 1072–1082 (2019).
- Houziaux, J.-S., Kerckhof, F., Degrendele, K., Roche, M. & Norro, A. The Hinder Banks: yet an important area for the Belgian marine biodiversity? (2008).
- Terwindt, J. H. J. Sand waves in the southern bight of the North Sea. *Mar. Geol.* **10**, 51–67 (1971).
- van Dijk, T. A. G. P. & Kleinans, M. G. Processes controlling the dynamics of compound sand waves in the North Sea, Netherlands. *J. Geophys. Res.* **110**, 1–15 (2005).
- McGave, N. Sand waves in the North Sea off the coast of Holland. *Mar. Geol.* **10**, 199–225 (1971).
- Ashley, G. M. Classification of large-scale subaqueous bedforms: a new look at an old problem. SEPM bedforms and bedding structures research symposium. *J. Sediment. Petrol.* **60**, 160–172 (1990).
- Damveld, J. H., Borsje, B. W., Roos, P. C. & Hulscher, S. J. M. H. Biogeomorphology in the marine landscape: Modelling the feedbacks between patches of the polychaete worm *Lanice conchilega* and tidal sand waves. *Earth Surf. Process. Landforms* **45**, 2572–2587 (2020).
- Borsje, B. W. *et al.* Modeling bio-geomorphological influences for offshore sandwaves. *Cont. Shelf Res.* **29**, 1289–1301

- (2009).
37. Borsje, B. W., de Vries, M. B., Hulscher, S. J. M. H. & de Boer, G. J. Modeling large-scale cohesive sediment transport affected by small-scale biological activity. *Estuar. Coast. Shelf Sci.* **78**, 468–480 (2008).
 38. Damveld, J. H., Roos, P. C., Borsje, B. W. & Hulscher, S. J. M. H. Modelling the two-way coupling of tidal sand waves and benthic organisms: a linear stability approach. *Environ. Fluid Mech.* **19**, 1073–1103 (2019).
 39. Borsje, B. W., Bouma, T. J., Rabaut, M., Herman, P. M. J. & Hulscher, S. J. M. H. Formation and erosion of biogeomorphological structures: A model study on the tube-building polychaete *Janice conchilega*. *Limnol. Oceanogr.* **59**, 1297–1309 (2014).
 40. Rabaut, M., van de Moortel, L., Vincx, M. & Degraer, S. Biogenic reefs as structuring factor in *Pleuronectes platessa* (Plaice) nursery. *J. Sea Res.* **64**, 102–106 (2010).
 41. Coolen, J. W. P. *et al.* Reefs, sand and reef-like sand: A comparison of the benthic biodiversity of habitats in the Dutch Borkum Reef Grounds. *J. Sea Res.* **103**, 84–92 (2015).
 42. Hendrick, V. J., Hutchison, Z. L. & Last, K. S. Sediment burial intolerance of marine macroinvertebrates. *PLoS One* **11**, (2016).
 43. Collins, K. Dorset marine habitat surveys: Maerl, worm reefs, bream nests, sea fans and brittlestars. *Dorset Wildlife Trust and English Nature report*. (2003).
 44. Damveld, J. H. The feedbacks among tidal sand waves, benthic organisms and sediment sorting processes. PhD Thesis. (University of Twente, 2020).
 45. Jenkins, C., Eggleton, J., Barry, J. & O'Connor, J. Advances in assessing *Sabellaria spinulosa* reefs for ongoing monitoring. *Ecol. Evol.* **8**, 7673–7687 (2018).
 46. Pearce, B., Fariñas-franco, J. M., Wilson, C., Pitts, J. & Somer, P. J. Repeated mapping of reefs constructed by *Sabellaria spinulosa* Leuckart 1849 at an offshore wind farm site. *Cont. Shelf Res.* **83**, 3–13 (2014).
 47. Fredsøe, J. & Deigaard, R. Mechanics of coastal sediment transport. (Advanced Series on Ocean Engineering: Volume 3, 1992).
 48. Zhou, J. *et al.* Giant sand waves on the Taiwan Banks, southern Taiwan Strait: Distribution, morphometric relationships, and hydrologic influence factors in a tide-dominated environment. *Mar. Geol.* **427**, 106238 (2020).
 49. Katoh, K., Kume, H., Kuroki, K. & Hasegawa, J. Development of sand waves and the maintenance of navigation channels in the Bisanseto Sea. *Proc. Coast. Eng. Conf.* **3**, 3490–3502 (1998).
 50. Aliotta, S. & Perolli, G. M. E. A sand wave field in the entrance to Bahia Blanca. *Mar. Geol.* **76**, 1–14. (1987).
 51. Kroodsmas, D. A. *et al.* Tracking the global footprint of fisheries. *Science*. **908**, 904–908 (2018).
 52. Amoroso, R. O., Parma, A. M., Pitcher, C. R., McConnaughey, R. A. & Jennings, S. Comment on “Tracking the global footprint of fisheries”. *Science* **361**, eaat6713 (2018).
 53. Piet, G. J. & Hintzen, N. T. Indicators of fishing pressure and seafloor integrity. *ICES J. Mar. Sci.* **69**, 1850–1858 (2012).
 54. Duplisea, D. E., Jennings, S., Warr, K. J. & Dinmore, T. A. A size-based model of the impacts of bottom trawling on benthic community structure. *Can. J. Fish. Aquat. Sci.* **59**, 1785–1795 (2002).
 55. van Denderen, P. D., Hintzen, N. T., van Kooten, T. & Rijnsdorp, A. D. Temporal aggregation of bottom trawling and its implication for the impact on the benthic ecosystem. *ICES J. Mar. Sci.* **72**, 952–961 (2015).
 56. Pitcher, C. R. *et al.* Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. *Methods Ecol. Evol.* **8**, 472–480 (2017).
 57. Hiddink, J. G., Jennings, S. & Kaiser, M. J. Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. *J. Appl. Ecol.* **44**, 405–413 (2007).
 58. Brown, C. J., Smith, S. J., Lawton, P. & Anderson, J. T. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast. Shelf Sci.* **92**, 502–520 (2011).
 59. Verduin, E. C., Tempelman, D. & van Moorsel, G. W. N. M. The macrobenthic fauna monitoring in the Dutch sector of the North Sea, MWTL 2009. *Grontmij Report*. (2011).
 60. ICES. Report of the International Bottom Trawl Survey Working Group (IBTSWG). *ICES Report CM 2015/SSGIEOM:24*. (2015).
 61. Sanderson, W. G. *et al.* Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. II. Epifauna recorded by divers and cameras. *J. Mar. Biol. Assoc. United Kingdom* **88**, 143–149 (2008).
 62. Rees, E. I. S., Sanderson, W. G., Mackie, A. S. Y. & Holt, R. H. F. Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea: III. Crevice, sediment infauna and epifauna from targeted cores. *J. Mar. Biol. Assoc. UK* **88**, 151–156 (2008).
 63. Brown, C. J., Smith, S. J., Lawton, P. & Anderson, J. T. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast. Shelf Sci.* **92**, 502–520 (2011).
 64. Sheehan, E. V. *et al.* An experimental comparison of three towed underwater video systems using species metrics, benthic impact and performance. *Methods Ecol. Evol.* **7**, 843–852 (2016).
 65. Rooper, C. N. & Zimmermann, M. A bottom-up methodology for integrating underwater video and acoustic mapping for seafloor substrate classification. *Cont. Shelf Res.* **27**, 947–957 (2007).
 66. Clements, A. J., Strong, J. A., Flanagan, C. & Service, M. Objective stratification and sampling-effort allocation of ground-truthing in benthic-mapping surveys. *ICES J. Mar. Sci.* **67**, 628–637 (2010).
 67. Rijnsdorp, A. D. *et al.* Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. *ICES J. Mar. Sci.* **73**, 127–138 (2015).
 68. Rijnsdorp, A. D. *et al.* Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol. Appl.* **28**, 1302–1312 (2018).
 69. de Groot, S. J. The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Manag.* **9**, 177–190 (1984).
 70. Shephard, S., Brophy, D. & Reid, D. G. Can bottom trawling indirectly diminish carrying capacity in a marine ecosystem? *Mar. Biol.* **157**, 2375–2381 (2010).
 71. Kaiser, M. J. *et al.* Global analysis of response and recovery of benthic biota to fishing. *Mar. Ecol. Prog. Ser.* **311**, 1–14 (2006).
 72. Batsleer, J. *et al.* Exploring habitat credits to manage the benthic impact in a mixed fishery. *Mar. Ecol. Prog. Ser.* **586**,

- 167–179 (2018).
73. Kraak, S. B. M. *et al.* 21st century fisheries management: a spatio-temporally explicit taroff-based approach combining multiple drivers and incentivising responsible fishing. *ICES J. Mar. Sci.* **69**, 590–601 (2012).
 74. Amoroso, R. O. *et al.* Bottom trawl fishing footprints on the world's continental shelves. *Proc. Natl. Acad. Sci.* **115**, 201802379 (2018).
 75. Eigaard, O. R. *et al.* The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J. Mar. Sci.* **74**, 847–865 (2017).
 76. Piet, G. J. & Hintzen, N. T. Indicators of fishing pressure and seafloor integrity. *ICES J. Mar. Sci.* **69**, 1850–1858 (2012).
 77. Rijnsdorp, A. D. *et al.* Different bottom trawl fisheries have a differential impact on the status of the North Sea seafloor habitats. *ICES J. Mar. Sci.* **77**, 1772–1786 (2020).
 78. Hiddink, J. G. *et al.* Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. *J. Appl. Ecol.* **57**, 1199–1209 (2020).
 79. O'Neill, F. G. & Ivanovic, A. The physical impact of towed demersal fishing gears on soft sediments. *ICES J. Mar. Sci.* **73**, i5–i14 (2016).
 80. Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M. & Stephens, D. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. *J. Sea Res.* **85**, 162–177 (2014).
 81. Jennings, S. & Kaiser, M. J. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* **34**, 201–352 (1998).
 82. Kaiser, M. J., Hornbrey, S., Booth, J. R., Hinz, H. & Hiddink, J. G. Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. *J. Appl. Ecol.* **55**, 1060–1070 (2018).
 83. Lambert, G. I., Jennings, S., Kaiser, M. J., Davies, T. W. & Hiddink, J. G. Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. *J. Appl. Ecol.* **51**, 1326–1336 (2014).
 84. Callaway, R., Engelhard, G. H., Dann, J., Cotter, J. & Rumohr, H. A century of North Sea epibenthos and trawling: Comparison between 1902–1912, 1982–1985 and 2000. *Mar. Ecol. Prog. Ser.* **346**, 27–43 (2007).
 85. Roberts, C. The unnatural history of the sea. (Island Press, 2007).
 86. Alward, G. The sea fisheries of Great Britain and Ireland. (Albert Gait, 1932).
 87. A correspondent. Reply to the so-called criticism and analysis of Professor M'Intosh on trawling and trawling investigations. (1899).
 88. Cunningham, J. T. A natural history of the marketable marine fishes of the British Islands. (Macmillan and Co. Ltd., 1896).
 89. Bennema, F. P. & Rijnsdorp, A. D. Fish abundance, fisheries, fish trade and consumption in sixteenth-century Netherlands as described by Adriaen Coenen. *Fish. Res.* **161**, 384–399 (2015).
 90. Rijnsdorp, A. D., van Leeuwen, P. I., Daan, N., L. Heessen Rijnsdorp, H. J. & Leeuwen, V. Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES J. Mar. Sci.* **53**, 1054–1062 (1996).
 91. Cook, R. *et al.* The substantial first impact of bottom fishing on rare biodiversity hotspots: A dilemma for evidence-based conservation. *PLoS One* **8**, e69904 (2013).
 92. Handley, S. J. *et al.* The importance of benchmarking habitat structure and composition for understanding the extent of fishing impacts in soft sediment ecosystems. *J. Sea Res.* **86**, 58–68 (2014).
 93. Lee, S. T. M., Kelly, M., Langlois, T. J. & Costello, M. J. Baseline seabed habitat and biotope mapping for a proposed marine reserve. *PeerJ* **3**, e1446 (2015).
 94. Cooper, K. M. & Barry, J. A big data approach to macrofaunal baseline assessment, monitoring and sustainable exploitation of the seabed. *Sci. Rep.* **7**, 12431 (2017).
 95. Fariñas-Franco, J. M., Allcock, A. L. & Roberts, D. Protection alone may not promote natural recovery of biogenic habitats of high biodiversity damaged by mobile fishing gears. *Mar. Environ. Res.* **135**, 18–28 (2018).
 96. Scheffer, M., Carpenter, S., Foley, J. a, Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001).
 97. Balke, T., Herman, P. M. J. & Bouma, T. J. Critical transitions in disturbance-driven ecosystems: Identifying windows of opportunity for recovery. *J. Ecol.* **102**, 700–708 (2014).
 98. Thrush, S. F. & Dayton, P. K. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Annu. Rev. Ecol. Syst.* **33**, 449–473 (2002).
 99. Paradis, S. *et al.* Spatial distribution of sedimentation-rate increases in Blanes Canyon caused by technification of bottom trawling fleet. *Prog. Oceanogr.* **169**, 241–252 (2018).
 100. Oberle, F. K. J., Storlazzi, C. D. & Hanebuth, T. J. J. What a drag: Quantifying the global impact of chronic bottom trawling on continental shelf sediment. *J. Mar. Syst.* **159**, 109–119 (2016).
 101. Kamermans, P. *et al.* Offshore wind farms as potential locations for flat oyster (*Ostrea edulis*) restoration in the Dutch North Sea. *Sustainability* **10**, (2018).
 102. Schulte, D. M., Burke, R. P. & Lipcius, R. N. Unprecedented restoration of a native oyster metapopulation. *Science*. **325**, 1124–1128 (2009).
 103. Sheehan, E. V., Stevens, T. F. & Attrill, M. J. A quantitative, non-destructive methodology for habitat characterisation and benthic monitoring at offshore renewable energy developments. *PLoS One* **5**, e14461 (2010).
 104. Barker, B. A. J. *et al.* A vessel-towed camera platform for surveying seafloor habitats of the Continental Shelf. *Cont. Shelf Res.* **19**, 1161–1170 (1999).
 105. Spencer, M. L., Stoner, A. W., Ryer, C. H. & Munk, J. E. A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: Comparison with beam trawls and divers. *Estuar. Coast. Shelf Sci.* **64**, 497–503 (2005).
 106. Mallet, D. & Pelletier, D. Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). *Fish. Res.* **154**, 44–62 (2014).
 107. Beisiegel, K., Darr, A., Gogina, M. & Zettler, M. L. Benefits and shortcomings of non-destructive benthic imagery for monitoring hard-bottom habitats. *Mar. Pollut. Bull.* **121**, 5–15 (2017).
 108. Vandermeulen, H. Drop and towed camera systems for ground-truthing high frequency sidescan in shallow waters. *Canadian Technical Report of Fisheries and Aquatic Sciences* 2687. (2007).
 109. Piechaud, N., Hunt, C., Culverhouse, P. F., Foster, N. L. & Howell, K. L. Automated identification of benthic epifauna with computer vision. *Mar. Ecol. Prog. Ser.* **615**, 15–30 (2019).

Appendices

Acknowledgements

Een PhD afronden wordt weleens vergeleken met een bevalling. Daar ben ik het niet mee eens. Nu kan ik veel verschillen opnoemen, maar één springt er voor mij uit. Waar ik bij de bevallingen zo min mogelijk mensen om me heen wilde hebben, heb ik tijdens mijn PhD juist met zoveel mogelijk mensen samengewerkt en dingen ondernomen. Dit proefschrift had er dan ook zeker niet geweest zonder hun hulp en inzet. Bedankt daarvoor!

Han, dank voor deze kans op een PhD over de Noordzee, en het vertrouwen tijdens het gehele proces. Onder jouw begeleiding heb ik mijn eigen visie kunnen ontwikkelen, mede omdat ik mijn mening en keuzes altijd goed moest onderbouwen in onze discussies. Daarnaast stimuleerde je mij om nieuwe samenwerkingen aan te gaan en breder te kijken dan de Noordzee. Met jouw nieuwe ideeën als relative outsider van Noordzee-onderzoek wist je mij te inspireren en jouw grote kennis van ecologie en statistiek was zeer welkom tijdens de data analyses.

Adriaan, jij bracht een zee van kennis in over de Noordzee, haar inwoners en gebruikers, en hun onderlinge uitdagingen. Op afstand keek je mee met mijn PhD, maar was altijd beschikbaar voor vragen en advies. Met geduld en een overduidelijke nieuwsgierigheid gaf je me een nieuwe kijk op relevante vraagstukken over Noordzeegebruik. Heel fijn dat je zo voor me klaarstond, dankjewel.

Laura, jij werd als laatste aan mijn begeleidend team toegevoegd. Wat ben ik daar blij mee! Jouw persoonlijke aanpak zorgde ervoor dat ik al mijn gedachten kon delen, over persoonlijke omstandigheden en werk gerelateerde uitdagingen. En altijd weer wist jij een positief perspectief te schetsen waardoor ik met nieuwe energie aan het werk ging. Bovendien resulteerde jouw input altijd in een verbetering van mijn output. Ik hoop dat we elkaar nog vaak tegenkomen voor werk!

Ook wil ik hier graag mijn leescommissie bedanken voor het grondig doornemen van mijn boekje. Jan Geert Hiddink, Klemens Eriksson, en Daphne van der Wal; ik ben benieuwd naar jullie vragen en weet zeker dat onze paden in de toekomst vaker zullen kruisen.

Mijn PhD vond plaats binnen het DISCLOSE consortium. Het spreekt voor zich dat mijn werk onmogelijk was geweest zonder mijn projectpartners. De inzet van Mirjam om ervoor te zorgen dat samenwerkingen binnen het project zo soepel mogelijk liepen; de vertaalslag van Leo en mij om elkaars vakgebied te kunnen begrijpen; de vele gesprekken met Christiaan over gerelateerde en niet-gerelateerde Noordzeevraagstukken; de nieuwe energie die Sebastiaan toevoegde aan het consortium; de vele discussies tijdens de consortium meetings, allen hebben bijgedragen aan de inhoud van dit boekje en mijn plezier tijdens het werken eraan.

Voor mijn onderzoek ben ik meerdere keren zelf de Noordzee op geweest. Tijdens de twee expedities van Stichting Duik de Noordzee Schoon aan boord van de Cdt. Fourcoul heb ik zelf kunnen zien hoe de Noordzeebodem eruit ziet. En tijdens de vijf onderzoeksreizen aan boord van de Pelagia en de Neptune hebben we de akoestische, videografische en benthische gegevens verzameld die gebruikt worden in verschillende hoofdstukken. Deze reizen waren onmogelijk geweest zonder de vaardige crews, en een stuk minder productief, gestructureerd en gezellig zonder de andere opvarenden aan boord. Mijn dank gaat verder uit naar Ben Stiefelhagen, Karline Soetaert, Ricardo Anguilar, Silvia Garcia, Rob Witbaard, Jip Vrooman en Helge Niemann voor de leiding tijdens de verschillende cruises. Daarnaast een speciale dankjewel voor Daniëlle, John, Nadia en Jan voor hun inzet aan mijn project tijdens de cruises, onder soms uitdagende omstandigheden. Johan, onze ontmoeting op de Pelagia heeft geleid tot een mooie samenwerking, die hopelijk nog wordt voortgezet. Justin and Chui, I remember our cruise(s) on board of the Pelagia with pleasure. Thank you both for the collaborations. All the best in your future careers, potentially with more collaborations ahead!

Mijn dank gaat uit naar de Fieldwork Company voor het meedenken, ontwikkelen, testen en aanpassen van "Bruce". Het is de laatste reis gelukt om scherpe videobeelden van de Noordzeebodem te maken met windkracht 6-7, dus ik zou zeggen dat ons ontwerp in elk geval werkt! Daarnaast ook

een dankjewel aan de studenten die mij hebben geholpen. Zo hielpen Lisa-Rose, Cameron, Jelmer, en Sietse in de analyse van verzamelde beelden, ging Danielle mee aan boord, en werkten Femke, Kasper, en Niek nieuwe ideeën uit. Daarnaast vond ik het superleuk om Jorn, Ruth, en Nina te begeleiden bij het uitwerken van andere maatschappelijk Noordzeevraagstukken. Ik wens jullie allen veel succes in jullie verdere carrières!

Tijdens mijn PhD project kon ik voortbouwen op de opgedane kennis tijdens mijn werk bij Wageningen Marine Research. Als gevolg daarvan kwam ik met regelmaat oud-collega's tegen. Heel leuk dat ik met sommigen nog echt kon blijven samenwerken! Veel dank aan Niels, Oscar en GerJan voor hun bijdragen aan deze thesis, en aan Nathalie, Marloes, Floor en Jan Jaap voor het doorzetten van onze paper over de samenwerking tussen wetenschappers en vissers.

This last year of my PhD, I have been a guest researcher with DTU Aqua. The mentoring of Ole and Grete made me feel welcomed and cared for in this new country. Thank you for all your effort to accommodate me, and the opportunity to work with you as a PostDoc. I am looking forward to continue our collaboration!

Veel van mijn werk vond plaats achter de computer, op kantoor in het CvL. Wat ben ik blij dat er altijd collega's waren om advies aan te vragen, koffie mee te drinken, te ouwehoeren of een balletje over te gooien. Jullie maakten de werkdagen en vaak genoeg ook de avonden of weekenden een stuk gezelliger! Dank daarom aan al mijn collega's: Guido, Hacen, Inger, Annelies, Rik, Yvonne, Nadia, Lisa, Drew, Janne, Max, Bea, Ruth, Kasper, Megan, Oscar, Michiel, Georgette, Izzy en alle anderen van de ConsEco-groep. Rik, ik vind het echt super dat je mijn paranimph wil zijn. Dat we naast elkaar zaten was niet altijd even productief, maar na een jaar thuiswerken kan ik uit ervaring zeggen dat dergelijke momenten noodzakelijk zijn 😊. Naast hun gezelligheid was de inzet van Joyce, Ingeborg, Joke, Jan en Jacob ook bijzonder waardevol voor mijn project. Bedankt dat ik met mijn vragen over IT, administratie of praktische zaken altijd bij jullie kon aankloppen!

Deze thesis was er niet geweest zonder alle activiteiten buiten werk om, zoals de vele spelletjesavonden met Rik en Jorien tot diep in de nacht. Heerlijk dat we die gewoon online hebben kunnen doorzetten, ook al wonen we nu verder weg. Marten, ik vond het altijd supergezellig als je weer even 'thuis' was. Zelfs als het betekende dat er weer voetbal werd gekeken. Gaan we GoT nog eens afkijken? Pepijn en Gerbrig, wanneer gaan we weer op wintersport? Er schijnt hier vlakbij een geschikte plek te zijn...

Daarnaast waren er natuurlijk altijd Calamari en Lycurgus. Sinds het begin van mijn studie ben ik een Calamariaan en hier heb ik me altijd thuis gevoeld. Ik heb genoten van de vele duikweekenden, borrels en commissie- en bestuursvergaderingen, net als van de vakanties naar Spanje, Corsica en Bretagne. Ik weet zeker dat ik velen van jullie nog tegen ga komen, aan de waterrand of juist tijdens werk. Bij mijn 'terugkomst' in Groningen ben ik ook met open armen ontvangen door D9. Lieve Anita, Astrid, Astrid, Elodie, Hanne, Jorien, Margreet, Suzanne, Wieke, en Willemijn, bedankt voor de fijne trainingen en mooie wedstrijden! Heerlijk om alle frustratie er soms even uit te kunnen slaan. Ik kom zeker nog eens een wedstrijd kijken! Ook John, Gertjan en Martijn, bedankt voor de trainingen!

Paps, van jou heb ik de liefde voor de natuur geerfd. Jij hebt me geleerd goed en aandachtig te kijken en te genieten van al het leven om ons heen. Het willen uitpuzzelen hoe iets zit of werkt, en het plannen, uitvoeren en analyseren van de benodigde onderzoeken heb ik dan weer van jou, mams. Daarnaast is ook jullie steun en interesse tijdens/in dit project belangrijk voor mij geweest. Anneke, Sandra, Erik, en alle aanhang; dezelfde steun en interesse hadden jullie ook. Maar nog veel belangrijker vond ik al onze momenten dat het niet over werk ging, en we heerlijk konden ouwehoeren over van alles en niets. Erik, heel leuk om mijn verdediging met jou te kunnen delen en je mijn paranimph wil zijn. Wellicht stap ik ooit nog eens bij je aan boord voor mijn onderzoek!

Luisterende oren en support vond ik ook altijd bij mijn extra familie. Paulus, Lenie en alle andere “de Boertjes”/“Brokjes”; dank voor de fijne gesprekken en discussies, al dan niet over werk, en gezelligheid. Jullie voelen echt aan als mijn familie!

Tot slot, lieve Bauke, ik zal niet beweren dat er zonder jou geen boekje had gelegen, maar ik weet zeker dat het compleet anders was geweest! Jij hielp me erdoor heen als alles tegen leek te zitten, en door jouw interesse wist je me vaak nog enthousiaster te maken. Ik kan met jou over alles praten, met onze wonderlijke, meestal nachtelijke, discussies over oa statistiek, natuurbeleid, klimaatverandering, boerenbedrijven, farmaceutische industrieën, en wereldproblematiek als kenmerkende voorbeelden. Daarnaast kan ik me geen betere vader wensen voor Lennart en Jelte.

Appendices

Biography

Karin Johanna van der Reijden was born on May 11, 1990 in Schiedam, the Netherlands. In 2008, she finished the preparatory scientific education from her high school (Schravenlant, Schiedam), with a focus on natural sciences. Hereafter, she started the bachelors 'Marine Biology' and 'Ecology and Evolution' at the University of Groningen, which she continued with a master in Marine Biology. This master included two research internships: a fundamental study on the effects of seagrass density on predator-prey interactions at the University of Groningen, and an applied study on the assessment methodology of discard quantity and composition in the Dutch demersal fisheries at Wageningen Marine Research. In 2013, Karin graduated *cum laude*.

From 2014 to 2016, Karin worked as a junior fisheries researcher at Wageningen Marine Research. She was active in multiple projects, that all focussed on discards in the Dutch demersal fisheries. She was responsible for the assessment of discard quantity and composition for the entire Dutch demersal fleet and lead three industry-surveys in which fishermen provide additional information for stock assessments. She further participated in research projects that estimated the survival of discarded fish, monitored cod bycatches by demersal gears, and studied spatial distributions of fisheries.

In May 2016, Karin returned to the University of Groningen, and started her PhD-research within the Conservation Ecology Group in the Groningen Institute for Evolutionary Life Sciences (GELIFES). This PhD was part of the DISCLOSE project; a collaboration between the Delft University of Technology, the University of Groningen, the Royal Netherlands Institute for Sea Research (NIOZ) and the North Sea Foundation. DISCLOSE aimed to study the distribution, structure, and functioning of low-resilient seafloor communities and habitats in the Dutch North Sea.

Since April 1st 2021, Karin works as PostDoc within the Ecosystem-Based Marine Management group at the National Institute of Aquatic Resources (DTU Aqua), Copenhagen. Here, she studies the benthic impact of demersal fisheries, with a special focus on the differences in impact between habitats.

Appendices

List of publications

van der Reijden KJ, Govers LL, Koop L, Damveld JH, Herman PMJ, Mestdagh S, Piet G, Rijnsdorp AD, Dinesen GE, Snellen M, Olff H (2021) Beyond connecting the dots: A multi-scale, multi-resolution approach to marine habitat mapping. *Ecological Indicators* 128, [107849], <https://doi.org/10.1016/j.ecolind.2021.107849>

van der Reijden KJ, Koop L, Mestdagh S, Snellen M, Herman PMJ, Olff H, Govers LL (2021): Conservation implications of Sabellaria spinulosa reef patches in a dynamic sandy-bottom environment. *Frontiers in Marine Science* 8, [642659], <https://doi.org/10.3389/fmars.2021.642659>

Leurs G, **van der Reijden KJ**, Yahya Lemrabott CS, Barry I, Nonque DM, Olff H, Ledo Pontes S, Regalla A, Gover LL (nd) Industrial fishing near West African Marine Protected Areas and its potential effects on mobile marine predators. *Frontiers in Marine Science* 8, [602917], <https://doi.org/10.3389/fmars.2021.602917>

Koop L, **van der Reijden KJ**, Mestdagh S, Ysebaert T, Govers LL, Olff H, Herman PMJ, Snellen M, Simons DG (2020) Measuring centimeter-scale sand ripples using multibeam echosounder backscatter data from the Brown Bank area of the Dutch Continental Shelf. *Geosciences* 10, [495], <https://doi.org/10.3390/geosciences10120495>

Hintzen NT, Aarts G, Poos JJ, **van der Reijden KJ**, Rijnsdorp AD (2020) Quantifying habitat preference of bottom trawling gear. *ICES Journal of Marine Science*, fsaa207. <https://doi.org/10.1093/icesjms/fsaa207>

Tiano JC, **van der Reijden KJ**, O'Flynn S, Beauchard O, van der Ree S, van der Wees J, Ysebaert T, Soetaert K (2020) Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front. *Marine Environmental Research*, 159, [104964]. [https://doi.org/\(...\)arenvres.2020.104964](https://doi.org/(...)arenvres.2020.104964)

Mestdagh S, Amiri-Simkooei A, **van der Reijden KJ**, Koop L, O'Flynn S, Snellen M, van Sluis C, Govers LL, Simons DG, Herman PMJ, Olff H, Ysebaert T (2020) Linking the morphology and ecology of subtidal soft-bottom marine benthic habitats: A novel multiscale approach. *Estuarine, Coastal and Shelf Science*, 238, [106687]. [https://doi.org/\(...\)0/j.ecss.2020.106687](https://doi.org/(...)0/j.ecss.2020.106687)

Steins NA, Kraan M, **van der Reijden KJ**, Quirijns F, van Broekhoven W, Poos JJ (2019) Integration collaborative research marine science: Recommendations from an evaluation of evolving science-industry partnerships in Dutch demersal fisheries. *Fish and Fisheries*, 21(1), 146-161. <https://doi.org/10.1111/faf.12423>

Amiri-Simkooei A, Koop L, **van der Reijden KJ**, Snellen M, Simons DG (2019). Seafloor characterization using multibeam echosounder backscatter data: Methodology and results in the North Sea. *Geosciences*, 9(7), [292]. [https://doi.org/\(...\)0/geosciences9070292](https://doi.org/(...)0/geosciences9070292)

Koop L, Amiri-Simkooei A, **van der Reijden KJ**, O'Flynn S, Snellen M, Simons DG (2019). Seafloor classification in a sand wave environment on the Dutch continental shelf using multibeam echosounder backscatter data. *Geosciences*, 9(3), [142]. <https://doi.org/10.3390/geosciences9030142>

van der Reijden KJ, Koop L, O'Flynn S, Garcia S, Bos O, van der Sluis C, Maaholm DJ, Herman PMJ, Simons DG, Olff H, Ysebaert T, Snellen M, Govers LL, Rijnsdorp AD, Aquilar R (2019). Discovery of Sabellaria spinulosa reefs in an intensively fished area of the Dutch Continental Shelf, North Sea. *Journal of Sea Research*, 144, 85-94. <https://doi.org/10.1016/j.seares.2018.11.008>

van der Reijden KJ*, Damveld JH*, Cheng C, Koop L, Haaksma LR, Walsh CAJ, Soetaert K, Borsje BW, Govers LL, Roos PC, Olff H, Hulscher SJMH (2018). Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophysical Research Letters*, 45(21), 11837-11846. <https://doi.org/10.1029/2018GL079858>

van der Reijden KJ, Hintzen NT, Govers LL, Rijnsdorp AD, Olff H. (2018). North Sea demersal fisheries prefer specific benthic habitats. *PLoS ONE*, 13(12), [e0208338]. <https://doi.org/10.1371/journal.pone.0208338>

Christianen MJA, van der Heide T, Holthuijsen SJ, **van der Reijden KJ**, Borst ACW, Olff H (2017). Biodiversity and food web indicators of community recovery in intertidal shellfish reefs. *Biological Conservation*, 213(Part B), 317-324. <https://doi.org/10.1016/j.biocon.2016.09.028>

van der Reijden KJ, Molenaar P, Chen C, Uhlmann SS, Goudswaard PCK, van Marlen B (2017). Survival of undersized plaice (*Pleuronectes platessa*), sole (*Solea solea*), and dab (*Limanda limanda*) in North Sea pulse-trawl fisheries. *ICES Journal of Marine Science*, 74(6), 1672-1680. <https://doi.org/10.1093/icesjms/fsx019>

de Fouw J, Govers LL, van de Koppel J, van Belzen J, Dorigo W, Sidi Cheikh MA, Christianen MJA, **van der Reijden KJ**, van der Geest M, Piersma T, Smolders AJP, Olff H, Lamers LPM, van Gils JA, van der Heide T (2016). Drought, mutualism breakdown, and landscape-scale degradation of seagrass beds. *Current Biology*, 26, 1051-1056. <https://doi.org/10.1016/j.cub.2016.02.023>

van der Zee EM, Angelini C, Govers LL, Christianen MJA, Altieri AH, **van der Reijden KJ**, Silliman BR, van de Koppel J, van der Geest M, van Gils JA, van der Veer HW, Piersma T, de Ruiter PC, van der Heide T (2016). How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 283(1826), 1-9. <https://doi.org/10.1098/rspb.2015.2326>

* These authors contributed equally