



## Effects of chronic bottom trawling on benthic macrofaunal communities

McLavery, Ciarán

*Publication date:*  
2020

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

[Link back to DTU Orbit](#)

*Citation (APA):*  
McLavery, C. (2020). *Effects of chronic bottom trawling on benthic macrofaunal communities*. DTU Aqua.

---

### General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

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.



DTU Aqua  
National Institute of Aquatic Resources

Section for Ecosystem Based Marine Management & Danish Shellfish Centre

## Effects of chronic bottom trawling on benthic macrofaunal communities

Ciarán McLaverty

PhD thesis

December 2019

Supervisor:

Ole Ritzau Eigaard

Co-supervisors:

Grete Elisabeth Dinesen & Jens Kjerulf Petersen



Ministry of Environment  
and Food of Denmark



European Union  
European Maritime and Fisheries Fund



## **Preface**

This thesis was submitted as part of the requirements for the degree of Doctor of Philosophy (PhD) at the Technical University of Denmark. The research presented in this thesis was carried out at the National Institute for Aquatic Resources (DTU Aqua) under the supervision of Senior Researcher Ole Ritzau Eigaard, Senior Consultant Grete Elisabeth Dinesen (both Section for Ecosystem Based Marine Management), and Professor Jens Kjerulf Petersen (Danish Shellfish Centre). An external research stay was undertaken at the University Centre in Svalbard (UNIS), in association with the University of Tromsø (Norway), hosted by UNIS Adjunct Professor Paul Renaud.

Funding for this PhD project was provided by the European Marine Fisheries Fund, the Danish Ministry of Environment and Food, and DTU Aqua, through the projects “Udvikling af bæredygtig forvaltning af følsomme habitater og arter i Kattegat” and “Påvirkning af økosystemkomponenten bundfauna i N2000 områder ved fiskeri med skrabende redskaber”. Travel and participation in international conferences, workshops, and research stays were partly supported by additional funding from the Otto Mønsted Fund and a scholarship from the Anglo-Danish Society.

## Acknowledgements

I would like to firstly thank my supervisors, Ole Ritzau Eigaard, Grete Elisabeth Dinesen, and Jens Kjerulf Petersen. You have all provided me with a great deal of support, encouragement, and guidance over the past years. I am particularly thankful for the trust placed in me, and I look forward to working with you again in the future. I would also like to pay a very special thanks to Henrik Gislason, who has been a kind, funny, and knowledgeable mentor.

A very big thank you to the crew of the RV *Havfisken*; Aage, Rene, Søren and Jens, and to the crew of the RV *Egon P*; Lars, Finn, and Kasper. I would like to thank Louise, Stine, Annegrete for help in the lab, and the many (many) students who have sorted samples; Andreas, Irene, Liv, Miguel, Kat, Mendelos, Virginia, Aurelia, Alondra, Paula, Romy, and Xiaoyu. The work contained in the thesis would not have been possible without you guys. Also thanks to Lis, Linda, Chris, and Leif for helping me along way with countless little tasks. A big thanks also to Pernille, Camille, Alex, and Mollie for chats and guidance along the way.

To my office mates, Elliot, Gildas, Marie, Esther, Aurore, Daniel, Neil, Tim (x2), it's been fun! To Sieme, Tobi and Jon – you've been great friends throughout the PhD. A very special mention to Katrina who has been there every step of the way over the past year – I owe you a lot and look forward to paying it back. To Aidan – congrats on your graduation this year – your work ethic and enthusiasm is (and I'm not joking) inspiring. To Mum and Dad – you have unquestionably supported my meandering wanderings every step of the way, always with love and support, and I am forever grateful.

# Contents

<b>Abstract.....</b>	<b>i</b>
<b>Resume .....</b>	<b>iii</b>
<b>1. General Introduction .....</b>	<b>6</b>
1.1. <i>The benthos of marine sediments .....</i>	6
1.2. <i>Bottom trawling .....</i>	9
1.3. <i>Ecological effects of bottom trawling .....</i>	12
1.4. <i>Challenges to the assessment of trawling effects .....</i>	14
1.5. <i>Assessing trawling effects in Danish waters.....</i>	16
1.6. <i>Aims of the thesis .....</i>	20
<i>References .....</i>	21
<b>2. Synopsis .....</b>	<b>28</b>
2.1. <i>Local and regional effects of bivalve dredging in a eutrophic estuarine system.....</i>	28
2.2. <i>Large benthic macrofauna as benthic indicators of trawling disturbance.....</i>	29
2.3. <i>The sensitivity of benthic life history traits to trawling .....</i>	30
<i>References .....</i>	32
<b>3. General discussion.....</b>	<b>33</b>
3.1. <i>Size-based indicators.....</i>	33
3.2. <i>Response of taxonomic and functional indicators.....</i>	35
3.3. <i>Reference areas.....</i>	39
<i>References .....</i>	42
<b>4. Local and regional effects of bivalve dredging on benthic macrofauna in a eutrophic estuarine system .....</b>	<b>49</b>
4.1. <i>Introduction.....</i>	51
4.2. <i>Materials and methods .....</i>	54
4.3. <i>Results .....</i>	62
4.4. <i>Discussion.....</i>	69
<i>References .....</i>	76
<b>5. Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance .</b>	<b>87</b>
5.1. <i>Introduction.....</i>	90
5.2. <i>Materials and methods .....</i>	92
5.4. <i>Results.....</i>	100

5.5. Discussion.....	108
References.....	114
<b>6. The sensitivity of benthic life history traits to chronic trawling disturbance.....</b>	<b>128</b>
6.1. Introduction.....	130
6.2. Materials and methods.....	132
6.3. Results.....	139
6.4. Discussion.....	145
References.....	150
<b>Supplementary contributions .....</b>	<b>160</b>
<b>Appendices.....</b>	<b>161</b>
Appendix A: Bromhall et al.....	161
Appendix B: Nielsen et al.....	162
Appendix C: Burgass et al.....	163

## Abstract

Marine sediments constitute one of the largest ecosystems on earth. The animal life which inhabit these environments are known as benthic fauna, and represent a remarkable range of taxonomic and functional diversity. Bottom trawling is a fishing method where nets or collection devices are actively dragged over the seafloor to capture commercial fish or invertebrate species. Commercial bottom trawl fisheries account for roughly one quarter of global seafood landings, and results in the widespread and chronic disturbance of seafloor habitats. In recent years, growing societal concern of the wider effects of fisheries has prompted the adoption of an 'Ecosystem Approach to Fisheries Management' (EAFM). This has seen increased scientific interest and resources dedicated to the monitoring and assessment of fishery impacts to the wider ecosystem. Trawling impacts can, however, vary considerably across habitat type, fishing method, and environmental setting. Accordingly, an EAFM requires assessment methods that can 'disentangle' trawling effects from other natural and human drivers, and respond effectively to shifts in ecological quality.

The aim of the research outlined in this thesis was to examine which characteristics of benthic communities are most sensitive to bottom trawling. This was done using two intensive trawl fisheries in Denmark as case-studies; shellfish dredging in shallow coastal waters, and otter trawling for Norway lobster in the Kattegat. Detailed benthic sampling programmes were undertaken to survey and analyse the response of benthic communities along spatially accurate gradients of trawling intensity. The results are presented in three research papers, which form the basis this thesis.

In Danish nearshore waters, dredging for blue mussel and oysters constitutes the main bottom trawl fishery. However, the fishing grounds here overlap with several marine protected areas, which are characterised by shallow, estuarine, and highly eutrophic conditions. Using high resolution fishing effort data, we investigated the relative effects of chronic dredging on benthic macrofauna at local and regional scales. Dredging resulted in a significant negative effect on community biomass, and led to small but significant changes in community composition. However, we were unable to detect an effect of dredging to several community metrics, which may be explained by the widespread occurrence of several stress-tolerant and opportunistic taxa. Furthermore, the observed trends were shown to vary considerably at local scales, demonstrating the importance of small scale assessments in nearshore areas.

Benthic indicators are widely used in fisheries management to track and monitor the ecological effects of trawling. However, many widely used ecological indicators have been shown to be ineffective in this regard. Given that trawling impacts to benthos are typically size-dependent, we size-separated benthic samples into

small and large size fractions to investigate their respective sensitivity. We observed that indicators derived from large macrofauna were highly responsive to trawling disturbance, and were less influenced by other environmental drivers. By contrast, indicators based on small individuals performed poorly, and those based on the whole community demonstrated a varied ability to detect trawling. The results highlight an underlying issue with using indicators of trawling disturbance based on the whole benthic community, and show how large benthic macrofauna can be used to improve indicator performance.

Biological traits are being increasingly used to interpret how changes in species composition can impact the functionality of ecosystems. Despite this, there are few examples of trait-based indicators being used to monitor and manage trawling impacts. Using size-separated benthic macrofauna, we examined the sensitivity of individual benthic traits to bottom trawling. Benthic fauna which possess traits relating suspension feeding, tube-dwelling, a lack of mobility (sessile), and long-lifespans (>10 years) were particularly sensitive to trawling disturbance. We additionally validated our observations using an independent benthic monitoring dataset, and observed largely corresponding results. This would suggest that chronic bottom trawling has a strong negative effect on specific traits of benthic macrofauna, and that data collected from a carefully designed one-off sampling event can provide results which are representative of long-term datasets. Given the importance of several of the above traits in processes such as benthic-pelagic coupling and sediment stabilisation, it is likely that loss or decline of these traits can have considerable implications for ecosystem functioning.

The thesis demonstrates that chronic bottom trawling has a significant impact on the structure, composition, and functioning of benthic communities. In addition, we show that the detection of fishery effects is challenging, and can be obscured by other manmade and environmental pressures. By focussing on the characteristics of benthos which are most sensitive to trawling, we present a number of potentially reliable trawling indicators. The findings of this thesis are highly relevant to the management of trawl fisheries in Danish waters, and have the potential to improve methods currently used to assess and monitor fishery impacts and seafloor status at a wider scale.

## Resume

Marine sedimenter udgør et af de største økosystemer på jorden. Dyrelivet, der findes i disse miljøer, kaldes bentisk fauna. Disse bentske faunasamfund har en meget høj biodiversitet og er af stor betydning for det marine økosystems funktioner. Fiskeri med bundslæbende redskaber er en fiskemetode, hvor en netpose slæbes henover havbunden for at fange fisk eller skaldyr. Bundtrawlfiskeri tegner sig for cirka en fjerdedel af de globale landinger af fisk og skaldyr og resulterer i en udbredt og – i visse områder - intensiv forstyrrelse af havbundenes levesteder.

I de senere år har der været en stigende samfundsmæssig bekymring for fiskeriets påvirkning af det marine miljø. Dette har medført en bred accept og implementering af en økosystem-baseret tilgang til fiskeriforvaltning (i.e. Ecosystem Approach to Fisheries Management, EAFM), hvilket har øget den videnskabelige interesse for, og ressourcer dedikeret til, vurdering og overvågning af fiskeriets påvirkninger af økosystemet. Trawlfiskeriets effekt på den bentske fauna kan variere betydeligt på tværs af naturtyper, fiskemetoder og miljøforhold. Derfor forudsætter anvendelse af EAFM, at der udvikles metoder, som dels kan skelne mellem effekter fra bundtrawling i forhold til andre menneskelige påvirkninger og naturlige miljøforhold, og dels responderer tydeligt på ændringer i miljøtilstanden. Formålet med denne PhD afhandling har været at undersøge, hvilke karakteristika ved bundfaunanen, der udviser størst følsomhed overfor påvirkninger fra bundtrawling. Undersøgelsen baserede sig primært på to videnskabelige studier: et som omhandler fiskeri med skrabere efter blåmuslinger i de indre danske farvande, og et om fiskeri med bundtrawl efter jomfruhummere i Kattegat. For begge fiskerier blev der taget kvantitative grabbeprøver af bundfauna og sediment langs en gradient af fiskeripåvirkning. Analyserne af bundfaunaens respons på forskellige påvirkningsgrader danner grundlaget for de tre videnskabelige artikler, der er beskrevet i PhD afhandlingen.

I de danske, kystnære havområder er fiskeriet med muslingeskrabere efter blåmuslinger og østers et af de væsentligste. Fiskepladserne i dette fiskeri overlapper med flere naturbeskyttede havområder, der er kendetegnet ved at være lavvandede, have lavt saltindhold og være meget nærringsaltberigede (eutrofe). I analysen af muslingefiskeriets var det muligt at anvende fiskerimoniteringsdata med meget høj rumlig og tidlig opløsning til at undersøge langtidseffekterne af muslingefiskeriet på bundfaunaen på både lokal og regional skala. Vi observerede, at selvom de bentske samfund var domineret af stresstolerante og opportunistiske arter, medførte fiskeriet en signifikant reduktion af bundfaunasamfundenes samlede biomasse målt på regional skala. Endvidere viste det sig, at effekten varierede betydeligt på len mere lokal

skala (de enkelte naturbeskyttelsesområder), hvilket viser vigtigheden af at anvende lokalskala-niveau i vurdering og monitorering af de kystnære havområders miljøtilstand.

Bentiske indikatorer anvendes i den marine miljø- og fiskeriforvaltning til at overvåge miljøtilstanden og til at vurdere påvirkningen fra bundtrawling. Flere af de mest anvendte indikatorer har dog vist sig, at være ineffektive med hensyn til at påvise fiskeribetingede ændringer af de bentiske faunasamfund. Ud fra en hypotese om, at effekterne af bundtrawling på den bentiske fauna er størrelsesafhængig, opdelte vi indsamlede bundfaunaprøver i en lille og stor størrelsesfraktion for at undersøge deres respektive følsomhed overfor bundtrawling. Vi observerede, at indikatorer baseret på de store individer var meget følsomme overfor trawling, mens de var mindre påvirkede af andre miljøfaktorer. I modsætning hertil var indikatorer baseret på små individer væsentlig dårligere til at opfange påvirkninger fra bundtrawling. Indikatorer baseret på hele samfundet, det vil sige både de store og små individer, udviste varierende evne til at opfange påvirkningen fra bundtrawling. Analysen påpegede således et underliggende problem med anvendelse af indikatorer, der er baseret på hele det bentiske samfund, og demonstrerede at en fokusering på de store individer kan forbedre indikatorens ydeevne.

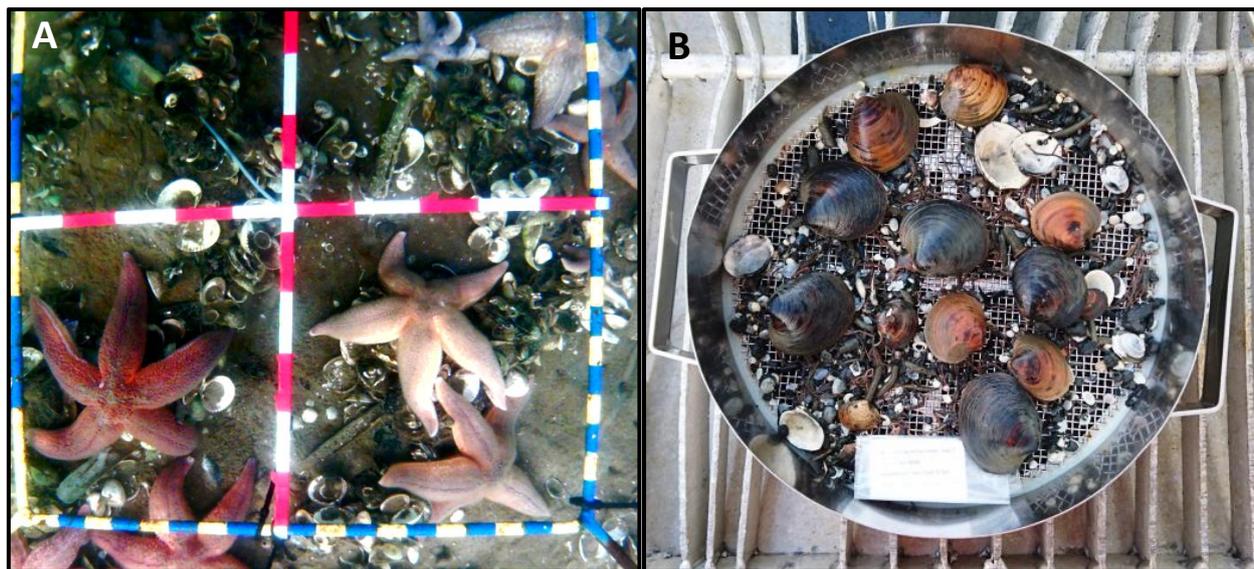
Biologiske karaktertræk bruges i stigende grad til at fortolke, hvordan ændringer i artssammensætning kan påvirke økosystemernes funktionalitet. Alligevel er der indtil nu kun få eksempler på, at karaktertræk-baserede indikatorer bruges til at vurdere og overvåge påvirkninger fra bundtrawling. Vi brugte størrelses-opdelt bentisk makrofauna til at undersøge følsomheden af individuelle karaktertræk overfor påvirkning fra bundtrawling. Bundfauna med følgende biologiske karaktertræk suspensionsernæring, overfladesediment-aflejrende, rør-boende og fastsiddende levevis, og >10 års maksimal levetid, var især følsomme over for forstyrrelse fra bundtrawling. Det var forventet at de fleste af disse karaktertræk udviste følsomhed overfor bundtrawling, men en rør-boende levevis er ikke tidligere blevet identificeret som følsom overfor fiskeriforstyrrelse. Vi validerede vores resultater ved hjælp af et uafhængigt monitoringsdatasæt med bentisk makrofauna, og fandt at analyserne af dette data sæt udviste tilsvarende resultater. Dette antyder, at kronisk bundtrawling har en stærk negativ effekt på specifikke biologiske karaktertræk hos bentisk makrofauna, og at øjeblikksbilleder af bundfaunaen, indsamlet i omhyggeligt tilrettelagte forsøgsdesign i forhold til fiskeripåvirkninger, kan give resultater, der er repræsentative for informationen indeholdt i datasættet indsamlet over længere tidsperioder. I betragtning af vigtigheden af flere af de ovennævnte træk i økosystemprocesser såsom kobling af energiudveksling mellem bunden og vandmassen over (bento-pelagisk kobling), samt stabilisering af sedimentet, er det sandsynligt, at tab eller tilbagegang af disse karaktertræk kan have betydelige konsekvenser for økosystemets funktion.

Tilsammen demonstrerer de tre databaserede undersøgelser beskrevet i denne afhandling, hvordan kronisk bundtrawling påvirker taksonomiske og funktionelle egenskaber hos bentiske makrofaunasamfund. Dette resultat blev opnået ved at analysere sensitiviteten af forskellige bentiske indikatorer overfor fiskeripåvirkning samt fiskeriets effekter på faunasammensætning, individuelle faunaarter og faunakaraktertræk. Disse effekter er blevet analyseret på tværs af intensitetsgradienter af kommercielt bundtrawlfiskeri i kystnære og åbne havområder, med forskellige miljøforhold og bentiske levesteder. Resultaterne af denne PhD afhandling har stor relevans for miljø- og fiskeriforvaltningen i danske farvande og har potentiale til at forbedre de metoder og indikatorer, der i øjeblikket anvendes til at vurdere og overvåge fiskeripåvirkning og havbundsstatus på international skala.

## **1. General Introduction**

### **1.1. The benthos of marine sediments**

Marine sediments constitute one of the largest ecosystems on earth (Snelgrove 1998) covering roughly 80% of the seafloor (Lenihan & Micheli 2001). Although often appearing featureless, sedimentary habitats contain a remarkably high diversity of marine life, and facilitate a range of marine and global ecosystem processes. The animals that inhabit the seafloor are referred to as benthic fauna (collectively known as the benthos), and are typically categorised according to their lifestyle or feeding modes. Benthos which burrow into the sediment and live within its physical matrix are known as infauna, while epifauna live on or attached to the sediment surface. Epifauna associated with soft sediments are typically less specious than infauna, but are relatively large and either mobile or sessile, such as starfish, decapods, and sponges (Figure 1-1 a). In contrast, the infauna are diverse and represent a large proportion of all invertebrate phyla. Characteristic taxa include bivalves, gastropods, echinoderms, polychaetes, flatworms, and small crustaceans. Such taxa are often highly abundant across a range of sediment types, and employ a wide variety of associated life history strategies (Figure 1-1 b). Aside from taxonomic grouping, infauna are normally categorised by their size. While the thresholds of these categories can differ slightly between studies, the infauna are generally categorised as benthic microfauna (<0.063mm), meiofauna (0.063mm - 1mm), and macrofauna (>1mm) (Gulliksen et al., 2009).



**Figure 1-1: Examples of benthic (a) epifauna and (b) infauna. Visible epifauna in (1-1 a) include common starfish *Asterias rubens* and blue mussels *Mytilus edulis*. Image acquired in Løgstør Broad, Limfjorden (April 2017). Visible infauna in (1-1 b) include the ocean quahog *Arctica islandica*, brittlestars *Amphiura sp.*, tube building polychaetes (e.g. *Spiophanes sp.*) and several species of small bivalve (e.g. *Kurtiella bidentata*). Sample collected in southern Kattegat (September 2016).**

The scientific sampling of benthic fauna is normally undertaken using grab samplers, core samplers, and dredges/trawls. Dredges and trawls were used exclusively prior to the early 1900s, and provide a relatively crude estimation of benthic abundance, diversity, and biomass. Although useful over large spatial scales, dredges and trawls are not spatially explicit and can only provide semi-quantitative assessments of the benthos. At the turn of the 20<sup>th</sup> century, the Danish fisheries scientist C.G.J. Petersen began to pioneer the use of benthic grab samplers. Although simple in design, benthic grabs are able to sample a distinct area of seabed, and allow for quantitative descriptions of benthic fauna. This represented a significant step forward in the study of benthic ecology, and allowed Peterson to achieve his goal of quantifying the distribution of benthos as a food resource for important commercial fish species. While carrying out this work in the coastal waters of Denmark, Peterson also noticed that distinctive groups of taxa would regularly occur in association with a particular habitat type. He subsequently used these fauna to formally describe distinctive benthic community types (Lie, 1968), and thus undertook some of the earliest research in the development of marine community ecology (Pearson et al., 1985). The concept of what represents an ecological ‘community’, and its explicit definitions, have since generated considerable debate (Ricklefs, 2008). While a strict consensus may not yet have been reached, there is a widely accepted interpretation that communities are groups of

species bound to a given location, shaped by their environment, and connected by a network of interdependence (Leveque, 2003; Barros, 2016).

### ***Factors structuring benthic communities***

The structure and function of benthic communities are governed by a combination of abiotic (e.g. environmental conditions) and biotic processes (e.g. ecological niche requirements of member species) (Gray & Elliot, 2009). The environmental conditions are considered to be the main structuring force of communities over large spatial scales, but decrease in importance at a local scale. Conversely, species interactions (e.g. predation and competition) are less important over larger areas, yet may account for small-scale differences in distribution. The extent to which biotic interactions shape communities in marine sediments has proven more difficult to demonstrate (Thrush and Dayton, 2002). This may be as interactions occur in a three-dimensional medium, and thus the vertical and horizontal partitioning of space results in less frequent encounters, unlike in rocky or hard bottom habitats. In addition, it has proven difficult to experimentally separate the effects of abiotic processes and rates of competition and predation in soft sediments (Wilson, 1990).

The manner to which soft sediment communities vary with respect to abiotic processes is, however, comparatively predictable. This is because benthic communities are relatively stable and stationary over time, and benthic species tend to exhibit specific tolerances to environmental variables (e.g. sediment type, salinity, temperature). Accordingly, the proportions of different species within a community will vary between areas and across environmental gradients. These subtle but ecologically important changes in species composition can be easily measured with modern statistical methods, and therefore patterns in benthos can be mechanistically linked to the type and strength of ambient environmental pressures (Gray et al., 2006). A classic example of such a stressor-response pattern has been described for benthic communities exposed to chronic eutrophication (Pearson and Rosenberg, 1978). Under the Pearson and Rosenberg model, benthic diversity will initially increase and then decline under increasing nutrient input, while the abundance of stress tolerant taxa increase (Pearson & Rosenberg 1978).

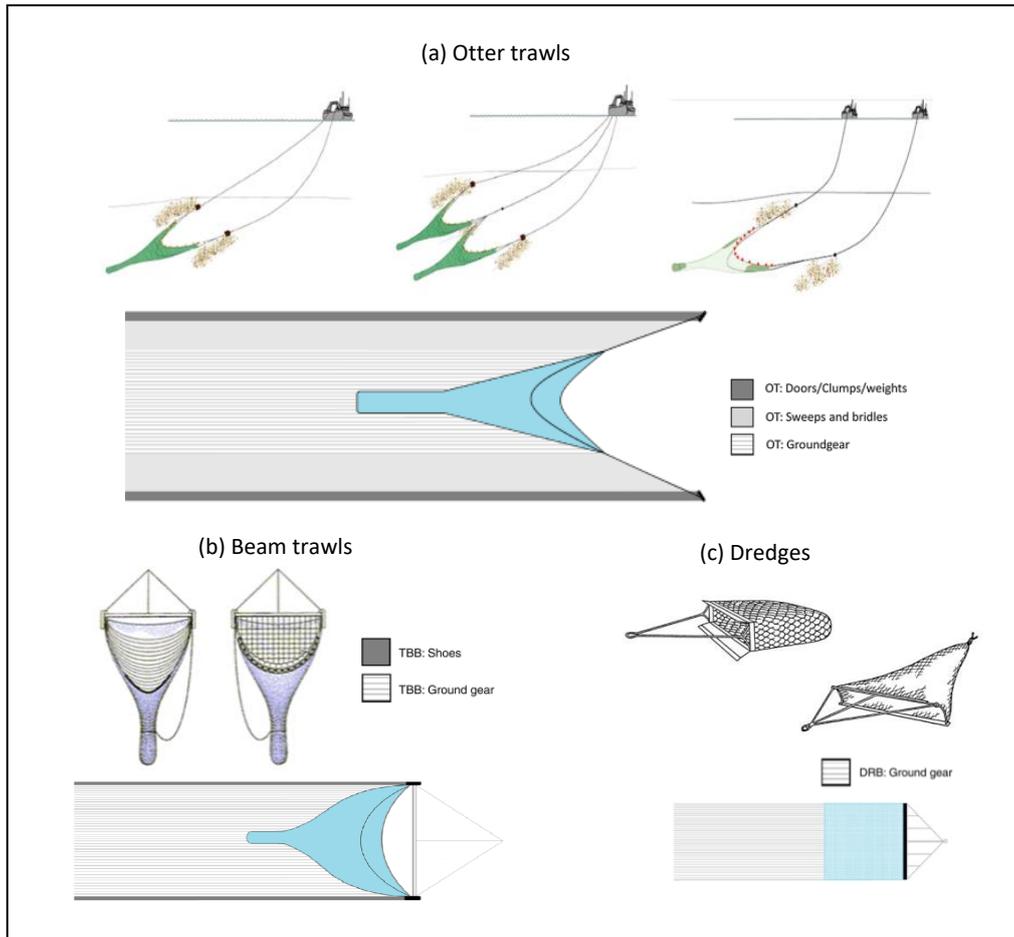
### ***Functional importance of benthic communities***

While it has proven difficult to accurately quantify the links between benthic diversity and ecosystem function (Bolam and Fernandes, 2002; Ieno et al., 2006), higher diversity is generally thought to improve the functionality of benthic ecosystems (Belley and Snelgrove, 2016). Furthermore, community or population biomass is also positively linked to functional capacity (Norkko et al., 2013). The benthos play an important role in ecosystem processes because of their feeding activity, in particular. This may be via the physical

reworking of sediments by selective and non-selective deposit feeders (i.e. bioturbation) or by filter feeding (by e.g. oysters and mussels). The filtration capacity of suspension feeders is considerable, and it has been suggested that the exploitation of oyster populations on the U.S. east coast led to a 200-fold decline in water filtration capacity. This decline has also been linked to large-scale phytoplankton blooms and poor water clarity (Kemp et al., 2005). In Danish fjords, the filtration capacity of blue mussels has been estimated to be between 23 to 180 m<sup>3</sup> m<sup>-2</sup> day<sup>-1</sup>, which equates to the filtration of the entire water column several times a day (Dolmer and Frandsen 2002). Deposit feeding infauna are primarily responsible for the oxygenation and irrigation of marine sediments, and bioturbation by benthic macrofauna play a role in key the consumption, remineralisation and sequestering of carbon and nitrogen (Queirós et al., 2013). The scale of this activity is thought to significantly affect global carbon budgets (Snelgrove, 1998). Of particular relevance to fisheries science is the role that benthos play in benthic-pelagic coupling, i.e. the coupling and exchange of energy, mass and nutrients between benthic and pelagic ecosystems (Griffiths et al., 2017). The conversion of energy generated from primary production into benthic biomass is known as benthic secondary production. This process is a key building block of marine food webs, and provides important food sources for human consumption (Snelgrove, 1998). However, secondary production and the functional capacity of benthic ecosystems are vulnerable to environmental and anthropogenic pressures (Bolam et al., 2017; S. G. Bolam et al., 2014; Cusson and Bourget, 2005).

## **1.2. Bottom trawling**

Bottom trawling constitutes one of the most widespread forms of anthropogenic pressure to marine benthic environments (Halpern et al., 2008). During this process, nets or other collection devices are actively dragged over the seabed to capture commercial fish or invertebrate species. The use of bottom trawls dates back hundreds of years, as do the concerns about how they affect seabed habitats. Concerns raised in the English Parliament about the adverse effects of trawling are recorded from as early as during the 14<sup>th</sup> century (Groot, 1984). While these early concerns were associated with sail-powered vessels, the introduction of steam powered trawlers in the late 1880s changed the dynamics of the fishery, allowing for the widespread use of heavier and larger gear types (Graham, 1938). Today, trawl gears are still widely used, and trawl fisheries are currently estimated to account for 19 million tonnes of seafood annually, or around 25% of global seafood landings (FAO, 2016). The most widely used gear types in bottom trawling include otter trawls, beam trawls, and dredges (collectively referred to as bottom trawls in this thesis) (Figure 1-2).



**Figure 1-2: Widely used bottom trawling gears. These include (a) otter trawls, (b) beam trawls and (c) dredges. Illustrations provided above and conceptual gear footprints below. OT = otter trawl, TBB = beam trawl, and DRB = dredge. Illustrations of gears from FAO: <http://www.fao.org/fishery/geartype/search/en>. Gear footprints modified from Buhl-Mortensen et al., (2013) and Eigaard et al., (2016).**

A demersal otter trawl is a cone shaped net that is towed by either one or two fishing vessels. The mouth of the trawl is held open horizontally by two otter boards, and vertically by a floating headline and by a ground rope (Figure 1-2 a). The ground rope is usually equipped with rubber discs or bobbins that allow the ground rope to move over the seabed, and avoid snagging or damage. This allows otter trawls to be used in both soft and coarse substrates. The deepest sediment penetration of the configuration is from the trawl doors, which can dig furrows of up to 35cm deep in soft sediments (Eigaard et al. 2016). Otter trawling results in a relatively large gear footprint on the seabed (doors may be up to 200m apart in large vessels), and is typically used to catch demersal fish species (whitefish and flatfish) as well as benthic invertebrates (Norway lobster *Nephrops norvegicus*). The nets used in beam trawls are smaller than in otter trawls, as they are restricted by the width of the beam which holds the net open (Figure 1-2 b). The beam generally does not reach widths greater than 12m, meaning that the beam trawl result in a smaller gear footprint than the otter trawl. The beam is held in

place by a shoe on either side of the gear, and when fishing for flatfish tickler chains attached to the ground gear scares the target species into the net. Both tickler chains and beam shoes can generate furrows of up to 10 cm depth in the sediment (Eigaard et al., 2016). Beam trawls are usually deployed in sandy and flat sedimentary habitats, and are typically used to catch flatfish species and some shrimp species. Dredges are the smallest of the three gear types in terms of spatial footprint, typically up to 2m in width, but can be deployed in varying numbers and gear set-ups (Figure 1-2 c). For scallop fishing, the front of the ground gear is often equipped with dredge teeth, which dig the scallops from just below the sediment surface. The penetration depth of the dredge is up to 6 cm in soft sediments (Eigaard et al., 2016), but this is highly dependent on the weight of the gear employed, which can vary between fisheries. Dredges can be used in a variety of sedimentary habitats, and are almost exclusively used to catch molluscs (oysters, clams, scallops and mussels).

### ***Estimating trawling pressure on benthic communities***

Spatially accurate fishing effort data are required to study the effects of trawling on benthic ecosystems (Rijnsdorp et al., 1998). Prior to the 2000s, fishing effort data were only available from EU vessel logbooks, and recorded at the scale of the ICES rectangles. This was problematic for those interested in the benthic effects of fishing, as ICES rectangles are large areas (approx. 30 x 30 nautical miles in northern Europe) and trawling activity is highly patchy, even at a scale of kilometres (Rijnsdorp et al., 1998). Coupled to this, benthic sampling is undertaken at a scale of meters, and therefore several orders of magnitude below that of a rectangle (Jennings et al., 2001b). Vessel monitoring systems (VMS) were introduced in the early 2000s as a mandatory on-board surveillance device for EU vessels (Hintzen et al. 2012). VMS data typically include information regarding the geographic coordinates and heading of a vessel, but are only transmitted every 1-2 hours, depending on EU member state requirements (every 1 hour in Denmark). In its raw form, the data can be used to describe the density of fishing activity, however additional processing can be undertaken to reconstruct trawl tracks and fishing footprints. This is done by combining the VMS points with gear information stored in the logbooks and interpolating between the individual data points (Hintzen et al., 2012; Eigaard et al. 2017). These methods have allowed for the investigation of trawling effort at a range of spatial scales, with recent improvements allowing for the estimation of trawling at a scale of 250 m (Sköld et al., 2018). However, as the temporal frequency of the VMS data is limited (1 or 2 pings every hour), the estimation of fishing effort at fine spatial scales is vulnerable to any error in the interpolation method. While some studies have acquired 'high-poll-rate data' (in agreement with the data providers) to test a specific hypothesis (Lambert et al., 2012), the vast majority of studies use processed VMS data provided by national fisheries institutes, typically analysed at a spatial resolution of 1nm x 1nm. Furthermore, VMS data are only

available for vessels  $\geq 12\text{m}$  in length, meaning that assessment undertaken in any areas with large numbers of smaller fishing vessels are likely to considerably underestimate trawling effort.

### ***Bottom trawling in the context of an ecosystem approach to management***

The traditional approach to fisheries management was centred on the assessment of fishery effects to the health and sustainability of the target species. The decline of numerous fish stocks (Worm et al., 2009) and the damage to marine systems (Crain et al., 2009) over the past century have raised questions about the validity of this approach (Gislason et al., 2000), and prompted growing societal and scientific concern regarding the wider effects and sustainability of fishing. This has seen the adoption of an ecosystem approach to fisheries management (EAFM) in recent years (Garcia et al., 2003). An EAFM aims to sustain healthy marine ecosystems and the fisheries that they support. Hence EAFM considers not only the health of the target species, but also the effects of fishing on non-target bycatch species, the structure and integrity of the seafloor, benthic communities, and wider trophic links (Kaiser et al., 2002). Trawling impact studies are therefore required to inform and guide an EAFM. The examination of fleet-level (or chronic) trawling impacts is particularly useful in this regard, and can reveal how commercial trawling activity impacts benthic macrofauna at local, regional, and ecosystem scales. We still, however, lack evidence regarding the effects of chronic trawling across all habitat types, and the potential interaction between trawling and other anthropogenic and natural drivers. As bottom trawl fisheries move into previously unfished environments, such as deep-water or polar areas, ecosystem-based research will be required to understand and predict potential ecosystem effects of bottom trawling (Hinz et al., 2009).

### **1.3. Ecological effects of bottom trawling**

The understanding of how trawling impacts benthic communities has greatly improved in recent years. Trawling can disturb benthos in several ways e.g. by causing changes to the biogeochemistry sediments (Sciberras et al., 2016), reduced structural complexity (Watling and Norse, 1998), resuspension of sediments (Duplisea et al., 2001), smothering of benthic organisms (Dayton et al., 1995), reduced water quality (Riemann and Hoffmann, 1991), or through direct contact with the trawl gear (Bergman and Van Santbrink, 2000; Rumohr and Krost, 1991). Trawling impacts are measured via a range of methods, and the way in which this is done can reveal different aspects of how communities respond to trawling.

#### ***Experimental vs. chronic trawling impact studies***

The impacts of trawling on the benthos are typically quantified using two main approaches; experimental and gradient (chronic) studies. Experimental impact studies sample the benthos before and after a trawling event, and usually takes the form of a BACI design (before-after-control-impact) (Underwood, 1992, Bromhall

et al. Appendix A). These experiments, in theory, allow for trawling to take place in controlled conditions, and can be used to describe small-scale (kilometres) and short-term (months) effects of trawling in ‘unfished’ conditions. Accurate information can be gathered regarding the immediate effects of trawling (e.g. direct mortality) and also be used to describe recovery times. However, experimental studies are often unable to replicate the effort and spatial scales of disturbance that result from chronic fishing (i.e. the effect of commercial fishing fleets). For this reason, experimental studies may be unable to describe ecosystem-level impacts, and the results of these studies must be carefully interpreted (Atkinson et al., 2011; Hinz et al., 2009).

Chronic impact studies form the basis of this thesis, and examines the long-term (years) and large-scale (kms) trawling effects that typically occur across fishing grounds. Sampling effort is typically concentrated across gradients of trawling pressure on comparable habitat. The introduction of VMS data has enabled the wider application of this type of study, without the need to use proxies of trawling effort (e.g. Kaiser et al., 2000). Chronic impact studies can be used to describe benthic community response to the cumulative effects of trawling over large areas, and thus test the predictions generated from experimental studies (Hinz et al., 2009). These studies are also more capable of describing the recovery dynamics of communities over large spatial scales. However, such studies are often resource demanding due to the large areas investigated, survey vessel time, and the numbers of samples required. Chronic impact studies are therefore relatively uncommon, and tend to be undertaken in areas that receive higher research funding. This has meant that the chronic effects of fishing at global scale remains poorly understood.

### ***Meta-analyses of trawling impact studies***

In recent years, comprehensive meta-analyses have helped synthesise the results of trawling impact studies. Meta-analyses are particularly useful at describing the overall direction and magnitude of change observed across studies in a standardised manner, while also benefiting from increased statistical power compared to one-off studies. Using this approach, Kaiser et al. (2006) demonstrated for the first time that trawling effects are highly habitat and fishing gear dependent. The results of this study revealed that while scallop dredging may exert a strong negative effect to the benthos regardless of habitat type, the effect of beam trawls varied significantly across habitats. The reason that trawling effects are so variable is explained by two main factors; (i) the penetration depth of the gear; and (ii) the sensitivity of the resident community to physical disturbance. In general, depletion rates are highly correlated with trawl penetration depth (Hiddink et al., 2017; Sciberras et al., 2018); i.e. the deeper the penetration of the trawl gear into the sediment, the higher the degree of disturbance and the greater the likelihood of biota coming into contact with the trawl gear. The sensitivity of the benthos is also habitat dependent. Depending on the ambient environmental

conditions, the community will be composed of varying proportions of stress-tolerant species and sensitive species. For example, benthic communities which occur in wave exposed sandy habitats are likely to be more resilient to trawling due to the greater proportions of small, short-lived, and free-living infauna found in these areas (Bolam et al., 2017; Tillin et al., 2006).

### ***Impacts of trawling on functional characteristics***

Bottom trawling alters the abundance (Gislason et al., 2017), diversity (Sköld et al., 2018), biomass (H. Reiss et al., 2009), and size-composition (Queirós et al., 2006) of benthic communities. Until recently, studies interested in the assessment of trawling impacts have focussed mainly on the taxonomic attributes of the community, in particular species richness. However, this approach has several limitations (J. Reiss et al., 2009) and taxonomic approaches are unable to convey information regarding ecosystem processes. Biological traits are now being increasingly used to describe the life history characteristics of communities and thus how changes in community composition can affect the functionality of the ecosystem (Bremner et al., 2005). Trait-based approaches can also help describe mechanisms of sensitivity, and therefore disentangle the ecological effects of multiple stressors (Bremner et al., 2006a). Trait-based research of trawling impacts has shown that the vulnerability of benthos is chiefly linked to aspects such as their position in the sediment, their fragility, longevity, and the frequency, method and fecundity of spawning (Bremner et al., 2005; de Juan et al., 2007; Rijnsdorp et al., 2018; Tillin et al., 2006). Less frequently trawled areas tend to contain higher proportions of filter-feeding, attached, hard bodied (exoskeleton), and large-bodied benthos. Conversely, small-bodied, deposit-feeding, mobile, and scavenging species are typically more abundant in highly fished areas (Tillin et al., 2006). These trawling-associated changes in trait composition may also have direct and indirect implications for the functioning of benthic ecosystems (Sciberras et al., 2016), although there is currently a lack of research supporting this.

### **1.4. Challenges to the assessment of trawling effects**

As our understanding of trawling impacts has advanced, studies have revealed various co-varying and interacting factors which can potentially mask the response of the community. As outlined above, trawling effects vary across habitat types and the gear used, but also in relation to auxiliary environmental drivers. Benthic habitats exposed to high levels of natural physical disturbance (i.e. high shear stress, wave action) are generally characterised by coarse sediments (such as sands and gravel) and low organic content in the interstitial waters. As grain size and sorting define the physical medium in which the infauna subsist, these aspects are particularly strong drivers of community composition. Coarse sediments would typically be inhabited by communities dominated by species tolerant to physical disturbance, sharing life-history traits

such as small body sizes, non-selective feeding strategies, early maturity, and large numbers of offspring (Van Denderen et al., 2015). By contrast, low energy environments found in sheltered and deep-water areas are often characterised by finer sediment particles and high silt content. These sediment properties are generally associated with lower oxygen levels and high organic content in interstitial waters. Accordingly, communities observed in these habitats are often dominated by organisms which may be sensitive to physical disturbance, and share traits such as late maturity and large body-size (Bremner et al., 2006b). As bottom trawl fisheries are often aggregated in nearshore and shelf areas (Amoroso et al., 2018), it may become difficult to ‘disentangle’ the effects of fishing from the intrinsic variability of these systems (Sciberras et al., 2013; Szostek et al., 2016). Although less well studied, the effects of trawling have also been shown to be difficult to demonstrate in estuarine conditions (Gibbs et al., 1980). Recent work from transitional waters bodies such as the Baltic Sea has shown that low-salinity areas mainly consist of short-lived species, and that these areas are therefore relatively resilient to the effects of trawling and hypoxia (van Denderen et al., 2019). Due to the similar effects of natural disturbance and trawling, benthic communities found across fishing grounds may strongly resemble naturally disturbed communities (Szostek et al., 2016; Van Denderen et al., 2015), which therefore can distort the results of trawling impact studies.

Furthermore, widespread bottom trawling has occurred along continental shelves for decades (Thurstan et al., 2010). This is problematic from the perspective of trawling impact studies, as adequate reference areas or defined gradients of disturbance are often lacking in coastal areas (de Juan et al., 2009). This issue ultimately limits the capacity of researchers to link benthic community components to trawling effort, and renders the results of assessments less meaningful.

### ***Need for benthic indicators***

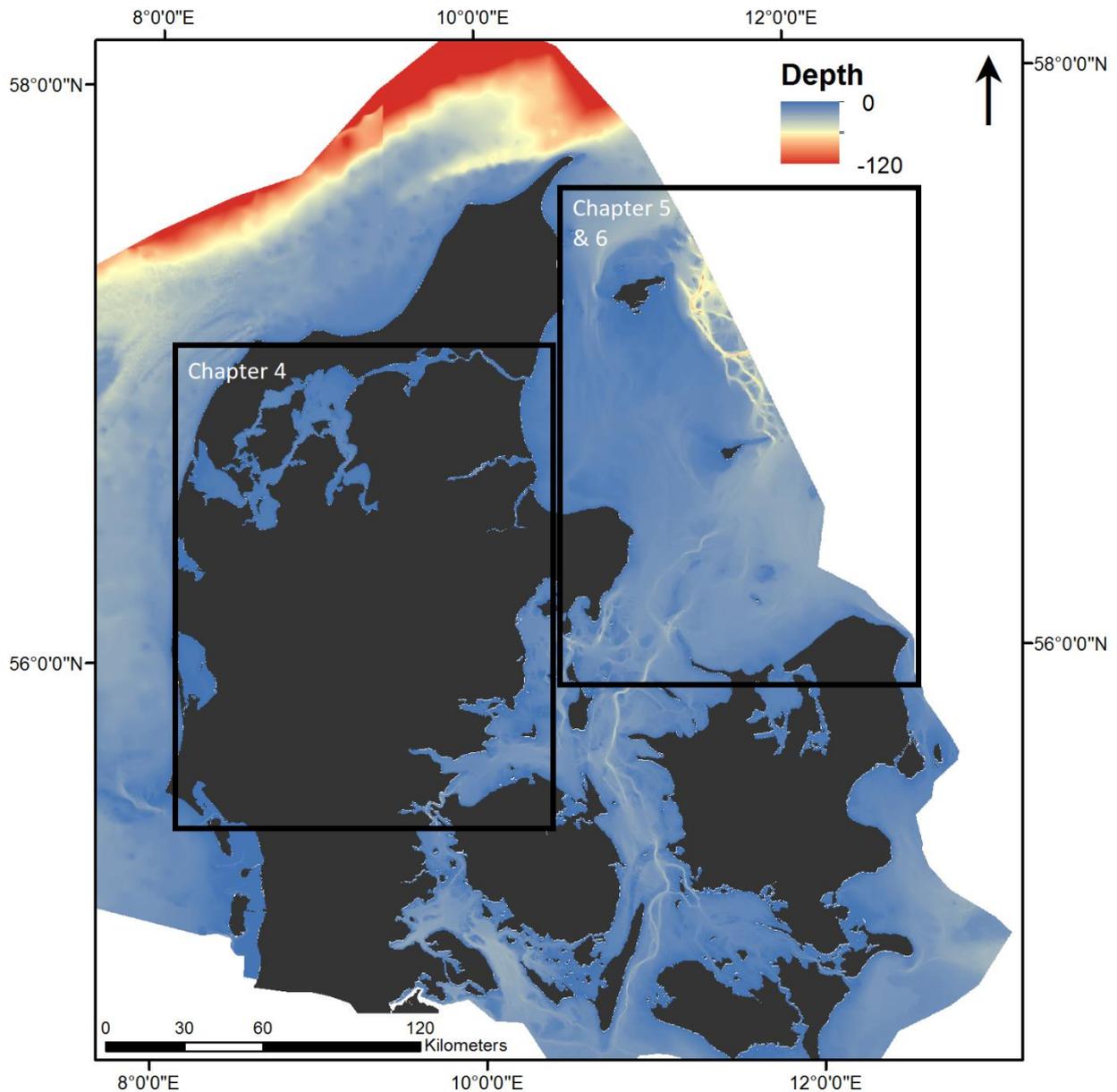
The implementation of the European Union Water Framework Directive (Anon. 2000) and the Marine Strategy Framework Directive (Anon. 2008) has led to increased monitoring of benthic communities in European waters (Nielsen et al, Appendix B). Under these directives, the status of benthic ecological quality are required in relation to a range of anthropogenic pressures (Rice et al., 2012; Van Hoey et al., 2010). Ecological indicators are often favoured in this regard as they are easily calculated and monitored, and allow complex information to be presented in a simple manner to a range of stakeholders (Jorgensen et al., 2013). However, for indicators to be effective, they must be able to link specific anthropogenic pressures to changes in ecological quality. Furthermore, they should not be overly affected by short-term variation or auxiliary environmental drivers. A clear link between anthropogenic pressure and indicator response is of great importance, as the successful management of ecologically adverse pressures is often dependent on the strength and quality of scientific evidence. If the links between pressures and responses are weak, managers

will be unlikely to act and apply change. The risk of this happening may be exacerbated in areas where ecologically damaging pressures are economically, politically or socially important (Gislason et al., 2017).

## **1.5. Assessing trawling effects in Danish waters**

### ***Background***

Denmark is one of the largest fish producing nations in Europe, and among the 20 largest exporters of fish and shellfish products in the world (Skov et al., 2019). Commercial fisheries take place in the North Sea, Skagerrak, Kattegat, Baltic Sea, as well as the Inner Danish waters and Limfjorden. Although landings have decreased sharply in recent years, the main fisheries for herring, sprat, mackerel, cod, flatfish, Norway lobster, blue mussel, and industrial species (sand eel, sprat and Norway pout) contribute to total landings of roughly 800,000 t year<sup>-1</sup> (Skov et al. 2019). In terms of gear type, bottom trawls dominate fishing effort (kilowatt-days) in Danish waters (Skov et al., 2019). The widespread use and importance of bottom trawls in Denmark therefore present several challenges to an EAFM. To highlight the needs of evidence-based management advice, and to provide context for the hypotheses and research objectives examined in this thesis, some of the main issues relating to trawling impact assessment in Danish waters are outlined in the following sections. In addition, two of the most intensive trawl fisheries in Denmark are introduced as case studies, one located in nearshore areas (Chapter 4) and the other in offshore areas (Chapter 5 & 6) (Figure 1-3).



**Figure 1-3: Danish waters and approximate study areas for the case studies.**

***National monitoring stations***

During the 1980s, a series of hypoxic events in the Kattegat, Belt Seas, and the Sound (Øresund) generated considerable public and scientific awareness regarding the deterioration of environmental and water quality in Danish waters (Conley et al., 2006; Ehrhardt and Wenck, 1984). Significant changes to environmental legislation came about as a response, and a harmonised national aquatic monitoring programme (known today as the NOVANA programme) was established (Conley et al., 2006). This programme represents one of

the most comprehensive aquatic monitoring programmes in the world. A key aim of the programme is to monitor nutrient enrichment in marine and freshwater areas (Svendsen et al., 2005). Sampling of benthic macrofauna takes place annually, with a focus on areas which are susceptible to low oxygen levels. The NOVANA programme has been used to assess the effectiveness of marine management measures under the Water Framework Directive (WFD), and now includes monitoring for the Marine Strategy Framework Directive (MSFD) and for sites within the Natura 2000 network of protected areas. (Jensen et al. 2016). The relevance of this from a fisheries management perspective is that the locations of these monitoring stations do not necessarily correspond with the range and distribution of trawling effort in Danish waters, and recent fisheries impact assessments using these data sets have produced mixed results (Gislason et al., 2017; Pommer et al., 2016). The spatial mismatch between monitoring stations and fishing pressure has been cited as a reason for this. Furthermore, this mismatch may present a hindrance to assessing the ecosystem effects of trawl fisheries in Danish waters, and in the fulfilment of monitoring commitments under the MSFD and the EU Habitats and Birds Directives (for Natura 2000 sites).

### ***Environmental gradients***

Danish waters are located in the transitional zone between the brackish Baltic Sea and the more marine North Sea. As a result, considerable salinity gradients exist across the NOVANA monitoring stations. This represents a potential challenge for benthic monitoring and the use of benthic indicators, as salinity is likely to be an important structuring driver of benthic communities in Danish waters (Conley et al., 2006). This issue is highlighted in a study by Gislason et al (2017), who examined the performance of several benthic indicators in detecting trawling impacts in Danish waters. The results demonstrated that several of the indicators adopted for monitoring purposes under the WFD, such as the Danish Quality Indicator (DKI), are poor indicators of trawling disturbance. One of the reasons for this is that variation may be unintendedly incorporated into these multimetric indicators during their calculation. Although a salinity standardisation is included in the DKI, the potential effects of other pressures (e.g. trawling, eutrophication, and hypoxia) are not considered at the salinity reference stations. Furthermore, indices such as the AMBI index (Borja et al. 2000) and unrefined species diversity (Shannon diversity) are used in the calculation of indicators such as the DKI. Given that the AMBI index can be a poor indicator of physical disturbance (Muxika et al., 2005), and that the use of unrefined species richness in the calculation of indicators can be highly problematic (see Gislason et al., (2017) for discussion), there is a need to test and develop new indicators. Ideally, these indicators should be able to effectively detect anthropogenic pressures, such as bottom trawling, and remain unaffected by auxiliary environmental drivers.

**PhD case studies**

In Danish nearshore and coastal areas ( $\leq 20$  m), dredging for blue mussel *Mytilus edulis* is associated with relatively high bottom trawling effort as well as significant landings (Gislason et al., 2014). This fishery chiefly occurs in Limfjorden and the Inner Danish waters (Figure 1-3), where lightweight dredges are used to exploit wild blue mussel and oyster stocks and collect blue mussel seed for cultivation. The bivalve fisheries generate landings of roughly 25 - 40,000 t year<sup>-1</sup>, yet several of the fishing grounds overlap with Natura 2000 areas, protected for a range of bird species and habitat types. This aspect has led to increased public and regulatory scrutiny of the fishery. In addition, the fishery primarily takes place in waters typical of many Danish estuaries i.e. shallow, with short residence times, high variability in physio-chemical conditions, and low oxygen levels (Conley et al., 2006). As fishing impacts can be difficult to detect and monitor in these environmental conditions, the situation presents a number of challenges to an EAFM (Dolmer and Frandsen, 2002). In Chapter 4 of this thesis, we examine the relative effects of dredge fisheries across and within these Natura 2000 areas.

In offshore areas ( $>20$  m), bottom trawling effort is dominated by the Norway lobster *Nephrops norvegicus* (and mixed bycatch) fishery (Gislason et al., 2014). This fishery takes place almost exclusively over muddy and sandy muds in the Kattegat and Skagerrak (Figure 1-3). *Nephrops* are gathered using demersal otter trawls and associated landings are roughly of 30,000 t year<sup>-1</sup>. The Kattegat represents a transitional sea separating the North Sea and Baltic Sea, and seabed conditions are characterised by significant gradients in depth, salinity, temperature, and current velocity. Further to this, significant trawl fisheries have taken place in the Kattegat for over 100 years (Petersen, 1918), and today the Kattegat is considered heavily trawled at a European (Eigaard et al., 2017) and global scale (Amoroso et al., 2018). It has been suggested that this level of historical fishing activities has led to significant changes in the composition and depth range of the resident benthic macrofauna (Josefson et al., 2018; Sköld et al., 2018). Although changes in community composition have been observed, several studies have either been unable to detect trawling impacts using standard indicators (Pommer et al., 2016), or the ability of indicators to detect trawling has been highly varied (Gislason et al., 2017; Sköld et al., 2018). This may suggest that trawling has deteriorated the community to such an extent that impacts are no longer detectable, or that the suite of indicators currently used to detect trawling effects in the Kattegat perform poorly. In Chapter 5 of this thesis, we test the performance of several community indicators, and investigate if their performance can be improved. In Chapter 6, we examine the functional characteristics of benthic communities and examine if individual benthic traits can act as effective indicators of trawling disturbance.

## **1.6. Aims of the thesis**

The overarching aim of this thesis is to determine which characteristics of benthic communities are the most sensitive to bottom trawling. To do this, I designed and executed two large-scale benthic sampling programmes. They were planned around spatially accurate gradients of trawling intensity, and accounted for key environmental gradients that may significantly influence community composition. As I intended to examine the effect of trawling on ecological condition and benthic functionality, I have combined both taxonomic and functional approaches in each of the research papers.

More specifically, the aim of Chapter 4 was to investigate the relative effects of mussel dredging on benthos in a shallow water system subject to high levels of natural and anthropogenic disturbance. Trends were observed at a regional scale (across the fishery) and at a local scale (within each Natura 2000 site).

In Chapter 5, I tested the performance of several widely used ecological indicators of bottom trawling disturbance. In addition, I examined whether the performance of these indicators could be improved by using only the large benthic fauna in their calculation.

Finally, in Chapter 6 I investigate (i) which benthic traits exhibit the strongest relationships with environment and trawling intensity in the Kattegat, and (ii) validate my snapshot sampling approach by comparing the results to a long-term monitoring dataset.

## References

- Amoroso RO, Pitcher CR, Rijnsdorp AD, McConnaughey RA, Parma AM, Suuronen P, Eigaard OR, Bastardie F, Hintzen NT, Althaus F, Baird SJ, Black J, Buhl-Mortensen L, Campbell AB, Catarino R, Collie J, Cowan JH, Durholtz D, Engstrom N, Fairweather TP, Fock HO, Ford R, Gálvez PA, Gerritsen H, Góngora ME, González JA, Hiddink JG, Hughes KM, Intelmann SS, Jenkins C, Jonsson P, Kainge P, Kangas M, Kathena JN, Kavadas S, Leslie RW, Lewis SG, Lundy M, Makin D, Martin J, Mazor T, Gonzalez-Mirelis G, Newman SJ, Papadopoulou N, Posen PE, Rochester W, Russo T, Sala A, Semmens JM, Silva C, Tsolos A, Vanelslander B, Wakefield CB, Wood BA, Hilborn R, Kaiser MJ, Jennings S (2018) Bottom trawl fishing footprints on the world's continental shelves. *Proc Natl Acad Sci* 115:E10275–E10282.
- Anon (2000) Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for the Community action in the field of water policy (Water Framework Directive).
- Anon (2008) Directive 2008/56/EC of the European Parliament and of the Council establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive).
- Atkinson L, Field J, Hutchings L (2011) Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages. *Mar Ecol Prog Ser* 430:241–255.
- Barros F. (2016) Soft Sediment Communities. In: Kennish M.J. (eds) *Encyclopedia of Estuaries*. Encyclopedia of Earth Sciences Series. Springer, Dordrecht.
- Belley R, Snelgrove PVR (2016) Relative Contributions of Biodiversity and Environment to Benthic Ecosystem Functioning. *Front Mar Sci* 3.
- Bergman MJN, Van Santbrink JW (2000) Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. In: *ICES Journal of Marine Science*. p 1321–1331.
- Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) 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.
- Bolam SG, Fernandes TF (2002) Dense aggregations of tube-building polychaetes: Response to small-scale disturbances. *J Exp Mar Bio Ecol* 269:197–222.
- Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, van Kooten T, Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Van Hoey G, Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar Environ Res* 126:1–13.
- Borja A, Franco J, Pérez V (2000) A marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Mar Pollut Bull* 40:1100–1114.
- Bremner J, Frid CLJ, Rogers SI (2005) Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? *Am Fish Soc Symp* 41:477–489.

Bremner J, Rogers S, Frid C (2006a) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecol Indic* 6:609–622.

Bremner J, Rogers SI, Frid CLJ (2006b) Matching biological traits to environmental conditions in marine benthic ecosystems. *J Mar Syst* 60:302–316.

Conley DJ, Kaas H, Møhlenberg F, Rasmussen B, Windolf J (2000) Characteristics of Danish estuaries. *Estuaries* 23:820–837.

Crain CM, Halpern BS, Beck MW, Kappel C V. (2009) Understanding and managing human threats to the coastal marine environment. *Ann N Y Acad Sci* 1162:39–62.

Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic habitats. *Mar Ecol Prog Ser* 297:1–14.

Dayton PK, Thrush SF, Agardy MT, Hofman RJ (1995) Environmental effects of marine fishing. *Aquat Conserv Mar Freshw Ecosyst* 5:205–232.

de Juan S, Demestre M, Thrush S (2009) Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: A Mediterranean case study. *Mar Policy* 33:472–478.

de Juan S, Thrush SF, Demestre M (2007) Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Mar Ecol Prog Ser* 334:117–129.

Dolmer P, Frandsen RP (2002) Evaluation of the Danish mussel fishery: Suggestions for an ecosystem management approach. *Helgol Mar Res* 56:13–20.

Duplisea DE, Jennings S, Malcolm SJ, Parker R, Sivyer DB (2001) Modelling potential impacts of bottom trawl fisheries on soft sediment biogeochemistry in the North Sea Presented during the ACS Division of Geochemistry symposium ?Biogeochemical Consequences of Dynamic Interactions Between Benthic Fauna, Microbes and Aqu. *Geochem Trans* 2:112.

Ehrhardt M, Wenck A (1984) Wind pattern and hydrogen sulfide in shallow waters of the Western Baltic Sea, a cause and effect relationship? *Meeresforschung* 30:101–110.

Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O'Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sørensen TK, Tully O, Zengin M, Rijnsdorp AD (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J Mar Sci* 73:i27–i43.

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanellander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *ICES J Mar Sci* 74:847–865.

Food and Agriculture Organization of the United Nations (FAO) (2016) The state of the World fisheries and aquaculture: contributing to food security and nutrition for all. FAO, Rome, Italy.

- Garcia, S. M., Zerbi, A., Aliaume, C., Do Chi, T., and Lasserre, G. (2003) The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. FAO Fisheries Technical Paper, 443. 71 pp.
- Gibbs P, Collins A, Collett L (1980) Effect of otter prawn trawling on the macrobenthos of a sandy substratum in a New South Wales estuary. *Mar Freshw Res* 31:509.
- Gislason H, Bastardie F, Dinesen GE, Egekvist J, Eigaard OR (2017) Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. *Ecol Indic* 82:260–270.
- Gislason, H., Dalskov, J., Dinesen, G. E., Egekvist, J., Eigaard, O., Jepsen, N., Larsen, F., Poulsen, L. K., Sørensen, T. K. & Hoffmann, E. 2014. Miljøskånsomhed og økologisk bæredygtighed i dansk fiskeri. DTU Aqua-rapport nr. 279-2014. Institut for Akvatiske Ressourcer, Danmarks Tekniske Universitet. 83 pp + bilag
- Gislason H, Sinclair M, Sainsbury K, O'boyle R (2000) Symposium overview: Incorporating ecosystem objectives within fisheries management. In: *ICES Journal of Marine Science*. p 468–475
- Graham M (1938) The trawl fisheries: A scientific and national problem. *Nature* 142:1143–1146.
- Gray, J. S., & Elliott, M., 2009. Ecology of marine sediments: from science to management. Oxford University Press.
- Gray JS, Dayton P, Thrush S, Kaiser MJ (2006) On effects of trawling, benthos and sampling design. *Mar Pollut Bull* 52:840–843.
- Griffiths JR, Kadin M, Nascimento FJA, Tamelander T, Törnroos A, Bonaglia S, Bonsdorff E, Brüchert V, Gårdmark A, Järnström M, Kotta J, Lindegren M, Nordström MC, Norkko A, Olsson J, Weigel B, Žydelis R, Blenckner T, Niiranen S, Winder M (2017) The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. *Glob Chang Biol* 23:2179–2196.
- Groot SJ De (1984) The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Manag* 9:177–190.
- Gulliksen B., Hop H. & Nilsen M. 2009. Benthic life. In E. Sakshaug et al. (eds.): *Ecosystem Barents Sea*. Pp. 167-208. Trondheim: Tapir Academic Press.
- Halpern BS, Walbridge S, Selkoe KA, Kappel C V., Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* (80- ) 319:948–952.
- Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazar T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci* 114:8301–8306.
- Hintzen NT, Bastardie F, Beare D, Piet GJ, Ulrich C, Deporte N, Egekvist J, Degel H (2012) VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fish Res* 115–116:31–43.

Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: Chronic effects and experimental predictions. *Ecol Appl* 19:761–773.

Ieno E, Solan M, Batty P, Pierce G (2006) How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Mar Ecol Prog Ser* 311:263–271.

Jennings S, Pinnegar J, Polunin N, Warr K (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Mar Ecol Prog Ser* 213:127–142.

Jensen, P.N., Boutrup, S., Fredshavn, J.R., Nielsen, V.V., Svendsen, L.M., Blicher-Mathiesen, G., Thodsen, H., Johansson, L.S., Hansen, J.W., Nygaard, B., Sogaard, B., Holm, T.E., Ellermann, T., Thorling, L. & Holm, A.G. 2016. Vandmiljø og Natur 2015 NOVANA. Tilstand og udvikling - faglig sammenfatning. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, 56 s. - Videnskabelig rapport fra DCE – Nationalt Center for Miljø og Energi nr. 211

Jorgensen SE, Burkhard B, Müller F (2013) Twenty volumes of ecological indicators-An accounting short review. *Ecol Indic* 28:4–9.

Josefson AB, Loo LO, Blomqvist M, Rolandsson J (2018) Substantial changes in the depth distributions of benthic invertebrates in the eastern Kattegat since the 1880s. *Ecol Evol*:1–13.

Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2002) Modification of marine habitats by trawling activities: Prognosis and solutions. *Fish Fish* 3:114–136.

Kaiser MJ, Ramsay K, Richardson CA, Spence FE, Brand AR (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. *J Anim Ecol* 69:494–503.

Kaiser M, Clarke K, Hinz H, Austen M, Somerfield P, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14.

Kemp WM, Boynton WR, Adolf JE, Boesch DF, Boicourt WC, Brush G, Cornwell JC, Fisher TR, Glibert PM, Hagy JD, Harding LW, Houde ED, Kimmel DG, Miller WD, Newell RIE, Roman MR, Smith EM, Stevenson JC (2005) Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. *Mar Ecol Prog Ser* 303:1–29.

Lambert GI, Jennings S, Hiddink JG, Hintzen NT, Hinz H, Kaiser MJ, Murray LG (2012) Implications of using alternative methods of vessel monitoring system (VMS) data analysis to describe fishing activities and impacts. *ICES J Mar Sci* 69:682–693.

Lenihan, H. S. and F. Micheli. (2001) Soft-sediment communities. In, *Marine Community Ecology* (M. D. Bertness, S. D. Gaines, and M. E. Hay, eds.), pp. 253–287. Sunderland, MA: Sinauer Associates.

Leveque C. (2003) Dynamics of communities and ecosystems. *Ecology From Ecosystem to Biosphere*. Enfield, NH: Science Publishers Inc. pp. 216–221.

Lie, U. (1968) A quantitative study of benthic infauna in Puget Sound, Washington. USA, in 1963-1964. *FiskDir. Skr. Ser. Havunders.* 14: 229-556.

- Muxika I, Borja Á, Bonne W (2005) The suitability of the marine biotic index (AMBI) to new impact sources along European coasts. *Ecol Indic* 5:19–31.
- Norkko A, Villnäs A, Norkko J, Valanko S, Pilditch C (2013) Size matters: Implications of the loss of large individuals for ecosystem function. *Sci Rep* 3:2646.
- Pearson TH, Josefson AB, Rosenberg R (1985) Petersen's benthic stations revisited. I. Is the Kattegatt becoming eutrophic? *J Exp Mar Bio Ecol* 92:157–206.
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol An Annu Rev* 16:229–311.
- Petersen CGJ (1918) The sea bottom and its production of fish food. A survey of the work done in connection with the valuation of the Danish waters from 1883-1917. *Rep Danish Biol Station* 25: 1–62.
- Pommer C, Olesen M, Hansen J (2016) Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. *Mar Ecol Prog Ser* 548:47–60.
- Queirós AM, Birchenough SNR, Bremner J, Godbold JA, Parker RE, Romero-Ramirez A, Reiss H, Solan M, Somerfield PJ, Van Colen C, Van Hoey G, Widdicombe S (2013) A bioturbation classification of European marine infaunal invertebrates. *Ecol Evol* 3:3958–3985.
- Queirós AM, Hiddink JG, Kaiser MJ, Hinz H (2006) Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. *J Exp Mar Bio Ecol* 335:91–103.
- Reiss H, Greenstreet SPR, Sieben K, Ehrich S, Piet GJ, Quirijns F, Robinson L, Wolff WJ, Kröncke I (2009) Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. *Mar Ecol Prog Ser* 394:201–213.
- Reiss J, Bridle JR, Montoya JM, Woodward G (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol Evol* 24:505–514.
- Rice J, Arvanitidis C, Borja A, Frid C, Hiddink JG, Krause J, Lorance P, Ragnarsson SÁ, Sköld M, Trabucco B, Enserink L, Norkko A (2012) Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. *Ecol Indic* 12:174–184.
- Ricklefs RE (2008) Disintegration of the ecological community. *Am Nat* 172:741–750.
- Riemann B, Hoffmann E (1991) Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. *Mar Ecol Prog Ser* 69:171–178.
- Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol Appl* 28:1302–1312.
- Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (1998) 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. In: *ICES Journal of Marine Science*. p 403–419

Rumohr H, Krost P (1991) Experimental evidence of damage to benthos by bottom trawling with special reference to *Arctica islandica*. *Meeresforschung/Rep Mar Res* 33:340–345.

Sciberras M, Hiddink JG, Jennings S, Szostek CL, Hughes KM, Kneafsey B, Clarke LJ, Ellis N, Rijnsdorp AD, McConnaughey RA, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2018) Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish* 19:698–715.

Sciberras M, Hinz H, Bennell JD, Jenkins SR, Hawkins SJ, Kaiser MJ (2013) Benthic community response to a scallop dredging closure within a dynamic seabed habitat. *Mar Ecol Prog Ser* 480:83–98.

Sciberras M, Parker R, Powell C, Robertson C, Kröger S, Bolam S, Geert Hiddink J (2016) Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. *Limnol Oceanogr* 61:2076–2089.

Sköld M, Göransson P, Jonsson P, Bastardie F, Blomqvist M, Agrenius S, Hiddink JG, Nilsson HC, Bartolino V (2018) Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Mar Ecol Prog Ser* 586:41–55.

Skov, C., Berg, S., Eigaard, O.R., Jessen, T.K. and Skov, P., (2019) Danish fisheries and aquaculture: past, present and future. *Fisheries*.

Snelgrove PVR (1998) The biodiversity of macrofaunal organisms in marine sediments. *Biodivers Conserv* 7:1123–1132.

Strain EMA, Allcock AL, Goodwin CE, Maggs CA, Picton BE, Roberts D (2012) The long-term impacts of fisheries on epifaunal assemblage function and structure, in a Special Area of Conservation. *J Sea Res* 67:58–68.

Svendsen, L.M. & Norup, B. (eds.) 2005: NOVANA. Nationwide Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments. Programme Description – Part 1. National Environmental Research Institute, Denmark. 53 pp. – NERI Technical Report No. 532

Szostek CL, Murray LG, Bell E, Rayner G, Kaiser MJ (2016) Natural vs. fishing disturbance: Drivers of community composition on traditional king scallop, *Pecten maximus*, fishing grounds. *ICES J Mar Sci* 73:i70–i83.

Thrush SF, Dayton PK (2002) Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. *Annu Rev Ecol Syst* 33:449–473.

Thurstan RH, Brockington S, Roberts CM (2010) The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nat Commun* 1.

Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45.

Underwood AJ (1992) Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *J Exp Mar Bio Ecol* 161:145–178.

Van Denderen PD, Bolam SG, Friedland R, Hiddink JG, Norén K, Rijnsdorp AD, Sköld M, Törnroos A, Virtanen EA, Valanko S (2020) Evaluating impacts of bottom trawling and hypoxia on benthic communities at the local, habitat, and regional scale using a modelling approach. *ICES J Mar Sci* 77:278–289.

Van Denderen PD, Bolam SG, Hiddink JG, Jennings S, Kenny A, Rijnsdorp AD, Van Kooten T (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar Ecol Prog Ser* 541:31–43.

Van Hoey G, Borja A, Birchenough S, Buhl-Mortensen L, Degraer S, Fleischer D, Kerckhof F, Magni P, Muxika I, Reiss H, Schröder A, Zettler ML (2010) The use of benthic indicators in Europe: From the water framework directive to the marine strategy framework directive. *Mar Pollut Bull* 60:2187–2196.

Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conserv Biol* 12:1180–1197.

Wilson WH (1990) Competition and predation in marine soft-sediment communities. *Annu Rev Ecol Syst* 21:221–241.

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA, Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PM, McClanahan TR, Minto C, Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R, Zeller D (2009) Rebuilding Global Fisheries. *Science* (80- ) 325:578–585.

## 2. Synopsis

### 2.1. Local and regional effects of bivalve dredging in a eutrophic estuarine system

Dredges are a type of bottom trawl primarily used in scallop, oyster, and blue mussel fisheries (FAO, 2016). Although relatively compact and of low spatial footprint, dredging can be associated with high macrofaunal mortality and deep sediment penetration (Hiddink et al., 2017). However, the impacts of dredging on benthic macrofauna can be variable across habitat types or environment settings. In Denmark, infralittoral populations of blue mussel *Mytilus edulis*, European flat oyster *Ostrea edulis*, and Pacific oyster *Crassostrea gigas*, are exploited by dredge fisheries in Limfjorden and Inner Danish waters. These areas are similar to many other Danish estuaries i.e. exhibiting short residence times, variable physico-chemical conditions, high levels of eutrophication, and being predominantly shallow and brackish (Conley et al., 2006). The mussel and oyster fishing grounds also overlap with several Natura 2000 (N2000) sites protected for various benthic habitat features. While experimental and comparative studies have investigated the short-term effects of mussel and oyster dredging in Danish waters, little is known about the ecosystem effects of chronic dredging, and how benthic macrofauna are affected along gradients of fishing disturbance in these dynamic systems.

Using ultra-high resolution fisheries data (~10m x 10m) we investigated the effects of chronic dredging on benthic macrofauna at both local (Natura 2000 site) and regional (fishery wide) scales. The results indicated that community biomass and community composition were significantly impacted by dredging. This decline was mainly accounted for by the loss of biomass of several large-bodied taxa (e.g. *Arctica islandica*, *Modiolus modiolus*, *Nephtys hombergii*, and *Alittla virens*) recorded in areas unaffected by both dredging (>10 years) and regular oxygen depletion. The trend, however, varied across the N2000 sites, with biomass exhibiting both positive and negative relationships with dredging intensity. An apparent positive relationship between dredging and biomass was observed in the Lovns Broad N2000 site, a basin which experiences chronic eutrophication and regular anoxic events. This result demonstrates the importance of local scale assessments in nearshore fisheries management.

In general, eutrophication had a strong effect on macrofaunal communities across the study area, with many sampling sites being characterised by high abundances of stress-tolerant and opportunistic taxa. This may explain why we were unable to detect an effect of dredging on metrics such as community density, functional richness, or trait composition. In general, the strongest responses to trawling were observed in N2000 sites which contained areas which had been subject to long-term fisheries closures. Based on this, we suggest that the monitoring and management of the fishery may benefit from the designation of reference areas within

the fishing grounds of each N2000 site. In summary, the results demonstrate how a detailed sampling program, high resolution fisheries data, and suitable reference areas can be used to detect specific fishery-related effects in highly stressed estuarine systems.

## **2.2. Large benthic macrofauna as benthic indicators of trawling disturbance**

Bottom trawling alters the abundance, diversity, size-composition, and function of benthic communities. Growing societal concern regarding fisheries effects has prompted the adoption of an ‘Ecosystem Approach to Fisheries Management’ (EAFM) (FAO, 2003) in the European Union. By definition, an EAFM requires assessments of human impacts at the level of species, communities, and ecosystems to guide management advice. Ecological indicators are often a favoured instrument in this regard as they are easily calculated, monitored, and interpreted. However, in order to be effective, indicators should be sensitive to changes in ecological state, capture and convey information on the ecosystem, and not be overly affected by short-term variation or auxiliary drivers. In addition to this, the detection of fishery impacts over large spatial scales can be obscured by various complicating factors, such as community adaptation to disturbance and co-varying environmental conditions. Such factors can obscure the measurable effects of trawling in benthic communities, and may explain why benthic indicators sometimes display varied performance (Atkinson et al., 2011; Kaiser et al., 1998; Mangano et al., 2014). Although size-based indicators are widely applied in the monitoring of fish communities (Greenstreet et al., 2011; Shin et al., 2005), their application in benthic systems has received relatively less attention.

We collected benthic macrofaunal samples at 21 sites across a Norway lobster *Nephrops norvegicus* fishing ground in the Kattegat, and separated the benthic community into small (1-4mm) and large (>4mm) size fractions. Four taxonomic indicators (total density, species density, Shannon diversity, and biomass) and four functional indicators (functional diversity, functional richness, functional evenness, and functional dispersion) were calculated based on each of the size fractions, as well as the two fractions combined (pooled community). The objective of this study was to explore if the performance of these indicators of trawling disturbance would improve if they were based on large macrofauna, rather than the whole community.

Our results show that macrofaunal indicators based on the pooled community demonstrated a varied performance, with four of the eight indicators exhibiting a significant negative response to trawling. This suggests that the standard approach of calculating benthic indicators using the whole macrofaunal community may be unsuitable for the assessment of trawling impacts. Conversely, each of the eight indicators based on large macrofauna declined significantly with trawling. Furthermore, these indicators were less influenced by other environmental drivers, such as depth, sediment grain size, bottom current

velocity, salinity, and temperature. By contrast, indicators derived from the small fraction performed poorly. Small macrofauna are typically characterised by high density, diversity, and population growth rates, and their relative resilience to trawling may mask the response of the more sensitive macrofauna. Together, these observations indicate that benthos displays a size-dependent sensitivity to trawling, and indicators based on body-size thresholds are able to better capture this sensitivity. By size-separating the community, improved indicator performance was achieved from numerically reduced subset of the whole community, comprising some 22% of all individuals and 52% of taxa. Considering this, we estimate that the time required to sort, identify, and estimate biomass for just for the large fraction, would have reduced the total laboratory processing time by approximately 75% compared with processing the entire community.

### **2.3. The sensitivity of benthic life history traits to trawling**

Traits are increasingly used in community ecology to characterise species composition (McGill et al., 2006) and to interpret how changes in the relative abundance of species can affect the functionality of systems (Bremner et al., 2005). In contrast to taxonomic methods, trait-based approaches can describe the physiological, behavioural, morphological, and life-history characteristics of communities, and therefore the vulnerability of communities to disturbance (Mouillot et al., 2013; Beauchard et al., 2017). While the longevity of benthic fauna has been successfully used to describe the sensitivity of benthic communities to trawling (Hiddink et al., 2018; Rijnsdorp et al., 2018), there are few other examples of the adoption of trait-based indicators in the monitoring and management of trawling impacts.

Community-weighted mean (CWM) traits describe the average trait value of species present in a sample, weighted by their relative biomass, and can therefore be used as univariate indicators (Beauchard et al., 2017). In this study we build upon the work outlined in Section 2.2, and use size-separated benthic data to compare the relative sensitivity of traits to trawling disturbance across size fractions. Ten candidate CWM traits were extracted from trait composition data using multivariate ordinations. This was done by calculating correlation coefficients between individual traits and the ordination axis that explained the majority variation in the data. This revealed that trawling had a relatively greater effect on the traits of large macrofauna, compared to the traits of small fauna, or traits based on the full community (large and small fractions combined).

CWM traits were subsequently analysed using generalised linear mixed models (GLMMs), and revealed that seven of the ten candidate traits exhibited a significant negative relationship with trawling. These traits spanned a number of trait categories, and included traits relating to feeding mode (suspension feeders), living habitat (tube-dwelling), sediment position (6-10cm deep), reproduction mode (planktotrophic larvae),

longevity (>10 year), bioturbation mode (surface deposition), and mobility (sessile). Given the importance of many of these traits in processes such as benthic-pelagic coupling, the results would suggest that trawling in the Kattegat is capable of significantly impacting the functionality of regional benthic ecosystems.

To investigate if the results were representative of chronic trawling impacts which occur over multiple years, we also investigated the sensitivity of these traits in a separate long-running monitoring (NOVANA) dataset. With the exception of one trait (suspension feeders), the same traits showed a significant negative response to trawling in the NOVANA data. These functional attributes may therefore be in a chronically disturbed state as a result of bottom trawling. Furthermore, this result suggests that a carefully designed one-off sampling event can provide results which are representative of long-term datasets.

## References

Atkinson LJ, Field JG, Hutchings L (2011) Effects of demersal trawling along the west coast of southern Africa: Multivariate analysis of benthic assemblages. *Mar Ecol Prog Ser* 430:241–255.

Beauchard O, Veríssimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecol Indic* 76:81–96.

Bremner J, Frid CLJ, Rogers SI (2005) Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? *Am Fish Soc Symp* 41:477–489.

Conley DJ, Kaas H, Møhlenberg F, Rasmussen B, Windolf J, Mohlenberg F, Windolf J (2006) Characteristics of Danish Estuaries. *Estuaries* 23:820.

Greenstreet SPR, Rogers SI, Rice JC, Piet GJ, Guirey EJ, Fraser HM, Fryer RJ (2011) Development of the EcoQO for the North Sea fish community. *ICES J Mar Sci* 68:1–11.

Hiddink JG, Jennings S, Sciberras M, Bolam SG, Cambiè G, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Parma AM, Suuronen P, Kaiser MJ, Rijnsdorp AD (2018) Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J Appl Ecol* 56:1075–1084.

Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci* 114:8301–8306.

Kaiser MJ, Edwards DB, Armstrong PJ, Radford K, Lough NEL, Flatt RP, Jones HD (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES J Mar Sci* 55:353–361.

Mangano MC, Kaiser MJ, Porporato EMD, Lambert GI, Rinelli P, Spanò N (2014) Infaunal community responses to a gradient of trawling disturbance and a long-term Fishery Exclusion Zone in the Southern Tyrrhenian Sea. *Cont Shelf Res* 76:25–35.

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185.

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends Ecol Evol* 28:167–177.

Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, Denderen PD van, Kooten T van (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol Appl* 28:1302–1312.

Shin YJ, Rochet MJ, Jennings S, Field JG, Gislason H (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J Mar Sci* 62:384–396.

### 3. General discussion

This thesis has demonstrated how chronic bottom trawling affects the taxonomic and functional properties of benthic macrofaunal communities, in terms of community indicators, community composition, and the response of individual species and traits. To achieve this, data were collected across wide gradients of commercial fishing effort in Danish waters. I have examined the relative effect of shellfish dredging in a eutrophic estuarine system (Chapter 4), the response of benthic biological traits to otter trawling in deeper offshore waters (Chapter 6), and presented a new method to refine and improve ecological indicators used to determine the impact on benthos arising from bottom trawling disturbance (Chapter 5). The following sections outline the main findings of the research conducted for the thesis. The potential implications of these findings are discussed from a fisheries management and monitoring perspective, as well as out of general academic interest.

#### 3.1. Size-based indicators

##### *Does size matter?*

The results of this thesis consistently demonstrate a strong effect of trawling on large-bodied macrofauna. In Limfjorden and Inner Danish waters, the biomass of vulnerable macrofauna were relatively high at unfished sites, or where dredging was infrequent. In the Kattegat, it was observed that benthic communities recorded at heavily fished areas were composed of relatively fewer and smaller benthic fauna, while the proportion of macrofauna over  $\geq 4$  mm in length was significantly greater in the unfished areas. These results suggest that while the whole community may be affected by bottom trawling, the impacts are disproportionately severe for larger-bodied individuals and species. From the perspective of an ecosystem approach to fisheries management, large macrofauna are functionally important members of the community. The presence of large individuals significantly improves local sedimentary characteristics, benthic biogeochemical fluxes, and community dominance structures (Thrush et al., 2006). Furthermore, it has been shown that large macrofauna may be more functionally important to ecological processes than the density or diversity of associated macrofauna (Norkko et al., 2013). In addition, a remarkable number of ecological processes scale in a simple and consistent manner with body-size (West et al., 1997). This can be explained as body-size is a 'master trait', due to its correlation with most other life history traits (Kiørboe et al., 2018). Size is easily measured and quantified, and represents a fundamental structuring force across marine systems (Andersen et al., 2016). Being unbound to taxonomic identity, body-size can also be used to compare communities from ecosystems with entirely different species compositions. So, it can be said that

size matters considerably, but how to best use it as an indicator of ecological status? At present, two major classes of size-based indicators are used to describe marine biotic communities; using the 'size spectrum' of aggregate size composition data; and using a proportion of numbers (or biomass) above some specified length or threshold (Rice et al., 2012)..

### ***Body-size spectra***

Analysis of the slopes of size spectra, which describe the relationship between organism size and abundance, is a widely used method to assess the state of marine ecosystems at regional and global scales (Shin et al., 2005). In fisheries science, size spectra are widely used to determine the slope of the size composition of fish populations. Fishing targets and disproportionately removes the larger members of the population, meaning the slope steepens following exploitation (Petchey and Belgrano, 2010). Early applications of this method were used to show that the slope of the spectra of North Sea fish size became about 1.5 times steeper between 1977 to 1993 (Rice and Gislason, 1996). Although bottom trawling does not target large benthos, the mortality rates experienced by large benthos are significantly greater than those of the smaller members of the community (Jennings et al., 2001a; McConnaughey et al., 2005). In view of this, size spectrum data have also been used as an indicator of bottom trawl disturbance (Duplisea et al., 2002; Queirós et al., 2006). The value of this indicator is that information on both ecosystem productivity (from the intercept parameter) and community mortality rates (from the slope parameter) can be inferred from the shape of the size spectra (Rice et al., 2012). In addition, there are a number of methodologies which have sought to improve the utility of size spectrum data. For example, the multimetric Index of Size-spectra Sensitivity (ISS) integrates information on the sensitivity of size classes to anthropogenic disturbance, as well as species richness measures, to calculate an 'asymmetric' size spectra model. ISS has so far shown a capability to discriminate between natural or anthropogenic pressures in coastal lagoons in the Mediterranean and Black Sea (Basset et al., 2012). However, it remains to be seen if and how this approach would translate to the assessment of fisheries impacts, and a potential barrier to this is that the sensitivity values for each size class are based on 'expert-opinion' (e.g. Borja et al. 2000). Nevertheless, a significant drawback of all the approaches based on community size spectra is the need to quantify and measure the spectrum. This is a relevant consideration to the analysis of benthic macrofauna, which requires all individuals (or a subset) to be measured or weighed. Given that a single benthic sample can contain hundreds or indeed thousands of individuals (e.g. I observed density values of up to 2,119 per 0.1 m<sup>2</sup> in Limfjorden), the application of size spectra methods for monitoring and assessment may be limited to programmes which have significant time and resources available.

***Body-size thresholds***

The method of separating the benthic community into body-size categories e.g. large and small is less widely applied, but has the considerable benefit of ease of calculation, integration into indicators (Chapter 5), as well as being simple to interpret and communicate. As with size-spectra estimations, this method has parallels in fisheries science, and a widely adopted example is the large fish indicator (LFI). The LFI simply provides a univariate description of the ‘state’ of a fish community by describing the proportion of fish over a length threshold (40 cm for the North Sea) (Greenstreet et al., 2011). The LFI is now used to support the OSPAR (Convention for the Protection of the Marine Environment of the North East Atlantic) Ecological Quality Objective (EcoQO) for the demersal fish communities in the Greater North Sea (Heslenfeld and Enserink, 2008). Conversely, this type of indicator has seen limited application as an indicator of the fishery effects on benthic communities. Chapter 5 thus provides, as far as I am aware, the first examination of how body-size thresholds can be combined with benthic community indicators. It is worth mentioning, however, that a potential limitation of this method could be that a great degree of ecological information is lost when using large sieve sizes. Relatively few species are represented on a large mesh size, and therefore little information regarding community composition can be gathered (Pinto et al., 2009). This may have implications for those interested in benthic biodiversity and community dynamics. The use of size thresholds may therefore be most suitable for tracking and monitoring specific anthropogenic pressures (such as outlined in this thesis), or as part of rapid ecological assessments. Several studies from Mediterranean lagoons have shown that the choice of sieve size (1 mm, 2 mm, and 4 mm) does not overly affect the outcome of ecological assessments (i.e. the assessment of ecological quality status category), while the use of a larger sieve size significantly reduced sampling and processing times (Pinna et al., 2014, 2013).

**3.2. Response of taxonomic and functional indicators*****Taxonomic metrics***

Given the responsiveness of density (Chapter 5) and biomass (Chapters 4 and 5), these metrics may provide effective indicators of bottom trawl disturbance at the community level. There are, however, a number of key differences between the two metrics. Density (or abundance) is the most basic measure of a benthic community, providing an absolute value for the total number of individuals in a sample. It is therefore estimated easily and quickly, and as a result is more commonly recorded in chronic trawling impact studies (Hiddink et al., 2017). Measures of density are useful in describing community structure, but are sensitive to recruitment and therefore the timing of sampling throughout the year. In addition, mortality rates based on count data are possibly more intuitive than those based on biomass. Density has also shown to be a good

indicator of trawl disturbance in several gradient studies (Gislason et al., 2017; Hinz et al., 2009; Sköld et al., 2018). However, it would anecdotally appear that many of these studies were conducted in more stable e.g. muddy environments. This may highlight a potential drawback of using density, whereby the sensitivity of density to fishing impacts may be masked in more disturbed systems. This is possibly highlighted by the results presented in Chapter 4, where I was unable to detect a significant effect of trawling on density in highly dynamic coastal waters, and in fact observed a non-significant positive relationship with dredging intensity. Ultimately, this trend was driven by large numbers of opportunistic macrofauna recorded at the most highly trawled sites. Similar responses have been recorded in small-scale experimental trawling studies (Tuck et al., 1998). This may therefore suggest that where fishing disturbance is spatially discrete (e.g. dredging effort in Natura 2000 sites, experimental trawling studies), the recovery in density of r-selected taxa may be comparatively high. The intermediate disturbance hypothesis (Connell, 1977) predicts that intermediate levels of disturbance may release some biota from the effects of competitive exclusion and thereby increase diversity and density. Furthermore, Pearson and Rosenberg's model of macrobenthic succession suggests that intermediate levels of disturbance (in the form of organic enrichment) correlates with a 'peak of opportunists' (Pearson and Rosenberg, 1978). While these hypotheses have their critics (Fox, 2013), the relationships between disturbance and density could potentially negate the effectiveness of density as an indicator of trawling impacts in highly disturbed systems.

An alternative explanation is that observations such as these are confounded with auxiliary processes which act on benthic community structure. Benthic recruitment dynamics can strongly influence estimates of density, and therefore assessments of response and recovery. The timing and success of recruitment is generally linked to seasonal differences in environmental conditions and productivity, and while benthic surveys are normally conducted prior to recruitment, there remains the possibility that a mismatch in timing can occur. If this were the case, then the communities may contain large numbers of recruits which have received relatively little exposure to trawling. This has the potential to drown out the signal of the previous year's fishing disturbance, and lead to the conclusion that fishery impacts were insignificant. This presents a possible limitation the use of data gathered from a 'snapshot' sampling event, such as those outlined in this thesis. However, the appropriate timing of surveys should normally negate this issue, or as in the case of Chapter 5, estimates of the potential effect of recruits can be integrated into the analysis.

On the other hand, biomass is thought to be more appropriate reflection of the functional capacity of an organism as it is closely linked to benthic secondary production (Bolam et al., 2014), and provides a better descriptor of the amount of carbon and other ecosystem resources an organism represents (Bremner et al., 2006b; Cesar and Frid, 2009). Additionally, community biomass has been shown to a reliable indicator of

chronic trawl disturbance (Hiddink et al., 2006b; Hinz et al., 2009). A significant response of biomass to trawling disturbance was observed in Chapters 4 and 5, where log biomass decreased linearly with fishing intensity. This indicates an exponential decrease in biomass, which typically occurs as a fixed fraction of biomass is lost with each pass of a trawl (Hiddink et al., 2006b). This means that the initial impacts of bottom trawling are much greater than subsequent trawling events (Jennings and Kaiser, 1998), and that repeated trawl passes will remove diminishing numbers of organisms. It has consequently been hypothesised that under heavy trawling communities may become entirely composed of trawling resistant species, and that further increases in disturbance would have little impact on biomass (Duplisea et al., 2002). If this were the case, then the use of community biomass may be of less value in highly disturbed areas, particularly in areas where there is an absence of unfished or low trawling intensity sites. However, research from heavily trawled areas of the southern North Sea suggest that this may not occur under the trawling frequencies exerted by commercial fleets, and that biomass will continue to significantly decline with increasing trawling disturbance (H. Reiss et al., 2009). Recent meta-analysis has further supported this, and have shown that trawling removes 6 – 41 % (gear depending, or on average 15 %) of faunal biomass per pass under chronic disturbance conditions (Hiddink et al., 2017). Moreover, it may be that biomass is quantifiably a better indicator of trawl disturbance than other taxonomic forms. Recent (currently unpublished) meta-analysis results from ICES (International Council for Exploration of the Sea) indicate that biomass is a more responsive indicator to trawling than abundance, evenness, Shannon diversity, or species richness (ICES, 2019). In summary, the choice of biomass as an indicator in trawling impact studies may therefore represent a trade-off, in that biomass is relatively sensitive to trawl disturbance, but it also is a relatively costly and resource demanding metric to estimate. However, as shown in Chapter 5, the implementation of body size thresholds can be used to reduce the cost and time needed to estimate biomass, while retaining or improving the sensitivity of the indicator.

### ***Diversity and richness-based metrics***

Species richness and diversity based indicators were examined in Chapter 5. Here, a poor response of species richness and Shannon diversity to trawling disturbance was observed corroborating the results of other chronic impact studies (Ball et al., 2000; Currie et al., 2011; H. Reiss et al., 2009) and the aforementioned meta-analysis (ICES 2019). The limitations of species richness as an indicator, and thus richness-based diversity indicators, in ecological monitoring are well described (Chase and Knight, 2013; Gotelli and Colwell, 2001). Where richness is not standardised for effort or area, it can lead to highly variable outcomes and interpretations of trends at both regional and local scales (Hillebrand et al., 2018). While this is generally an issue for ecological monitoring, its relevance to the monitoring of fisheries impacts is that richness and

diversity estimates are used either directly under the WFD and MSFD, or indirectly in the calculation of multi-metric indices (Gislason et al., 2017). It has been suggested that no single indicator can suitably describe and summarize biodiversity changes (Purvis and Hector, 2000). Consequently, there is considerable potential for improvement of the current suite of biodiversity metrics used to monitor trawling impacts. In this regard, measures of beta-diversity i.e. nestedness and turnover, could be considered (Baselga, 2010). Turnover is driven by changes in species identity and reflects the replacement of species between sites, whereas nestedness is driven by differences in species richness and occurs when species loss or gain cause sites to share varying proportions of the same species. In either case, these indicators are capable of capturing changes in the similarity or dissimilarity of communities, and therefore allow for much more meaningful assessment of changes in biodiversity. The mismatch between the ability of indicators to detect pressures, and their application in biodiversity monitoring, is the subject of growing introspection (Nicholson et al. 2012; Burgass et al. Appendix C)), and those concerned with the monitoring the biodiversity impacts of fisheries should also consider these limitations.

### ***Trait-based metrics***

Taxonomic information alone cannot convey the changes in ecological condition and benthic functionality caused by trawling (Bremner et al., 2003). Furthermore, trait-based approaches have previously been successful in the detection of trawling impacts (Bolam et al., 2014; de Juan et al., 2007; Tillin et al., 2006). Despite this, most benthic impact assessments are performed without considering the effects of trawling on the functional or trait attributes of the community. My intention was therefore to make use of trait-based approaches at each step, and thus test their applicability in Danish waters and in a wider context. Chapter 5 examined the performance of functional diversity (Rao's quadratic entropy), as well as functional richness, functional evenness (Villéger et al., 2008), and functional divergence (Laliberté and Legendre, 2010). Interestingly, the results demonstrated that functional richness and functional divergence responded negatively to trawling across each size fraction (large, small and combined fractions). In contrast, none of the taxonomic indicators detected an effect of trawling to the smallest macrofauna (small fraction), and suggest that the functionality of small macrofauna is also impinged by trawling disturbance. In Chapter 6, I highlight the sensitivity of several community-weighted mean (CWM) traits to trawling across size fractions, and compare the results of our snapshot sampling event with a long-term monitoring dataset. The increased sensitivity of trait-based community indicators (Chapter 5) and CWM traits (Chapter 6) based on the communities recorded in the large fraction suggests that utilising the traits of large macrofauna may represent the basis to develop new trait-based indicators. Aside from longevity (Hiddink et al., 2018; Rijnsdorp et al., 2018), individual traits or trait modalities have received little attention as potential indicators

of trawl disturbance. As a consequence, there is considerable potential to further test functional indicators, and to deepen our understanding of the links between pressure and trait variation. It was my original intention to also examine the links between groups of traits and the sensitivity of key species, and this may be an obvious avenue to explore at a later date. In this regards, future work may consider ‘RLQ’ analysis as a potential method to develop this understanding (Dray et al., 2014). This multivariate approach combines datasets on species abundance, environmental variables, and trait information, and can be used to estimate trait–environment relationships (Beukhof et al., 2019). Furthermore, RLQ has advantages over CWM-based regression analysis, as it considers inter- and intraspecific variation in the calculation of the trait value (CWM provides only a mean value), and can also be used to quantify the role of key species in the functional composition of the community (Beauchard et al., 2017).

Functional approaches are increasingly being applied in benthic studies and as part of monitoring requirements. However, the relatively recent adoption of these approaches in the field of benthic ecology, and pace at which it develops, may mean that methods are applied without due consideration of the ecological response being investigated, or the ecological meaning of the results. Throughout the research carried out in this PhD, I made use of a fuzzy coded trait database developed by Bolam et al. (2017). This has been greatly valuable to the analysis carried out, yet there are likely to be a number of limitations to its use. While fuzzy coding allows for taxa to be assigned and weighted to several traits, it is likely that trait characteristics will vary between conspecifics within a given assemblage, and also between habitat type, life-stage, and ambient environmental conditions. Furthermore, a considerable issue is that the knowledge of the natural history of most benthic species is still lacking (Bremner et al., 2003; Tyler et al., 2012). To account for this, I often used trait information based on closely related species. For some species, trait information is shared between entire taxonomic families. While there is practical and ecological merit to this approach, as phylogenetically similar species are likely to be functionally similar, the legitimacy of this approach is unproven, and there is in fact evidence to suggest the contrary (Bevilacqua et al., 2012). However, considerations such as this may not be relevant to studies undertaken at the scales such those examined in this thesis. Given the considerable potential of functional approach, future work should not only aim to develop new methods, but to also improve and strengthen existing approaches.

### **3.3. Reference areas**

Nearly 20 years ago, Jeremy Collie and co-authors published the first significant meta-analysis of trawling impact studies (Collie et al., 2000). They concluded by suggesting that future studies should seek to move away from short-term, small-scale pulse experiments, and to focus on larger-scale impacts via “press and relaxation experiments”. To do this, the authors noted that “*one half of the experiment has already been*

*done – since fishing activity has been providing the press for many years, what we now require are carefully designed closed area contrasts*". This would, at least initially, appear to be a relatively achievable objective. Although European waters are some of the most heavily trawled in the world, the proportion of untrawled seabed varies from ~80% off the west of Scotland to ~20% in the Adriatic Sea (Amoroso et al., 2018). However, in a recently published meta-analysis of large-scale gradient studies (such as those described by Collie et al. (2000)), only 5 of the 24 studies included unfished reference areas (Hiddink et al. 2017). Given the awareness of the need to include reference areas in studies of fisheries effects, and spatial heterogeneity of trawl fisheries, then why is there a lack of reference areas in trawling impact studies? There may not be a single answer to this, but it is likely that that a significant proportion of untrawled seabed is either unsuitable, compromised, or somehow unrepresentative of impacted areas (Hewitt et al., 2001), and that temporal and spatial restriction placed on fisheries data (e.g. VMS) hinder the identification of potentially untrawled areas. As a consequence, the selection of representative reference areas for control-impact experiments is a remarkably difficult task (Gray et al., 2006).

Commercial fishing grounds often comprise a mosaic of areas which are regularly trawled and those which remain unimpacted over many years (Piet and Hintzen, 2012). Given recent improvements in the spatial and temporal resolution of fisheries data, it is now possible to identify less impacted areas which may serve as potential reference sites. This approach would have the advantage of securing reference areas without the need for specific management action (Hiddink et al., 2006a). Such a management suggestion is provided in Chapter 4, whereby small-scale reference sites within the fishing grounds could benefit the management and monitoring of the fishery. Unlike fish populations, the sessile nature of benthic macrofauna means that reference areas do not require large geographic areas to be protected, and should therefore be comparatively easy to establish (Botsford et al., 2003; Collie et al., 2000). Benthic reference areas can also serve to improve the reproductive capability of target species (Beukers-Stewart et al., 2005), and potentially provide a source of larvae and adults for non-target species in surrounding areas (Attrill et al. 2011). Any attempts to designate reference areas, however, need to be undertaken in areas free from other manmade pressures, and consideration of the potential effects of fisheries displacement is required (Agardy et al., 2011). Furthermore, areas are likely to differ in their potential as sources and sinks of larvae (particularly in coastal areas), while larval transport, abundance and cohort strength, and connectivity represent important considerations before we can design suitable reference areas (White et al., 2019). Nonetheless, carefully selected reference areas can help meet a range of conservation and fisheries management objectives (Roberts et al., 2003).

In a wider context, as little as 3.7% of the world's oceans are currently protected from human activities (Morgan et al., 2018), well short of the 10% by 2020 Aichi target set out under the Convention of Biological Diversity (CBD, 2010). Of these protected areas, roughly half (or 2%) is subject to strong protection, and the remaining areas are designated as 'multiple use' areas or 'partially protected' areas, which allow regulated human activities to continue (Mascia 2004). This low level of conservation ambition is compounded by the mismatch between marine protected areas and areas where high biological and functional diversity occurs (Lindegren et al. 2018). In this thesis, I have been in the fortunate position to be able to design and plan fishing impact studies in close proximity to suitable reference areas. Areas such as Øresund and Trachten (closed to fishing for 87 years - Chapters 5 & 6), the closed area in Løgstør Natura 2000 site (closed for 31 years), and Horsens Natura 2000 site (closed for 10 years) (Chapter 3) were utilised to provide 'true zeroes' of fishing intensity. This aspect has enhanced my ability to detect and characterise the effects of chronic trawling throughout each of the research papers. The EU MSFD and Habitats Directive explicitly aim for seabed habitats to meet 'good environmental status', and 'favourable conservation status', respectively, and to apply the precautionary principle in environmental decision making. If we aim to meet these objectives, suitable reference areas are essential to properly characterise the impact of trawling, and to ensure a fully integrated ecosystem approach to fisheries management.

## References

- Agardy T, di Sciara GN, Christie P (2011) Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Mar Policy* 35:226–232.
- Amoroso RO, Pitcher CR, Rijnsdorp AD, McConnaughey RA, Parma AM, Suuronen P, Eigaard OR, Bastardie F, Hintzen NT, Althaus F, Baird SJ, Black J, Buhl-Mortensen L, Campbell AB, Catarino R, Collie J, Cowan JH, Durholtz D, Engstrom N, Fairweather TP, Fock HO, Ford R, Gálvez PA, Gerritsen H, Góngora ME, González JA, Hiddink JG, Hughes KM, Intelmann SS, Jenkins C, Jonsson P, Kainge P, Kangas M, Kathena JN, Kavadas S, Leslie RW, Lewis SG, Lundy M, Makin D, Martin J, Mazor T, Gonzalez-Mirelis G, Newman SJ, Papadopoulou N, Posen PE, Rochester W, Russo T, Sala A, Semmens JM, Silva C, Tsolos A, Vanellander B, Wakefield CB, Wood BA, Hilborn R, Kaiser MJ, Jennings S (2018) Bottom trawl fishing footprints on the world's continental shelves. *Proc Natl Acad Sci*:201802379.
- Andersen KH, Berge T, Gonçalves RJ, Hartvig M, Heuschele J, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer AB, Olsson K, Palacz A, Prowe AEF, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T (2016) Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. *Ann Rev Mar Sci* 8:217–241.
- Attrill, M.J., Austen, M.C., Bayley, D.T.I., Carr, H.L., Downey, K., Fowell, S.C., Gall, S.C., Hattam, C., Holland, L., Jackson, E.L., Langmead, O., Mangi, S., Marshall, C., Munro, C., Rees, S., Rodwell, L., Sheehan, E.V., Stevens, J., Stevens, T.F. & Strong, S. (2011). Lyme Bay – a case-study: measuring recovery of benthic species; assessing potential “spillover” effects and socio-economic changes, 2 years after the closure. Report 1: Response of the benthos to the zoned exclusion of bottom towed fishing gear in Lyme Bay, June 2011. Report to the Department of Environment, Food and Rural Affairs from the University of Plymouth-led consortium. Plymouth: University of Plymouth Enterprise Ltd. 108 pages.
- Ball BJ, Fox G, Munday BW (2000) Long- and short-term consequences of a Nephrops trawl fishery on the benthos and environment of the Irish Sea. *ICES J Mar Sci* 57:1315–1320.
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr* 19:134–143.
- Basset A, Barbone E, Borja A, Brucet S, Pinna M, Quintana XD, Reizopoulou S, Rosati I, Simboura N (2012) A benthic macroinvertebrate size spectra index for implementing the Water Framework Directive in coastal lagoons in Mediterranean and Black Sea ecoregions. *Ecol Indic* 12:72–83.

- Beauchard O, Veríssimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecol Indic* 76:81–96.
- Beukers-Stewart BD, Vause BJ, Mosley MWJ, Rossetti HL, Brand AR (2005) Benefits of closed area protection for a population of scallops. *Mar Ecol Prog Ser* 298:189–204.
- Beukhof E, Frelat R, Pecuchet L, Maureaud A, Dencker TS, Sólmundsson J, Punzón A, Primicerio R, Hidalgo M, Möllmann C, Lindegren M (2019) Marine fish traits follow fast-slow continuum across oceans. *Sci Rep* 9:17878.
- Bevilacqua S, Terlizzi A, Claudet J, Fraschetti S, Boero F (2012) Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. *J Appl Ecol* 49:357–366.
- Bolam S, Eggleton J, Garcia C, Kenny A, Buhl-Mortensen L, Gonzalez G, Kooten T, Dinesen G, Hansen J, Hiddink J, Sciberras M, Smith C, Papadopoulou N, Gumus A, Hoey G Van, Laffargue P, Eigaard O, Bastardie F (2014) Biological traits as functional indicators to assess and predict (using statistical models) the status of different habitats.
- Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) 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.
- Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, Kooten T van, Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Hoey G Van, Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar Environ Res* 126:1–13.
- Borja A, Franco J, Pérez V (2000) A marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Mar Pollut Bull* 40:1100–1114.
- Botsford LW, Micheli F, Hastings A (2003) Principles for the design of marine reserves. *Ecol Appl* 13.
- Bremner J, Frid CLJ, Rogers SI (2003) Assessing Marine Ecosystem Health: The long-term effects of fishing on functional biodiversity in North Sea benthos. In: *Aquatic Ecosystem Health and Management* p 131–137.
- Bremner J, Rogers SI, Frid CLJ (2006) Matching biological traits to environmental conditions in marine benthic ecosystems. *J Mar Syst* 60:302–316.

- CBD (2010) The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets, [www.cbd.int/doc/decisions/cop-10/cop-10-dec-02-en.pdf](http://www.cbd.int/doc/decisions/cop-10/cop-10-dec-02-en.pdf).
- Cesar CP, Frid CLJ (2009) Effects of experimental small-scale cockle (*Cerastoderma edule* L.) fishing on ecosystem function. *Mar Ecol* 30:123–137.
- Chase JM, Knight TM (2013) Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecol Lett* 16:17–26.
- Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts shelf-sea benthos. *J Anim Ecol* 69:785–798.
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Currie DR, Dixon CD, Roberts SD, Hooper GE, Sorokin SJ, Ward TM (2011) Relative importance of environmental gradients and historical trawling effort in determining the composition and distribution of benthic macro-biota in a large inverse estuary. *Fish Res* 107:184–195.
- Dray S, Choler P, Dolédec S, Peres-Neto PR, Thuiller W, Pavoine S, Ter Braak CJF (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95:14–21.
- Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-based model of the impacts of bottom trawling on benthic community structure. *Can J Fish Aquat Sci* 59:1785–1795.
- Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends Ecol Evol* 28:86–92.
- Gislason H, Bastardie F, Dinesen GE, Egekvist J, Eigaard OR (2017) Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. *Ecol Indic* 82:260–270.
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391.
- Gray JS, Dayton P, Thrush S, Kaiser MJ (2006) On effects of trawling, benthos and sampling design. *Mar Pollut Bull* 52:840–843.
- Greenstreet SPR, Rogers SI, Rice JC, Piet GJ, Guirey EJ, Fraser HM, Fryer RJ (2011) Development of the EcoQO for the North Sea fish community. *ICES J Mar Sci* 68:1–11.
- Heslenfeld P, Enserink EL (2008) OSPAR Ecological Quality Objectives: The utility of health indicators for the North Sea. *ICES J Mar Sci* 65:1392–1397.

Hewitt JE, Thrush SE, Cummings VJ (2001) Assessing environmental impacts: Effects of spatial and temporal variability at likely impact scales. *Ecol Appl* 11:1502–1516.

Hiddink JG, Hutton T, Jennings S, Kaiser MJ (2006) 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.

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE, Piet GJ (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can J Fish Aquat Sci* 63:721–736.

Hiddink JG, Jennings S, Sciberras M, Bolam SG, Cambiè G, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Parma AM, Suuronen P, Kaiser MJ, Rijnsdorp AD (2018) Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J Appl Ecol* 56:1075–1084.

Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci* 114:8301–8306.

Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, Filstrup CT, Harpole WS, Hodapp D, Larsen S, Lewandowska AM, Seabloom EW, Waal DB Van de, Ryabov AB (2018) Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *J Appl Ecol* 55:169–184.

Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: Chronic effects and experimental predictions. *Ecol Appl* 19:761–773.

ICES (2019) Interim Report of the Working Group on Fisheries Benthic Impact and Trade-offs (WGFBIT), 12–16 November 2018, ICES Headquarters, Copenhagen, Denmark. ICES CM 2018/HAPISG:21. 74 pp.

Jennings S, Dinmore TA, Duplisea DE, Warr KJ, Lancaster JE (2001) Trawling disturbance can modify benthic production processes. *J Anim Ecol* 70:459–475.

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol*:201–212.

Juan S de, Thrush SF, Demestre M (2007) Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Mar Ecol Prog Ser* 334:117–129.

- Kjørboe T, Visser A, Andersen KH, Browman H (2018) A trait-based approach to ocean ecology. *ICES J Mar Sci* 75:1849–1863.
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.
- Lindegren M, Holt BG, Mackenzie BR, Rahbek C (2018) A global mismatch in the protection of multiple marine biodiversity components and ecosystem services. *Sci Rep* 8:4099.
- Mascia MB (2004) Social dimensions of marine reserves. Pages 164–186 in C. Dahlgren and J. Sobel, editors. *Marine reserves: a guide to science, design, and use*. Island Press, Washington, D.C..
- McConnaughey R a, Syrjala SE, Dew CB (2005) Effects of chronic bottom trawling on the size structure of soft-bottom benthic invertebrates. *Benthic habitats Eff fishing Am Fish Soc Symp* 41:425–437.
- Morgan L, Pike E, Moffitt R (2018) How much of the ocean is protected? *Biodiversity*:1–4.
- Nicholson E, Collen B, Barausse A, Blanchard JL, Costelloe BT, Sullivan KME, Underwood FM, Burn RW, Fritz S, Jones JPG, McRae L, Possingham HP, Milner-Gulland EJ (2012) Making robust policy decisions using global biodiversity indicators. *PLoS One* 7.
- Norkko A, Villnäs A, Norkko J, Valanko S, Pilditch C (2013) Size matters: Implications of the loss of large individuals for ecosystem function. *Sci Rep* 3:2646.
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol An Annu Rev* 16:229–311.
- Petchey OL, Belgrano A (2010) Body-size distributions and size-spectra: universal indicators of ecological status? *Biol Lett* 6:434–437.
- Piet GJ, Hintzen NT (2012) Indicators of fishing pressure and seafloor integrity. *ICES J Mar Sci* 69:1850–1858.
- Pinna M, Marini G, Mancinelli G, Basset A (2014) Influence of sampling effort on ecological descriptors and indicators in perturbed and unperturbed conditions: A study case using benthic macroinvertebrates in Mediterranean transitional waters. *Ecol Indic* 37:27–39.
- Pinna M, Marini G, Rosati I, Neto JM, Patrício J, Marques JC, Basset A (2013) The usefulness of large body-size macroinvertebrates in the rapid ecological assessment of Mediterranean lagoons. *Ecol Indic* 29:48–61.

Pinto R, Patrício J, Baeta A, Fath BD, Neto JM, Marques JC (2009) Review and evaluation of estuarine biotic indices to assess benthic condition. *Ecol Indic* 9:1–25.

Purvis A, Hector A (2000) Getting the measure of biodiversity. *Nature* 405:212–219.

Queirós AM, Hiddink JG, Kaiser MJ, Hinz H (2006) Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. *J Exp Mar Bio Ecol* 335:91–103.

Reiss H, Greenstreet SPR, Sieben K, Ehrich S, Piet GJ, Quirijns F, Robinson L, Wolff WJ, Kröncke I (2009) Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. *Mar Ecol Prog Ser* 394:201–213.

Rice J, Arvanitidis C, Borja A, Frid C, Hiddink JG, Krause J, Lorange P, Ragnarsson SÁ, Sköld M, Trabucco B, Enserink L, Norkko A (2012) Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. *Ecol Indic* 12:174–184.

Rice J, Gislason H (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES J Mar Sci* 53:1214–1225.

Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, Denderen PD van, Kooten T van (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol Appl* 28:1302–1312.

Roberts CM, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KD, Leslie H, Lubchenco J, McArdle D, Ruckelshaus M, Warner RR (2003) Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecol Appl* 13:215–228.

Shin YJ, Rochet MJ, Jennings S, Field JG, Gislason H (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J Mar Sci* 62:384–396.

Sköld M, Göransson P, Jonsson P, Bastardie F, Blomqvist M, Agrenius S, Hiddink JG, Nilsson HC, Bartolino V (2018) Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Mar Ecol Prog Ser* 586:41–55.

Thrush SF, Hewitt JE, Gibbs M, Lundquist C, Norkko A (2006) Functional role of large organisms in intertidal communities: Community effects and ecosystem function. *Ecosystems* 9:1029–1040.

Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45.

Tuck ID, Hall SJ, Robertson MR, Armstrong E, Basford DJ (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Mar Ecol Prog Ser* 162:227–242.

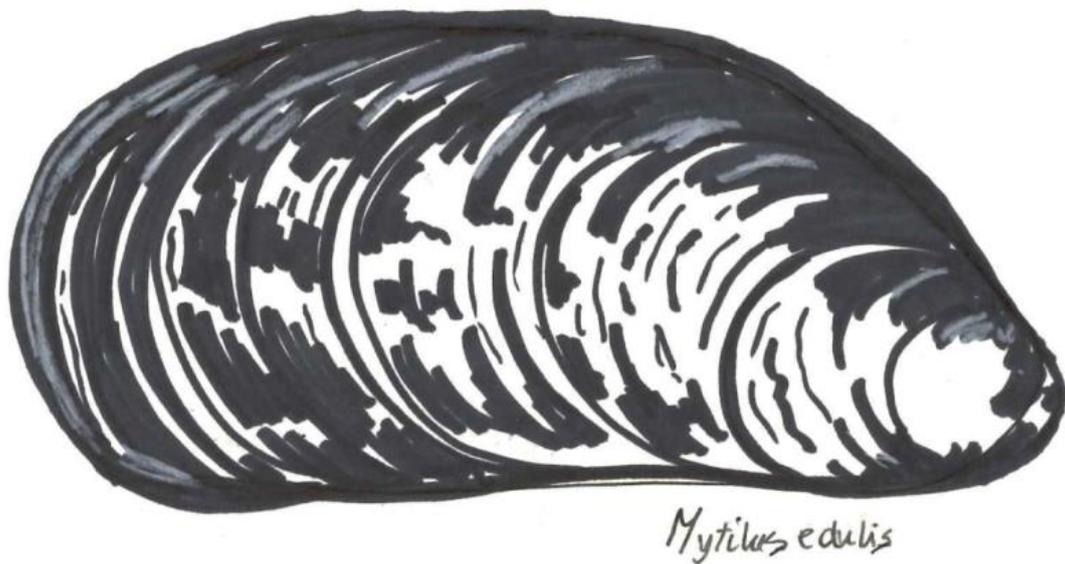
Tyler EHM, Somerfield PJ, Berghe E Vanden, Bremner J, Jackson E, Langmead O, Palomares MLD, Webb TJ (2012) Extensive gaps and biases in our knowledge of a well-known fauna: Implications for integrating biological traits into macroecology. *Glob Ecol Biogeogr* 21:922–934.

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* (80- ) 276:122–126.

White JW, Carr M, Caselle J, Washburn L, Woodson CB, Palumbi S, Carlson P, Warner R, Menge B, Barth J, Blanchette C, Raimondi P, Milligan K (2019) Connectivity, Dispersal, and Recruitment: Connecting Benthic Communities and the Coastal Ocean. *Oceanography* 32:50–59.

**4. Local and regional effects of bivalve dredging on benthic macrofauna in a eutrophic estuarine system**



This chapter has been submitted to Marine Ecology Progress Series:

McLaverty C, Eigaard OR, Dinesen GE, Gislason H, Kokkalis A, Erichsen AC, & Petersen JK (*submitted*) Local and regional effects of bivalve dredging on benthic macrofauna in a eutrophic estuarine system

## Local and regional effects of bivalve dredging on benthic macrofauna in a eutrophic estuarine system

Ciarán McLaverty<sup>1,2\*</sup>, Ole R. Eigaard<sup>1</sup>, Grete E. Dinesen<sup>1</sup>, Henrik Gislason<sup>1</sup>, Alexandros Kokkalis<sup>1</sup>, Anders C. Erichsen<sup>3</sup>, Jens Kjerulf Petersen<sup>2</sup>

<sup>1</sup> DTU Aqua, National Institute of Aquatic Resources, Denmark

<sup>2</sup> Danish Shellfish Centre, Øroddevej 80, 7900 Nykøbing Mors, Denmark

<sup>3</sup> DHI A/S, Agern Allé 5, 2920 Hørsholm, Denmark

\*Corresponding author: [cimc@aqu.dtu.dk](mailto:cimc@aqu.dtu.dk). Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, Building 201, Room 049, 2800 Kgs. Lyngby, Denmark.

### Keywords:

Bottom trawling; Benthic fauna; Coastal fisheries; Ecosystem based management; Fishing impact; Marine protected areas; *Mytilus edulis*; Natura 2000;

### Abstract

Commercial dredging for blue mussel (*Mytilus edulis*) and oysters (*Ostrea edulis*, *Crassostrea gigas*) constitutes the main bottom-trawl fishery in Danish nearshore areas. However, the fishing grounds overlap with several Natura 2000 sites, characterised by shallow, estuarine, and highly eutrophic conditions. This presents several challenges to an ecosystem approach to fisheries management. Using ultra-high resolution fisheries data (~10m x 10m) we investigated the effects of chronic dredging on benthic macrofauna at both local (Natura 2000 site) and regional (fishery wide) scales. Our results indicate that community biomass was particularly high in areas unaffected by both dredging (>10 years) and regular oxygen depletion. Outside of these areas, dredging resulted in reduced biomass and changes to community composition. In addition, eutrophication (in the form of sediment organic content) strongly impacted macrofauna across the study area, and may explain the wide distribution and high abundances of stress-tolerant and opportunistic taxa. Furthermore, this may have reduced our ability to detect an effect of dredging on community density, traits richness, or trait composition. At local scales, observed relationships between biomass, community composition and dredging varied considerably, and an apparent positive relationship between dredging and biomass was observed in the Lovns Broad N2000 site. However, this site experiences chronic eutrophication and regular anoxic events, meaning that the detection of dredging disturbance was likely compromised in this site. Our results demonstrate how a detailed sampling program, high resolution fisheries data, and suitable reference areas can be used to detect fishery effects in highly stressed estuarine systems.

#### 4.1. Introduction

Bottom trawl fisheries account for nearly one-quarter of global seafood landings (FAO, 2016), resulting in widespread disturbance of shelf sea habitats (Eigaard et al. 2017, Amoroso et al. 2018). In recent years, there has been a shift in fisheries management toward a more integrated ecosystem approach i.e. an ecosystem approach to fisheries management (EAFM) (Gislason et al. 2000). For bottom trawl and dredge fisheries, this has meant an increased focus on the assessment of effects to benthic fauna, functional composition, production, and higher trophic levels (Jennings et al. 2002, Tillin et al. 2006, Olsgard et al. 2008, Hinz et al. 2017, Sciberras et al. 2018).

Dredges are a type of bottom trawl primarily used in scallop, oyster, and blue mussel fisheries (FAO, 2016). Despite being relatively compact and of low spatial footprint, dredges may weigh up to several hundred kilos and are designed to disturb the upper layers of the sediment (Eigaard et al. 2016). Dredging is consequently associated with deeper penetration and higher macrofaunal depletion than other forms of bottom trawling (Hiddink et al. 2017). However, the effects of dredging vary considerably by habitat type or environment setting. Dredging in vulnerable habitats, such as circalittoral and deep-sea biogenic reefs, are particularly damaging and will typically result in substantial declines in associated benthic species and long recovery times (Kaiser et al. 2006, Hall-Spencer & Moore 2000, Cook et al. 2013). On the other hand, dredging in shallow water sedimentary habitats which experience high natural disturbance can often result in negligible or short-term effects (Sciberras et al. 2013, Moritz et al. 2015, Szostek et al. 2016, Lambert et al. 2017). This is as macrofaunal communities are typically well adapted to ambient environmental pressures. The level of resilience and recoverability of benthos in fishing grounds is governed by their life history characteristics (Kaiser et al. 2018). Environmental pressures, such as high shear stress or eutrophication, typically select for communities which are numerically dominated by few stress-tolerant taxa (Pearson & Rosenberg 1978, Dornie et al. 2003). In order to be successful in such conditions, traits relating to short lifespans, high mobility, and high population growth rates (r-strategists) are common, while traits relating to large body-size, slow growth, and late maturity are rarer (K-strategists) (MacArthur & Wilson 1967). Incidentally, the adaptation of benthic assemblages to natural disturbance can lead to community compositions which closely resemble those found in highly trawled areas (Jennings & Kaiser 1998, Diesing et al. 2013, Van Denderen et al. 2015).

In Denmark, infralittoral populations of blue mussel *Mytilus edulis* (Linnaeus, 1758) (hereafter referred to as mussels), European flat oyster *Ostrea edulis* (Linnaeus, 1758), and Pacific oyster *Crassostrea gigas* (Thunberg, 1793) (hereafter referred to as oysters), are exploited in Limfjorden and the Inner Danish waters. These areas are similar to many other Danish estuaries i.e. predominantly shallow brackish waters, short residence times, variable physico-chemical conditions, and high levels of eutrophication (Conley et al. 2006). In many coastal

areas of Denmark, nitrogen and phosphorous loadings have increased six-fold over the last century (peaking in the 1980s) as a result of intensified agriculture (Tomczak et al. 2013). In Limfjorden (Figure 4-1), a significant alteration in water quality has been linked to the collapse of several commercial finfish fisheries (Hoffmann & Dolmer 2000), regime shifts (Tomczak et al. 2013), and a concomitant increase in mussel and oyster biomass (Maar et al. 2010). While widespread nutrient loading has declined in recent years, long-running and regular anoxic and hypoxic events remain persistent in some areas (Jørgensen 1980, Conley et al. 2006), resulting in the intermittent mass mortality of shellfish stocks and other benthos (Dolmer et al. 1999). The considerable environmental and ecological changes in these areas, combined with the emergence of a significant dredge fishery, has led to increased political and public focus on the effects of mussel and oyster dredging (Dolmer & Frandsen 2002).

Mussel dredging in Denmark has been shown to impact local sediment biogeochemistry (Riemann & Hoffmann 1991), and physically remove hard substrates (shells, stones, live mussel matrix) that are important for mussel recruitment and juvenile survival (Dolmer & Frandsen 2002). Studies which have examined how these activities impact the associated macrofauna have reported mainly short-term effects. For example, experimental dredging trials in Limfjorden resulted in an increase in the density of scavenging brown shrimps (*Crangon crangon*) in the days immediately after dredging, but reduced species richness for up to 40 days post-disturbance (Dolmer et al. 2001). Comparative studies of epibenthos in unfished and fished areas have reported largely similar communities (Hoffmann & Dolmer 2000), while in other areas densities of the large suspension feeding plumose anemone *Metridium senile* were comparatively higher in unfished areas. Furthermore, the size and density of *M. senile* was found to be positively correlated with the weight of shell hash in the sediment, indicating the importance of this material as a hard substrate (Riis et al. 2003). While these studies have provided the basis for scientific understanding regarding short-term dredging effects, little is known about the ecosystem effects of chronic (long-term) dredging and how benthic macrofauna are affected along gradients of fishing disturbance in these dynamic systems.

This knowledge gap is problematic as the mussel and oyster fishing grounds overlap with several Natura 2000 (N2000) sites. These areas are designated under the EU Birds Directive (Anon, 1979) and Habitats Directive (Anon, 1992), for features such as sandbanks, large shallow inlets and bays, and reefs, as well as several protected species (e.g. harbour seal *Phoca vitulina* Linnaeus, 1758 and a number of mussel-eating and wading birds). In 2013, the Danish Mussel Policy was set up to regulate and sustainably manage fisheries in these areas (Ministry of Foreign Affairs of Denmark, 2019). This policy includes several management strategies designed to reduce dredging impacts to designating features, and has implemented exclusion zones in areas with depths between 0-3m, and for vulnerable habitats such as eel grass beds (*Zostera marina*) and boulder

reefs. Also under the policy, vessels are restricted on engine size (< 175 HP), total vessel length (< 12 m), and maximum weight of the iron frame of the dredges deployed (<50 kg), and fishing is restricted to areas with mussel densities above 1 kg m<sup>-2</sup> (Frandsen et al. 2015). Furthermore, licences are limited (52 in Limfjorden, and 8 in the Inner Danish waters), and vessels are only permitted to cumulatively impact up to 15% of seabed within each N2000 site. To monitor this, all dredging activities in N2000 areas are conditional on the use of ‘black-box’ devices. The black-box monitors fishing effort by logging vessel position, speed, and winch activity every 10 seconds. This represents an unusually high temporal and spatial resolution for fisheries data, as Vessel Monitoring Systems (VMS) used in the EU are typically restricted to an hourly polling frequency.

The availability of high-resolution fisheries data is uncommon, and allows for research questions to be examined at a wide range of spatial scales. The relevance of this is that relationships between ecological systems and environmental processes are often scale-dependent (Wiens 1989), and therefore perceptions of disturbance and its underlying processes are similarly conditional. Accordingly, spatial scales are an important consideration in analyses of fishing effort, and in the estimation of benthic mortality from bottom trawl fisheries (Piet & Quirijns 2009). The main aim of this study was therefore to investigate the effects of dredging to benthic communities in fishing grounds which experience high levels of eutrophication and natural variability. To achieve this, we made use of black-box data to examine potential effects at both local (N2000 sites) and regional (fishery-wide) scales. We collected macrofaunal data from 34 locations across the main mussel and oyster fishing grounds in Denmark. The effects of dredging to the benthos were examined in terms of taxonomic and functional (biological trait) characteristics, while accounting for environmental differences between fishing grounds, as well as sediment characteristics and hydrodynamic properties. The findings of this study provide new evidence regarding the ecosystem effects of bottom trawling in estuarine and eutrophic systems, and are of particular relevance to the management of fisheries in highly dynamic coastal waters.

## 4.2. Materials and methods

### **Study area**

**Limfjorden:** The N2000 sites of ‘Nissum Broad’ (hereafter ‘Nissum’), ‘Lovns Broad’ (hereafter ‘Lovns’), and ‘Løgstør Broad, Livø, Feggesund and Skarrebage’ (hereafter ‘Løgstør’) are located within Limfjorden. Limfjorden represents a large microtidal sound (1,500 km<sup>2</sup>) connecting the North Sea and Kattegat (Figure 4-1). The fjord is physically and hydrodynamically complex, being composed of several sills and basins, and has an overall mean depth of ~6 m. Salinity decreases from ~34 PSU in the west to ~26 PSU in the east (Tomczak et al. 2013) but is locally influenced by large seasonal freshwater influxes. Water temperatures fluctuate considerably between ice cover and >25°C during the summer, while surface and bottom currents are predominantly wind driven. The area is highly eutrophic due to nutrient rich run-off from a 7500 km<sup>2</sup> watershed (Dolmer et al. 1999) which causes considerably reduced water quality, and persistent seasonal hypoxia and anoxia (Maar et al., 2010). Despite this, a highly productive mussel fishery takes place in the central Limfjorden. The majority of landings come from Lovns and Løgstør, and reached a peak in Limfjorden of ~100,000 t year<sup>-1</sup> in the late 1990s (Dinesen et al. 2011). Since then, a decline in mussel biomass and increased fisheries regulation has seen landings fall to roughly 30,000-40,000 t year<sup>-1</sup>. To protect vulnerable eelgrass habitats, the northern parts of the Løgstør N2000 site have been closed to bottom fishing since 1988 (Kristensen & Hoffman, 1999). A valuable oyster fishery has taken place in Nissum for over 100 years, and in recent years a significant oyster biomass has begun to establish in Løgstør. Oyster landings peaked at 1,489 t in 2008, and an associated stock biomass of over 10,000 t (Nielsen & Petersen 2019). However in recent years the fishery has become more restricted, and the total allowable catch was 129 t in 2016, and an associated with a stock biomass of less than 2,000 t. Oyster dredges used in this fishery are considerably lighter (~35 kg) and smaller than the dredges used in the mussel fishery (~100 kg).

**Inner Danish waters:** The N2000 site ‘Horsens Fjord and the sea east of Endelave’ (hereafter ‘Horsens’) is located along the eastern coast of Jutland in the Inner Danish waters. It comprises an area of ~458 km<sup>2</sup> and extends from the mouth of Horsens fjord east into the southern Kattegat. Although geographically distinct from Limfjorden, seabed conditions here are similar and the area has supported a significant mussel fishery since the decline of water quality in Limfjorden in the late 1990s. The site ranges from shallow (~3 m) estuarine and heavily eutrophic waters in the west, to deeper (~20 m) and more marine conditions in the east (Markager et al. 2010). Mussel landings peaked at ~20,000 t year<sup>-1</sup> in the 1990s; however no fisheries took place in the N2000 site between 2007 and 2016. Fisheries recommenced for a single season prior to sampling (2016/2017), yielding landings of 12,012 t from an estimated mussel biomass of 160,000 t

(Nielsen et al., 2017). This meant that at the point of sampling, large areas of Horsens were unfished for a minimum of 10 years (Figure 4-1 d).

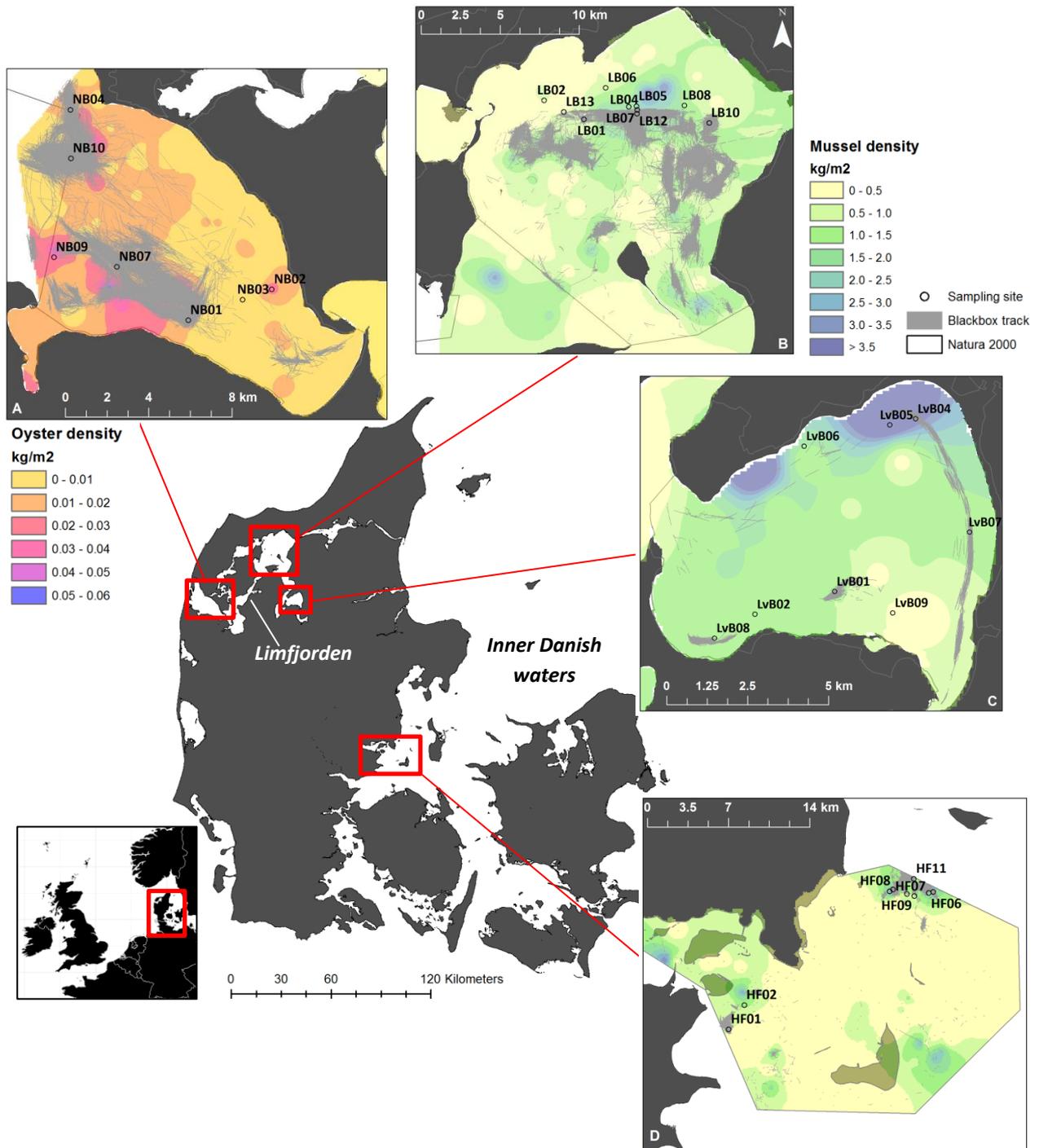


Figure 4-1: Location of sampling sites in (a) Nissum Broad, (b) Løgstør Broad, (c) Lovns Broad, and (d) Horsens Fjord. The black-box tracks represent the footprint of individual hauls. Estimated mussel and oyster densities are based on annual bivalve stock monitoring surveys.

### **Sampling design**

Within each basin, macrofaunal sampling effort was distributed equally between unfished and dredged areas to account for the low spatial extent and discrete nature of fishing effort, and to deal with the expected variation in the benthos in both types of sampling sites. Using composite GIS maps, the following criteria were applied to select sampling sites; (i) dredged seabed (impacted  $\leq 1.5$  years prior to April 2017) (described in *Estimation of dredging intensity*), (ii) unfished seabed (unimpacted since 2012 and  $> 100$  m away from fished areas), (iii) mud and sandy mud habitat (determined from habitat maps provided by the Danish Shellfish Centre), (iv)  $\leq 3$  m depth range (within a given basin) (v) presence of mussel/oyster beds (using shellfish density maps provided by the Danish Shellfish Centre (Figure 4-1)) (vi) absence of seabed anoxia (between 2016 - April 2017) (using maps provided by the Danish Centre for Environment and Energy: <http://bios.au.dk/raadgivning/vand/havmiljoe/iltsvind/arkiv/>). Given the likely importance of mussel beds to improve benthic diversity (Norling & Kautsky 2008), we used camera transects to determine the percentage cover of mussels at each site. This step ensured that stations in unfished areas of bare sand were moved or excluded. Furthermore, we included mussel biomass (in grams ash-free dry weight) as a predictor in the statistical analysis, and tests for collinearity were undertaken to ensure mussel biomass was not confounded with other predictors, such as fishing effort. Although mussels occur in Nissum, they are generally sparse and do not form significant or consolidated subtidal beds. Therefore, the shellfish bed criterion was not applied in this basin, and sampling sites were selected based on fishing effort, sediment type, and depth.

### **Data collection and sample processing**

A total of 34 sites were sampled between April and June 2017 (Horsens = 8, Løgstør = 10, Lovns = 8, Nissum = 8) (Figure 4-1 a-d). At each site, a single camera transect was undertaken (10 minutes at  $\sim 0.6 - 0.8$  knots, or roughly 200m), and five replicate grab samples were obtained using a 0.1 m<sup>2</sup> Van-Veen grab sampler. Four replicates were analysed for benthic macrofauna, while the fifth was used to determine sediment grain size and organic content. Macrofaunal samples were sieved over a 1mm mesh and preserved in 4% formalin seawater solution buffered with borax (sodium borate). In the laboratory, the residuum was rinsed, sorted, and all animal material identified to the lowest taxonomic level possible. Biomass estimates were determined via ash-free dry weight. The nomenclature of all taxa were validated and standardised in accordance to the World Register of Marine Species (WoRMS Editorial Board, 2018, correct as of 05/01/2019). Sediment particle size analysis (PSA) was undertaken via mass loss following wet sieving (Danish Standard (DS) 405.9), resulting in the estimation of the percentage of mud ( $< 63\mu\text{m}$ ), sand (0.063–2mm), and gravel ( $\geq 2\text{mm}$ ). Organic content was calculated via loss-on-ignition (LOI%) by estimating the mass loss of 4mg of homogenised sediment placed in a muffle furnace at 560°C for 4 hours, or until a constant weight was

achieved (DS 204). During data collection it was observed that sediment samples often comprised of large quantities of shell hash (empty shells and fragments). Accordingly, all shell hash > 4mm were weighed in the laboratory, and the weight used as a predictor in the analysis. In some areas, large numbers of *Asterias rubens* and *Carcinus maenas* were sampled. These epifaunal species are highly mobile and may be unrepresentative of chronic fishing effects. Furthermore, permutation based tests of homogeneity of dispersions (PERMDISP) (Anderson et al., 2008) were estimated with and without these species. This revealed significant multivariate dispersion between basins when *A. rubens* and *C. maenas* were included in biomass estimates (PERMDISP  $F = 2.9176$ ,  $p = 0.037$ ). These species, along with *Mytilus edulis*, were excluded from the analysis.

### **Biological traits**

To describe the functional structure of the community we calculated the composition of biological traits of the macrofauna in each sample. To do this, we used a trait database (Bolam et al. 2017) that describes 10 trait categories and 48 descriptive modalities (Table 4-1) scored using a ‘fuzzy coding’ approach (Chevene et al. 1994). Fuzzy coding allows for more than one trait modality to be expressed in a category, and also indicates the relative importance of each modality. For example, if a taxa exhibited full affinity to a single modality within a trait (e.g. longevity), a score of 3 was assigned, while if a taxa exhibited multiple modalities (e.g. several feeding modes may be used), each modality was assigned a score relative to its importance (e.g. Predator = 2, Scavenger/Opportunist = 1). Modality scores were standardised within each trait category, and then combined with biomass data. This resulted in a trait-by-site matrix carried forward for analysis.

**Table 4-1: Biological traits and associated modalities used in the study**

Trait	Modalities	
Size range	<10mm 11-20mm 21-100mm	101-200mm 201-500mm >500mm
Longevity	<1 year 1-<3 years 3-10 years >10 years	
Larval Development	Planktotrophic Lecithotrophic Direct	
Morphology	Soft Crustose Cushion	Tunic Stalked Exoskeleton (chitin/calcium carbonate)
Egg development	Asexual/Budding Sexual: shed eggs pelagic Sexual: shed eggs benthic	

	Sexual: brood eggs	
Living habit	Tube-dwelling Burrow-dwelling Free-living	Crevice/hole/under stone Attached to substratum Epi/endozoic/phytic
Sediment position	Surface Infauna: 0-5cm Infauna: 6-10cm Infauna: >10cm	
Feeding mode	Suspension Scavenger/Opportunist Surface Deposit	Subsurface deposit Predator Parasite
Mobility	mob Sessile Burrower Swim Crawl/creep/climb	
Bioturbators	Diffusive mixing Surface deposition Downwards conveyer	Upward Conveyor None

### ***Estimation of dredging intensity***

Dredging intensity was estimated as swept-area ratio (SAR) values. We aggregated the total area swept (dredged) within a 10m radius around each benthic sampling position, over a period of 1.5 years prior to the date of sampling. A SAR value was calculated for each sample as the accumulated dredged area within this circle, divided by the area of the circle. These SAR values provide estimates of how many times a sampled community was impacted by a dredge during the 1.5 year period. For the purposes of this study, black-box data were filtered and fishing activity defined as; (i) when vessel speed is between 1.5 and 4.0 knots, (ii) this speed interval is met for at least 80 sec (8 consecutive loggings), and (iii) when these loggings match registered winch activity. Black-box data were then combined with logbook information to determine gear configuration (type and size of dredge, and the number of dredges). The mussel fishing season is closed annually during January-February and June-August each year. Therefore, in order to analyse the equivalent of roughly 1 year of fishing effort, we aggregated fishing data over 1.5 years prior to the sampling to account for the closed periods. For ease of interpretation, SAR values are presented as equivalent values year<sup>-1</sup>.

### ***Natural and anthropogenic drivers***

Several anthropogenic and natural pressures are present across the study area. We therefore gathered information on hydrodynamic (salinity, temperature, current velocity), physical (sediment grain size, depth, mussel biomass, and shell hash) and anthropogenic (nutrient loading) gradients. Data regarding depth, sediment organic content via loss-on-ignition (LOI), sediment mud content, mussel biomass, and shell hash were collected in the field. Hydrodynamic data in the form of bottom current velocity (max + range), bottom

salinity, bottom temperature (mean + range for both) were extracted from the MIKE 3 HD Flexible Mesh (FM) models (DHI 2013) (see Supplement – Text S1 for more information). The models were calibrated to consider the specific hydrodynamic conditions of Limfjorden and Inner Danish waters, and therefore provided spatial resolutions of between 100 and 1000m in Limfjorden, and between 40 and 400 m for Horsens. Hydrodynamic data were estimated at each sampling site at a monthly scale and averaged over 2016.

### **Data analysis**

**Predictor variables:** In addition to the predictors listed above, the categorical variable ‘basin’ was included in the analysis to capture auxiliary sources of variation potentially not described by the other variables. This resulted in thirteen predictor variables (dredging intensity, salinity (mean and range), temperature (mean and range), current velocity (max and range), mud content, LOI, depth, mussel biomass, shell hash, and basin). The variables ‘dredging intensity’, ‘mussel biomass’, and ‘shell hash’ were log transformed ( $\log_e+1$ ) to reduce the weighting of outliers and normalise skewed distributions. Prior to formal statistical analysis, all potential predictors were checked for multicollinearity. Pair-wise plots were used to calculate correlation coefficients and correlation coefficients  $>0.7$  were excluded from further analysis (Dormann et al, 2013) (Supplement – Figure S1). Bottom temperature range ( $r = 0.858$ ), bottom temperature mean ( $r = 0.741$ ), and bottom current velocity range ( $r = 0.781$ ) were excluded as they were collinear with depth. Bottom salinity range ( $r = 0.797$ ) and bottom salinity mean ( $r = 0.776$ ) were also excluded as deemed collinear with ‘basin’, while sediment grain size (mud content) was excluded as collinear with LOI ( $r = 0.771$ ). As salinity was expected to be a potentially important predictor, we verified the choice to exclude this term by examining the GLMM fits with either salinity (mean/range) or basin included. In each case, models containing the categorical ‘basin’ term had a lower Akaike’s Information Criterion (AIC). Variance inflation factor (VIF) values were checked for the remaining seven predictors; basin, maximum bottom current speed (current), depth, dredging, LOI, mussel biomass, and shell hash (Supplement Table S1). While some level of correlation was present across the remaining predictors, the VIF were all below the acceptable threshold of 5 (Kutner et al. 2004).

**Habitat comparability:** To investigate the comparability of environmental conditions at local and regional scales, analyses of similarity were undertaken using multivariate clustering analysis, using the package PRIMER v.7 (Clarke and Gorley, 2015). Clustering of predictor variables (except dredging intensity) were based on normalised Euclidean distances. Significance was determined using the SIMPROF routine, which tests for statistically significant site clusters. At the regional scale, the analysis resulted in four distinct clusters based on each basin. To account for potential differences in habitat type, we therefore forced the inclusion

of basin in the calculation of all statistical models at the regional scale. At the local scale, the analysis resulted in a single cluster for each basin (Supplement – Figure S2).

**Univariate analysis - community indicators:** Generalised linear mixed models (GLMMs) were used to model three community indicators; density, biomass, and functional richness, chosen based on their sensitivity to trawling disturbance in elsewhere in Danish waters (McLaverly et al. 2020). Density and biomass were calculated at the total number and biomass of individuals in a sample, respectively. Functional richness describes the richness of traits expressed in the community, measured by the total volume of multivariate trait space occupied by the community, and ranges from 0 to 1 (Villéger et al. 2008). Each model included a site-specific random term to account for the non-independence of replicate samples at each site. Community biomass was log transformed, and indicators were modelled using either a negative binomial (density), Gaussian (biomass), or beta (functional richness) distribution. To estimate the relative effects of each predictor, calculated the relative variable importance (RVI) of each predictor via multi-model inference using the R package ‘MuMin’ (Barton 2013). This method quantifies the importance of each predictor regardless of significance level. RVI values are determined from the weighted AIC, calculated across all permutations of a global model (Burnham & Anderson 2002). RVI values can be interpreted as  $>0.9$  = highly important,  $>0.6$  = moderately important,  $<0.6$  = low importance, and  $<0.5$  = little/no importance. Statistical significance and the direction of the relationship (i.e. negative or positive) were also calculated using the coefficients of the best fitting models ( $\Delta AIC < 4$ ). Selection of the final model was based on AICc. GLMM diagnostics were checked via simulation-based approach suited for mixed models using the R package ‘DHARMA’ (Hartig, 2016). GLMMs were fit using the R package ‘glmmTMB’ (Brooks et al., 2017). To streamline the analysis, we included the interaction term ‘basin x dredging’. A significant interaction term would indicate if the relationship between indicators and dredging varied at the basin scale. The marginal effects and interaction terms of GLMMs were plotted using the sjPlot package (Lüdtke, 2016). All univariate analysis were carried out using R version 3.6.0 (R Development Core Team, 2018)

**Multivariate analysis - community composition:** Distance-based linear models (DistLMs) were used to analyse the effect of predictor variables on three estimates of community composition; density composition, biomass composition, and trait composition. This approach provided an analogous approach to the univariate indicators used at the regional scale. DistLMs are based on a distance-based redundancy analysis (dbRDA) (Legendre & Anderson 1999), which models the relationship between a multivariate response and environmental predictors. The approach partitions variance in the response among the predictors. Model selection was undertaken using the ‘step-wise’ selection procedure and p-values were obtained based on 999 permutations. Selection of the final model was based on AICc. Density was fourth root transformed and

biomass data were log transformed prior to analysis. Resemblance matrices of taxonomic and trait data were calculated based on Bray-Curtis similarity, and based on Euclidean distance for environmental data. To test for differences in community composition between fished and unfished areas we used a two-way crossed PERMANOVA design with 'basin' and 'dredging' as factors. Where differences in unfished and dredged areas were identified, post-hoc tests using pair-wise PERMANOVA and similarity percentage breakdowns (SIMPER) were used to determine the species or traits which made the greatest contribution to the observed dissimilarity within significant pairwise contrasts. PERMANOVA models were based on 999 permutations of residuals under a reduced model, and using Type III (partial) sums of squares (SS) to account for the asymmetry in the sampling design. All multivariate analyses were carried out using PRIMER v.7 with PERMANOVA+ (Anderson et al., 2008).

### 4.3. Results

#### ***Fishing effort***

The distribution of dredging effort during the study period was confined to relatively small areas within each basin (Figure 4-1 a-d). Dredging generally took place at intermediate water depths within each basin i.e. seaward of the 0-3m restricted zone, and away from deeper areas which may suffer low oxygen conditions. Dredging intensity (SAR) values were relatively uniform in Løgstør (mean SAR 2.17) and Nissum (mean SAR 2.52), and Lovns (mean SAR 1.42). Conversely, the mean fishing intensity observed in Horsens (mean SAR 10.22) was approximately 4 to 5 times higher than the other areas.

#### ***Macrofaunal community***

A total of 20,042 individuals, 160 taxa, and 13 main phylogenetic groups, were recorded across the 34 sampling sites. These included Polychaeta (71 taxa), Malacostraca (26), Bivalvia (22 taxa), Gastropoda (20 taxa), Echinodermata (8 taxa), Clitellata, Polyplacophora, Ascidiacea, Hexanauplia (all represented by 2 taxa), and a single taxon within the Anthozoa, Nemertea, Phoronida, and Pycnogonida. Blue mussels *Mytilus edulis* dominated measures of density and biomass (Table 4-2). The occurrence of mussels in samples from dredged and unfished areas was largely similar (~51% and ~55%, respectively). Video transects revealed that shellfish beds were highly variable in coverage, and ranged from large consolidated beds (e.g. Løgstør), to mosaics of fragmented beds (e.g. Horsens), to a sparse coverage of individuals (both mussel and oysters) (e.g. Nissum). Some of the most abundant taxa recorded included a number of deposit feeding polychaetes (*Streblospio shrubsolii*, *Capitella* sp.), bivalves (*Petricolaria pholadiformis*, *Kurtiella bidentata*), a deposit feeding gastropod (*Peringia ulvae*), small crustaceans (*Microdeutopus* sp., *Monocorophium insidiosum*), and two taxa within the subclass Oligochaeta (*Tubificoides benedii* and *Oligochaeta* indet.). In general, the most abundant taxa were also widely occurring (e.g. *S. shrubsolii* and *K. bidentata* were present in >80% of samples). On the other hand, biomass was dominated by fewer taxa which exhibited lower spatial coverage. These included relatively large and long-lived bivalves (*Actica islandica*, *Modiolus modiolus*, *Petricolaria pholadiformis*, *Venerupis corrugata*), scavenging and deposit feeding gastropods (*Tritia reticulata*, *Aporrhais pespelecani*, *Peringia ulvae*, *Littorina littorea*) and larger predatory polychaetes (*Alitta virens* and *Nephtys hombergii*).

**Table 4-2: Dominant taxa recorded in terms of density and biomass. Occurrence (%) indicates the percentage occurrence of taxa across all samples.**

Taxa	Count	Occurrence (%)	Taxa	Biomass (g)	Occurrence (%)
<i>Mytilus edulis</i> *	2817	65	<i>Mytilus edulis</i> *	4532.7	65
<i>Peringia ulvae</i>	1430	45.5	<i>Arctica islandica</i>	239.4	3
<i>Streblospio shrubsolii</i>	1145	81.8	<i>Asterias rubens</i> *	115.3	18.2
<i>Tubificoides benedii</i>	1141	45.5	<i>Carcinus maenas</i> *	88.9	33.3
<i>Capitella sp.</i>	1035	48.5	<i>Crepidula fornicata</i>	78.2	33.3
<i>Petricolaria pholadiformis</i>	1027	18.2	<i>Modiolus modiolus</i>	73.2	3
<i>Oligochaeta</i>	1003	78.8	<i>Petricolaria pholadiformis</i>	46.3	18.2
<i>Kurtiella bidentata</i>	1002	87.9	<i>Tritia reticulata</i>	12.9	27.3
<i>Scoloplos armiger</i>	666	72.7	<i>Aporrhais pespelecani</i>	12.2	9.1
<i>Heteromastus filiformis</i>	510	39.4	<i>Alitta virens</i>	8.2	45.5
<i>Corbula gibba</i>	472	30.3	<i>Venerupis corrugata</i>	7.3	3
<i>Nephtys hombergii</i>	459	72.7	<i>Peringia ulvae</i>	6.5	45.5
<i>Bittium reticulatum</i>	457	24.2	<i>Littorina littorea</i>	5.6	6.1
<i>Microdeutopus sp.</i>	389	72.7	<i>Psammechinus miliaris</i>	5.6	12.1
<i>Mediomastus sp.</i>	385	51.5	<i>Mya arenaria</i>	5.0	15.2
<i>Pygospio elegans</i>	315	57.6	<i>Nephtys hombergii</i>	4.1	72.7
<i>Polydora cornuta</i>	294	60.6	<i>Echinoidea</i>	2.7	6.1
<i>Monocorophium insidiosum</i>	292	63.6	<i>Ensis leei</i>	2.6	3
* excluded from the formal analysis					

### **Regional effects of dredging – community indicators**

Relative variable importance (RVI) scores indicate that spatial patterns in density of individuals were best explained by sediment organic content (LOI) (RVI: 0.96), mussel biomass (RVI: 0.93) and shell hash (RVI: 0.68). LOI demonstrated a negative relationship with density (Figure 4-2 (d)), while relationships with mussel biomass (Figure 4-2 b) and shell hash (Figure 4-2 c) were positive. In addition, basin (RVI: 1) was a significant term in the most parsimonious model for density (Figure 4-2 a). The RVI score of 1 however is due to the inclusion of the term in all permutations of the global model. Dredging and density exhibited a non-significant positive trend (RVI: 0.36). In contrast, dredging and biomass exhibited a significant negative relationship (RVI: 0.62). In addition, the quantity of shell hash (RVI: 0.71) showed a significant positive relationship with biomass (Figure 4-2 f). Although the interaction term between basin and dredging was significant (discussed in *Local effects of dredging – community indicators*), ‘basin’ was not a significant term in the final biomass model (Table 4-3). Basin (RVI: 1, Figure 4-2 g) and mussel biomass (RVI: 0.99, Figure 4-2 h) were the only

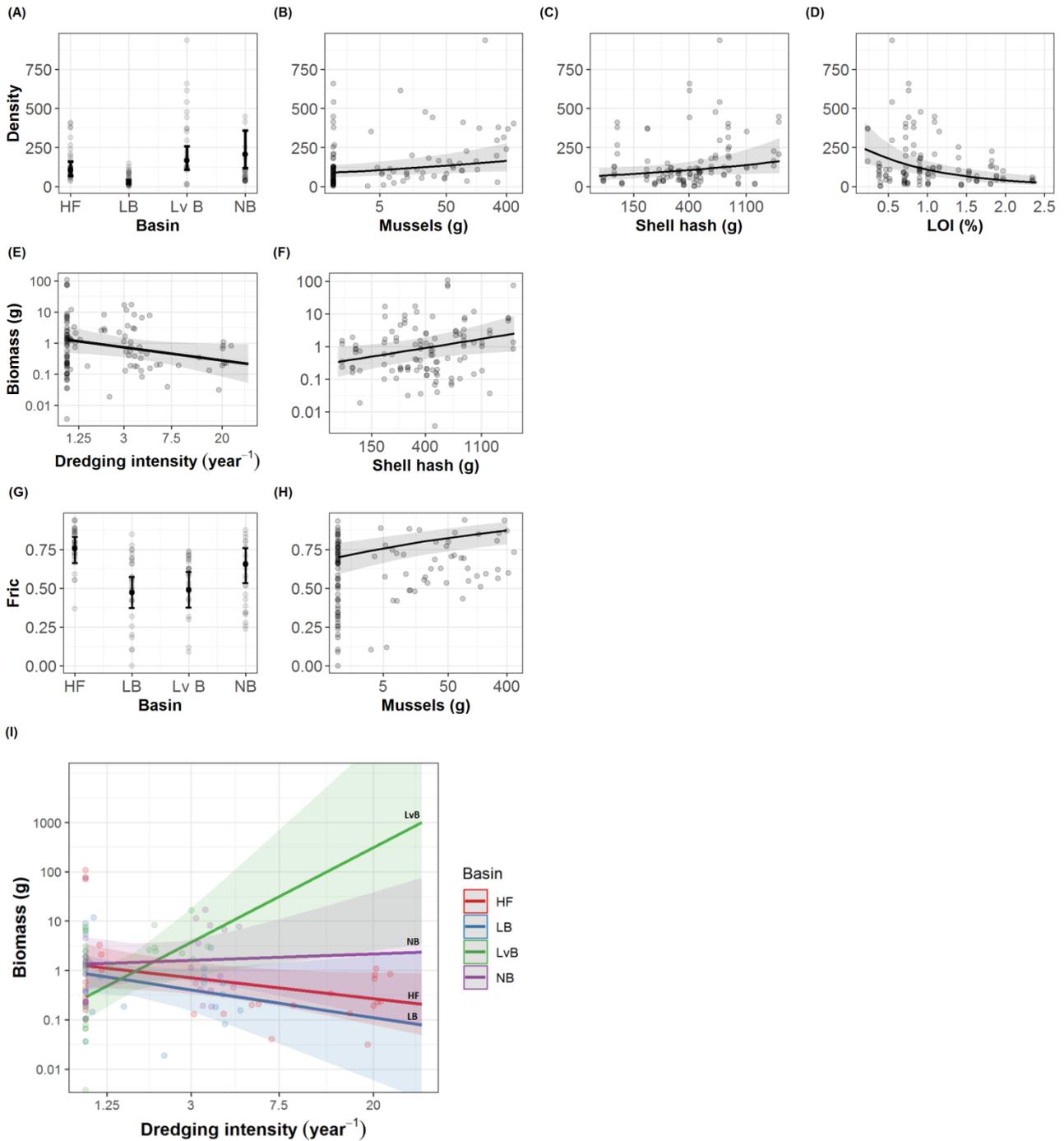
significant predictors in the final model of functional richness. Functional richness also demonstrated a non-significant negative trend with dredging (RVI: 0.27).

**Table 4-3: Summary results of GLMMs of macrofaunal indicators. The importance of each predictor in the model represented by the relative variable importance (RVI) scores. Positive relationships are denoted by (+), and negative relationships by (-). Interaction term is denoted by 'x'. Statistically significant parameters are shown in bold. Conditional R<sup>2</sup> values describe the proportion of variance explained by both fixed and random terms.**

Community indicator	Basin	Basin x Dredging	Dredging	LOI	Mussel biomass	Shell hash	Current	Depth	Conditional R <sup>2</sup>
Density	<b>1.00</b>	0.07	0.36 (+)	<b>0.96 (-)</b>	<b>0.93 (+)</b>	<b>0.68 (+)</b>	0.37 (-)	0.43 (+)	0.83
Biomass	1.00	<b>0.49</b>	<b>0.62 (-)</b>	0.40 (-)	0.54 (+)	<b>0.71 (+)</b>	0.32 (+)	0.49 (+)	0.38
Functional richness	<b>1.00</b>	0.09	0.27 (-)	0.29 (-)	<b>0.99 (+)</b>	0.53 (+)	0.29 (+)	0.44 (+)	0.78

#### ***Local effects of dredging – community indicators***

The significant interaction term observed in the biomass model (RVI: 0.49) revealed that the relationship between dredging and biomass varied significantly between basins (Figure 4-2 i). The relationship observed in Horsens and Løgstør was also similar to the overall trend at the regional scale (Figure 4-2 f), indicating the importance of these basins at the regional scale, while biomass showed little variation as a function of dredging in Nisum. However, biomass exhibited a positive relationship with dredging in Lovns (Figure 4-2 i). The predicted values at the higher dredging intensities were however characterised by high uncertainty (indicated by 95% confidence intervals). This was as dredging intensity was relatively low in Lovns, and did not exceed 2.58 SAR year<sup>-1</sup>.



**Figure 4-2: Marginal effects plots of the relationship between community indicators and significant predictors shown in Table 4-3. Regression lines represent the predicted values from GLMMs and shaded areas represent 95% confidence intervals. Note that the axes for values of biomass (g), dredging intensity (SAR year<sup>-1</sup>), mussel (g), and shell hash (g) are shown on a natural logarithmic scale. HF = Horsens, LB = Løgstør, LvB = Lovns, NB = Nissum.**

***Regional effects of dredging – community composition***

The percentages of community variance explained by predictors in distance based linear models (DistLMs) models are outlined in Table 4-4. In each model, the majority of explained variance was accounted for by basin. This was particularly the case for density-based composition (21.3 %) and trait based-composition (10.4 %), while biomass was comparatively similar across basins (7.5 %). Variance in community composition was significantly linked to depth (density = 9.5 %, biomass = 4.9 %, traits = 2.4 %), mussel biomass (density = 5.4 %, biomass = 2.4 %, traits = 4.2 %), and shell hash (density = 3.3 %, biomass = 2.1 %, traits = 4.2 %). Dredging (density = 3.3 %, biomass = 2.95 %) and LOI (density = 5.5 %, biomass = 3.3 %) were significant predictor of taxonomic community characteristics only, with no observed effect on trait composition.

**Table 4-4: Percentage of community variance explained by dredging and environmental predictors. Variance partitioning based on distance based linear models of community composition. The total variance explained by the model is provided by the R<sup>2</sup>.**

Community composition	Dredging	LOI	Mussel biomass	Shell hash	Current	Depth	Basin	R <sup>2</sup>
Density	3.3	5.5	5.4	3.3	1.3	9.5	21.3	49.6
Biomass	2.5	3.3	2.4	2.1	-	4.9	7.5	23.9
Traits	-	-	4.2	1.5	-	2.4	10.4	18.5

***Local effects of dredging – community composition***

A significant interaction term was observed in the models of density-based (pseudo-F = 3.25, p = 0.001), and biomass-based composition (pseudo-F = 2.11, p = 0.001) (Table 4-5), indicating that differences between unfished and fished areas varied by basin. Post-hoc pairwise tests described the degree of variation in each of the four basins for density, and the marginally larger pseudo-t values in Horsens (pseudo-t = 2.33) and Lovns (pseudo-t = 2.2) indicated that differences were larger in these basins. In the case of biomass-based composition, the community varied significantly in each basin except exception Nissum (pseudo-f = 1.2, p = 0.134). No differences were detected in trait composition between unfished and dredged areas.

**Table 4-5: (A) Results of two-way PERMANOVA models, testing for differences in community composition between basins and between unfished and dredged areas. Interaction term is denoted by 'x'. (B) Pairwise tests between pairs of 'unfished vs. dredged'. Significant P values are indicated in bold. Tests were based on 999 permutations.**

	Density		Biomass		Traits	
<b>(A) Two-way analysis</b>						
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p
<b>Basin</b>	22.61	<b>0.001</b>	6.53	<b>0.001</b>	4.22	<b>0.001</b>
<b>Dredging</b>	2.79	<b>0.001</b>	1.70	<b>0.027</b>	1.77	0.094
<b>Basin x Dredging</b>	3.25	<b>0.001</b>	2.11	<b>0.001</b>	1.27	0.186
<b>(B) Pairwise comparisons (unfished vs. dredged)</b>						
	Pseudo-t	p	Pseudo-t	p	Pseudo-t	p
<b>Horsens</b>	2.33	<b>0.001</b>	1.61	<b>0.002</b>	-	-
<b>Løgstør</b>	1.13	<b>0.001</b>	1.41	<b>0.025</b>	-	-
<b>Lovns</b>	2.20	<b>0.001</b>	1.85	<b>0.004</b>	-	-
<b>Nissum</b>	1.44	<b>0.041</b>	1.20	0.134	-	-

The taxa which contributed most to the observed dissimilarities are presented in Table 4-6. The densities of these taxa exhibited several opposing trends, either within basins (e.g. Horsens) or between basins (Løgstør and Lovns). However, the densities of sedentary taxa (e.g. *Prionospio fallax*, *Streblospio shrubsolii*, *Phoronis* sp., *Kurtiella bidentata*, *Galathowenia oculata*) were typically reduced in dredged areas. Similarly consistent responses were observed for the predatory polychaetes *Pholoe inornata* and *Kefersteinia cirrhata*, and the amphipod *Microdeutopus* sp.. Conversely, mobile gastropods (*Bittium reticulatum*, *Peringia ulvae*, and *Odostomia* sp.), and opportunistic oligochaetes (*Tubificoides benedii* and *Oligochaeta indet.*) were observed at higher densities in the dredged areas. The response of community biomass was more consistent within basins, and generally reflected the response of the community indicators. Large-bodied taxa were characteristic of the unfished areas of Horsens and Løgstør, and included taxa such as *Arctica islandica*, *Alitta virens*, *Nephtys caeca*, and *Psammechinus miliaris*. Conversely, a higher biomass composed of *Petricolaria pholadiformis*, *Peringia ulvae*, and *Mya arenaria* was observed in the dredged areas of Lovns.

**Table 4-6: SIMPER (similarity percentages) analysis describing the species with the greatest contribution to observed dissimilarity between unfished and dredged areas. Species are ranked based on their percentage contribution. Taxa which contributed to up to 15 % (density) and 50% (biomass) of the dissimilarity between groups are shown. “±” indicates if density/biomass was higher (▲) or lower (▼) in dredged areas. “Cum. contrib.” stands for the cumulative contribution to dissimilarity between fishing effort (%). “Fished/unfished” describes the mean abundance/biomass in fished and unfished areas.**

Density	Group	Fished	Unfished	±	Cum. contrib. (%)	Biomass	Group	Fished	Unfished	±	Cum. contrib. (%)
<i>Nereididae</i> sp.		3.25	0.00	▲	4.96	<i>Crepidula fornicata</i>		0.31	1.24	▼	23.40
<i>Prionospio fallax</i>		0.86	1.59	▼	7.25	<i>Arctica islandica</i>		-	1.83	▼	42.76
<i>Phoronis</i> sp.		0.46	1.46	▼	9.36	<i>Alitta virens</i>		0.14	0.65	▼	55.49
<i>Odostomia</i> sp.		1.30	0.00	▲	11.42	<i>Nephtys caeca</i>		0.01	0.14	▼	61.16
<i>Streblospio shrubsolii</i>		0.92	1.35	▼	13.44						
<i>Tubificoides benedii</i>		2.11	1.48	▲	15.72						
<i>Microdeutopus</i> sp.		0.2	1.49	▼	4.63	<i>Crepidula fornicata</i>		0.75	0.49	▲	18.08
<i>Pholoe inornata</i>		0.71	1.61	▼	9.15	<i>Psammechinus miliaris</i>		-	0.49	▼	35.16
<i>Kefersteinia cirrhata</i>		0.71	1.49	▼	13.43	<i>Tritia reticulata</i>		0.37	0.38	▼	48.65
<i>Kurtiella bidentata</i>		0.66	1.27	▼	17.54	<i>Alitta virens</i>		0.03	0.32	▼	55.20
						<i>Mya arenaria</i>		-	0.19	▼	61.01
<i>Peringia ulvae</i>		3.9	1.27	▲	5.98	<i>Petricolaria pholadiformis</i>		1.61	0.79	▲	28.08
<i>Petricolaria pholadiformis</i>		3.29	1.03	▲	11.78	<i>Peringia ulvae</i>		0.94	0.06	▲	48.37
<i>Oligochaeta</i> indet.		3.97	1.81	▲	17.14	<i>Mya arenaria</i>		0.6	-	▲	61.43
<i>Bittium reticulatum</i>		2.73	-	▲	6.74						
<i>Galathowenia oculata</i>		1.41	1.81	▼	10.59						
<i>Microdeutopus</i> sp.		0.25	1.58	▼	15.67						

 = Polychaeta (sedentaria)     
 = Amphipoda     
 = Bivalvia     
 = Phoronida  
 = Polychaeta (errantia)     
 = Gastropoda     
 = Echinoidea     
 = Oligochaeta

#### 4.4. Discussion

In this study, we have described the effects of chronic shellfish dredging to macrofaunal communities in eutrophic estuarine systems, and further demonstrated how effects can be spatially dependent. At the fishery scale, community biomass declined along the gradient of dredging intensity, while small but significant changes in the taxonomic composition of the community were also observed. Environmental variables, such as sediment organic content (negative effect), mussel biomass, shell hash (both positive), and geographic location (i.e. basin) were also strong drivers of community composition. We were, however, unable to detect a significant effect to functional attributes of the community, namely functional richness and trait composition. Our ability to estimate dredging intensity at a fine spatial resolution revealed that the effects to macrofaunal communities varied at local scales, and this demonstrated the importance of this aspect in nearshore fishing impact assessments. In the following sections we discuss these findings and outline their management implications.

##### 1.1. Regional effects of dredging

Community biomass decreased exponentially over the gradient of dredging intensity, as indicated by the log-log linear relationship between the variables. This relationship commonly occurs as bottom trawling is thought to remove a fixed proportion of benthic biomass with each respective pass of the gear (Hiddink, Jennings, Kaiser, et al. 2006). While there was relatively high variation in biomass at the unfished and lightly fished sites, biomass was consistently low at frequencies of SAR  $>5 \text{ yr}^{-1}$  (all samples less than 5 g) (Figure 4-2 e). The high variation of biomass at low dredging intensities may also indicate the influence of other environmental pressures at these sites. While the biomass of taxa such as *Crepidula fornicata* and *Scoloplos armiger* remained stable regardless of dredging intensity, high biomass taxa such as *Arctica islandica*, *Modiolus modiolus*, *Nephtys hombergii*, and *Alitta virens* were present only at unfished sites. Large differences in biomass between open and closed areas has also been observed in fully marine circalittoral scallop grounds in the Irish Sea (Kaiser et al. 2000, Hinz et al. 2011, Cook et al. 2013), and suggest that large-bodied individuals are unable to withstand chronic fishing disturbance. Community biomass has been shown to be an effective indicator of trawl disturbance across fishing grounds (Hiddink, Jennings, & Kaiser 2006) and also in heavily fished sedimentary environments (Reiss et al. 2009). Under regular disturbance, the biomass of macrofaunal communities will typically shift from a dominance of few large individuals, to those composed of highly abundant small macrofauna (Kaiser et al. 2000). While both large and small bodied macrofauna are vulnerable to direct contact with fishing gear (Bergman & Van Santbrink 2000), large-bodied fauna are unable to recover due to inherently low population growth rates (Jennings, Dinmore, et al. 2001, Queirós et al. 2006). Despite the widespread use of biomass-based indicators, there is little information regarding their use in

mussel and oyster fisheries, and in shallow brackish environments. Nevertheless, the sensitivity of large epifauna to mussel dredging has been demonstrated in studies from Limfjorden using comparative (open vs. closed) areas (Dolmer 2002). In areas closed to fisheries for four months, higher abundances of sponges, anthozoans, crustaceans, and ascidians were observed compared to fished areas, while epibenthic community composition remained altered in some areas for up to four years.

A result common to our study and several other assessments of bivalve fisheries is the observed impact to community composition. Changes in taxonomic composition have been observed from fisheries in the Irish Sea (Hill et al. 1999, Lambert et al. 2014), Portugal (Constantino et al. 2009), Australia (Currie & Parry 1996) and New Zealand (Thrush et al. 1995). Changes in community composition are often detectable as trawling results in uneven mortality of benthos, and thereby altering the relative proportions of different species (Jennings, Pinnegar, et al. 2001). However, these changes are often subtle, and may explain why community-level indicators such as total density did not respond significantly, despite its effectiveness elsewhere in Danish waters (Gislason et al., 2017, McLaverty et al., 2020). Rather unusually, density exhibited a non-significant but positive relationship with dredging intensity. Although dredging reduced the density of several taxa in our study, we also observed high densities of opportunistic taxa at the most heavily dredged sites. For example, densities of 250-500 m<sup>2</sup> were observed for *Heteromastus filiformis*, *Scoloplos armiger*, and *Streblospio shrubsolii* at dredging intensities of >20 year<sup>-1</sup> (in Horsens sites HF01, HF04). While these polychaete species may proliferate under high nutrient enrichment (Rouse & Pleijel 2001), we would expect such high dredging intensities to significantly reduce macrofaunal density. However, dredging in these areas are characterised by highly aggregated effort (Figure 4-1 a-d), and it is likely that a high degree of recovery from adjacent unaffected areas may occur via immigration between dredging events.

Although trait-based approaches can effectively describe trawling effects to macrofaunal communities across regional scales (Lundquist et al. 2018), we were unable to detect any such differences in our study. This result was somewhat unexpected, and may indicate that unfished and fished communities are composed of functionally similar trait combinations. Communities which subsist in highly dynamic or otherwise naturally disturbed habitats (e.g. inherently low species richness in brackish waters) may exhibit traits which favour high resilience and recoverability (Bolam et al. 2017). This was evident in our results, whereby the most widely distributed taxa shared a number of traits such as generalist feeding strategies, high mobility, short-longevity, and small body-size (e.g. *Peringia ulvae*, *Streblospio shrubsolii*, *Tubificoides benedii*, *Capitella* sp., and *Oligochaeta* indet.). Furthermore, the abundance of these taxa and therefore their traits were seemingly unaffected by dredging intensity. Similar effects of hydrodynamic disturbance and trawling to macrofauna have been observed in the North Seas and English Channel (Van Denderen et al. 2015, Szostek et al. 2016),

and our results suggest that areas which experience chronic eutrophication may be also functionally resistant to bottom trawl fisheries (Dinesen et al. 2015).

### ***Local effects of dredging***

A unique aspect of our study was the examination of fishing gradients at the scale of individual N2000 sites. This revealed that the observed decline in biomass at the regional level was not generalised across spatial scales. At the local scale, biomass decreased with dredging intensity in Horsens and Løgstør, showed little relationship in Nissum, and increased with dredging intensity in Lovns. Although populations of scavenging species have been shown to increase in response to bottom trawling disturbance (Dolmer et al. 2001, Mangano et al. 2013), an increase in community biomass represents a particularly unusual observation. However, it is likely that the environmental conditions present in Lovns may strongly impact local community composition, while at the same time constricting our ability to accurately measure the effects of dredging. Due to mainly agricultural runoff, nitrogen and phosphorus loadings in Lovns are three times higher than average for Limfjorden (Markager et al. 2006). These remarkably high levels of eutrophication, combined with high residence times, means that regular and widespread oxygen depletion is prevalent in Lovns. In the summer prior to sampling, extensive anoxia occurred on two separate occasions (June and September) in the central parts of the basins (Hansen 2018). Furthermore, we observed a mean temperature range of  $\sim\pm 20^{\circ}\text{C}$  across sampling sites in Lovns. Such large variation may be outside of the thermal limits of boreal benthic species, and favour more generalist species. Differences in biomass between unfished and dredged sites in Lovns were mainly accounted for by 3 taxa; namely, *Oligochaeta* indet., *Peringia ulvae*, and *Petricolaria pholadiformis*. In the southern North Sea, greater densities of *P. ulvae* and *P. pholadiformis* have been observed in areas impacted by sediment dredging works (Gutperlet et al. 2015), while in addition, several studies have shown oligochaetes to be relatively unaffected by bottom trawl disturbance (Collie et al. 2000, Fariñas-Franco et al. 2018, Sciberras et al. 2018). This combination of a highly resilient macrofaunal community and unusually low abundance and biomass observed at some of the unfished sites (e.g. LvB06, LvB08, and LvB09), may explain the apparent positive relationship between biomass and dredging intensity.

Community composition varied significantly between unfished and dredged areas in each of the basins. In our density-based estimates, several species exhibited opposing relationships with dredging. This may partly explain the lack of significant effect on community density at the regional scale, while also providing evidence of how specific species respond to chronic bottom trawl disturbance. Most of the taxa which exhibited a positive response to trawling were either gastropod or oligochaete species. Oligochaetes are pioneer species, characteristic of highly eutrophic systems, and have been observed to be the first macrofauna to recolonise heavily trawled areas (Engel & Kvitek 1998). Although shown to be vulnerable to the direct effects of trawling

(Ramsay et al. 2000), gastropods are relatively mobile compared to most benthic macrofauna. Furthermore, the widespread occurrence of the group across the study area would suggest that the potential for immigration to fished areas is high, and this mechanism may explain the generally short recovery times of gastropods observed in meta-analyses (Sciberras et al. 2018). In respect to biomass, several taxa demonstrated a consistent negative response to dredging. Although the occurrence of *Arctica islandica* was low, its presence in unfished areas was a distinguishing feature. Despite its thick shell and periodic deep sediment position, *A. islandica* can experience high mortality rates (up to ~20% per trawl pass) (Bergman & Van Santbrink 2000). This species also exhibits late maturity and slow recoverability, and is often absent from heavily fished areas. The loss of *Alitta virens* and *Nephtys caeca* have been observed in several other trawl studies (Dolmer et al. 1999, Ball et al. 2000, Craeymeersch et al. 2013, Sköld et al. 2018) indicating the susceptibility of these species to physical damage. These polychaetes are relatively large, soft-bodied and may be exposed to direct contact with dredge gear while feeding in the mussel bed matrix.

### **Auxiliary drivers**

Mussel biomass and shell hash had a strong positive effect to the structure and composition of macrofaunal communities. In soft sediment habitats, hard structures such as living organisms and shell debris provide additional important habitat elements. Furthermore, mussels and oysters are capacious filter feeders, and therefore recognised as habitat modifying organisms, altering resource availability and modifying physical environmental conditions. Aggregations of mussels increase food resources, reduce turbidity via filtration, and provide hotspots of biodiversity in species-poor systems (Norling & Kautsky 2008). Empty mussel shells and shell hash provide similar benefits to benthic diversity as live mussels by providing structure, a substrate for epizoic growth, and by accumulating sediments (Norling & Kautsky 2007). While the filtration capacity of mussel beds has been discussed as a potential mitigation tool for nutrient enrichment in Limfjorden and Inner Danish waters (Dolmer & Frandsen 2002), the benefits of shellfish beds to the ecosystem are generally not considered. Given that dredging removes mussel and oyster biomass from the system, and has been shown to reduce the quantity of shell hash in sediments in Limfjorden (Riis et al. 2003), management may seek to examine such trade-offs in future. We observed a roughly equal occurrence of mussels in samples taken in fished and unfished areas, which would suggest that the positive effects of mussel biomass was balanced across the treatment of fishing effort. However, future work may seek to further investigate the mechanisms behind the community response to dredging by quantifying the interactive effects between these variables.

Although the total biomass of macrofauna did not vary between N2000 sites, 'basin' was a significant term in the final models of density, functional richness, and the various measures of community composition. Although the study area was dominated by several stress-tolerant species, this result indicates that the

communities observed in each basin were formed of distinct combinations of species and traits. The divergence of these combinations likely to be due to the effects of dispersal, a key driver of community composition across regions (Young et al. 1997). Accordingly, the degree of connectivity and dynamics of water movements between basins will have had a strong effect on the nestedness of these communities. Aside from this, salinity is also a key driver of species composition in Danish waters, and is often positively correlated with benthic species richness (Josefson & Hansen 2004). However, we are unable to formally test the effect of this variable as we opted to exclude salinity during the preliminary analysis (see *material and methods: data analysis*), due to its collinearity with other variables, and inability to improve model fits. Examination of x-y plots between salinity and the diversity indicators further validated this choice. This demonstrated that, Nissum (the most saline basin) exhibited relatively moderate to low species and functional richness, while Horsens (the least saline) exhibited by far the highest richness. By contrast, levels of organic enrichment in the sediment were highest in Nissum and lowest in Horsens. These observations contradict our *a-priori* assumptions regarding the positive relationship between salinity and benthic indicators, and suggest that typical relationships observed elsewhere in Danish waters are disrupted under high eutrophication and high fishing pressure conditions.

Benthic communities in Danish waters are affected by organic enrichment and associated hypoxia (Jørgensen 1980, Petersen et al. 2002). Although our sampling design aimed to exclude areas of regular oxygen depletion, our results show that community density and community composition were significantly affected by elevated sediment organic content. Despite recent improvements under the Water Framework Directive (WFD; 2000/60/EC), eutrophication remains a significant issue in Danish coastal waters, and our ability to accurately describe the impacts of dredging are likely hampered by the interactive effects of nutrient enrichment and oxygen depletion. Given that dissolved oxygen concentrates of the global ocean are expected to drop by 1-7% by 2100 (Schmidtke et al. 2017), scientific knowledge regarding the combined effects of trawling and low oxygen on benthic communities is considerably lacking.

### ***Management perspectives***

Our study has shown that it is difficult to detect fishery effects in heavily modified areas. Like many nearshore areas in Denmark (Conley et al. 2006), the fishing grounds examined here are characterised by high nutrient enrichment and variability in environmental conditions. Anthropogenic and natural pressures have the potential to distort the outcome of fishing impact assessments, as benthic communities may become stress-adapted irrespective of fishing effort (Kaiser et al. 2002). This was potentially reflected in our results from Nissum and Lovns, where the ability of indicators to detect dredging impacts were significantly impaired. Although Løgstør is subject to similar levels of nutrient enrichment and natural disturbance, a clear negative

effect of dredging to macrofaunal communities was observed here. This is likely attributable to the presence of a long-standing fisheries closure in the north of the basin, in an area of the seabed which also experiences stable oxygen conditions. In these areas, the sampled communities were comparatively less disturbed and thus provided unfished reference conditions relative to the rest of the basin. Similar unfished reference conditions were not present in Lovns and Nissum, and therefore dredging activities takes place on a rotational basis across the majority of available shellfish beds. This practice is undertaken to allow the stock to reach marketable size (~4.5 cm for mussels, >80 g for oysters) (Frandsen et al. 2015, Nielsen & Petersen 2019), and means that mussel beds are fished roughly every 2.5 years (Dolmer 1998), and 3-4 years in the case of oysters (Nielsen & Petersen 2019). This may result in a situations where there is little remaining comparable seabed in these areas, which is not impacted by fisheries, or by high organic content and/or low oxygen conditions. Therefore, the conservation of small reference sites could provide for the maintenance of ecosystem services, while also improving local habitat diversity and function. The preservation of unfished shellfish beds also has the potential to improve monitoring and management by providing suitable and permanent 'control' (reference) areas adjacent to the fishing grounds (e.g. Lindeboom 1995). Such a strategy would not require closure of large areas or entire basins, given the black-box data has demonstrated that reference sites (and associated sensitive macrofauna) can be maintained in close proximity (~100 m) to high intensity dredging (Figure 4-1 a & d). The inclusion of a number small reference sites into future monitoring studies could thus potentially help meet several conservation and management objectives relative to the fishery activities, and help reduce the need to implement large sampling programs to inform ecosystem based fisheries management advice. In addition to this, the preservation of such areas are necessary for a management scenario were shifting baselines are not ignored (Brown & Trebilco 2014).

### **Acknowledgements**

Thanks to Jens Würgler Hansen, Aarhus University, for providing oxygen depletion maps of the study area. Thanks to Pernille Nielsen and Camille Saurel, both the Danish Shellfish Centre, for discussions regarding the planning of field work and interpretation of results. Thanks to Daniel van Denderen for advice regarding the planning of the study. Thanks to Jeppe Olsen for providing black-box data and associated shapefiles. We thank the captains of RV *Egon P*: Lars Kyed Andersen and Finn Bak, and to Kasper Lenda Andersen, Louise Scherffenberg Lundgaard, and Stine Kærulf Andersen for assistance during field work. Thanks to the several student assistants for laboratory assistance in sorting benthic samples into higher taxonomic groups. This study was funded by The Danish Fisheries Agency, Ministry of Environment and Food of Denmark, through the European Maritime and Fisheries Fund (EMFF) via the project “Påvirkning af økosystemkomponenten bundfauna i N2000 områder ved fiskeri med skrabende redskaber” (grant agreement number 33-113B-16-056) and DTU Aqua.

### **Supplementary information**

[See supplement below]

## References

- Amoroso RO, Pitcher CR, Rijnsdorp AD, McConnaughey RA, Parma AM, Suuronen P, Eigaard OR, Bastardie F, Hintzen NT, Althaus F, Baird SJ, Black J, Buhl-Mortensen L, Campbell AB, Catarino R, Collie J, Cowan JH, Durholtz D, Engstrom N, Fairweather TP, Fock HO, Ford R, Gálvez PA, Gerritsen H, Góngora ME, González JA, Hiddink JG, Hughes KM, Intelmann SS, Jenkins C, Jonsson P, Kainge P, Kangas M, Kathena JN, Kavadas S, Leslie RW, Lewis SG, Lundy M, Makin D, Martin J, Mazor T, Gonzalez-Mirelis G, Newman SJ, Papadopoulou N, Posen PE, Rochester W, Russo T, Sala A, Semmens JM, Silva C, Tsolos A, Vanelslander B, Wakefield CB, Wood BA, Hilborn R, Kaiser MJ, Jennings S (2018) Bottom trawl fishing footprints on the world's continental shelves. *Proc Natl Acad Sci* 115:E10275–E10282.
- Anon (1979) Birds Directive: Council Directive 79/409/EEC of 2 April 1979.
- Anon (1992) Habitats Directive: Council Directive 92/43/EEC of 21 May 1992.
- Ball BJ, Fox G, Munday BW (2000) Long- and short-term consequences of a Nephrops trawl fishery on the benthos and environment of the Irish Sea. *ICES J Mar Sci* 57:1315–1320.
- Barton, K. (2013) MuMIn: Multi-Model Inference. R Package Version 1.40.4 <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Bergman MJN, Santbrink JW Van (2000) Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. In: *ICES Journal of Marine Science*. p 1321–1331.
- Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, Kooten T van, Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Hoey G Van, Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar Environ Res* 126:1–13.
- Brown CJ, Trebilco R (2014) Unintended Cultivation, Shifting Baselines, and Conflict between Objectives for Fisheries and Conservation. *Conserv Biol* 28:677–688.
- Chevène F, Doledec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshw Biol* 31:295–309.
- Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts shelf-sea benthos. *J Anim Ecol* 69:785–798.
- Conley DJ, Kaas H, Møhlenberg F, Rasmussen B, Windolf J, Mohlenberg F, Windolf J (2000) Characteristics of Danish Estuaries. *Estuaries* 23:820.
- Constantino R, Gaspar MB, Tata-Regala J, Carvalho S, Cúrdia J, Drago T, Taborda R, Monteiro CC (2009) Clam dredging effects and subsequent recovery of benthic communities at different depth ranges. *Mar Environ Res* 67:89–99.

- Cook R, Fariñas-Franco JM, Gell FR, Holt RHF, Holt T, Lindenbaum C, Porter JS, Seed R, Skates LR, Stringell TB, Sanderson WG (2013) The Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A Dilemma for Evidence-Based Conservation. *PLoS One* 8:1–10.
- Craeymeersch J, Jansen J, Smaal A, van Stralen M, Meesters E, Fey F (2013) Impact of mussel seed fishery on subtidal macrozoobenthos in the western Wadden Sea. IMARES report number PR 7 C003/13. 123 pp.
- Currie D, Parry G (1996) Effects of scallop dredging on a soft sediment community: a large-scale experimental study. *Mar Ecol Prog Ser* 134:131–150.
- Danish Ministry of the Environment (2013). Natura 2000-basisanalyse 2015-2021 for Horsens Fjord, havet øst for og Endelave Natura 2000-område nr. 56 Habitatområde H52 Fuglebeskyttelsesområde F36. ISBN nr. 978-87-7091-092-7.
- Dernie KM, Kaiser MJ, Warwick RM (2003) Recovery rates of benthic communities following physical disturbance. *J Anim Ecol* 72:1043–1056.
- DHI (2013). MIKE 21 & MIKE 3 Flow Model FM. Hydrodynamic and Transport Module. Scientific Documentation. DHI Water Environment Health, Hørsholm, Denmark, 54 pp.
- Diesing M, Stephens D, Aldridge J (2013) A proposed method for assessing the extent of the seabed significantly affected by demersal fishing in the Greater North Sea. *ICES J Mar Sci* 70:1085–1096.
- Dinesen GD, Canal-Vergés P, Nielsen P, Filrup K, Geitner K & Petersen JK 2015. Effekter af blåmuslingefiskeri på bundfauna. DTU Aqua Rapport 305-2015, 33 pp.
- Dinesen GE, Timmermann K, Roth E, Markager S, Ravn-Jensen L, Hjorth M, Holmer M, Støttrup JG (2011) Mussel Production and Water Framework Directive Targets in the Limfjord, Denmark: an Integrated Assessment for Use in System-Based Management. *Ecol Soc* 16:art26.
- Dolmer P (1998) Seasonal and spatial variability in growth of *Mytilus edulis* L. in a brackish sound: Comparisons of individual mussel growth and growth of size classes. *Fish Res* 34:17–26.
- Dolmer P, Frandsen RP (2002) Evaluation of the Danish mussel fishery: Suggestions for an ecosystem management approach. *Helgol Mar Res* 56:13–20.
- Dolmer P, Kristensen T, Christiansen ML, Petersen MF, Kristensen PS, Hoffmann E (2001) Short-term impact of blue mussel dredging (*Mytilus*). *Hydrobiologia* 465:115–127.
- Dolmer P, Sand Kristensen P, Hoffmann E (1999) Dredging of blue mussels (*Mytilus edulis* L.) in a Danish sound: Stock sizes and fishery-effects on mussel population dynamic. *Fish Res* 40:73–80.
- Dolmer, P. (2002). Mussel dredging: Impact on epifauna in Limfjorden, Denmark. *Journal of Shellfish Research*, 21(2), 529-538.
- Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O'Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sørensen TK, Tully O, Zengin M, Rijnsdorp AD

(2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J Mar Sci* 73:i27–i43.

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanellander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *ICES J Mar Sci* 74:847–865.

Engel J, Kvitek R (1998) Effects of Otter Trawling on a Benthic Community in Monterey Bay National Marine Sanctuary. *Conserv Biol* 12:1204–1214.

Fariñas-Franco JM, Allcock AL, Roberts D (2018) Protection alone may not promote natural recovery of biogenic habitats of high biodiversity damaged by mobile fishing gears. *Mar Environ Res* 135:18–28.

Frandsen RP, Eigaard OR, Poulsen LK, Tørring D, Stage B, Lisbjerg D, Dolmer P (2015) Reducing the impact of blue mussel (*Mytilus edulis*) dredging on the ecosystem in shallow water soft bottom areas. *Aquat Conserv Mar Freshw Ecosyst* 25:162–173.

Gislason H, Bastardie F, Dinesen GE, Egekvist J, Eigaard OR (2017) Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. *Ecol Indic* 82:260–270.

Gislason H, Sinclair M, Sainsbury K, O'boyle R (2000) Symposium overview: Incorporating ecosystem objectives within fisheries management. In: *ICES Journal of Marine Science*. p 468–475

Gutperlet R, Capperucci RM, Bartholomä A, Kröncke I (2015) Benthic biodiversity changes in response to dredging activities during the construction of a deep-water port. *Mar Biodivers* 45:819–839.

Hall-Spencer, J.M., & Moore, P.G. (2000). Impact of scallop dredging on maerl grounds. p. 105-118, in: M.J. Kaiser and S.J. De Groot. *Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues*. Oxford: Blackwell Science.

Hansen, J.W. (red.) (2018). *Marine områder 2016*. NOVANA. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, 140 s. - Videnskabelig rapport fra DCE - Nationalt Center for Miljø og Energi nr. 253 <http://dce2.au.dk/pub/SR253.pdf>.

Hiddink JG, Jennings S, Kaiser MJ (2006a) Indicators of the ecological impact of bottom-trawl disturbance on seabed communities. *Ecosystems* 9:1190–1199.

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE, Piet GJ (2006b) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can J Fish Aquat Sci* 63:721–736.

Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci* 114:8301–8306.

Hill AS, Veale LO, Pennington D, Whyte SG, Brand AR, Hartnoll RG (1999) Changes in Irish Sea Benthos: Possible effects of 40 years of dredging. *Estuar Coast Shelf Sci* 48:739–750.

Hinz H, Moranta J, Balestrini S, Sciberras M, Pantin JR, Monnington J, Zalewski A, Kaiser MJ, Sköld M, Jonsson P, Bastardie F, Hiddink JG (2017) Stable isotopes reveal the effect of trawl fisheries on the diet of commercially exploited species. *Sci Rep* 7:6334

Hinz H, Tarrant D, Ridgeway A, Kaiser MJ, Hiddink JG (2011) Effects of scallop dredging on temperate reef fauna. *Mar Ecol Prog Ser* 432:91–102

Hoffmann E, Dolmer P (2000) Effect of closed areas on distribution of fish and epibenthos. *ICES J Mar Sci* 57:1310–1314.

Hoffmann, E. (2005). Fisk, fiskeri og epifauna: Limfjorden 1984-2004. Charlottenlund: Danmarks Fiskeriundersøgelser. DFU-rapport, No. 147-05 (in Danish).

Jennings S, Dinmore TA, Duplisea DE, Warr KJ, Lancaster JE (2001) Trawling disturbance can modify benthic production processes. *J Anim Ecol* 70:459–475.

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol*:201–212.

Jennings S, Nicholson MD, Dinmore TA, Lancaster JE (2002) Effects of chronic trawling disturbance on the production of infaunal communities. *Mar Ecol Prog Ser* 243:251–260.

Jennings S, Pinnegar J, Polunin N, Warr K (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Mar Ecol Prog Ser* 213:127–142.

Jørgensen BB, Jørgensen BB (1980) Seasonal Oxygen Depletion in the Bottom Waters of a Danish Fjord and Its Effect on the Benthic Community. *Oikos* 34:68.

Josefson AB, Hansen JLS (2004) Species richness of benthic macrofauna in Danish estuaries and coastal areas. *Glob Ecol Biogeogr* 13:273–288.

Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14.

Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2002) Modification of marine habitats by trawling activities: Prognosis and solutions. *Fish Fish* 3:114–136.

Kaiser MJ, Hormbrey S, Booth JR, Hinz H, Hiddink JG (2018) Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. *J Appl Ecol* 55:1060–1070.

Kaiser MJ, Ramsay K, Richardson CA, Spence FE, Brand AR (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. *J Anim Ecol* 69:494–503.

Kutner MH, Nachtsheim CJ, Neter J, Li W (2004) *Applied Linear Statistical Models*. McGraw-Hill Irwin

Lambert GI, Jennings S, Kaiser MJ, Davies TW, Hiddink JG (2014) Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. *J Appl Ecol* 51:1326–1336.

- Lambert GI, Murray LG, Hiddink JG, Hinz H, Lincoln H, Hold N, Cambiè G, Kaiser MJ (2017) Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance. *Sci Rep* 7:5440.
- Legendre P, Andersson MJ (1999) Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24.
- Lenihan, B.S. (1999). Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. *Ecological Monographs* 69: 251-275.
- Lüdecke, D., (2016) sjPlot: Data Visualization for Statistics in Social Science. 2019; Available online: <http://cran.r-project.org/package=sjPlot>.
- Lundquist CJ, Bowden D, Cartner K, Stephenson F, Tuck I, Hewitt JE (2018) Assessing Benthic Responses to Fishing Disturbance Over Broad Spatial Scales That Incorporate High Environmental Variation. *Front Mar Sci* 5:1–14.
- Maar M, Markager S, Madsen KS, Windolf J, Lyngsgaard MM, Andersen HE, Moller EF (2016) The importance of local versus external nutrient loads for chl a and primary production in the western Baltic Sea. *Ecol Modell* 320:258–272.
- Maar M, Timmermann K, Petersen JK, Gustafsson KE, Storm LM (2010) A model study of the regulation of blue mussels by nutrient loadings and water column stability in a shallow estuary, the Limfjorden. *J Sea Res*
- Maar M, Timmermann K, Petersen JK, Gustafsson KE, Storm LM (2010) A model study of the regulation of blue mussels by nutrient loadings and water column stability in a shallow estuary, the Limfjorden. *J Sea Res* 64: 322–333
- MacArthur, R. H., and E. O. Wilson. (1967). *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Mangano M, Kaiser M, Porporato E, Spanò N (2013) Evidence of trawl disturbance on mega-epibenthic communities in the Southern Tyrrhenian Sea. *Mar Ecol Prog Ser* 475:101–117.
- Markager, S., Bassompierre, M. & Petersen, D.J. (2010) *Analyse af miljøtilstanden i Horsens Fjord fra 1985 til 2006. Empirisk modellering*. National Environmental Research Institute, Aarhus University. 84 pp. – NERI Technical Report No. 733.
- Markager, S., Storm, L.M. & Stedmon, C.A. (2006) *Limfjordens miljøtilstand 1985 til 2003. Sammenhæng mellem næringsstofftilførsler, klima og hydrografi belyst ved hjælp af empiriske modeller*. Danmarks Miljøundersøgelser. 219 s. - Faglig rapport fra DMU, nr. 577.
- McLaverty C, Eigaard OR, Gislason H, Bastardie F, Brooks ME, Jonsson P, Lehmann A, Dinesen GE (2020) Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. *Ecol Indic* 110:105811.
- Moritz C, Gravel D, Savard L, McKindsey CW, Brêthes J-C, Archambault P (2015) No more detectable fishing effect on Northern Gulf of St Lawrence benthic invertebrates. *ICES J Mar Sci J du Cons* 72:2457–2466.

Nielsen P, Petersen JK (2019) Flat oyster fishery management during a time with fluctuating population size. *Aquat Living Resour* 32:22.

Nielsen, P., Canal-Vergés, P., Nielsen, M. M., Geitner, K., & Petersen, J. K. (2017). Konsekvensvurdering af fiskeri efter blåmuslinger ved og øst for Horsens Fjord samt Endelave 2017. Institut for Akvatiske Ressourcer, Danmarks Tekniske Universitet. DTU Aqua-rapport, No. 319-2017 (in Danish).

Norling P, Kautsky N (2007) Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. *Mar Ecol Prog Ser* 351:163–175.

Norling P, Kautsky N (2008) Patches of the mussel *Mytilus* sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic sea. *Aquat Biol* 4:75–87.

Olsgard F, Schaanning MT, Widdicombe S, Kendall MA, Austen MC (2008) Effects of bottom trawling on ecosystem functioning. *J Exp Mar Bio Ecol* 366:123–133.

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol An Annu Rev* 16:229–311.

Petersen JK, Stenalt E, Hansen BW (2002) Invertebrate re-colonisation in Mariager Fjord (Denmark) after a severe hypoxia. II. Blue mussels (*Mytilus edulis* L.). *Ophelia* 56:215–226.

Piet GJ, Quirijns FJ (2009) The importance of scale for fishing impact estimations (B Sainte-Marie, Ed.). *Can J Fish Aquat Sci* 66:829–835.

Queirós AM, Hiddink JG, Kaiser MJ, Hinz H (2006) Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. *J Exp Mar Bio Ecol* 335:91–103.

Ramsay K, Kaiser M., Richardson C., Veale L., Brand A. (2000) Can shell scars on dog cockles (*Glycymeris glycymeris* L.) be used as an indicator of fishing disturbance? *J Sea Res* 43:167–176.

Reiss J, Bridle JR, Montoya JM, Woodward G (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol Evol* 24:505–514.

Riemann B, Hoffmann E (1991) Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. *Mar Ecol Prog Ser* 69:171–178.

Riis A, Dolmer P, Riis A (2003) The distribution of the sea anemone *Metridium senile* (L.) related to dredging for blue mussels (*Mytilus edulis* L.) and flow habitat. *Ophelia* 57:43–52.

Rouse, G., & Pleijel, F. (2001). *Polychaetes*. Oxford university press.

Schloerke B, Crowley J, Cook D, Hofmann H, Wickham H, Briatte F, Marbach M, Thoen E (2014) *GGally*: extension to *ggplot2*. In: R package version 0.4.8, Vienna, Austria.

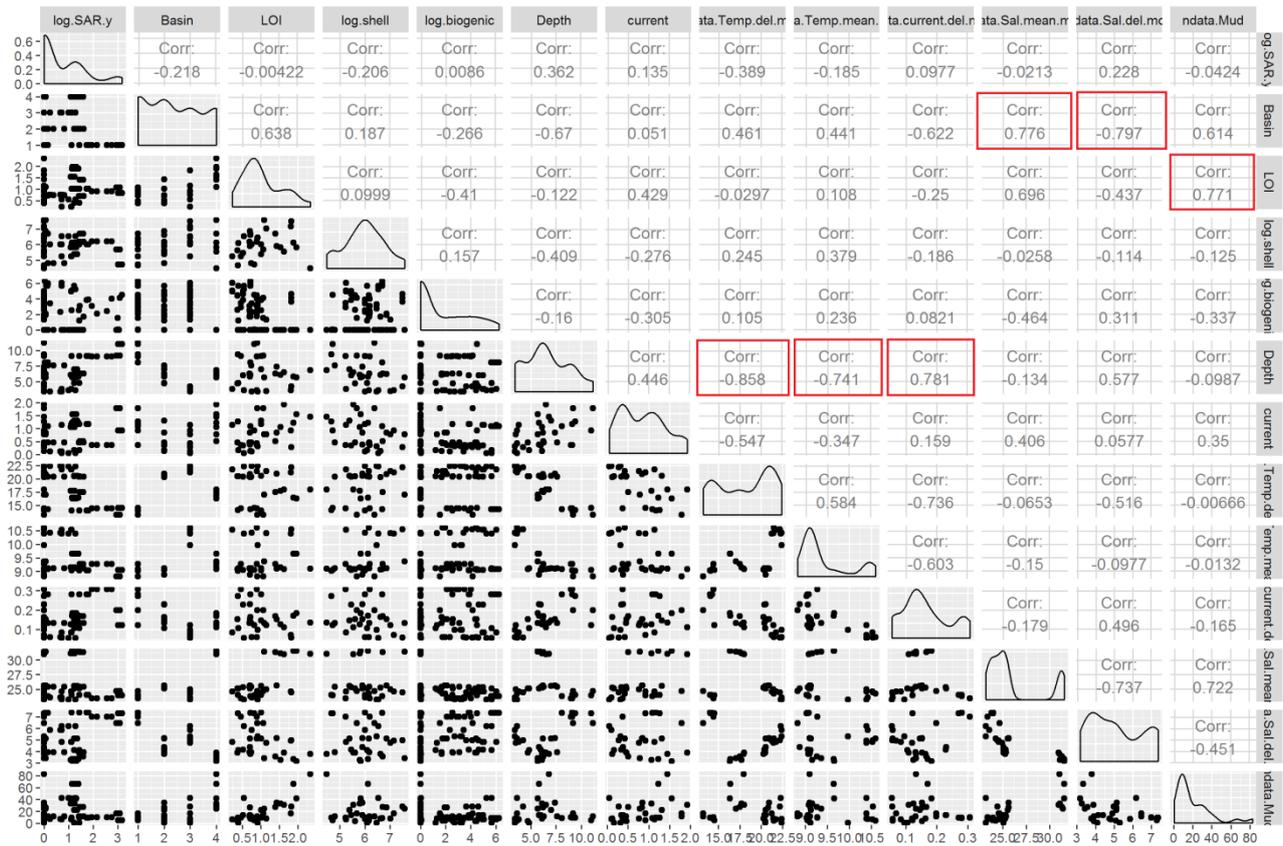
Schmidtko S, Stramma L, Visbeck M (2017) Decline in global oceanic oxygen content during the past five decades. *Nature* 542:335–339.

- Sciberras M, Hiddink JG, Jennings S, Szostek CL, Hughes KM, Kneafsey B, Clarke LJ, Ellis N, Rijnsdorp AD, McConnaughey RA, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2018) Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish* 19:698–715.
- Sciberras M, Hinz H, Bennell JD, Jenkins SR, Hawkins SJ, Kaiser MJ (2013) Benthic community response to a scallop dredging closure within a dynamic seabed habitat. *Mar Ecol Prog Ser* 480:83–98.
- Sköld M, Göransson P, Jonsson P, Bastardie F, Blomqvist M, Agrenius S, Hiddink JG, Nilsson HC, Bartolino V (2018) Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Mar Ecol Prog Ser* 586:41–55.
- Szostek CL, Murray LG, Bell E, Rayner G, Kaiser MJ (2016) Natural vs. fishing disturbance: Drivers of community composition on traditional king scallop, *Pecten maximus*, fishing grounds. *ICES J Mar Sci* 73:i70–i83.
- Thrush SF, Hewitt JE, Cummings VJ, Dayton PK (1995) The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Mar Ecol Prog Ser* 129:141–150.
- Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45
- Tomczak, M. T., Dinesen, G. E., Hoffmann, E., Maar, M., & Støttrup, J. (2012) Integrated trend assessment of ecosystem changes in the Limfjord (Denmark): evidence of a recent regime shift? *Estuarine, Coastal and Shelf Science*, 117, 178-187.
- Ministry of Foreign Affairs of Denmark (2019). Målsætninger og forvaltningsprincipper for muslinge- og østersskrab og øvrig muslinge- og østersproduktion i og udenfor Natura 2000 områder.  
<http://www.fiskeristyrelsen.dk/erhvervsfiskeri/muslinger-og-oesters/muslinge-og-oesterspolitikken>
- Van Denderen PD, Bolam SG, Hiddink JG, Jennings S, Kenny A, Rijnsdorp AD, Van Kooten T (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar Ecol Prog Ser* 541:31–43.
- Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.
- Wiens JA (1989) Spatial Scaling in Ecology. *Funct Ecol* 3:385.
- Young CM, Sewell MA, Tyler PA, Metaxas A (1997) Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: The role of larval dispersal. *Biodivers Conserv* 6:1507–1522.

Supplementary information

Local and regional effects of bivalve dredging on benthic macrofauna in a eutrophic estuarine system

Figure S1: Pair-plot of predictor variables considered for the analysis. Values provided are Pearson R correlation coefficients. Correlations of >0.70 were excluded from the analysis. Colinear relationships that resulted in the dropping of variables are highlighted by the red boxes. The  $r=0.736$  relationship between temp delta and current delta is not highlighted as both terms were removed from the analysis. Variance Inflation Factor values are provided below based on a model containing all variables. Terms are explained below.

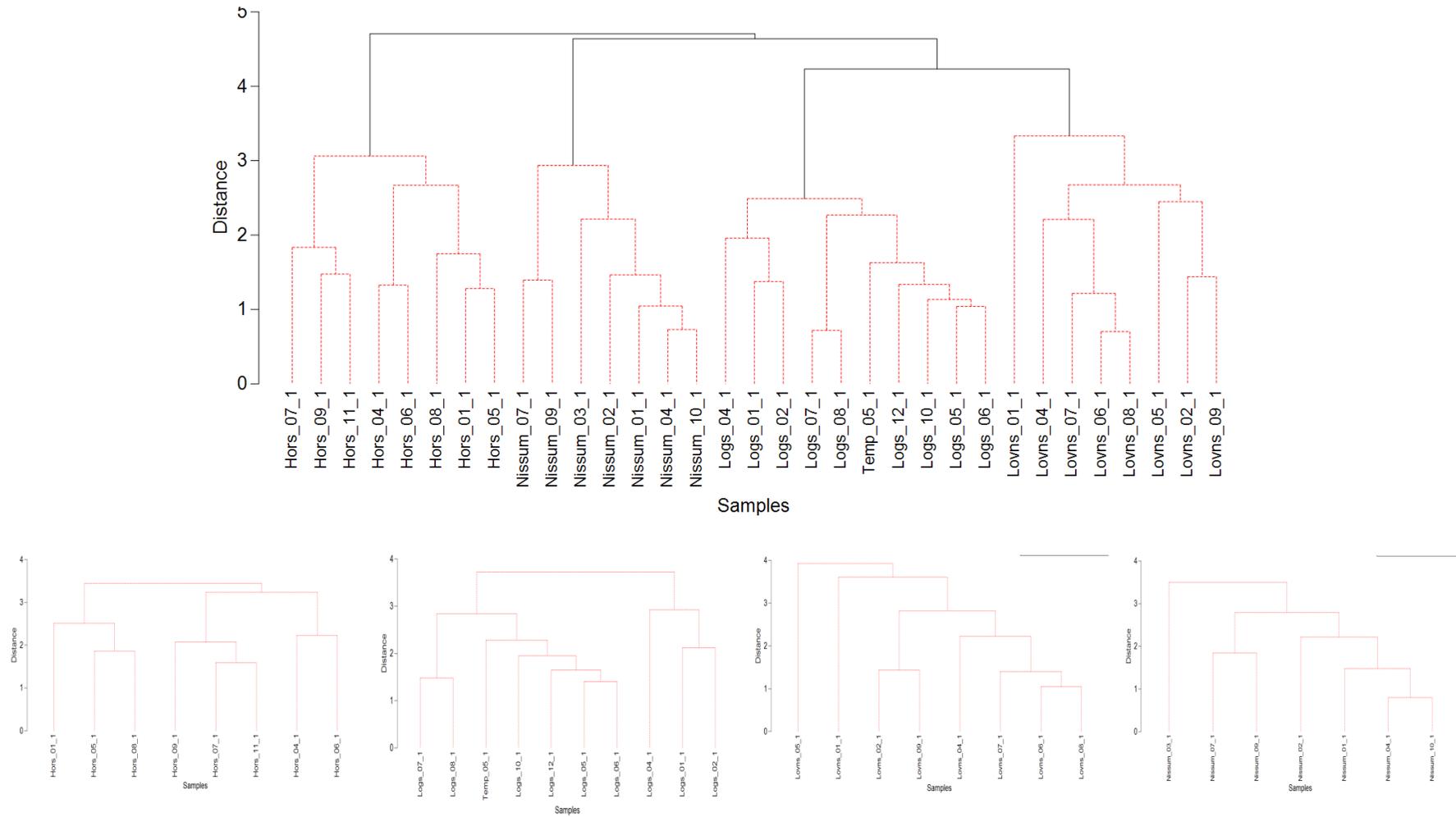


Terms : LOI = loss on ignition (organic content). Temp = temperature. Sal = salinity. Del = delta (range). SAR = dredging intensity. Mud = mud fraction. Shell = shell hash. Muss = mussel biomass.

**Table S1: Variance Inflation Factor (VIF) values for the predictors carried forward for analysis. VIF based on  $GVIF^{(1/(2 \cdot Df))}$  due to presence of categorical terms.**

Final terms:	Response ~ Basin*Dredging + LOI + Shell hash + Mussel biomass + Temperature + Current + (1 Site)						
	Basin	Dredging	LOI	Shell hash	Mussel biomass	Temperature	Current
VIF values	1.823625	1.108752	1.566026	1.145600	1.091511	3.677804	1.430279

**Figure S2: Cluster analysis of environmental characteristics of sampling sites. Clustering based on Euclidean distance. Red line indicate statistically significant clusters.**



**Text S1- MIKE 3 HD Flexible Mesh (FM) model**

For the hydrodynamic model results we have applied DHIs model software (DHI 2013); The hydrodynamic MIKE 3 HD Flexible Mesh (FM) models were set up to represent the specific hydrodynamic conditions of the Limfjord and the Northern Belt sea. MIKE 3 HD FM is applicable for the study of a wide range of physical phenomena, for instance: tidal exchange and currents, including stratified flows, salinity and heat transfer. MIKE 3 HD FM solves the time-dependent conservation equations of mass and momentum in three dimensions, the so-called Reynolds-averaged Navier-Stokes equations. The flow field and pressure variation are computed in response to bathymetry, bed resistance, wind and atmospheric pressure field, hydrographical boundary conditions, etc. MIKE 3 HD FM uses the UNESCO equation for the state of seawater as the relation between salinity, temperature and density (UNESCO 1981). The unstructured flexible mesh and finite volume solution technique of MIKE 3 FM allow for a variation of the horizontal resolution of the model grid mesh within the model area to obtain a finer resolution of selected sub-areas. Hence, the model mesh resolution varies between 100 and 1000 m for the Limfjord and between 40 and 400 m for Horsens Fjord. The vertical resolution is based on a sigma-z layer approach (DHI 2013); The Limfjord having 5 sigma-layers of 1 m and 15 z-layers of 1 m, whereas the Horsens Fjord has 10 sigma layers of 1 m followed by 1 m z-layers to the bottom. The Limfjord model was first developed as part of the Danish River Basin Management Plans 2015-2021 (Erichsen & Timmermann, 2017) and are now being updated as part of the Danish River Basin Management Plans 2021-2027 together with the model covering the Horsens Fjord. The hydrodynamic models have been calibrated during the period 2002-2011 and validated during 2012-2016 (data not shown).

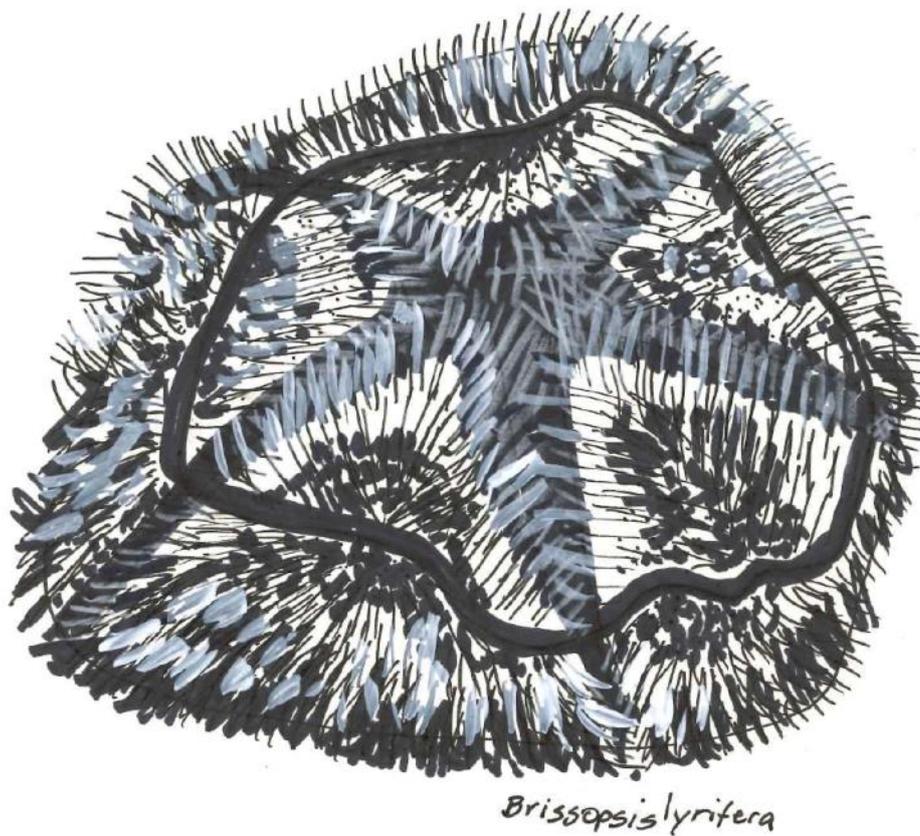
**References**

DHI (2013). MIKE 21 & MIKE 3 Flow Model FM. Hydrodynamic and Transport Module. Scientific Documentation. DHI Water Environment Health, Hørsholm, Denmark, 54 pp.

UNESCO (1981) The practical salinity scale 1978 and the international equation of state of seawater 1980. UNESCO technical papers on marine science.

Erichsen AC (Ed.), Timmermann K (Ed.), Christensen JPA, Kaas H, Markager S, Møhlenberg F (2017) Development of models and methods to support the Danish River Basin Management Plans. Scientific documentation. Aarhus University, Department of Bioscience and DHI, 191 pp.

**5. Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance**



This chapter has been published in Ecological Indicators:

McLaverty C, Eigaard OR, Gislason H, Bastardie F, Brooks ME, Jonsson P, Lehmann A, Dinesen GE (2020) Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. *Ecol Indic* 110:105811. <https://doi.org/10.1016/j.ecolind.2019.105811>

## Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance

Ciarán McLaverty<sup>1,\*</sup>, Ole R. Eigaard<sup>1</sup>, Henrik Gislason<sup>1</sup>, Francois Bastardie<sup>1</sup>, Mollie E. Brooks<sup>1</sup>, Patrik Jonsson<sup>2</sup>, Andreas Lehmann<sup>3</sup>, Grete E. Dinesen<sup>1</sup>

<sup>1</sup>DTU Aqua, National Institute of Aquatic Resources, Denmark

<sup>2</sup>Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, 453 30 Lysekil, Sweden

<sup>3</sup>GEOMAR Helmholtz Centre for Ocean Research, Düsternbrooker Weg 20, 24105 Kiel, Germany

\*Corresponding author: [cimc@aqu.dtu.dk](mailto:cimc@aqu.dtu.dk). Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, Building 201, Room 049, 2800 Kgs. Lyngby, Denmark.

### Keywords

Keywords: benthic community; benthic indicators; ecosystem-based approach; fisheries management; functional traits; seafloor disturbance; trawling impacts.

### Abstract

Bottom trawling alters the abundance, diversity, size-composition, and function of benthic communities. However, the ability to detect these impacts over large spatial scales can be obscured by various complicating factors, such as community adaptation to disturbance and co-varying environmental conditions. An ecosystem-based approach to fisheries management therefore requires ecological indicators which can ‘disentangle’ trawling effects from other natural and human drivers, and respond effectively to shifts in ecological quality. We collected benthic macrofaunal samples at 21 sites across a Norway lobster *Nephrops norvegicus* fishing ground in the Kattegat, and separated the benthic community into small (1-4mm) and large (>4mm) size fractions. Four taxonomic indicators (total density, species density, Shannon diversity, and biomass) and four functional indicators (functional diversity, functional richness, functional evenness, and functional dispersion) were calculated based on each size fraction, and the two fractions combined (pooled community). Here, we compare the ability of these indicators to detect trawling impacts across size categories. We show that indicators derived from large macrofauna were highly effective in this regard, and were less influenced by other environmental drivers, such as depth, sediment grain size, bottom current velocity, salinity, and temperature. This suggests that the taxonomic and functional characteristics of benthic communities display a size-dependent sensitivity to trawling disturbance, and therefore community metrics based on large benthic macrofauna may provide useful indicators. By contrast, indicators derived from the small fraction performed poorly, and those based on the pooled community demonstrated a varied ability to detect trawling. Small macrofauna are typically characterised by high density, diversity, and population growth rates, and their relative resilience to trawling may mask the response of the more sensitive

macrofauna. This highlights an underlying issue with calculating indicators based on the whole benthic community. The approach outline here is easily applied, improves indicator performance, and has the potential to reduce laboratory workloads due to the fewer taxa and individuals required for analyses.

## 5.1. Introduction

In recent years, the mapping and quantification of commercial trawling effort has greatly improved. This has come about due to the increased availability of spatially resolved information on fishing vessel activities, and the development of open source methods to estimate fishing effort (Bastardie et al., 2010; Hintzen et al., 2012). As a result, there is an improved understanding of the distribution of commercial trawling effort (Amoroso et al., 2018; Eigaard et al., 2017; Puig et al., 2012), and how gradients of trawling intensity alter the structure and ecological functioning of benthic macrofaunal communities (Bolam et al., 2017; Hiddink et al., 2017; Hinz et al., 2009; Tillin et al., 2006). Growing societal concern regarding fisheries effects has prompted the adoption of an 'Ecosystem Approach to Fisheries Management' (EAFM) (FAO, 2003) in the European Union. This has seen increased scientific interest and resources dedicated to the monitoring and assessment of 'Sea-floor Integrity' (Anon., 2010) and 'Good Environmental Status' of seafloor ecosystems, under the European Union Marine Strategy Framework Directive (MSFD) (Anon., 2008). By definition, an EAFM requires assessments of human impacts at the level of species, communities, and ecosystems to guide management advice. Ecological indicators are often a favoured instrument in this regard as they are easily calculated, monitored, and interpreted. However, in order to be effective, indicators should be sensitive to changes in ecological state, capture and convey information on the ecosystem, and not be overly affected by short-term variation or auxiliary drivers. Measuring all aspects of ecosystem state is neither practical nor possible, and well-designed indicators of bottom trawling impacts are therefore required to support management (Rice et al., 2012; Van Hoey et al., 2010).

As knowledge of the benthic effects of trawling has advanced, various co-varying and interacting factors have also been revealed. These can include the sensitivity of specific seabed habitats (Kaiser et al., 2006), the impact of different gear types (Eigaard et al., 2016; Hiddink et al., 2017), the magnitude of background human and natural disturbance (Diesing et al., 2013; Van Denderen et al., 2015), and gradual adaptations of macrofaunal communities to disturbance (Kaiser et al., 2000; Reiss et al., 2009). Alone, or in combination, such factors can obscure the measurable effects of trawling in benthic communities, and may explain why indicators sometimes display varied performance (Atkinson et al., 2011; Kaiser et al., 1998; Mangano et al., 2014). On the other hand, experimental and model based studies have revealed that large macrofauna are disproportionately sensitive to chronic trawling disturbance (Duplisea et al., 2002; Jennings et al., 2001; McConnaughey et al., 2005; Queirós et al., 2006). This vulnerability is linked to a relationship between body size and several key life history traits (Begon et al., 2006), whereby larger macrofauna tend to grow and reach maturity at a slower rate, have comparatively lower mortality and population growth rates, and are therefore more vulnerable to trawling induced mortality. Although small benthic fauna are also vulnerable trawling

disturbance (Hinz et al., 2008), they often display relatively high growth and turnover rates, resulting in shorter recovery times.

While body size and sensitivity may vary across taxa, sensitivity may also change within the lifespan of an individual. During development from offspring to adult, sensitivity to physical disturbance can vary across size classes, trophic levels, and functional roles (Brose et al., 2016). For this reason, indicators based on e.g. the fraction of individuals above a certain minimum body size have been suggested and applied to monitor fish communities (Greenstreet et al., 2011; Shin et al., 2005), yet no such size-based indicators exist for benthic macrofauna. Recent studies by Hiddink et al., (2018) and Rijnsdorp et al., (2018) have shown that the relative abundances of long-lived macrofauna can indicate the sensitivity of benthic communities to trawling. This approach combines information on age composition of the community with fishing pressure data, and allows for the assessment of risks and impacts of trawling to taxa with defined longevity or recovery times (Hiddink et al., 2018). While this approach has shown to be effective, the longevity of macrofauna can be difficult to measure, may be uncertain, and may be lacking for many species in less studied areas. It would therefore be advantageous if macrofaunal indicators of trawling impacts could be devised based on the size composition of the benthic organisms. Such indicators could be easily and accurately quantified, would not require knowledge of life history traits, would have the potential to be applied across habitat type and geographic region, and could potentially reduce sample processing times.

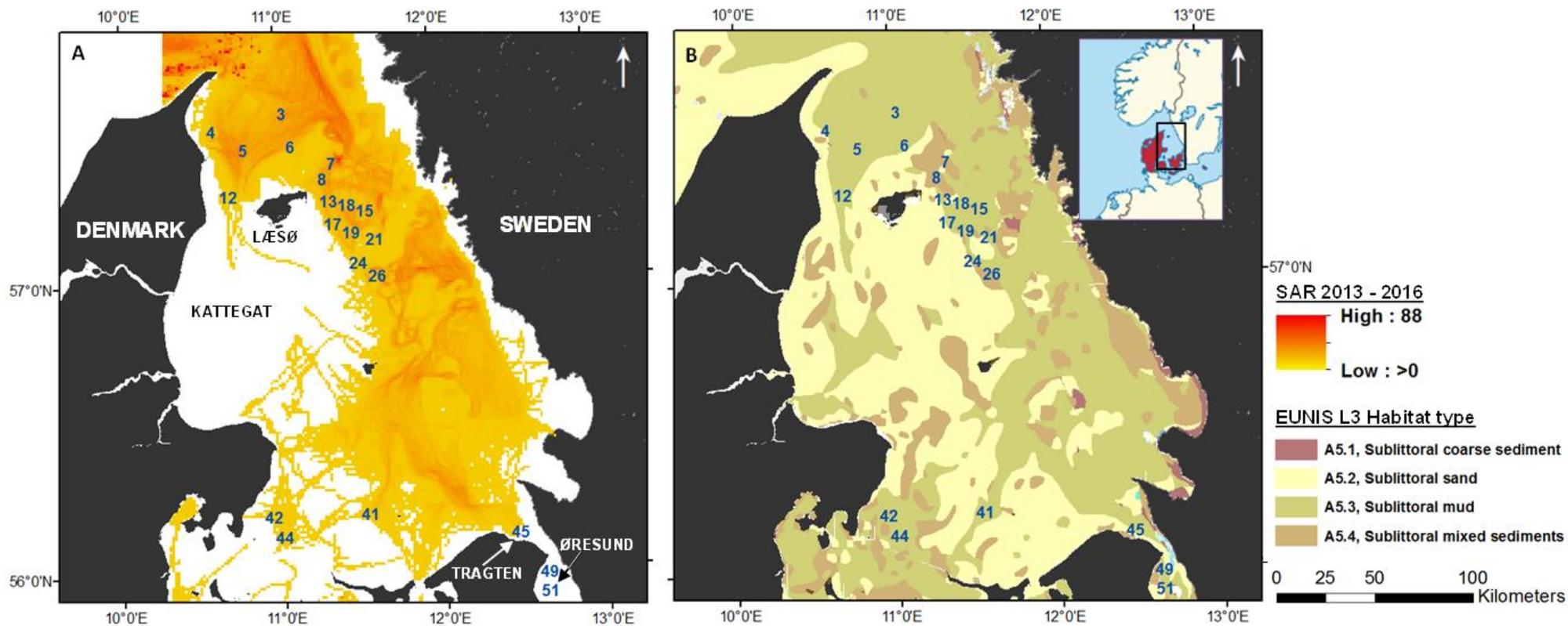
The main objective of this study is to explore if the performance of several taxonomic and functional indicators of trawling disturbance would improve if they were based on large macrofauna, rather than the whole community. To test this, data were collected in a fishing ground with a long history of bottom trawling. Sampling sites were selected to represent a wide spatial gradient of trawling intensity, ranging from zero (determined by long-standing closed areas) to regionally high trawling intensities. During sampling, sieves were used to separate the benthic community into two size fractions. Eight macrofaunal indicators were then calculated within each size fraction (small and large), as well as the fractions combined (pooled community). We investigate and compare the ability of these indicators to detect bottom trawling impacts across size categories using generalised linear mixed models (GLMMs).

## 5.2. Materials and methods

### *Study area*

The Kattegat is a shallow transitional sea separating the marine North Sea and the brackish Baltic Sea (Figure 5-1). Its seabed is composed of sandy sediments in the west, and of mud and mixed sediments in the north, east, and deeper areas (Figure 5-1b). Physical conditions on the seabed are characterised by gradients in salinity, temperature, current velocity, and by a two-layer stratified flow pattern. An inflow of saline water from the North Sea occurs in the deeper areas, which is offset by an outflow of brackish water from the Baltic Sea at the surface. The two water masses are separated by a pycnocline which sits between 15m (westwards) and 25m (eastwards) (Al-Hamdani et al., 2007). Commercial fishing for cod *Gadus morhua* (Linnaeus, 1758) and plaice *Pleuronectes platessa* (Linnaeus, 1758) has taken place in the Kattegat for over 100 years (Petersen, 1918). In recent years, high fishing effort has led to significant declines in the cod population and associated quota (Svedäng and Bardou, 2003; ICES, 2018). Conversely, there has been a considerable rise in landings of Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). Although this may occur as a result of population increase (ICES, 2018b), or community shifts associated with reduced predation pressure (Howarth et al., 2014), time series data of commercial CPUE (catch per unit effort) suggest that increased fishing effort is the likely explanation (Eggert and Ulmestrand, 1999). *Nephrops*, now the primary target species in the Kattegat, is caught almost exclusively by Danish and Swedish vessels using demersal otter trawls (Hornborg et al., 2017). As *Nephrops* reside in shallow burrows, the fishery is characterised by relatively low catchability and high trawling intensity. As a result, the Kattegat is an area of relatively high trawling intensity at European (Eigaard et al., 2017) and global scale (Amoroso et al., 2018). Based on trawling effort in 2017, we estimate that ~53% of all sublittoral mud habitat in the Kattegat (A5.3 - EUNIS level 3) (Figure 5-1b) was impacted by mobile bottom-contacting fishing gear.

Figure 5-1: Map of sampling sites in respect to (a) trawling effort and (b) EUNIS Level 3 habitat types. Trawling intensity is described as the swept Area Ratio (SAR), and represents the cumulative trawling effort over 3 years (September 2013 to September 2016) for all Danish and Swedish vessels >12m, using bottom contacting gears.



### **Sampling design**

Sampling sites were selected within areas characterised by the sediment type and depth suitable for *Nephrops*. The locations of sites were restricted to Danish waters and were chosen based on, i) a minimum depth of 15m, ii) mud (EUNIS A5.3) and mixed sand/mud (EUNIS A5.4) habitat (Figure 5-1b), iii) within a gradient of trawling intensity between 2013 -2016 (see section *Estimating trawling pressure*) (Figure 5-1a). Furthermore, some sites were determined by side scan sonar and consultation with local fishermen. As depth has been shown to be a potentially confounding factor in similar studies (Pommer et al., 2016), we selected areas of high and low trawling intensity in both shallow and deeper areas. The sampling design also included three sites located in areas subject to long-standing trawling closures; two in the Øresund, and the a third in nearshore areas of the 'Tragten' (Figure 5-1a). These areas have been subject to a trawl ban since 1932 under a Danish-Swedish Royal Convention (Ministry of Foreign Affairs of Denmark, 1933a; 1933b, 2009). Comparability of abiotic habitat characteristics were verified post-sampling by means of statistical analysis (detailed in the section *Environmental drivers*).

### **Data collection and sample processing**

Macrofauna communities were sampled at 21 sites (Figure 5-1) between 22 September and 6 October 2016. Five sediment samples were taken at each site using a 0.1m<sup>2</sup> Van-Veen grab. Four samples were processed for faunal analysis, and a fifth was sub-sampled for particle size analysis (PSA) and organic content. The faunal samples were sieved consecutively over 4mm and 1mm mesh sizes to separate the community into two size fractions. A 1mm mesh size is widely used as benthic macrofauna are generally defined as metazoans retained by a 1mm sieve, and a 4mm threshold is used to distinguish larger macrofauna (also known as megafauna). The sieved samples were then fixed in 4% borax-buffered formaldehyde in ambient seawater. In the laboratory, all animal material were identified to the lowest taxonomic level possible, and biomass estimates per species were determined as ash-free dry weight. All tubicolous polychaetes were removed from their tubes prior to weighing. Taxa were validated and standardised in accordance with World Register of Marine Species (WoRMS Editorial Board, 2018). The size-separation the community provided three datasets carried forward for analysis; the 1-4mm (small) fraction, the ≥4mm (large) fraction, and the two fractions combined (pooled community). Samples acquired for PSA and LOI% were first frozen on board at -18°C. PSA was undertaken via mass loss following wet sieving (Danish Standard (DS) 405.9), and resulted in the estimation of mud% (<63µm), sand% (0.063–2mm), and gravel% (≥2mm). Organic content was estimated via loss-on-ignition (LOI%), and calculated by mass loss of 4mg of homogenised sediment placed in a muffle furnace at 560°C for 4 hours, or until a constant weight was achieved (DS 204).

### **Biological trait classification**

An overview of the biological traits and associated categories (modalities) used to describe the functional characteristics of the community is presented in Table 5-1. Some 10 traits and 48 descriptive modalities were developed by Bolam et al. (2017), based on their potential sensitivity to trawling. As marine taxa often exhibit more than one modality within a trait (e.g. multiple feeding modes), we followed a ‘fuzzy coding’ approach (Chevene et al., 1994). If a species exhibited full affinity to a single modality within a trait (e.g. age), a score of 3 was assigned. Where species exhibited more than one modality, they were assigned a score relative to its importance (e.g. a predator which occasionally scavenges was coded as Predator = 2, Scavenger = 1). After coding, the scores for each modality were standardised to 1 within each trait type. The coded trait scores (taxa-by-trait matrix) were then combined with abundance data (abundance-by-site), to generate a trait-by-site matrix.

**Table 5-1: Biological traits and associated modalities used in the study**

<b>Trait</b>	<b>Modalities</b>
Size range	<10mm   11-20mm   21-100mm   101-200mm   201-500mm   >500mm
Longevity	<1 year   1-<3 years   3-10 years   >10 years
Larval development	Planktotrophic   Lecithotrophic   Direct
Morphology	Soft   Crustose   Cushion   Stalked   Tunic   Exoskeleton (chitin/calcium carbonate)
Egg development	Asexual/Budding   Sexual: shed eggs pelagic   Sexual: shed eggs benthic   Sexual: brood eggs
Living habit	Tube-dwelling   Burrow-dwelling   Free-living   Crevice/hole/under stone   Attached to substratum   Epi/endozoic/phytic
Sediment position	Surface   Infauna: 0-5cm   Infauna: 6-10cm   Infauna: >10cm
Feeding mode	Suspension   Scavenger/Opportunist   Surface Deposit   Subsurface deposit   Predator   Parasite
Mobility	mob Sessile   Burrower   Swim   Crawl/creep/climb
Bioturbators	Diffusive mixing   Surface deposition   Downwards conveyer   Upward Conveyer   None

### **Ecological indicators**

Ecological indicators were based on the benthic macrofauna, and chosen to reflect the ecological, taxonomic, and functional characteristics of the community. Taxonomic indicators (density, species density, Shannon diversity and biomass) were calculated using PRIMER v.7 (Clarke and Gorley, 2015) and functional indicators (functional diversity, functional richness, functional evenness, and functional dispersion) were calculated using the R package ‘FD’ (Laliberte, Legendre & Shipley, 2015). Table 5-2 provides a description of the indicators and their interpretation. The functional indicators were weighed using density data, as this data is

more commonly recorded in benthic impact studies (Hiddink et al., 2017). For completeness, we also provide the results of functional indicators based on biomass data (Supplement – Table S2).

**Table 5-2: Macrofaunal indicators used in the study**

Indicator	Label	Description	Range of values	Reference
Density	N	Total number of individuals per sample.	0 - $\infty$	
Species density	S	Total number of species per sample.	0 - $\infty$	
Shannon diversity	H'	A measure of taxonomic diversity, which accounts for S and N, and the structure (dominance) of a community. Calculated using $\text{Log}_e$ .	0 - $\infty$	(Shannon, 1948)
Log biomass	Biomass	Total ash free dry weight biomass per sample. $\text{Log}_e$ transformed.	0 - $\infty$	
Functional diversity	RaoQ	A measure of trait diversity, which accounts for trait richness and relative abundance. Rao's quadratic entropy measures the trait dissimilarity of two random individuals (akin to Simpson's diversity).	0-1	(Botta-Dukát, 2005; Lepš et al., 2006)
Functional richness	Fric	A measure of the richness of traits expressed in the community, measured by the total volume of multivariate trait space occupied by the community. Calculated using minimum convex hull.	0-1	(Villéger et al., 2008)
Functional evenness	Feve	A measure of trait dominance, defined by the evenness in distribution of trait abundance in multivariate trait space. Calculated using minimum convex hull.	0-1	(Villéger et al., 2008)
Functional dispersion	Fdis	A measure of the average distance of species to the centre of multivariate trait space.	0 - $\infty$	(Laliberté and Legendre, 2010)

### **Potential recruitment effect on indicators**

The recruitment of benthic macrofauna typically takes place between August and November in the Kattegat. As sampling was conducted in mid-September/early October, there is the risk that newly settled recruits may be recorded in the data. These individuals may consequently have had little or no exposure to trawling, and could potentially bias results. However, recruits would need to settle (or begin ontogenetic development) and reach  $\geq 1\text{mm}$  in size by the end of September for this to occur. We therefore considered the potential contribution of new recruits to our measures of density (N). Of the most abundant taxa (Table 5-3), early juveniles of *Phoronis* sp., *Kurtiella bidentata*, *Nucula nitidosa*, *Thyasira flexuosa* and *Scalibregma inflatum*, were considered too small or soft bodied to be retained on a 1mm sieve at the time of sampling. Moreover,

early juveniles of these taxa were not observed during the processing of samples. Conversely, *Amphiura filiformis* and *Amphiura chiajei* are relatively large macrofaunal taxa and have the potential for rapid post-settlement growth rates (Josefson and Jensen, 1992). Recently settled (<1 year) individuals were also observed in the small fraction during sample processing. We thus estimated the potential growth rate of newly settled *Amphiura* spp., in accordance with Sköld et al. (2001), to determine if our results could be affected by an influx of *Amphiura* spp. prior to sampling. The details of these estimates are outlined in the Supplement – Text S1. Accordingly, we took the conservative measure of also removing 50% of all *Amphiura* spp. from the dataset, and re-analysing pooled community N and small fraction N without these individuals. The results are provided in *results: potential effect of recruits on abundance*.

### ***Estimating trawling pressure***

Since 2012, all fishing vessels  $\geq 12$ m operating in European Union waters have been required to carry a vessel monitoring system (VMS) receiver on board. VMS receivers collect and send data regarding the vessel location, heading, and speed, with an hourly polling frequency (in Danish and Swedish waters). Raw VMS data were cleaned and filtered to retain only ‘trawling activity’ (defined as speed ranging between 2 and 4 knots, with a minimum distance of 3km from port). These raw data points were then used to reconstruct vessel trawl tracks using cubic Hermite spline interpolation (Hintzen et al., 2012). The tracks were coupled with information on vessel size (from EU logbooks) and gear dimensions (Eigaard et al., 2016) to estimate gear-width, and aggregated to calculate the area of seabed ‘swept’ during each logbook trip. Trawling effort and swept areas were estimated using the VMStools package (Hintzen et al., 2012). The total swept areas (for all Danish and Swedish  $\geq 12$ m vessels and trips) were aggregated within a 1km radius around each benthic sampling site. This spatial scale represents a trade-off between precision limitations in i) VMS-positioning, ii) gear position in relation to vessel position, and iii) interpolation of trawl tracks. With the choice of a 1 km radius, trawling would tend to be randomly distributed within years and uniformly spread on longer timescales (Amaroso et al., 2018; Ellis et al., 2014), and the potential error associated with the spline interpolations is likely to be limited (Lambert et al., 2012). Trawling intensity is described as swept-area ratio (SAR) values, defined as the accumulated swept area within a circle divided by the size of the circle. SAR can therefore be interpreted as the number of times the seabed within the circle is trawled within the given time period. To account for inter-annual variation in trawling activity at infrequently fished sampling sites, and due to the focus of the analysis on larger, longer-lived, macrofauna, SAR estimates were based on three years of fishing effort. Trawling intensity was back-calculated from the day prior to sampling for each replicate sample (September/October 2013 to September/October 2016).

### ***Environmental drivers***

The structure and composition of benthic communities are known to be closely linked to ambient environmental conditions. To account for key natural drivers, and ascertain potentially confounding effects, we included six environmental parameters in addition to trawling intensity. Depth (*in situ*), LOI%, and mud% (described above) were collected in the field. Hydrodynamic data in the form of bottom current velocity (m/s), bottom temperature (°C), and minimum bottom salinity (PSU), were extracted from the high-resolution Kiel Baltic Sea Ice-Ocean Model (BSIOM) (Lehmann et al., 2014) (further information can be found in the Supplement – Text S2). Hydrodynamic data were back-calculated at a monthly scale and averaged over the year prior to sampling (September 2015 - September 2016). The same environmental data values were applied to each replicate with a site. To investigate comparability of environmental conditions across sampling sites, an analysis of similarity was undertaken by multivariate clustering analysis, using the package PRIMER v.7 (Clarke and Gorley, 2015). Clustering was based on normalised Euclidean distances and significance was determined using the SIMPROF routine, which tests for statistically significant station clusters. The analysis resulted in one single cluster of similar habitat characteristics (Supplement – Figure S1). Tests for collinearity between predictors are discussed below.

### ***Statistical approach***

We used generalised linear mixed models (GLMMs) to test the ability of macrofaunal indicators to detect trawling impacts across size fractions. As each replicate sample represented an observation, we analysed the data using mixed effects models. This modelling approach is particularly suitable to quantify potential correlations in repeated measure designs (i.e. replicate samples nested within sites) (Bolker et al., 2009). ‘Sampling site’ was therefore included as a random effect term to account for non-independence of samples, while all other predictors were included as fixed effect terms. The exception to this was for models which contained species density (S) as a response variable. In such cases density (N) was included an additional predictor, as per Gislason et al., (2017) and Sköld et al., (2018). This step was taken to account for changes in the detection rate new species as abundance increases (Gotelli and Colwell, 2001), and therefore improve our ability to detect the effects of other predictors, aside from N. Indicators were modelled using either a negative binomial, Poisson, or Gaussian distribution depending on the data type (count/discrete or continuous). The response variable Biomass was log transformed. To avoid issues related to multicollinearity of predictor variables, pair-wise correlations between the predictor variables were determined. Predictors with correlation coefficients  $>0.7$  were excluded from the analysis (Dormann et al, 2013). As a result, LOI% was removed due to a high correlation with mud% ( $R = 0.95$ ,  $p = <0.001$ ). Pairwise correlation coefficients were visualised using the corrplot package (Wei and Simko, 2016) and are presented in the Supplement –

Figure S2. Variance inflation factor (VIF) values were checked in a model of the remaining predictor variables (Fox and Weisberg, 2011). VIF values for all predictor variables were  $<2$ . GLMMs were fit using the glmmTMB package (Brooks et al., 2017). To determine the best fit model for each indicator, we used the MuMin package (Barton, 2013) to calculate all possible combinations of the predictor variables. The routine returns all sub-models in ascending order based on small-sample size corrected Akaike information criterion (AICc) value. The most parsimonious models were selected based on the lowest AICc (Burnham and Anderson, 2004). To deal with potential difficulties associated with model validation of mixed models, we applied a quantitative (simulation) based approach for determining model diagnostics using the DHARMA package (Hartig, 2016). Marginal effects of GLMMs were plotted using the sjPlot package (Lüdtke, 2016). All analyses were conducted using R version 3.5.0 (R Development Core Team, 2018).

## 5.4. Results

### **Dataset description**

The study identified 30,783 individuals across 285 different taxa. Of these, 276 (97%) were identified to species level, 7 (2%) to genus, 1 (<1%) to class, and 1 (<1%) to phylum. Out of the total number of taxa recorded, 91% were represented in the small fraction (268 taxa), 52% represented in the large fraction (147 taxa), and 26% were unique to the large fraction (74 taxa). The dominant taxa in the pooled community were *Amphiura filiformis* (Class Ophiuroidea), *Phoronis* sp. (Phylum Phoronida), *Kurtiella bidentata*, *Nucula nitidosa*, *Thyasira flexuosa*, *Eunucula tenuis*, *Abra nitida* (Class Bivalvia), *Scalibregma inflatum*, *Diplocirrus glaucus*, *Spiophanes kroyeri*, *Rhodine gracilior*, *Prionospio fallax*, *Scoloplos armiger*, *Pholoe inornata* (Class Polychaeta), and *Hyala vitrea* (Class Gastropoda) (Table 5-3). A similar group of dominant taxa, and relative contributions to total density, were observed in the small fraction, indicating the importance of this fraction to the overall community. The relative contribution of dominant taxa in the large fraction was greater than in the other size categories, with the top 15 taxa contributing 89% of total density (Table 5-3). The dominant taxa in the large fraction also included *Amphiura chiajei* and *Ophiura* spp. (Class Ophiuroidea), *Maldane sarsi*, *Terebellides stroemii*, *Praxillella praetermissa* (Class Polychaeta), *Turritella communis* (Class Gastropoda), and *Echinocardium cordatum* (Class Echinoidea).

### **Trawling effort**

Over the three year period, fishing intensity (SAR) ranged from 0 to 43.4 (equivalent to  $\sim 14.5 \text{ yr}^{-1}$ ). Sites 3, 5 and 6 (northern Kattegat), and Sites 17 and 19 (south east Læsø) were subject to the highest fishing intensities. Untrawled conditions were observed in the closed areas (Sites 45, 49, 51), and low SAR values were observed at various locations across the study area, particularly at Sites 8, 12, 24, and 41. Figure 5-2 illustrates the relative abundance of the dominant taxa as a function of trawling intensity. The polychaetes *Anobothrus gracilis*, *P. fallax*, *S. inflatum*, and the unrelated horseshoe worm *Phoronis* sp., were observed in relatively high densities at the untrawled and lightly trawled sites (left of the plot), while being either absent or observed at low densities in the highly trawled sites (right of the plot). This same pattern was also observed for the bivalve species *T. flexuosa* and *N. nitidosa*. Conversely, *A. filiformis* and *K. bidentata* were recorded at high densities across the range of trawling intensity, while numbers of *D. glaucus* were also relatively consistent. The tubicolous polychaete *S. kroyeri* were observed to peak in numbers at intermediate levels of trawling, while *H. vitrea* occurred in relatively high densities at the most heavily trawled sites. Summary information of site-by-site SAR values and macrofaunal counts are provided in the Supplement – Table S1.

Table 5-3: Dominant macrofauna (based on density) of the pooled community, small fraction, and large fractions

Pooled community		Small fraction (1-4mm)		Large fraction (>4mm)	
Taxa	Density (cumulative contribution %)	Taxa	Density (cumulative contribution %)	Taxa	Density (cumulative contribution %)
<i>Amphiura filiformis</i>	8153 (26%)	<i>Amphiura filiformis</i>	5358 (22%)	<i>Amphiura filiformis</i>	2795 (41%)
<i>Phoronis</i> sp.	3942 (38%)	<i>Kurtiella bidentata</i>	3729 (37%)	<i>Phoronis</i> sp.	1498 (62%)
<i>Kurtiella bidentata</i>	3729 (50%)	<i>Phoronis</i> sp.	2444 (46%)	<i>Spiophanes kroyeri</i>	364 (68%)
<i>Nucula nitidosa</i>	1370 (54%)	<i>Nucula nitidosa</i>	1192 (51%)	<i>Rhodine gracilior</i>	343 (72%)
<i>Thyasira flexuosa</i>	1110 (58%)	<i>Scalibregma inflatum</i>	1062 (55%)	<i>Amphiura chiajei</i>	202 (75%)
<i>Scalibregma inflatum</i>	1068 (61%)	<i>Thyasira flexuosa</i>	1015 (59%)	<i>Nucula nitidosa</i>	178 (78%)
<i>Hyalia vitrea</i>	749 (63%)	<i>Hyalia vitrea</i>	749 (62%)	<i>Turritella communis</i>	124 (80%)
<i>Diplocirrus glaucus</i>	732 (66%)	<i>Diplocirrus glaucus</i>	725 (65%)	<i>Ophiura</i> sp.	113 (81%)
<i>Spiophanes kroyeri</i>	611 (68%)	<i>Ennucula tenuis</i>	540 (68%)	<i>Maldane sarsi</i>	100 (83%)
<i>Ennucula tenuis</i>	550 (69%)	<i>Pholoe inornata</i>	497 (70%)	<i>Thyasira flexuosa</i>	95 (84%)
<i>Rhodine gracilior</i>	527 (71%)	<i>Prionospio fallax</i>	493 (72%)	<i>Anobothrus gracilis</i>	87 (86%)
<i>Prionospio fallax</i>	504 (72%)	<i>Scoloplos armiger</i>	489 (73%)	<i>Terebellides stroemii</i>	56 (86%)
<i>Scoloplos armiger</i>	503 (74%)	<i>Abra nitida</i>	362 (75%)	<i>Abra nitida</i>	54 (87%)
<i>Pholoe inornata</i>	499 (76%)	<i>Anobothrus gracilis</i>	303 (76%)	<i>Praxillella praetermissa</i>	52 (88%)
<i>Abra nitida</i>	416 (77%)	<i>Cylichna cylindracea</i>	303 (77%)	<i>Echinocardium cordatum</i>	51 (89%)
<b>Pooled community total</b>	<b>30,783</b>	<b>Small fraction total</b>	<b>23,996</b>	<b>Large fraction total</b>	<b>6,787</b>

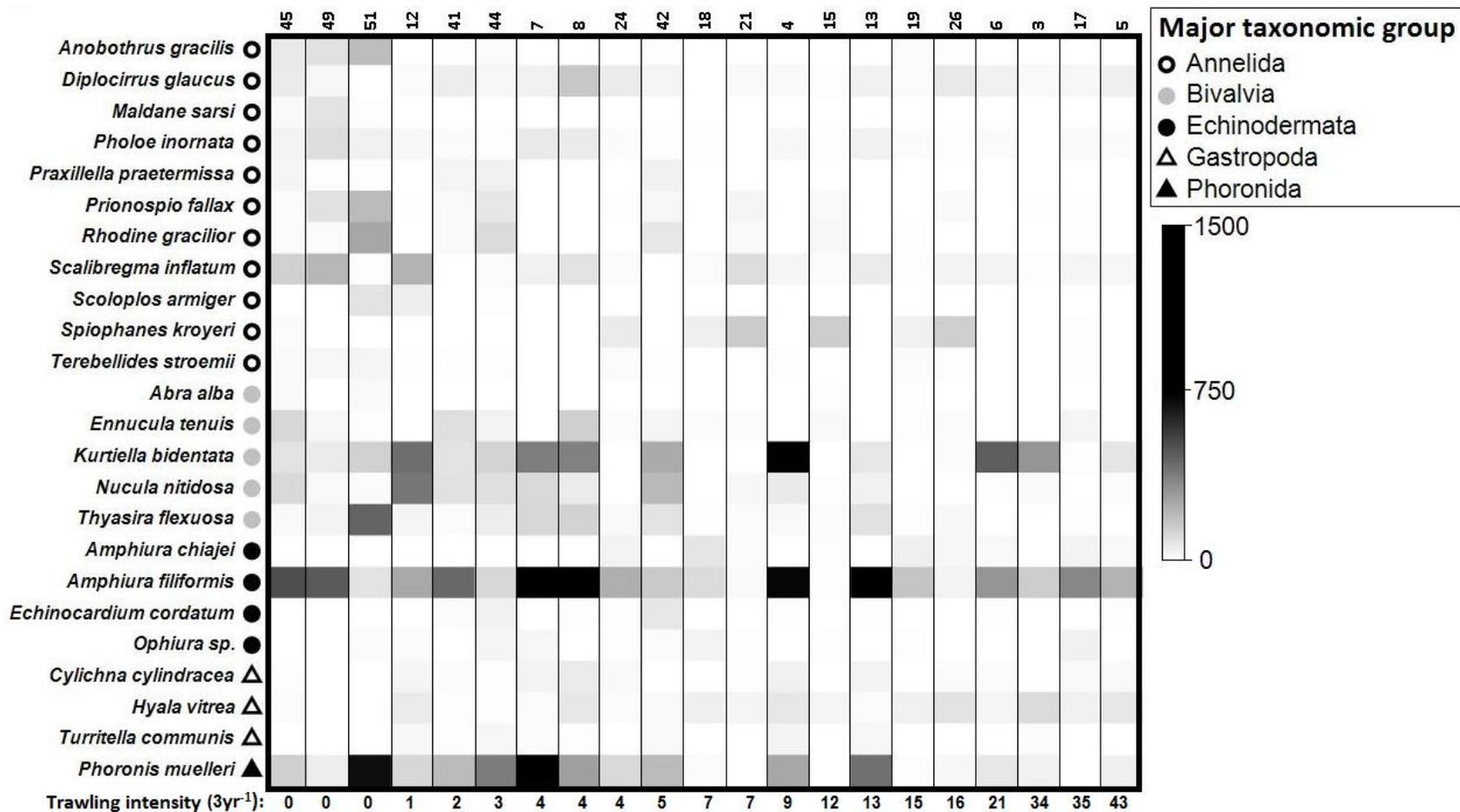


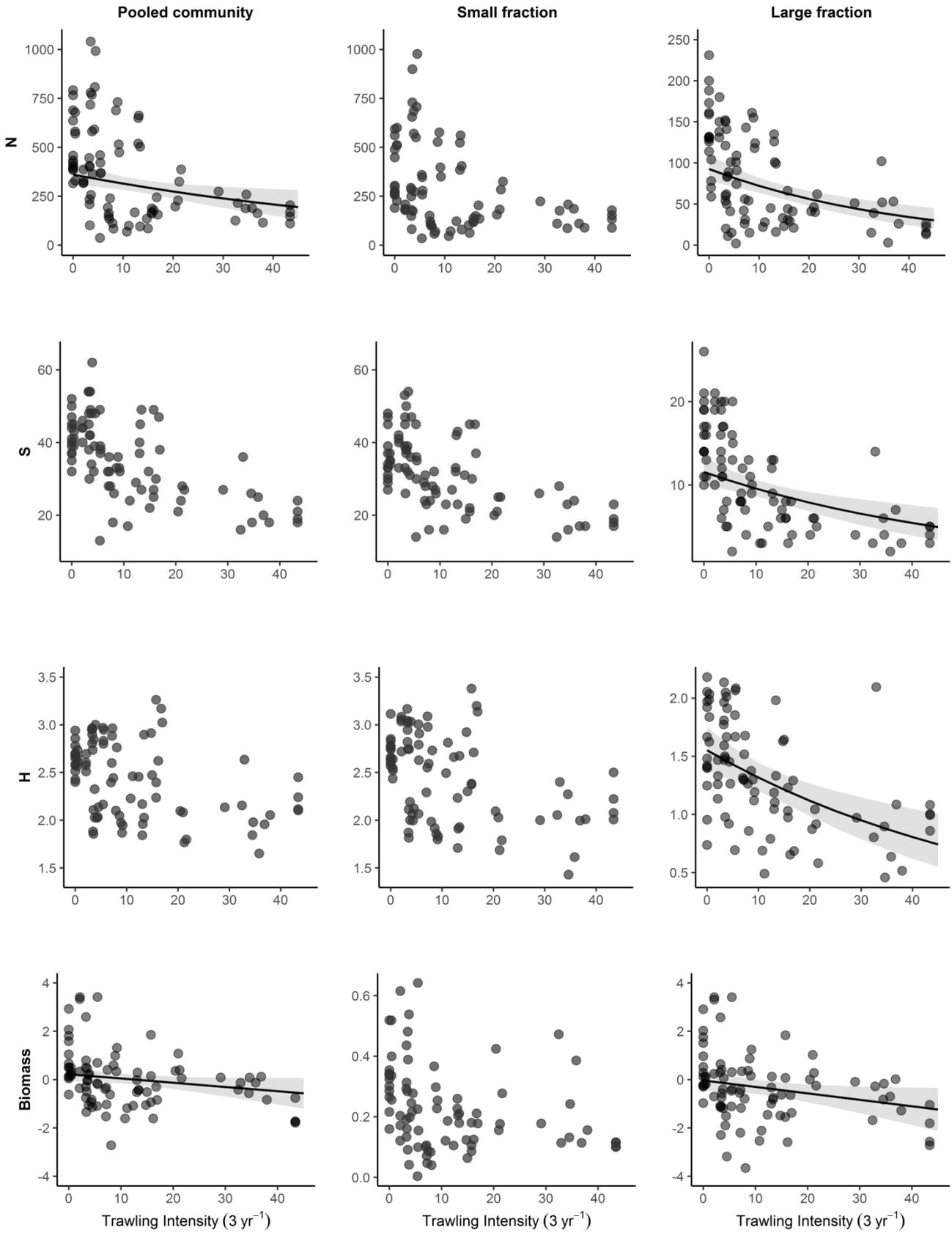
Figure 5-2: Relative density of dominant fauna across the gradient of trawling intensity, illustrated as a shade plot. Dark shading indicates high density, light shading indicates low density, and values represent the total density of macrofauna per site (or per 0.4 m<sup>2</sup>). SAR values are based on three years of trawling effort (3 yr<sup>-1</sup>), and increase from left to right (bottom of the plot). Sampling site numbers are provided at top of the plot.

***Response of macrofaunal indicators to trawling***

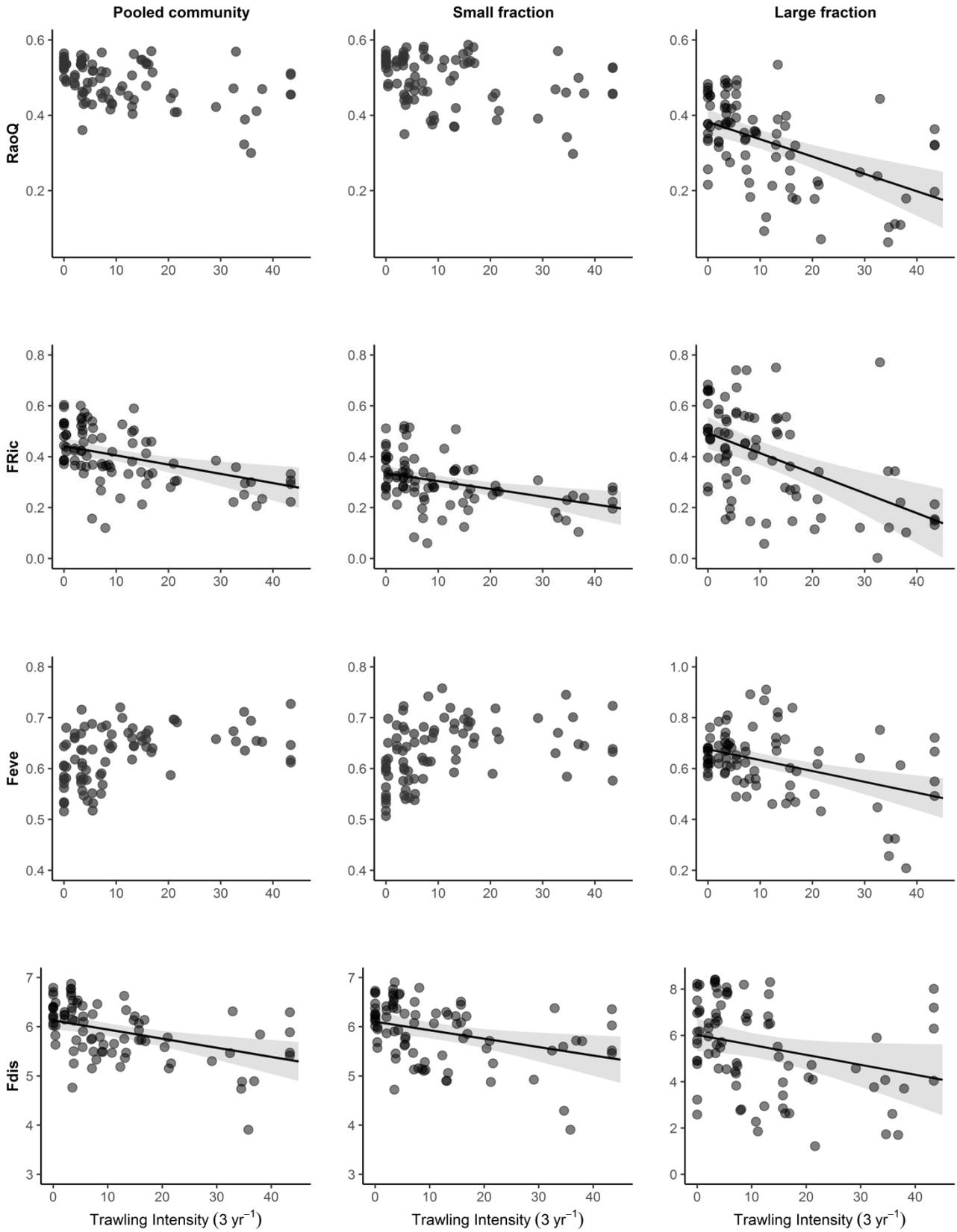
Macrofaunal indicators based on the pooled community demonstrated a varied performance, with four of the eight indicators exhibiting a significant negative response to trawling. These included density (N), biomass, functional richness (Fric), and functional dispersion (Fdis) (Table 5-4). Although species density (S), Shannon diversity (H'), functional diversity (RaoQ) also showed a tendency to decline over the gradient of trawling intensity (Figure 5-3), these relationships were not statistically significant. On the contrary, functional evenness (Feve) slightly increased over the trawling gradient, although again this trend was not significant. In the small fraction, none of the taxonomic based indicators (N, S, H', biomass) responded to trawling, whereas two of the functional indicators (Fric and Fdis) demonstrated significant negative relationships with trawling. These indicators were distinctive, in that they demonstrated significant negative relationships with trawling intensity across all size categories. In the large fraction, each of the eight indicators examined declined significantly with trawling. Moreover, trawling was the sole explanatory variable in the most parsimonious models of S, H', Fric, Feve, and Fdisp. Comparison of model parameter estimates across size fractions indicates that there was also a larger effect of trawling per unit N, biomass, RaoQ and Fdisp, in the large fraction. Results for the functional indicators calculated using biomass data are presented in Table S2, and in general, these indicators performed similarly to their density-based counterparts. The main discrepancies being that Fdis (pooled community) showed no relationship with trawling, and RaoQ (small fraction) responded to negatively to trawling.

**Table 5-4: Summary output for generalised linear mixed models of macrofaunal indicators. The values shown are parameter estimates, and associated standard error (shown in brackets). The significance level is denoted by asterisks (\* = P < 0.05; \*\* =P < 0.01; \*\*\* = P < 0.001). Conditional R<sup>2</sup> values describe the proportion of variance explained by both the fixed and random terms.**

	Indicator	Intercept	Current	Depth	Mud%	Temperature	Trawling	Salinity	Density <sup>†</sup>	Conditional R <sup>2</sup>
<b>Pooled</b>	N	7.16(0.19)	-0.206 (0.065)**	-0.017 (0.003)***	-0.007 (0.001)***		-0.013 (0.005)*		-	0.79
	S	4.63 (0.29)			-0.005 (0.001)***	-0.139 (0.037)***			0.25 (0.004)***	0.75
	H'	3.56 (0.58)	0.066 (0.027)*			-0.08 (0.031)*			-	0.33
	Biomass	4.19 (1.20)		-0.032 (0.006)***		-0.368 (0.147)*	-0.017 (0.009)*		-	0.35
	RaoQ	0.64(0.07)	0.020 (0.009)*			-0.025 (0.010)*			-	0.52
	Fric	0.47(0.01)			-0.001 (<0.001)**		-0.004 (0.001)**		-	0.47
	Feve	0.31(0.07)						0.010 (0.002)***	-	0.51
	Fdis	5.86(0.16)	0.167 (0.076)*				-0.018 (0.005)**		-	0.48
<b>Small fraction</b>	N	6.92(0.22)	-0.240 (0.077)**	-0.017 (0.003)***	-0.011 (<0.002)***				-	0.82
	S	2.67 (0.46)	0.101 (0.031)***	0.004 (0.001)*	-0.005 (0.001)***	-0.138 (0.03)***			0.005 (0.002)***	0.73
	H'	2.07(0.15)	0.243 (0.066)**			0.250 (0.075)			-	0.76
	Biomass	-0.81(0.14)		-0.018 (0.003)***	-0.004 (0.002)*				-	0.38
	RaoQ	0.779(0.08)	0.022 (0.009)**			-0.042 (0.011)***			-	0.58
	Fric	0.38 (0.02)		-0.001 (>0.001)*			-0.003 (0.001)**		-	0.38
	Feve	0.26(0.06)						0.011 (0.002)**	-	0.48
	Fdis	7.63(0.78)				-0.202 (0.103)*	-0.017 (0.006)*		-	0.46
<b>Large fraction</b>	N	7.07(0.73)		-0.018 (0.003)***		-0.246 (0.089)**	-0.025 (0.005)***		-	0.53
	S	0.66(0.28)					-0.016 (0.004)*		0.423 (0.06)***	0.75
	H'	1.55(0.08)					-0.019 (0.005)***		-	0.43
	Biomass	0.95(0.32)		-0.027 (0.008)***			-0.027 (0.012)*		-	0.31
	RaoQ	0.43(0.02)		-0.001 (<0.0001)*			-0.004 (0.001)***		-	0.50
	Fric	0.49 (0.03)					-0.007 (0.001)***		-	0.47
	Feve	0.67(0.01)					-0.004 (0.001)***		-	0.21
	Fdis	7.77(0.55)		-0.048 (0.013)***			-0.042 (0.021)*		-	0.65
N = density, S = species density, H' = Shannon diversity, RaoQ = functional diversity, Fric = Functional richness, Feve = Functional evenness, Fdis = Functional dispersion Model families: N = Negative binomial. S = Poisson. H/Biomass/RaoQ/Fric/Feve/Fdis = Gaussian. Models of H were fitted using a log link. † = density (N) included as a predictor for models of species density (S), only										



Continued...



**Figure 5-3: Relationships between trawling intensity and macrofaunal indicators derived from the pooled, small, and large fractions, respectively. Regression lines represent the predicted values from GLMMs**

presented in Table 5-4. Greyed area represent 95% confidence intervals. The raw observations are overlaid as data points. Note: Y-axis scale differs in large fraction plots, with the exception of biomass, RaoQ, and Fric.

### ***Response to environmental drivers***

Overall, the indicators based on the pooled community and small fraction were strongly influenced by environmental drivers. A number of significant relationships were observed between indicators and current speed (mainly positive relationships) and temperature (mainly negative relationships) in both these categories, while depth was more prominent in the small fraction. Salinity was observed to be a poor predictor overall (pooled, small and large fractions), with Feve being the only indicator to respond to salinity. The overall influence of environmental drivers on large fraction indicators was considerably less. The large fraction indicators of N, biomass, RaoQ, and Fdis responded significantly to depth, while N also responded to temperature.

### ***Potential effect of recruits on abundance***

Based on estimates provided by Sköld et al. (2001), the post-metamorphic settlers of *Amphiura* spp. would be expected to be ~0.4 - 0.5mm in diameter. In the event of an early settlement from August onwards, and a daily increase in disk diameter of 0.42% and arm length of 1.76%, individual *Amphiura* spp. would thus need a minimum of 75 days to reach  $\geq 1$ mm in diameter. As data collection was completed ~65 days after the beginning of August, it was deemed unlikely that many recruits would have reached  $\geq 1$ mm by the time of sampling. Furthermore, empirical evidence of Sköld et al 2001 also show that the vast majority of *Amphiura* spp. sampled in early October in the Kattegat were  $< 1$ mm in length. Nevertheless, the precautionary step to exclude 50% of *Amphiura* spp. individuals from pooled community N and small fraction N did not change the overall outcome. , The model for N minus 50% *Amphiura* spp. included trawling ( $\beta = -0.017$ , se = 0.004, p =  $< 0.001$ ), Mud% ( $\beta = -0.006$ , se = 0.001, p =  $< 0.001$ ), depth ( $\beta = -0.02$ , se = 0.001, p =  $< 0.001$ ), and current ( $\beta = -0.117$ , se = 0.05, p = 0.002). Likewise, the model for small fraction N minus 50% *Amphiura* spp. included Mud% ( $\beta = 0.01$ , se = 0.002, p =  $< 0.001$ ), depth ( $\beta = 0.017$ , se = 0.003 p =  $< 0.001$ ), and current ( $\beta = -0.188$ , se = 0.07, p = 0.009). The conditional  $R^2$  for these models were 0.77 and 0.81, respectively. Although spring sampling would have been optimal (logistical constraints did not allow for this), the retrospective steps taken to validate our results demonstrate that recruitment effects are unlikely to have affected our results. Furthermore, we provide the results of biomass and biomass based indicators, which are less likely to be affected by recent recruitment events.

## 5.5. Discussion

In this analysis we describe and compare the ability of eight ecological indicators to detect trawling impacts across macrofaunal size categories. Our results suggest that benthos display a size-dependent sensitivity to trawling, whereby large fauna ( $\geq 4\text{mm}$ ) and their associated traits are most affected. Indicators derived from large fauna were able to capture this sensitivity, effectively detect trawling disturbance, while being less affected by other environmental drivers. Studies which apply macrofaunal indicators to assess human and natural pressures in the marine environment are typically undertaken using indicators based on all members of the benthic community (equivalent of the pooled community in this study). This approach may therefore not be the most suitable for the assessment of trawling impacts to benthic communities. In the following sections, we discuss the performance of indicators, as well as the ecological and management implications of these findings.

### ***Response of pooled community indicators to trawling***

The community-level indicators of density (N), biomass, functional richness (Fric), and functional dispersion (Fdis) declined significantly with increasing trawling disturbance in our study. Under chronic trawling conditions, rates for the depletion of biota (density and biomass combined) have been estimated at  $\sim 6\%$  per pass of an otter trawl (Hiddink et al., 2017). As the most heavily fished sites in this study were associated with SAR values of up to 43.4 over a three year period (or  $\sim 14.5 \text{ yr}^{-1}$ ), N and biomass would be expected to considerably decline in heavily trawled areas. In general, declines in these indicators will occur when the fishery exerts mortality rates higher than what can be replaced by the wider population, either through recruitment or potentially immigration. Although this rate may vary between location, the efficacy of N as indicator of trawling impacts in gradient studies has been demonstrated in a number of regions, including in the Kattegat (Gislason et al., 2017), Irish Sea (Hinz et al., 2009), Mediterranean (Mangano et al., 2014), and New Zealand (Thrush et al., 1998). Equally, biomass has been shown to be an effective indicator of trawling disturbance. Repeated and intense trawling will typically result in shifts from communities dominated by high biomass taxa, to those dominated by highly abundant small macrofauna (Hiddink et al., 2006; Jennings et al., 2002; Kaiser et al., 2000). Furthermore, total biomass has been shown to persistently decline in highly trawled areas, even when other indicators (such as N) have become unresponsive (Reiss et al., 2009). Despite this, the performance of N and biomass can also vary across studies. A good example of this is provided by Sköld et al., (2018). This study was undertaken in nearby *Nephrops* grounds, and across a similar gradient of trawling intensity (up to  $15.8 \text{ yr}^{-1}$ ), yet did not detect significant shifts in N or biomass. A possible explanation is that the models used in their study were characterised by high uncertainty at the heavily fished sites (due to relatively few observations), which may have affected overall trends. Furthermore, samples were collected

from long-standing monitoring sites, while our data are based on a ‘snapshot’ sampling event. While our approach has the disadvantage of lacking information on inter-annual trends, it does allow for the sampling design to be tailored to the observed range of recent trawling effort, while accounting for effort across other environmental factors, such as depth. Aside from these differences, Sköld et al., (2018) also observed that the density of *Amphiura chiajei*, a particularly dominant taxa in their dataset, showed a positive relationship with trawling. This may demonstrate that when a community is dominated by ‘robust’ taxa, their response has the potential to mask that of the remaining community. By contrast, abundances of *Amphiura* spp. (mostly *A. filiformis*, but also *A. chiajei*) were relatively stable over the trawling gradient in our study (Figure 5-2), while taxa which increased over the trawling gradient (e.g. *Hyala vitrea*) contributed less to total abundance. Moreover, taxa such as *H. vitrea* were completely absent from the large fraction, and may partly explain the clearer trends observed in this size category (discussed in section *Response of large and small fraction indicators to trawling*). Observations from *Nephrops* grounds in the Irish Sea have conversely shown *A. filiformis* to be highly sensitive to trawling (Queirós et al., 2006; Hinz et al., 2009). While the exact reasons for these discrepancies are unclear, it is possible that local sedimentary and hydrodynamic conditions may affect the relationship between some taxa and trawling.

Although species density and diversity (S and H’) showed a negative relationship with trawling in our study, these relationships were not significant. This lack of response is in agreement with other trawling gradient studies (Ball et al., 2000; Currie et al., 2011; Reiss et al., 2009), and may add weight to general concerns about their suitability in ecological monitoring. Measures of species richness can be highly sensitive to factors such as the size of sampling area, sampling intensity, and taxonomic properties of the species in question (Fleishman et al., 2006). A further complicating factor is that species density is often positively correlated with density (Gislason et al., 2017; Gotelli and Colwell, 2001). To account for observed variation in N between our sampling stations, we included N as a predictor for models of S. Although this step allows for a more accurate assessment of the role of other predictors, this did not result in the detection of trawling. Nonetheless, this relationship between N and S is theoretically relevant for all indicators derived from estimates of species richness, such as diversity measures (e.g. Shannon-diversity, functional diversity), and for multi-metric indicators commonly used in national benthic monitoring programs. Currently, most diversity indicators are applied without accounting for this relationship, or by e.g. using rarefied species richness. For this reason we did not attempt to standardize our diversity indicators with respect to N, but followed common practice, and future work is needed to quantify the effect of this relationship and its relevance for indicator use.

Our study also tested the performance of several functional indicators, which provide alternative and complimentary information to taxonomic measures. Trawling has been shown to negatively affect trait composition, and characteristics such as the size, age, nutrient cycling, and trophic profile of benthic communities (Bolam et al., 2017; Bremner et al., 2003; Tillin et al., 2006). Nonetheless, comparatively few studies have formally tested the ability of functional indicators to reflect these changes. In contrast to measures of species density and diversity, functional richness (Fric) and functional dispersion (Fdis) demonstrated significant negative relationships with trawling, doing so across all size categories. Fric is largely influenced by the loss or addition of unique traits, while Fdis provides a measure of the distinctiveness of traits within the community. The results thus suggest that trawling may have a greater effect on trait richness/diversity than on taxonomic counterparts. If that were the case, then communities in heavily trawled areas may become functionally impoverished, while a base level of species diversity may be comparatively unaffected. This would have implications for the functionality of benthic communities across fishing grounds, and suggests that monitoring of functional indicators should be undertaken in conjunction with taxonomic approaches.

#### ***Response of large and small fraction indicators to trawling***

It has been suggested that the body-size composition of a community can provide a proxy for a large degree of embedded ecological information, such as ecological quality and sensitivity to disturbance (Woodward et al., 2005). This is supported by our results, where each of the indicators derived from the large size fraction displayed significant negative relationships with trawling. Although previous studies have investigated trawling impacts to large epifauna (Hinz et al., 2009), and the production rates of large macrofauna ( $\geq 4\text{mm}$ ) (Reiss et al., 2009), none have explicitly tested community indicators based on body-size. Accordingly, the results of this study are not readily comparable to others, although the processes which underpin the sensitivity of large fauna are relatively well described. While, some large-bodied taxa are comparatively unaffected by trawling, due to e.g. burrowing depth, high mobility, or robust physical structure, populations of larger fauna are unable to withstand the high rates of mortality imposed by chronic trawling (Duplisea et al., 2002). Consequently, trawling leads to the disproportionate loss of large individuals, and an associated steepening in the slope of the size spectrum (Jennings et al., 2001; Queirós et al., 2006). The effects of trawling on large fauna is also thought to be greater than that of other influential environmental factors, such as depth and sediment characteristics (Duplisea et al., 2002), and may explain the reduced influence of natural drivers to indicators based on this size fraction. By the time an individual is near its asymptotic size, ambient environmental conditions will have selected for certain species or traits. Large fauna may therefore be less susceptible to variation caused by natural processes and local recruitment success, which are known

to complicate the outcome of trawling impact assessments, and may be better suited to track trawling impacts over time and space. Furthermore, large fauna are considerably less abundant than small fauna, meaning that fewer individuals and species are required for analysis and monitoring. Overall, indicators derived from the small fraction were less responsive to trawling, and demonstrated several significant relationships with environmental drivers such as depth, current speed, mud content, and temperature. Small macrofauna typically exhibit higher growth rates, earlier reproductive onset, wide-spread recruitment, and elevated abundances of small fauna have been shown to be effective indicators of other environmental pressures, such as nutrient enrichment (Pearson and Rosenberg, 1978). Nevertheless, trawling is thought to reduce community abundance and biomass across a range of benthic size classes (Hinz et al., 2008), and may explain why proliferations of opportunistic species have not been observed in highly trawled area (Hinz et al., 2009; Jennings et al., 2001). While indicators based on small fauna were relatively unresponsive in our study, individual taxa (and traits) within this fraction may be potentially affected by trawling. A more detailed size-based investigation of species and trait-level responses would therefore help to clarify potential relationships. Such results may also be relevant for less productive areas, where comparatively lower abundances and biomass of large fauna may reduce the effectiveness of large community indicators. Regardless, the varying responses observed between the two size fractions highlight an underlying issue with using pooled community indicators to detect trawling impacts. This is as species, taxonomic groups, and traits may display contradictory responses to trawling and to other environmental drivers.

### ***Ecological implications***

The ecosystem effects of trawling can range from changes in the functioning of marine sediments (Sciberras et al., 2016), to bottom-up interactions with higher trophic levels (Eddy et al., 2017; Hiddink et al., 2011; Hinz et al., 2017). The results of this study provide additional evidence that chronic trawling has a strong negative effect on the abundance (i.e. density and biomass) (see Hiddink et al., 2017; Sciberras et al., 2018) and functional capacity of benthic macrofaunal communities (see Bremner et al., 2003; de Juan et al., 2007; Tillin et al., 2006), while demonstrating the value of closed areas to scientific studies of demersal fishing. In particular, we show that highly trawled communities are associated with significant reductions in large macrofauna, and their associated traits. Large macrofauna play a particularly important role in several benthic processes, and it is thought that their importance in nutrient cycling is such that losses cannot be replicated, or offset, by smaller species (Solan et al., 2004). Manipulative experiments have shown that the removal of large individuals from intertidal communities have significant negative effects on local sedimentary characteristics, biogeochemical fluxes, and community dominance structures (Thrush et al., 2006). In addition, variation in intraspecific size has been recognised as a stronger predictor of ecosystem

function than that of density or species density (Norkko et al., 2013). Theoretical and empirical evidence would therefore suggest that the loss of large fauna may have significant consequences for the functionality of benthic communities. The role and decline of large fauna from wider ecological systems has received increased attention in recent years (see Malhi et al., 2016), yet the significance of this for benthic systems across fishing grounds is poorly understood.

### ***Conclusions and applications***

Using a whole community approach, four of the eight macrofaunal indicators examined were unable to detect trawling impacts. By contrast, all indicators based on large macrofauna responded consistently and effectively to trawling intensity. These results were demonstrated using data from a one-off sampling event, and in an area where fisheries may have altered the benthic community over time (Josefson et al., 2018). Although this approach cannot be retrospectively applied to existing data, our findings may have implications for future ecological monitoring of bottom trawling activities. By size-separating the benthic community, improved indicator performance was achieved from a numerically reduced subset, comprising some 22% of all individuals and 52% of taxa. The laboratory based processing of macrofaunal samples is a labour intensive and costly task. Considering this, we estimate that the time taken to screen the whole community (i.e. pick all biota from the sieved residuum), and taxonomically identify and determine biomass just for the large fraction, would have reduced the total laboratory processing time by approximately 75%. This time difference is mainly due to the fewer individuals and species requiring identification. The approach outlined in this study is easily employed, does not require prior ecological knowledge of the system, and future work should seek to test its application across different habitat types and geographic regions. We suggest that this, along with other promising methodologies (Hiddink et al., 2018; Rijnsdorp et al., 2018), have the potential to provide a suite of improved tools to better detect, assess, and monitor bottom trawling impacts on benthic communities.

### **Acknowledgements**

We thank the captains and crew of the DTU Aqua RV *Havfisken*: Aage Thaarup, Rene Nyholm Erlandsen, Søren Larsen Grønby and Jens Holm, and Eva Maria F. Pedersen and Martin Veicherts for assistance during fieldwork. Thanks to Annegrete D. Hansen and Louse Louise Scherffenberg Lundgaard for assistance with laboratory work, and to Andreas Vratsistas, Irene Saez Devis, Liv Dramshøj and Miguel Martin for assistance in sorting benthic samples into higher taxonomic groups. We thank Tobias Mildenberger and Alexandros Kokkalis for assistance regarding data analysis. We also thank the anonymous reviewers for their time and helpful suggestions to improve the manuscript. The work was funded by The Danish Fisheries Agency, Ministry of Environment and Food of Denmark, through the European Maritime and Fisheries Fund (EMFF) via the project “Udvikling af bæredygtig forvaltning af følsomme habitater og arter i Kattegat” (grant agreement number 33113-B-16-024) and DTU Aqua.

### **Supplementary information**

[See supplement below]

## References

- Al-Hamdani ZK, Reker J, Leth JO, Reijonen A, Kotilainen AT, Dinesen GE (2007) Development of marine landscape maps for the Baltic Sea and the Kattegat using geophysical and hydrographical parameters. *Geol Surv Denmark Greenl Bull* 13:61–64.
- Amoroso RO, Pitcher CR, Rijnsdorp AD, McConnaughey RA, Parma AM, Suuronen P, Eigaard OR, Bastardie F, Hintzen NT, Althaus F, Baird SJ, Black J, Buhl-Mortensen L, Campbell AB, Catarino R, Collie J, Cowan JH, Durholtz D, Engstrom N, Fairweather TP, Fock HO, Ford R, Gálvez PA, Gerritsen H, Góngora ME, González JA, Hiddink JG, Hughes KM, Intelmann SS, Jenkins C, Jonsson P, Kainge P, Kangas M, Kathena JN, Kavadas S, Leslie RW, Lewis SG, Lundy M, Makin D, Martin J, Mazor T, Gonzalez-Mirelis G, Newman SJ, Papadopoulou N, Posen PE, Rochester W, Russo T, Sala A, Semmens JM, Silva C, Tsolos A, Vanellander B, Wakefield CB, Wood BA, Hilborn R, Kaiser MJ, Jennings S (2018) Bottom trawl fishing footprints on the world's continental shelves. *Proc Natl Acad Sci* 115:E10275–E10282.
- Anon. (2008) 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).
- Anon. (2010) Commission Decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters 2010/477/EU.
- Atkinson L, Field J, Hutchings L (2011) Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages. *Mar Ecol Prog Ser* 430:241–255.
- Ball BJ, Fox G, Munday BW (2000) Long- and short-term consequences of a Nephrops trawl fishery on the benthos and environment of the Irish Sea. *ICES J Mar Sci* 57:1315–1320.
- Barton, K. (2013) MuMIn: Multi-Model Inference. R Package Version 1.40.4 <http://CRAN.R-project.org/package=MuMIn>.
- Bastardie F, Nielsen JR, Ulrich C, Egekvist J, Degel H (2010) Detailed mapping of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel geo-location. *Fish Res* 106:41–53.
- Begon, M., Harper, J.L., Townsend, C.R., 2006. *Ecology: From Individuals to Ecosystems*, fourth ed. Blackwell Science, Oxford.
- Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, van Kooten T, Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Van Hoey G, Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar Environ Res* 126:1–13.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135.
- Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J Veg Sci* 16:533–540.
- Bremner J, Frid CLJ, Rogers SI (2003) Assessing Marine Ecosystem Health: The long-term effects of fishing on functional biodiversity in North Sea benthos. In: *Aquatic Ecosystem Health and Management*. p 131–137

Brose U, Blanchard JL, Eklöf A, Galiana N, Hartvig M, R. Hirt M, Kalinkat G, Nordström MC, O’Gorman EJ, Rall BC, Schneider FD, Thébault E, Jacob U (2016) Predicting the consequences of species loss using size-structured biodiversity approaches. *Biol Rev* 49:684–697.

Burnham KP, Anderson DR (2004) Multimodel Inference. *Sociol Methods Res* 33:261–304.

Chevenet F, Doleadec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshw Biol* 31:295–309.

Clarke KR, Gorley RN (2015) Primer v7:user manual/tutorial. PRIMER-E Ltd, Plymouth. [www.primer-e.com/primer7\\_download.htm](http://www.primer-e.com/primer7_download.htm).

Currie DR, Dixon CD, Roberts SD, Hooper GE, Sorokin SJ, Ward TM (2011) Relative importance of environmental gradients and historical trawling effort in determining the composition and distribution of benthic macro-biota in a large inverse estuary. *Fish Res* 107:184–195.

de Juan S, Thrush SF, Demestre M (2007) Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Mar Ecol Prog Ser* 334:117–129.

Diesing M, Stephens D, Aldridge J (2013) A proposed method for assessing the extent of the seabed significantly affected by demersal fishing in the Greater North Sea. *ICES J Mar Sci* 70:1085–1096.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop)* 36:27–46.

Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-based model of the impacts of bottom trawling on benthic community structure. *Can J Fish Aquat Sci* 59:1785–1795.

Eddy TD, Lotze HK, Fulton EA, Coll M, Ainsworth CH, de Araújo JN, Bulman CM, Bundy A, Christensen V, Field JC, Gribble NA, Hasan M, Mackinson S, Townsend H (2017) Ecosystem effects of invertebrate fisheries. *Fish Fish* 18:40–53.

Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O’Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sørensen TK, Tully O, Zengin M, Rijnsdorp AD (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J Mar Sci* 73:i27–i43.

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanellander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *ICES J Mar Sci* 74:847–865.

Ellis N, Pantus F, Pitcher CR, II TQ (2014) 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.

FAO (2003) Fisheries management 2: The ecosystem approach to fisheries. FAO Technical Guidelines for

Responsible Fisheries (FAO, Rome), 4(Suppl 2):112.

Fleishman E, Noss RF, Noon BR (2006) Utility and limitations of species richness metrics for conservation planning. *Ecol Indic* 6:543–553.

Fox J, Weisberg S (2014) An R Companion to Applied Regression: Appendices. *Robust Regres R*:1–17.

Gislason H, Bastardie F, Dinesen GE, Egekvist J, Eigaard OR (2017) Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. *Ecol Indic* 82:260–270.

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391.

Greenstreet SPR, Rogers SI, Rice JC, Piet GJ, Guirey EJ, Fraser HM, Fryer RJ (2011) Development of the EcoQO for the North Sea fish community. *ICES J Mar Sci* 68:1–11.

Hartig, F. (2016). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models . DHARMA version 0.2.0. URL <https://cran.r-project.org/web/packages/DHARMA/index.html>.

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE, Piet GJ (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can J Fish Aquat Sci* 63:721–736.

Hiddink JG, Jennings S, Sciberras M, Bolam SG, Cambiè G, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Parma AM, Suuronen P, Kaiser MJ, Rijnsdorp AD (2019) Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J Appl Ecol* 56:1075–1084.

Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci* 114:8301–8306.

Hiddink JG, Johnson AF, Kingham R, Hinz H (2011) Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. *J Appl Ecol* 48:1441–1449.

Hintzen NT, Bastardie F, Beare D, Piet GJ, Ulrich C, Deporte N, Egekvist J, Degel H (2012) VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fish Res* 115–116:31–43.

Hinz H, Hiddink JG, Forde J, Kaiser MJ (2008) Large-scale responses of nematode communities to chronic otter-trawl disturbance. *Can J Fish Aquat Sci* 65:723–732.

Hinz H, Moranta J, Balestrini S, Sciberras M, Pantin JR, Monnington J, Zalewski A, Kaiser MJ, Sköld M, Jonsson P, Bastardie F, Hiddink JG (2017) Stable isotopes reveal the effect of trawl fisheries on the diet of commercially exploited species. *Sci Rep* 7:6334.

Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: Chronic effects and experimental predictions. *Ecol Appl* 19:761–773.

framework directive to the marine strategy framework directive. *Mar Pollut Bull* 60:2187–2196.

Howarth LM, Roberts CM, Thurstan RH, Stewart BD (2014) The unintended consequences of simplifying the sea: Making the case for complexity. *Fish Fish* 15:690–711.

ICES, 2018. ICES Advice on fishing opportunities, catch, and effort, Greater North Sea Ecoregion. Cod (*Gadus morhua*) in Subdivision 21 (Kattegat). Published 29 June 2018

Jennings S, Dinmore TA, Duplisea DE, Warr KJ, Lancaster JE (2001) Trawling disturbance can modify benthic production processes. *J Anim Ecol* 70:459–475.

Jennings S, Nicholson MD, Dinmore TA, Lancaster JE (2002) Effects of chronic trawling disturbance on the production of infaunal communities. *Mar Ecol Prog Ser* 243:251–260.

Josefson AB, Jensen JN (1992) Growth patterns of *Amphiura filiformis* support the hypothesis of organic enrichment in the Skagerrak-Kattegat area. *Mar Biol* 112:615–624.

Josefson AB, Loo LO, Blomqvist M, Rolandsson J (2018) Substantial changes in the depth distributions of benthic invertebrates in the eastern Kattegat since the 1880s. *Ecol Evol*:1–13.

Kaiser M, Clarke K, Hinz H, Austen M, Somerfield P, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14.

Kaiser MJ, Edwards DB, Armstrong PJ, Radford K, Lough NEL, Flatt RP, Jones HD (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES J Mar Sci* 55:353–361.

Kaiser MJ, Ramsay K, Richardson CA, Spence FE, Brand AR (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. *J Anim Ecol* 69:494–503.

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.

Laliberté, E., Legendre, P., & Shipley, B. (2015). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Package, Version 1.0-12.

Lambert GI, Jennings S, Hiddink JG, Hintzen NT, Hinz H, Kaiser MJ, Murray LG (2012) Implications of using alternative methods of vessel monitoring system (VMS) data analysis to describe fishing activities and impacts. *ICES J Mar Sci* 69:682–693.

Lehmann A, Hinrichsen HH, Getzlaff K, Myrberg K (2014) Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. *J Mar Syst* 134:20–28.

Lepš J, De Bello F, Lavorel S, Berman S (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78:481–501.

Lüdecke, D., 2016 *sjPlot: Data Visualization for Statistics in Social Science*. 2019; Available online: <http://cran.r-project.org/package=sjPlot>.

Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning J-C, Terborgh JW (2016) Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc Natl Acad Sci* 113:838–846.

- Mangano MC, Kaiser MJ, Porporato EMD, Lambert GI, Rinelli P, Spanò N (2014) Infaunal community responses to a gradient of trawling disturbance and a long-term Fishery Exclusion Zone in the Southern Tyrrhenian Sea. *Cont Shelf Res* 76:25–35.
- McConnaughey R a, Syrjala SE, Dew CB (2005) Effects of chronic bottom trawling on the size structure of soft-bottom benthic invertebrates. *Benthic habitats Eff fishing Am Fish Soc Symp* 41:425–437.
- Ministry of Foreign Affairs of Denmark, 1933b. Anordning om frednings- og ordensbestemmelser af fiskeriet i det til kongerigerne Danmark og Sverige grænsende farvande. Royal Regulation, AND no. 230 of 29/06/1933, 2 pp. DOI: <https://www.retsinformation.dk/Forms/R0710.aspx?id=79587>
- Ministry of Foreign Affairs of Denmark. 1933a. Bekendtgørelse om en under 31. December 1932 mellem Danmark og Sverige angaaende fiskeriforholdene i de til Danmark og Sverige grænsende farvande. BEK no. 228 of 21/06/1933, Ministry of Foreign Affairs of Denmark, J.nr. 63.D.31, pp 1-5. DOI: <https://www.retsinformation.dk/pdfPrint.aspx?id=163290>
- Ministry of Foreign Affairs of Denmark. 2009. Bekendtgørelse om forbud mod visse former for fiskeri i nærmere afgrænsede områder i Kattegat og nordlige del af Øresund. BEK no. 182 of 13/03/2009, Ministry of Food, Agriculture and Fishery, Fisheries Agency, J.nr. 2009-01657, pp 1-8. DOI: <https://www.retsinformation.dk/pdfPrint.aspx?id=123851>
- Norkko A, Villnäs A, Norkko J, Valanko S, Pilditch C (2013) Size matters: Implications of the loss of large individuals for ecosystem function. *Sci Rep* 3:2646.
- Pearson, T.H., Rosenberg, R., (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 16, 229–311.
- Petersen CGJ (1918) The sea bottom and its production of fish food. A survey of the work done in connection with the valuation of the Danish waters from 1883-1917. *Rep Danish Biol Station* 25: 1–62
- Pommer C, Olesen M, Hansen J (2016) Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. *Mar Ecol Prog Ser* 548:47–60.
- Puig P, Canals M, Company JB, Martín J, Amblas D, Lastras G, Palanques A, Calafat AM (2012) Ploughing the deep sea floor. *Nature* 489:286–289.
- Queirós AM, Hiddink JG, Kaiser MJ, Hinz H (2006) Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. *J Exp Mar Bio Ecol* 335:91–103.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL. <https://www.R-project.org/>.
- Reiss H, Greenstreet SPR, Sieben K, Ehrich S, Piet GJ, Quirijns F, Robinson L, Wolff WJ, Kröncke I (2009) Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. *Mar Ecol Prog Ser* 394:201–213.
- Rice J, Arvanitidis C, Borja A, Frid C, Hiddink JG, Krause J, Lorance P, Ragnarsson SÁ, Sköld M, Trabucco B, Enserink L, Norkko A (2012) Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. *Ecol Indic* 12:174–184.

- Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol Appl* 28:1302–1312.
- Sciberras M, Hiddink JG, Jennings S, Szostek CL, Hughes KM, Kneafsey B, Clarke LJ, Ellis N, Rijnsdorp AD, McConnaughey RA, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2018) Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish* 19:698–715.
- Sciberras M, Parker R, Powell C, Robertson C, Kröger S, Bolam S, Geert Hiddink J (2016) Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. *Limnol Oceanogr* 61:2076–2089.
- Shannon CE, Weaver W, Blahut RE (1949) The mathematical theory of communication. Urbana Univ Illinois Press 117:379–423.
- Shin YJ, Rochet MJ, Jennings S, Field JG, Gislason H (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J Mar Sci* 62:384–396.
- Sköld M, Göransson P, Jonsson P, Bastardie F, Blomqvist M, Agrenius S, Hiddink JG, Nilsson HC, Bartolino V (2018) Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Mar Ecol Prog Ser* 586:41–55.
- Sköld M, Josefson A, Loo L (2001) Sigmoidal growth in the brittle star *Amphiura filiformis* (Echinodermata: Ophiuroidea). *Mar Biol* 139:519–526.
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* (80- ) 306:1177–1180.
- Svedäng H, Bardon G (2003) Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. *ICES J Mar Sci* 60:32–37.
- Thrush ASF, Hewitt JE, Cummings VJ, Dayton PK, Cryer M, Turner SJ, Funnell GA, Budd RG, Milburn CJ, Wilkinson MR (2008) Disturbance of the Marine Benthic Habitat by Commercial Fishing : Impacts at the Scale of the Fishery. 8:866–879.
- Thrush SF, Hewitt JE, Gibbs M, Lundquist C, Norkko A (2006) Functional role of large organisms in intertidal communities: Community effects and ecosystem function. *Ecosystems* 9:1029–1040.
- Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45.
- Van Denderen PD, Bolam SG, Hiddink JG, Jennings S, Kenny A, Rijnsdorp AD, Van Kooten T (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar Ecol Prog Ser* 541:31–43.
- Van Hoey G, Borja A, Birchenough S, Buhl-Mortensen L, Degraer S, Fleischer D, Kerckhof F, Magni P, Muxika I, Reiss H, Schröder A, Zettler ML (2010) The use of benthic indicators in Europe: From the water framework directive to the marine strategy framework directive. *Mar Pollut Bull* 60:2187–2196.

Villéger S, Mason NWH, Moullot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.

Wei T, Simko V (2016) Package ‘corrplot’. R package version 0.77. <https://cran.r-project.org/web/packages/corrplot/>.

Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. *Trends Ecol Evol* 20:402–409.

WoRMS Editorial Board (2018) World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ. Accessed 05/06/2018.

## Supplementary information

### Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance

#### Text S1 - Post-metamorphic growth of *Amphiura sp.*

Since the recruits of most species recorded herein settle during autumn (from September to November), sampling in mid-September to early October could have resulted in an overrepresentation of newly settled individuals in the small fraction (and therefore also the full community). Thus recruits could result in low response/lack of response to trawling in the small fraction and full community. Of the six most abundant species (>1000 individuals in the total dataset) in the small fraction, and in the full community, notable numbers of juveniles were not encountered for *Phoronis muelleri*, *Kutiella bidentata*, *Nucula nitidosa*, *Thyasira flexuosa* and *Scalibregma inflatum*. This is probably due to the early juveniles being too small and/or soft bodied to be retained on a 1mm sieve. However, few juvenile individuals of *Amphiura spp.* were encountered in the samples. The absence of significant numbers of (<1 year) juveniles is in line with earlier findings in the Kattegat area, where total diameter of *Amphiura* individuals in October is typically <1mm (Sköld et al 2001) (see below). Furthermore, daily mortality of post-metamorphic juveniles are considered high (estimated 160 individuals day<sup>-1</sup> in Sköld *et al.*, 2001) and annual recruitment into adult populations appears low (Muus, 1981; Sköld *et al.*, 2001). Recruitment of *Amphiura* takes place between August and November (peaking in October). Typically, the diameter of post-metamorphic settlers is ~0.46mm (disc diameter ~0.3mm and 2x arm length ~0.08mm in Muus, 1981 and Sköld *et al.*, 2001). Using the estimated growth models of Sköld *et al.* (2001), and a daily increase in disk diameter of 0.42% and arm length of 1.76%, even early August recruits are unlikely to have reached a total size of 1mm prior to the sampling time (considering that sampling began ~50 days after August 01, and ended ~65 days after). Furthermore, empirical evidence from Sköld et al 2001 (frequency distributions of the mean arm length and disk diameter) show that the vast majority of individuals sampled in early October were <1mm in length. To be allow for a precautionary approach, we excluded 50% off all *Amphiura sp* from the dataset and analysed N (small fraction). Model output is provided in section 3.3.3.

#### Calculation of post-metamorphic growth of *Amphiura filiformis* from Sköld et al 2001:

	Average size at settlement (µm)	Daily growth (in % day <sup>-1</sup> )			
Disc diameter:	300 µm	0.42%			
Arm length:	80 µm	1.76%			
<b>Growth equation: Size x (1+ (%/100))<sup>n</sup></b> where <b>size</b> is the length at Day 0, <b>%</b> is the daily growth in percentages, and <b>n</b> is the number of days of growth					
	Day 0	Day 30	Day 60	Day 75	Day 90
Disc diameter	300	300 x (1+ (0.42/100)) <sup>30</sup> =340	300 x (1+ (0.42/100)) <sup>60</sup> =386	411	300 x (1+ (0.42/100)) <sup>90</sup> =438
Arm length (two arms)	80 (160)	80 x (1+ (1.76/100)) <sup>30</sup> =135 (270)	80 x (1+ (1.76/100)) <sup>60</sup> =228 (456)	296 (592)	80 x (1+ (1.76/100)) <sup>90</sup> =385 (770)
<b>Total diameter, µm</b>	<b>460</b>	<b>510</b>	<b>842</b>	<b>1003</b>	<b>1208</b>

(1 disc + 2 arms):					
--------------------	--	--	--	--	--

**References**

Sköld, M., Josefson, A., Loo, L., 2001. Sigmoidal growth in the brittle star *Amphiura filiformis* (Echinodermata: Ophiuroidea). *Mar. Biol.* 139, 519–526. <https://doi.org/10.1007/s002270100600>

### Text S2 - Kiel Baltic Sea Ice-Ocean Model

We used hydrological data from the high-resolution hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM, Lehmann and Hinrichsen, 2000; Lehmann et al. 2002) which covers the period 1979-2016. The horizontal resolution of the coupled sea-ice ocean model is at present 2.5 km, and in the vertical 60 levels are specified, meaning that the upper 100 m are resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat and Skagerrak. The oxygen conditions in the entire Baltic Sea are described by an oxygen consumption sub-model coupled to BSIOM (Lehmann et al. , 2014). At the western boundary, a simplified North Sea is connected to the model domain to represent characteristic North Sea water masses in terms of characteristic temperature and salinity profiles resulting from different forcing conditions. The model is forced by low frequency sea level variations in the North Sea/Skagerrak calculated from the BSI (Baltic Sea Index, Lehmann et al., 2002; Novotny et al., 2006). The current model setup is forced by ERA-Interim reanalysis data (Dee et al. 2011) which provide surface air pressure, 2 m air temperature, 2 m dew point temperature, cloudiness at 6-hourly, and total precipitation at 12-hourly resolution. The atmospheric forcing have a horizontal resolution of 0.5x0.5 degrees, and the 6- and 12-hourly base data are linearly interpolated onto 3-hourly resolution to force the ocean model. Wind speed and direction at 10 m height are calculated from geostrophic winds according to the gradient in surface air pressure, where the impact of differences in surface roughness of coastal and open sea areas on wind speed and direction are accounted for (Bumke et al. 1998). Surface heat and momentum fluxes (from wind stress, short wave radiation and sensible and latent heat) are calculated according to Rudolph and Lehmann (2006). River runoff into the Baltic Sea is prescribed from a runoff dataset for the period 1979–2016 corrected using annual accumulated river runoff for extension into the year 2016 (Kronsell and Andersson 2012, see e.g. Lehmann et al. 2014). Modelled data extracted and used in the analysis included average bottom current velocity (m/s), bottom temperature (°C), and bottom salinity (PSU) values.

### References

- Bumke, K., Karger, U., Hasse, L. Niekamp, K., 1998. Evaporation over the Baltic Sea as an example of a semi-enclosed sea. *Contr. Atmos. Phys.*, 71(2), 249-261
- Dee DP, et al. 2011. The ERA-interim reanalysis: configuration and performance of the data assimilation system. *Quart. J. Roy. Meteor. Soc.* 137, 1972 – 1990.
- Kronsell, J., Andersson, P., 2012. Total regional runoff to the Baltic Sea. HELCOM Indicator Fact Sheets 2011. Online. (<http://www.helcom.fi/environment2/ifs>).
- Lehmann, A., Krauß, W., Hinrichsen, H.-H., 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus*, 54A: 299–316.
- Lehmann, A., Hinrichsen, H.-H., Getzlaff, K., Myrberg, K., 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. *Journal of Marine Systems*, 134:20-28.
- Novotny, K., Liebsch, G., Lehmann, A., Dietrich, R., 2006. Variability of sea surface heights in the Baltic Sea: An intercomparison of observations and model simulations, *Marine Geodesy*, 29, 113-134.
- Rudolph, C., Lehmann, A., 2006. A model-measurements comparison of atmospheric forcing and surface fluxes of the Baltic Sea. *Oceanologia*, 48(3), 333-380.

Figure S1: (a) nMDS plot of environmental characteristics of sampling sites (b) Cluster analysis of environmental characteristics of sampling sites. Parts (a) and (b) are based on Euclidean distance.

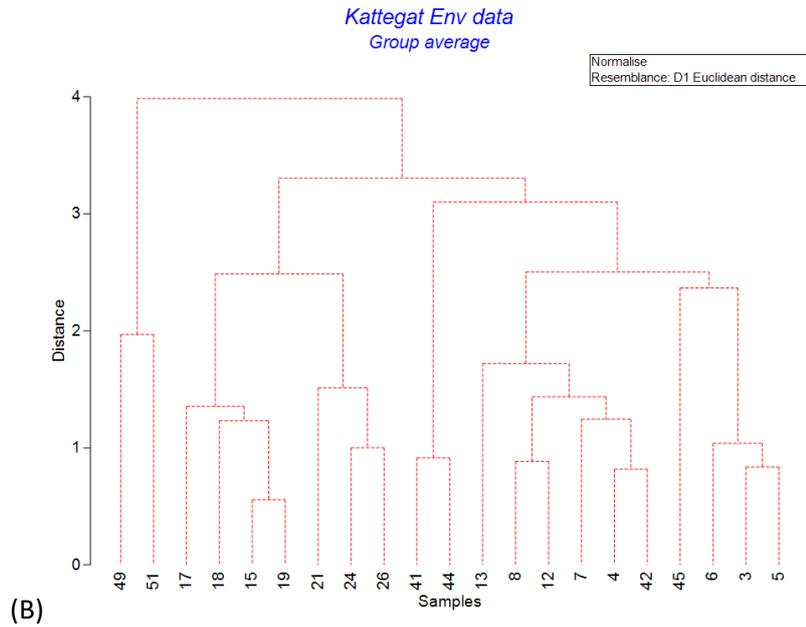
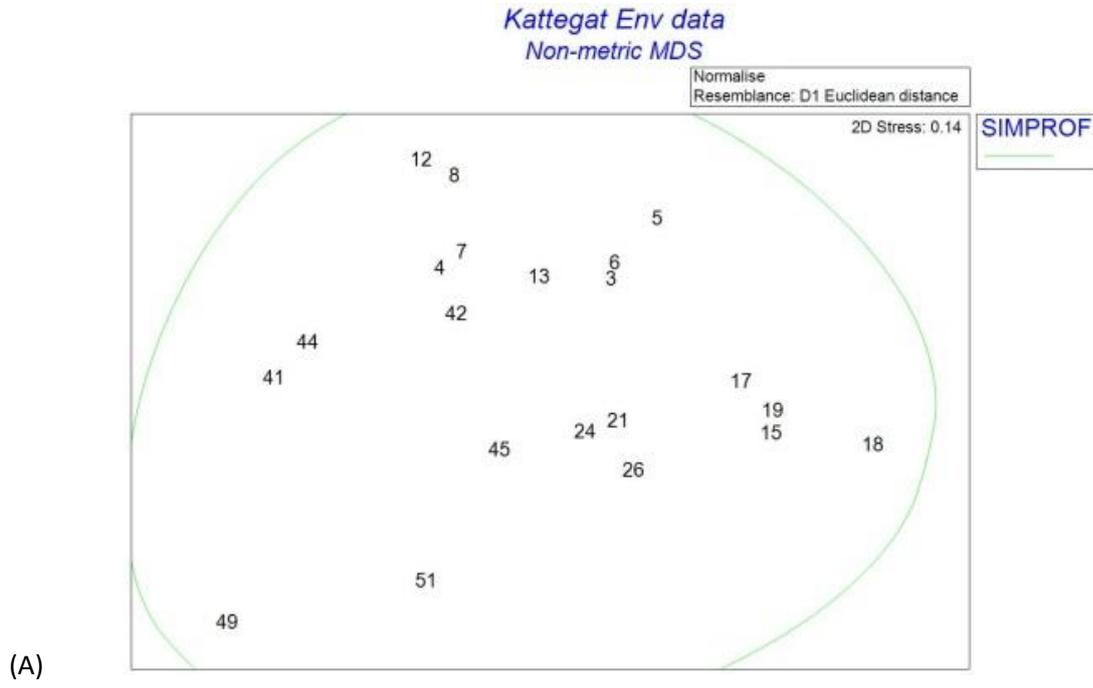
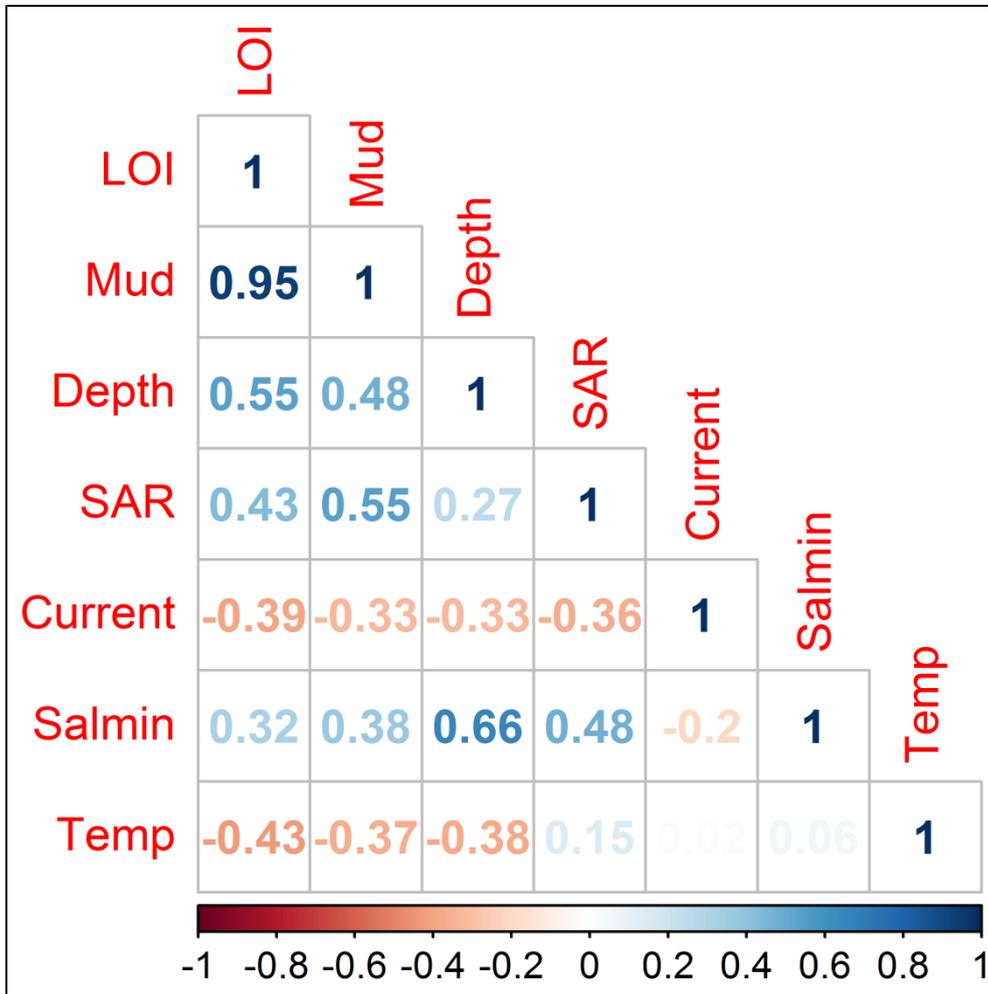


Figure S2: Pairs plot of predictor variables (fishing intensity and environmental variables) and associated Pearson correlation coefficients. LOI = loss on ignition. SAR = swept area ratio. Correlations of >0.7 were excluded from the analysis, which resulted in Loss-on-ignition (LOI) being removed.



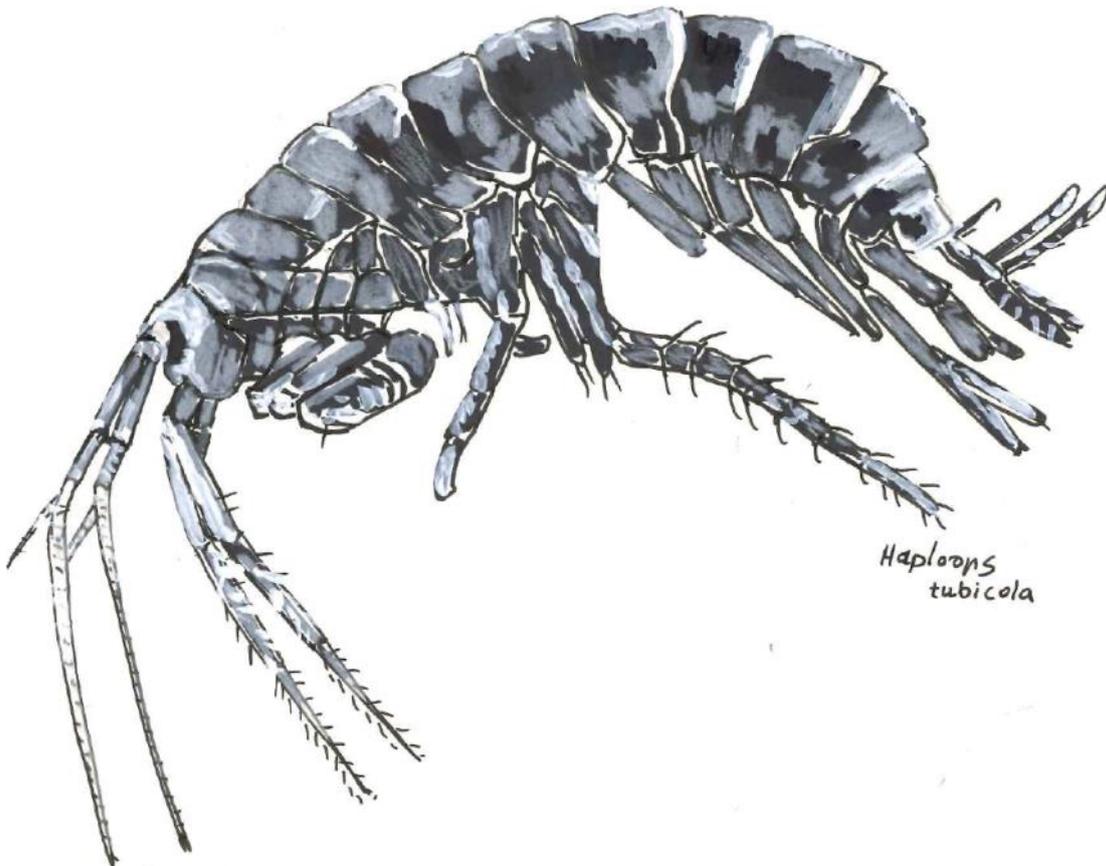
**Table S1: Site-by-site summary information for macrofaunal density, species density, trawling intensity, and environmental variables. Density and species density are totals over four replicates. As SAR values were calculated and analysed for each replicate sample, the values presented here are averaged over four replicates (standard deviation shown in brackets). Data for environmental variables were calculated per sampling site.**

Sampling site	Density			Species density			Trawling Intensity	Current speed	Depth	Mud content	Min Salinity	Temperature
	1-4mm	>4mm	Full community	1-4mm	>4mm	Full community	SAR (3 yr <sup>-1</sup> )	cm/s	m	% <63µm	PSU	Celsius
3	629	144	773	36	7	39	33.53 (3.7)	1.66	34.43	79.59	32.20	8.12
4	1850	558	2408	52	22	59	8.95 (0.2)	1.69	16.25	13.67	29.16	8.98
5	552	76	628	36	10	38	43.4 (0)	1.36	32.90	96.54	33.15	8.54
6	947	189	1136	40	10	44	21.06 (0.4)	0.84	33.18	67.08	33.04	8.17
7	2889	219	3108	73	18	81	4.14 (0.4)	1.86	38.65	3.78	30.76	8.54
8	2882	286	3168	75	33	89	3.64 (0.1)	1.02	33.00	5.10	29.28	8.85
12	1847	311	2158	62	31	73	0.42 (0)	0.98	18.58	3.57	30.03	8.99
13	1872	461	2333	73	25	81	13.15 (0.2)	0.73	28.03	11.89	33.72	7.82
15	318	111	429	47	11	50	11.91 (1.1)	1.45	63.68	96.16	34.31	6.92
17	558	197	755	47	18	52	35.02 (1.6)	0.42	60.90	60.77	34.26	6.95
18	258	214	472	42	17	46	7.2 (1.2)	0.41	81.08	95.76	34.34	6.80
19	403	166	569	51	14	53	15.3 (0.5)	0.95	64.90	92.67	34.24	7.02
21	480	155	635	53	16	57	7.11 (0.1)	2.54	59.93	44.93	34.22	7.33
24	709	246	955	83	38	101	3.54 (0.3)	1.93	59.30	4.32	34.04	7.50
26	624	122	746	73	14	80	16.39 (0.5)	1.35	62.08	10.90	34.47	6.89
41	752	599	1351	74	36	82	2.08 (0)	4.11	22.45	24.67	30.37	7.54
42	1242	375	1617	61	31	69	5.48 (0.1)	1.46	19.88	12.46	30.78	7.77
44	975	483	1458	78	33	89	3.28 (0.1)	3.56	23.13	5.48	30.83	7.89
45	1100	535	1635	53	33	62	0 (0)	2.35	26.78	57.94	32.07	6.77
49	1018	548	1566	52	27	63	0 (0)	1.76	19.25	25.68	21.63	6.41
51	2091	792	2883	67	39	75	0 (0)	1.10	20.93	56.17	26.66	6.25

**Table S2: Output of generalised linear mixed models for macrofaunal indicators. Parameter estimates are presented and standard error is shown in brackets. Significance level is denoted by asterisks (\* = P < 0.05; \*\* =P < 0.01; \*\*\* = P < 0.001).**

Macrofaunal indicator	Intercept	Current	Depth	Mud%	Temperature	Trawling	Salinity	Density <sup>†</sup>	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>
<b>Pooled community</b>										
RaoQ	0.23 (0.02)		-0.001 (<0.001)*	-0.001 (<0.001)*					0.09	0.18
Fric	0.47(0.01)			-0.001 (<0.001)*		-0.003(0.001)**			0.36	0.47
Feve	0.20(0.09)						0.006(0.003)*		0.08	0.24
Fdis	4.31(0.40)		0.022(0.010)*	-0.013(0.006)*					0.09	0.13
<b>Small (1-4mm) fraction</b>										
RaoQ	0.43(0.06)				0.014(0.008)	-0.001 (<0.001)***			0.17	0.17
Fric	0.38(0.02)		-0.001 (<0.001)*			-0.003(0.001)**			0.26	0.38
Feve	0.21(0.08)						0.007(0.002)**		0.11	0.11
Fdis	5.76(0.13)					-0.025(0.008)**			0.10	0.11
<b>Large (≥4mm) fraction</b>										
RaoQ	0.28(0.02)	-0.024) 0.011)*		-0.001 (<0.001)*		-0.002(0.001)***			0.28	0.28
Fric	0.49(0.03)					-0.007(0.001)***			0.26	0.46
Feve	0.46(0.03)					-0.005(0.001)**			0.11	0.11
Fdis	4.37(0.30)					-0.053(0.018)**			0.12	0.21
N = density, S = species density, H' = Shannon diversity, RaoQ = functional diversity, Fric = Functional richness, Feve = Functional evenness, Fdis = Functional dispersion Model families: N = Negative binomial. S = Poisson. Biomass/RaoQ/Fric/Feve/Fdis = Gaussian † = density (N) included as a predictor for models of species density (S), only										

## 6. The sensitivity of benthic life history traits to chronic trawling disturbance



This chapter is currently in preparation:

McLaverty C, Dinesen GE, Brooks ME, Eigaard OR (*In prep*) The sensitivity of benthic life history traits to chronic trawling disturbance

## **The sensitivity of benthic life history traits to chronic trawling disturbance**

Ciarán McLaverty<sup>1,\*</sup>, Grete E. Dinesen<sup>1</sup>, Mollie E. Brooks<sup>1</sup>, Ole R. Eigaard<sup>1</sup>

<sup>1</sup>DTU Aqua, National Institute of Aquatic Resources, Denmark

\*Corresponding author: [cimc@aqu.dtu.dk](mailto:cimc@aqu.dtu.dk). Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, Building 201, 2800 Kgs. Lyngby, Denmark.

### **Keywords**

Bottom trawling; Benthic community; Biological trait approach; Community-weighted mean; Ecosystem function; Tweedie distribution

### **Abstract**

Bottom trawling results in the widespread disturbance of seabed habitats and benthic communities. An Ecosystem Approach to Fisheries Management aims to strike a balance between the exploitation of marine resources, and inevitable impacts to benthic biodiversity and ecosystem function. In this regard, trait-based approaches represent a promising method to understand the impacts of trawling on benthic communities. In this study, we describe the sensitivity of benthic communities to trawling using community-weighted mean (CWM) traits, which have the potential to act as univariate indicators of trawling disturbance. Using benthic data collected from commercial fishing grounds in the Kattegat, we demonstrate that the traits of large benthic macrofauna are particularly sensitive to trawling impacts. In addition, benthic fauna which are sessile, suspension feeding, surface depositing, tube-dwelling and demonstrating long lifespans, were also particularly sensitive in this regard. Given the importance of many of these traits in processes such as benthic-pelagic coupling, it is therefore likely that the loss or decline of these traits may have implications for the functioning of benthic ecosystems across fishing grounds. Additionally, we validated our observations using an independent benthic monitoring dataset. Our results suggest that chronic bottom trawling has a strong negative effect the traits of benthic macrofauna, and that data collected from a carefully designed one-off sampling event can provide results which are representative of long-term datasets.

## 6.1. Introduction

Traits are increasingly used in community ecology to characterise species composition (McGill et al. 2006) and to interpret how changes in the relative abundance of species can affect the functionality of systems (Bremner et al. 2005). In contrast to taxonomic methods, trait-based approaches can be used to describe physiological, behavioural, morphological, and life-history characteristics of communities. Knowledge of these attributes can therefore be used to predict the vulnerability of communities to disturbance (Mouillot et al., 2013; Beauchard et al., 2017).

Understanding the balance between fisheries exploitation, biodiversity, and ecosystem function forms the basis of an Ecosystem Approach to Fisheries Management (EAFM) (FAO, 2003; Pikitch et al., 2004). Traditionally, research of trawling impacts have mainly focussed on an understanding of the linkages between fishing pressure and changes to the structure, diversity, taxonomic composition of benthic communities (Kaiser et al. 2006, Hiddink et al. 2017, Sciberras et al. 2018). However, taxonomic information alone cannot convey the changes in ecological condition and benthic functionality caused by bottom-trawling (Bremner et al. 2003). Furthermore, taxonomic approaches are generally unable to describe mechanisms of sensitivity, or disentangle the ecological effects of multiple stressors (Bremner et al. 2006a). While the longevity of benthic fauna has been successfully used to describe the sensitivity of benthic communities to trawling (Rijnsdorp et al. 2018, Hiddink et al. 2018), there are few examples of the adoption of trait-based indicators in the monitoring and management of trawling impacts. Accordingly, there is considerable potential to explore the viability of, and develop, benthic trait-based approaches.

A recent study demonstrated that trait-based community indicators show a mixed ability to detect trawling impacts (McLaverty et al. 2020). However, recalculating the same trait-based indicators using large-bodied macrofauna resulted in considerably improved detection rates of bottom trawling disturbance (McLaverty et al. 2020). This approach of combining large-bodied benthos with biological traits may therefore represent the basis to develop trait-based indicators. The potential of this approach lies in the fact that the body-size of an organism is tightly linked to several other life history characteristics, such as feeding, growth, metabolism, mortality, and the main physical constraints of an organism (Begon 2006). Accordingly, the size of an individual may reflect its sensitivity to, and ability to recover from, disturbance. In other fields of ecology, traits such as reproductive method and frequency have been suggested as key traits to define organisms (Kiørboe et al. 2018). Such trait may also prove useful in the development of benthic indicators, as benthic populations with early reproduction and fast growth rates (*r*-strategists) may have greater ability to withstand fishing mortality (Blanchard et al. 2004).

The main objective of this study was therefore to assess sensitivity of community-weighted mean (CWM) traits as indicators of chronic trawling disturbance. To do this, data were collected in a fishing ground with a long history of bottom trawling. Sampling sites were positioned along a gradient of recent trawling intensity, covering both unfished sites (from long-standing closed areas) and sites representative of regionally high trawling intensity. Furthermore, we size-separated the community during sampling into small (1 – 4mm) and large ( $\geq 4$ mm) fractions to allow for indicators to be tested for both large-bodied and small-bodied benthic macrofauna. Candidate traits were identified using multivariate ordinations, and these were used to model the effect of trawling and environmental variables on trait biomass. Finally, to examine if our results were representative of long-term impacts caused by bottom trawling, we repeated our analysis using data from an independent monitoring dataset from the same area.

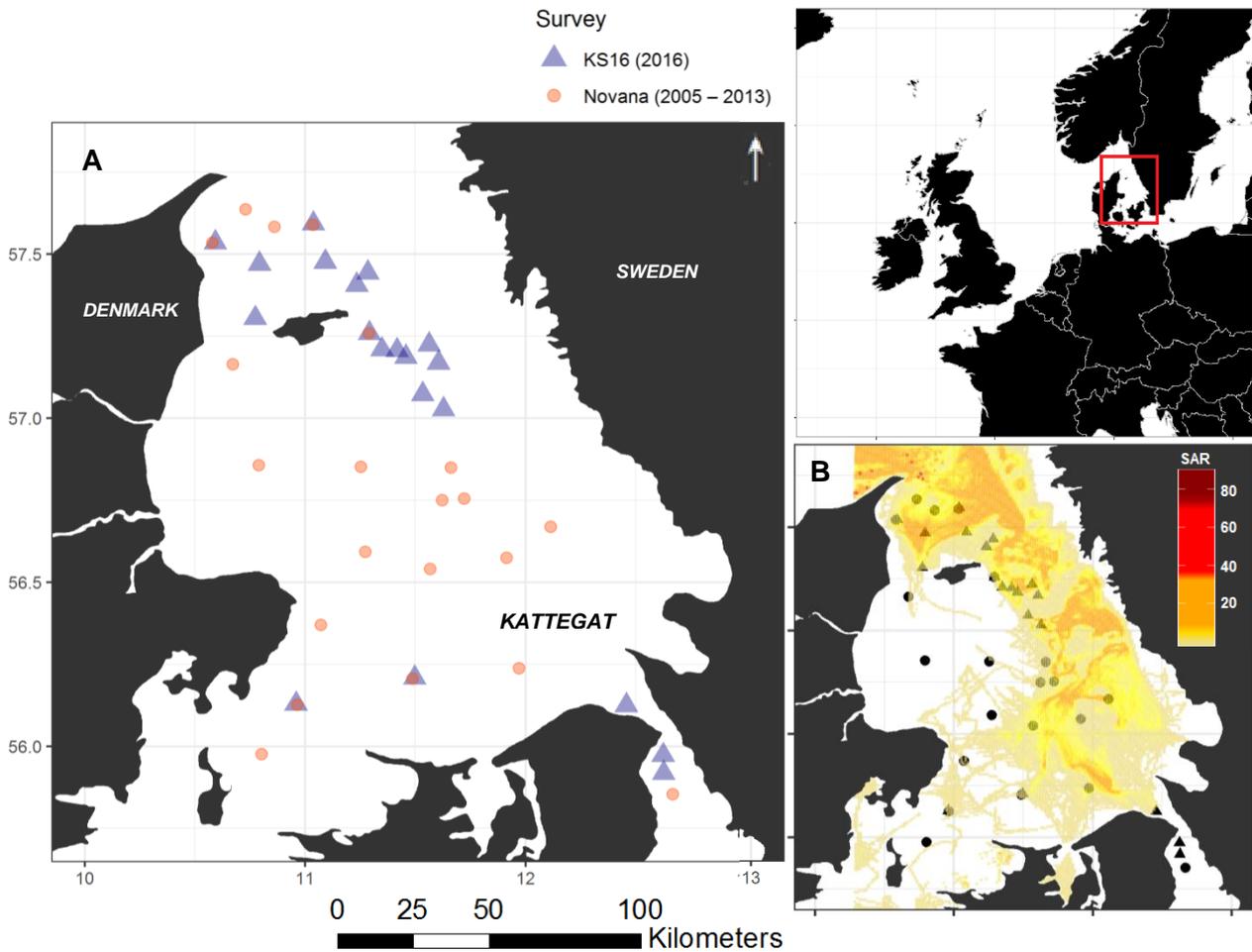
## 6.2. Materials and methods

### **Data sources**

The analyses undertaken in this study were based on two independent benthic surveys undertaken in Danish waters between 2005 and 2016. The KS16 survey was undertaken as a one-off or ‘snapshot’ survey in September 2016, and gathered benthic samples from 21 locations. The samples were size-separated into large and small size fractions, and therefore represent three separate datasets; the 1-4mm (small) fraction, the  $\geq 4$ mm (large) fraction, and the two fractions combined (full community). The Danish National Monitoring programme (NOVANA) dataset was generated from a long-running benthic monitoring program. Data were gathered from 22 sites (i.e. fixed locations) in the Kattegat for the years 2005–2008, 2010, 2011 and 2013. The locations of NOVANA sampling sites were originally selected to assess the effect of anthropogenic impacts such as effects of nutrient enrichment in Danish waters (Svendsen et al., 2005).

### **Study area**

Both the KS16 and NOVANA surveys were undertaken in the Kattegat with the Danish Exclusive Economic Zone (EEZ) (Figure 6-1a). The area represents an important fishing ground for Danish and Swedish vessels targeting mainly Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). The western areas of the Kattegat are shallow and sandy, while the northern and eastern areas are generally deeper, composed of a mosaic of muddy canyons and mounts of mixed sediments. *Nephrops* habitats generally occur below 20m depth. The highest levels of trawling intensities are typically in the northern areas, around a trench system in the east, and sporadic areas in the south.



**Figure 6-1. (a) Location of sampling sites for KS16 and NOVANA surveys (b) location of sampling sites in respect to typical trawling effort in the Kattegat (based on fishing effort between 2013 and 2016).**

#### ***Data collection and sample processing***

*KS16 survey (2016).* The sampling stations in the KS16 survey were selected based on the sediment type (mud and mixed sand/mud), depth ( $\geq 15\text{m}$ ), and spread across a trawling gradient based on 2013-2016 data (Figure 6-1b). Five sediment samples were taken at each site using a  $0.1\text{m}^2$  Van Veen grab. One was sub-sampled for particle size analysis (PSA) and four samples were processed for faunal analysis. This resulted in the collection of 84 faunal samples in total. The faunal samples were sieved consecutively over 4mm and 1mm mesh sizes to separate the community into two size fractions. This size-separation of the community provided three datasets, which were carried forward for analyses; the 1-4mm (small) fraction, the  $\geq 4\text{mm}$  (large) fraction, and the combined full community (full community). The sieved samples were then fixed in 4% borax-buffered

formaldehyde in ambient seawater. In the laboratory, all animal material was identified to the lowest taxonomic level possible, and biomass estimates per species were determined as ash-free dry weight.

*NOVANA survey (2005 – 2013)*. At each station, five replicate sediment samples are typically collected with a 0.0143m<sup>2</sup> Haps corer for faunal analysis. The combined data between 2005 and 2013 resulted in a total of 827 samples. Samples were rinsed over a 1mm sieve, and persevered in 96% ethanol solution. In the laboratory, all animal material was sorted into individuals, identified to the lowest taxonomic level possible and enumerated prior to biomass determination as wet weight. Core samples for particle size analysis (PSA) were conducted at all stations in 2006. For both surveys, PSA was undertaken via mass loss following wet sieving (Danish Standard (DS) 405.9), and resulted in the estimation of mud% (<63µm), sand% (0.063–2mm), and gravel% (≥2mm).

### ***Estimating trawling pressure***

Trawling intensity was calculated for the KS16 and NOVANA surveys as swept area ratio (SAR). The SAR values were calculated within a circle of ~2km radius around the position of each faunal replicate sample (KS16) or monitoring station (NOVANA). SAR represents the accumulated gear specific trawled (swept) area ratio within the circle divided by the size of the circle, and is an estimate of the number of times the seabed within the circle is trawled in a given time period. The area swept was estimated by combining Vessel Monitoring System (VMS) data with information regarding vessel and gear specifications, provided by EU logbooks. VMS receivers collect and send data regarding the vessel location, heading, and speed, at an hourly polling frequency for Danish and Swedish vessels. Raw VMS data were processed to preserve only points which represented 'trawling activity'. This was defined as speed between 2 and 4 knots, with a minimum distance of 3km from port. To reconstruct trawling tracks, the raw data points were interpolated using a cubic Hermite spline method (Hintzen et al. 2012). Trawling tracks are then combined with logbook data on vessel size and gear dimensions (Eigaard et al. 2016). From this, the gear-width can be estimated and then aggregated to calculate the area of seabed 'swept' during each logbook trip. All processing of VMS data and estimation of SAR were done using the VMStools package (Hintzen et al. 2012). Since 2012, VMS has been mandatory on all vessels ≥12m operating in European waters. Between 2005 and 2012, the device was mandatory for vessels ≥15m. As the NOVANA survey runs prior to 2012, we were therefore unable to consider the effort of vessels <15m. Thus, all SAR values calculated for the NOVANA data were based on vessels ≥15m and including the effort of both Danish and Swedish vessels. SAR values calculated for the KS16 data were based on vessels ≥15m and also include the effort of Swedish fishing vessels.

### ***Environmental drivers***

Aside from trawling intensity, data for five important environmental drivers of benthic communities were collated. These included mud content (%), depth (m), bottom current speed ( $\text{cm}^{-\text{s}}$ ), bottom water salinity, and bottom temperature ( $^{\circ}\text{C}$ ). Data regarding depth (in situ) and mud content (described above) were collected in the field. Modelled hydrodynamic data on current speed, salinity, and temperature were extracted from the high-resolution Baltic Sea Ice-Ocean Model (BSIOM) (Lehmann et al., 2014). These data were back-calculated for a 2\*2km grid cell at each benthic sampling position at a monthly scale and averaged over the 12 months prior to sampling. Due to the resolution of the environmental data, the same values were applied to all replicates at a given station.

### ***Calculation of trait composition and indicators***

We used a suite of 10 biological traits and 48 descriptive modalities from an existing trait database (EU BENTHIS, e.g. see Bolam et al., 2017) to describe the trait composition of the communities recorded in the KS16 and NOVANA datasets (Table 6-1). Additionally, 10 genera were coded based on information from the literature. Traits were categorised in relation to ecosystem functions, such as food acquisition, recovery capability, resilience to disturbance, and sediment stability (Beauchard et al. 2017). Community trait composition was calculated using 368 (NOVANA), 285 (KS16 full community), 144 (KS16 large fraction) and 259 (KS16 small fraction) taxa. As benthic species often exhibit multiple trait modalities, the traits were described using a ‘fuzzy coding’ approach (Chevenet et al. 1994). Fuzzy coding allows for several modalities to be expressed within a trait category, and indicates the relative importance of each modality. Where taxa showed full affinity to a single modality (e.g. its maximum age or body size) a score of 3 was assigned. If taxa exhibited multiple modalities per category, they were assigned a score relative to its importance. For example, the brittlestar *Amphiura filiformis* is a deposit feeder and facultative suspension feeder. *A. filiformis* would therefore be scored as suspension = 2 and surface deposit = 2. After all modalities were scored, the values were standardised to 1 within each category. Trait scores were combined with biomass data to generate trait-by-site matrices. This was done by averaging the trait scores of the species present in a sample, weighted by their relative biomass, which results in a community-weighted mean (CWM) trait value. CWM values were calculated using absolute values, to preserve spatial and temporal contrasts in trait biomass across the study area. The trait matrices were used to first determine the most sensitive traits in the community (multivariate analysis), and then directly test the sensitivity of individual traits to trawling disturbance (univariate analysis, as per Beauchard et al., 2017). Biomass was chosen to weight the trait values as it is considered to better reflect an organism role in ecosystem functioning (Bolam & Eggleton 2014).

**Table 6-1. Biological traits and associated modalities used in the study.**

<b>Function</b>	<b>Trait</b>	<b>Modality</b>
Food acquisition	Feeding mode	Suspension Scavenger/Opportunist Surface Deposit Subsurface deposit Predator Parasite
Recovery	Larval Development	Planktotrophic Lecithotrophic Direct
	Egg development	Asexual/Budding Sexual: eggs pelagic Sexual: eggs benthic Sexual: brood eggs
	Mobility	Sessile Burrower Swim Crawl/creep/climb
Resilience	Size range	<10mm 11-20mm 21-100mm 101-200mm 201-500mm >500mm
	Longevity	<1 year 1-3 years 3-10 years >10 years
	Morphology	Soft Crustose Cushion Stalked Tunic Exoskeleton (chitin/calcium carbonate)
Sediment stability	Living habit	Tube-dwelling Burrow-dwelling Free-living Crevice/hole/under stone Attached to substratum Epi/endozoic/phytic
	Sediment position	Surface Infauna: 0-5cm Infauna: 6-10cm Infauna: >10cm
	Bioturbators	Diffusive mixing Surface deposition Downwards conveyer Upward Conveyor None

### **Statistical approach**

#### *Multivariate analysis – determining sensitive traits*

Analyses of functional trait composition were carried out using distance-based linear models (DistLMs). DistLMs fit the relationship between community (multivariate) data and environmental predictors using a distance-based redundancy analysis (dbRDA) approach (Legendre & Andersson 1999). Constrained ordinations are undertaken using non-Euclidean distance measures. Firstly, trait scores were log transformed ( $\log(x+1)$ ), and resemblance matrices were based on Bray-Curtis similarity. Step-wise sequential tests and the small-sample size corrected Akaike information criterion (AICc) were used for the selection of predictors in the DistLM. P-values were obtained based on 999 permutations. Following this, dbRDAs visualised the fitted values from the DistLM model. dbRDA vector overlays visualise the multiple partial correlations for the significant predictors. We also used multiple partial correlations to compare the importance of trawling in each of the datasets. To determine the most sensitive traits, we calculated the correlation (Pearson's R) between individual traits and the axis that explained most of the variation (providing the axis also correlated with trawling intensity). Traits with larger correlation coefficients were thus considered to have a larger contribution to the dbRDA ordination. This approach has been suggested as a useful method to generate exploratory hypotheses from multivariate data (Anderson et al., 2008), and has been used in recent trawling impact studies to examine the sensitivity of individual species to trawling disturbance (Sköld et al. 2018). We limited our analysis to the ten traits with the largest correlation coefficients in each dataset. Multivariate analyses were carried out using PRIMER v.7 with PERMANOVA+ (Anderson et al. 2008).

#### *Univariate analysis - Sensitivity of CWM traits to trawling*

As each replicate sample represented an observation, we analysed the data using mixed effects models. This modelling approach is particularly suitable to quantify potential correlations in repeated measure designs (Bolker et al. 2009). The biomass-weighted CWM trait data were non-negative, continuous, containing zeros, and right skewed. Log-transformations are widely applied to ecological data to deal with such data, however, this approach can potentially produce spurious results while also distorting the underlying meaning of the measurement (Feng et al. 2014). Instead of transforming the data, we applied the Tweedie distribution because it can handle continuous data that is greater than or equal to zero. The Tweedie distribution and its extensions have been demonstrated to provide an effective method to fit fish biomass data (Foster & Bravington 2013). We fitted generalized linear mixed models (GLMMs) with a Tweedie distribution and a log-link using the glmmTMB package (Brooks et al., 2017). To avoid issues related to multicollinearity of predictor variables, all pair-wise correlations were checked, and all demonstrated correlation values of  $<0.7$  (Dormann et al., 2013). Pairwise correlation coefficients are presented in the Supplement – Table S1. Model selection

was undertaken via backwards model selection and likelihood ratio tests. Model diagnostics were checked using the DHARMA package (Hartig, 2016), a quantitative (simulation) based approach suitable for mixed models. All analyses were conducted using R version 3.5.0 (R Development Core Team, 2018).

### 6.3. Results

A summary of sampling effort, gross community metrics, and trawling intensities over the two datasets are outlined in Table 6-2. Despite the KS16 survey comprising a considerably lower number of samples, the area of seabed sampled in the two datasets were comparable. This was due the 0.1 m<sup>2</sup> Van Veen grab sampler used in the KS16 survey, which is considerably larger than the 0.0143m<sup>2</sup> Haps corer used in the NOVANA survey. Although the difference in biomass estimation between the surveys does not allow for direct comparisons, roughly 90% of KS16 biomass was accounted for by the large fraction. The mean and range of trawling intensity estimated at sampling sites was similar between the datasets, indicating that the gradient of trawling effort sampled in the KS16 survey was representative of temporal patterns in the 10 years prior to sampling.

**Table 6-2. Summary of the sampling effort, benthic community parameters, and fishing intensity recorded in the KS16 (2016) and NOVANA surveys (2005-2013).**

	KS16 large fraction 2016	KS16 small fraction 2016	KS16 Full community 2016	NOVANA 2005 – 2013
Number of samples	84			827
Areas of seabed sampled	8.4 m <sup>2</sup>			11.8 m <sup>2</sup>
Trait modalities represented	46	48	48	48
Total biomass	199.04 g*	21.46 g*	220.50 g*	4,814.13 g <sup>†</sup>
Total number of taxa	144	259	285	368
Range of trawling intensity (SAR)	0 - 12.6 yr <sup>-1</sup>			0 - 14.8 yr <sup>-1</sup>
Mean trawling intensity (SAR)	3.8 yr <sup>-1</sup>			3.4 yr <sup>-1</sup>
* Ash free dry weight biomass				
† Wet weight (blotted) biomass				

#### ***Determining sensitive traits***

Multivariate redundancy analyses (dbRDAs) were used to examine the relationship between CWM trait composition and the predictor variables. In each of the dbRDAs, the first axis (dbRDA1) explained considerably higher trait variance than the other axes, and was significantly correlated with trawling. This axis was therefore used to calculate the sensitivity of CWM traits across the respective datasets. Table 6-3 (a) presents the strength of correlations between dbRDA1 and individual CWM traits. The ten CWM traits which exhibited the largest correlation coefficients in each dataset are presented, representing a total of 22 traits.

**Table 6-3. Linear relationships between CWM traits and respective dbRDA axes which best contributed to the total variation (dbRDA1). The ten traits which demonstrated the strongest correlations in each dataset are presented.**

		KS16 large	KS16 small	KS16 Full community	NOVANA
(a)					
Trait group	CWM trait				
Food acquisition	Predator		-0.45		
	Subsurface deposit		-0.43		
	Suspension	-0.52		-0.55	-0.20
Recovery	Lecithotrophic		-0.46		
	Planktotrophic	-0.48		-0.5	
	Sessile	-0.47	-0.45	-0.51	-0.24
	Sexual: eggs pelagic	-0.48	-0.52	-0.5	
	Surface deposition	-0.49		-0.51	
Resilience	1 – 3 years				-0.20
	>10 years	-0.50		-0.51	
	21 - 100mm				-0.22
	101 - 200mm	-0.49		-0.49	
	Exoskeleton	-0.47		-0.49	
	Soft		-0.51	-0.54	
Sediment stability	Burrow-dwelling		-0.41	-0.48	-0.26
	Crevise-dwelling				+0.42
	Diffusive mixing		-0.43		
	Infauna: 0-5cm		-0.47		-0.23
	Infauna: 6-10cm	-0.45	-0.53		-0.23
	Free-living				+0.21
	Tube-dwelling	-0.47			
	Non-bioturbator				-0.21
(b)					
	Predictor				
	Trawling	0.45	0.30	0.41	0.13

Responsive CWM traits identified in the KS16 full community and large fraction showed a high degree of similarity. The exceptions to this were the trait ‘Infauna: 6-10cm’ and ‘tube-dwelling’, and ‘soft’. The most sensitive traits in the KS16 small fraction were relatively dissimilar from those of the KS16 large fraction and KS16 full community, and included distinctive traits such as ‘subsurface deposit’, ‘lecithotrophic’, predators, ‘infauna: 0-5cm’, and ‘diffusive mixing’. Across the surveys, ‘suspension’, ‘sessile’, ‘burrow-dwelling’,

‘infauna: 0-5cm’ and ‘infauna: 6-10cm’’, were common to both the NOVANA surveys and KS16 surveys. The ‘free-living’ and ‘crevice dwelling’ were the only traits to exhibit a positive relationship with dbRDA1. Multiple partial correlations between trawling and dbRDA1 revealed a marginally larger correlation in the KS16 large fraction, indicating a proportionally greater effect of trawling to trait variance in this dataset Table 6-3 (b). The full dbRDAs are provided in Figure S1 of the Supplement.

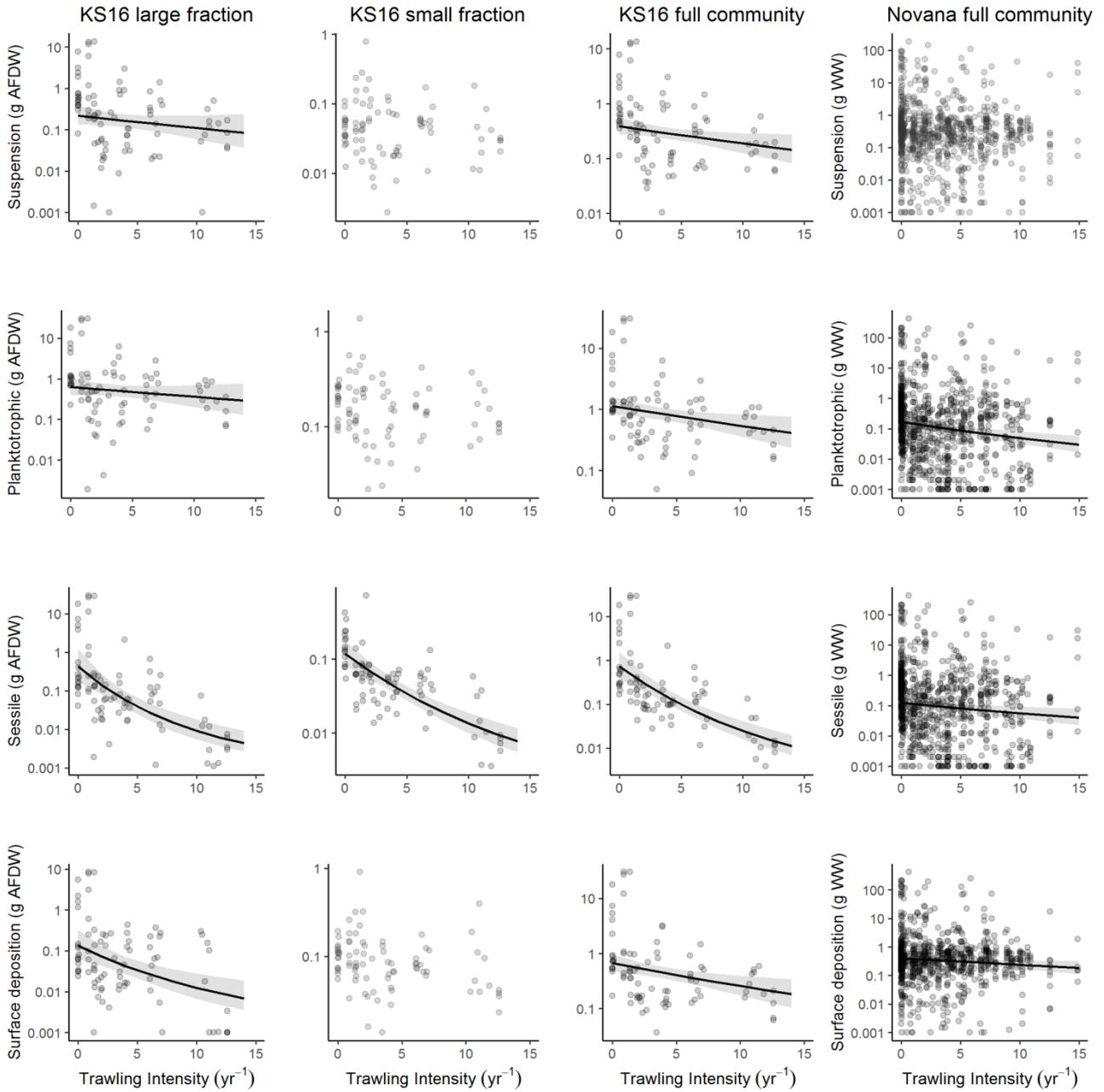
### ***Sensitivity of CWM traits to trawling***

Given the relative importance of trawling to trait ordination in the large fraction, we carried forward the traits identified in this dataset for further analysis. These traits included ‘suspension’, ‘>10 years’, ‘surface deposition’, ‘101-201mm’, ‘sexual: eggs pelagic’, ‘planktotrophic’, ‘exoskeleton’, ‘tube-dwelling’, ‘sessile’, and ‘infauna: 6-10cm’. Summary results of the GLMMs are presented in Table 6-4, and significant relationships are visualised in Figure and Figure. Of the ten traits examined, seven exhibited a significant relationship with trawling in the large fraction i.e. ‘suspension’, ‘planktotrophic’, ‘sessile’, ‘surface deposition’, ‘>10 years’, ‘infauna: 6-10cm’ and ‘tube-dwelling’. These results showed a high degree of similarity with the result from the KS16 full community (with the exception of >10 years, and Infauna: 6-10cm). Similarly, the results from the large fraction were mostly reflected in the NOVANA datasets, the only exception being ‘suspension’. This suggests that the traits identified from the large fraction were both highly sensitive to chronic trawling, and able to reflect the effects of long-term trawling on the benthic communities better than the full community traits. Of the environmental predictors included in the analysis, depth, temperature, and current speed were particularly important. Model outputs from the GLMMs are provided in Table S3 in the Supplement.

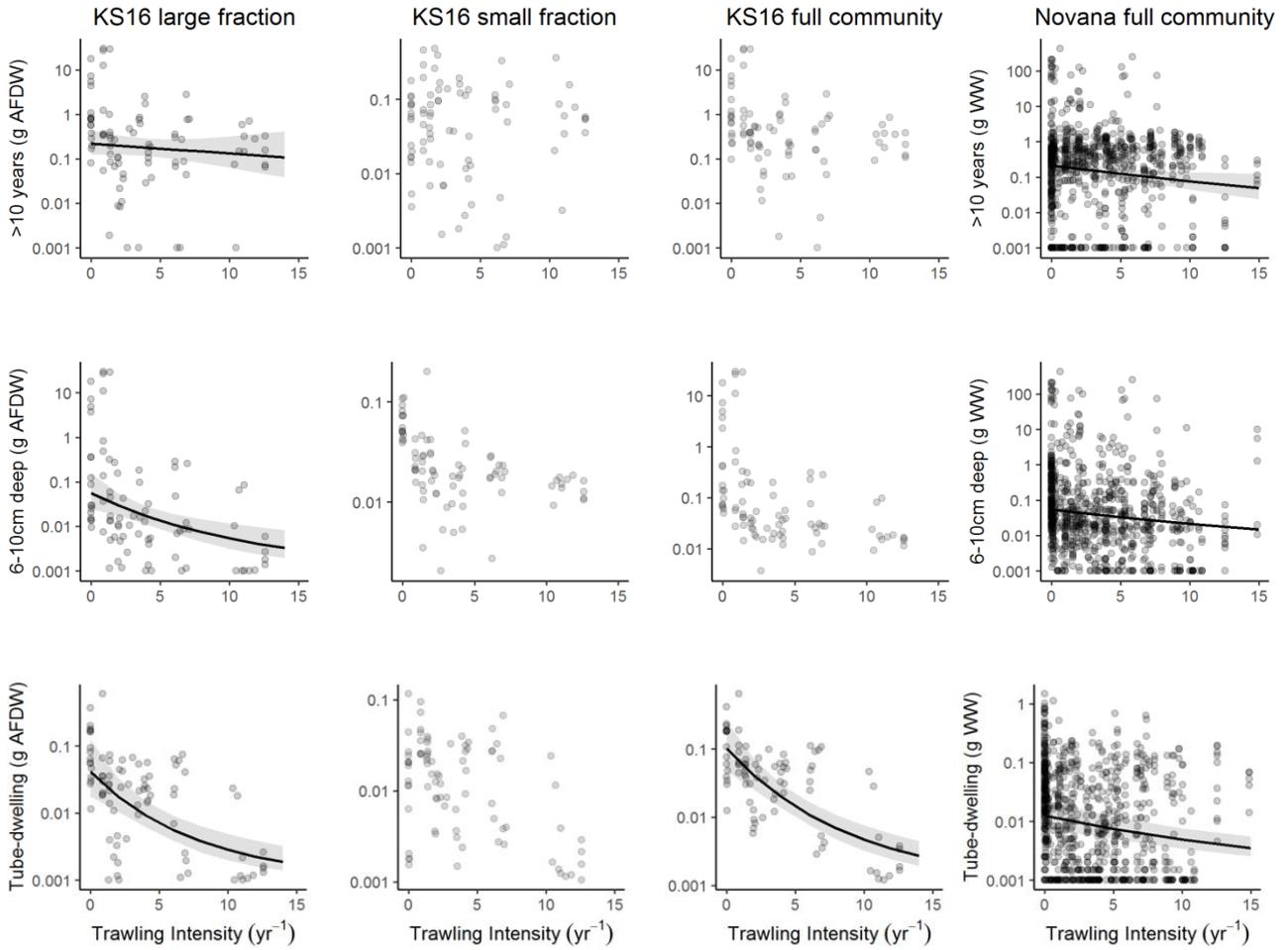
**Table 6-4. Summarised output of GLMMs of CWM traits. Significant relationships with trawling are denoted with a tick (✓). Significant relationships with other environmental variables are shown in the ‘Other’ column. Direction of the relationship is shown as positive (+) or negative (-). Model coefficients of determination ( $R^2$ ) are provided as conditional  $R^2$  values (marginal and random effects combined). All traits were modelled using a Tweedie distribution.**

Functional group	Trait modality	KS16 (2016)									NOVANA (2005 – 2013)		
		Large fraction			Small fraction			Full community			Full community		
		Trawling	Other	R2	Trawling	Other	R2	Trawling	Other	R2	Trawling	Other	R2
Food acquisition	Suspension	✓-	D-	0.69		S+, T-	0.48	✓-	D-	0.72		C+, M-	0.43
Recovery	Planktotrophic	✓-	D-	0.58		S-, T+	0.42	✓-	D-	0.61	✓-	C+, S+	0.41
	Sessile	✓-	D-	0.83	✓-	C-	0.74	✓-	D	0.82	✓-	C+, M+, S+, T-	0.90
	Sexual: eggs pelagic		D-, T-	0.58		S-, T+	0.40		C+, D-, T-	0.62		S+, T+	0.42
	Surface deposition	✓-	D-, T-	0.67		S-, T-	0.44	✓-	D-	0.69	✓-	C+, M-, S+	0.43
Resilience	>10 years	✓-	D-	0.70		D-	0.67		D-, T-	0.69	✓-	C+, D+, T+	0.41
	101-200mm		D-, T-	0.68		M-, S-	0.48		D-, T-	0.70		C+, M+	0.52
	Exoskeleton		C+, D-, T-	0.57		T+	0.52		D-, T-	0.61		C+, S+	0.29
Sediment stability	Infauna: 6-10cm	✓-	D-, T-	0.83		M-, S-	0.67		D-, T-	0.81	✓-	C+, D-, M-, S+	0.67
	Tube-dwelling	✓-	T-	0.80		M-, T-	0.81	✓-	T-	0.87	✓-	C+, M-, T-	0.82

*C = bottom current speed*  
*D = depth*  
*M = mud content*  
*T = bottom temperature*  
*S = bottom salinity*



**Figure 6-2. Relationships between trawling intensity and respective CWM traits (food acquisition and recovery) derived from the KS16 large, KS16 small, KS16 full fraction, and NOVANA datasets. Regression lines denote a significant relationship, and represent the predicted values from GLMMs presented in Table 6-4. Shaded areas represent 95% confidence intervals. The raw observations are overlaid as data points. To aid visual interpretation, CWM trait values are shown on a log scale.**



**Figure 6-3. Relationships between trawling intensity and respective CWM traits (resilience and sediment stability) derived from the KS16 large, KS16 small, KS16 full fraction, and NOVANA datasets. Regression lines denote a significant relationship, and represent the predicted values from GLMMs presented in Table 6-4. Shaded areas represent 95% confidence intervals. The raw observations are overlaid as data points. To aid visual interpretation, CWM trait values are shown on a log scale.**

## 6.4. Discussion

Trait-based approaches provide a promising method to understand the effect of chronic trawling disturbance on benthic macrofaunal communities. Although the Kattegat is one of the most heavily trawled areas in Europe (Eigaard et al., 2017), few studies have sought to investigate the functional implications of trawling in this region. Here, we describe the sensitivity of the benthic community to trawling by investigating the responsiveness of community-weighted mean (CWM) traits. Our results show that the traits of large benthic macrofauna are particularly sensitive to trawling impacts. Furthermore, the majority of these traits were shown to be highly responsive to trawling in separate time-series dataset. This may suggest that trait information gathered during a one-off sampling program may be suitable to use in the detection of chronic trawling impacts over longer timescales. In the following sections we discuss the sensitivity of benthic traits to trawling disturbance, and how changes in their biomass may affect ecosystem functioning.

### ***Indicators of trawling disturbance***

‘Sessile’ was an unusual trait in our analysis, in that it was highly responsive to trawling regardless of size fraction. Although several studies have demonstrated that large sessile benthos are sensitive to trawling (Kaiser et al. 2000, 2018, Sciberras et al. 2018), this observation provides evidence that both large and small sessile fauna are equally vulnerable to trawling impacts. Sessile fauna are functionally important members of the macrofauna. These fauna typically possess an exoskeleton or inhabit tubes or burrows, therefore creating important physical complexity in soft-sediment habitats. Allied to this, our results show that suspension feeders were also significantly impacted by trawling. Suspension feeders are often also non-mobile, and often have fragile feeding appendages. Trawling may also cause sediment resuspension which impacts suspension feeders indirectly by clogging feeding apparatus and effecting their ability to feed (Jennings & Kaiser 1998). Furthermore suspension feeders are important in regards to benthic-pelagic coupling in sedimentary environments (Griffiths et al. 2017). This can take the form of nutrient cycling via the transfer of organic material (phytoplankton, bacteria, particulate organic matter) to deeper sediments (Rosenberg 2001) or through the conversion of this material to benthic biomass which is an important food source for higher trophic levels (Hiddink et al., 2011; 2016). Tube-building organisms are also sessile by nature. Our results show that the unfished and lightly fished sites in both surveys were characterised by relatively high biomass tube-building maldanid polychaetes (e.g. *Rhodine gracilior* and *Maldane sarsi*), terebellid polychaetes (e.g. *Anobothrus gracilis*), and horseshoe worms (*Phoronis* sp.) Although trawling is known to reduce the abundance of polychaetes (Kenchington et al. 2006) and phoronid worms (Hinz et al. 2009), tube-building has not previously been commonly identified as sensitive trait in trawling impact studies. Tube-building macrofauna typically live at the sediment surface and require stable substrate to construct

tubes. Furthermore, few tube-building species are broadcast spawners and thus some exhibit low larval dispersal potential. As a result, tube-building polychaetes may be slow to recolonise areas after disturbance events, despite being relatively short-lived (Bolam & Fernandes 2002). Similarly to sessile and suspension feeders, tube-building macrofauna play an important role in benthic-pelagic coupling and in providing habitat which may promote taxonomic and functional diversity. Aggregations of tubicolous worm have been shown to actively support increased benthic diversity (Bolam, 1999), and benefit other species by improving sediment stability (Noji and Noji, 1991; Friedrichs et al., 2000). Furthermore, high densities of tubes have been shown to improve conditions for larval settlement (Bolam & Fernandes 2002), and promote increased food supply for associated benthic species (Holte 2001).

This combination of sessile, suspension feeding, and tube building traits may therefore point to a potential trait combination that may be relevant for the development of trait-based indicators. Species which share these traits are likely to experience both high direct and in-direct mortality rates, whilst the localised reproductive strategies of some species may suggest these fauna may be unable to recover between regular trawling events. This combination of traits also points to the sensitivity of *Haploops* sp., a tube building amphipod which has experienced large-scale declines across the Kattegat. *Haploops* sp. are recognised for their functional importance (Rigolet et al. 2014), and were once a dominant component of the macrofauna in the Kattegat at the beginning of the 1990s (Petersen, 1913). It has been previously suggested that the large-scale loss of these species from the area may be directly due to bottom trawling (Göransson, 1999, Josefson et al., 2018; Sköld *et al.*, 2018), although this has yet to be proven. Nevertheless, we are unable to discuss the sensitivity of this species as it was recorded at only a handful of stations across our datasets. This would suggest that the current distribution of *Haploops* sp. in the Kattegat is limited to such an extent that it can no longer act as an indicator of trawling disturbance.

In contrast to the traits discussed above, the responsiveness of long-lived macrofauna (>10 years) to trawling was chiefly accounted for by a single class of macrofauna. A longevity of >10 years is a relatively uncommon trait for high density species such as polychaetes, and this trait is more common in larger-bodied bivalves which often dominate estimates of biomass. Despite their hard external shells, marine bivalves often experience relatively high rates of trawling induced mortality (Bergman & Van Santbrink 2000). Species such as *Nucula nitidosa*, *Thyasira flexuosa*, and *Arctica islandica* contributed significantly to the biomass in unfished and lightly fished sites. *A. islandica*, although a periodically deep living bivalve, is highly sensitive to chronic trawling disturbance (Craeymeersch et al. 2000). Species such as *T. flexuosa* have relatively fragile shells and are sensitive to regular trawling impacts (Thrush et al. 1995, Ball et al. 2000). The sensitivity of long-lived fauna to disturbance is common across ecological groups (Begon 2006), and the longevity

distribution of benthic macrofauna has been shown to be an effective indicator of trawling disturbance (Rijnsdorp et al. 2018, Hiddink et al. 2018). Surface depositing bioturbators deposit faeces or egested particles at the sediment surface. This form of bioturbation is typical for a large number of bivalve and tube-building species. The sensitivity of this trait is likely due to its close association with the sediment-water interface, meaning that fauna sharing this trait are negatively impacted by bottom trawling (Van Denderen et al. 2015). Finally, the sensitivity of macrofauna with planktotrophic larval development is less intuitive. Although this trait can reflect an adaptation to variable environmental conditions (Paganelli et al. 2012), it was one of the most common traits in the datasets analysed in this study, and instead may reflect the general decline in biomass observed at the community level, rather than the sensitivity of particular species or taxonomic group.

### ***Effect of environmental variables***

The results of GLMMs based on the KS16 data revealed a strong effect of depth on trait biomass. Depth is recognised as an important structuring factor in the vertical distribution of benthic macrofaunal communities (Rosenberg 1995), and has previously been recognised as a significant predictor of marine benthic macrofaunal trait composition (Bremner et al. 2006b). Nevertheless, defining the mechanistic effects of depth is often difficult as depth can co-vary with several other environmental drivers, thus describing more than the effect of hydrostatic pressure alone. Depth in the Kattegat is likely to be related to food availability, due to the attenuation of light and organic matter during vertical transport. It has been suggested that trawling may exhibit an interactive effect with depth in the Kattegat (Pommer et al. 2016). Although this was not tested in the present study, this aspect may have important implications for the future research in fishing grounds which experience strong depth gradients. The relevance of this from a functional perspective is that as deep areas are likely to be more functionally sensitive to trawling than shallower areas (Bolam et al. 2017). Although temperature has been shown to be a significant driver of benthic trait composition in the Irish sea and English Channel (Bremner et al. 2006b), there is little research linking the effect of temperature to individual traits such as sessile or suspension feeding organisms. Temperature exhibited both positive and negative trends with the sensitive traits, which likely reflects the strong structuring effect of temperature (Rosenberg et al. 1992) and the locally variable temperatures associated with the transitional nature of the Kattegat.

### ***Conclusions***

The monitoring of ecological systems is often constrained by high ecosystem complexity, and there is a need to develop ecological indicators which effectively distil this information into easily interpreted and communicated measures of ecological impact and state. In this study we have demonstrated the sensitivity

of CWM traits as indicators of trawling disturbance, and outlined some of the mechanisms which may underpin their sensitivity. Our results indicate the benthic fauna which share sensitive traits e.g. sessile, suspension feeding, surface depositing, tube-dwelling and long longevity, are strongly impacted by chronic trawling disturbance. Given the importance of many of these traits in processes such as benthic-pelagic coupling and nutrient cycling, it is likely that the loss or decline of these traits will have considerable implications for the functioning of benthic ecosystems across fishing grounds. While trait-based approaches have the advantage of communicating information on how trawling may impact ecosystem function, there are currently few studies which have looked to empirically test these predictions. The separation of the KS16 data into small and large categories demonstrated that analysing only a subset of the full community can improve our ability to detect trawling, and supports the observations of McLaverty et al. (2020). The size-separation also allowed us to determine a group of traits which were highly sensitive to trawling over both spatial (KS16) and spatio-temporal (NOVANA) scales. The validation of our observations using the NOVANA data suggests that a carefully designed one-off sampling event can provide results which are representative of the information contained in long-term datasets.

### **Acknowledgements**

Thanks to the captains and crew on-board the DTU Aqua *RV Havfisken* for facilitating all aspects of field work. Thanks to the laboratory technicians for assistance in sediment analysis, biomass estimation, and the sorting benthic samples into higher taxonomic groups. The NOVANA data were extracted from the ODA database. Thanks to Daniel van Denderen for advice regarding the methods used in study. The work was funded by The Danish Fisheries Agency, Ministry of Environment and Food of Denmark, through the European Maritime and Fisheries Fund (EMFF) via the project “Udvikling af bæredygtig forvaltning af følsomme habitater og arter i Kattegat” (grant agreement number 33113-B-16-024) and DTU Aqua.

### **Supplementary information**

[See supplement below]

## References

- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER : t. *Guid to Softw Stat Methods* 1:186.
- Ball BJ, Fox G, Munday BW (2000) Long- and short-term consequences of a Nephrops trawl fishery on the benthos and environment of the Irish Sea. *ICES J Mar Sci* 57:1315–1320.
- Beauchard O, Veríssimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecol Indic* 76:81–96.
- Begon M (2006) *Ecology: From Individuals to Ecosystems*.
- Bergman MJN, Santbrink JW Van (2000) Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. In: *ICES Journal of Marine Science*.p 1321–1331.
- Blanchard F, LeLoc’h F, Hily C, Boucher J (2004) Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. *Mar Ecol Prog Ser* 280:249–260.
- Bolam SG, Eggleton JD (2014) Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. *J Sea Res* 88:47–58.
- Bolam SG, Fernandes TF (2002) Dense aggregations of tube-building polychaetes: Response to small-scale disturbances. *J Exp Mar Bio Ecol* 269:197–222
- Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, Kooten T van, Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Hoey G Van, Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar Environ Res* 126:1–13.
- Bolam, S, Eggleton J D., Garcia C, Kenny A J., Buhl-Mortensen L, Gonzalez G, Kooten T, Dinesen G., Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou K. N, Gumus A, Van Hoey G, Laffargue P, Eigaard O, Bastardie F (2014). Biological traits as functional indicators to assess and predict (using statistical models) the status of different habitats -. EU-FP7 Benthis Deliverable D3.4. <https://archimer.ifremer.fr/doc/00310/42140/>.
- Bolam, S.G., 1999. An investigation into the processes responsible for the generation of the spatial pattern of the spionid polychaete *Pygospio elegans* Clapare`de. PhD Thesis, Napier University, Edinburgh.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135.
- Bremner J, Frid CLJ, Rogers SI (2003) Assessing Marine Ecosystem Health: The long-term effects of fishing on functional biodiversity in North Sea benthos. In: *Aquatic Ecosystem Health and Management*. p 131–137
- Bremner J, Frid CLJ, Rogers SI (2005) Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? *Am Fish Soc Symp* 41:477–489.

- Bremner J, Rogers SI, Frid CLJ (2006a) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecol Indic* 6:609–622.
- Bremner J, Rogers SI, Frid CLJ (2006b) Matching biological traits to environmental conditions in marine benthic ecosystems. *J Mar Syst* 60:302–316.
- Brooks M E, Kristensen K, van Benthem K J, Magnusson A, Berg C W, Nielsen A, Skaug H J, Mächler M, and Bolker B M. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9: 378-400.
- Chevenet F, Doleadec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshw Biol* 31:295–309.
- Clarke KR, Gorley RN (2015) Primer v7:user manual/tutorial. PRIMER-E Ltd, Plymouth. [www.primer-e.com/primer 7 \\_ download.htm](http://www.primer-e.com/primer7_download.htm).
- Craeymeersch JA, Piet GJ, Rijnsdorp AD, Buijs J (2000) Distribution of macrofauna in relation to the micro-distribution of trawling effort. In: Kaiser MJ, de Groot SJ (eds) *Effects of fishing on non-target species and habitats*. Blackwell Science, Oxford, p 187–197.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop)* 36:27–46.
- Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O’Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sørensen TK, Tully O, Zengin M, Rijnsdorp AD (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J Mar Sci* 73:i27–i43.
- FAO (2003) *Fisheries management 2: The ecosystem approach to fisheries*. FAO Technical Guidelines for Responsible Fisheries (FAO, Rome), 4(Suppl 2):112.
- Feng C, Wang H, Lu N, Chen T, He H, Lu Y, Tu XM (2014) Log-transformation and its implications for data analysis. *Shanghai Arch Psychiatry*.
- Foster SD, Bravington M V. (2013) A Poisson–Gamma model for analysis of ecological non-negative continuous data. *Environ Ecol Stat* 20:533–552.
- Friedrichs M, Graf G, Springer B (2000) Skimming flow induced over a simulated polychaete tube lawn at low population densities. *Mar Ecol Prog Ser* 192:219–228.
- Griffiths JR, Kadin M, Nascimento FJA, Tamelander T, Törnroos A, Bonaglia S, Bonsdorff E, Brüchert V, Gårdmark A, Järnström M, Kotta J, Lindegren M, Nordström MC, Norkko A, Olsson J, Weigel B, Žydelis R, Blenckner T, Niiranen S, Winder M (2017) The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. *Glob Chang Biol* 23:2179–2196.

- Hiddink JG, Jennings S, Sciberras M, Bolam SG, Cambiè G, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Parma AM, Suuronen P, Kaiser MJ, Rijnsdorp AD (2018) Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J Appl Ecol* 56:1075–1084.
- Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci* 114:8301–8306.
- Hiddink JG, Johnson AF, Kingham R, Hinz H (2011) Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. *J Appl Ecol* 48:1441–1449.
- Hiddink JG, Moranta J, Balestrini S, Sciberras M, Cendrier M, Bowyer R, Kaiser MJ, Sköld M, Jonsson P, Bastardie F, Hinz H (2016) Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. *J Appl Ecol* 53:1500–1510.
- Hintzen NT, Bastardie F, Beare D, Piet GJ, Ulrich C, Deporte N, Egekvist J, Degel H (2012) VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fish Res* 115–116:31–43.
- Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: Chronic effects and experimental predictions. *Ecol Appl* 19:761–773.
- Holte B (2001) Possible ecological effects from maldanid (annelida, polychaeta) “super-dominance” in a small North Norwegian sill system. *Ophelia* 55:69–75.
- ICES. 2019. Interim Report of the Working Group on Fisheries Benthic Impact and Trade-offs (WGFBIT), 12–16 November 2018, ICES Headquarters, Copenhagen, Denmark. ICES CM 2018/HAPISG:21. 74 pp.
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol*:201–212.
- Josefson AB, Loo LO, Blomqvist M, Rolandsson J (2018) Substantial changes in the depth distributions of benthic invertebrates in the eastern Kattegat since the 1880s. *Ecol Evol*:1–13.
- Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14.
- Kaiser MJ, Hormbrey S, Booth JR, Hinz H, Hiddink JG (2018) Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. *J Appl Ecol* 55:1060–1070.
- Kaiser MJ, Ramsay K, Richardson CA, Spence FE, Brand AR (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. *J Anim Ecol* 69:494–503.
- Kenchington ELR, Gilkinson KD, MacIsaac KG, Bourbonnais-Boyce C, Kenchington TJ, Smith SJ, Gordon DC (2006) Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean. *J Sea Res* 56:249–270.

- Kjørboe T, Visser A, Andersen KH, Browman H (2018) A trait-based approach to ocean ecology. *ICES J Mar Sci* 75:1849–1863.
- Legendre P, Andersson MJ (1999) Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24.
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185.
- McLaverty C, Eigaard OR, Gislason H, Bastardie F, Brooks ME, Jonsson P, Lehmann A, Dinesen GE (2020) Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. *Ecol Indic* 110:105811.
- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends Ecol Evol* 28:167–177.
- Paganelli D, Marchini A, Occhipinti-Ambrogi A (2012) Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): A study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). *Estuar Coast Shelf Sci* 96:245–256.
- Petersen CGJ (1918) The sea bottom and its production of fish food. A survey of the work done in connection with the valuation of the Danish waters from 1883-1917. *Rep Danish Biol Station* 25: 1–62.
- Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E., Link, J., Livingston, P., Mangel, M., McAllister, M., Pope, J. & Sainsbury, K. (2004) Ecosystem-based fishery management. *Science*, 305:346–347.
- Pommer CD, Olesen M, Jhansen ØLS (2016) Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. *Mar Ecol Prog Ser* 548:47–60.
- Rigolet C, Dubois SF, Thiébaud E (2014) Benthic control freaks: Effects of the tubicolous amphipod *Haploopsis nirae* on the specific diversity and functional structure of benthic communities. *J Sea Res* 85:413–427.
- Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, Denderen PD van, Kooten T van (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol Appl* 28:1302–1312.
- Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. *Netherlands J Sea Res* 34:303–317.
- Rosenberg R (2001) Marine benthic faunal successional stages and related sedimentary activity. *Sci Mar* 65:107–119.
- Rosenberg R, Loo LO, Möller P (1992) Hypoxia, salinity and temperature as structuring factors for marine benthic communities in a eutrophic area. *Netherlands J Sea Res* 30:121–129.
- Sciberras M, Hiddink JG, Jennings S, Szostek CL, Hughes KM, Kneafsey B, Clarke LJ, Ellis N, Rijnsdorp AD, McConnaughey RA, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2018) Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish* 19:698–715.

Sköld M, Göransson P, Jonsson P, Bastardie F, Blomqvist M, Agrenius S, Hiddink JG, Nilsson HC, Bartolino V (2018) Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Mar Ecol Prog Ser* 586:41–55.

Svendsen, L.M. & Norup, B. (eds.) 2005: NOVANA. Nationwide Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments. Programme Description – Part 1. National Environmental Research Institute, Denmark. 53 pp. – NERI Technical Report No. 532.

Thrush SF, Hewitt JE, Cummings VJ, Dayton PK (1995) The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Mar Ecol Prog Ser* 129:141–150.

Van Denderen PD, Bolam SG, Hiddink JG, Jennings S, Kenny A, Rijnsdorp AD, Van Kooten T (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar Ecol Prog Ser* 541:31–43.

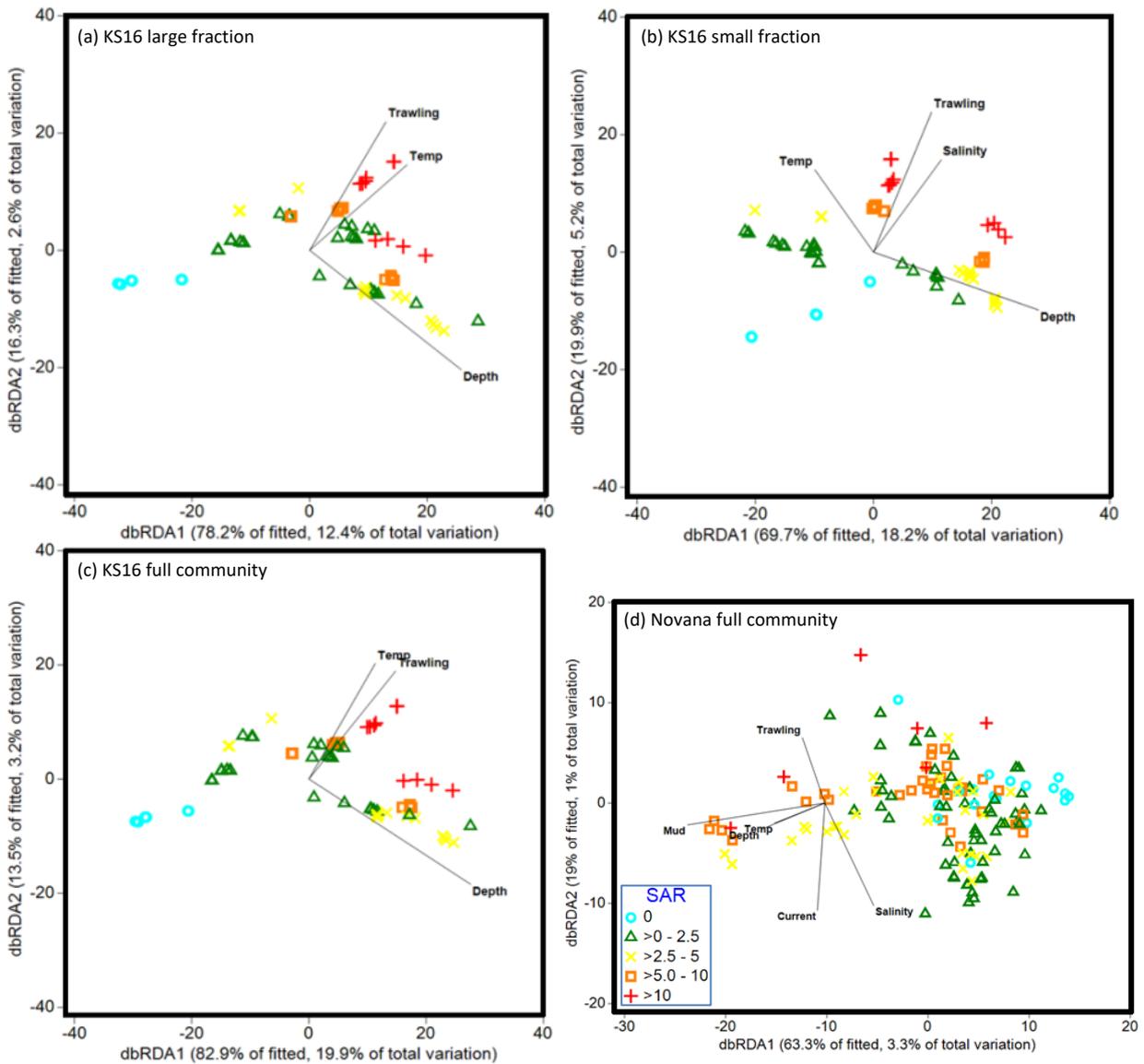
## Supplementary information

## The sensitivity of benthic life history traits to chronic trawling disturbance

**Table S1. Pair-wise correlations between the predictor variables used in the analyses of the KS16 NOVANA benthic fauna data. Values represent Pearson's R values and range between -1 and 1.**

KS16	Trawling	Mud	Depth	Current	Salinity
Mud	0.58813				
Depth	0.288834	0.475688			
Current	-0.38924	-0.3251	-0.32779		
Salinity	0.51561	0.378989	0.662901	-0.20062	
Temp	0.159995	-0.35519	-0.37505	0.020433	0.058533

NOVANA	Trawling	Mud	Depth	Current	Salinity
Mud	0.347546				
Depth	0.600782	0.690657			
Current	-0.17703	-0.16523	-0.19854		
Salinity	0.42274	0.349985	0.509452	-0.14439	
Temp	-0.23702	-0.24371	-0.56769	0.020077	-0.03251



**Figure S1.** Distance-based redundancy analysis (dbRDA) ordinations of trait composition, in the (a) KS16 large fraction, (b) KS16 small fraction, (c) KS16 full community, and (d) NOVANA datasets. Sampling stations are colour coded by their associated trawling intensity (SAR) category. The length and direction of the vectors indicate the relative effect of each predictor variable on the constrained ordination.

**Table S2. Multiple partial correlations correlation coefficients between predictor variables and dbRDA1 axes . Large fraction:  $\geq 4$  mm mesh size; small fraction: 1 – 4 mm mesh size.**

	dbRDA1	Pearson's R					
	Variance explained	Current	Depth	Mud	Salinity	Temp	Trawling
KS16 (full community)	19.91%		<b>0.82</b>			<b>0.34</b>	<b>0.41</b>
KS16 (small fraction)	18.22%		<b>0.83</b>		0.35	<b>-0.29</b>	<b>0.30</b>
KS16 (large fraction)	12.38%		<b>0.75</b>			<b>0.49</b>	<b>0.45</b>
Novana	3.29%	n/s	<b>0.37</b>	0.81	-0.29	<b>0.29</b>	<b>0.13</b>
Pearson correlation critical values: KS16 = 0.21   Novana = 0.07							

**Table S3. Summary output for generalised linear mixed models. The values shown are parameter estimates, and associated standard error (shown in brackets). The significance level is denoted by asterisks (\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ). Conditional  $R^2$  values describe the proportion of variance explained by both the fixed and random terms.**

KS 16 Full community	Intercept	Current	Depth	Mud	Salinity	Temperature	Trawling	$R^2$
>10	6.99 (2.52)		-0.05 (0.01)***			-0.69 (0.3)*		0.58
101-200mm	7.81 (2.51)		-0.04 (0.01)***			-0.82 (0.30)**		0.61
Exoskeleton (chitin/calcium carbonate)	5.94 (2.04)		-0.03 (<0.01)***			-0.55 (0.24)*		0.57
Infauna: 6-10cm	11.51 (3.23)		-0.08 (0.01)***			-1.33 (0.39)***		0.74
Planktotrophic	1.73 (0.37)		-0.02 (<0.01)**				-0.12 (0.04)**	0.47
Sessile	1.5 (0.51)		-0.03 (0.01)**				-0.35 (0.06)***	0.82
Sexual shed eggs-pelagic	4.68 (1.86)	0.39 (0.17)*	-0.03 (0.01)***			-0.51 (0.21)*		0.62
Surface deposition	1.7 (0.42)		-0.03 (<0.01)***				-0.15 (0.05)**	0.69
Suspension	1.34 (0.36)		-0.04 (<0.01)***				-0.12 (0.04)**	0.72
Tube-dwelling	3.70 (1.59)					-0.79 (0.21)***	-0.27 (0.04)***	0.84

KS16 Large fraction	Intercept	Current	Depth	Mud	Salinity	Temperature	Trawling	$R^2$
>10	1.49 (0.64)		-0.03 (0.01)*				-0.44 (0.08)***	0.45
101-200mm	9.75 (2.89)	0.89 (0.36)*	-0.05 (0.01)**			-1.08 (0.35)*		0.68
Exoskeleton (chitin/calcium carbonate)	6.24 (2.16)	0.40 (0.19)*	-0.03 (0.01)***			-0.70 (0.25)**		0.57
Infauna: 6-10cm	11.79 (4.01)		-0.08 (0.02)***			-1.30 (0.50)**	-0.31 (0.11)**	0.83
Planktotrophic	1.65 (0.45)		-0.03 (0.01)				-0.13 (0.05)*	0.58
Sessile	1.49 (0.64)		-0.03 (0.01)*				-0.44 (0.08)***	0.76
Sexual shed eggs-pelagic	9.28 (2.2)		-0.05 (0.01)***			-0.92 (0.27)***		0.55
Surface deposition	7.18 (2.47)		-0.05 (0.01)**			-0.67 (0.30)*	-0.13 (0.05)*	0.46
Suspension	1.38 (0.42)		-0.04 (0.01)**				-0.13 (0.05)*	0.69
Tube-dwelling	4.24 (1.85)					-0.93 (0.24)***	-0.27 (0.05)***	0.80

KS16 Small fraction	Intercept	Current	Depth	Mud	Salinity	Temperature	Trawling	R <sup>2</sup>
>10	-2.15 (0.46)		-0.02 (0.01)*					0.67
101-200mm	-2.51 (1.69)				-0.07 (0.04)*	0.31 (0.15)*		0.54
Exoskeleton (chitin/calcium carbonate)	-5.74 (1.4)					0.47 (0.18)**		0.52
Infauna: 6-10cm	1.13 (1.01)			-0.01 (<0.01)*	-0.14 (0.03)***			0.67
Planktotrophic	-2.42 (1.19)				-0.06 (0.02)**	0.35 (0.10)**		0.51
Sessile	-1.69 (0.31)	-0.23 (0.13)*					-0.21 (0.03)***	0.74
Sexual shed eggs-pelagic	-1.04 (1.04)				-0.08 (0.02)***	0.26 (0.09)**		0.40
Surface deposition	-2.09 (1.27)				-0.07 (0.03)**	0.29 (0.11)*		0.46
Suspension	-2.91 (1.72)				-0.09 (0.04)*	0.38 (0.16)*		0.48
Tube-dwelling	6.65 (2.08)			-0.02 (<0.01)***		-1.35 (0.26)***		0.81

NOVANA	Intercept	Current	Depth	Mud	Salinity	Temperature	Trawling	R <sup>2</sup>
>10	-6.07	0.37 (0.07)***	0.05 (0.01)***			0.37 (0.11)**	-0.09 (0.02)**	0.41
101-200mm	-2.54 (0.22)	0.32 (0.06)***		0.01 (<0.01)***				0.52
Exoskeleton (chitin/calcium carbonate)	-2.62 (0.51)	0.23 (0.06)***			0.05 (0.01)***			0.29
Infauna: 6-10cm	-6.81 (0.71)	0.31 (0.07)***	-0.05 (0.01)***	-0.01 (<0.01)***	0.18 (0.02)***		-0.11 (0.03)***	0.84
Planktotrophic	-2.39 (0.47)	0.21 (0.05)***			0.06 (0.01)***		-0.05 (0.02)*	0.41
Sessile	-0.16 (1.14)	0.35 (0.08)		0.03 (<0.01)***	0.09 (0.02)***	-0.56 (0.11)***	-0.09 (0.03)**	0.91
Sexual shed eggs-pelagic	-2.30 (0.47)				0.04 (0.01)***	0.25 (0.05)**		0.42
Surface deposition	-2.76 (0.51)	0.13 (0.05)*		-0.01 (<0.01)*	0.06 (0.01)***		-0.04 (0.02)*	0.43
Suspension	-1.67 (0.22)	0.27 (0.06)***		-0.01 (<0.01)**				0.43
Tube-dwelling	3.78 (0.78)	0.37 (0.06)***		-0.02 (<0.01)***		-1.09 (0.09)***	-0.12 (0.02)***	0.82

## Supplementary contributions

### Research papers:

Mildenberger, T. K., Omar, O. H., **McLavery, C.**, Jiddawi, N., & Wolff, M. (2018). Indicators of stock status for large-pelagic fish based on length composition from driftnet fisheries in Zanzibar. Western Indian Ocean Journal of Marine Science, 17(2), 51-65. DOI: 10.4314/wiojms.v17i2.5

### Master thesis:

Irene Sàez Devís (2018) Assessment of the ecosystem impacts of mussel fishing in Natura 2000 areas using underwater video techniques. *MSc thesis (C. McLavery co-supervisor)*

Katrina Bromhall (2018) To fish or not to fish; implications of mussel dredging for soft sediment benthic macrofauna. *MSc thesis (C. McLavery co-supervisor)*

## Appendices

### Appendix A: Bromhall et al

#### Using experimental trawling to assess the impact of mussel dredging on soft bottom benthic habitat (*In prep*)

Katrina Bromhall, Grete Dinesen, **Ciarán McLaverty**, Ole Eigaard, Jens Kjerulf Petersen and Camille Saurel

##### Abstract

Ecosystem-based fisheries management (EBFM) for bottom-contacting fisheries aims to account for the effect of fishing on the seabed habitats. In the Limfjord, Denmark, dredging for wild blue mussels (*Mytilus edulis*) occurs within Habitats Directives a Special Area of Conservation (SAC). To reduce the cumulative impact of the fishery on the seabed, strict spatial restrictions apply to mussel dredging activity within the SAC. Here we carried out a Before-After-Control-Impact (BACI) experiment to determine if experimental mussel dredging resulted in short term effects to the associated macrofauna. Using diver collected benthic samples our results confirm that dredging causes an immediate decline in the macrofaunal density and species richness within the direct footprint of the dredge (i.e. the dredge track). Macrofaunal density and species richness also decline, but to a lesser degree, in the areas immediately adjacent to the dredge tracks, indicating a larger area of impact than is currently estimated. After four months and subsequent to summer recruitment, species richness remained low in the fished site. Changes in the habitat conditions caused by physical disturbance are thought to reduce the recruitment success of certain species. Whilst the decline in macrofaunal density and species richness is undesirable, restricting the outcome to a small area has been deemed acceptable. Whereas underestimating the area of impact is may be more cause for concern, and of importance in reaching conservation goals.

## **Appendix B: Nielsen et al**

### **Management of bivalve fisheries in marine protected areas (*In prep*)**

Pernille Nielsen, Mette Møller Nielsen, **Ciarán McLaverty**, Kasper Kristensen, Kerstin Geitner, Jeppe Olsen, Camille Saurel, Anja Gadgaard Boye, and Jens Kjerulf Petersen

#### **Abstract**

Marine protected areas can often overlap with important fishing grounds. Within the European Union, the Natura 2000 is a network of nature protection areas, which consists of Special Areas of Conservation and Special Protection Areas designated under the Habitats Directive and Birds Directive, respectively. In Denmark, an innovative ecosystem-based approach to fisheries management has been applied to ensure the sustainability of bivalve fisheries in Natura 2000 sites and the conservation status of the designated sites. The main management strategies implemented has included the enforcement of mandatory monitoring systems on all vessels, a maximum of 15% cumulative fishery impacted area of ecosystem components (seagrass, macroalgae, benthic fauna), and a comprehensive research effort to provide high spatial resolution habitat mapping. We also describe several additional management benefits brought about by the implementation of an adaptive ecosystem-based approach. The results and lessons learned are discussed in the context of an ecosystem approach to bivalve fisheries management within the marine Natura 2000 sites.

## **Appendix C: Burgass et al**

### **Key considerations for biodiversity conservation in multilateral agreements (*Submitted to Conservation Letters*)**

Michael J. Burgass, Derek Tittensor, Cecilia Larossa, Hernan Caceres, Abbey Camaclang, Shannon Hampton, **Ciarán McLaverty**, Carolina M. Pinto, Victor K. Muposhi, Jessica Rowland, Simone Stevenson, Emily Nicholson, Kate Watermayer, and E.J. Milner-Gulland.

#### **Abstract**

It is nearly three decades since the world recognised the need for a global multilateral treaty aiming to address accelerating biodiversity loss. Despite the Convention on Biological Diversity (CBD) being adopted in 1992 and biodiversity being a central component of other multilateral agreements such as the Millennium and Sustainable Development Goals, biodiversity continues to decline at a concerning rate. If we are serious about protecting and restoring biodiversity, then actions will need to be wide-reaching in scope and geography – merely formulating new targets as updates of the existing targets is unlikely to create meaningful change. Here we focus on three key areas which can be of use for the development of the CBD Post-2020 Agenda; (i) Formulating robust theories of change to define agreed, adaptive plans for achieving each target; (ii) using models to evaluate assumptions and effectiveness of different plans and targets; and, (iii) identifying common but differentiated responsibilities of different actors/states/countries within these plans. We demonstrate how future multilateral agreements must not focus only on what needs to be done but also on how it should be done, using measurable steps which make sense at the scales at which biodiversity change happens.