The effect of modified and lightweight fishing gears on benthic macrofauna

Bromhall, Katrina

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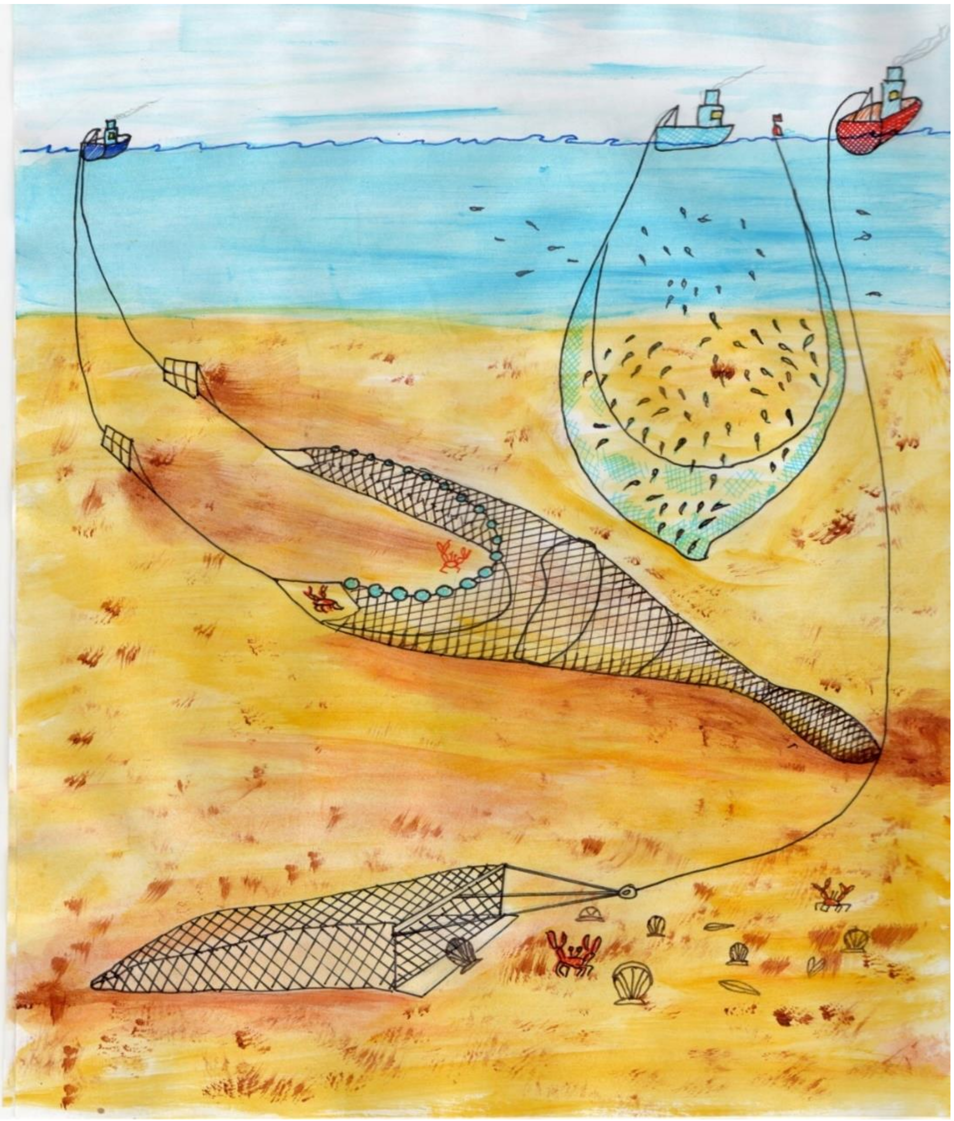
The effect of modified and lightweight fishing gears on benthic macrofauna

PhD Thesis

Katrina Bromhall



Supervisor: Ole Ritzau Eigaard. Co-supervisors: Grete Elisabeth Dinesen & Finbarr G. O' Neill.

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Illustrations by Neil Bromhall

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 (Section for Ecosystem Based Marine Mangement) and Professor Finbarr G. O'Neill (Section for Fisheries Technology). An external research project was carried with Professor Jan Geert Hiddink at Bangor University.

Funding for this PhD was provided by the European Marine Fisheries Fund, and the Danish Ministry of Environment and Food, and DTU Aqua, through the projects 'Sandbanker og fiskeripåvirkning i relation til EU's fiskeri-og miljøpolitik' and 'Development of benthic indicators for assessment of fisheries impacts on marine benthic fauna and habitats'. Travel and participation in international conferences and research stays were partly supported by a scholarship from the Anglo-Danish Society.

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Contents

Abstract

Fishing with bottom-towed gears represents the largest anthropogenic impact to benthic habitats. In order to mitigate further degradation, fisheries manager are adopting an Ecosystems Approach to Fisheries Management, in which the impact of trawling on the seabed and associated biota is taken into consideration. The magnitude of benthic impact from a single pass of a fishing gear can be attributed, in part, to the correlation between gear penetration depth and benthic faunal depletion rates. As such, bottom-towed gears that penetrate less deeply into the sediment are thought to cause less benthic mortality. The use of lighter-weight bottom-towed fishing gears has therefore been suggested as a potential solution to reduce benthic impact from conventional fishing gears, whilst retaining an active fishery. Thus, gear modifications have been developed, and interest into lightweight conventional gears has been stimulated. Some modified fishing gears have been adopted into Danish fisheries. However, quantification of the effects that modified and light weight gears have on benthic macrofauna is rather limited. Therefore, in order to support whether gear modifications have the potential to reduce benthic habitat damage, an assessment of their impact to benthic macrofauna is necessary. Here we examine the effect of three lightweight or modified bottom-towed fishing gears on benthic macrofauna. The results are presented in three research papers, which form the basis of this thesis

Research Paper 1: In Danish inshore waters, blue mussels (*Mytilus edulis*) are fished from wild stocks using a lightweight mussel dredge. In this chapter, we quantified the instantaneous impact of mussel dredging directly in the dredge track, the area adjacent to the track, as well as the short-term recovery after 4 months. Density and species richness was significantly reduced in the dredge track, and density significantly differed in the adjacent area. After 4 months, density and species richness remained affected, but signs of recovery may be indicated. No effect of dredging was observed on biomass in the dredge track, the adjacent area or over time.

Research Paper 2: In nearshore open coast, the Danish seine is used to catch mixed demersal fish species. The Danish seine is thought to impose very little physical impact to the seabed, as the footprint consist mainly (99%) of long ropes used to herd fish into the net, and only 1% from the ground gear and net. In this chapter, we quantified the effect of the two gear components of the Danish seine on benthic macrofauna. The impact on benthic fauna was examined after a single and multiple hauls of the Danish seine. We observed little effect of either the ropes or ground gear on benthic macrofaunal indicators.

However, for an individual taxa, the tube-building horseshoe worm, *Phoronis* spp, density was reduced by ~90% after multiple hauls of the Danish seine ropes.

Research Paper 3: On an offshore sandbank, the Dogger Bank, one of Denmark's largest fisheries targets sandeel (Ammodytes sp.) using otter trawls. In an effort to reduce the benthic impact, a modified sandeel otter trawl (SOT) was developed and tested. In this Chapter, we compared the benthic impact of conventional SOT with the modified SOT. The conventional SOT resulted in a greater reduction of benthic faunal biomass, specifically of the large-bodied fauna, living at the sediment surface, and also reduced the overal footprint by 33%. From these results, it would appear that by switching to the modified gear, the benthic impact of the sandeel fishery could be reduced.

Despite the relatively large losses in some components of the community, the modified gears generally exhibited small effects to seabed macrofauna and benefits to seabed habitats could be expected from replacing conventional gears with these lighter weight modified gears.

Dansk Resume

Fiskeri med bundslæbende redskaber, som f.eks. bundtrawl, udgør den største fysiske påvirkning af havbundens habitater fra menneskelige aktiviteter. For at minimere de uønskede effekter af fiskeriet anvendes der i forvaltningen en økosystemtilgang, hvor fiskeriets indvirkning på havbunden og de tilhørende organismer tages i betragtning. Den dødelighed, som fiskeriet påfører bunddyrene, afhænger i høj grad af hvor dybt redskabet trænger ned i havbunden, og derfor forårsager mindre tunge redskaber en lavere dødelighed. På den baggrund er udviklingen af lettere bundslæbende redskaber blevet foreslået som en mulighed for at reducere de negative effekter af konventionelt fiskeri, samtidig med at der bevares et aktivt fiskeri. Flere modificerede bundslæbende fiskeredskaber er allerede udviklet og implementeret i dansk fiskeri, men dokumentation og kvantificering af deres effekt er utilstrækkelig. Derfor er der et påtrængende behov for at få klarlagt og kvantificereret i hvilket omfang modifikationer af bundslæbende fiskeredskaber har potentiale til at reducere den uønskede påvirkning af havbundens levesteder. Her undersøger vi effekten af tre forskellige typer af modificerede bundslæbende redskaber på bunddyrssamfundene i hhv. kystnære og åbne havområder. Resultaterne præsenteres i tre forskningsartikler, som danner grundlag for denne afhandling.

Artikel 1: I de danske kystnære farvande og fjorde fiskes blåmuslinger (Mytilus edulis) fra vilde bestande i stigende grad med en modificeret letvægts-muslingeskraber. I dette kapitel har vi kvantificeret den umiddelbare påvirkning af bunddyr direkte i skrabesporet fra redskabet og i området ved siden af sporet, samt graden af genopretning fire måneder efter påvirkningen fra skraberen. Tætheden og artsrigdommen af bunddyr blev væsentligt reduceret i selve skrabesporet, mens kun tætheden blev reduceret i det tilstødende område. Efter fire måneder var tæthed og artsrigdom i sporet stadigt lavere end før fiskeripåvirkningen, men højere end umiddelbart efter påvirkningen. Der var ikke nogen signifikant effekt på den samlede biomasse, hverken i skrabesporet eller det tilstødende område, eller over tid.

Artikel 2: På den åbne kyst i Danmark anvendes snurrevod til fangst af bundlevende fisk som rødspætter og torsk. Snurrevoddet anses for at have en lille fysisk påvirkning af havbunden og lav effekt på bunddyrene, da redskabets fodaftryk primært afsættes af to meget lange reb, mens under en procent afsættes af et let bundgear under selve voddet. I dette kapitel har vi kvantificeret effekten af hver af de to forskellige redskabskomponenter på bunddyrene. Desuden blev effekterne estimeret efter både et enkelt og efter gentagne slæb med snurrevoddet. Vi observerede ingen effekt af hverken rebene eller

bundgearet på den samlede tæthed, biomasse eller artsrigdom af bunddyrene, men for en enkelt art, den rørbyggende hesteskoorm (Phoronis spp), blev tætheden reduceret med ~90% efter gentagne slæb med snurrevoddet.

Artikel 3: På det åbne hav, midt i Nordsøen, understøtter Dogger banke et af Danmarks største fiskerier, hvor der anvendes bundtrawl til fangst af tobis (Ammodytes sp.). I et forsøg på at reducere havbundspåvirkningen fra dette fiskeri, blev der udviklet og testet et modificeret letvægts-trawl. I dette kapitel sammenlignede vi bundpåvirkningen fra et konventionelt tobistrawl med påvirkningen fra det modificerede trawl. Den konventionelle trawl medførte en større reduktion af bentisk faunabiomasse end det modificerede trawl, som også havde et 33% mindre fodaftryk, og resultaterne viser, at man ved at skifte til det modificerede redskab kan reducere havbundspåvirkningen fra tobisfiskeriet.

På trods af relativt stor påvirkning af enkelte arter, udviste de modificerede redskaber generelt små effekter på bunddyrssamfundene som helhed og overordnet set må der forventes en reduktion i de uønskede effekter på havbunden ved at erstatte konventionelle redskaber med de undersøgte, modificerede redskaber.

1. Introduction

1.1. Bottom contacting fishing

Fishing with bottom-towed fishing gear (hereafter trawling) presents the largest anthropogenic pressure on the seafloor (Halpern et al., 2008). Yet, trawling is a socioeconomically and culturally important industry, which contributes one quarter of wild marine landings (FAO, 2010). The first description of trawling dates back to 1376, but by 1885 the first occurrences of habitat damage from trawling was being reported (Thurstan et al., 2010). Today, European fishing grounds are exposed to some of the highest trawling intensities worldwide (Amoroso et al., 2018), and accordingly have some of the most deteriorated seabed conditions (Pitcher et al., 2022). In order to address issues such as seabed degradation, and other negative ecological effects of fishing, an Ecosystems Approach to Fisheries Management (EAFM) has been adopted into European fisheries (Jennings and Rice, 2011). While an EAFM has improved the sustainability of fisheries where it has been adopted, it does not provide a silver-bullet solution. In this regard, an alternative and complimentary strategy to minimise the seabed impact of trawling, whilst maintaining an active fishery, is to use lightweight or modified fishing gears in place of commercial gears (McConnaughey et al., 2020; Suuronen et al., 2012).

1.2. Physical effect of fishing gear on seabed

In European fisheries the main types of bottom-towed gears are: otter trawls, beam trawls, dredges and seines (Figure 1). These gears are used to catch demersal fish species, crustaceans and molluscs (FAO, 2001). Otter trawls can be generally described as a large conical net towed along the seabed by a moving vessel. The net is kept open by two otter boards that stay in contact with the seabed. Otter trawls are deployed in most sedimentary habitat types (Kaiser et al., 2006), and for this reason numerous riggings and ground gears exist that target different species (Eigaard et al., 2016). Beam trawls mostly catch flatfish or crustaceans on sandy, muddy-sand habitats (Kaiser at al., 2006). They consist of a cone-shaped net held open by a metal bar (the beam), and typically include tickler chains that stirs up the sediment to encourage fish to swim into the net. Dredges are relatively small, and commonly used to harvest bivalves (shellfish), mostly in sandy, muddy-sand, or gravel habitats (Kaiser et al., 2006). A metal rectangular frame comprises the mouth of the dredge and mesh nets or chain bags contains the catch. As target species often live slightly submerged in the sediment, dredges are designed to dig into the seabed. Demersal seines (e.g. Danish seines) are used to catch flatfish on relatively homogenous sedimentary habitats. Danish seines differ from the aforementioned gears, in that the gear is pulled in by winch whilst the boat is anchored, instead of being actively towed by the vessel. The net of a Danish seine is conical, and is attached to long ropes on each wing (several hundred meters). The ropes are first laid on the seabed, and then hauled in to herd fish into the net from a relatively large area.

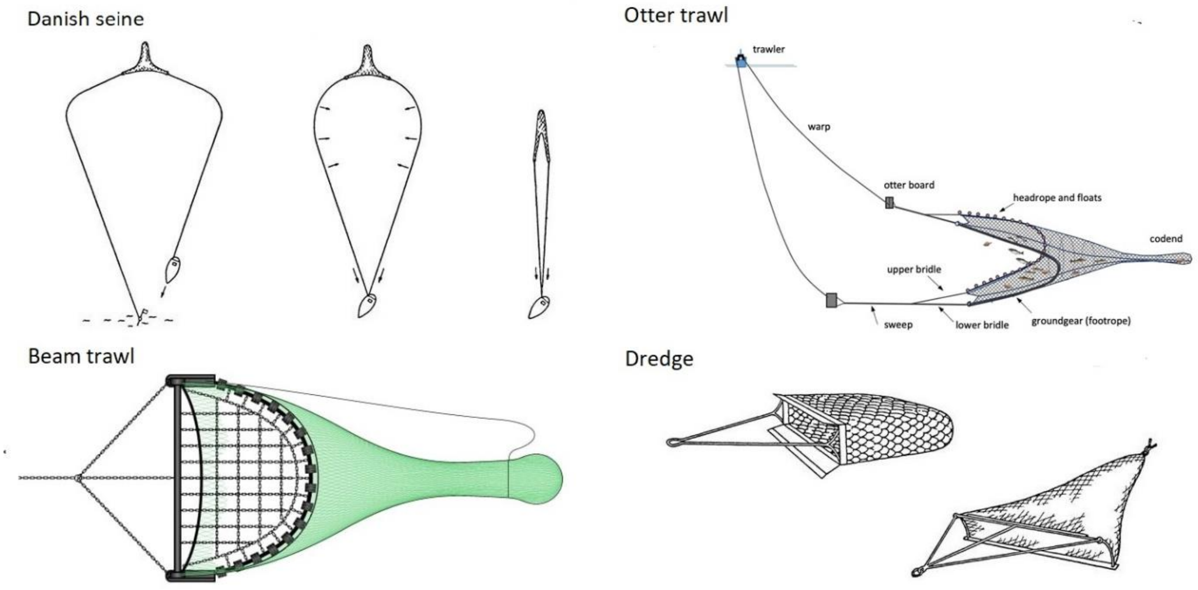


Figure 1: Commerically used bottom-contacting fishing gears: a Danish seine, an otter trawl, a beam trawl and a dredge. Illustrations from FAO: http://www.fao.org/fishery/geartype/search/en

The physical effect of these fishing gears on the seabed can be divided into surface and subsurface effects (Eigaard et al., 2016). Generally, beam trawls and dredges have relatively smaller footprints (i.e. the area directly impacted by the gear), but cause subsurface impacts as they are typically heavier and designed to dig into the sediment. Otter trawls and Danish seines have larger footprints, but the majority of the impact is at the surface level as they are designed to sweep the seabed. Nonetheless, the sweeping action may homogenise seabed features like sand ripples (Noack et al., 2019). Furthermore, otter trawls and Danish seines have a heterogeneous footprint, which arises from having different gear components, such as the sweeps, clumps, and nets, which vary in size and weight, and interact differently with the seabed. For example, the otter trawl doors can inflict some of the greatest impact on the seabed due to their weight and physical structure, resulting in depressions of up to 35cm in the sediment, but only make up approximately 1% of the total footprint (Eigaard et al., 2016).

Gear penetration, the action of fishing gears digging into the sediment, occurs as a result of the mechanical force exerted by the gear structure on the seabed. This action causes sediment to be displaced laterally (O’Neill and Ivanović, 2016) and results in distinctive tracks on the seabed. Gear penetration depth has been found to correlate closely with benthic faunal depletion, such that gears that penetrate deeper result in higher faunal depletion (Hiddink et al., 2017). In addition, fishing gears also mobilise sediment in their wake, due to the hydrodynamic effect of a heavy object moving through water (O’Neill and Ivanović, 2016). The re-suspended material alters water turbidity and can increase the nutrient concentration in the water column (Bradshaw et al., 2021) which has the potential to stimulate phytoplankton growth (Riemann and Hoffmann, 1991).

1.3. Fishing impacts on benthos

Marine sedimentary habitats constitute the largest habitat on earth (Snelgrove, 1998). Within these habitats live the benthic fauna, which are generally divided into infauna and epifauna. Infauna are composed of organisms that live in the sediment matrix, while epifauna live at or on the sediment surface. Benthic fauna exhibit great diversity, and their distribution over large spatial scales generally follow abiotic gradients, such as depth, sediment grain size, or temperature (Gislason et al., 2017; Rice et al., 2012). The close, and predictable, relationship with ambient environment conditions make benthic invertebrates ideal indicators of environmental conditions, and are therefore widely used in environmental monitoring and management (Gray et al., 2006). In addition to closely reflecting changes in their environment, their importance as indicators also arises from their key role in ecosystem function, where they directly shape the environment and support higher trophic levels. Their habitual activities drive key ecosystem processes. For example, the movement of a burrowing polychaete, on the search for food, oxygenates and irrigates the sediment; a tube-dwelling amphipod transports nutrients into the sediment by consuming particles at the surface, and excreting them at depth; a bivalve consumed by a bird provides a food source that sustains higher trophic levels. Communities of benthic fauna also facilitate large scale processes, such as nutrient regeneration, primary- and secondary production, and benthic-pelagic coupling, which can be termed as ecosystem services (Millennium Ecosystem Assessment, 2005).

Fishing with bottom contacting gear is well documented to negatively impact seabed biota, reducing benthic faunal density, species richness, and biomass (Collie et al., 2000; Hiddink et al., 2017; Kaiser et al., 2006; Sciberras et al., 2018). These activities affect seabed complexity by removing physical structures (boulders, large, sessile organisms) (Rijnsdorp and Vingerhoed, 2001), and homogenise the seabed. Bottom trawling can also diminish the quality of the habitat making it is less suitable for larval settlement (Piersma et al., 2001), weakening ecosystem resilience through a decrease in functional diversity (de Juan et al., 2007), and impairing ecosystem function by reducing biodiversity (Hooper et al., 2005).

Sensitivity to trawling impact varies between habitats. Habitats formed of large and long lived organisms such as biogenic reefs are generally more sensitive to trawling (Cook et al., 2013; Kaiser et al., 2006). On the other hand, habitats exposed to high levels of natural physical disturbance are often chiefly composed of small and short lived taxa (Lambert et al., 2017; van Denderen et al., 2015). Similarly, poorly sorted muddy or gravel sediments are considered relatively sensitive to trawling impacts, whilst well sorted, coarse sediments are less sensitive (Bolam et al., 2014; Kaiser and Spencer, 1996; Queirós et al., 2006).

Over time, bottom trawling can disproportionally remove larger and more sensitive organisms from a community, leading to chronically impacted fishing grounds appearing less sensitivity to trawling impact (Sciberras et al., 2018). In such circumstances, trawling can reduce ecosystem function, as large, attached, fragile fauna are removed and replaced with small motile scavenging fauna (Kenchington et al., 2007; Tillin et al., 2006). Due to their size, large organisms are particularly important to ecosystem function. Larger species are e.g. more effective at bioturbation, and ingest and excrete particulates at a higher rates (Solan et al., 2004). As a result, shifts in community dominance towards small-bodied taxa can have large consequences for ecosystem processes such as nutrients fluxes and benthic production (Solan et al., 2004; Thrush et al., 2006). In addition, the removal of sessile upright epifauna reduces the complexity of the seabed (Howarth et al., 2011), which in turn can negatively affect species diversity associated with these structures (Bradshaw et al., 2003).

1.4. Management – an ecosystems approach

In recognition of the degradation of natural ecosystems caused by commercial fisheries, a new way of managing fisheries emerged in the early 2000s. An Ecosystems Approach to Fisheries Management aims to sustainably manage fisheries by recognising the impacts on the environment and incorporating them into management plans (Pikitch et al., 2004). Given the extensive evidence of the impact of bottom trawling on benthos, and the need to balance an EAFM, the future for bottom-towed fishing is debated, and often a political matter (Kaiser, 2019). Some conservations groups have called for a complete ban of trawling in some circumstances, but the socio-economic consequence of such drastic measures make it unlikely to happen any time soon. As a result, fisheries managers have suggested multiple strategies to mitigate benthic habitat degradation from fishing (McConnaughey et al., 2020).

1.4.1. Spatial closures

Closing areas to damaging human impacts is the leading strategy to halt biodiversity loss (Worm, 2017). Since the 1960's, the number of Marine Protected Areas (MPAs) have increased exponentially, and currently 8% of the ocean is ‘protected’ (Worm, 2017). However, the success of MPA’s has been variable, and their pitfalls can often be traced back to a lack of funding or clear objectives (Worm, 2017). Prohibiting trawling in MPAs (hereafter termed spatial closures when referring to prohibited areas) creates a refuge for species and habitat alike. Within a few years of establishment, the density, biomass, average size, and diversity of organisms have been shown to increase inside spatial closures (Halpern, 2003). Over time, and with effective management, spatial closures can lead to the export of larvae, juveniles, and adults into nearby areas (Beukers-Stewart et al., 2005; Palumbi, 2004). This in turn may enhance the fishable stocks outside the closed area, known as spillover. Proximity to areas with high abundance and biomass of benthic fauna speeds up recovery time, suggesting spatial closures could also support the recovery of habitat exposed to trawling (Lambert et al., 2014). In addition to the considerable ecological benefits, spatial closures also provide a reference point for which the impact from trawling can be compared. This in turn allows for a more accurate estimate of impact (McLaverty et al., 2020), and facilitates sustainable fisheries management. Nonetheless, some disadvantages of spatial closures should be considered. Spatial closures that overlap with existing commercially important fishing grounds may lead to the displacement of fishing effort into previously unfished or low-level fished areas (Hiddink et al., 2006). Displacement into less suitable fishing grounds, may require higher fishing effort as catch rates may be reduced (McConnaughey et al., 2020) leading to an overall increase in the impact on the seabed. In addition, there can be economic costs associated with spatial closures (McConnaughey et al., 2020) such as fuel costs associated with increased distance to new fishing grounds, longer fishing hours, or reduced landings. Therefore, in some cases the use of alternative or supplementary management measures may be considered (Agardy et al., 2011).

1.4.2. Gear modifications

While spatial closures have many potential benefits, the extent and scale of such closures are limited by human activities in the marine environment (Agardy et al., 2011). In this regard, fishing gear modifications can provide a solution that potentially improves the condition of natural habitats, but does not significantly impinge on the productivity of the fishing industry. Unlike spatial closures, which provide more localised benefits through habitat protection, gear modifications reduce benthic impacts per unit effort (McConnaughey et al., 2020). Gear modifications have traditionally aimed to fine-tune the fishing process, and have largely focused on improving catch selectivity (Kennelly and Broadhurst, 2002). A well-known example of gear modifications are those for bycatch reduction. This has included modifications to the gear design of *Nephrops* trawls, whereby multiple sweeps are used to deter unwanted fish in the trawl, and escape panels for unwanted species. In more recent years, and in line with a greater focus on the ecosystem effects of fishing, gear modifications have been increasingly used to reduce the weight of the gear, and thus the overall seabed impact (Suuronen et al., 2012). Such modifications include alterations to the materials gears are fabricated from, and changes to gear configuration to reduce seabed disturbance e.g. pelagic otter trawl doors (Jørgensen and Valdemarsen, 2010). Additionally, simple modifications such as the addition of floats or bobbins can increase the buoyancy of gear, reducing gear penetration depth, or lift gear components off the seabed (Lindholm et al., 2014). While the development of less physically impacting gears has increased greatly, relatively little attention has yet been given to documenting how these modified gears affect the associated benthic macrofauna (Sciberras et al., 2018; Surronen et al., 2012).

1.4.3. Natura 2000 network

The EU is home to the largest coherent network of protected areas, known as the Natura 2000 network. In compliance with the Convention of Biological Diversity, the Nature Directives ('the Habitats Directive' and 'Bird Directive') set out to preserve and restore the habitats and species that are important to Europe's biodiversity. As authorities of the 28 Member states are fully responsible for managing sites in their jurisdiction, no general rules apply for Natura 2000 sites. This means each site is managed on an individual basis, determined by the habitat and species composition, and the socio-economic conditions. In some circumstances, spatial closures are included in management plans for Natura 2000 sites, and are mostly used to protect reef habitats (Species and Habitats Directive (92/43/EEC), Annex 1 Habitat 1170 (reefs) and Habitat 1180 (submarine structures made by leaking gases)) that are sensitive to fishing impact (European Environment Agency, 2013). 'Sandbanks' are a designated habitat under the Natura 2000 network. Despite this, sandbanks are regularly and widely fished in European waters. Whilst these features may appear superficially uniform, sandbanks are thought to exhibit physical and biological heterogeneity, with differences in benthic communities associated with the troughs and crests, as well as the sand waves and even small-scale-ripples (Mestdagh et al., 2020). Furthermore, they are known to host the biogenic reef forming species, such as the tube-building worm *Lanice conchilega*, which can positively benefit wider species diversity (Rabaut et al., 2008). However, these submerged, sandy features are not protected from bottom trawling. This is as they are primarily designated due to their importance to higher organisms (fish nursery areas and bird feeding grounds), as oppose to benthic macrofauna. The ecology of habitats such as sandbanks are, however, poorly described, and the associated impacts of trawling not well understood. This has the potential to be problematic for Danish fisheries, as several fishing grounds overlap with sandbanks in the Jammerbugt and Skagerrak, and in many areas of the North Sea. In these areas, and for many of these fisheries, there is a lack of available evidence regarding how fishing gears impact benthic fauna. Assessments of trawling impacts on sandbanks are therefore currently needed to meet these knowledge gaps, and in order for fisheries to implement an ecosystem approach to management.

1.5. Outline

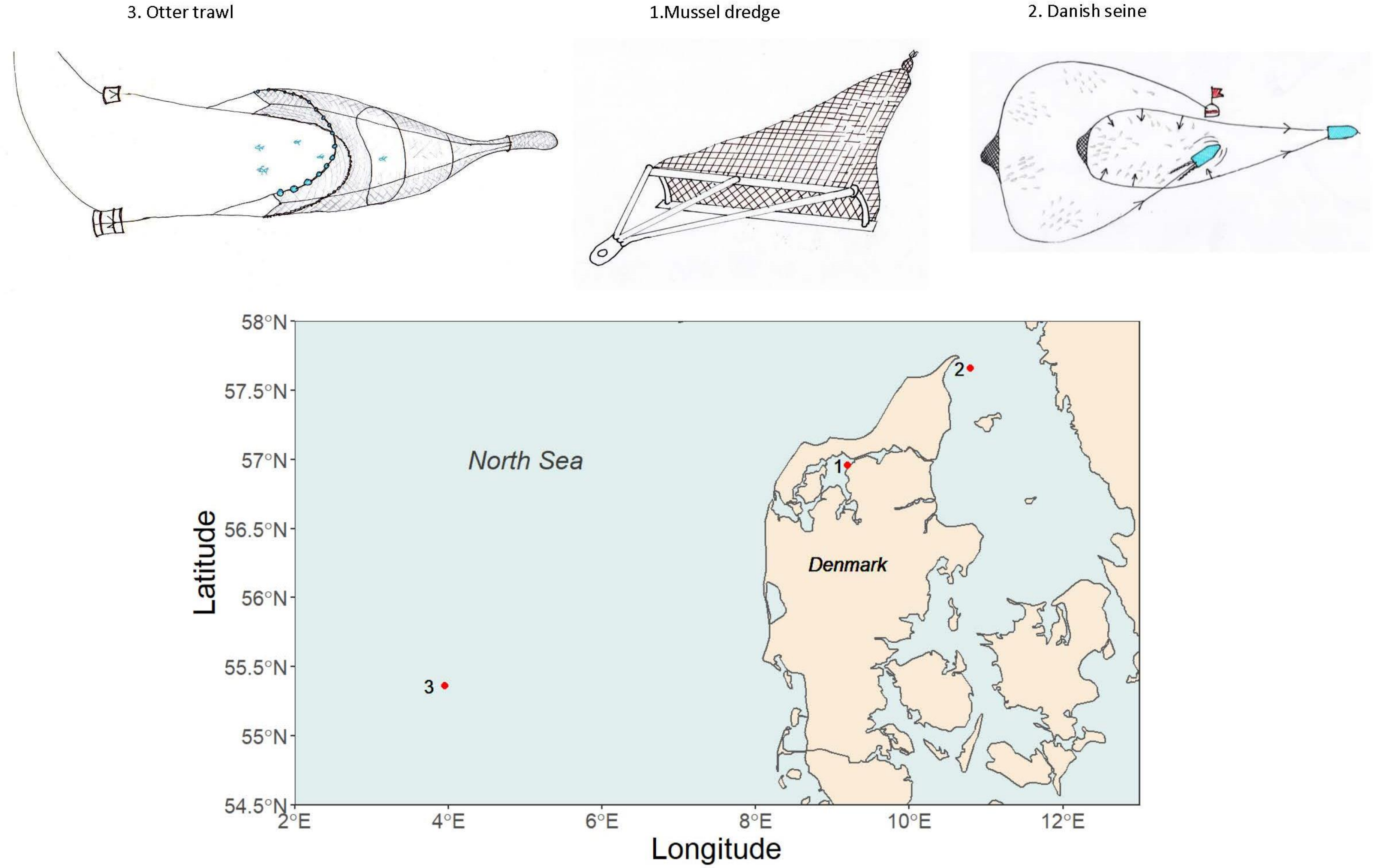
The need to reduce seabed degradation from trawling is no longer negotiable. One management strategy being explored is the use of lightweight or modified fishing gear as alternatives for the heavier conventional gears (McConnaughey et al., 2020). However, limited empirical evidence exists on the impact of such gears on benthic macrofauna. In this thesis, the benthic impact of three lightweight or modified fishing gears used by, or under testing for, commercial Danish fisheries are examined. In each case, the gears are evaluated in terms of their ability to reduce the impact of fishing gear on benthic macrofauna.

In a eutrophic coastal fjord system, blue mussels (*Mytilus mytilus*) are dredged from wild populations. A modified 'lightweight' mussel dredge was introduced into the blue mussel fishery in 2012, in line with the Danish Mussel Policy, as fishing grounds overlapped with Natura 2000 areas (Frandsen et al., 2015). In **Chapter 3 (Figure 2)**, we used experimental trawling to assess the effect of the lightweight mussel dredge on benthic macrofauna, using a Before-After-Control-Impact set up. We quantified the effect of dredging directly in the dredge track, and from areas immediately adjacent to the track. We followed up with sampling after 4-months to gain insights into recovery from dredging.

In nearshore open coast areas, the Danish seine fishery targets mixed demersal fish species. The relatively large and heterogeneous footprint of the Danish seine is thought to inflict a low seabed impact, as 90% of the trawl footprint is caused by relatively lightweight ropes. An interest has developed in the Danish seine as an alternative to more damaging gears (Suuronen et al., 2012). However, no empirical evidence exists to support the assumption that Danish seining results in low, or lower, seabed impacts. In **Chapter 4 (Figure 2)**, we quantify the effect of the Danish seine on benthic macrofaunal invertebrates. We separated the effect of the two gear components to improve the power of detect an effect from this expectedly low-impact fishing gear. We applied this approach in terms of a one-off impact (single haul), as well as for cumulative impacts (multiple hauls) using a BACI experimental design.

Moving to offshore sandbanks, the Dogger Bank is the location of Denmark's largest commercial fishery targeting sandeels (*Ammodytes sp.*)(Gislason et al., 2014). As an isolated, shallow, feature in the central North Sea, Dogger Bank supports a diversity of wildlife, where the viability of trawling has been questioned. In order to improve the sustainability of the fishery, a modified otter trawl that minimises the physical footprint on the seabed has been trailed. The modified design, made of lighter weight materials in the net and ground gear, floating sweeps, and pelagic trawl doors, has been shown to successfully reduce the footprint of the gear by 33%. However, it is not known how this reduced footprint translates in terms of impacts on benthic fauna. In **Chapter 5 (Figure 2)** we used a Control-Impact experimental design and compared the benthic macrofaunal impact of this modified sandeel otter trawl with the conventional sandeel otter trawl.

Across the three case studies, we applied different experimental setups, but consistently used targeted sampling of specific gear components or the gear tracks to capture potentially varying effects across the trawl footprint. This approach was followed to improve the resolution of our impact estimates, and contribute new evidence in regards the benthic impacts of the gear and their specific components. The results from this thesis can therefore support the future management of these fisheries, and also provide findings which are applicable in a wider EAFM context.



3. Otter trawl

1.Mussel dredge

2. Danish seine

Figure 2: Illustration of the fishing gears used in this thesis and a map of the North Sea and Danish waters where the studies took place.

References

Agardy, T., di Sciara, G.N., Christie, P., 2011. Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar. Policy 35, 226–232. https://doi.org/10.1016/j.marpol.2010.10.006

Amoroso, R.O., Pitcher, C.R., Rijnsdorp, A.D., McConnaughey, R.A., Parma, A.M., Suuronen, P., Eigaard, O.R., Bastardie, F., Hintzen, N.T., Althaus, F., Baird, S.J., Black, J., Buhl-Mortensen, L., Campbell, A.B., Catarino, R., Collie, J., Cowan, J.H., Durholtz, D., Engstrom, N., Fairweather, T.P., Fock, H.O., Ford, R., Gálvez, P.A., Gerritsen, H., Góngora, M.E., González, J.A., Hiddink, J.G., Hughes, K.M., Intelmann, S.S., Jenkins, C., Jonsson, P., Kainge, P., Kangas, M., Kathena, J.N., Kavadas, S., Leslie, R.W., Lewis, S.G., Lundy, M., Makin, D., Martin, J., Mazor, T., Gonzalez-Mirelis, G., Newman, S.J., Papadopoulou, N., Posen, P.E., Rochester, W., Russo, T., Sala, A., Semmens, J.M., Silva, C., Tsolos, A., Vanelslander, B., Wakefield, C.B., Wood, B.A., Hilborn, R., Kaiser, M.J., Jennings, S., 2018. Bottom trawl fishing footprints on the world's continental shelves. Proc. Natl. Acad. Sci. 115, E10275–E10282. https://doi.org/10.1073/pnas.1802379115

Beukers-Stewart, B., Vause, B., Mosley, M., Rossetti, H., Brand, A., 2005. Benefits of closed area protection for a population of scallops. Mar. Ecol. Prog. Ser. 298, 189–204. https://doi.org/10.3354/meps298189

Bolam, S.G., Coggan, R.C., 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. https://doi.org/10.1016/j.seares.2013.05.003

Bradshaw, C., Collins, P., Limited, B.S., Brand, A.R., 2003. To what extent does upright sessile epifauna affect benthic biodiversity and community composition? Mar. Bio. 4, 783-791. https://doi.org/10.1007/s00227-003-1115-7

Bradshaw, C., Jakobsson, M., Brüchert, V., Bonaglia, S., Mörth, C.M., Muchowski, J., Stranne, C., Sköld, M., 2021. Physical Disturbance by Bottom Trawling Suspends Particulate Matter and Alters Biogeochemical Processes on and Near the Seafloor. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.683331

Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. J. Anim. Ecol. 69, 785–798.

Cook, R., Fariñas-Franco, J.M., Gell, F.R., Holt, R.H.F., Holt, T., Lindenbaum, C., Porter, J.S., Seed, R., Skates, L.R., Stringell, T.B., Sanderson, W.G., 2013. The Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A Dilemma for Evidence-Based Conservation. PLoS One 8, e69904. https://doi.org/10.1371/journal.pone.0069904

de Juan, S., Demestre, M., 2007. Effects of commercial trawling activities on benthic communities in a fishing ground from the NW Mediterranean Sea. Dep. Ecol. 334, 158 pp. https://doi.org/https://doi.org/10.1016/j.marpol.2008.11.005

Eigaard, O.R., Bastardie, F., Breen, M., Dinesen, G.E., Hintzen, N.T., Laffargue, P., Mortensen, L.O., Nielsen, J.R., Nilsson, H.C., O'Neill, F.G., Polet, H., Reid, D.G., Sala, A., Sköld, M., Smith, C., Sørensen, T.K., Tully, O., Zengin, M., Rijnsdorp, A.D., 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. 73, i27–i43. https://doi.org/10.1093/icesjms/fsv099

European Environment Agency. 2013. 1180 Submarine structures made by leaking gases, Report under the Article 17 of the Habitats Directive Period 2007-2017 [Online] Available at: https://forum.eionet.europa.eu/habitat-art17report/library/2007-2012-reporting/factsheets/habitats/coastal-habitats/1180-submarine-structures-made-leaking-gases/download/en/1/1180-submarine-structures-made-by-leaking-gases.pdf

European Commission, 2003. Directive 2003/6/EC of the European Parliament and the Council. Off. J. Eur. Union 22–142. https://doi.org/2004R0726 - v.7 of 05.06.2013

FAO. 2001. Fishing gear types. Technology fact sheets. In: FAO Fisheries and Aquaculture Department [Online].Available at: http://www.fao.org/fishery/ geartype/search/en

FAO. 2010. Total World Fisheries. The State of World Fisheries and Aquaculture, 10.

Frandsen, R.P., Eigaard, O.R., Poulsen, L.K., 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. https://doi.org/10.1002/aqc.2455

Gislason, H., Bastardie, F., Dinesen, G.E., Egekvist, J., Eigaard, O.R., 2017. Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. Ecol. Indic. 82, 260-270. https://doi.org/10.1016/j.ecolind.2017.07.004

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 Report.

Gray, J.S., Dayton, P., Thrush, S., Kaiser, M.J., 2006. On effects of trawling, benthos and sampling design. Mar. Pollut. Bull. 52, 840–843. https://doi.org/10.1016/j.marpolbul.2006.07.003

Halpern, B.S., 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecol. Appl. 13, S117–S137. https://doi.org/https://doi.org/10.1890/1051-0761(2003)013[0117:TIOMRD]2.0.CO;2

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A Global Map of Human Impact on Marine Ecosystems. Science. 319, 948–952. https://doi.org/10.1126/science.1149345

Hiddink, J.G., Hutton, T., Jennings, S., Kaiser, M.J., 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. https://doi.org/10.1016/j.icesjms.2006.02.006

Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proc. Natl. Acad. Sci. 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35. https://doi.org/10.1890/04-0922

Howarth, L.M., Wood, H.L., Turner, A.P., Beukers-Stewart, B.D., 2011. Complex habitat boosts scallop recruitment in a fully protected marine reserve. Mar. Biol. 158, 1767–1780. https://doi.org/10.1007/s00227-011-1690-y

Jennings, S., Rice, J., 2011. Towards an ecosystem approach to fisheries in Europe: A perspective on existing progress and future directions. Fish Fish. 12, 125–137. https://doi.org/10.1111/j.1467-2979.2011.00409.x

Jørgensen, B.T., Valdemarsen, J.W., 2010. Pelagic trawling for cod. Inst. Mar. Res. Havforkningsinstitutet. 5, 5–6.

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. https://doi.org/10.3354/meps311001

Kaiser, M.J., 2019. Recent advances in understanding the environmental footprint of trawling on the seabed. Can. J. Zool. 762, 755–762. https://doi.org/10.1139/cjz-2018-0248

Kaiser, M.J., Spencer, B.E., 1996. The Effects of Beam-Trawl Disturbance on Infaunal Communities in Different Habitats. J. Anim. Ecol. 3, 348-358. https://doi.org/10.2307/5881

Kenchington, E.L., Kenchington, T.J., Henry, L.A., Fuller, S., Gonzalez, P., 2007. Multi-decadal changes in the megabenthos of the Bay of Fundy: The effects of fishing. J. Sea Res. 58, 220–240. https://doi.org/10.1016/j.seares.2007.04.001

Kennelly, S.J., Broadhurst, M.K., 2002. By-catch begone: Changes in the philosophy of fishing technology. Fish Fish. 3, 340–355. https://doi.org/10.1046/j.1467-2979.2002.00090.x

Lambert, G.I., Jennings, S., Kaiser, M.J., Davies, T.W., Hiddink, J.G., 2014. Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. J. Appl. Ecol. 51, 1326–1336. https://doi.org/10.1111/1365-2664.12277

Lambert, G.I., Murray, L.G., Hiddink, J.G., Hinz, H., Lincoln, H., Hold, N., Cambiè, G., Kaiser, M.J., 2017. Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance. Sci. Rep. 7, 5440. https://doi.org/10.1038/s41598-017-04715-4

Lindholm, J., Gleason, M., Kline, D., Clary, L., Rienecke, S., Cramer, A., Los Huertos, M., 2014. Ecological effects of bottom trawling on the structural attributes of fish habitat in unconsolidated sediments along the central California outer continental shelf. Fish. Bull. 113, 82–96. https://doi.org/10.7755/FB.113.1.8

McConnaughey, R.A., Hiddink, J.G., Jennings, S., Pitcher, C.R., Kaiser, M.J., Suuronen, P., Sciberras, M., Rijnsdorp, A.D., Collie, J.S., Mazor, T., Amoroso, R.O., Parma, A.M., Hilborn, R., 2020. Choosing best practices for managing impacts of trawl fishing on seabed habitats and biota. Fish Fish. 21, 319–337. https://doi.org/10.1111/faf.12431

McLaverty, C., Eigaard, O.R., Dinesen, G.E., Gislason, H., Kokkalis, A., Erichsen, A.C., Petersen, J.K., 2020. High-resolution fisheries data reveal effects of bivalve dredging on benthic communities in stressed coastal systems. Mar. Ecol. Prog. Ser. 642, 21–38. https://doi.org/10.3354/meps13330

Mestdagh, S., Amiri-Simkooei, A., van der Reijden, K.J., Koop, L., O'Flynn, S., Snellen, M., Van Sluis, C., Govers, L.L., Simons, D.G., Herman, P.M.J., Olff, H., Ysebaert, T., 2020. Linking the morphology and ecology of subtidal soft-bottom marine benthic habitats: A novel multiscale approach. Estuar. Coast. Shelf Sci. 238, 106687. https://doi.org/10.1016/j.ecss.2020.106687

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis World Resources Institute, Washington, DC

Noack, T., Stepputtis, D., Madsen, N., Wieland, K., Haase, S., Krag, L.A., 2019. Gear performance and catch process of a commercial Danish anchor seine. Fish. Res. 211, 204–211. https://doi.org/10.1016/j.fishres.2018.11.012

O'Neill, F.G., Ivanović, A., 2016. The physical impact of towed demersal fishing gears on soft sediments. ICES J. Mar. Sci. 73, i5–i14. https://doi.org/10.1093/icesjms/fsv125

Palumbi, S.R., 2004. Marine reserves and ocean neighborhoods: The Spatial Scale of Marine Populations and Their Management. Annu. Rev. Environ. Resour. 29, 31–68. https://doi.org/10.1146/annurev.energy.29.062403.102254

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., Essink, K., 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. J. Appl. Ecol. 38, 976–990. https://doi.org/10.1046/j.1365-2664.2001.00652.x

Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-Based Fishery Management. Science. 305, 346–347. https://doi.org/10.1126/science.1098222

Pitcher, C.R., Hiddink, J.G., Jennings, S., Collie, J., Parma, A.M., Amoroso, R., Mazor, T., Sciberras, M., McConnaughey, R.A., Rijnsdorp, A.D., Kaiser, M.J., Suuronen, P., Hilborn, R., 2022. Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. Proc. Natl. Acad. Sci. 119. e2109449119. https://doi.org/10.1073/pnas.2109449119

Queirós, A.M., Hiddink, J.G., Kaiser, M.J., 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. https://doi.org/10.1016/j.jembe.2006.03.001

Rabaut, M., Braeckman, U., Hendrickx, F., Vincx, M., Degraer, S., 2008. Experimental beam-trawling in Lanice conchilega reefs: Impact on the associated fauna. Fish. Res. 90, 209–216. https://doi.org/10.1016/j.fishres.2007.10.009

Rice, J., Arvanitidis, C., Borja, A., Frid, C., Hiddink, J.G., Krause, J., Lorance, P., Ragnarsson, S.Á., 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. https://doi.org/10.1016/j.ecolind.2011.03.021

Riemann, B., Hoffmann, E., 1991. Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark 69, 171–178.

Rijnsdorp, A.D., Vingerhoed, B., 2001. Feeding of plaice Pleuronectes platessa L. and Sole Solea solea (L.) in relation to the effects of bottom trawling. J. Sea Res. 45, 219–229. https://doi.org/10.1016/S1385-1101(01)00047-8

Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish Fish. 19, 698–715. https://doi.org/10.1111/faf.12283

Snelgrove, P.V.R., 1998. The biodiversity of macrofaunal organisms in marine sediments. Biodivers. Conserv. 7, 1123–1132. https://doi.org/10.1023/A:1008867313340

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and Ecosystem Function in the Marine Benthos. Science. 306, 1177–1180. https://doi.org/10.1126/science.1103960

Suuronen, P., Chopin, F., Glass, C., Løkkeborg, S., Matsushita, Y., Queirolo, D., Rihan, D., 2012. Low impact and fuel efficient fishing-Looking beyond the horizon. Fish. Res. 119–120, 135–146. https://doi.org/10.1016/j.fishres.2011.12.009

Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A., 2006. Functional Role of Large Organisms in Intertidal Communities: Community Effects and Ecosystem Function. Ecosystems 9, 1029–1040. https://doi.org/10.1007/s10021-005-0068-8

Thurstan, R.H., Brockington, S., Roberts, C.M., 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat. Commun. 1, 15. https://doi.org/10.1038/ncomms1013

Tillin H.M, Hiddink J.G, Jennings S, Kaiser M.J, 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 284–286. https://doi.org/10.3354/meps318031 van Denderen, P., Bolam, S., Hiddink, J., Jennings, S., Kenny, A., Rijnsdorp, A., 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. https://doi.org/10.3354/meps11550

Worm, B., 2017. How to heal an ocean. Nature 543, 630–631. https://doi.org/10.1038/nature21895

2. Methods

2.1. Experimental trawling

A prerequisite to understanding human effects on the environment is an assessment that can isolate human effects from background natural variation. There are many challenges in this pursuit, and hence a number of experimental designs have been proposed. Measuring the effects of bottom-towed fishing gears from field observations poses similar challenges. One of the main challenges is that benthic invertebrate assemblages, which are used as the indicators of fishing impact, vary naturally in space and time (Currie and Parry, 1996; Kaiser and Spencer, 1996). This variation can be a product of local distributions, predator-prey interactions, or the effect of environmental pressures, such as physical disturbance caused by waves (Ellis et al., 2000). This means that the choice of location, and the placement of treatment areas, are important considerations for experimental trawling studies. For example, if one was to compare disturbed and undisturbed samples from two locations in a 'Control-Impact' design at one point in time (Figure 1 A), this assumes that there were no major natural differences between the two locations prior to fishing (i.e. minimal spatial variance). Similarly, if one were to gather samples before and after a disturbance, in Before-After design (Figure 1 B), this assumes that no major differences occured over time aside from arising from the introduced disturbance (i.e. minimal temporal variance). While these experimental set-ups are valid, and have been used herein (Chapter 5) and in a large number of experimental trawling studies (Sciberras et al., 2018), more robust designs can be applied, if resources allow.

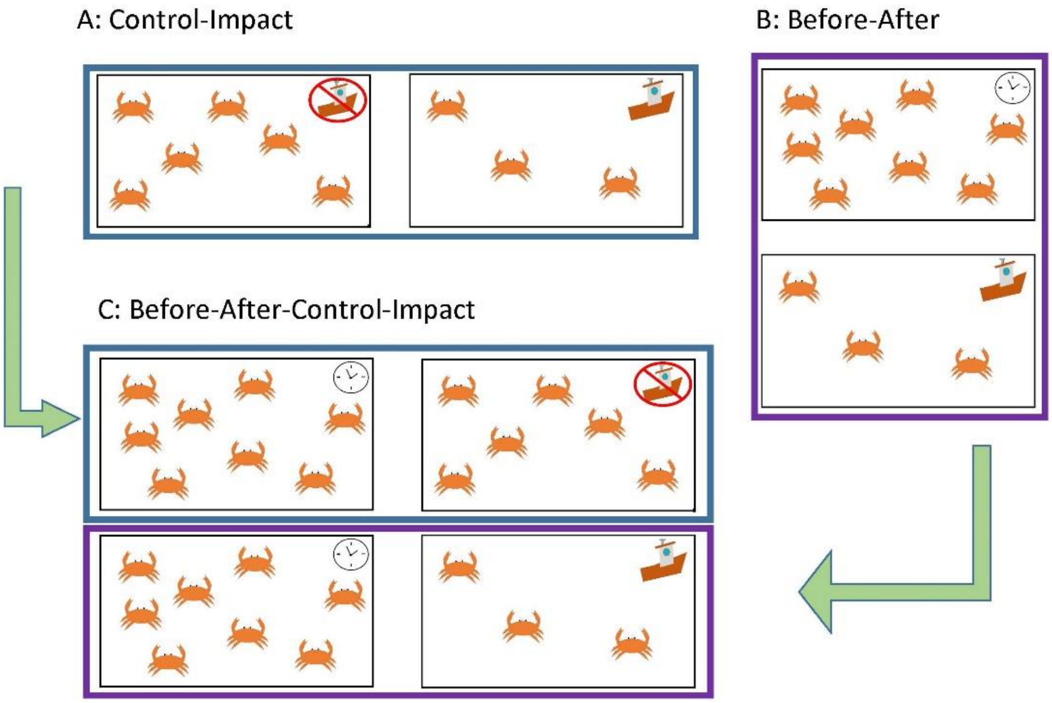


Figure 1: Conceptualisation of three experimental designs.

2.2. Before-After-Control-Impact

The Before-After-Control-Impact (BACI) design includes both temporal and spatial sampling controls (Green, 1979) (Figure 1 C). It is a factorial design which determines whether an impact has taken place based on the significance of an interaction between time (e.g., before, after) and treatment (e.g. control, impact) (Green, 1979). A significant interaction occurs when a change over time (determined by the slope between before and after experimental disturbance) differs in the control and impact treatment. The BACI design is typically the preferred method used in environmental monitoring or assessment studies (Smokorowski and Randall, 2017). However, its strengths and weaknesses have been subject to much debate. The basic BACI design has been criticised for the inclusion of only a single treatment site (control and impact), and a single time (before and after) (Hulbert 1984; Underwood 1992). It was argued that the impact site was not random and therefore subject to objectivity, and a lack of replicate 'treatments' (i.e. multiple impact/control sites) resulted in 'pseudoreplication' (Hurlbert, 1984). Stewart-Oatsen (1986) contested this, and highlighted that it is not always reasonable, or possible, to have multiple impact sites (he took the example of building power plants) and suggested that in order to negate pseudoreplication, sampling should be replicated in time. To put it simply, this means sampling multiple times before and multiple times after impact, in an approach known as BACIPS (Before-After-Control-Impact-Paired Sites). To quantify differences between treatments, a comparison of the mean response can be made for the 'before' and 'after' samples. Underwood (1992) argued that this method still risked wrongful inference, as for example, benthic indicators from a single control site could naturally have a different trajectory, and this could be interpreted as a human disturbance. He went on to describe a sampling design which includes sampling multiple times before and after, and multiple controls, a designed he called 'Beyond BACI'. The Beyond BACI is likely the most robust BACI design, and confidence can be had in the results. However, a significant drawback to this approach is the extensive resources needed to sample at numerous time intervals and across multiple treatments. Furthermore, the complexity of the design has the potential to introduce large variance to the data, meaning that true effects can go undetected (Hewitt et al., 2001). For these reasons, it is conceivable that some aspects of the design are often conceded upon. For example, in a particularly large-scale BACI experiment undertaken by Lambert et al. (2017), the design included four controls and 13 different impact treatments (fishing intensities), but sampling only took place at three time intervals (once before, three days after, and again 4 months later). This suggests that even the larger-scale experiments also require some level of compromise in the design, in order to be practical.

In this thesis, a combination of BACI and Control-Impact designs were used to measure the effects of trawling on benthic macrofauna using direct field observations. In Chapter 3, we applied a BACI using a single control and single impact site to evaluate the effect of mussel dredging on benthic macrofauna. The sampling design included three sampling times, once before dredging, an after (3-days) to measure the immediate impact, and an after (4-months) to assess recovery. In Chapter 4, we conducted a BACI sampling design to evaluate the effect of the Danish seine gear components on benthic macrofauna applied at two fishing intensities. We had two experimental sites, one to measure the effects of a single impact (1 haul) and another to measure multiple impacts (3 consecutive hauls). At each location, we collected samples before and 3-days after experimental fishing. In Chapter 5, we used a control-impact design to compare the effect of a conventional sandeel otter trawl (SOT) with a lightweight modified SOT (hereafter Dyneema). Samples were collected from three locations - a control, and two impact treatments (conventional gear and Dyneema) - after trawling, with sampling repeated in two consecutive years (2013, 2014).

2.3. Component specific sampling

It is widely accepted that fishing gear impacts differ between bottom-towed gears, mainly due to differences in the gear penetration depth (Eigaard et al., 2016; Hiddink et al., 2017; Rijnsdorp et al., 2016; Sciberras et al., 2018). Similarly, the various components of a given gear type interact with the seabed differently, and produce a heterogeneous footprint. Benthic impacts from respective gear components are thus thought to vary considerably across the footprint (Eigaard et al., 2016), although the quantification of this aspect is lacking for many gear types. Furthermore, assuming that modified and lightweight gears have shallower penetration depths, presumably they should result in smaller benthic faunal impact than the published estimates for conventional gears (e.g. those in Sciberras et al., 2018). If this were the case, then the accuracy of sampling (e.g. directly within the path of the gear track) may be of particular importance for lighter gears in order to observe the true effect.

In each of the case studies in this thesis, we applied relatively direct and specific sampling methods to target desired areas of the gear footprint. In Chapter 3, we targeted sampling within the dredge track, and area immediately adjacent to the track to evaluate the direct and indirect effects of the mussel dredge on seabed macrofauna. To do this, a SCUBA-diver collected samples across the BACI design by hand. In addition to improving the accuracy of sampling, using a diver allowed us to control for differences in substrate type by collecting samples only from within the mussel patches, and for differences in patch size and patch position. In Chapter 4 we followed the methods of Noack et al. (2019), and used surface mounted GPS devices attached to the gear components of the Danish seine using dog leashes. This enabled us to accurately track the movements of the gear components during hauling, and produce maps of the gear footprint with high accuracy. This facilitated targeted sampling within the footprints of the main gear components. In Chapter 5 we identified the position of the otter trawl ground gear using side scan sonar, and matched this with positions from SCANMAR sensors attached to each otter door. Samples were then targeted within the ground gear impacted area only.

References

Currie, D.R., Parry, G.D., 1996. Effects of scallop dredging on a soft sediment community: A large-scale experimental study. Mar. Ecol. Prog. Ser. 134, 131–150. https://doi.org/10.3354/meps134131

Eigaard, O.R., Bastardie, F., Breen, M., Dinesen, G.E., Hintzen, N.T., Laffargue, P., Mortensen, L.O., Nielsen, J.R., Nilsson, H.C., O'Neill, F.G., Polet, H., Reid, D.G., Sala, A., Sköld, M., Smith, C., Sørensen, T.K., Tully, O., Zengin, M., Rijnsdorp, A.D., 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. 73, i27–i43. https://doi.org/10.1093/icesjms/fsv099

Ellis, J.I., Norkko, A., Thrush, S.F., 2000. Broad-scale disturbance of intertidal and shallow sublittoral soft-sediment habitats; Effects on the benthic macrofauna. J. Aquat. Ecosyst. Stress Recover. 7, 57–74. https://doi.org/10.1023/A:1009923530894

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. JWS, NY.

Hewitt, J.E., Thrush, S.E., Cummings, V.J., 2001. Assessing environmental impacts: Effects of spatial and temporal variability at likely impact scales. Ecol. Appl. 11, 1502–1516. https://doi.org/https://doi.org/10.1890/1051-0761(2001)011[1502:AEIEOS]2.0.CO;2

Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proc. Natl. Acad. Sci. 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114

Hurlbert, S.H., 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecol. Monogr. 54, 187–211. https://doi.org/10.2307/1942661

Kaiser, M.J., Spencer, B.E., 1996. The Effects of Beam-Trawl Disturbance on Infaunal Communities in Different Habitats. J. Anim. Ecol. 65, 348-358. https://doi.org/10.2307/5881

Lambert, G.I., Murray, L.G., Hiddink, J.G., Hinz, H., Lincoln, H., Hold, N., Cambiè, G., Kaiser, M.J., 2017. Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance. Sci. Rep. 7, 5440. https://doi.org/10.1038/s41598-017-04715-4

Noack, T., Stepputtis, D., Madsen, N., Wieland, K., Haase, S., Krag, L.A., 2019. Gear performance and catch process of a commercial Danish anchor seine. Fish. Res. 211, 204–211. https://doi.org/10.1016/j.fishres.2018.11.012

Rijnsdorp, A.D., Bastardie, F., Bolam, S.G., Buhl-Mortensen, L., Eigaard, O.R., Hamon, K.G., Hiddink, J.G., Hintzen, N.T., Ivanović, A., Kenny, A., Laffargue, P., Nielsen, J.R., O'Neill, F.G., Piet, G.J., Polet, H., Sala, A., Smith, C., van Denderen, P.D., van Kooten, T., Zengin, M., 2016. Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. ICES J. Mar. Sci. 73, i127–i138. https://doi.org/10.1093/icesjms/fsv207

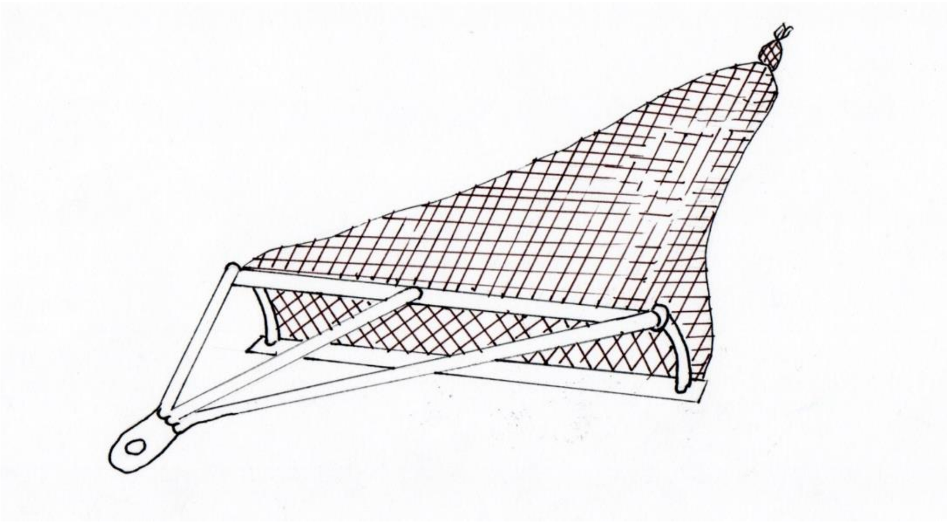
Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish Fish. 19, 698–715. https://doi.org/10.1111/faf.12283

Smokorowski KE, Randall RG., 2017. Cautions on using the Before-After-Control-Impact design in environmental effects monitoring programs. FACETS. 2017;2(1):212-232. doi:10.1139/facets-2016-0058

Stewart-Oaten, A., Murdoch, W.W., Parker, K.R., 1986. Environmental Impact Assessment : “Pseudoreplication" in Time ? Ecology 67, 929–940.

Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J. Exp. Mar. Bio. Ecol. 161, 145–178. https://doi.org/10.1016/0022-0981(92)90094-Q

3. Experimental effects of a lightweight mussel dredge on benthic fauna in a eutrophic MPA



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Experimental effects of a lightweight mussel dredge on benthic fauna in a eutrophic MPA

Katrina Bromhall[1]*, Grete E. Dinesen[1], Ciarán McLaverty[1], Ole R. Eigaard[1], Jens Kjerulf Petersen[2], Camille Saurel[2]

[1] DTU Aqua, National Institute of Aquatic Resources, Denmark

[2] Danish Shellfish Centre, Øroddevej 80, 7900 Nykøbing Mors, Denmark

* Corresponding author: krmb@aqua.dtu.dk. Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, Building 201, 2800 Kgs. Lyngby, Denmark

Key words: Before-After-Control-Impact (BACI); biological traits; bivalve fishery; ecosystem based fisheries management; fisheries effects; mussel; *Mytilus edulis*

Abstract

Dredging for wild mussels *Mytilus edulis* Linnaeus, 1758 takes place in Marine Protected Areas (Natura 2000 sites) in Denmark. The fishery is strictly regulated to limit the impact of dredging to the benthic environment, and requires the use of modified lightweight mussel dredges. Nevertheless, the depletion of the benthic macrofauna associated with *M. edulis* beds after impact from such dredges is yet to be quantified. Here, dredging is shown to result in a significant decline in the density, species richness, and biological traits directly in the dredge track but no significant impact on the community composition. Species richness remained significantly affected four months post dredging, although the positive trend after four months may signal recovery. An effect of dredging was also detected in areas adjacent (~5 m) to the dredge tracks, but needs further investigation to understand this impact. The results provide an estimate of benthic macrofaunal depletion in the dredge track as well as of the short-term recovery, which may be of use in the management of the fishery. Finally, it is suggested that species richness may be a more sensitive indicator than density in a eutrophic and species-poor system.

3.1. Introduction

Globally, 15 million tonnes of bivalve molluscs are produced each year for human consumption of which 11% are exploited from wild stocks (Wijsman et al., 2019). In Europe, scallops, blue mussels, and cockles dominate wild bivalve landings (FAO, 2020). Exploited bivalves live in or on the seabed, thus the fishing gear used for harvesting comes into direct contact with the seabed. The interaction causes a disturbance to the benthic habitat and the associated fauna (Kaiser et al., 2006). Bivalve harvesting is typically undertaken using dredges, which are relatively small, compact, and heavy towed gear that can include a bar or teeth to penetrate the surface sediments (Eigaard et al., 2016). Most research regarding the impacts of bivalve dredging to benthos stems from studies conducted on scallop fisheries (Thrush et al., 1995; Currie and Parry, 1999; Hall-Spencer and Moore, 2000; LeBlanc et al., 2015; Sciberras et al., 2016). Scallop dredging is deemed by some to be one of the more damaging fishing gears, although a large body of literature shows there to be a variable response of benthic communities to scallop dredging (Kaiser et al., 2006; Sciberras et al., 2018). Far less is known about other forms of bivalve dredging, some of which occur in dynamic, shallow systems, prone to high levels of natural (e.g. waves and storms) and anthropogenic (e.g. eutrophication) disturbance.

The Limfjord in Northern Denmark is a shallow microtidal-tidal system in which blue mussels (*Mytilus edulis*, Linnaeus 1758) are dredged from wild stocks. In 2012, new legislation initiated the switch from a heavier traditional Dutch dredge to a modified lightweight dredge (hereafter termed light dredge) in part to mitigate the damage to the seabed from dredging. While the light dredge has been shown to cause significantly less physical impact to the seabed by reducing sediment retention and drag resistance (Frandsen et al., 2015), the direct impact to the benthic macrofauna from the light dredge is less well understood. A comparative (gradient) study found a decline in macrofaunal biomass and a change in species composition correlated with light-dredging intensity, although were highly dependent on local environmental conditions (McLaverty et al., 2020). In addition, experimental trawling using a 1:2 scaled version of the Dutch dredge resulted in 2-5 cm furrows in the sediment, and a short-term decline in species richness (Dolmer et al., 2001). Thus, to meet the objectives of an Ecosystems Approach to Fisheries Management (EAFM), a direct assessment of the effect of the light dredge to seabed macrofauna is of particular interest to fisheries managers.

An obstacle to an EAFM in the Danish blue mussel fishery is the fact that the areas where *M. edulis* fisheries occur are also characterised by remarkably high levels of eutrophication associated with intense agricultural runoff (Ærtebjerg et al., 2003). Although this nutrient enrichment has promoted blue mussel growth and high mussel biomass (Dolmer et al., 1998), eutrophication also causes periodic oxygen depletion in some areas of the Limfjord. Eutrophication has a strong and predictable structuring influence on benthic communities (Pearson and Rosenberg, 1978). Under high nutrient enrichment, communities tend to be dominated by opportunistic fauna that can tolerate low oxygen and rapidly re-colonise areas when mass mortality occurs. Whilst the effects of eutrophication on benthos is relatively well understood, there is a paucity of research regarding the effects of trawling in organically enriched areas.

Fishing grounds for *M. edulis* in Denmark overlap with a number of Natura 2000 sites designated for their conservation value under the EU Habitats Directive (European Union, 1992). To ensure sustainable fisheries in these areas, strict regulations of the mussel fishery were instated in 2012 (Foreign Ministry of Denmark, 2019). This introduced the use of mandatory black box devices on fishing vessels operating in Natura 2000 areas (Nielsen et al., 2021). The black box data are used for several purposes, including to limit the footprint of dredging activity (≤ 15% of seabed) within Natura 2000 sites. The spatial footprint of dredging activity is calculated using the black-box data and the gear dimension. Estimating gear-based fisheries footprints in such a manner is common practice in the EU (Eigaard et al., 2017, ICES, 2019). Nevertheless, this method does not currently consider the indirect effects of dredging, for example on the area immediately adjacent to the dredge track (within meters), where there is potential for organisms to be exposed to sedimentation from dredging activity (Pastor et al., 2020), possibly leading to an underestimation of the impact footprint.

The aim of this study was to investigate the direct (dredge track) and indirect (adjacent to the dredge track) effects of the light dredge on *M. edulis* associated macrofauna in a highly eutrophic system. The study represents the first experimental dredging study on benthic macrofauna using this type of fishing gear. Using black box data, an area of seabed unfished for four years prior to the study was identified. At this location, a Before-After-Control-Impact (BACI) experiment was conducted. In order to sample the direct and indirect effects of mussel dredging accurately, a scuba diver collected macrofaunal samples from within the dredge track, immediately adjacent to the dredge track (up to 5 m distance), and in a control site. Samples were also collected four months after dredging to assess short-term recovery.

3.2. Material and Methods

3.2.1. Study area

Løgstør Broads is a large shallow basin situated in the North-East of the Limfjord, Denmark (Figure 1). The mean water depth is 7.2 m and salinity 27.3 (Josefson and Hansen, 2004). Seabed conditions in Løgstør are categorized as sandy or sandy mud substrates. Patches of *M. edulis* form on top of the substrate and create a seabed with a mosaic of bare sand and complex biogenic structure. Annual water temperature fluctuate between 0 - 22°C (Hoffmann and Dolmer, 2000) and water movement is predominantly driven by westerly winds (Dolmer and Frandsen, 2002). Low levels of wind and high temperatures during summer can lead to thermal stratification. In the Løgstør Broad a Natura 2000 site with surrounding coastal area covers an area of 441 km^2. Active environmental monitoring of the site started in 2004 and management commenced in 2011, in compliance with the Habitats Directive.

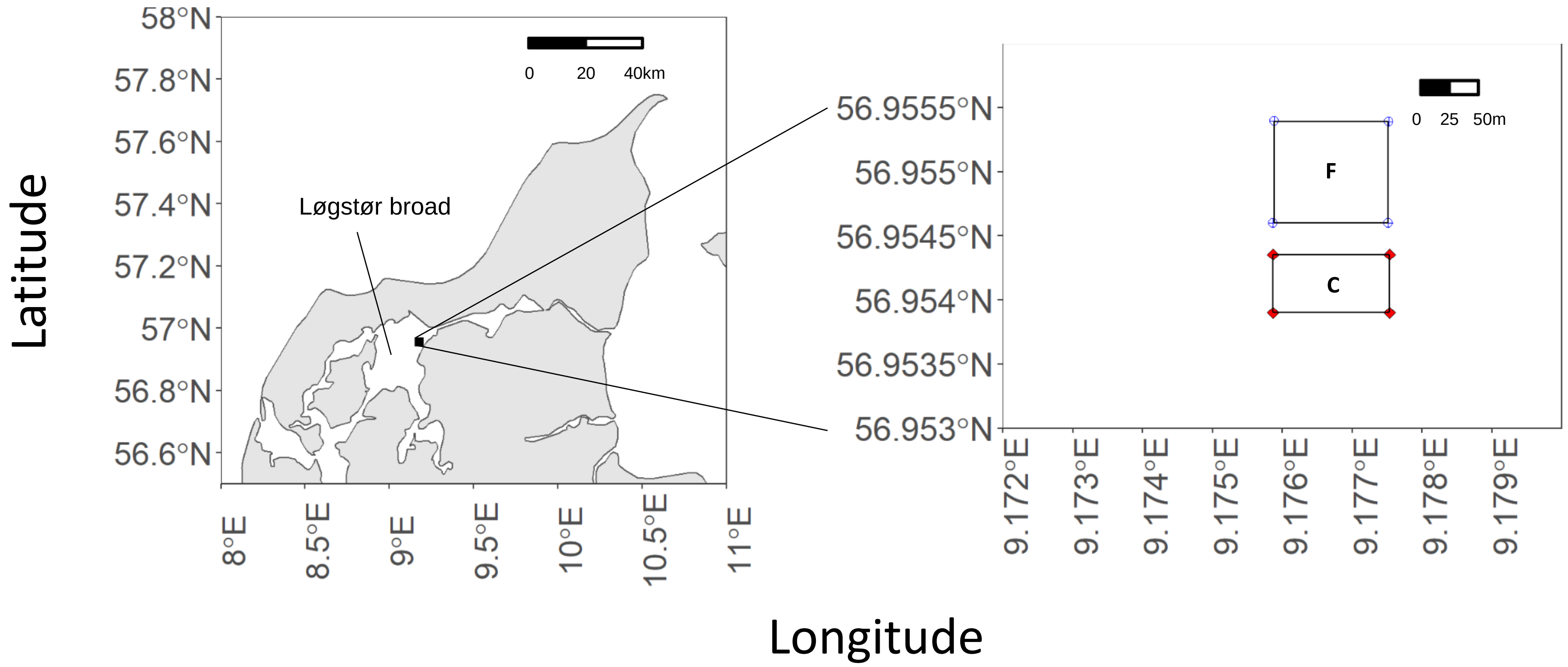

Figure 1: Map of the **study site in Løgstør broad, Limfjord, Denmark and location of respective fished (F) and control (C) sites.**

3.2.2. Experimental design

To quantify the effect of the light dredge a BACI experimental design was conducted. A BACI uses a factorial design to determine an impact based on a significant interaction between 'Time' (before, after) and 'Treatment' (control, impact) (Green, 1979). A significant interaction occurs when the change in time (i.e. the slope between before and after experimental disturbance) differs in the control and impact treatments. Black box data were used to locate an area where dredging had been absent for multiple years, and validated that the study sites had not been dredged for four years prior to the experiment (Figure 1). Due to the scarcity of large mussel beds in areas unfished for more than 3 years, the study was constrained to including only one control and one impact site. Although the criticism of such designs are recognised (Underwood, 1992), the viewpoint of Stewart-Oaten and Bence (2001) was taken. The control sites are not typical experimental controls (as conducted in laboratory experiments), but instead highly correlated co-variates and serve to represent the treatment site in an undisturbed condition (Stewart-Oaten and Bence, 2001). Thus, the efforts made to ensure that the control site represented the impact site, allowed for the examination of the experimental disturbance.

The fished site was experimentally dredged using the commercial light dredge, while the control site remained unfished for the duration of the study period. The boundary of the fished site marks the southernmost dredge track based on black box data and the minimum measured distance to the control site was 30 m. As the predominant bottom currents were northwards, the control site was located south of the fished site to reduce the possibility that sediment plumes from the dredging activity affected the control site.

Experimental dredging took place in the fished site on the 15th and 22nd of May 2017. The gear was as shown in Figure 2, with each dredge weighing 123.4 kg (Frandsen et al., 2015). A licensed fishing vessel conducted the experimental dredging rigged with two light dredges on each side (four in total). The catch efficiency of the dredge is variable, depending on the mussel bed structure, percentage cover and substratum. In some instance, catch efficiency has been recorded to be as low as 50 %, meaning that after dredging, some mussel patches remain in the dredge track (Dolmer et al., 1999). Macrofaunal samples were collected from mussel patches at three time intervals: before dredging on 10th May 2017 ('before'), the day after dredging on 23rd May 2017 ('after'), and four months after dredging on 20th September 2017 ('four-months after'). In the fished site, samples taken after dredging were collected from inside and outside of the gear path. Samples taken inside the gear path are referred to as 'dredge track', whilst those outside (~5 m from the dredge track) are referred to as 'adjacent to the track', shown in Figure 3.

As the recovery of seabed habitats after trawling is thought to occur through immigration from the surrounding area and through local recruitment (Lambert et al., 2017), samples were also taken four months after dredging to assess recovery from dredging.

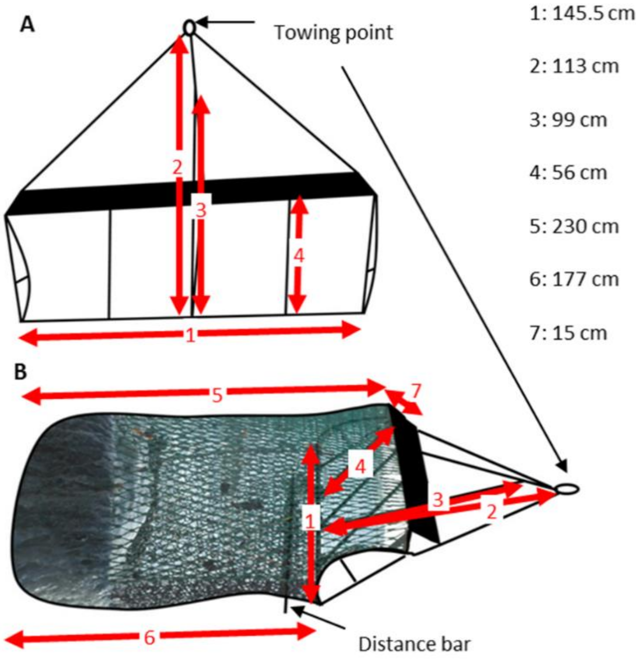

Figure 2: The dimensions of the light dredge seen from the front (A) and the side (B) reproduced from Frandsen et al., 2015

3.2.3. Data collection and processing

Benthic macrofaunal samples were collected using SCUBA and a hand-held sediment corer (HAPS; ø136mm, L; 315mm, V; 4.5L) at a depth of 4.5 m. The HAPS corer was chosen as it is the most commonly used sampler in Danish coastal waters and is used in annual benthic monitoring under the Danish National monitoring programme (Hansen, 2021). With as much accuracy as possible, samples were taken from a central position within similar-sized mussel patches. Four replicate core samples were taken from each treatment at each sampling time (Figure 3). The cores were brought to the surface and sieved through a 1-mm sieve prior to preservation in 80% ethanol (EtOH). In the laboratory, organisms were removed from the sediment residue and identified to species level where possible. Identification was aided using taxonomic keys (Kirkegaard, 1992a; Kirkegaard, 1992b; Tebble, 1976; Lincoln, 1979) and online taxonomic resources (species-identification.org; naturalhistory.museumwales.ac.uk). Verification of nomenclature was based on WoRMs (marinespecies.org; 10/09/21). Individual taxa were counted and biomass (ash free dry weight; AFDW) was determined following incineration at 550°C.

3.2.4. Biological traits

Biological Trait Analysis uses the morphological, behavioural, and reproductive traits of taxa as indicators of ecological function (Bremner et al., 2006). The ten trait categories chosen for analysis are shown in Table 1, which describe the functional composition of the associated macrofauna based on an existing trait database (Bolam et al., 2017). These trait categories were chosen based on their expected sensitivity to dredging disturbance. The ten trait categories were subdivided into trait modalities (Table 1). As some taxa may exhibit more than one trait modality within a trait category, the traits were 'fuzzy coded'. Fuzzy coding uses a scale of 0-3 to rank taxa affinity to each trait modality (zero equals no affinity, and three equals full affinity) (Chevenet et al., 1994). The fuzzy coded trait categories were standardised to 1, such that the trait modalities made up a proportion of the trait category. The trait scores were subsequently multiplied by the density of each taxa per site, which gave a density-weighted trait by site matrix used for analysis. Biological trait information was coded for the species identified in this study from the EU BENTHIS database (Bolam et al., 2017). Where taxa were not coded in the BENTHIS database, relevant literature was used to code taxa trait profiles.

Table 1: Biological traits and corresponding trait modalities analysed in the study.

Biological trait category	Modalities	Biological trait category	Modalities	Biological trait category	Modalities	Biological trait category	Modalities
Size	10 mm	Feeding	Suspension	Living Habit	Tube dwelling	Bioturbation	Diffusive mixer
	11-20 mm		Surface deposit.		Burrow dwell		Surface deposition
	21-100 mm		Subsurf. deposit.		Free living		Up- conveyor
	101-200 mm		Scavenger		Crevice		Down-conveyor
	201-500 mm		Predator		Endo/Epi-phytic		
	> 500 mm						
Mobility	Sessile	Larval Development	Planktotrophic	Sediment Position	Surface	Morphology	Exoskeleton
	Crawl		Lecithortrophic		Infauna-top		Soft
	Swim		Direct		Infauna-mid		Tunic
	Burrow				Infauna-deep		Crustose
			Budding				Cushion
							Stalked
Longevity	< 1 yr	Egg Development	Pelagic eggs				
	1-2 yrs		Benthic eggs				
	3-10 yrs		Brooding				
	10+ yrs						

3.2.5. Data analysis

Univariate

Statistical analyses were undertaken on three univariate community metrics, namely: density, species richness and biomass. Generalised linear models (GLMs) were applied using a Negative binomial, Poisson and Gamma variance distribution for density, species richness and biomass respectively in the ‘stats’ package in R. Studio. The model was as follows:

$$\mu_{ij} = \beta_0 + \beta_1 Tr_j + \beta_2 T_i + \beta_3 TrT + \varepsilon_{ij}$$

Where μ_{ij} denotes the response metric (density, species richness, biomass). β_0 is the intercept of the model, Tr_j is the treatment (dredge track, adjacent to the track, control). T is the time interval associated with μ_{ij}. β’s are the parameters for the predictors, where β_3 describes the interaction between treatment and time i.e. the BACI interaction term and the key parameter for this type of analysis. ε_{ij} is the residuals for the model. As the species richness and biomass of macrofauna associated with *Mytilus edulis* correlates with mussel patch size (Norling and Kautsky, 2007), mussel abundance was included in the model. During model selection, *M. edulis* abundance was not significantly contributing to any of the model, and hence was not selected in the most parsimonious model.

Multivariate

To compare the differences in macrofaunal community composition and biological trait composition, a permutation-based analysis of variance (PERMANOVA) was carried out in Primer 7 (PERMANOVA add on) (Anderson et al., 2008). If a significant interaction in the main test was observed, it was followed by post-hoc pairwise tests of time within site. A Similarity Percentage routine (SIMPER) set at 70 % was used to identify taxa or traits that contributed most to the dissimilarity between interacting time and treatment pairs. Macrofaunal composition required fourth root transformation to reduce within group dispersion, indicated by a significant PERMDISP test on non-transformed data. A non-significant PERMDISP result after transformation reduced uncertainty upon finding a significant main test PERMANOVA result. No transformation was necessary for the trait data.

Dredge track

To quantify the direct impact within the dredge track a statistical model compared the control and fished site before and after disturbance. ‘Before’ samples were taken 14 days prior to experimental dredging, and ‘after’ samples were taken 1 day post experimental dredging. In this analysis the fished site samples after dredging were collected from within the dredge track (Figure 3 – A: red squares).

Adjacent to the dredge track

To quantify the indirect effects of dredging adjacent to the dredge track (within 5 m), a statistical model compared the control and fished site before and after dredging. Here the fished site samples after dredging were taken adjacent to the dredge track (Figure 3 – A: yellow diamonds).

Short-term recovery (4months)

To quantify the short-term recovery from dredging, the fished and control sites were compared at three time intervals (before, after (1 day), four months after). After four months, it was no longer possible to see the dredge track and samples were taken randomly from within the fished site, conceivably from either track or adjacent area. To account for this, the dredge track and adjacent to the track samples ‘after’ were combined in the analysis (n = 8). To evaluate the effect of combining the two ‘after’ treatments, a model excluding time ‘after’ was used for comparison. It showed that combining treatments resulted in a conservative estimate of impact, but overall had the same outcome. Thus, the model including time ‘after’ was used for the analysis (Figure 3 – B).

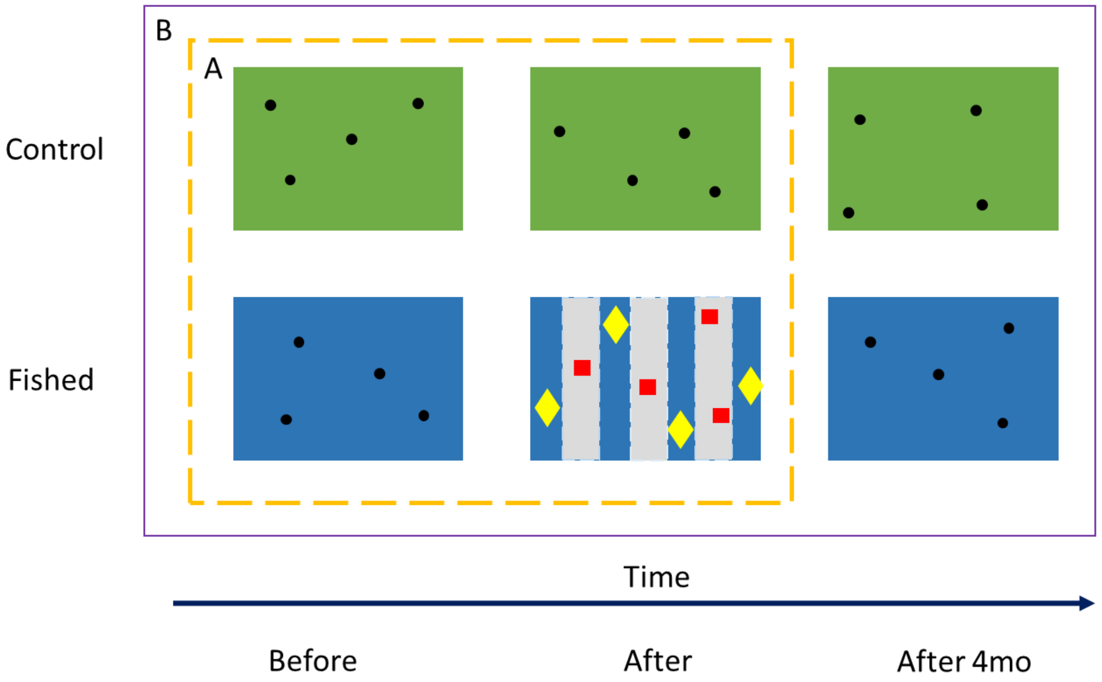

Figure 3: Experimental design comprising two sites and three time intervals. Dashed yellow line (A) Direct/indirect effect of dredging: Sampling undertaken before and after dredging. Black dots denote random samples from within the site. Two impact treatments are shown in the fished site (after): red dots within the grey bands denote samples taken within the dredge track; yellow dots within the blue area denote samples taken adjacent to the dredge track. Solid purple line (B) Short-term effects of dredging: sampling undertaken before, after, and after four months.

3.3. Results

3.3.1. Community composition

In total, 525 individuals and 54 species were identified in the HAPS core samples, after removing all individuals of *M. edulis*. The species represented four phyla: Annelida, Mollusca, Crustacea, and Echinodermata. The Annelida were numerically dominant, contributing 73 % of total density, followed by Crustacea, (23 %), Mollusca (3 %), and Echinodermata (1 %). In terms of species richness, Annelida and Crustacea made up the majority of species with 26 and 19 species, respectively (48 % and 35 %). Additionally, seven species of Mollusca were identified and one species of Echinodermata. The polychaete *Capitella capitata* (Blaineville, 1828) was found in high density and made up 43 % (227 individuals) of the total density. Taxa such as the amphipod *Microdeutopus* sp. were also abundant contributing to 7 % of total density (37 individuals). As expected, samples from September, after summer recruitment, exhibited the greatest density and species richness.

3.3.2. Dredge track

A decline in macrofaunal density and species richness within the dredge track (Figure 4) resulted in a significant BACI interaction term (β_3) (Table 2). Of the ten most common taxa, five taxa decreased in density after dredging in the fished site (*Microdeutopus gryllotalpa* (Costa 1853)*, Mediomastus fragilis* (Rasmussen 1973)*, Pseudopolydora pulchra* (Carazzi 1893)*, Tubifex* sp.*, Kurtiella bidentata* (Gofas & Salas 2008)), whilst three species increased (*Capitella capitata, Harmothoe impar* (Kinberg 1856)*, Harmothoe imbricata* (Kinberg 1856)) and two remained the same (Table 3). The density and species richness increased in the control site after dredging, which strengthened the significant interaction. In contrast, no effect of dredging was observed on biomass in the dredge track. The PERMANOVA analysis of biological trait scores showed a significant interaction (pseudo F 4.73, $p = 0.003$), indicating that dredging also had an effect on biological trait composition (Table 4). The biological traits which differed after dredging were remarkably similar at both sites (Table 5). The difference was that all the biological traits declined in the dredge track, and increased in the control site (Table 5). Of the ten biological traits studied, nine declined in the dredge track. These included sediment position (infaunal-top), living habit (burrow dwelling), egg development (brooding), mobility (sessile), morphology (soft), longevity (1-2 yrs), larval development (planktonic, direct development), feeding mode (subsurface deposit), size (21-100 mm). No significant effect of dredging was detected on multivariate community composition in the dredge track (Table 4).

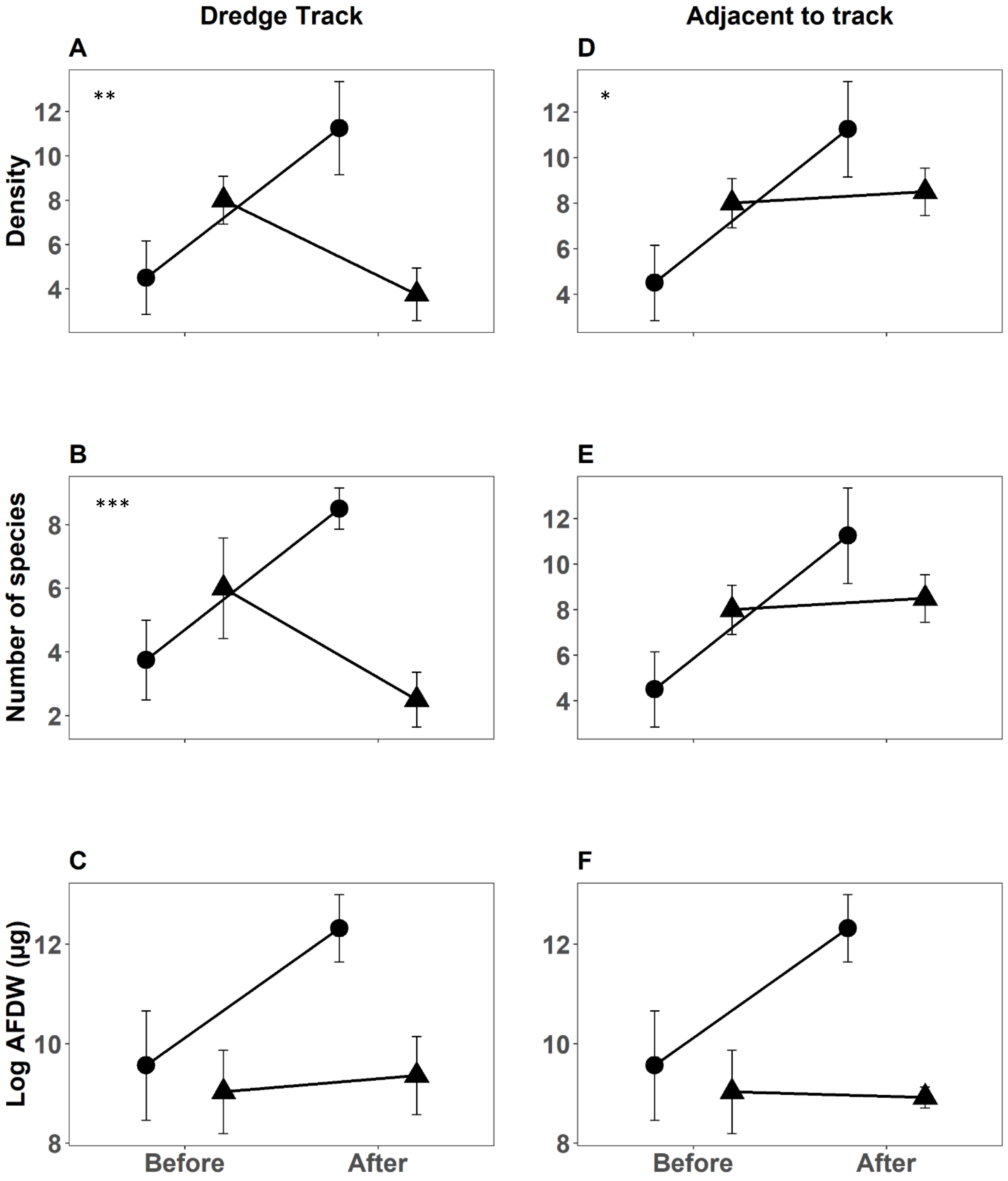

Figure 4: The mean (±SE) macrofaunal density (A, D), species richness (B, E), biomass (C, F) before dredging and after dredging in the control site (circles) and impact site (triangles). Asterisk indicates significant interaction level (* <0.001, ** <0.01, * <0.05).**

Table 2: Analysis of Variance (likelihood ratio test) of Generalised Linear Models for response variables (density, species richness, biomass) in the dredge track, adjacent to the track and four months after dredging.

	LR Chisq	Df	P value
Dredge track: density			
Treatment	2.33	1	0.12
Time	0.91	1	0.34
Treatment x Time	17.33	1	**>0.0001**
Dredge track: species richness			
Treatment	2.72	1	0.1
Time	0.30	1	0.5
Treatment x Time	13.20	1	**0.0002**
Dredge track: biomass			
Treatment	3.77	1	**0.05**
Time	2.93	1	0.08
Treatment x Time	1.16	1	0.28
Adjacent to the track: density			
Treatment	0.06	1	0.79
Time	6.58	1	**0.01**
Treatment x Time	5.44	1	**0.02**
Adjacent to track species: richness			
Treatment	0.01	1	0.92
Time	4.48	1	**0.05**
Treatment x Time	3.15	1	0.09
Adjacent to the track: biomass			
Treatment	6.12	1	**0.01**
Time	2.76	1	0.09
Treatment x Time	2.28	1	0.13
Short term: density			
Treatment	0.6	1	0.44
Time	186.7	2	**<0.0001**
Treatment x Time	8.4	2	**0.01**
Short-term: species richness			
Treatment	7.5	1	**0.006**

Time	10.4	2	**0.005**
Treatment x Time	9.6	2	**0.008**
Short-term: biomass			
Treatment	21.1	1	**<0.0001**
Time	5.6	2	0.06
Treatment x Time	0.7	2	0.7

Table 3: Average density (SD) of the most abundant taxa before and after dredging the three treatments (control, dredge track, adjacent to the track). Arrows indicate whether the change over time is positive (↑) or negative (↓)

	Control			Dredge track			Adjacent track		
Species	**Before**	**After**		**Before**	**After**		**Before**	**After**	
Capitella capitata	1 (0.8)	0.25 (0.5)	↓	0.25 (0.5)	0.75 (0.96)	↑	0.25 (0.5)	0	↓
Microdeutopus grylloptalpa	0	0.5 (0.5)	↑	0.75 (0.95)	0	↓	0.75 (0.95)	0.5 (0.5)	↓
Semibalanus balanoides	0	1.75 (3.5)	↑	0	0		0	1 (0.8)	↑
Mediomastus fragilis	0.75 (0.5)	1.75 (2.2)	↑	2.25 (1.8)	0.75 (0.96)	↓	2.25 (1.8)	0.75 (0.9)	↓
Harmothoe impar	0.75 (0.5)	1.25 (0.9)	↑	0.5 (0.5)	1 (0.5)	↑	0.5 (0.5)	2 (0.8)	↑
Harmothoe imbricata	0	0		0	0.25 (0.5)	↑	0	0	
Caprella linearis	0.25 (0.5)	0.5 (0.5)	↑	0	0		0	0	
Pseudopolydora pulchra	0	0.75 (0.95)	↑	0.25 (0.5)	0	↓	0.25 (0.5)	1.25 (1.2)	↑
Psamathe fusca	0.5 (1)	1.25 (0.5)	↑	0.25 (0.5)	0.25 (0.5)		0.25 (0.5)	0	↓
Tubifex sp.	0.5 (1)	0.25 (0.5)	↓	0.25 (0.5)	0	↓	0.25 (0.5)	0.5 (0.5)	↑
Kurtiella bidentata	0.25 (0.5)	0	↓	0.75 (0.5)	0	↓	0.75 (0.5)	0	↓

Table 4: PERMANOVA results showing differences in trait composition and community composition before and after dredging. The response was analysed in the dredge track (direct effect), adjacent to the track (indirect effects), and after four months (short-term effects). Asterisk indicates the significance level:* <0.001, ** <0.01, * <0.05**

Traits composition							**Community composition**				
	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**	**df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
Dredge track	Treatment	1	626.3	626.3	0.628	0.7	1	1375.7	1375.7	0.5122	0.8
	Time	1	798.19	798.19	0.8	0.5	1	1800.9	1800.9	0.6704	0.7
	Time x Treatment	1	4713.6	4713.6	4.726	**0.003****	1	5094.8	5094.8	1.8967	0.07
Adjacent to track	Treatment	1	988.3	988.3	1.215	0.2	1	3789	3789	1.628	0.1
	Time	1	2037.3	2037.3	2.505	**0.02***	1	3642.1	3642.1	1.5648	0.1
	Time x Treatment	1	1221.5	1221.5	1.502	0.15	1	2558.7	2558.7	1.0998	0.4
Short term	Treatment	1	583.9	583.9	0.687	0.5	1	2383.7	2383.7	1.0163	0.4
	Time	2	23584	11792	13.87	**0.001****	2	17159	8579.4	3.6579	**0.001****
	Time x Treatment	2	3327.2	1663.6	1.956	0.07	2	5978.7	2989.4	1.2745	0.2

Table 5: SIMPER analysis showing the differences in trait composition in the control and the fished site before and after dredging. Arrows indicate whether the change over time is positive (↑) or negative (↓)

Control site

Trait modality	Before Av. abundance	After Av. abundance	Av.Diss	Diss/SD	Contrib %	Cum.%
Soft	3.75	7.5 ↑	3.07	1.38	6.07	6.07
Surf-depos	1.88	6.38 ↑	2.93	1.98	5.8	11.86
brood	3.4	7.19 ↑	2.57	1.3	5.08	16.95
Crawl	1.67	4.92 ↑	2.38	1.73	4.69	21.64
yr1-2	3.13	5.5 ↑	2.14	1.39	4.22	25.86
Plankto	2.33	5.83 ↑	2.08	0.98	4.11	29.97
Surface	1.56	4.13 ↑	2.04	1.65	4.03	34
21-100mm	2.58	5.17 ↑	1.98	1.52	3.91	37.92
Burrow-	1.19	4.06 ↑	1.82	1.4	3.59	41.5
dwelling	2.63	4.25 ↑	1.79	1.1	3.54	45.04
Sessile	2.31	4.96 ↑	1.77	0.94	3.5	48.54
Inf-top	1.27	3.08 ↑	1.7	1.45	3.36	51.9
Direct	0.75	3.5 ↑	1.69	1.07	3.34	55.24
Exoskeleton	1.37	3.29 ↑	1.66	1.5	3.27	58.52
Free-living	0.58	2.5 ↑	1.54	1.54	3.03	61.55
eggs-pel	0.88	3 ↑	1.51	1.36	2.98	64.53
yr3-10	1.33	3.05 ↑	1.44	1.42	2.84	67.37
Pred	0.16	2.4 ↑	1.39	2.32	2.75	70.12
Surf-Dep						

Fished site (dredge track)

Inf-top	5.85	2 ↓	3.45	2.58	6.89	6.89
Burrow-	3.94	0.38 ↓	3.03	3.23	5.78	18.73
dwelling	5.65	2.63 ↓	2.89	1.58	5.36	24.09
brood	4.63	1.5 ↓	2.68	1.59	5.33	29.42
Sessile	6.25	3.5 ↓	2.67	1.45	5.15	34.57
Soft	5.25	2.38 ↓	2.58	2.3	4.86	39.43
yr1-2	4.46	2.75 ↓	2.43	1.2	4.05	43.48
Plankto	3.5	1.5 ↓	2.03	1.24	3.75	47.23
Subsurf-dep	4.28	2.5 ↓	1.88	1.52	3.67	50.9

21-100mm	2.33	0.5 ↓	1.84	1.71	3.65	54.55
Direct	3.19	1.75 ↓	1.83	1.3	3.55	58.11
Surf-depos	2.16	0.19 ↓	1.78	1.59	3.23	61.34
Surf-Dep	2.25	1.13 ↓	1.62	1.29	3.21	64.54
yr3-10	2.56	0.94 ↓	1.61	1.05	2.77	67.31
Up-Conveyor	1.75	0.25 ↓	1.39	1.95	2.77	70.08
Exoskeleton 10mm	1.58	0 ↓	1.39	1.98	6.05	12.95

3.3.3. Adjacent to the dredge track

A significant interaction on macrofaunal density was observed adjacent to the track (Table 2). Yet, unlike in the dredge track, density remained relatively stable in the area adjacent to the track, and the significant interaction term was driven by an increase in density in the control (Figure 4). The higher density in the control site occurred due to the emergence of new taxa, and an increase in density of most taxa already present before dredging (Table 6). The main effect 'Time' was the only significant predictor for species richness adjacent to the track (Table 2) suggesting changes over time had a greater effect on species richness than dredging in the adjacent area. Similar to in the dredge track, no effect of dredging on biomass was recorded (Table 2). Further, there was no indication of an effect of dredging on the biological traits examined or the community composition (Table 4).

Table 6: Species differences in the control site before and after fishing. Number of individuals shown in brackets. Arrows indicate whether the change over time is positive (↑) or negative (↓)

Before (9)	After (21)	Change	
	Asterias	+1	↑
Alitta succinea (1)	Alitta succinea (2)	+1	↑
	Alitta virens	+2	↑
Capitella capitata (4)	Capitella capitata (1)	-3	↓
Caprella linearis (1)	Caprella linearis (2)	+1	↑
	Corophium	+1	↑
	Ensis ensis	+1	↑
	Eunereis	+1	↑
	Gammarus	+2	↑
Harmothoe impar (3)	Harmothoe impar (5)	+ 2	↑
	Heteromastus	+1	↑
	Hinia	+1	↑
Kurtiella bidentata (1)	Kurtiella bidentata (2)	+1	↑
Mediomastus fragilis (3)	Mediomastus fragilis (7)	+4	↑
	Microdeutopus gryllotalpa	+2	↑
Mya arenaria (1)	Mya arenaria (2)	+1	↑
Psamathe fusca (2)	Psamathe fusca (5)	+3	↑
	Pseudopolydora	+3	↑
	Scoloplos armiger	+2	↑
	Semibalanus balanoides	+7	↑
Tubificidae (2)	Tubificidae (1)	-1	↓

3.3.4. Short-term effect

Four months after dredging species richness remained low, possibly suggesting a longer-term impact compared to that of density or biomass (Figure 5). Species richness declined immediately after dredging in the fished site, and then showed signs of recovery after four months (Figure 5). After four months, three of the ten most common species were absent from the fished site (*Microdeutopus grylloptalpa, Tubifex* sp.*, Kurtiella bidentata*) (Table 7). In addition, the diversity of amphipods was particularly low in the fished site. Here, only four species of amphipod were recorded after four months, of which there were five individuals. In contrast, the control site had eight species with 59 individuals. Whilst the density of macrofauna declined immediately after dredging, a considerable increase occurred thereafter, resulting in a similar macrofaunal density in the fished site as in the control site after four months (Figure 5). This indicates that the effect of dredging on macrofaunal density did not persist for the four month study period. In both sites, the density increased after four months mainly due to a single species of opportunistic polychaete, *Capitella capitata*, which made up 60 % and 81 % of the density in the control and fished site, respectively. Biomass was observed to remain relatively stable over the study period (Figure 5), and accordingly no short-term effect of dredging was detected on macrofaunal biomass (Table 2). The results of the PERMANOVA analysis indicated that there were no significant interactions on biological trait composition, which suggests that dredging did not impact the biological trait composition of the community in the short-term (Table 4). Finally, there was no effect of dredging on macrofaunal community composition as indicated by the non-significant PERMANOVA interaction term (Table 4).

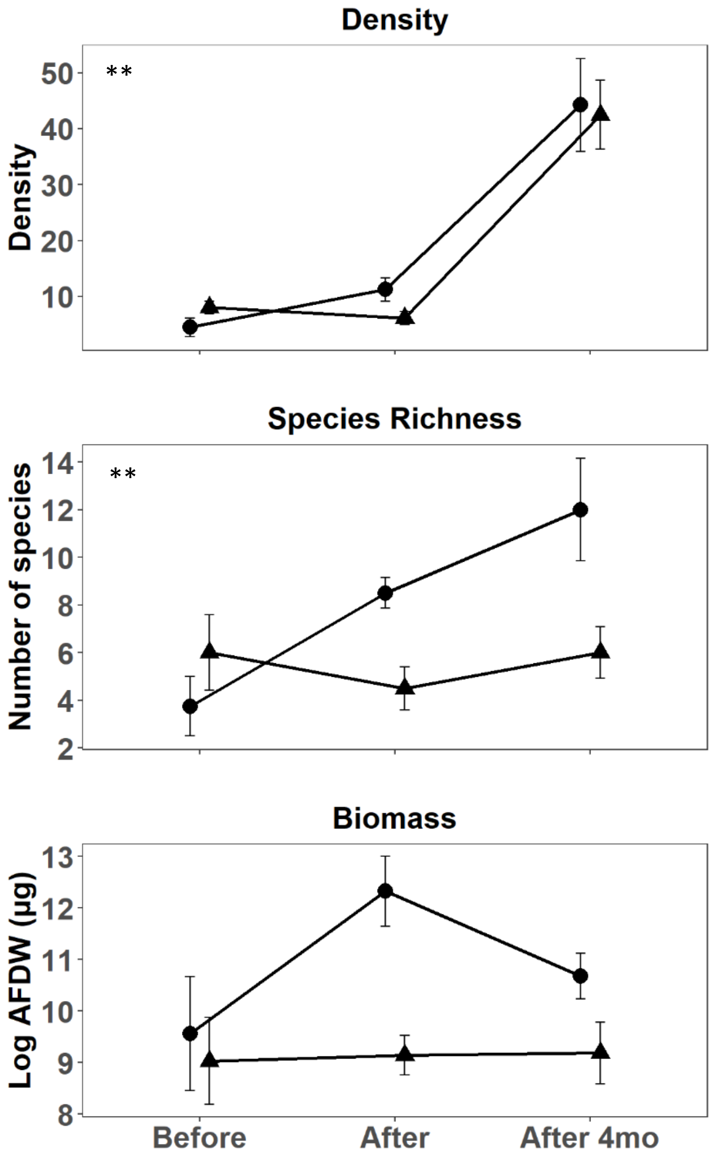

Figure 5: The difference in macrofaunal density, species richness, biomass (±SE) before dredging, after dredging, and four months after dredging in the control site (circles) and fished site (triangles). Asterisk indicates significant interaction level (* <0.001, ** <0.01, * <0.05)**

Table 7: The average density of the ten most abundant taxa ‘before’, ‘after’ and ‘four months after’ dredging in the control and fished site. Arrows indicate whether the change over time is positive (↑) or negative (↓)

	Control					**Fished**				
	Before	After		4 mon. After		Before	After		4 mon. After	
Capitella capitata	1	0.25	↓	19.25	↑	0.25	0.375	↑	35.25	↑
Microdeutopus grylloptalpa	0	0.5	↑	7.25	↑	0.75	0.25	↓	0	↓
Semibalanus balanoides	0	1.75	↑	3.25	↑	0	0.5	↑	0.5	↑
Mediomastus fragilis	0.75	1.75	↑	2.5	↑	2.25	0.75	↓	0.25	↓
Harmothoe impar	0.75	1.25	↑	0.5	↓	0.5	1.125	↑	0.5	
Harmothoe imbricata	0	0		2	↑	0	0.125	↑	2	↑
Caprella linearis	0.25	0.5	↑	2.25	↑	0	0		0.5	↑
Pseudopolydora pulchra	0	0.75	↑	0	↓	0.25	0.625	↑	0.75	↑
Psamathe fusca	0.5	1.25	↑	0	↓	0.25	0.125	↑	0.25	
Tubifex sp.	0.5	0.25	↓	0.75	↑	0.25	0.25		0	↓
Kurtiella bidentata	0.25	0	↓	0	↓	0.75	0	↓	0	↓

3.4. Discussion

3.4.1. Direct effects of the light dredge

The physical impacts to the seabed from fishing gears, besides removing the target species and habitat materials, arise from two processes (O'Neill and Ivanović, 2016). First, there are pressure driven changes which occur as the gear physically interacts with the seabed and leads to gear penetration, shearing, and lateral distribution of sediments (O'Neill and Ivanović, 2016). Second, hydrodynamic processes at the wake of the gear generates turbulence and pressure drop, leading to the mobilisation of sediment (O'Neill and Ivanović, 2016). The immediate decline in density and species richness shown in the dredge track is thought to be caused by the former, i.e. the direct physical interaction with the gear. The dredge itself consists of a metal frame and a polyethylene collection bag, which create a relatively homogenous impact across the footprint (Eigaard et al., 2016). Within the width of the gear and length of the path (i.e. gear footprint), the benthos are first impacted by the iron frame, followed by the trailing 177-cm long netted bag (Figure 2). Direct contact with the iron frame likely causes the greatest impact, potentially crushing infauna with exoskeletons such as thin-shelled bivalves (Rumohr and Krost, 1991) and crustaceans. The netted bag may be less impactful, but has the potential to snag and tear soft-bodied benthos such as polychaetes and ascidians. Accordingly, a relatively greater mortality can be expected from the direct physical interaction with the gear (Bergman and Van Santbrink, 2000), compared to indirect effects from the mobilisation of sediments. For that reason many experimental fishing studies have reported a decline in the density (Hall et al., 1990; Thrush et al., 1995; Carvalho et al., 2011), species richness (Hall et al., 1990; Thrush et al., 1995; Dolmer et al., 2001; Carvalho et al., 2011), and biomass (Carvalho et al., 2011) of macrofauna in the days following fishing impact.

The light dredge is designed to reduce the physical impact to the seabed, and compared to the traditional Dutch dredge, the sediment retention and drag is significantly reduced (Frandsen et al., 2015). A lack of gear trials meant making a direct comparison of the macrofaunal depletion from the Dutch dredge and light dredge not possible. Even so, a similar study was undertaken in the Løgstør broads using a scaled model of the Dutch dredge, roughly a third of the size and weight of the commercial configuration (Dolmer et al., 2001). In the study, species richness was significantly affected by dredging, and reported to decline by ~ 33 % 40 days after dredging. In comparison, the present study showed that the light dredge resulted in a 44 % decrease in species richness one day after dredging. The greater depletion of species in the present study may be caused by the heavier gear weight. The down-scaled model used by Dolmer et al. (2001) weighed ~ 80 kg, compared to the commercial light dredge which weighed 123 kg. The weight and towing speed of fishing gears determines the penetration into the sediment (Rijnsdorp et al., 2016), and gear penetration depth correlates with benthic macrofaunal mortality (Sciberras et al., 2018). Therefore, as the Dutch dredge weighs 235.6 kg (approximately double the weight of the light dredge), it can be assumed that the switch to the light dredge will have resulted in reduced macrofaunal depletion from fishing.

The depletion of benthic fauna can be influenced by the morphological, behavioural, and reproductive characteristics. Certain biological traits are known to be more sensitive to trawling than others (Thrush and Dayton, 2002; de Juan et al., 2007) such as shell thickness (Rumohr and Krost, 1991), mobility (Thrush and Dayton, 2002), and egg development. Accordingly, a negative effect of dredging was found on the biological trait composition in the dredge track. Sensitive biological traits, such as shallow sediment position (infauna top: 0-5 cm), low mobility (sessile), and soft morphology declined in the dredge track, however, so did the biological traits which are thought to be more tolerant to physical disturbance such as short lifespan (1-2 yrs), small size (10 mm, 21-100 mm), and hard morphology (exoskeleton). The general decline of biological traits in the dredge track suggests that dredging was not only detrimental to the sensitive traits, and instead may reflect the overall loss in density in the dredge track.

3.4.2. Indirect effects of the light dredge

In a BACI experimental design, a significant interaction usually implies a negative effect of the treatment, particularly if the significant interaction is caused by a decline in the impact site. Here, the significant interaction on density adjacent to the dredge track was driven by a higher density of macrofauna in the control site. As these results are not derived from a decline in the fished site, caution must be taken in the interpretation of the results.

A positive effect of time was shown for the density of macrofauna in the control site which was not apparent in the fished site. The first and simplest explanation is patchy distribution. Environmental parameters can vary over small spatial scales and as a consequence, macrofauna are patchily distributed. Adding to this, beds of *Mytilus edulis* are also known to be hotspots for biodiversity. Benthic macrofaunal density, biomass, species richness and trait richness all increase with *M. edulis* density and patch size (Norling and Kautsky, 2007; McLaverty et al., 2020). Therefore, differences in *M. edulis* density, size structure, or biomass could drive differences in macrofaunal density and species richness. To mitigate the effect of mussel patch size, a diver made his best efforts to sample from a central position in similar sized mussel patches. These efforts were reflected in the fact that the shell length and biomass of *M. edulis* were not significantly different after dredging in the control and adjacent area (t-test comparing *M. edulis* shell length and biomass after dredging: t= 1.6, Df= 4.1, p= 0.2, t= 0.6, Df= 3.5, p= 0.6, respectively). Although mussel density was significantly higher in the adjacent area after dredging than in the control (t= 93.1, Df= 6, p= 0.02), mussel density in the adjacent area did not differ before and after fishing (t = 0.2, df = 4.6, p = 0.8). The lower macrofaunal density in the adjacent area associated with higher mussel density, relative to the control, is contrary to the positive effect of mussel density on macrofaunal density previously shown (Norling and Kautsky, 2007; McLaverty et al., 2020). Therefore, the results may reflect that the hand-held sediment corer was not optimal for sampling larger epifauna such as *M. edulis*, and that differences in the mussel bed structure may still have existed between sites. In addition, an assumption was made that the sediment grain size were the same due to the close proximity of the sites to one another yet, a significant differences in the grain size of the top layer of sediment (0-2 cm) was detected before experimental dredging took place, but no difference in the organic material (loss on ignition). These small-scale differences between sites could also have influenced the results.

One effect of dredging that perceivably affects the benthos indirectly is the mobilisation of sediment. Sedimentation can smother benthic fauna if it exceeds natural levels and thus faunal tolerance (Miller et al., 2002). Sedimentation can also cause deterioration of water quality due to increased turbidity. An empirical based model showed that the sediment plume from the light dredge in the Limfjord can extend 260-540 m depending on current speed, and that sediment resuspension was similar to background (natural) re-suspension (Pastor et al., 2020). The model showed that fishing intensity correlated with sediment accumulation. Therefore, the comparatively higher fishing intensity in this study (~ 28 dredge tracks 100 m^{-2} versus 4.5 dredge tracks 100 m^{-2}), may have led to higher sediment accumulation. Further, sediment accumulation was highest closest to the dredging activity (Pastor et al., 2020), which suggests that localised sediment accumulation could have been high in the dredge track and adjacent areas. Based on the sediment type (sand >125 µm) it was estimated that 80 % of the resuspended sediment would fall within 0.3 - 0.9 m from the dredge track. As sediment accumulation was not quantified in this study, it was not possible to conclude on whether sedimentation from dredging activity exceeded natural sedimentation. Further investigation into the extent of sediment accumulation in the adjacent areas would clarify whether sedimentation from dredging negatively effects benthic macrofauna.

3.4.3. Short-term effects of the light dredge

Seasonal recruitment causes macrofaunal density and species richness to increase from its lowest point at the onset of spring, to its highest in late autumn (Peterson and Jensen, 1911). In the Limfjord, recruitment follows a similar seasonal pattern. This has been disrupted in some years, where species richness remains at a constant low between spring and autumn, due to mass mortality caused by oxygen depletion (Hylleberg, 1993). In this study, species richness remained relatively constant in the fished site from spring to autumn, whereas species richness increased in the control site. There was no indication of oxygen depletion at the study site during the study period. Therefore the lack of increase in species richness may indicate a negative effect of dredging on recruitment. Nonetheless, while species richness was lower in the fished site than in the control, the trend four months after dredging was positive, which may signify recovery was in progress. The recovery in terms of density was dominated by the polychaete *Capitella capitata* which made up 81 % and 60 % of the density in the fished and control sites, respectively. This resulted in both sites having relatively low species richness, but high density, which is characteristic of benthic communities affected by eutrophication (Pearson and Rosenberg, 1987).

As organic enrichment increases, water quality deteriorates, and the number of species that can tolerate the conditions decline. Meanwhile, the proliferations of opportunistic taxa can occur (Pearson and Rosenberg, 1987). The polychaete *Capitella capitata* thrives in eutrophic conditions as it can tolerate hypoxic sediments (Macleod et al., 2008), expresses opportunistic reproduction (Quian and Chai, 1994), and rapidly colonises defaunated patches (Bolam and Fernandes, 2002). The effect of eutrophication on the density of macrofauna may help explain the lack of detectable fishery effect in this part of the study, and may signify that density is a poor indicator of the short-term effects of dredging in eutrophic systems. It is recognised that the results of this study are limited to the discussion of impacts to the benthos over the short term, i.e. after four months. Ideally, given the large structuring effect winter mortality can have on benthic communities, additional sampling would have taken place after the winter to fully assess recovery. This is of particular importance in systems such as the Limfjord where large fluctuations in temperature occurs between seasons. Given the practical and financial restraints of using diver-collected samples, this was not possible.

High levels of benthic disturbance, whether anthropogenic or natural, will shape macrofaunal community composition and select for biological traits that are more resilient to disturbance. Here, the results showed that while dredging negatively affected biological traits in the dredge track, no negative effect on biological traits was evident after four months. This suggests that other environmental drivers may have a greater structuring effect on benthic composition than dredging in the Limfjord. These findings are also corroborated by the results of a large scale gradient analysis of dredging effects in Danish Natura 2000 sites, where dredging intensity did not result in any significant impacts to trait composition or trait richness (McLaverty et al., 2020). This can occur as stressors such as nutrient pollution and hydrodynamic disturbance have a similar structuring effect on benthic trait composition as trawling, i.e. a dominance of small-bodied, short-lived, deposit feeding taxa (Macleod et al., 2008; Van Denderen et al., 2015). Given the century-long effect of nutrient enrichment in the area, it is not surprising that dredging is not the main driver of species and trait composition across the study area.

3.4.4. Management perspectives

For the first time, these results provide an estimate for the depletion of benthic macrofauna, and information on the dynamics of recovery, directly relevant to the dredging gear used across the Danish mussel fishery. The Danish Mussel Policy was set up with the aim to regulate and sustainably manage fisheries in Natura 2000 sites, and permits vessels to impact ≤ 15 % of the seabed cumulatively over a period of 2-5 years depending on recovery time of benthic fauna within a given Natura 2000 site (Foreign Ministry of Denmark, 2019). As benthic macrofaunal depletion rates are not currently considered in the assessment of dredging impacts, the results are of particular relevance, and improve the understanding of dredging effects on seabed biota in the Løgstør broad. Provided depletion rates are supplemented with depletion rates for the other main habitat types in the Limfjord, these can be combined with black box data to predict impacts quantitatively in areas that are not currently assessed (Rijnsdorp et al., 2016).

Of the biological metrics examined in this study, the results suggest that species richness was relatively sensitive to dredging, remaining in an altered state for up to four months after disturbance. This supports the observations of Dolmer et al. (2001), who observed that although species richness initially increased straight after dredging (due to an influx of scavengers), it subsequently declined and remained reduced for up to 40 days after. Species richness has been shown to be a more sensitive indicator of trawling than density in deeper (35 m) muddy benthic habitats (Ragnarsson and Lindegarth, 2009), and has been shown to remain impacted for up to eight months after experimental shrimp trawling (Tulp et al., 2020). To more accurately define the effect of dredging on species richness in the Limfjord, future studies may seek to undertake experiments over longer time periods than four months. The choice to limit this experiment to four months was mainly logistical, but also reflected normal dredging activity followed by a closed period during the summer months (beginning of July – beginning of September).

The experiment was designed to target benthic communities that are representative of those impacted by this fishery. As a result, the macrofaunal depletion and recovery are described for communities associated with established mussel beds. Therefore, the results of this study may be less relevant for predicting depletion rates in other habitat types such as soft bottoms (sand and mud) which are not associated with biogenic structures. Until recently, the management of mussel fisheries in Denmark has used data collected from the Danish national monitoring programme to estimates benthic community regeneration times in each Natura 2000 site. Notably, these monitoring data are collected in areas of Løgstør that do not support large or consolidated mussel beds. These reference communities may not be representative of those found in close association with mussel beds, and therefore impacted by the fishery. Compared to bare sand habitats, mussel beds in Løgstør are associated with higher benthic density and species richness (Ysebaert et al., 2009; McLaverty et al., 2020), and more generally, mussels significantly enhance benthic diversity in disturbed or eutrophic systems (Norling and Kautsky, 2008). It would be advantageous that the estimation of regeneration times are based on data collected from surveys such as this one, which target benthic communities found in association with dense mussel beds.

A cumulative impact of 15 % of the seabed in Natura 2000 sites was considered suitable as it is lower than 25 % which the European commission defines to be ‘unfavourable’ for conservation status (Foreign Ministry of Denmark, 2019). Nonetheless, the Biodiversity Strategy for 2030 proposes to have 30 % of land and sea legally protected by 2030 of which 10 % should be strictly protected i.e. permanently closed to bottom contacting fishing (European Commission, 2020). While the Natura 2000 site in the Løgstør broad already meets this proposition, as a section of the Natura 2000 site is voluntarily closed to protect eelgrass beds, other Natura 2000 sites in Danish waters do not. The value of having areas permanently closed to bottom contacting fishing, may not only to support biodiversity, but also enhance the ability to sustainably manage fisheries. A study carried out in the Limfjord and inner Danish waters showed that non-fished reference sites were essential for detecting dredging impacts (McLaverty et al., 2020). Therefore, permanently closed MPAs within the Natura 2000 network in European waters may be a consideration for future ecosystem based fisheries management.

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References

Alves, F., Chícharo, L., Nogueira, A., Regala, J. 2003. Changes in benthic community structure due to clam dredging on the Algarve coast and the importance of seasonal analysis. J. Mar. Biol. Assoc. 83, 719–729. https://doi.org/10.1017/S0025315403007707h

Anderson, M., Gorley, R., Clarke, K. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. https://doi.org/10.1002/9781118445112.stat07841

Bergman, M. J. N., & Van Santbrink, J. W. 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES J. Mar. Sci. 57, 1321–1331. doi: 10.1006/jmsc.2000.0917

Bolam, S. G., Garcia, C., Eggleton, J., Kenny, A. J., Buhl-Mortensen, L., Gonzalez-Mirelis, G., van Kooten, T., Dinesen, G., Hansen, J., Hiddink, J. G., Sciberras, M., Smith, C., Papadopoulou, N., Gumus, A., Van Hoey, G., Eigaard, O. R., Bastardie, F., Rijnsdorp, A. D. 2017. Differences in biological traits composition of benthic assemblages between unimpacted habitats. Mar. Environ. Res. 126, 1–13. https://doi.org/10.1016/j.marenvres.2017.01.004

Bolam, S. G., Fernandes, T. F. 2002. Dense aggregations of tube-building polychaetes: response to small-scale disturbances. J. Exp. Mar. Bio. Ecol. 269, 197–222. https://doi.org/10.1016/S0022-0981(02)00003-5

Bremner, J., Rogers, S. I., & Frid, C. L. J. 2006. Matching biological traits to environmental conditions in marine benthic ecosystems. J. Mar. Syst. 60, 302–316. doi: 10.1016/j.jmarsys.2006.02.004

Buschbaum, C. 2001. Selective settlement of the barnacle *Semibalanus balanoides* (L.) facilitates its growth and reproduction on mussel beds in the Wadden Sea. Helgol. Mar. Res. 55, 128–134. https://doi.org/10.1007/s101520100070

Carvalho, S., Constantino, R., Pereira, F., Ben-Hamadou, R., Gaspar, M. B. 2011. Relationship between razor clam fishing intensity and potential changes in associated benthic communities. J. Shellfish Res. 30, 309–323. https://doi.org/10.2983/035.030.0217

Chevenet, F., Doledec, S. & Chessel, D. 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw, Biol. 31, 295–309. doi: 10.1111/j.1365-2427.1994.tb01742.x

Chícharo, L., Regala, J., Gaspar, M., Alves, F., Chícharo, A. 2002. Macrofauna spatial differences within clam dredge-tracks and their implications for short-term fishing effect studies. Fish. Res. 54, 349-354. doi: 10.1016/S0165-7836(01)00272-7

Currie, D., Parry, G. 1999. Impacts and efficiency of scallop dredging on different soft substrates. Can. J. Fish. Aquat. Sci. 56, 539–550. doi: 10.1139/cjfas-56-4-539

van Denderen, P., Bolam, S., Hiddink, J., Jennings, S., Kenny, A., Rijnsdorp, A., 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. https://doi.org/10.3354/meps11550

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. doi: 10.1016/S0165-7836(97)00081-7

Dolmer, P., Kristensen, T., Christiansen, M. L., Petersen, M. F., Kristensen, P. S., Hoffmann, E. 2001. Short-term impact of blue mussel dredging (*Mytilus edulis* L.) on a benthic community. Hydrobiologia. 465, 115–127. https://doi.org/10.1023/A:1014549026157

Dolmer, P. & Frandsen, R. 2002. Evaluation of the Danish mussel fishery: suggestions for an ecosystem management approach. Helgol. Mar. Res. 56, 13–20. https://doi.org/10.1007/s10152-001-0095-6

Eigaard, O. R., Bastardie, F., Breen, M., Dinesen, G. E., Hintzen, N. T., Laffargue, P., Mortensen, L. O., Nielsen, J. R., Nilsson, H. C., O'Neill, F. G., Polet, H., Reid, D. G., Sala, A., Sköld, M., Smith, C., Sørensen, T. K., Tully, O., Zengin, M., Rijnsdorp, A. D. 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. 73, i27–i43. https://doi.org/10.1093/icesjms/fsv099

Eigaard, O. R., Bastardie, F., Hintzen, N. T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G. E., Egekvist, J., Fock, H. O., Geitner, K., Gerritsen, H. D., González, M. M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J. R., Papadopoulou, N., Posen, P. E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C. J., Vanelslander, B., Rijnsdorp, A. D. 2017. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES J. Mar. Sci. 74, 847–865. https://doi.org/10.1093/icesjms/fsw194

European Commission. 2020. EU Biodiversity Strategy for 2030. Brussels: 20.5.2020 COM (2020) 380

European Union. 1992. Habitats directive: Council Directive 92/43/ EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Off. J. Eur. Union. L. 206, 7−50

FAO. 2020. Fisheries and Aquaculture Information and Statistics Branch [Statistics Query Results]. Available at http://www.fao.org/fishery/statistics

Frandsen, R. P., Eigaard, O. R., Poulsen, L. K., Tørring, D., Stage, B., Lisbjerg, D., Dolmer, P. 2015. Reducing the impact of blue mussel (*Mytilus edulis* L.) dredging on the ecosystem in shallow water soft bottom areas. Aquat. Conserv. Mar. Freshw. Ecosyst. 25, 162–173. https://doi.org/10.1002/aqc.2455

Foreign Ministry of Denmark. 2019. Målsætninger og forvaltningsprincipper for muslinge- og østersskrab og øvrig muslinge- og østers produktion i og udenfor Natura 2000 områder. Available at: https://fiskeristyrelsen.dk/media/10650/muslinge-og-oesterspolitik.pdf

Glorius, S. T., Tulp, I., Meijboom, A., Bolle, L. J., Chen, C., 2018. Developments in benthos and fish in gullies in an area closed for human use in the Wadden Sea: 2002-2016. WOt-technical report 129. https://doi.org/10.18174/464873

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A Global Map of Human Impact on Marine Ecosystems. Science (80-.). 319, 948–952. https://doi.org/10.1126/science.1149345

Hansen, J. W. 2012. Marine områder 2011. NOVANA. Videnskabelig rapport fra DCE-Nationalt Center for Miljø og Energi nr. 34. Available at: http://www.dmu.dk/Pub/SR34.pdf

Hall-Spencer, J., Moore, P. G. 2000. Scallop dredging has profound, long-term impacts on maerl habitats. ICES J. Mar. Sci. 57, 1407–1415. https://doi.org/10.1006/jmsc.2000.0918

Hall, S. J., Basford, D., Robertson, M. R. 1990. The impact of hydraulic dredging for razor clams *Ensis* sp. (S.) on an infaunal community. Netherlands J. Sea Res. 27, 119–125. https://doi.org/10.1016/0077-7579(90)90040-N

Hoffmann, E., Dolmer, P. 2000. Effect of closed areas on distribution of fish and epibenthos. ICES J. Mar. Sci. 57, 1310–1314. https://doi.org/10.1006/jmsc.2000.0921

Hylleberg, J. 1993. Extinction and immigration of benthic fauna. The value of historical data from Limfjorden, Denmark. Ist. Sci. Ambientali. Mar. Santa-Margherita Ligure (Italy). 43-70. Available at https://www.academia.edu/10220679

ICES. 2019. Working Group on Spatial Fisheries Data (WGSFD). ICES Sci. Rep. 1-52. http://doi.org/10.17895/ices.pub.5648

Jones, J. B. 1992. Environmental impact of trawling on the seabed: a review. New Zeal. J. Mar. Freshw. Res. 26, 59–67. https://doi.org/10.1080/00288330.1992.9516500

Josefson, A. B., Hansen, J. L. S., 2004. Species richness of benthic macrofauna in Danish estuaries and coastal areas. Glob. Ecol. Biogeogr. 13, 273–288. https://doi.org/10.1111/j.1466-822X.2004.00091.x

de Juan, D., Thrush, S., 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. https://doi.org/10.3354/meps334117

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. https://doi.org/10.3354/meps311001

Kaiser, M. J., Spencer, B. E. 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. J. Anim. Ecol. 65, 348. https://doi.org/10.2307/5881

Kirkegaard, J. B. 1992a. Havbørsteorme I: Errantia. Danmarks Fauna, 83: 1-416

Kirkegaard, J. B. 1992b. Havbørsteorme II: Sedentaria. Danmarks Fauna, 83: 1-451

Lambert, G. I., Murray, L. G., Hiddink, J. G., Hinz, H., Lincoln, H., Hold, N., Cambiè, G., Kaiser, M. J. 2017. Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance. Sci. Rep. 7, 5440. https://doi.org/10.1038/s41598-017-04715-4

LeBlanc, S. N., Benoît, H. P., Hunt, H. L. 2015. Broad-scale abundance changes are more prevalent than acute fishing impacts in an experimental study of scallop dredging intensity. Fish. Res. 161, 8–20. https://doi.org/10.1016/j.fishres.2014.06.001

Lincoln, R. J. 1979. British Marine *Amphipoda: Gammaridea*. British Museum (Natural History). 818: 1-658

Macleod, C., Moltschaniwskyj, N., Crawford, C. 2008. Ecological and functional changes associated with long-term recovery from organic enrichment. Mar. Ecol. Prog. Ser. 365, 17–24. https://doi.org/10.3354/meps07534

McLaverty, C., Eigaard, O. R., Dinesen, G. E., Gislason, H., Kokkalis, A., Erichsen, A. C., Petersen, J. K. 2020. High-resolution fisheries data reveal effects of bivalve dredging on benthic communities in stressed coastal systems. Mar. Ecol. Prog. Ser. 642, 21–38. https://doi.org/10.3354/meps13330

Miller, D. C., Muir, C. L., Hauser, O. A. 2002. Detrimental effects of sedimentation on marine benthos: what can be learned from natural processes and rates? Ecol. Eng. 19, 211–232. https://doi.org/10.1016/S0925-8574(02)00081-2

Nielsen, P., Nielsen, M. M., McLaverty, C., Kristensen, K., Geitner, K., Olsen, J., Saurel, C., Petersen, J. K., 2021. Management of bivalve fisheries in marine protected areas. Mar. Policy 124, 104357. https://doi.org/10.1016/j.marpol.2020.104357

Norling, P., Kautsky, N. 2007. Structural and functional effects of *Mytilus edulis* (L.) on diversity of associated species and ecosystem functioning. Mar. Ecol. Prog. Ser. 351, 163–175. https://doi.org/10.3354/meps07033

O'Neill, F. G., Ivanović, A. 2016. The physical impact of towed demersal fishing gears on soft sediments. ICES J. Mar. Sci. 73, i5–i14. https://doi.org/10.1093/icesjms/fsv125

O'Neill, F. G., Summerbell, K., Breen, M. 2008. The suspension of sediment by scallop dredges. Fisheries Research Services Internal Report, 08/08. FRS Marine Laboratory, Aberdeen Scotland

Olive, P. J. W. 1995. Annual breeding cycles in marine invertebrates and environmental temperature: Probing the proximate and ultimate causes of reproductive synchrony. J. Therm. Biol. 20, 79–90. https://doi.org/10.1016/0306-4565(94)00030-M

Pastor, A., Larsen, J., Mohn, C., Saurel, C., Petersen, J. K., Maar, M. 2020. Sediment transport model quantifies plume length and light conditions from mussel dredging. Front. Mar. Sci. 7:576530. doi: 10.3389/fmars.2020.576530

Pearson, T., Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16, 229-311

Peterson, C., Jensen, P. 1911. Valuation of the sea: animal life of the sea-bottom, its food and quantity. Am. Nat. 47, 378–384. doi: 10.2983/035.034.0121u1.10

Qian, P. Y., Chia, F. S. 1994. In situ measurement of recruitment, mortality, growth, and fecundity of *Capitella* sp. (Annelida: Polychaeta). Mar. Ecol. Prog. Ser. 111, 53-62.

Ragnarsson, S., Lindegarth, M. 2009. Testing hypotheses about temporary and persistent effects of otter trawling on infauna: changes in diversity rather than abundance. Mar. Ecol. Prog. Ser. 385, 51–64. https://doi.org/10.3354/meps08056

Rhoads, D. C., Young, D. 1970. The influence of deposit-feeding organisms on sediment stability and community structure. J. Mar. Res. 28, 150-178

Rijnsdorp, A. D., Bastardie, F., Bolam, S. G., Buhl-Mortensen, L., Eigaard, O. R., Hamon, K. G., Hiddink, J. G., Hintzen, N. T., Ivanović, A., Kenny, A., Laffargue, P., Nielsen, J. R., O'Neill, F. G., Piet, G. J., Polet, H., Sala, A., Smith, C., van Denderen, P. D., van Kooten, T., Zengin, M. 2016. Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. ICES J. Mar. Sci. 73, i127–i138. https://doi.org/10.1093/icesjms/fsv207

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

Sciberras, M., Parker, R., Powell, C., Robertson, C., Kröger, S., Bolam, S., Hiddink, J. G. 2016. Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. Limnol. Oceanogr. 61, 2076–2089. https://doi.org/10.1002/lno.10354

Sciberras, M., Hiddink, J. G., Jennings, S., Szostek, C. L., Hughes, K. M., Kneafsey, B., Clarke, L. J., Ellis, N., Rijnsdorp, A. D., McConnaughey, R. A., Hilborn, R., Collie, J. S., Pitcher, C. R., Amoroso, R. O., Parma, A. M., Suuronen, P., Kaiser, M. J. 2018. Response of benthic fauna to experimental bottom fishing: a global meta-analysis. Fish Fish. 19, 698–715. https://doi.org/10.1111/faf.12283

Stewart-Oaten, A., Bence, J. R. 2001. Temporal and spatial variation in environmental impact assessment. Ecol. Monogr. 71, 305–339. https://doi.org/10.1890/0012-9615(2001)071[0305:TASVIE]2.0.CO;2

Tebble, N. 1976. British Bivalve Seashells: A Handbook for Identification (2nd ed.) Royal Scottish Museum. 1:212

Thrush, S. F., Hewitt, J. E., Cummings, V. J., Dayton, P. K. 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. doi: 10.3354/meps129141

Thrush, S. F., Dayton, P. K. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Ann. Rev. Ecol. Syst. doi:10.1146/annurev.ecolsys.33.010802.150515

Tomasetti, S. J., Morrel, B. K., Merlo, L. R., Gobler, C. J. 2018. Individual and combined effects of low dissolved oxygen and low pH on survival of early stage larval blue crabs, *Callinectes sapidus* (R.). PLoS ONE, 13, 1–16. doi: 10.1371/journal.pone.0208629

Tulp, I., Glorius, S., Rippen, A., Looije, D., Craeymeersch, J. 2020. Dose-response relationship between shrimp trawl fishery and the macrobenthic fauna community in the coastal zone and Wadden Sea. J. Sea Res. 156, 101829. https://doi.org/10.1016/j.seares.2019.101829

Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J. Exp. Mar. Biol. Ecol. 161, 145–178. doi: 10.1016/0022-0981(92)90094-Q.

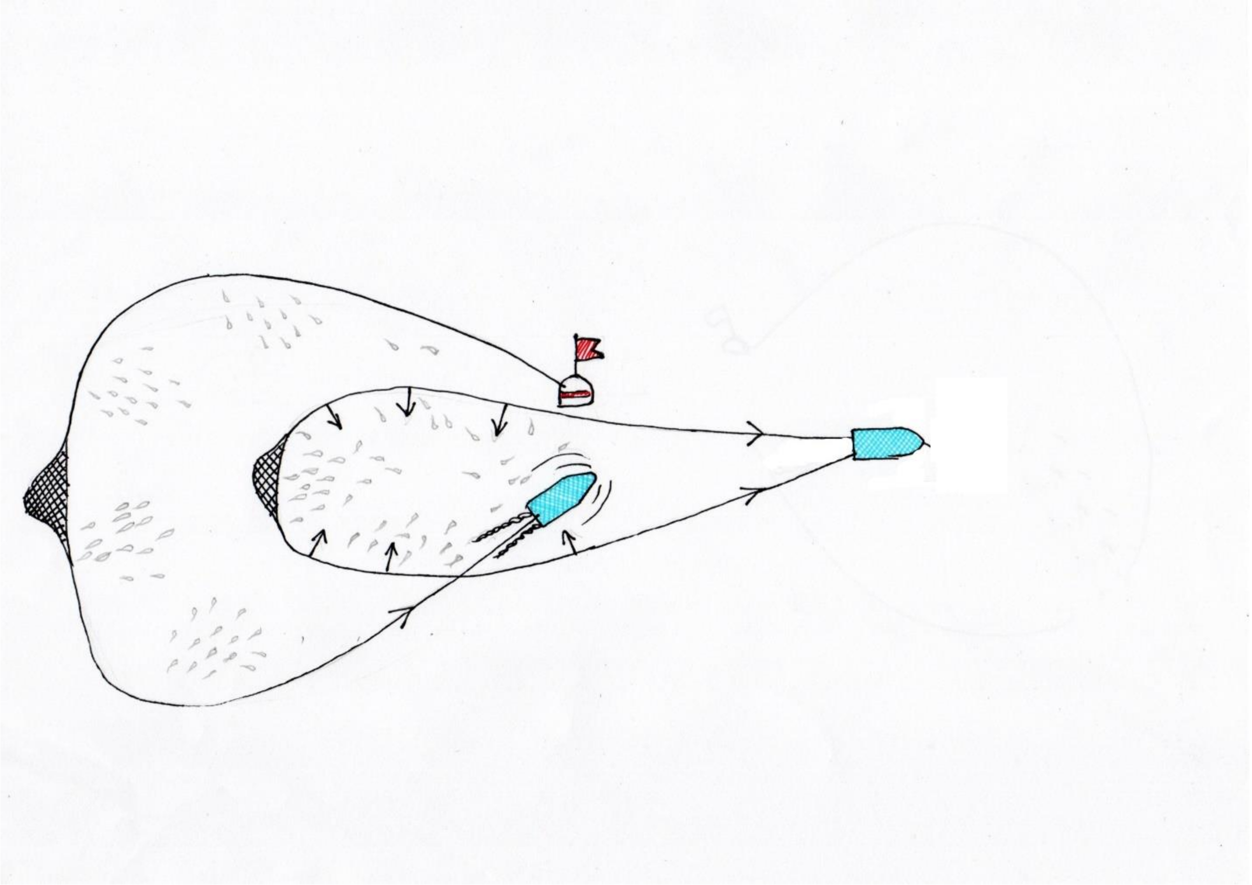
Wijsman, J. W. M., Troost, K., Fang, J., Roncarati, A. 2019. Global production of marine bivalves. Trends and challenges. In Goods and services of marine bivalves. 7-26. Springer [Online]. Available at: https://doi.org/10.1007/978-3-319-96776-9

Ysebaert, T., Hart, M. & Herman, P. M .J. 2009. Impacts of bottom and suspended cultures of mussels *Mytilus* spp. (L.) on the surrounding sedimentary environment and macrobenthic biodiversity. Helgol. Mar. Res. 63, 59–74. doi:10.1007/s10152-008-0136-5

Ærtebjerg, G., Andersen, J. H., Hansen, O. S. 2003. Nutrients and eutrophication in Danish marine waters: A challenge for science and management. National Environmental Research Institute, *126*. Ministry of the Environment. Available at:

https://www.dmu.dk/1_viden/2_publikationer/3_Ovrige/rapporter/Nedmw2003_0-23.pdf

4. Quantifying the impact of the Danish Seine - a ‘low environmental impact’ fishing gear - on seabed macrofauna



Katrina Bromhall, Ole R. Eigaard, Tim J.G. Wilms, Thomas Noack, Ciarán McLaverty, Finbarr G. O’Neill, Grete E. Dinesen (*In prep*) Quantifying the impact of the Danish Seine - a ‘low environmental impact’ fishing gear - on seabed macrofauna

Quantifying the impact of the Danish Seine - a ‘low environmental impact’ fishing gear - on seabed macrofauna

Katrina Bromhall[1], Ole R. Eigaard[1], Tim J.G. Wilms[1], Thomas Noack[2], Ciarán McLaverty[1], Finbarr G. O’Neill[3], Grete E. Dinesen[1]

[1]Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, 2800 Kongens Lyngby, Denmark

[2] Thünen Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, Rostock, 18069, Germany

[3]Technical University of Denmark, National Institute of Aquatic Resources, Willemoesvej 2, 9850 Hirtshals, Denmark

Abstract

The Danish ‘anchor’ seine is a commercial fishing gear used worldwide to catch demersal fish. It is assumed to have a low seabed impact due to its light weight and shallow penetration depth. However, relatively little is known about the effect of Danish seining on benthic macrofauna. By applying single and multiple experimental hauls, we quantified the effect of the Danish seines gear components on benthos using BACI ratios estimated from Bayesian models. We found greater reductions of benthic macrofauna from the seine ropes relative to the heavier ground gear, and the greatest loss after multiple hauls of the seine ropes. The reduction of benthic macrofauna were, nevertheless, low for density, species richness and biomass, and coupled with uncertainty (credible intervals (CI) overlapped zero). In contrast, multiple hauls of seine ropes resulted in high levels of loss for individuals of the erect tube-building *Phoronis* spp.. (mean, 95% CI: - 90%, -99% to -60%). Despite the high loss of *Phoronis* spp., generally the reduction of macrofaunal was low at the community level, suggesting the Danish seine has an overall low impact on this component of seabed biota. We suggest that the use and promotion of fishing gears with a low benthic macrofaunal impact such as the Danish seine can help to fulfil the objectives of an Ecosystem Approach to Fisheries Management.

4.1. Introduction

Mobile bottom contacting fishing gears account for almost one quarter of wild marine fisheries landings worldwide (FAO 2010). The extensive literature on seabed impact from bottom trawling suggests a widespread consensus on the environmental burden of these activities (Kaiser et al., 2006; Hiddink et al., 2017; Sciberras et al., 2018). Although less widely used, bottom-towed gears such as the Danish seine are thought to exert comparatively low level of physical impact on the seabed (Suuronen et al., 2012). Accordingly, it is assumed that Danish seines inflict relatively low impacts to benthic macrofauna, although this has yet to be formally examined.

The Danish anchor seine (hereafter Danish seine) was invented in Denmark in 1848, where a beach seine was adapted to catch plaice (*Pleuronectes platessa*) from a rowing boat. The boat operating the Danish seine has since evolved into a bigger, diesel-engine powered vessel, which many countries worldwide have adapted for use in their demersal seine fisheries (Walsh and Winger, 2011). The assumed low seabed impact of the Danish seine is, in part, due to the hauling procedure (Figure 1). The haul consists of a net towed by two long ropes, attached on each wing to an anchored vessel. The two ropes are laid out in a roughly triangular area from an anchor point and are winched in from the vessel. This reduces the area between the ropes until the net closes around the catch. The procedure creates a large footprint on the seabed (~5 km2) relative to other commercial gears (Eigaard et al., 2016; Noack et al., 2019). That said, 99% of the footprint comes from the ropes moving across the surface of the seabed, and 1% is from the ground gear and net (Noack et al., 2019). The two gear components interact with the seabed differently creating a heterogeneous footprint, where the physical effect varies within the gear footprint.

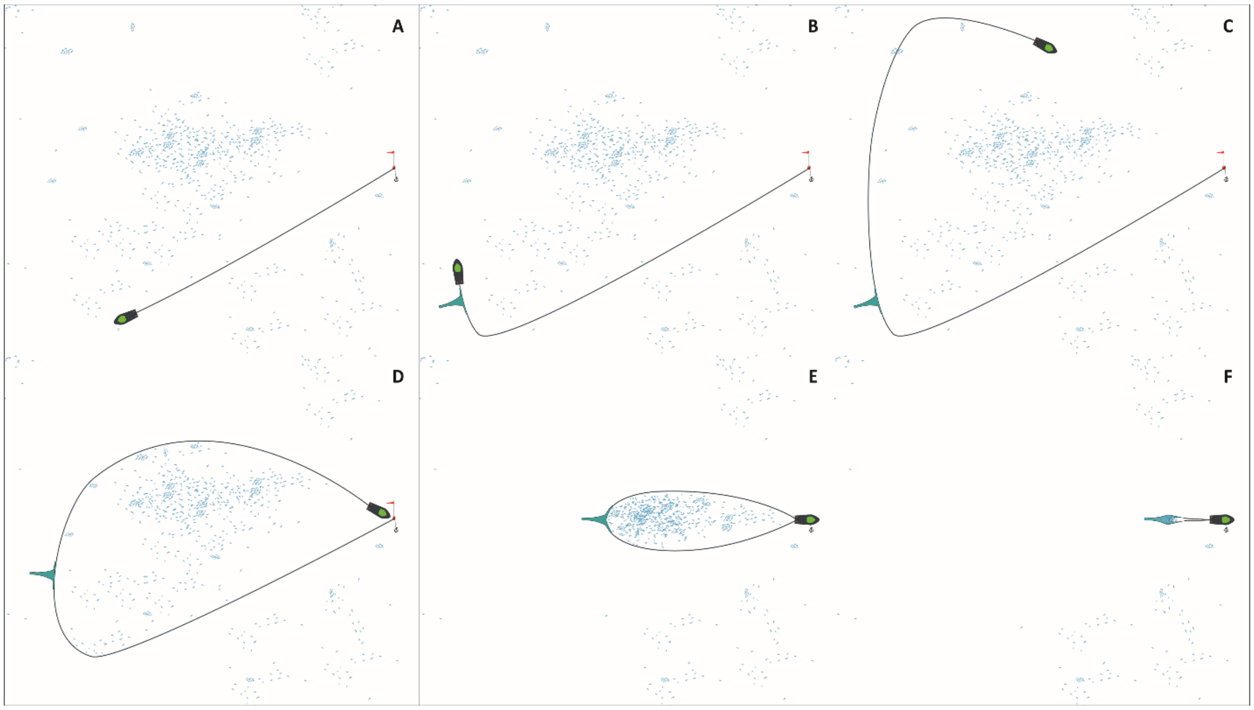


Figure 1: The main phases of the Danish seine fishing process (A) setting rope 1 (B) deploying the ground gear and net (C) setting rope 2 (D) returning to the anchor (E) herding phase (F) catching phase. (Reproduced from Noack et al., 2019).

The physical effects of a bottom-towed gear can typically be characterised as being hydrodynamic or mechanical (O'Neill and Ivanovic, 2015). The hydrodynamic effects mainly occur at the wake of the gear where the associated turbulence can create a sediment plume. The mechanical effects occur at the interface of the gear and seabed and cause the gear to penetrate the seabed and displace sediment (O'Neill and Ivanovic, 2015). The associated mechanical (or contact) forces are of particular interest, as fishing gear penetration depth has been correlated with benthic faunal depletion (Hiddink et al., 2017). The ground gear and the net, which sweep about 1% of the Danish seine footprint (Noack et al., 2019), are thought to be responsible for most of the penetration into the sediment (Eigaard et al., 2016). Very little, or no penetration, is thought to occur from the Danish seine ropes (Suuronen et al., 2012), and thus it is expected that minimal effect on macrofaunal occurs within 99% of the footprint where the rope passes.

In addition to the reduction of benthic faunal density and biomass, bottom-towed gears can also alter benthic ecosystem structures and functioning (Thrush et al., 2006). Ecosystem functioning can be described as the processes (e.g. nutrient cycling), properties (e.g. stability) and energy flow through an ecosystem (Bremner et al., 2003). Benthic organisms play a major role in many ecosystem processes and are commonly used to detect changes in environmental condition (MSFD; 2008/56/EC). This is as the reduction of benthic macrofauna has been shown to affect ecosystem functioning through the loss of certain biological characteristics (Norling et al., 2007). These characteristics are also commonly referred to as biological traits, which can be used by proxy to assess the impacts of fishing on ecosystem functioning (Tillin et al., 2006). Some traits are known to make taxa more sensitive to the effects of bottom-towed gears e.g., living at the sediment surface exposes taxa to direct contact with bottom-towed gears (de Juan et al., 2007). Similarly certain traits, e.g., short life span, enable taxa to recolonise rapidly post trawling (Hiddink et al., 2019). Using biological traits to characterise the community can therefore provide a complementary approach to taxonomic analysis, and improve our understanding of how bottom-towed gears can impact the integrity of ecosystems.

In European marine waters, demersal fisheries impact 28% to 85% of shelf seas, or areas less than 200 m deep (Eigaard et al., 2017). Meanwhile, 551,898 km^2 of European seabed (~ 9.5% of total area) are designated as protected areas under the Natura 2000 network (European Commissions, 2018). The Natura 2000 network encompasses a range of coastal landscapes, habitats and species which have been selected for their importance in protecting biodiversity. Some of these species are highly sensitive to trawling, for example horse mussel beds, *Modiolus modiolus* (Cook et al., 2013). Although trawling can be prohibited in Natura 2000 sites containing sensitive benthic species, many sites are primarily designated for the protection of bird and cetacean species, or specific habitat features that are not directly impacted by bottom-towed gears. As a result, a large number of Natura 2000 sites are regularly trawled (Dureuil et al., 2018). While some stakeholders (NGOs) suggest bottom-towed gears should be prohibited in all Natura 2000 sites, a possible alternative to this is the promotion of fishing fleets operating with ‘low-impacting’ gear types.

The primary objective of this study was to quantify the impact of the Danish seine to benthic macrofauna via experimental trawling. By targeted sampling within the areas affected by two different gear components, we aim to assess whether the loss of benthic macrofauna differed across the Danish seine gear footprint. We also tested whether multiple impacts of the Danish seine reduced benthic macrofaunal metrics to a greater extent by comparing the outcomes of single and multiple hauls in two nearby impact areas. To achieve this, two BACI experiments were carried out at two sandy locations off the North-East Jutland, Denmark, using a commercial Danish seiner. Our findings provide new evidence on the ecological impacts of Danish seines, and provides insights into whether the Danish seine can offer a low impact alternative to more damaging bottom-towed fishing gears.

4.2. Material and Methods

4.2.1. Study area

The study took place in Ålbæk Bay located at the North-Eastern tip of Jutland, Denmark (Figure 2), a shallow (20 m) and sheltered bay in northern Kattegat. The location was selected for the absence of commercial fishing in the nine years prior to the study determined by Vessel Monitoring System (VMS), Automatic Identification System (AIS), and local fishermen knowledge. Two adjacent sites adjacent were selected for experimental trawling in comparable coastal conditions to nearby fishing grounds (Figure 2). The sites each covered ~5.5 km^2 and were oriented perpendicular to the coast, resulting in a depth range between 6-10 m. The sediment type at both locations was sand. At the northerly site, the Danish seine was deployed once and referred to hereafter as the 'single haul' site. At the southerly site, the Danish seine was deployed three times in succession and referred to as the 'multiple haul' site.

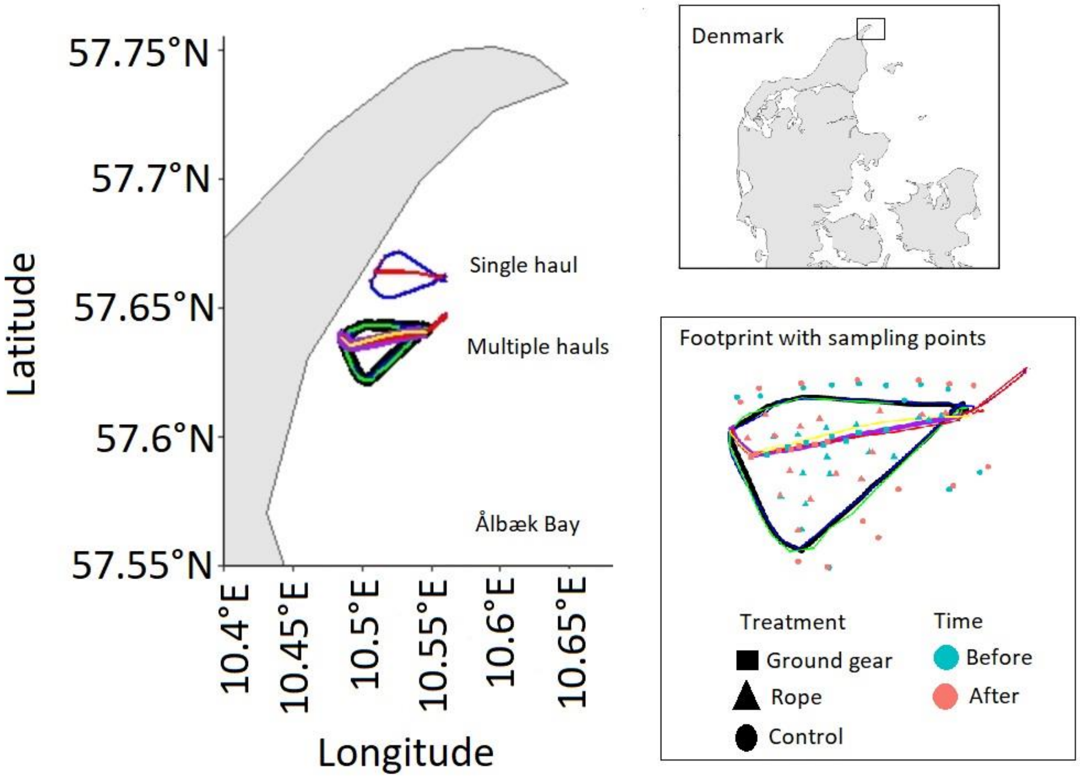


Figure 2: Map of the study sites in Ålbæk Bay showing the gear footprints at each site (left). An example of the sampling point is given on the bottom left (bottom right).

4.2.2. Experimental design and data collection

To understand the direct ecological effects of fishing with bottom-towed gears on benthos, a Before-After-Control-Impact (BACI) experiment set can be used. A BACI experiment aims to isolates the effect of fishing by using a factorial design that includes a comparison in time (before and after experimental fishing) and in space (impacted and unfished sites). A significant interaction between time (e.g., before, after) and treatment (e.g. control, impact) indicates an effect of fishing (Green, 1979). However, it is possible that significant interactions occur when there has been a greater change in the control treatment (Chevalier et al., 2019). According to Underwood (1992), to satisfy a causal relationship with the known disturbance, the change over time should be greater in the impact treatment than in the control treatment. To negate this possible issue, and to quantify the grounds for a significant BACI interaction, we followed the approach from Chevalier et al. (2019) by applying two additional metrics. First, the Control-Impact (CI) Contribution, which calculates the absolute change over time at each treatment and therefore quantifies which treatment 'contributes' most to the significant interaction. Second, the CI Divergence measures the dissimilarity between treatment means after disturbance. Assuming a negative effect of the experimental fishing, it was would be expected that the impact treatment contributes most to the significant interaction (as measured by the CI Contribution), and that the treatment means became more dissimilar after impact (as measured by the CI Divergence).

Our BACI sampling design provides additional resolution via targeted sampling in each of the main gear components, i.e., the rope and ground gear within the Danish seine footprint (Figure 2). Benthic samples were collected once before and once after fishing at both the single and multiple haul site. Each site was divided into five zones with two control zones (the area just north and south of the gear footprint), two rope zones (the footprint on either side of the ground gear), and the ground gear zone (the middle part of the footprint) (Figure 2). Benthic macrofaunal samples were collected using a Van Veen grab (sampling area: 0.1 m^2) on the 18th and 19th June 2019 (before fishing) and 26th and 27th June 2019 (after fishing). Experimental fishing was carried out at both sites on the 21st June 2019 by the commercial Danish seiner S15 *Vera Maria* (length 16.3 m, engine power: 140 kW). The Danish seine gear was made up of 15 coils of 26 mm leaded seine rope on each side of the net. Each coil was 220 m in length (giving 3300m on each side each) and weighed approx 0.56 kgm−1 in air and 0.12 kgm−1 in water. The ground gear was 38m long and made up of rubber disks that were approximately 15 cm in diameter and 4 cm thick and which were 10 – 12 cm apart and separated by small rubber cookies (approx. 4.5 cm in diameter and 2 cm thick). The impact caused by the rope and ground gear was determined by mapping the gear footprint whilst hauling using GPS loggers (Canmore G-PORTER GP-102+; accuracy: 2.5 m) following the methodology described in Noack et al. (2019). Briefly, we retained one GPS on the boat and attached one to each of the wings of the seine net. In the interest of having paired 'before' and 'after' samples, we used pre-defined anchor points for each site, and overlaid theoretical modelled gear footprints based on Noack et al. (2019).

After collection, each sediment sample was sieved through a 4 mm and 1 mm sieve to divide the faunal sample into two size fractions. Benthic macrofauna ≥4 mm have been shown to be comparatively sensitive to fishing disturbance (McLaverty et al., 2020), although this approach has not been tested in the context of a BACI experiment. Benthic macrofaunal samples were preserved in borax-saturated 4% formaldehyde prior to taxonomic identification and enumeration in the laboratory. Biomass (wet weight) was determined for the 4 mm fraction of the community. At the single haul site, seven Van Veen grab samples were taken from the control and rope treatments (3 or 4 replicates per zone), and seven macrofaunal samples were taken from within the ground gear at each time (N = 42). At the multiple haul site, 6-9 replicates were taken per zone (N = 77). To visually examine the physical impact of the seine, side-scan sonar (Edgetech 4125 SAR 600/1600) was used to scan a section of each site before and after fishing. The side scan sonar was towed 3-4 m above the seabed with a range of 55 m on either size. A scanning a frequency of 600kHz was used at a towing speed of 1 knot.

4.2.3. Data analysis

Univariate analysis

Generalised linear models were fitted using a Bayesian framework to assess the effect of the Danish seine on 10 benthic macrofaunal indicators. We modelled the effect on community indicators (density, species richness and biomass) for the pooled community (>1 mm) and for large taxa (> 4 mm) separately. In addition, the response of two of the most commonly occurring tube-building species (*Lanice conchilega* and *Phoronis* spp.) and three functional traits (scavenger density, suspension feeder density, tube builder density) from the pooled community were also modelled. All the indictors were chosen based on their documented responsiveness to fishing (Ketchington et al., 2006; Reiss et al., 2009; Sköld et al., 2018; Hiddink et al., 2020; McLaverty et al., 2021). We used a Poisson distribution for count data and a gamma distribution for biomass data. When overdispersion was detected, a negative binomial distribution was used in place of Poisson (Supplementary Figure 1). All models included the BACI factorial predictors (Time, Treatment, Site). We used 'leave-one-out' (LOO) cross-validation (Vehtari et al., 2017) and WAIC (Watanabe, 2010) to select the most parsimonious model for each of the response variables. Additional covariates included in the models were water depth (m) and *L. conchilega* tube biomass (g). The inclusion of *L. conchilega* relates to its role as a habitat forming species, which has the potential to correlate with local species richness and density (Callaway, 2006). As no prior information was available on the impact from the Danish seine, we defined weakly-informative priors with a normal distribution for the parameters and intercept (Supplementary Table 1) and a half-Cauchy prior for the dispersion parameter in negative binomial models (Gelman et al., 2008). Models were run using the R package 'brms' (Bürkner, 2017). We used 20,000 iterations across 4 chains with a 'burn-in' of 10,000, yielding a total of 40,000 post 'warm-up' iterations per model. Additional steps were taken to check for zero inflation or deflation (Supplementary Figure 2A), and spatial autocorrelation. Moran I's tests using the DHARMa package (Hartig, 2019) were used to validate the models (Supplementary Figure 2B). No spatial auto-correlation was identified for any of the response variables.

BACI ratios

Following the protocol described in Conner et al. (2016), we employed Markov Chain Monte Carlo (MCMC) sampling and BACI ratio computation to assess the impact of the Danish seine. We compared the rope impact and the ground gear impact at the two sites (Single/ Multiple haul) separately, such that we ended with four BACI ratios for each indicator (i.e., response variable); a rope and a ground gear impact from the single and multiple haul site. The posterior samples for each time and treatment were extracted for all models, with N number of samples equal to the post-warm up iterations (Supplementary Table 1). Then, the 'before' and 'after' ratios were calculated as follows:

$$R_{i\,|Before} = \frac{\hat{Y}_{i|I_{Before}}}{\hat{Y}_{i|C_{Before}}};\ R_{i\,|After} = \frac{\hat{Y}_{i|I_{After}}}{\hat{Y}_{i|C_{After}}};\ i = 1, \dots, N \qquad (1)$$

Where $R_{i\,|Before}$ is the 'before ratio' and $R_{i\,|After}$ is the 'after ratio' for the *i*-th iteration for each of the impact treatments (rope or ground gear) at each of the sites (single or multiple haul). $\hat{Y}_{i|I}$ and $\hat{Y}_{i|C}$ represent the fitted values on the response scale for the *i*-th iteration of the impact and control, respectively. The BACI ratios were then calculated by:

$$R_{i|BACI} = \frac{R_{i|After}}{R_{i|Before}}; i = 1, \dots, N \qquad (2)$$

yielding a posterior distribution of N BACI ratios for each model. A BACI ratio of 1 implies that the 'before' and 'after' ratios are equal, i.e. no difference in the slope for time between the impact and control treatments. A BACI ratio of < 1 therefore indicates a decline in the impact response variable relative to the control after fishing. We calculated the probability of benthic indicators declining in the impact treatments relative to the control, by computing the proportion of BACI ratios (out of N ratios) corresponding to a ratio < 1 for each indicator. Here we qualify the probability as high referring to values 0% to 10% and 90% to 100%.

CI Contribution and CI Divergence

To improve the interpretation of BACI interactions, we included two additional metrics in the analysis proposed by Chevalier et al. (2019). The first measure, 'CI Contribution' is calculated as follows:

$$CI\ Contribution_i = \left|\hat{Y}_{i|I_{After}} - \hat{Y}_{i|I_{Before}}\right| - \left|\hat{Y}_{i|C_{After}} - \hat{Y}_{i|C_{Before}}\right| \quad i = 1, \dots, N \tag{3}$$

A positive CI Contribution value indicates that there has been a greater change in the impact (rope/ground gear) treatment relative to the control treatment and goes some way to satisfy Underwood's criteria to determine an effect (Underwood, 1992).

The second measure, 'CI Divergence' was calculated as follows:

$$CI\ Divergence_i = \left|\hat{Y}_{i|I_{After}} - \hat{Y}_{i|C_{After}}\right| - \left|\hat{Y}_{i|I_{Before}} - \hat{Y}_{i|C_{Before}}\right|;\ i = 1, \dots, N \tag{4}$$

A negative fisheries effect would be seen as a high CI Contribution and a high CI Divergence (here high refers to probabilities > 90%) such that the largest change occurs in the impact treatment, and the difference in mean values increases after fishing. We used the 40,000 post warm-up MCMC samples to calculate the probability of a positive CI Contribution and positive CI Divergence, similar to the probabilities derived from the BACI ratios.

Multivariate analysis

To assess the effect of the Danish seine on benthic macrofaunal community composition and biological trait composition we used a Bayesian ordination and multivariate regression analysis. The macrofaunal community composition consisted of counts of individual taxa present in more than three samples (rare taxa removed). The biological traits were coded for the identified taxa at the genus level or higher using the EU BENTHIS database (Bolam et al., 2017), and calculated following the procedure described in Bolam et al. (2014). First, we performed a Bayesian unconstrained ordination by fitting a pure Latent Variable Model (LVM). The LVM represents a model-based ordination approach that treats the ordination scores as unobserved random effects, i.e., 'latent variables' (Hui et al., 2015). Therefore, this approach estimates the correlation between species without any predictor variables. In addition, the LVM identifies any indicator species associated with different clusters (Hui et al., 2015). To consider differences in both density and species composition, we omitted the row effect (Hui, 2016). We then fitted three Correlated Response Models (CRM), which included the latent variables and one of our other predictors (BACI interaction; Depth; *Lanice conchilega* tube biomass). Unconstrained ordinations from the LVM were compared to the residual ordinations from the CRMs to determine whether community patterns were explained by any of the predictors. Initially we used a Poisson distribution to model the density of species in the community, but information criteria and model validation plots indicated that a negative binomial distribution would provide an improved model fit (Supplementary Figure 1 and 2). The boral package for R (Hui, 2016) was used to implement the LVMs and CRMs.

All statistical analyses were carried out in R programming language (R Core Team, 2020).

4.3. Results

4.3.1. Univariate

Rope - single haul

After a single haul of the Danish seine rope the pooled community species richness was reduced, as was the density, biomass and species richness of the large fauna (> 4 mm fauna) (Figure 3). The effect on these indicators ranged between - 3% (CI: -27% to 25%) for pooled species richness to - 11% (CI: -32% to 52%) for large fauna density, but all included zero in the 95% credible interval, signalling uncertainty in the mean (Table 1). The probability of a negative BACI ratio (i.e., a decline in the impact treatment response variable relative to the control) was between 62% and 69% (Table 1). As a BACI probability of 50% means there is equal probability of a positive or a negative effect, the probabilities here provided little evidence of a negative effect from a single haul of a Danish seine rope. The probability of a positive CI Contribution (i.e., a greater change in the impact treatment relative to the control) and positive CI Divergence (i.e. treatment means were less similar after fishing relative to before fishing) can be used to support whether, or not, a BACI ratio was associated with the fishing activity. The strongest support for a fisheries effect occurs when both the CI Contribution and CI Divergence probabilities approach 100%. In contrast, probabilities closer to 50% indicate uncertainty of the cause of the BACI effect. The CI Contribution and CI Divergence for community indicators were all close to 50% (Table 1), indicating uncertainty on whether the effects were caused by fishing.

At the species level, there was a > 80% probability that the density of the sandmason worm (*Lanice conchilega*) and the horseshoe worm (*Phoronis* spp.) declined after impact from a single haul of the Danish seine rope (Table 1). However, the CI Contribution (*L. conchilega*: 21%, *Phoronis* spp.: 80%) and CI Divergence (*L. conchilega*: 52%, *Phoronis* spp.: 25%) were not shown to support a fisheries effect for either taxon.

Rope - multiple hauls

After multiple hauls of the Danish seine rope there was a mean loss in all of the community indicators, except for the species richness of the large fauna (Table 1). The effect ranged between –4% (CI: -43% to 15) for large fauna density and -13% (CI:-55% to 140%) for large fauna biomass, but again all included zero in the 95% credible interval. There was an 80% probability that pooled density declined after fishing relative to the control, although the cause of the decline was unclear from the CI Contribution (72%) and

CI Divergence (49%) (Table 1). The probability of a negative fishing effect on the remaining community indicators ranged between 40 – 61 % (Table 1).

For species, there was a 99% probability that *Phoronis* spp. density declined relative to the control (Figure 3G). The mean effect was - 90% (CI: -99% to – 60%) and the CI contribution (72%) and CI divergence (95%) supported that these results were possibly linked to experimental fishing.

For traits, there was a 98% probability that tube builder density declined after multiple hauls of the rope (Figure 3J). The loss of tube builder density was estimated to be - 35% (CI: -59% to -3%) relative to the control (Table 1). Support for a fisheries effect was indicated by the CI Contribution (77%) and CI Divergence (96%). The probability of suspension feeder density declining was 94%, although there was no concerted support that it was associated with fishing (CI Contribution 14%, CI Divergence 92%).

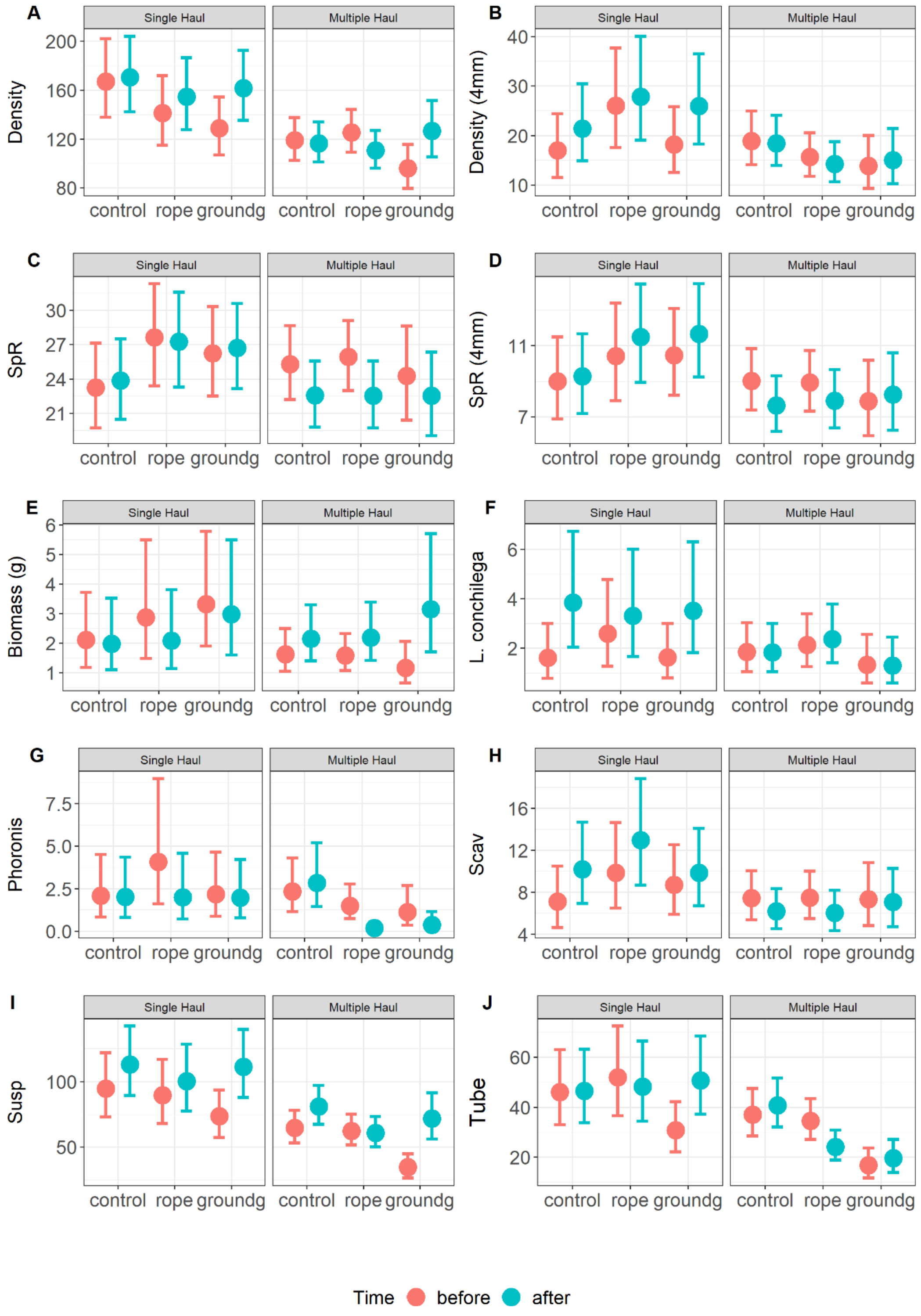


Figure 3: Mean response (+/-95% credible interval) following a single and multiple impact from the Danish seine for (A) Density (pooled), (B) Density (4 mm component), (C) Species richness (pooled) (D) Species richness (4 mm component), (E) Biomass (4 mm component), (F) Lanice conchilega density, (G) Phoronis spp. density, (H) Scavenger density, (I) Suspension feeder density, (J) Tube builder density.

Ground gear - single haul

After a single haul of the ground gear the density of large fauna was estimated to decline by -8 % (CI: -112% to 66%) and the pooled species richness by - 1% (-24 to 28%) (Table 1). However, the observation that both indicators increased after fishing in the impact treatment (Figure 3B, 3C), combined with the large credible intervals suggests uncertainty in these mean values. Pooled density, large fauna species richness, and biomass were all estimated to increase after a single haul of the ground gear (Figure 3A, 3D, 3E). The increase were estimated to be 24% (CI: -14% to 72%), 10% (CI-39% to 63%) and 11% (CI: -69% to 185%), respectively (Table 1). There was an 11% probability that pooled density decreased, implying an 89% probability that density increased after a single haul of the ground gear relative to the control. However, whether the increase in density was associated with fishing impact was unclear from the CI Contribution (79%) and CI Divergence (16%).

For traits, the density of all three traits increased after a single haul of the ground gear: mean (CI); scavengers: 76% (- 35% to 250%); suspension feeder: 85% (- 18% to 96%), and tube builders: 96% (- 8% to 148%), as shown in (Table 1). An explanation for the observed increase was uncertain from the CI Contribution (scavengers: 31%, suspension: 80%, tube: 88%) and CI Divergence (scavenger: 48%, suspension: 32%, tube: 25%).

Ground gear - multiple hauls

After multiple hauls of the ground gear, the community indicators increased relative to the control (Figure 3). The estimated increase ranged from 4% (CI; - 20% to 36%) in pooled species richness to 132% (CI: -24% to 460%) in large fauna biomass. The probability of a positive trend for biomass after fishing was 92%, and CI Contribution 90%, CI Distribution 69% gave some indication this could have been associated with fishing. Similarly, the probability that pooled density increased after fishing was 97.6%, although concerted support for a fisheries effect was not apparent from the CI Contribution (93%) CI Distribution (25%).

For species, there was a 94% probability that the *Phoronis* spp. declined after multiple hauls of the ground gear (Figure 3G) with an estimated loss of -64% (CI -97% to 41%). However, there was not concerted support for a fisheries effect from the CI contribution (47%) and CI Distribution (51%).

For traits, there was a 99% probability that suspension feeders increased after multiple hauls of the ground gear. Suspension feeders were estimated to increase by 69% (CI: 10% to 148%) relative to the control. Whether this related to the fishing activity was unclear from the CI Contribution (95%) and CI

Divergence (5%). Similarly, scavenger density was estimated to increase: mean: (CI) 22% (-38% to 220%), and so was tube builder density: 10% (-39% to 83%) (Table 1).

Table 1: Summary of the mean effect sizes with the 95% Bayesian credible interval, probabilities of a negative BACI ratio (i.e. negative effect of fishing relative to the control), probability of a positive CI contribution (i.e. absolute change in impact samples was greater than control), and probability of CI divergence (i.e. sites became more dissimilar after disturbance)

	Variable	No. hauls	Mean effect (95% CI)	P(BACI ratio <1)	P(CI contribution >0)	P(CI divergence >0)
Rope	Density (P)	Single	8% (-32% to 52%)	35%	54%	39%
		Multiple	-10% (-43% to 15%)	*80%*	72%	49%
	Density (4mm)	Single	-11% (-32% to 52%)	69%	51%	38%
		Multiple	-4% (-43% to 15%)	61%	47%	58%
	Species richness (P)	Single	-3% (-27% to 25%)	62%	57%	39%
		Multiple	-3% (-22% to 20%)	60%	60%	48%
	Species richness (4mm)	Single	-9% (-31% to 65%)	38%	62%	62%
		Multiple	6% (-26% to 48%)	40%	41%	51%
	Biomass (4mm)	Single	-8% (-76% to 150%)	67%	65%	38%
		Multiple	-13% (-55% to 140%)	46%	52%	61%
	Lanice conchilega	Single	-37% (-83% to 59%)	*87%*	21%	52%
		Multiple	20% (-53% to 165%)	40%	58%	60%
	Phoronis spp.	Single	-35% (-89% to 110%)	*83%*	*80%*	25%
		Multiple	-90% (-99% to -60%)	99%	72%	95%
	Scavengers	Single	20% (-50% to 220%)	41%	52%	52%
		Multiple	0% (-40% to 70%)	54%	53%	48%
	Suspension feeders	Single	-4% (-41% to 40%)	61%	39%	60%
		Multiple	-22% (-45% to 8%)	94%	14%	92%
	Tube builders	Single	-4% (-49% to 65%)	61%	57%	45%
		Multiple	-35% (-59% to -3%)	98%	77%	96%
	Density (P)	Single	24% (-14% to 72%)	11%	79%	16%
		Multiple	36% (3% to 81%)	2.4%	93%	25%
	Density (4mm)	Single	-8% (-112% - 66%)	65%	68%	66%
		Multiple	16% (-61% to 99%)	36%	53%	38%
	Species richness (P)	Single	-1% (-24% to 28%)	52%	54%	48%
		Multiple	4% (-21% to 36%)	38%	43%	44%
	Species richness (4mm)	Single	10% (-29% to 63%)	*36%*	62%	66%
		Multiple	20% (-20% to 89%)	16%	39%	41%
	Biomass (4mm)	Single	11% (-69% to 185%)	54%	65%	45%
		Multiple	132% (-24% to 460%)	8%	90%	69%

Ground gear	*Lanice conchilega*	Single	5% (-70% to 167%)	7%	41%	73%
		Multiple	13% (-67% to 185%)	52%	50%	51%
	Phoronis spp.	Single	21% (-78% to 281%)	53%	54%	50%
		Multiple	-64% (-97% to 41%)	94%	47%	*86%*
	Scavengers	Single	35% (-35% to 250%)	24%	31%	48%
		Multiple	22% (-38% to 220%)	68%	48%	51%
	Suspension feeders	Single	29% (-18 % to 96 %)	15%	80%	32%
		Multiple	69% (10 % to 148%)	1%	95%	5%
	Tube builders	Single	70% (-8% to 187%)	4%	*88%*	25%
		Multiple	10% (-39% to 83%)	41%	39%	55%

4.3.2. Multivariate

The community composition differed after impact from multiple hauls of the Danish seine rope. This was shown in the unconstrained ordination from the Latent Variable Model (LVM) where clusters associated with the rope treatment were not overlapping before and after fishing (Figure 4A). The species driving the difference in the two clusters were the starfish *Asterias rubens*, the amphipod *Melita obtusata*, which were more abundant after fishing, and *Phoronis* spp., and the ribbon worm *Nemertea* sp., which were less abundant after fishing (Figure 4C). The Correlated Response Models (CRMs) showed that the difference in community composition was associated with the fishing activity, as clusters overlapped in the residual ordination when the BACI interaction was included in the model (Figure 4B). Clustering in the residual ordination continued in the CRMs which included depth or *Lanice* conchilega tube weight, suggesting that these variables were unimportant for driving community patterns (Supplementary Figure 3). No cluster separation was apparent in the unconstrained ordination of the LVM for the single haul pooled community, or for either single or multiple hauls in the 4 mm community or the biological traits (Supplementary Figure 4).

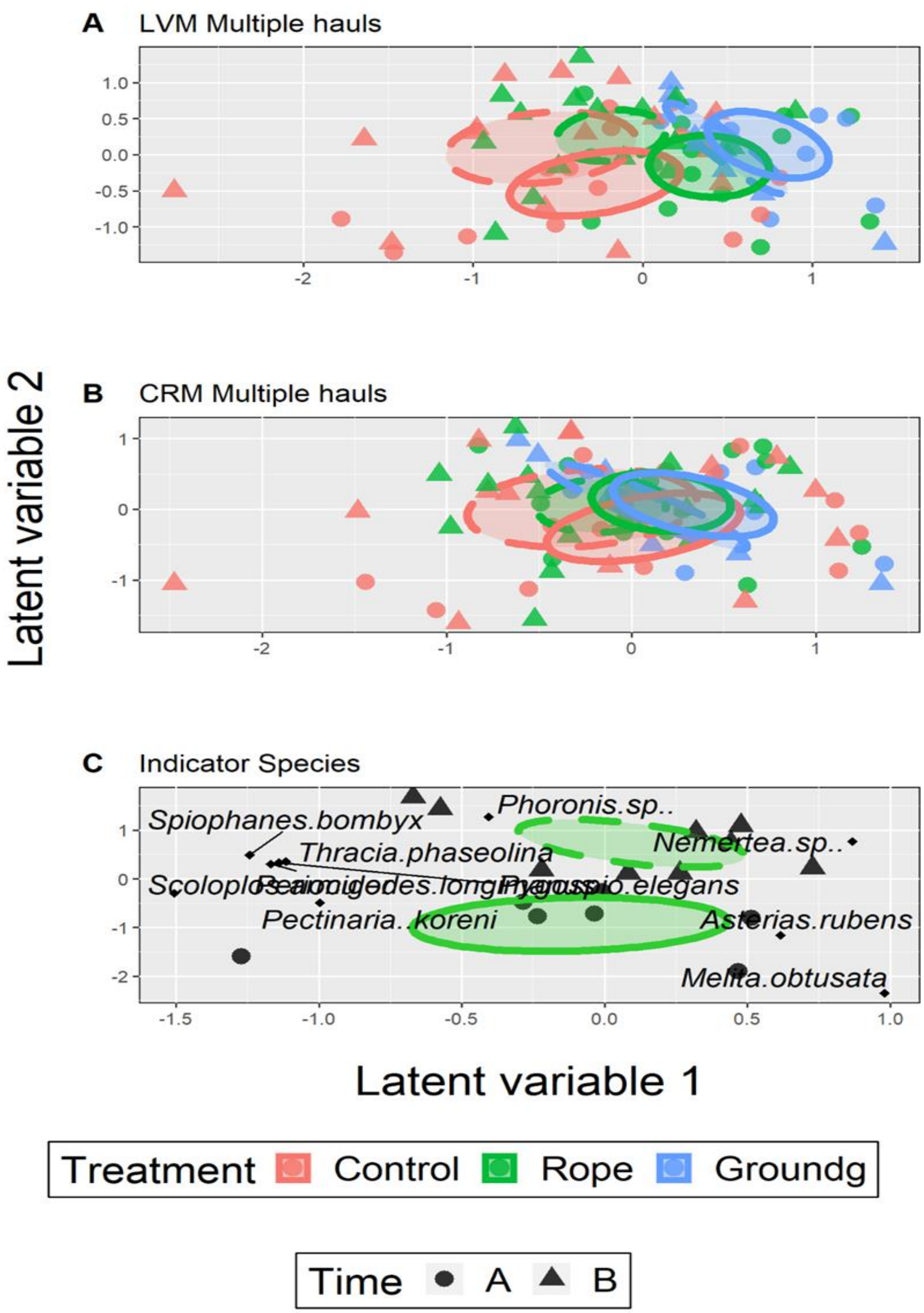


Figure 4: The multivariate regression analysis showing (A) the unconstrained ordination of the Latent Variable Model (LVM) for the pooled community - multiple haul site (B) the ordination of the Correlated Response Model for the pooled community at the multiple haul site with the BACI interaction included in the model and (C) the unconstrained ordination of the LVM showing the 25 species that contributed most to differences between clusters. Time: A (after), B (before).

4.3.3. Side scan sonar images

At the single haul site the section of seabed covered by side scan sonar coincided with the active hauling phase. The active phase occurs as the boat has returned to the anchor point, and the gear is hauled in by winch, causing the gear to gradually narrow around the catch. A scour mark was evident in the single haul site, which was identified to be where the ground gear passed, using the GPS loggers (Figure 5). The scour mark from the ground gear occurred in the final stage of the haul where the water depth was deepest (being furthest from the coast), and where benthic communities would be impacted to a lesser degree by wave action. In contrast, the section of seabed examined by side scan sonar in the multiple haul site was earlier in the hauling phase, and in shallower water depth. During this part of the haul the gear may not be actively hauling (prior to the vessel reaching the anchor). No scour marks were observed in the section of the multiple haul site covered by the side scan sonar.

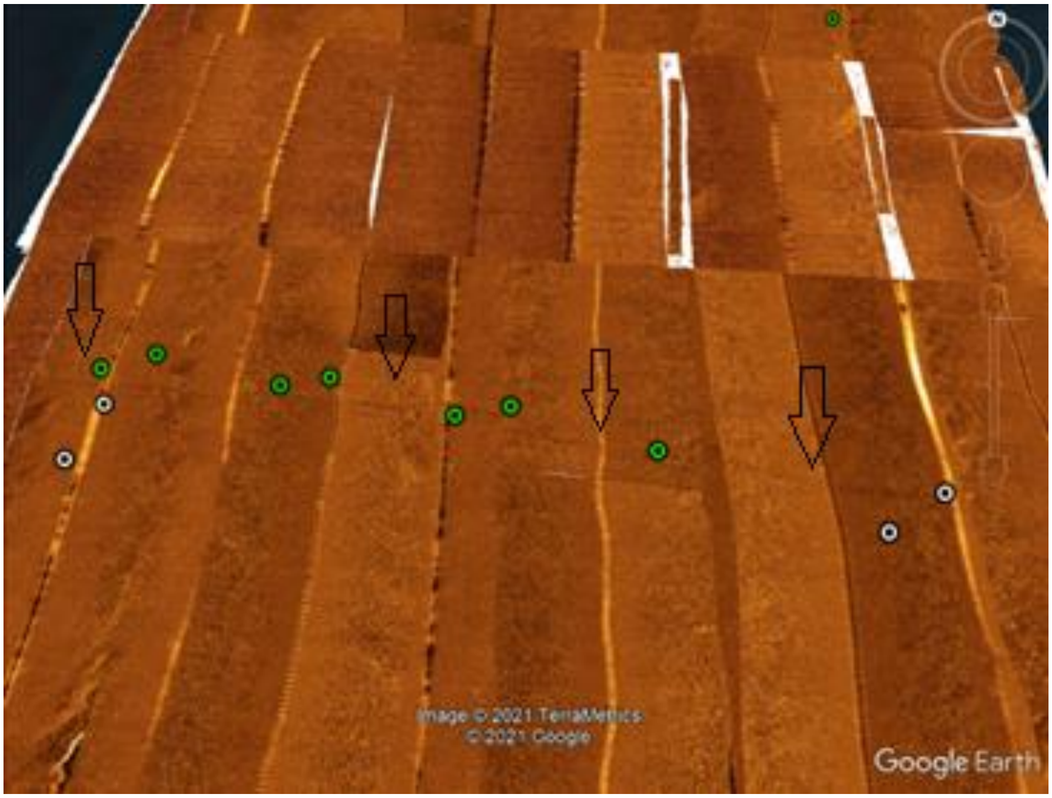


Figure 5: Side scan sonar image from the Single haul site showing a scour mark (darker line below arrows) running through where we have GPS co-ordinates from the ground gear (green circles)

4.4. Discussion

The Danish seine is considered a 'low-impact' fishing gear due to its lightweight, lack of deep penetrating gear components (e.g. doors/shoes/weights/clumps/tickler chains), and its associated low fuel consumption (Suuronen et al., 2012; Eigaard et al., 2016; Noack et al., 2017; Dinesen et al., 2018). Given the low penetrative force, in theory, the loss of benthic macrofauna should also be relatively low. Our study supports this assumption, by observing only small reduction in several community indicators (density, biomass and species richness) after impact from the Danish seine. Nonetheless, we also found that the loss could be high for individual species (*Phoronis* spp.) and similarly for individual traits ('tube-builders'). These indicators both exhibited high rates of loss, and were supported for a fisheries effect using the CI Contribution and CI Distribution. In addition, our study detected differing effects from the two main gear components, and unexpectedly found higher losses of benthic fauna from the seine ropes. Below we discuss these findings, and describe the results in terms of their relevance to the seabed ecology and the management implications.

4.4.1. Effect of the Danish seine ropes

The Danish seine ropes are described from *in situ* video footage to skim the surface of a sandy seabed and create 'dust clouds not visible after two minutes' (Noack et al., 2019). Despite this, our results found the greatest probability of a fisheries effect within the rope treatment. In particular, there was a high likelihood (>98%) that *Phoronis* spp. density and tube-builder density were depleted by the Danish seine ropes. These observations are inherently linked, as *Phoronis* spp. is a tube building taxon and was one of the most common taxa in the community. The sensitivity of *Phoronis* spp. has been previously documented, with densities negatively correlated with gradients of fishing intensity (Hinz et al., 2009; Sköld et al., 2018; McLaverty et al., 2020). The relatively high loss of *Phoronis* spp. may be explained by their biological traits, given that they are sessile and surface dwelling (de Juan et al., 2007; McLaverty et al., 2021), which places them in direct contact with demersal fishing gears regardless of sediment penetration depth. Functionally, the loss of *Phoronis* spp. (-90%) has the potential to negatively affect nutrient flux to the seabed, as *Phoronis* spp. live in vertical tubes that extend twice their body length (Temereva et al., 2020).

Given the close relationship between macrofaunal depletion and gear penetration depth (Hiddink et al., 2017), it was unexpected that the greatest effect occurred in the rope-impacted area, where penetration is only thought to be at the surface level, if any (Eigaard et al., 2016). Considering the physical effect of the fishing gear more closely, we know that in addition to sediment penetration, fishing gears have a hydrodynamic effect which can lead to the suspension of sediment (O'Neill and Ivanović, 2016). The effect of suspended sediment on benthic macrofauna from fishing activity are, by comparison, poorly understood. However, it has been shown that the twenty most abundant taxa in the sediment plume of a scallop dredge were mainly swimming crustaceans (amphipods and mysids), along with two tube-dwelling polychaete species (*L. conchilega* and Terrebellinae sp.)(O'Neill et al., 2013). The polychaetes were sampled higher in the water column (45-60 cm) than the swimming crustaceans (35-40 cm) which may suggest that some characteristic of such polychaetes cause them to be entrained higher into the water column; possibly related to their body weight, volume and shape. The swimming crustaceans are thought to be transported passively until the turbulence in the sediment plume dissipates, at which point they can actively return to the seabed (O'Neill et al., 2013). The sessile taxa, however, are completely at the fate of the prevailing water movement. This could make them prone to loss from the area, especially in the presence of currents. Possible support for this comes from the observed change in community composition after impact from the seine rope, which was in part due to a lower occurrence of two worm-like taxa (*Phoronis* spp. and Nemertea indet.).

Whilst our results showed high levels of loss for only one taxa, the relatively large spatial scale which the ropes affect (km^2) may be grounds for more concern. Moreover, fragile, erect taxa, like *Phoronis* spp. are less common in the majority of sandy habitats compared to fine, muddy sediment and may suggest that greater losses could occur in fine sediment habitats. These results may indicate that other mechanisms than gear penetration may be acting to deplete benthic fauna.

4.4.2. Effect of the Danish seine ground gear

The ground gear is thought to impose the greatest mechanical force on the seabed due to its greater weight (Eigaard et al., 2016) and, thus, it was where we expected to see the largest impact from the Danish seine. Counter to our expectations, benthic macrofauna were not reduced in the area impacted by the ground gear. Instead, there was a positive trend in the community indicators after fishing. We observed, with high probability (> 92%), an increase in density, biomass, and suspension feeder density. Whilst the increase in suspension feeder density has no ecological explanation, the result may be an example of an issue with the way biological traits are analysed, whereby spurious results can occur due to inherent correlations with other traits (detailed in Hinz et al., 2021). In contrast, the increase in community density and biomass after impact from the ground gear may be explained by an increase in scavenger density (Kaiser and Spencer, 1994; Ramsay et al., 1997; Groenewold and Fond 2000). Although we observed a mean increase in scavenger density after both the single (35%) and multiple (22%) ground gear hauls, there was uncertainty in the mean values given the wide credible intervals, and potentially little support that this was due to fishing. In addition, we deliberately waited 72 hours before sampling after fishing, to allow potential scavengers to disperse (Goenewold and Fond, 2000). An alternative explanation for the positive response may be related to the suitability of the control, given the difference in macrofaunal density betweem treatments before fishing. This was also indicated by the CI metric, as although density increased to a greater extent in the impact treatment (CI Contribution: single: 78% multiple: 93%), the means converged (CI Divergence: single: 16% multiple: 25%) which has been suggested to signify a poorer comparison (Chevalier et al., 2019). The greater geographical distance between the ground gear and control treatments may be a reason for the dissimilarity, compared to the control-rope treatments (Figure 1). As an alternative, we could have used control treatments east and west of the DS footprint (as opposed to north and south) to reduce the distance between treatments, but we instead we prioritised the depth gradient and minimised its range within near-coastal study site.

4.4.3. Single vs Multiple hauls

Experimental studies assessing the effect of fishing on benthic fauna are faced with large natural variation in community composition and environmental parameters (Currie and Parry, 1996). Detecting small effects can be difficult to pinpoint in amongst the natural variance. As such, we were unable to detect an effect of a single haul of a Danish seine. While it is likely that the impact was not greater than natural variability, the power to detect an effect may also have been affected by the number of replicates, and subsequent high variation observed within treatments. In spite of that, we were able to detect an effect of multiple hauls of the Danish seine rope on *Phoronis* spp. density and tube builder density. Identifying an impact after multiple hauls may indicate a cumulative impact, whereby the effect increases with increased fishing. Understanding the cumulative impact of the Danish seine may therefore be an important aspect to consider for future studies, as cumulative impacts are expected at the fisheries scale.

4.4.4. Implications for management

A key tenant of an Ecosystems Approach to Fisheries Management (EAFM) is to minimise the environmental impact from fishing to the wider ecosystem, whilst maintaining economically feasible fisheries. Striking a balance between the two has been an ongoing challenge. Marine Protected Areas (MPAs) have been used as a tool to support EAFM, and have rapidly increased in numbers since the 1990’s (Halpern et al., 2008). However, some estimates have suggested commercial trawling occurs in 59% of

MPAs in Europe, and that trawling intensity is higher inside MPA's than outside (Dureuil et al., 2018). While not all MPAs are designated to protect the seabed, the indirect benefits of reducing the seabed impact in these areas has the potential to contribute to wider conservation goals. For example, the reduction of benthic impacts through management has increased the density of commercially sized target species (Beukers-Stewart et al., 2005), and increased habitat complexity leading to higher densities of juvenile demersal fish and shellfish (Howarth et al., 2015). Given that the state of the seabed in European fishing grounds are some of the most deteriorated worldwide (Pitcher et al., 2022), alternative fishing methods could be prioritised to improve the environmental status of seabed habitats. We therefore suggest that the replacement of beam and otter trawls with lighter or low-impact gears, particularly in ecologically important areas such as MPAs, could help to improve seabed status. This has the potential to provide a desirable middle ground for management, reducing impacts to benthic species and ecosystem functionality, and thereby allowing fishing to continue in commercially important areas. Our results show that Danish seines can provide a gear with low benthic impact , which also has relatively high fuel (Dinesen et al., 2018) and catch efficiency (Noack et al., 2017), that could be favoured in areas subject to nature conservation designations, and where the use of low impacting gears may improve fisheries sustainability.

References

Beukers-Stewart, B. D., Vause, B. J., Mosley, M. W. J., Rossetti, H. L., Brand, A. R. (2005). Benefits of closed area protection for a population of scallops. Marine Ecology Progress Series, 298, 189–204. https://doi.org/10.3354/meps298189

Bremner, J., Rogers, S. I., Frid, C. L. J. (2003). Assessing functional diversity in marine benthic ecosystems: A comparison of approaches. Marine Ecology Progress Series, 254, 11–25. https://doi.org/10.3354/meps254011

Bolam, S.G., Coggan, R.C., 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. Journal of Sea Research, 85, 162–177. https://doi.org/10.1016/j.seares.2013.05.003

Bolam, S.G., Garcia, C., Eggleton, J., Kenny, A.J., Buhl-Mortensen, L., Gonzalez-Mirelis, G., van Kooten, T., Dinesen, G., Hansen, J., Hiddink, J.G., Sciberras, M., Smith, C., Papadopoulou, N., Gumus, A., Van Hoey, G., Eigaard, O.R., Bastardie, F., Rijnsdorp, A.D. (2017). Differences in biological traits composition of benthic assemblages between unimpacted habitats. Marine Environmental Research, 126, 1–13. https://doi.org/10.1016/j.marenvres.2017.01.004

Büerkner (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software, 80, 1-28. doi:10.18637/jss.v080.i01

Callaway, R. (2006). Tube worms promote community change. Marine Ecology Progress Series, 308, 49–60. https://doi.org/10.3354/meps308049

Chevalier, M., Russell, J. C., Knape, J. (2019). New measures for evaluation of environmental perturbations using Before-After-Control-Impact analyses. Ecological Applications, 29, 1–12. https://doi.org/10.1002/eap.1838

Conner, M. M., Saunders, W. C., Bouwes, N., Jordan, C. (2016). Evaluating impacts using a BACI design, ratios, and a Bayesian approach with a focus on restoration. Environmental Monitoring and Assessment, 188(10). https://doi.org/10.1007/s10661-016-5526-6

Cook, R., Fariñas-Franco, J.M., Gell, F.R., Holt, R.H.F., Holt, T., Lindenbaum, C., Porter, J.S., Seed, R., Skates, L.R., Stringell, T.B., Sanderson, W.G., (2013). The Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A Dilemma for Evidence-Based Conservation. PLoS ONE, 8(8), e69904. https://doi.org/10.1371/journal.pone.0069904

Currie, D.R., Parry, G.D., 1996. Effects of scallop dredging on a soft sediment community: A large-scale experimental study. Marine Ecology Progress Series. 134, 131–150. https://doi.org/10.3354/meps134131

de Juan, D., Thrush, S., Demestre, M. (2007) Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Marine Ecology Progress Series. 334, 117–129. https://doi.org/10.3354/meps334117

Dinesen, G.E., Rathje, I.W., Højrup, M., Bastardie, F., Larsen, F., Sørensen, T.K., Hoffmann, E., Eigaard, O.R. (2018). Individual transferable quotas, does one size fit all? Sustainability analysis of an alternative model for quota allocation in a small-scale coastal fishery. Marine Policy, 88, 23–31. https://doi.org/10.1016/j.marpol.2017.10.038

Dureuil, M., Boerder, K., Burnett, K.A., Froese, R., Worm, B. (2018). Elevated trawling inside protected areas undermines conservation outcomes in a global fishing hot spot. Science, 362, 1403–1407. https://doi.org/10.1126/science.aau0561

European Commission. (2018). Marine protected areas in Europe's seas. An overview and perspectives for the future. EEA Report No 3/2015

Eigaard, O. R., Bastardie, F., Breen, M., Dinesen, G. E., Hintzen, N. T., Laffargue, P., Mortensen, L. O., Nielsen, J. R., Nilsson, H. C., O'Neill, F. G., Polet, H., Reid, D. G., Sala, A., Sköld, M., Smith, C., Sørensen, T. K., Tully, O., Zengin, M., Rijnsdorp, A. D. (2016). Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES Journal of Marine Science. https://doi.org/10.1093/icesjms/fsv099

Eigaard, O. R., Bastardie, F., Hintzen, N. T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G. E., Egekvist, J., Fock, H. O., Geitner, K., Gerritsen, H. D., González, M. M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J. R., Papadopoulou, N., Posen, P. E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C. J., Vanelslander, B., Rijnsdorp, A. D. (2017). The footprint of bottom trawling in European waters: Distribution, intensity, and seabed integrity. ICES Journal of Marine Science, 74, 847–865. https://doi.org/10.1093/icesjms/fsw194

FAO. (2010). Total World Fisheries. The State of World Fisheries and Aquaculture, 10.

Gelman, A., A. Jakulin, M. G. Pittau, and Y. S. Su. (2008) A weakly informative default prior distribution for logistic and other regression models. Annals of Applied Statistics 2:1360–1383. DOI: 10.1214/08-AOAS191

Green, R. H. (1979). Sampling design and statistical methods for environmental biologists. John Wiley & Sons.

Groenewold, S., Fonds, M. (2000). Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES Journal of Marine Science, 57, 1395–1406. https://doi.org/10.1006/jmsc.2000.0914

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R. (2008). A Global Map of Human Impact on Marine Ecosystems. Science, 319(5865), 948–952. https://doi.org/10.1126/science.1149345

Hartig, F. (2016). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1. 0.

Hiddink, J. G., Jennings, S., Sciberras, M., Szostek, C. L., Hughes, K. M., Ellis, N., Rijnsdorp A. D., McConnaughey, R. A., Mazor, T., Hilborn, R., Collie, J. S., Pitcher, C. R., Amoroso, R. O., Parma, A. M., Suuronen, P., Kaiser, M. J. (2017). Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proceedings of the National Academy of Sciences, 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114

Hiddink, J.G., Jennings, S., Sciberras, M., Bolam, S.G., Cambiè, G., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Parma, A.M., Suuronen, P., Kaiser, M.J., Rijnsdorp, A.D. (2019). Assessing bottom trawling impacts based on the longevity of benthic invertebrates. Journal of Applied Ecology. 56, 1075–1084. https://doi.org/10.1111/1365-2664.13278

Hiddink, J. G., Kaiser, M. J., Sciberras, M., McConnaughey, R. A., Mazor, T., Hilborn, R., Collie, J. S., Parma, A. M., Suuronen, P., Rijnsdorp, A. D., Jennings, S. (2020). Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. Journal of Applied Ecology, 57, 1199–1209. https://doi.org/10.1111/1365-2664.13617

Hinz, H., Prieto, V., Kaiser, M. J. (2009). Trawl disturbance on benthic communities: Chronic effects and experimental predictions. Ecological Applications. https://doi.org/10.1890/08-0351.1

Hinz, H., Törnroos, A., de Juan, S. (2021) Trait-based indices to assess benthic vulnerability to trawling and model loss of ecosystem functions. Ecological Indicators. 126, 107692. https://doi.org/10.1016/j.ecolind.2021.107692

Howarth, L. M., Pickup, S. E., Evans, L. E., Cross, T. J., Hawkins, J. P., Roberts, C. M., & Stewart, B. D. (2015). Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve. Marine environmental research, 107, 8-23.

Hui, F. K. C., Taskinen, S., Pledger, S., Foster, S. D., Warton, D. I. (2015). Model-based approaches to unconstrained ordination. Methods in Ecology and Evolution, 6, 399–411. https://doi.org/10.1111/2041-210X.12236

Hui, F. K. C. (2016). boral – Bayesian Ordination and Regression Analysis of Multivariate Abundance Data in r. Methods in Ecology and Evolution, 7, 744–750. https://doi.org/10.1111/2041-210X.12514

Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C. V. (2006). Global analysis of response and recovery of benthic biota to fishing. Marine Ecology Progress Series. 331, 1-14. https://doi.org/10.3354/meps311001

Kaiser, M. J., Spencer, B. E. (1994). Fish scavenging behaviour in recently trawled areas. Marine Ecology Progress Series, 112, 41–50. https://doi.org/10.3354/meps112041

Kenchington, E. L. R., Gilkinson, K. D., MacIsaac, K. G., Bourbonnais-Boyce, C., Kenchington, T. J., Smith, S. J., Gordon, D. C. (2006). Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean. Journal of Sea Research, 56, 249–270. https://doi.org/10.1016/j.seares.2006.03.010

McLaverty, C., Eigaard, O.R., Gislason, H., Bastardie, F., Brooks, M.E., Jonsson, P., Lehmann, A., Dinesen, G.E., (2020). Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. Ecological Indicators. 110, 105811. https://doi.org/10.1016/j.ecolind.2019.105811

McLaverty, C., Dinesen, G., Gislason, H., Brooks, M., Eigaard, O. (2021). Biological traits of benthic macrofauna show sizebased differences in response to bottom trawling intensity. Marine Ecology Progress Series. 671, 1–19. https://doi.org/10.3354/meps13790

Noack, T., Frandsen, R. P., Wieland, K., Krag, L. A., Berg, F., Madsen, N. (2017). Fishing profiles of Danish seiners and bottom trawlers in relation to current EU management regulations. Fisheries Management and Ecology, 24, 436–445. https://doi.org/10.1111/fme.12244

Noack, T., Stepputtis, D., Madsen, N., Wieland, K., Haase, S., Krag, L. A. (2019). Gear performance and catch process of a commercial Danish anchor seine. Fisheries Research, 211, 204–211. https://doi.org/10.1016/j.fishres.2018.11.012

Norling, K., Rosenberg, R., Hulth, S., Grémare, A., & Bonsdorff, E. (2007). Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. Marine Ecology Progress Series, 332, 11-23. doi:10.3354/meps332011

O'Neill, F. G., Robertson, M., Summerbell, K., Breen, M., & Robinson, L. A. (2013). The mobilisation of sediment and benthic infauna by scallop dredges. Marine Environmental Research, 90, 104–112. https://doi.org/10.1016/j.marenvres.2013.06.003

O'Neill, F. G., Ivanović, A. (2016). The physical impact of towed demersal fishing gears on soft sediments. ICES Journal of Marine Science, 73(suppl_1), i5–i14. https://doi.org/10.1093/icesjms/fsv125

O'Neill, F. G., Noack, T. (2021). The geometry and dynamics of Danish anchor seine ropes on the seabed, ICES Journal of Marine Science, 78, 125–133. https://doi.org/10.1093/icesjms/fsaa198

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Pitcher, C.R., Hiddink, J.G., Jennings, S., Collie, J., Parma, A.M., Amoroso, R., Mazor, T., Sciberras, M., McConnaughey, R.A., Rijnsdorp, A.D., Kaiser, M.J., Suuronen, P., Hilborn, R. (2022) Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. Procedings of the National Academy of Sciences 119. https://doi.org/10.1073/pnas.2109449119

Ramsay, K., Kaiser, M. J., Moore, P. G., Hughes, R. N. (1997). Consumption of Fisheries Discards by Benthic Scavengers: Utilization of Energy Subsidies in Different Marine Habitats. The Journal of Animal Ecology, 66, 884-896. https://doi.org/10.2307/6004

Reiss, H., Greenstreet, S. P. R., Sieben, K., Ehrich, S., Piet, G. J., Quirijns, F., Robinson, L., Wolff, W. J., Kröncke, I. (2009). Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Marine Ecology Progress Series, 394, 201–213. https://doi.org/10.3354/meps08243

Sciberras, M., Hiddink, J. G., Jennings, S., Szostek, C. L., Hughes, K. M., Kneafsey, B., Clarke, L. J., Ellis, N., Rijnsdorp, A. D., McConnaughey, R. A., Hillborn, R., Collie, J. S., Pitcher, C. R., Amoroso, R. O., Parma, A. M., Suuronen, P., Kaiser, M. J. (2018). Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish and Fisheries, 19, 698–715. https://doi.org/10.1111/faf.12283

Sköld, M., Göransson, P., Jonsson, P., Bastardie, F., Blomqvist, M., Agrenius, S., Hiddink, J. G., Nilsson, H. C., Bartolino, V. (2018). Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. Marine Ecology Progress Series, 586, 41–55. https://doi.org/10.3354/meps12434

Suuronen, P., Chopin, F., Glass, C., Løkkeborg, S., Matsushita, Y., Queirolo, D., Rihan, D. (2012). Low impact and fuel efficient fishing-Looking beyond the horizon. Fisheries Research, 119–120, 135–146. https://doi.org/10.1016/j.fishres.2011.12.009

Temereva, E., Shcherbakova, T., Tzetlin, A. (2020). First data on the structure of tubes formed by phoronids. Zoology, 143, 125849. https://doi.org/10.1016/j.zool.2020.125849

Tillin H.M, Hiddink J.G, Jennings S, Kaiser M.J. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology Progress Series. 318, 284–286. https://doi.org/10.3354/meps318031

Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A., (2006). Functional Role of Large Organisms in Intertidal Communities: Community Effects and Ecosystem Function. Ecosystems 9, 1029–1040. https://doi.org/10.1007/s10021-005-0068-8

Underwood, A. J. (1992). Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. Journal of Experimental Marine Biology and Ecology, 161, 145–178. https://doi.org/10.1016/0022-0981(92)90094-Q

Vehtari, A., Gelman, A., Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing, 27, 1413–1432. https://doi.org/10.1007/s11222-016-9696-4

Walsh, S. J., & Winger, P. D. (2011). Bottom Seining in Canada, 1948-2010 : Its development, fisheries and ecosystem impacts. Canadian Technical Report of Fisheries and Aquatic Sciences. No. 2922

Watanabe, S. (2010). Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. Journal of Machine Learning Research, 11, 3571–3594.

Supplementary information

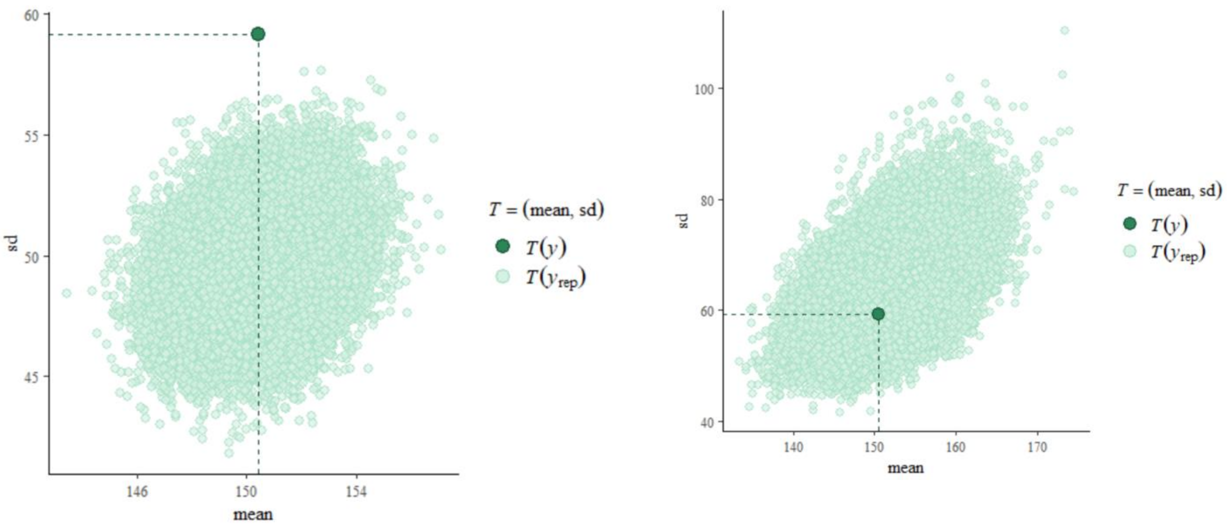
Supplementary Table 1: Prior distributions.

Parameter	Prior distribution	Model applied
Intercept	Normal (0,3)	Poisson, Neg Bin, Gamma
Beta	Normal (0,3)	Poisson, Neg Bin, Gamma
Dispersion	Half Cauchy (0, 2.5)	Neg Bin

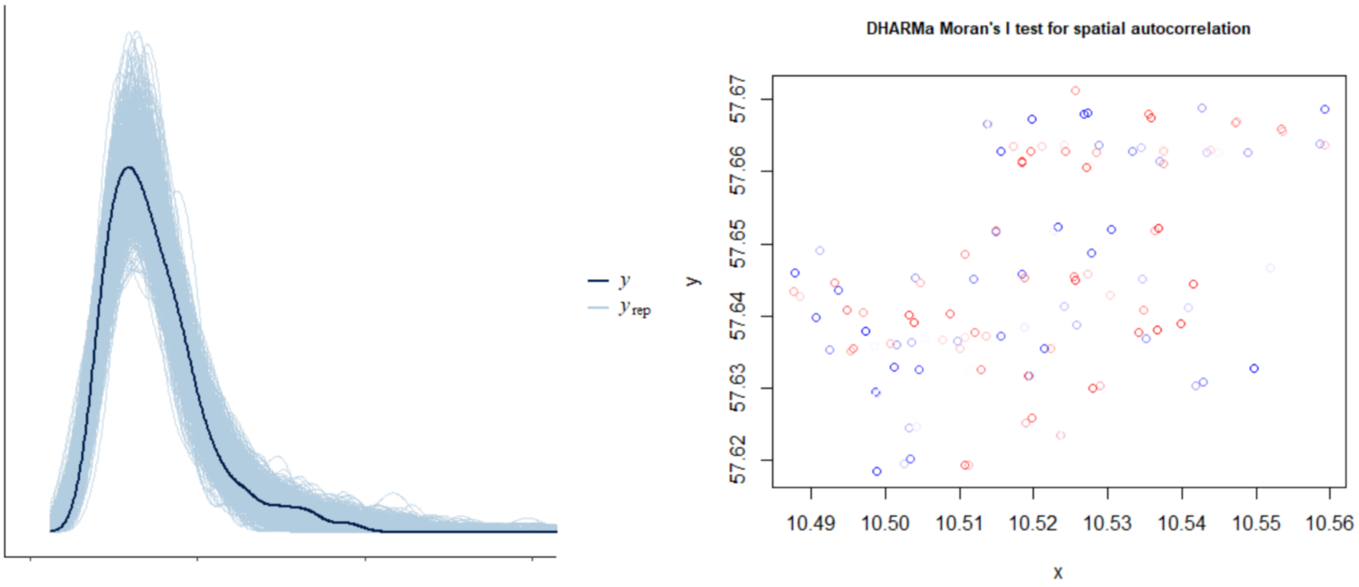
Supplementary Table 1
T = time, Trt = Treatment, S = Site, D = Depth, LT = Lanice tube , FD = faunal density, biomass, ‘x’ indicates an interaction

Response variable	Distribution	Priors	Fixed effects	Correlation structure	Post warm up interations
Density (pooled)	NB Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$ $\phi \sim hCauchy\ (0, 2.5)$	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000
Density (4mm)	NB Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$ $\phi \sim hCauchy\ (0, 2.5)$	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000
Species richness (pooled)	NB Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$ $\phi \sim hCauchy\ (0, 2.5)$	T, Trt, S D, LT, FD, T x Trt, T x S, Trt x S	None	40,000
Species richness (4mm)	NB Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$ $\phi \sim hCauchy\ (0, 2.5)$	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000
Biomass (4mm)	Gamma Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$	T, Trt, S D, T x Trt, T x S, Trt x S	none	40,000
Lanice conchilega	NB Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$ $\phi \sim hCauchy\ (0, 2.5)$	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000
Phoronis sp.	NB Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$ $\phi \sim hCauchy\ (0, 2.5)$	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000
Scavengers	NB Link (log)	$\beta_0 \sim N\ (0, 3)$ $\beta_{1\text{-}14} \sim N\ (0, 3)$ $\phi \sim hCauchy\ (0, 2.5)$	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000

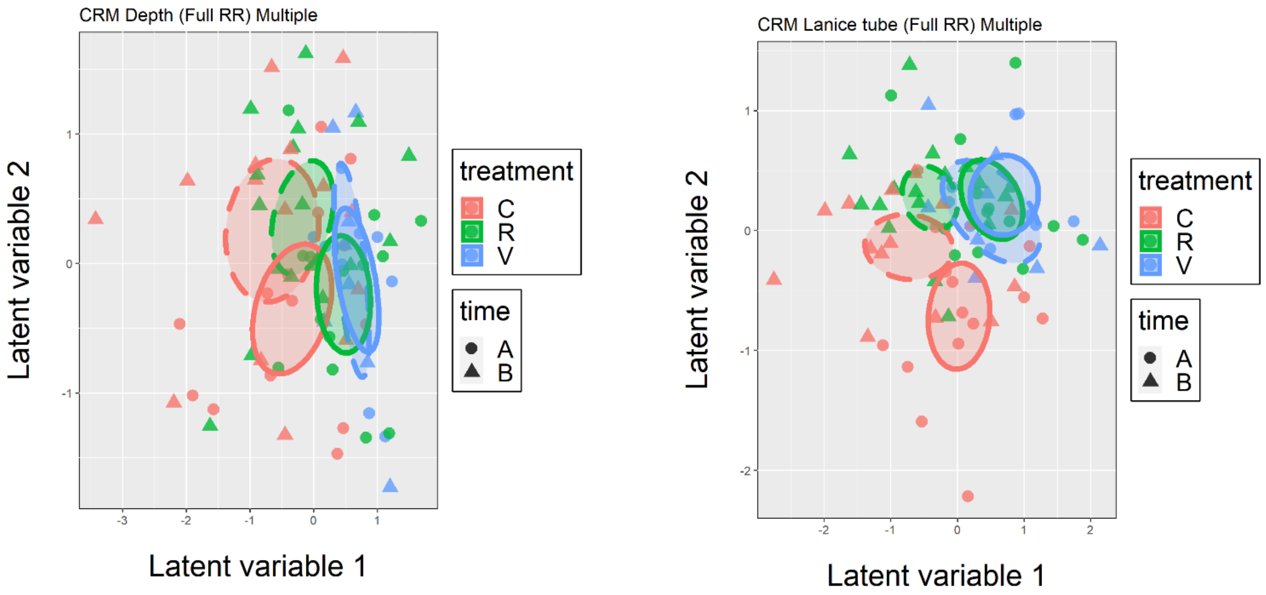
Suspension feeders	NB Link (log)	$\beta_0 \sim N(0, 3)$ $\beta_{1-14} \sim N(0, 3)$ $\phi \sim$ *hCauchy* (0, 2.5)	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000
Tube builders	NB Link (log)	$\beta_0 \sim N(0, 3)$ $\beta_{1-14} \sim N(0, 3)$ $\phi \sim$ *hCauchy* (0, 2.5)	T, Trt, S D, LT, T x Trt, T x S, Trt x S	none	40,000



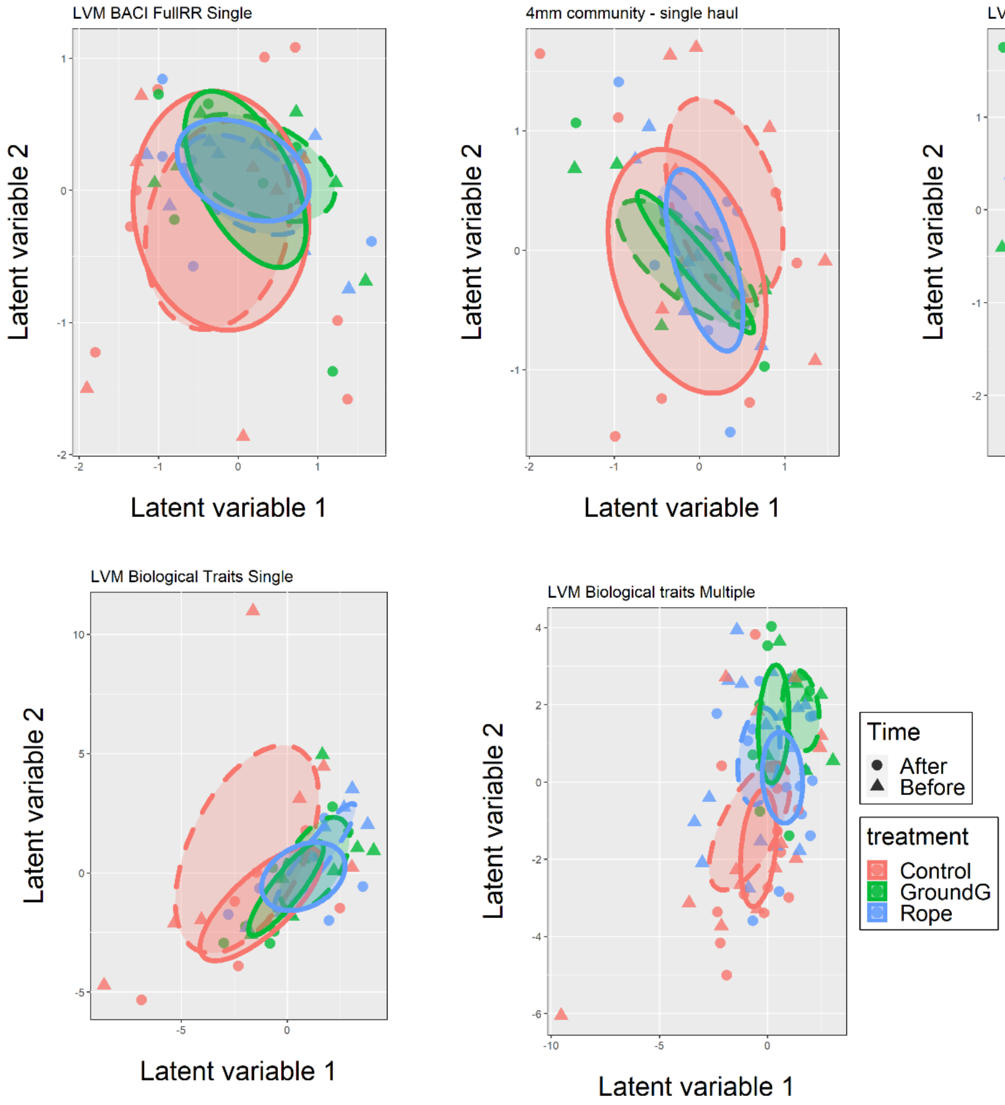
Supplementary Figure 1: Example of the distribution family validation to check it fits the dispersion in the data. Left side Poisson distribution (bad fit), right side Negative Binomial distribution (good fit).



Supplementary Figure 2: Example of model validation checks carried out for each model selected. A) checks for zero inflation/deflation; B: Moran I's test for spatial autocorrelation

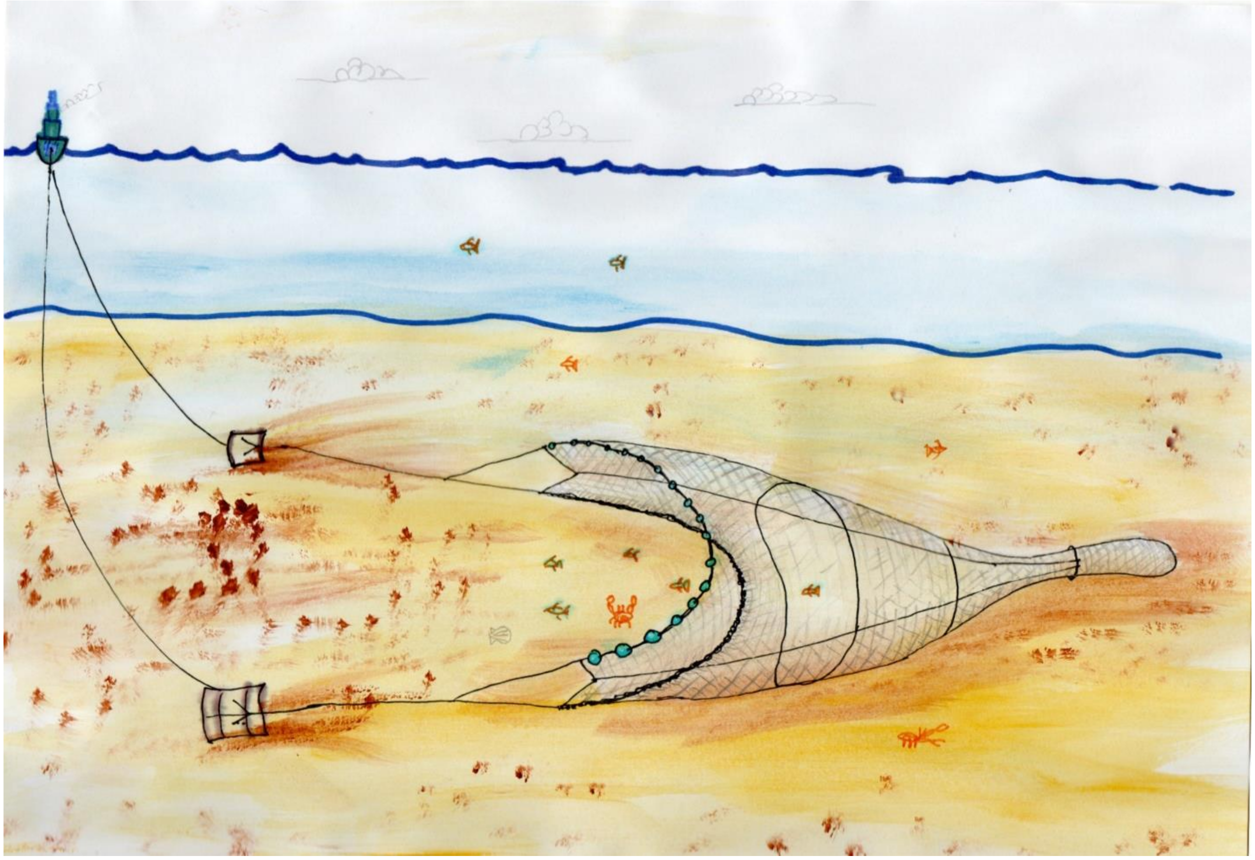


Supplementary Figure 3: Ordination of the Correlated Response Model for the Pooled community at the Multiple haul site with (A) Depth, and (B) *Lanice conchilega* tube weight included at predictors with the latent variables.



Supplementary Figure 4: Unconstrained ordination of the Latent Variable Model for (A) Pooled community single haul, (B) 4mm community Single haul, (C) 4mm community Multiple haul, (D) Biological traits Single haul, (E) Biological traits Multiple haul.

5. Comparing the impact on benthic fauna of a conventional sandeel trawl with a modified lightweight sandeel trawl on the Dogger Bank (southern North Sea)



Katrina Bromhall, Grete E. Dinesen, Ole R. Eigaard, Jan G. Hiddink (*In prep*) Comparing the impact on benthic fauna of a conventional sandeel trawl with a modified lightweight sandeel trawl on the Dogger Bank (southern North Sea)

Comparing the impact on benthic fauna of a conventional sandeel trawl with a modified lightweight sandeel trawl on the Dogger Bank (southern North Sea)

Katrina Bromhall[1], Grete E. Dinesen[1], Ole R. Eigaard[1], Jan G. Hiddink[2]

[1]Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, 2800 Kongens Lyngby, Denmark

[2]School of Ocean Science, University of Wales-Bangor, Menai Brdige, Anglesey, LL59 5AB, United Kingdom

Abstract

Bottom trawling for lesser sandeel (*Ammodytes marinus*) is an economically important fishery that takes place with high intensity on Dogger Bank in the southern North Sea. The sustainability of the fishery, in particular in relation to seafloor integrity, is increasingly being questioned as UK, Netherlands, and Germany have designated Dogger Bank as part of the Natura 2000 network of protected areas under the EU Habitats Directive. Here we used an *in-situ* Control-Impact experiment in two successive years to show that reduced benthic impacts could be achieved by using a modified sandeel otter trawl. The modified trawl replaced heavy bottom-towed doors and sweeps made of combination rope (steel and nylon) with lighter pelagic doors, Dyneema sweeps, and parts of the trawl netting with lightweight Dyneema netting. The modified trawl had a 33% smaller footprint on the seabed. From infaunal grab samples we observed a significant reduction of benthic biomass from the conventional sandeel trawl relative to the control, whereas the modified gear showed no such loss. The estimated loss from the conventional gear was 28%. However, this estimate is associated with substantial uncertainty as sampling was confined to the ground gear of the trawls, and not done across the full width of the gear-footprint. Accounting for the other gear components, the benthic faunal loss for the footprint would be ~ 14%. Further, both control and impact sites were contaminated with non-experimental trawling during the study period. Nonetheless, the results are highly relevant for the movement towards an ecosystems approach to fisheries management and for an objective of maintaining a productive fishery, whilst reducing the adverse effect of the fishery on the habitat and wider ecosystem.

5.1. Introduction

Bottom trawling with mobile bottom-contacting fishing gears disturbs and modifies marine benthic habitats, biodiversity and community composition (Engel and Kvitek, 1998; Thrush and Dayton 2002; Kaiser et al., 2006). Generally, macrofauna that live attached to the seabed surface (sessile), and are fragile, large in body size, long lived and suspension feeding, are more sensitive to fishing pressure and are reduced in numbers or removed as a result of trawling (Tilin et al., 2006; Kenchington et al., 2006). Recovery time for taxa with these sensitive traits often exceeds that of mobile opportunistic (e.g., short lived capacious recruiters) taxa (Sciberras et al., 2018). Nonetheless, the impact of trawling has been shown to also depend on the type of gear being deployed, where the greatest impacts occur from fishing gears that penetrate deepest into the seabed (Sciberras et al., 2018; Hiddink et al., 2017). Of the four most common commercial bottom trawls (otter trawls, beam trawls, towed dredges, hydraulic dredges otter trawling resulted in the lowest depletion of benthic macrofauna, and correspondingly had the smallest gear penetration depth (Hiddink et al., 2017).

The otter trawl is a widely used commercial bottom trawl, which can be rigged in different ways to target various species. In common, otter trawls all have otter boards (trawl doors) that ensures the gear stays open when towed through the water. In addition, they have sweeps and bridles that connect the doors to the trawl net and sometimes, depending on species, act to heard fish into the net. They also have a ground gear with the primary function of protecting the trawl net, which is often in contact with the seabed. The otter trawl type used to harvest the lesser sandeel (*Ammodytes marinus*) differs from a typical otter trawl designed for larger demersal fish. They have a high opening and appear more like a pelagic trawl with very large meshes in the front part of the trawl that gradually reduce in size towards the aft (i.e., codend) of the trawl. Like many gear adaptations, the design of the sandeel trawl takes advantage of the behavioural characteristics of the target species, which shoal in large densities just above the seabed (Freeman et al., 2004) and are prone to being herded by the large meshes in the trawl mouth (Eigaard et al., 2011). In addition to improving the catchability for shoaling fish, the gear design is thought to reduce the physical impact with the seabed compared to a more traditional otter trawl designed to catch larger demersal species for human consumption (Gislason et al., 2014). Nonetheless, the environmental impact of the sandeel fishery is being brought into question as it predominantly occurs on a distinct topographic feature in the North Sea known as the Dogger Bank.

Dogger Bank is a 17,600 km^2 sandbank located in the southern central North Sea (Stride, 1959). The outer boundary of Dogger Bank is defined by the 40 m depth contour, and the shallowest depth is ~ 18 m.

Situated between stratified waters to the North and mixed waters to the South, Dogger Bank hosts distinct benthic communities across the bank (Dyer et al., 1983). Unlike the surrounding area, there is continuous phytoplankton production year-round on Dogger Bank due to vertical mixing (Kröncke and Knust, 1995). The abundance of fish is likely what attracts the seabirds, and accordingly Dogger Bank is recognised as an important feeding ground for many seabirds, which forms the grounds for Natura 2000 designation. In addition, Dogger Bank has always been an important feature for commercial fisheries targeting cod, haddock, plaice, sole, dab and sandeel. For Denmark, the Dogger Bank supports the sandeel fishery, which in terms of landings, is the largest commercial fishery in the country (Gislason et al., 2014) with landings fluctuating around 200.000 metric tons in recent years (Skov et al., 2019). The different aspects of Dogger Bank falls within the exclusive economic zones (EEZs) of the UK, Germany, Netherlands, and Denmark, whereby the UK, Netherlands, and Germany designated Dogger Bank as part of the EU Habitats Directive under the Natura 2000 network of protected areas (Habitats Directive, 92/43/EEC). In the designation process, the Netherlands and Germany identified fishing with mobile bottom-contacting gears as one of the greatest threats to the Dogger Bank habitats (https://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=DE1003301; https://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=NL2008001). However, fishing with mobile bottom-contacting gear continues on Dogger Bank and the environmental status is monitored on an annual basis by the three designating EU member states.

In fisheries management, it has been suggested that gear modifications may offer an alternative strategy to spatial closures, whereby fishing may be allowed to continue with gears, which have a reduced physical impact on the seabed (McConnaughey et al., 2020). The trawl doors are the heaviest component of an otter trawl and penetrate the deepest into the sediment (up to 35 cm in muddy sediment) but represent only a small proportion of the overall gear footprint (1-3%)(Eigaard et al., 2016). The sweeps and bridles generally make up ~ 60-85 % of an otter trawl footprint, and these have only a low level of penetrative force (Buhl-Mortensen et al., 2013; Eigaard et al., 2016). Although, the lateral force of the sweeps and bridles can damage any protruding structures. The ground gear of an otter trawl constitutes the remaining ~ 15-40 % of the gear footprint and can penetrate up to 2 cm into sandy sediment, and more depending on the ground gear and sediment type (Buhl-Mortensen et al., 2013; Eigaard et al., 2016). Therefore, gear modifications that reduce the impact of an otter trawl may include lighter or pelagic doors, discs or bobbins on the sweeps and bridles (to lift them off the seabed) and fewer and lighter components and materials for the ground gear, trawl net and cod end (Valdemarsen et al., 2007). For example, the seabed contact of a shrimp otter trawl was reduced five-fold, by removing a number of bobbins on the ground gear (He et al., 2002). However, the subsequent impact of reducing the physical contact with the seabed was not tested on benthic macrofaunal indicators, and empirical studies on the changes in benthic macrofaunal from fishing gear modifications are somewhat scarce.

The aim of this study was to assess whether it was possible to reduce the impact to benthic macrofauna from the sandeel fishery by using a modified sandeel trawl, where heavy bottom-towed doors were replaced with lighter pelagic doors and parts of the trawl netting with lightweight Dyneema netting. Here, experimental trawling was conducted with a conventional sandeel otter trawl (SOT) and a modified SOT to directly compare the loss of benthic macrofauna. The reduction of benthic macrofauna from the two trawls was estimated relative to an un-trawled control site in two successive years. The results are of relevance for management of the Natura 2000 habitat type ‘1110 Sandbanks’, and fisheries management based on an ecosystems approach.

5.2. Materials and Methods

5.2.1. Study area

The study took place in a southern-Central North Sea area of the Dogger Bank (Figure 1A). The study site was a 3.6 nm^2 area located within the Dutch EEZ. The depth at the study site was ~35m and the sediment was homogenous across the site, consisting of 89-98% fine sand and 1-10% gravel with very low (<1%) concentration of fine particles. The site was chosen for the absence of sandeel trawling by Danish vessels for 5 years prior to the study. However, upon conducting side scan sonar prior to experimental fishing, it became apparent that the site had been trawled more recently as there were a number of trawl tracks visible. Based on the track dimensions they were likely to have been made by beam trawls and from the sonar data it is estimated that the intensity of the fishing with beam trawls was similar in the three treatment areas (two experimental and one control) of the study. Nonetheless, our best efforts were made to sample outside of the tracks.

5.2.2. Experimental design

To assess the benthic faunal depletion from a conventional sandeel otter trawl (hereafter conventional SOT) and a modified Dyneema sandeel otter trawl (hereafter Dyneema SOT) a Control-Impact experiment was conducted. Two experimental treatments and a control treatment were designated within the study site, whereby experimental trawling took place in the two former areas (Figure 1B). Benthic faunal depletion was estimated by comparing community indicators from the fished treatments with indicators from the non-fished control treatment. The benthic community indicators which were used were: biomass (ash free dry weight), species richness, community composition; and a life history trait: sediment position. To assess the impact to seabed structure from the two fishing gears side-scan sonar images were taken before and after experimental trawling.

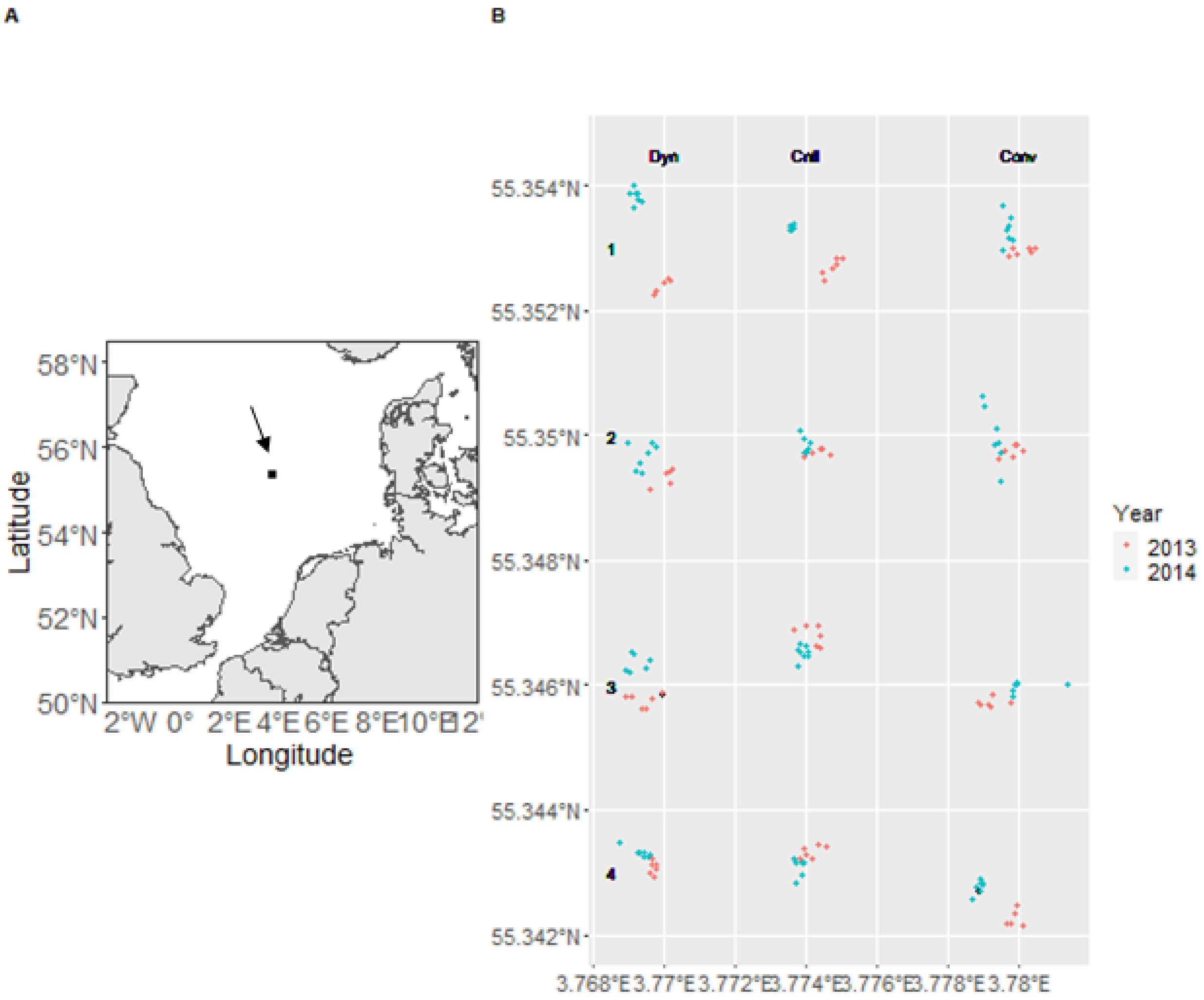


Figure 1: Left: location of study site in the North Sea. Right: the three treatment transects of the study ('Dyn' = transect with samples impacted from modified (Dyneema) sandeel otter trawl, 'Cntl' = transect with control samples, and 'Conv' = transect with samples impacted from conventional sandeel otter trawl). Samples were taken at Stations (1-4) in 2013 and 2014 and the dots show the sample points each year (pink dots for 2013 and blue for 2014).

5.2.3. Data collection and experimental trawling

Sample collection and experimental trawling took place in June 2013 and 2014 on-board the commercial fishing vessels Lonny Hedvig (L526) with Captain Rene Schmidt and vessel Lotte Vohnsen (L455) with Captain Lars Vohnsen. The conventional SOT had steel warps (26 mm in diameter), two demersal steel doors (weight 4.5 tons per door), sweeps and bridles of 118 meters combination rope (polypropylene coated steel wire), and the trawl netting was constructed of nylon (Figure 2A). The Dyneema SOT was modified to have warps made of Dyneema (a lightweight polyethylene-polymer) with a diameter of 26 mm, two pelagic steel doors (weight: 2 tons per door), 101 meters of sweeps and bridles made of combination rope (similar to the conventional SOT) and 21.5 meters of steel chain connecting the bridles and the lower wing-ends, as well as a trawl netting where several panels were made of Dyneema instead of nylon (Figure 2B). The ground gears of the two trawls were identical and made of combination rope, coated with small rubber discs.

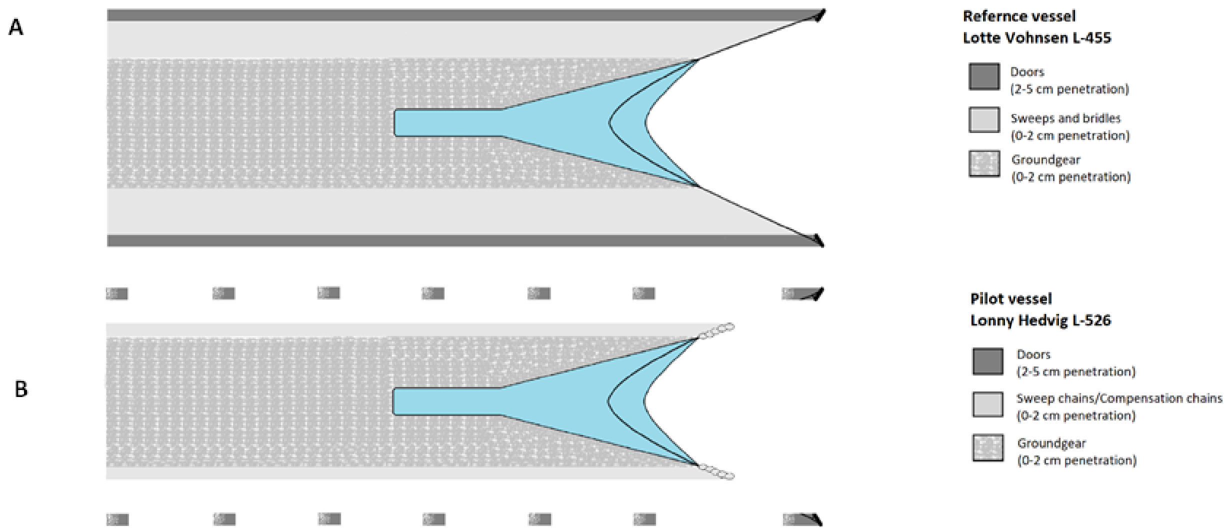


Figure 2: A conceptual footprint made by (A) the conventional sandeel trawl and (B) the modified Dyneema sandeel trawl.

The diameter of the Dyneema warps was equal to that of the conventional steel wires, but was only one tenth of the weight. The overall reduction in weight and total filament surface of the netting by switching to Dyneema meant there was a 10% lower drag compared to the conventional SOT as well as an approx. 20% larger trawl opening. As demersal doors play a role in ensuring that the fishing gears remains on the seafloor (weight function), the use of pelagic doors requires another form of weight to hold the gear down. This was achieved using approx. 20 meters of compensation chain, which was attached in front of each of the lower wing-ends, replacing an approx. similar length of the lower bridle. In front of this section of compensation chain all gear components were off the bottom (bridles, sweeps, doors, warps) resulting in the Dyneema SOT being assessed to have an approx. 30% narrower footprint, even though the wing spread and trawl height were greater than for the conventional SOT.

Benthic infaunal samples were taken after experimental trawling in June 2013 and 2014 using a Van Veen grab (0.1m^2). In total 120 infaunal samples were collected from within the three treatments (conventional SOT, Dyneema SOT, control). The treatments consisted of one transect, within which there were four stations (Figure 1). Five replicates were taken per station (N = 20 per treatment), and the whole setup repeated in 2013 and 2014 (N = 60 samples per year). The infaunal samples were sieved through a 4mm and 1mm sieve which made two infaunal community size fractions. These two fractions are referred to as the large component (> 4mm) and the full community (>1mm). The large component of the community has been shown to be a more responsive indicator of trawling that the full community (>1mm) (McLaverty et al., 2020a). In the laboratory, taxa were sorted from the sediment residue and identified to species level where possible. Biomass was measured as ash-free-dry-weight after incineration at 500°C.

5.2.4. Sediment Position

The life history trait 'sediment position' may contribute to an organisms sensitivity to fishing gear impact in that those which live at the sediment surface or top 0-5 cm are more likely to come into contact with the fishing gear. Comparatively, those that live deeper in the sediment (5-10 cm, >10 cm) may experience less physical disturbance. Therefore, we estimated the loss of biomass for four sediment positions (surface, 0-5 cm, 6-10 cm, >10 cm) after impact with the two otter trawls studied. To do this, a sediment position was determined for each taxa with a value assigned using a fuzzy-coding approach based on the database of Bolam et al. (2017). The fuzzy coded trait scores were multiplied by the taxon biomass and summed over all species to give a biomass-weighted trait score per sample for the analysis.

5.2.5. Statistical analysis

Generalised linear models were used to assess the impact of the conventional SOT and of the Dyneema SOT relative to the control. A Poisson distribution was applied for species richness and checked for over- or under-dispersion. A Conway-Maxwell-Poisson distribution was used in cases of under- or over dispersion. For biomass and the sediment position, a Gamma distribution was used. All models included 'Gear' as a main effect and a random effect of Station. An additional covariate, the factor 'Year' (2013, 2014), was included when it improved the model fit. Model selection used AIC to determine the most parsimonious model. Full models are detailed in Table 1. An ANOVA (walds chi-squared test) determined whether there was a significant treatment effect i.e. whether the response variable was different in the two gear treatments relative to the control. Following a significant treatment effect, pairwise comparisons were made using the *emmeans* package in R (Lenth, 2021). The above modelling was carried out using R 3.959 (R Core Team, 2018).

5.2.6. Loss of benthic biomass

To estimate the effect of trawling on benthic faunal biomass we calculated the loss of benthic biomass, as the relative difference in biomass for each gears and control treatment.

$$Loss\ of\ benthic\ biomass = 1 - \frac{gear_i}{control}$$

Data from the two years were combined to give a single depletion rate per gear. Whereby ‘$gear_i$’ is the mean response for the convention SOT or Dyneema SOT, and ‘control’ is the mean response for the control.

5.2.7. Physical footprint

To assess whether the footprint of the Dyneema SOT differed in physical impact from the conventional SOT we used side scan sonar imaging. Side scan sonar (SSS) transects were taken using an Edgetech 4125 SAR, 600 kHz combined with an AirMar PB150 Weather Station for geographical positioning. Scanning used a low frequency (600kHz) with a viewing width of 120 m either side and 10m above the seabed. SSS transects were taken before and after trawling in 2013 and 2014 at each of the three treatment locations.

5.2.8. Community composition

The experimental effect on benthic species composition was assessed using PERMANOVA (Anderson et al., 2008). The model includd a fixed effect of ‘Gear’ and ‘Year’ and their interaction. A random effect of ‘Station’ was also included. Observing a significant main effect of ‘Gear’ was followed by pairwise PERMANOVA. A square-root transformation reduced the contribution of heavy taxa (Clarke and Gorley, 2015), and a Bray-curtis similarity matrix was used to calculate similarity coefficients. A SIMPER analysis set with a 70% cut-off was used to identify species driving significant differences between ‘Gear’ treatments and ‘Years’.

5.3. Results

5.3.1. Whole community indicators

Full community biomass was on average 28% lower after impact with the conventional SOT relative to the control, whereas faunal biomass was on average 10% higher in the Dyneema SOT (Table 2). A significant effect of gear was observed from the statistical analysis (Table 1), although pairwise comparisons showed no significant contrast between the either gear and the control. There was however, a significant difference between the two gears (p = 0.02). The biomass of the large biota (> 4mm) was 43% lower after impact with the conventional SOT relative to the control, and large biota biomass increased by ~17% after impact with the Dyneema SOT (Table 2). The statistical analysis showed a significant effect of gear on the large biota biomass (Table 1). Pairwise contrasts showed significant differences between the conventional SOT and the control, and the conventional SOT and the Dyneema SOT (Figure 3). The loss of large faunal biomass after impact from the conventional SOT was greater in 2013 (-54%) compared to 2014 (-27%) (Figure 3B). The greater effect in 2013 compared to 2014 was due to a decline in biomass in the control treatment in the second year (Figure 3). The organisms driving the difference in biomass between the control and the conventional SOT in 2013 were *Gari fervensis*, *Owenia fusiformis*, *Amphiura chiajei*, *A. filiformis*, *Echinocardium cordatum*, and *Campanulariidae* indet.. It is important to note that these taxa were also present in the conventional SOT treatment but their biomass was lower. No effect of the either SOT was shown for species richness (Figure 3C, Figure 3D).

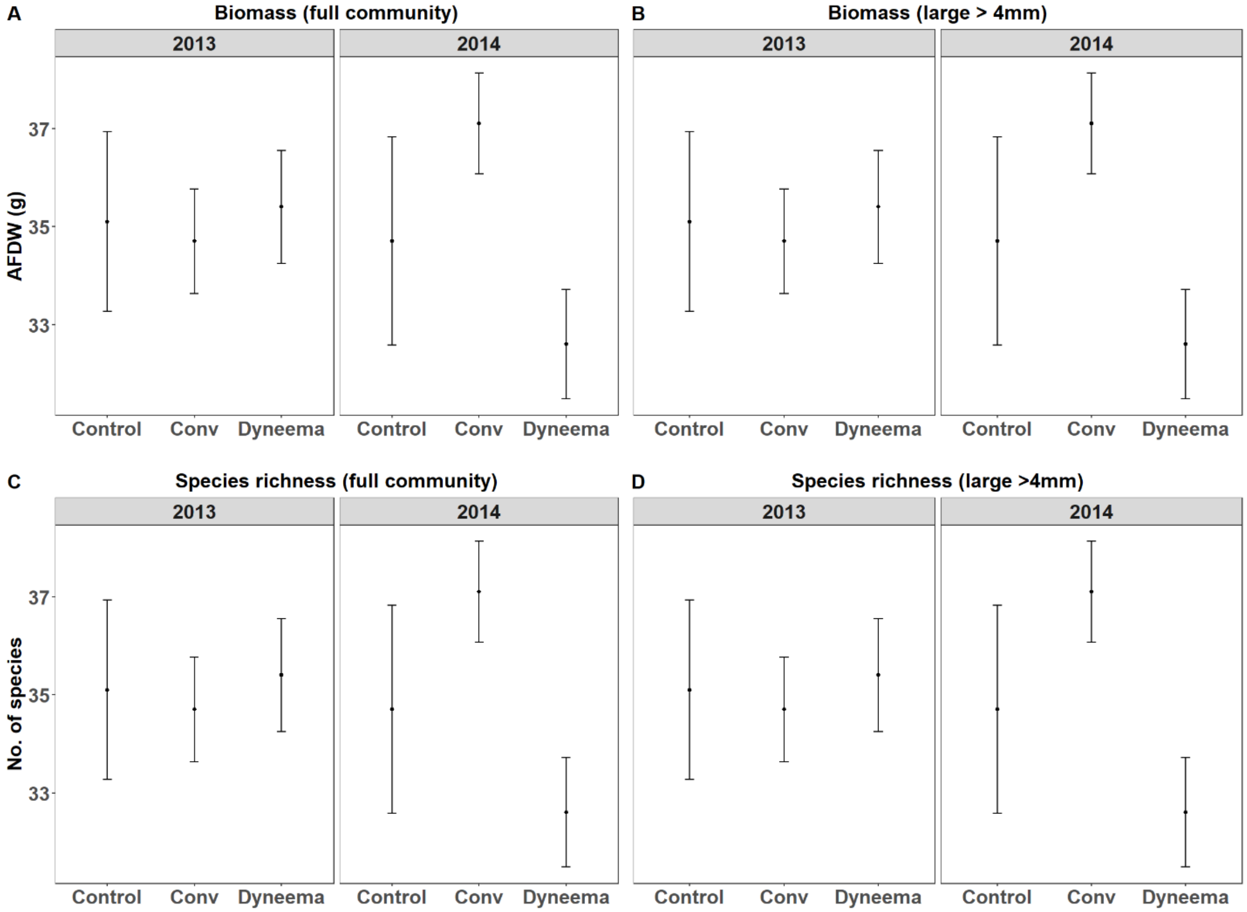


Figure 3: Mean (± SE) of (A) biomass full community (B) biomass in large (> 4mm) component, (C) species richness full community and (D) species richness in the large component in the three treatments Control, Conventional sandeel otter trawl (Conv) and the modified Dyneema sandeel otter trawl (Dyneema)

Table 1: Results from the Generalised Linear Mixed Models's (GLMM) for the control-impact experiment comparing a conventional sandeel trawl and a modified Dyneema sandeel trawl with a control (C). The fixed effects were G = Gear, Yr = Year. All models included Station as a random effect. Significant p values at alpha = 0.05 are in bold.

	Fixed effects	Dist.	Chisq	Df	p
Biomass (pooled)	G	Gamma	7.8	2	**0.01**
Biomass (4mm)	G	Gamma	12.4	2	**0.002**
Species richness (pooled)	G	Poisson	2.1	2	0.35
Species richness (4mm)	G	ComPois	0.1	2	0.95
Surface	G	Gamma	15.9	2	**0.004**
	Yr		59.99	1	**< 0.0001**
	G * Yr		28.4	2	**< 0.0001**
Top (0-5cm)	G	Gamma	6.0	2	0.051
	Yr		4.9	1	**0.02**
Mid (6-10cm)	G	Gamma	3.4	2	0.2
Bottom >10cm	G	Gamma	2.6	2	0.3

Table 2: showing the loss of benthic biomass relative to the control treatment in 2013, 2014 and an average of both years (Av)

Gear-Year	Biomass full	Biomass 4mm
Conv. – 2013	- 35%	- 54%
Conv. - 2014	- 19%	- 27%
Conv. – Av.	**- 28%**	**- 43%**
Dyn. 2013	- 8%	- 12%
Dyn. 2014	37%	60%
Dyn. Av.	**10%**	**17%**

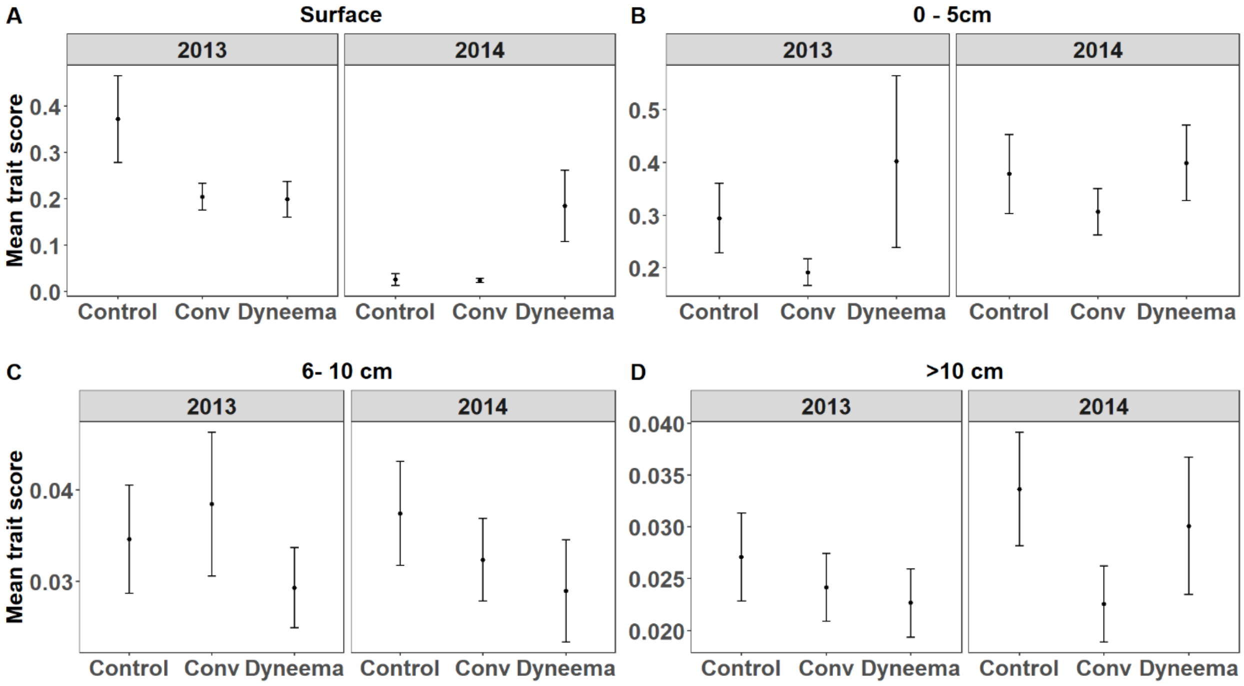


Figure 4: Mean (± SE) biomass of four vertical sediment positions sampled in 2013 and 2014 from the Control, Conventional sandeel otter trawl (Conv) and the modified Dyneema sandeel otter trawl

5.3.2. Sediment position

After fishing with the conventional SOT there were significantly fewer taxa that lived at the sediment surface relative to the control (Table 1). There was also a signifcant effect of Year and the interaction between Gear and Year on surface fauna (Table 1) indicating different relationships for gears between years. The significant interaction was likely to be driven by loss of surface fauna in the control and conventional SOT in 2014 (Figure 4 A). In contrast, very little change was apparent for the surface taxa after impact from the Dyneema SOT (Figure 4 A). The taxa that live in the top layer of sediment (0-5cm) were also reduced after impact from the conventional SOT relative to the control, and this was more pronounced in 2013 than 2014 (Figure 4 B). Although, the statistical analysis showed no signficant difference between Gears. Benthic fauna living deeper in the sediment (6-10 cm & < 10 cm) were not shown to significantly differ between Gears or Years (Table 1).

5.3.3. Physical footprint

Side scan images showed there to be a number of trawl tracks at the study site prior our experimental trawling (Figure 5). Nonetheless, it was possible to identify the trawl tracks made by the experimental sandeel trawls. The side scan sonar images showed that the width of the Dyneema SOT footprint was 70 m (Figure 6, right), whereas the track width of the conventional SOT was 105 m (Figure 6, left). The 33% narrower footprint for the Dyneema SOT can be attributed to the pelagic doors and a large part of each sweep being lifted. Due to currents the pelagic doors periodically came into contact with the seafloor, which is visible in the sonar image as two close parallel lines in the left part of Dyneema SOT footprint, where the outer door-line is dashed (Figure 6). This mechanism periodically extended the width of the Dyneema footprint with by 10-15 m.

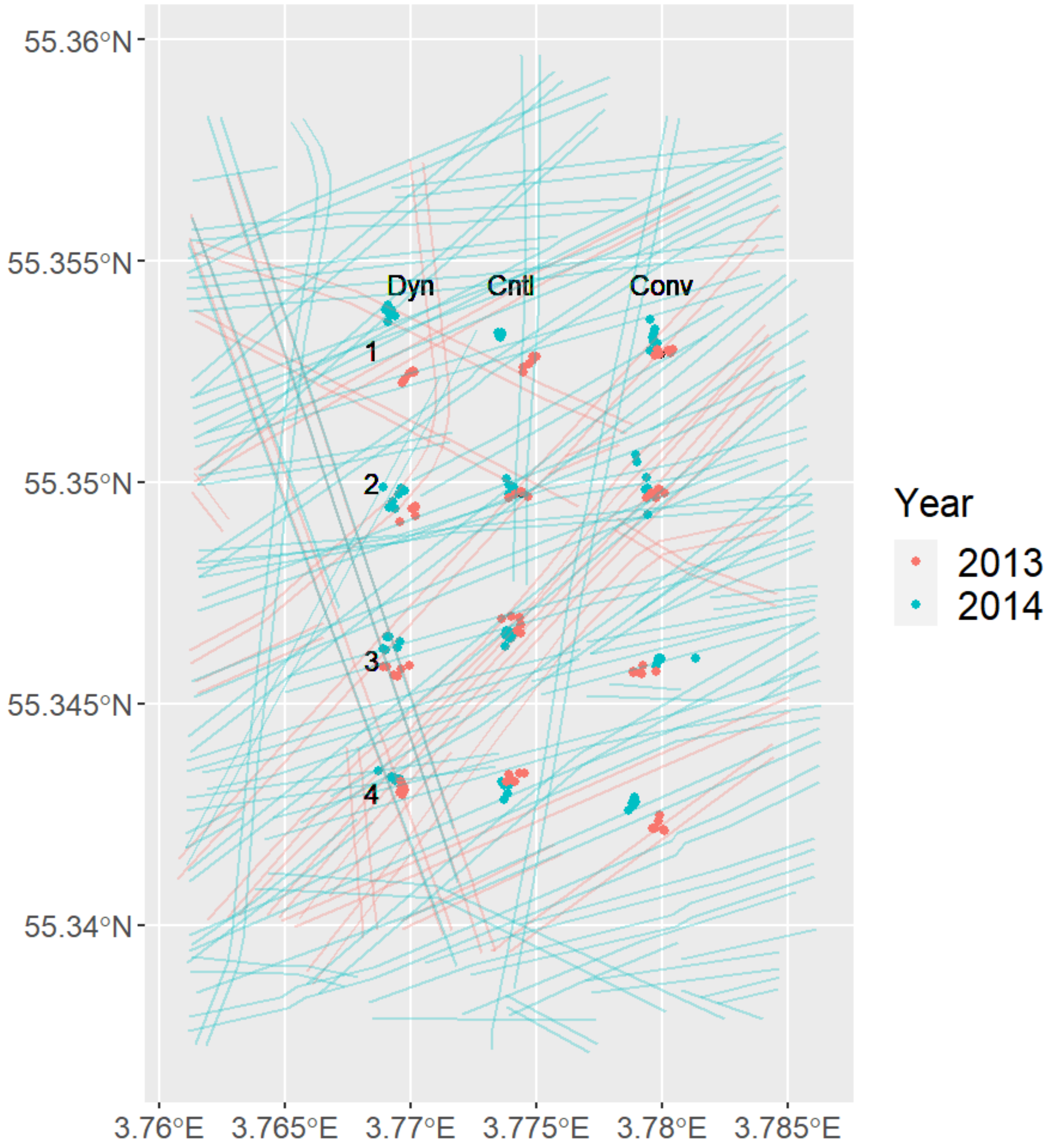


Figure 5: Side scan images identified trawl tracks (lines) at the study site each year (pink lines for 2013 and blue for 2014). The dots show the sample points each year.

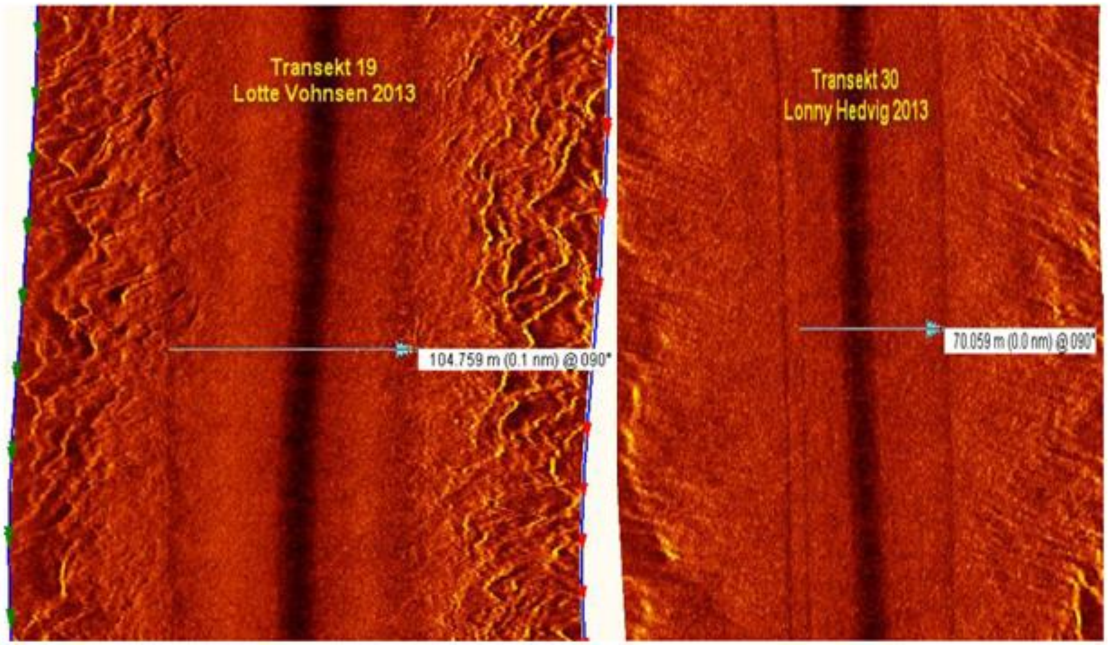


Figure 6: Side scan images showing the trawl track from the conventional sandeel trawl (left) and from the Dyneema sandeel trawl (right). The gear tracks are detected based on the smoothness of the image (harder substrate due to compacting). The width of gear track can be identified where a piling of sediment at extent of the track creates a shadow, seen here as darker line. Two darker lines in parallel are distinct on the left hand of the Dyneema track caused by the pelagic door coming into contact with the seabed.

5.3.4. Community composition

In the multivariate PERMANOVA, 'Gear' was not shown to have a significant effect on the species composition (p = 0.1). The 'Gear-Year' interaction was neither significant (p = 0.43), indicating that gear had the same effect on species composition in both years. The species composition was significantly different between year (p = 0.002) (Figure: 7) and the random effect 'Station' indicated significant variation in species composition between stations (p = 0.001). The differences in species composition between years was largely driven by the absence of the taxa Campanularidae in 2014, and the increase of *Echinocaridum cordatum*, *Amphiura chiajei* and *Lanice conchilega* in 2014 (Supplementary Table 1).

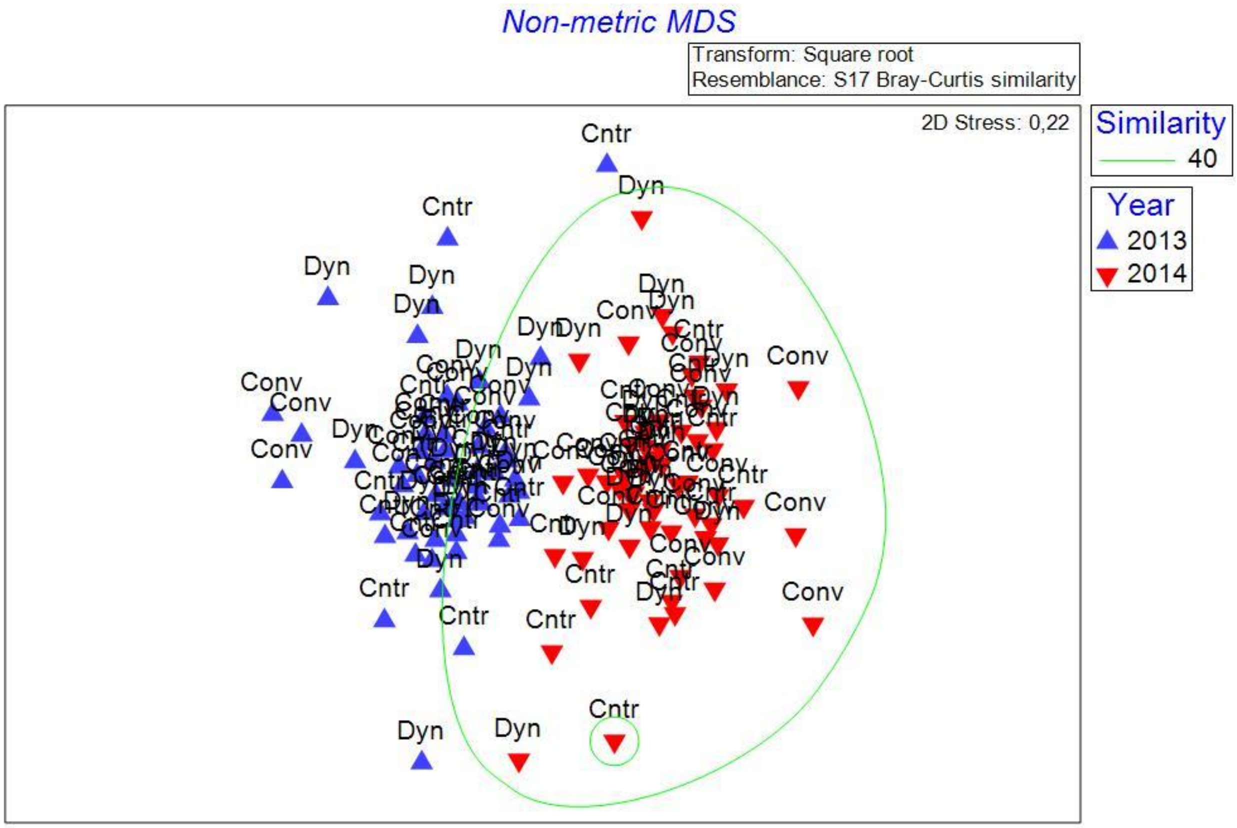


Figure 7: non-metric multi-dimensional scaling plot showing the infaunal species composition on Dogger Bank. The species composition differed significantly by fixed effect 'Year' (p= 0.002) but not between treatment (p = 0.1) ('Conv' – conventional trawl, 'Dyn' – Dyneema trawl, Cntr - Control).

5.4. Discussion

In this study, we compared the impact of a modified Dyneema sandeel otter trawl to that of a conventional SOT to evaluate whether the depletion of benthic macrofauna was reduced when using the modified gear. Our analyses showed no significant loss of faunal biomass after impact with the Dyneema SOT, whereas biomass of large fauna was significantly lower after impact from the conventional SOT. The conventional SOT may have had a greater impact on the benthic fauna living at the surface and top sediment layer (0-5 cm), than those living deeper in the sediment (> 6cm). The statistical analyses showed no significant effect of either gear on species richness or on the community composition. These results suggest that switching to a modified SOT may reduce the benthic impact from this fishery.

5.4.1. Large fauna

Of the benthic indicators assessed here, biomass was more responsive to trawling than species richness, corroborating the findings of Hiddink et al. (2020). The strength of biomass as an indicator pertains to its consistent response to trawling impact, declining exponentially with trawling intensity (Hiddink et al., 2020). The exponential response occurs as large individuals (representing most of the biomass) are removed in the first few trawl passages, and relatively less biomass is removed subsequently (Hiddink et al., 2006). We observed significantly lower biomass of the large fauna after impact with the conventional SOT relative to the control, but no significant difference for the full community biomass. These results suggest that larger individuals are more sensitive to impact from the conventional SOT than smaller organisms. Support for this notion comes from the lower biomass, rather than absence, of the *Gari fervensis*, *Owenia fusiformis*, *Amphiura chiajei*, *A. filiformis*, *Echinocardium cordatum*, and *Campanulariidae* indet in the conventional SOT. This possibly indicating that larger individuals were removed by the gear impact, whilst small individuals were less affected. Although small fauna are vulnerable to trawling mortality (Hinz et al., 2009), they tend to be less sensitive as they are thought to come into less direct contact with the gear (Bergman and Santbrink et al., 2000), and generally have faster growth rates allowing them to recovery quickly. On the other hand, large fauna are often more sensitive to trawling (Tillin et al., 2006, Querios et al., 2006, McConnaughey et al., 2005; McLaverty et al., 2020a), as body size often correlates with other vulnerable life history traits such as slow growth rates and older maturation age (Begon et al., 2006). While the relationship between large body sizes and trawling is relatively well-understood (Queirós et al., 2006), it is less clear how this relationship changes over a species life span. As such, some species may be sensitive to trawling at their maximum size, but robust to trawling whilst juvenile (i.e. smaller). By physically separating the large bodied fauna in the community, we were able to isolate the more sensitive part of the community and detect an effect from the conventional SOT. These results support the findings of McLaverty et al. (2020a) that showed the large biota (> 4mm) may be a more sensitive indicator of trawling, and that the response at the full community level could be obscured by the antagonistic response of the large- and small-bodied fauna

5.4.2. Loss of benthic fauna

Benthic faunal mortality from trawling occurs as organisms are crushed due to direct contact with the fishing gear (Bergman and Santbrink, 2000), or consumed after exposure as gears dig into the sediment and displace fauna residing deeper in the sediment. A correlation has been shown between the gear penetration depth and the depletion rate of benthic fauna (Hiddink et al., 2017). Fishing gear that penetrates deeper into the sediment causes greater depletion. We observed a reduction in benthic faunal biomass from the conventional sandeel trawl by - 28% (full community), and - 43% (large fauna). In comparison, after fishing with the Dyneema SOT benthic biomass had increased by 10% (full community) and 17% (large fauna). Given that the ground gear of the conventional- and Dyneema SOT were identical, we may infer that the lower benthic impact from the Dyneema SOT arose from the lighter weight of the net in the Dyneema SOT.

Of the commercial trawl gears used in European fisheries, hydraulic dredges cause the greatest impact, and are estimated to penetrate 16 cm into the sediment and reduce benthic biomass by -40 % (Hiddink et al., 2017; Sciberras et al., 2018). Considering that the penetration depth for the conventional SOT ground gear was assumed to be no more than 2 cm (Eigaard et al., 2016), a 28% reduction of biomass was greater than had been expected. An explanation for the higher than expected loss may be that our sampling approach targeted the ground gear path only, which makes up ~35 % of the footprint of typical sandeel trawls and likely inflicts a greater impact than the sweeps (~60 % of the footprint) (Eigaard et al., 2016). Typically, benthic faunal loss is estimated for the entire footprint (e.g., Hiddink et al., 2017) and if the other gear components were included into our calculations, the reduction of faunal biomass from the conventional SOT would approximately be halved (~ 14%).

The effect of bottom-towed gears on faunal sediment position was expected to have been greater for the surface fauna than for fauna living deeper in the sediment (Bolam et al., 2014). While the relative biomass of surface fauna was lower in the conventional SOT than the control in 2013, an absence of surface fauna in both control and conventional SOT in 2014, meant this pattern was not consistent between years. Nevertheless, the decline of surface fauna after the conventional SOT in 2013 compared to the lack of negative effect from the Dyneema SOT, may indicate that the gear modification reduced seabed penetration, and therefore the overall impact on the seabed biota.

5.4.3. Uncertainties

The statistical analysis demonstrated a significant reduction in large fauna biomass from the conventional SOT but not from the lightweight modified Dyneema SOT, and that surface dwelling taxa were the most affected by the conventional SOT. Overall, these result are not surprising. However, when considering that the ground gears were identical in design, and the magnitude of the effect was higher than expected (- 28%), it could suggest that external factors and/or methodological aspects contributed to the observed differences in faunal biomass. Firstly, the methodology applied may have some limitations that pertains to the inference of an effect (Green, 1979). The control-impact design is without a temporal comparison and therefore risks inferring an effect when the differences are due to natural spatial variation. Further to this, unquantified background trawling occurred at the study site, likely to have been from beam trawls, and we cannot distinguish whether the observed effect were in fact not, from our experimental trawling. However, the experimental design was repeated in two successive years, and generally the trends were similar in both years (lower biomass in the conventional SOT relative to the control, similar biomass in the Dyneema SOT and the control). The similarly between years may provide more confidence that the observed response was at least not related to background trawling, as we would expect the Dyneema SOT treatment to similarly have been exposed to such effects. Nevertheless, the total biomass decreased in the control treatment in 2014, largely due to the loss of a surface-dwelling hydroid Campanularidae. Thus, the difference between the control and conventional gear may have been a sampling artefact causes by a large biomass taxa. The decline in Campanularidae may also have contributed to the observed effect on surface fauna, which was most pronounced in 2013. Hydriods are often emitted from benthic faunal analyses, as they can exhibit patchy distribution, and as colonial organisms are difficult to enumerate. It may therefore be useful to omit the Campanularidae in a further analysis.

5.4.4. Management perspectives

Gear modifications may offer a supplementary solution to spatial closures, allowing fishing activity to continue whilst reducing the impact to the seabed (McConnaughey et al., 2020). Here we demonstrate that by using pelagic doors on the sandeel otter trawl the gear footprint and seabed area impacted were reduce by 33%. We also estimated a significantly lower impact to the benthic fauna in the ground gear path of the conventional SOT, which may be explained by reduced bottom contact (ground gear penetration) from the lower weight and sediment-resuspension of the trawl-netting.

Previously, studies conducted on the Dogger Bank have shown no effect of trawling on functional composition (Tillin et al., 2006), or benthic biomass, production and size spectra (Querios et al., 2006). The ongoing anthropogenic pressure that occurs on the Dogger Bank, which has both current and historically high levels of fishing, may be grounds for the lack of detectable fishing effect. It's possible that the history of fishing contributed to the absence of an effect for the modified Dyneema SOT. Over time, the effect of chronic trawling causes the community to shift towards shorter-lifespans and higher resilience to fishing disturbance (Hiddink et al., 2017, Jennings et al., 1998). As such, conducting fishing impact assessments that take place in previously fished locations may give an underestimation of the impact relative to the unfished conditions (Sciberras et al., 2018). This was exemplified in a highly disturbed coastal system in Denmark where it was shown that effects of trawling were only evident in areas associated with an unimpacted reference site (McLaverty et al., 2020b). Therefore, spatial closures have a value, not only in conservation, but also in order to detect 'true' fishing impact (Beukers-Stewart et al., 2005).

A commitment has been made in the EU to create an ecologically coherent Natura 2000 network of protected areas, whereby '1110 Sandbanks' are one of the habitat nature types identified to be of importance (Habitats Directive 92/43/EEC). Dogger Bank is among the largest sandbank habitats in European waters and recognition of its importance is implied by its designation as a Natura 2000 site by three of the four countries which share its jurisdiction. Fishing with bottom-towed fishing gears was listed as one of the greatest threats to the Dogger Bank habitat. Therefore, in order to assess the impact of trawling, it is recommended that undisturbed references areas, free from bottom trawling, be instated. This will allow the fisheries effects on seabed habitats to be measured and monitored relative to undisturbed conditions. Only then will it be seen whether gear modifications offer a solution to the age-old problem of maintaining a productive fishery, whilst reducing the adverse effect of bottom trawling on seabed habitats and ecosystems.

References

Anderson, M., Gorley, R., and Clarke, K. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd, Plymouth. www.primer-e.com/PERMANOVA_download.htm.

Begon, M., Harper, J.L., Townsend, C.R., 2006. Ecology: From Individuals to Ecosystems, fourth ed. Blackwell Science, Oxford.

Bergman, M. J. N., and Van Santbrink, J. W. 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES Journal of Marine Science, 57: 1321–1331.

Beukers-Stewart, B., Vause, B., Mosley, M., Rossetti, H., and Brand, A. 2005. Benefits of closed area protection for a population of scallops. Marine Ecology Progress Series, 298: 189–204. http://www.int-res.com/abstracts/meps/v298/p189-204/.

Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M., and Stephens, D. 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. Journal of Sea Research, 85: 162–177. http://dx.doi.org/10.1016/j.seares.2013.05.003.

Bolam, S.G., Garcia, C., Eggleton, J., Kenny, A.J., Buhl-Mortensen, L., Gonzalez-Mirelis, G., van Kooten, T., Dinesen, G., Hansen, J., Hiddink, J.G., Sciberras, M., Smith, C., Papadopoulou, N., Gumus, A., Van Hoey, G., Eigaard, O.R., Bastardie, F., Rijnsdorp, A.D., 2017. Differences in biological traits composition of benthic assemblages between unimpacted habitats. Mar. Environ. Res. 126, 1–13. https://doi.org/10.1016/j.marenvres.2017.01.004

Buhl-Mortensen, B. L., Aglen, A., Breen, M., Ervik, A., Husa, V., Løkkeborg, S., I, R., et al. 2013. Impacts of fisheries and aquaculture on sediments and benthic fauna: suggestions for new management approaches. 1–69. https://www.hi.no/hi/nettrapporter/fisken-og-havet/2013/fh-2-2013.

Clarke, K. R., and Gorley, R. N. 2015. PRIMER V7: User Manual/Tutorial. PRIMER-E Ltd, Plymouth. www.primer-e.com/primer 7_download.htm.

Dyer M.F., Fry W.G., Fry P.D., Cranmer G.J. 1983. Benthic Regions within the North Sea. J. Mar. Biol. Ass. 63, 683-693

Eigaard, O. R., Rihan, D., Graham, N., Sala, A., Zachariassen, K. 2011. Improving fishing capacity descriptors: modelling engine power and gear-size relations of five European trawl fleets. Fisheries Research, 110, 39–46

Eigaard, O. R., Bastardie, F., Breen, M., Dinesen, G. E., Hintzen, N. T., Laffargue, P., Mortensen, L. O., Nielsen, J. R., Nilsson, H. C., O'Neill, F. G., Polet, H., Reid, D. G., Sala, A., Sköld, M., Smith, C., Sørensen, T. K., Tully, O., Zengin, M., Rijnsdorp, A. D. 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. 73, i27–i43. https://academic.oup.com/icesjms/article/73/suppl_1/i27/2573989.

Engel, J., and Kvitek, R. 1998. Society for Conservation Biology Effects of Otter Trawling on a Benthic Community in Monterey Bay National Marine Sanctuary Linked references are available on JSTOR for this article : Effects of Otter Trawling on a Benthic Community in Monterey Bay Nation. Cons. Biol. 12, 1204–1214. https://www.jstor.org/stable/2989838.

EU, 1992. EU Habitat Directive 92/43. https://doi.org/2004R0726

Freeman, S., Mackinson, S., and Flatt, R. 2004. Diel patterns in the habitat utilisation of sandeels revealed using integrated acoustic surveys. J. Exp. Mar. Biol. Ecol. 305, 141–154. https://doi.org/10.1016/j.jembe.2003.12.016.

Gislason, H., Dalskov, J., Dinesen, G. E., Egekvist, J., Eigaard, O., Jepsen, N., Larsen, F., Poulsen, L. K., Sørensen, T. K., Hoffman, E. 2014. Miljøskånsomhed og økologisk bærdygtihed i dansk fiskeri. DTU Aqua-rapport nr. 279-2014. Institut for Akvatiske Ressourcer, Danmarks Teknisje Universitet. 83

Green, R. H. (1979). Sampling design and statistical methods for environmental biologists. John Wiley & Sons.

Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E., Piet, G.J., 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. https://doi.org/10.1139/f05-266

Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proc. Natl. Acad. Sci. 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114

Hiddink, J.G., Kaiser, M.J., Sciberras, M., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Parma, A.M., Suuronen, P., Rijnsdorp, A.D., Jennings, S., 2020. Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. J. Appl. Ecol. 57, 1199–1209. https://doi.org/10.1111/1365-2664.13617

Hinz, H., Prieto, V., Kaiser, M.J., 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecol. Appl. 19, 761–773. https://doi.org/10.1890/08-0351.1

Jennings, S., and Kaiser, M. J. 1998. The Effects of Fishing on Marine Ecosystems. Elsevier Masson SAS. 201–212, 212e, 213–352 pp. http://dx.doi.org/10.1016/S0065-2881(08)60212-6.

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. https://doi.org/10.3354/meps311001

Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G., Bourbonnais-Boyce, C., Kenchington, T.J., Smith, S.J., Gordon, D.C., 2006. Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean. J. Sea Res. 56, 249–270. https://doi.org/10.1016/j.seares.2006.03.010

Kroncke, I., Knust, R. 1995. The Dogger Bank: A Special Ecological Region in the Central North Sea. Hel. Meeres. 49, 335- 353.

Lenth RV. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. https://cran.r-project.org/package=emmeans.

McConnaughey, R.A., Syrjala, S.E., Dew, C.B., 2005. Effects of chronic bottom trawling on the size structure of soft-bottom benthic invertebrates. Am. Fish. Soc. Symp. 41, 425–437.

McConnaughey, R.A., Hiddink, J.G., Jennings, S., Pitcher, C.R., Kaiser, M.J., Suuronen, P., Sciberras, M., Rijnsdorp, A.D., Collie, J.S., Mazor, T., Amoroso, R.O., Parma, A.M., Hilborn, R., 2020. Choosing best practices for managing impacts of trawl fishing on seabed habitats and biota. Fish Fish. 21, 319–337. https://doi.org/10.1111/faf.12431

McLaverty, C., Eigaard, O.R., Gislason, H., Bastardie, F., Brooks, M.E., Jonsson, P., Lehmann, A., Dinesen, G.E., 2020a. 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

McLaverty, C., Eigaard, O. R., Dinesen, G. E., Gislason, H., Kokkalis, A., Erichsen, A. C., and Petersen, J. K. 2020b. High-resolution fisheries data reveal effects of bivalve dredging on benthic communities in stressed coastal systems. Mar. Ecol. Prog. Ser. 642, 21–38. https://www.int-res.com/abstracts/meps/v642/p21-38/.

R Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

Queirós, A.M., Hiddink, J.G., Kaiser, M.J., 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. https://doi.org/10.1016/j.jembe.2006.03.001

Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J. 2018. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish Fish, 19: 698–715. http://doi.wiley.com/10.1111/faf.12283.

Skov, C., Berg, S., Eigaard, O.R., Jessen, T.K., Skov, P.V., 2020. Danish Fisheries and Aquaculture: Past, Present, and Future. Fisheries 45, 33–41. https://doi.org/10.1002/fsh.10330

Stride, A. 1959. On the Origin of the Dogger Bank, in the North Sea. Geological Magazine, 96(1), 33-44. doi:10.1017/S0016756800059197

Thrush, S.F., Dayton, P.K., 2002. Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annu. Rev. Ecol. Syst. 33, 449–473. https://doi.org/10.1146/annurev.ecolsys.33.010802.150515

Tillin H.M, Hiddink J.G, Jennings S, and Kaiser M.J. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318: 284–286. http://dx.doi.org/10.3354/meps318031.

Valdemarsen, J.W., Suuronen, P., 2003. Modifying fishing gear to achieve ecosystem objectives. Responsible Fisheries in the Marine Ecosystem. CABI Publishing, UK, pp. 321–341. https://doi.org/10.1079/9780851996332.0321

Supplementary information

Supplementary A: SIMPER results comparing the community composition in 2013 and 2014.

	Group 2013	Group 2014				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Campanulariidae indet.	0.41	0.05	9.26	1.68	15.56	15.56
Echinocardium cordatum	0.06	0.19	4.53	1.61	7.62	23.18
Amphiura chiajei	0.24	0.31	4.30	1.34	7.23	30.41
Owenia fusiformis	0.27	0.23	3.98	1.33	6.69	37.10
Euspira nitida	0.13	0.01	3.00	1.51	5.05	42.15
Lanice conchilega	0.05	0.12	2.39	1.28	4.01	46.16
Dosinia lupinus	0.05	0.07	2.34	0.70	3.93	50.09
Amphiura filiformis	0.09	0.04	2.00	1.28	3.37	53.46
Spiophanes bombyx	0.11	0.14	1.86	0.92	3.13	56.59
Ampelisca macrocephala	0.00	0.09	1.80	0.32	3.02	59.61
Edwardsia sp.	0.06	0.10	1.43	1.33	2.41	62.02
Echinocyamus pusillus	0.06	0.07	1.14	1.05	1.91	63.93
Nephtys longosetosa	0.05	0.04	1.05	1.19	1.76	65.69
Ensis ensis	0.03	0.01	0.98	0.47	1.65	67.35
Tellina fabula	0.02	0.02	0.98	0.62	1.64	68.99
Sigalion mathildae	0.04	0.06	0.94	1.23	1.59	70.57

Supplementary B: SIMPER results comparing the community composition in the conventional sandeel trawl treatment (Group K) with the control treatment (Group O).

	Group K	Group O				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Campanulariidae indet.	0.39	0.48	6.82	1.22	14.96	14.96
Owenia fusiformis	0.25	0.30	3.58	1.29	7.85	22.81
Amphiura chiajei	0.20	0.26	3.56	1.44	7.81	30.62
Dosinia lupinus	0.04	0.09	2.01	1.12	4.42	35.03
Euspira nitida	0.14	0.13	1.95	1.13	4.28	39.32
Amphiura filiformis	0.09	0.09	1.64	1.15	3.60	42.91
Echinocardium cordatum	0.03	0.05	1.38	0.53	3.02	45.93
Lanice conchilega	0.04	0.06	1.32	1.15	2.89	48.82
Echinocyamus pusillus	0.07	0.06	1.31	0.88	2.88	51.70
Spiophanes bombyx	0.13	0.10	1.28	1.16	2.81	54.51
Gari fervensis	0.00	0.06	1.23	0.29	2.71	57.21

Ensis ensis	0.05	0.01	1.18	0.57	2.60	59.81
Phoronis muelleri	0.02	0.04	1.12	0.96	2.47	62.28
Chaetozone setosa	0.02	0.05	0.97	0.32	2.13	64.41
Edwardsia sp.	0.06	0.06	0.93	1.29	2.03	66.44
Nephtys hombergii	0.03	0.02	0.87	0.83	1.90	68.34
Tellina fabula	0.03	0.01	0.81	0.60	1.78	70.13

Supplementary C: SIMPER results comparing the community composition in the modified sandeel trawl treatment (Group N) with the control treatment (Group O).

	Group N	Group O				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Campanulariidae indet.	0.36	0.48	6.80	1.22	14.33	14.33
Owenia fusiformis	0.25	0.30	3.80	1.31	8.01	22.34
Amphiura chiajei	0.26	0.26	2.99	1.36	6.29	28.63
Echinocardium cordatum	0.10	0.05	2.63	0.61	5.53	34.16
Gari fervensis	0.09	0.06	2.44	0.35	5.14	39.30
Euspira nitida	0.11	0.13	2.37	1.27	4.99	44.29
Dosinia lupinus	0.03	0.09	1.89	1.08	3.98	48.27
Amphiura filiformis	0.09	0.09	1.58	1.19	3.32	51.59
Phoronis muelleri	0.05	0.04	1.34	0.81	2.83	54.41
Lanice conchilega	0.05	0.06	1.31	1.15	2.75	57.17
Spiophanes bombyx	0.11	0.10	1.30	1.22	2.74	59.91
Echinocyamus pusillus	0.05	0.06	1.05	1.13	2.22	62.13
Nephtys hombergii	0.04	0.02	1.00	0.78	2.12	64.24
Edwardsia sp.	0.06	0.06	0.98	1.16	2.07	66.31
Chaetozone setosa	0.01	0.05	0.93	0.30	1.96	68.27
Ensis ensis	0.03	0.01	0.90	0.54	1.89	70.16

6. Discussion

6.1. Evaluating the results

6.1.1. Overview

With the condition of the seabed in European fishing grounds deteriorated (Pitcher et al., 2022), and an increasing emphasis on marine biodiversity being reflected in future policy instruments (e.g. EU's biodiversity strategy for 2030), efforts are being made to protect coastal and offshore waters from further degradation. In some circumstances, bottom-towed gears (hereafter trawling) will be forbidden in order to meet new EU regulations. While the implementation of closed areas will likely have several benefits (Jacquemont et al., 2022), there are risks associated with the closure of established fishing grounds, such as in the form of displacement of fishing effort into surrounding areas (Hiddink et al., 2006b). On the other hand, gear modifications may provide an alternative approach which allows fisheries to continue in established areas, but with a reduced seabed impact (McConnaughey et al., 2020).

In this thesis, I examined the effect of three lightweight fishing gears used in different commercial and nationally important Danish fisheries. The three research papers together evaluate the extent to which these gear affect seabed macrofauna, and thus assess whether gear modifications can achieve the goal of reducing seabed impact. Overall, the modified gears resulted in low levels of benthic impact, but measurable effects were still detected. We observed reduced benthic density and species richness in the dredge track of the light weight mussel dredge, with possible lasting effects on species richness (Chapter 3); high levels of depletion of the erect, tube-building horseshoe worm (*Phoronis* spp.) after multiple hauls of the Danish seine rope, but little evidence of an effect on whole community indicators (e.g. density, species richness, biomass) (Chapter 4); and no effect of the modified sandeel trawl on benthic biomass whereas the biomass of large biota was reduced by the conventional sandeel trawl (Chapter 5).

6.1.2. Effect of modified gears

While some impacts of experimental trawling were observed, these effects were relatively limited and inconsistent across the respective studies. The loss of benthic fauna from trawling has been strongly linked to gear penetration depth, whereby greater penetration depths result in higher depletion rates (Hiddink et al., 2017). Accordingly, the relatively low benthic impacts observed in this thesis are reflective of this relationship. The reduction of benthic fauna from commercial fishing gears has been quantified from a meta-analysis of experimental fishing studies. The results of which estimate that a commercial otter trawl, towed dredge, and beam trawl reduces faunal density by - 3%, -8%, - 12% per pass, respectively (Sciberras et al., 2018). To put the results of this thesis in context, the following sections compare our observed losses of benthic fauna with published values. Due to differences in the way losses of benthic fauna are calculated between studies, I will refer these as collectively as 'treatment effects'. As such, treatment effects were not explicitly reported in the mussel dredge study (Chapter 3). I have accordingly calculated the treatment effects for the mussel dredge in line with the Danish Seine[1] for the purposes of this discussion.

Mussel dredge

The estimated treatment effect from the lightweight mussel dredge directly in the dredge track was – 86%, and from the adjacent area - 65%. At face value, these treatment effects suggest that impacts from mussel dredging far exceeds that of commercial dredging (- 8%), despite this gear being a lightweight modification. However, fishing for wild blue mussels (*Mytilus edulis*) is a unique situation where the fishery targets a biogenic reef. As a habitat forming species, blue mussels support a diverse community of invertebrates (Norling & Kautsky, 2007). Yet in contrast to other biogenic reefs, blue mussels have fast growth rates and are considerably mobile. Comparing the treatment effect to a commercially used towed dredge (deployed in mud and sand habitats) overlooks the nature of the biogenic reef. A better comparison may therefore be the effect on biogenic reefs. One study quantified the impact of scallop dredging on maerl beds, with 70% of the maerl lost after scallop dredging (Hall-Spencer and Moore, 2000). In addition, a meta-analysis has shown that benthic macrofauna were reduced in biogenic habitats by - 96% after scallop dredging, and ~ - 70% after otter trawling (Kaiser et al., 2006). These loss estimates are closer to our observations for the mussel dredge, and provide and more realistic comparison.

Given these large impacts on the benthic fauna, the viability of the blue mussel fishery could seem unsustainable. However, the difference in the mussel fishery lies in the ability to recover from such a large losses. The recovery of biogenic reef forming taxa have in some cases exceeded the duration of the study

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[1]

$$R_{before} = \frac{\mu\, I_{before}}{\mu\, C_{before}}\ ;\ R_{after} = \frac{\mu\, I_{after}}{\mu\, C_{after}}$$

Treatment effect = $1 - (\frac{R_{before}}{R_{after}})$

Where μ is the mean value for impact (I) and control (C) treatments 'before' and 'after' fishing.

e.g. Hall-Spencer and Moore, 2000 [4 years] and Cook et al., 2013 [5 years], with others estimating some long-lived taxa in the phyla Cnidaria and Porifera can take up to 20 years to recover (Kaiser et al., 2018). In contrast, we observed rapid recolonization of blue mussels after 4-months, such that impacts in the dredge track were no longer visible, and the effect on the invertebrate community was short-lived i.e. signs of recovery for density and species richness. Rapid recolonization could be facilitated by the dominance of polychaete worms and amphipod crustaceans in the community composition, as these organisms show some of the lowest sensitivity to bottom-towed gear disturbance and the fastest recovery rates (Bolam et al., 2014). Unlike other dredge fisheries, the sharp decline in density observed for the mussel dredge is likely caused by the removal of the mussel matrix, rather than high mortality associated with deep penetration. Furthermore, mussel fisheries that take place in Danish Natura 2000 sites are spatially restricted to impact only 15% of the basin on an annual basis (see Chapter 3 for more details). This means that dredging impacts take place on relatively low spatial scales, and large areas (~85%) of the basin are unfished in a given year. Assuming these unfished areas host higher benthic density and diversity, this aspect may also facilitate relatively fast recovery into fished areas through nearby immigration (Lambert et al., 2014).

Danish seine

Prior to this thesis, no studies had quantified the effect of the Danish seine on benthic fauna. In Chapter 4, we quantified the loss of benthic fauna specific to the two gear components, as opposed to the whole gear footprint. After a single haul of the Danish seine, faunal density was not reduced by either gear component. In comparison, otter trawls have been shown to reduce benthic faunal density by an average of -3% per pass (Sciberras et al., 2018). In the case of multiple hauls, the Danish seine ropes reduced benthic faunal density by - 10%, species richness (- 3%), and large fauna biomass (– 13%), while no losses were observed in the ground gear. Comparisons between the Danish seine and otter trawl are often made due to some similarities between the gears, and accordingly the gear belong to the same legislative category in European fisheries (Noack et al., 2017). As a result, it has been assumed that seabed impacts would similar and estimates for the impact of the Danish seine have been based on empirical data from an otter trawl (Eigaard et al. 2016). The use of Danish seines, however, only overlap with otter trawls in some habitats, as otter trawls can be in a range of sediment types (Kaiser et al., 2006). By comparison, the Danish seines are restricted to flat sedimentary habitats, or in areas between rough spots (FAO, 2022). In Denmark, the Danish seine is predominantly used in the Jammerbugt (Jammer Bay) and Skagerrak area, where the fishery overlaps considerably with the international beam trawl fishery. This overlap has generated considerable debate around the respective environmental effects of these two gear types, particularly as they target the same species. As beam trawls used in these fishing grounds target flatfish, they have tickler chains designed to penetrate into the sediment. As a result, the entire footprint of a beam trawl causes subsurface impacts (>2cm) and can penetrate as deep as 10cm (Eigaard et al., 2016). This is significant as subsurface penetration (>2cm) has a particularly strong effect on the benthic community, and can result in increases in the prevalence of small-short lived organisms (Rijndorp et al 2018). By comparison, Danish seines are not thought to cause any subsurface penetration (Eigaard et al., 2016), and in addition to this, fuel consumption estimates for flatfish fisheries have shown beam trawl use ~ 2.6 litres fuel per kg of flatfish, while Danish seiners use ~ 0.2 litres per kg flatfish caught (Thrane, 2005). The results of this thesis provide new evidence supporting the environmental benefits of the Danish seine compared to more widely used commercial gears, by showing relatively low impacts of single and multiple hauls on benthic fauna.

Otter trawl

In Chapter 5, we calculated the reduction of benthic fauna for the conventional sandeel otter trawl (SOT) and the lightweight Dyneema SOT, which represent the first quantification of benthic impact for these gears. We observed a reduction of the full community biomass (~ - 28%), and the large biota (> 4mm) biomass (~ - 43%) after fishing with the conventional SOT. Previously, the reduction of benthic macrofauna from commercial otter trawling has been up to ~ - 55%, although such losses are typically associated with trawling in muddy habitats (Kaiser et al., 2006). Thus, the treatment effect for the conventional SOT was higher than expected, considering SOT's are deployed on sandy substrata, and are light relative to other commercial otter trawls (Gislason et al., 2014). Comparatively, after impact from the Dyneema SOT benthic biomass was not reduced, but instead biomass increased. An increase in faunal biomass after otter trawling has been observed from other sandy habitats, possibly caused by immigration of scavenging fauna (Kaiser et al., 2006), or as a sampling artefact as fishing disturbance increases exposure to sampling gear (Kaiser et al., 2019). In spite of that, the contrasting results for the two gears may indicate that the modified SOT reduces the benthic impact. This is further supported by the consistency of the results between years i.e. biomass was lower in the conventional SOT relative to the control in 2013 and 2014, whereas biomass in the Dyneema SOT did not differ from the control. However, the treatment effect calculated in Chapter 5 are based on the relative differences between control and impact site alone (control-impact design) as opposed to treatment effects in Chapter 3 and 4 (BACI design). Therefore, it cannot be discounted that the observed lower biomass in the conventional SOT could equally be due to natural differences between sites.

6.1.3. Indicators

It is commonplace that community level indicators are used in fisheries impact assessment and monitoring. Across studies, community level indicators (community numbers, biomass, number of species) have been shown to be better measures of trawling impact than those based on individual taxa (numbers or biomass) (Hiddink et al., 2020). However, we found the response of community indicators to experimental trawling was inconsistent. In Chapter 4, we observed no negative effect of the Danish seine on density, species richness or large biota biomass. Similarly, in Chapter 3 we found no effect of the mussel dredge on biomass, and no effect on species richness from the conventional SOT or Dyneema SOT in Chapter 5. Despite their ability to detect impacts of chronic trawling, these indicators have shown a general lack of response in BACI experimental studies (Tuck et al., 1998; Drabsch., et al 2001; Brown et al., 2005; Ragnarsson and Lindegarth, 2009; Prantoni et al., 2013; Lambert et al., 2017).

A large scale assessment of trawling impact indicators found biomass-based community metrics to be the most effective. This was due to their consistent response to fishing impact across studies, and links between biomass and ecosystem function (Hiddink et al., 2020). In contrast to this, we observed greater variance in our biomass data than in the other indicators, which reduced the power to detect an effect with this metric (Chapter 3 Figure 5, Chapter 4 Figure 3E). Accordingly, we did not find community biomass to be the most informative indicator (Chapter 3, 4). In general, the effect of trawling on benthic biomass follows an exponential trend, whereby the greatest reduction in biomass occurs with the first trawl, and subsequently less biomass is removed for each trawl (Hiddink et al., 2006a). This relationship, however, is expected in undisturbed habitats where the size-, age-, and longevity distribution of the community includes a high biomass of old and larger organisms (Rijnsdorp et al., 2018; Hiddink et al., 2019). Fishing mortality rates tend to be greater for these large biota, relative to small biota (Bergman and Santbrink 2002), and therefore fishing effects the size-, age-, and longevity distribution by shifting it towards one dominated by small, short-lived biota (Hiddink et al., 2006a; Rijnsdorp et al., 2018). As such, losses of benthic fauna from trawling is highly dependent on the history of fishing at a given location (Sciberras et al., 2018). European fishing grounds generally have an extensive history of fishing, and significant changes in the benthic community composition have occurred since the turn of the century (Bradshaw and Brand, 2002). The seabed condition in the Kattegat-Skagerrak region has be identified to be one of the most heavily impacted fishing grounds worldwide (Chapter 4), and in the North Sea the total unfished area is only ~11% (Chapter 5) (Pitcher at al., 2022). Similarly, the Limfjord has a long history of fishing and has undergone significant changes from anthropogenic nutrient enrichment (Chapter 3) (Hoffman and Dolmer, 2000). Therefore, our observed lack of response in biomass may be reflective of the historic or background levels of disturbance in these areas. This issue may be worsened by the absence of true reference areas, which I will discuss in more detail in section 6.2.3.

Overall, the sensitivity of community indicators depends on the outcome of synergistic, or antagonistic, relationships between individual species and trawling (Hiddink et al, 2006a). Dominant taxa in terms of numbers or biomass can accentuate, or disguise, species-specific responses. This was apparent in Chapter 3, where the polychaete *Capitella* sp. increased rapidly after spring recruitment, and made up > 80% of community density. Due to the dominance of *Capitella* sp., the declining densities of other species were masked. Similarly, in Chapter 4, total density was not observed to decline after fishing, while, the erect tube-building horseshoe worm *Phoronis* spp. was estimated to decline by ~90%. This highlights how sensitive, and potentially important, components of the community can go undetected using community indicators alone.

Species-specific responses to fishing impact are ecologically important, and can provide information on the consequences of losses to functionality (Thrush et al., 2006). In spite of this, species-specific responses can be difficult to extrapolate across different geographic areas and fisheries. Species-specific responses also have been shown to vary between locations composed of similar community composition (Bremner et al., 2003). One reason for this is that the response of a given species may not always be consistent, and as such, it is not uncommon to observe contrasting responses between studies. For example, a decline in *Phoronis* sp. density has been correlated with high fishing intensities (Hinz et al., 2009; Sköld et al., 2018, McLaverty et al., 2020b), which is in accordance with our results from the Danish seine rope (Chapter 4). Yet, Reiss et al., (2009) observed relatively high densities of *Phoronis muelleri* in heavily trawled sites. The grounds for this may be as species sensitivities can change depending on ambient environmental conditions, or habitat type. In either case, this can make interpretation of species-specific responses (e.g. the development of indicator species) difficult across fisheries, and thus harder to translate at the management level.

The identification of benthic invertebrates to species (or taxa) level substantially increases the processing time of benthic samples. Nevertheless, the species level resolution improved the analytical approach by combining species level information (multivariate analysis) with community indicators (e.g. in linear models). Multivariate metrics can evaluate changes in the relative abundance/diversity/biomass of species simultaneously, and can be used as diagnostics tool for identifying sensitive species, allowing for a more detailed understanding of how the gears impacts the community. An example of this comes from Chapter 5 where the multivariate analysis flagged the possibility that the significant responses in the community indicators (biomass and surface sediment position) were being driven by an individual taxa. The taxa in question was a colony forming hydroid (Campanularidae indet.), which can grow to be large in size and can be patchily distributed. The observation that Campanularidae decreased as a result of trawling made sense, but its absence in the control was what led us question whether it should be included in further analyses. The multivariate analysis also allowed us to link changes in individual species to the potential mechanisms of the impact. For example, in Chapter 4, we found *Phoronis* spp.. declined (90%) after multiple hauls of the Danish seine rope. Given the discussed hydrodynamic impacts of the seine ropes, we expect small, surface-living species like *Phoronis* spp. to be particularly sensitive to re-suspension. Therefore, the use of multivariate analyses in this thesis would suggest that studies dealing with similarly small effect sizes would benefit from these methods.

6.1.4. Summary

In each case, the modified gear had a comparable or lower benthic impact than published depletion rates for the equivalent conventional gear. The exception was possibly the mussel dredge, where no direct comparison could be made to a commercial gear. Nevertheless, the relatively high benthic loss observed for the mussel dredge is potentially mitigated by the rapid recolonization of the blue mussels and associated benthic community, and also by the lighter gear required by the management of the fishery. The Danish seine had a low overall impact. Given the greater benthic faunal impact associated with beam trawls and otter trawls, replacing these gears with Danish seines, where possible, would likely have great benefits to the ecological condition of the seabed. In terms of the sandeel otter trawl, the results here have shown that fishing with the modified Dyneema gear results in lower benthic impact relative to the conventional gear.

The main benefit of the community indicators in this thesis was the comparability of these metrics with other studies, allowing for a straight forward contextualisation of our observations. On the other hand, multivariate approaches were useful diagnostics tools, helping to identify species-specific effects. This is as individual species were in some cases more responsive.

6.2. Evaluating the methods

6.2.1. Experimental design

In order for human activities to be environmentally sustainable, it is critical to understand how they impact the environment, and understand how the environment will respond. In cases where damage is unavoidable, as is the case for fisheries, an acceptable level of impact should be defined from the best available science. A Before-After-Control-Impact experimental design is particularly useful in this regard, as it can isolate the human effects (in this case trawling), which uses an unimpacted control site to account for natural temporal variability (Green, 1979). The advantage of using BACI experiments in a fishing context is the ability to capture the instantaneous effect of the fishing gear, and quantify the community response to a known impact intensity. In the respective thesis research chapters, we applied Before-After Control-Impact (BACI) and Control-Impact (CI) experimental designs to assess the effect of modified fishing gears on benthic macrofauna.

Although the BACI design follows a relatively straight forward approach, some caution is required in its interpretation. The point of interest in the BACI analysis is an interaction between 'Time' (before-after) and 'Treatment' (control-impact), which is a comparison of the slope between the impacted and control site. However, a significant interaction alone does not necessarily mean there has been an experimental effect. This is as the interaction does not specify the direction of change (positive or negative), or whether a greater change occurred in the control or impact site. Without careful inspection, spurious interpretations can be made following the standard BACI approach (Smith et al., 1993). In this regard, metrics such as the CI Contribution and CI Divergence (Chapter 4) were highly useful in informing and quantifying the direction and extent of change.

It has been suggested that multiple spatially-replicated controls should be included in a BACI design (also known as Beyond BACI) to improve inference of experimental effects from other background effects (Underwood, 1992). In Chapter 4 we included spatially replicated controls over two fishing intensities. While this enabled the analysis to better capture natural variability in the system, a potential drawback of multiple controls can be added variability within treatment, particularly when assessing small effects (Hewitt et al., 2001). Whilst we observed relatively low impacts from the Danish seine this likely reflects the low impact of the gear rather than as a result of high variability in the control. This is as the degree of variability in the control was not considerably larger than the experimental treatments. Therefore the similar level of variability would suggest that the additional control did not influence the outcome of our results. In comparison, we included a single control in Chapter 3, where we observed a significant effect of trawling in the dredge track and the adjacent area. In this case, the temporal variability in the control (positive trend) strengthened the significant BACI interaction, and contributed to clear treatment effects in both the dredge track and adjacent area. In the case of the adjacent area, the treatment effect was driven by the increase in the control rather than a decline in the adjacent area. In Chapter 3 we benefited from having nearby and representative control which added confidence to the interpretation of our results. However, in highly variable systems it is likely that multiple controls be required to best capture the natural variability. Ultimately, the most appropriate design comes down to a trade-off between the systems being examined, and the resources available for the assessment.

6.2.2. Variance

Given the inherent variability of natural systems, it is likely that the number of samples taken in a BACI will strongly influence the level of variance observed. An example of this is in Chapter 4, where we observed notable differences in variation (as shown by the error bars) between the two fishing intensities. In this case, it is possible that the greater variance was caused by fewer samples taken at the single haul site. The power to detect an effect depends on the magnitude of the impact (effect size), the variability in the data, and the number of independent samples. Following this, large effects require fewer samples to be detected, whilst small effects, in theory, require more samples in order to be detected. Using unfished areas in Iceland, Ragnarsson et al. (2009) used a power analysis to show that the effect size needed to detect a fisheries effect ranged between 10% -35%. The effect size varied between response variables (abundance and diversity) and temporal scale (short-term or persistent effects) due to within treatment variability. In contrast, Pitcher et al. (2009) compared several BACI designs, and found that using between 32 and 128 stations could detect an effect size of 79% and 55%, respectively. This would suggest that a (very) large number of samples may be needed to detect a small effect size. However, the intensity and scale of sampling (particularly for benthic communities) is typically influenced by resource availability, and therefore compromises in sampling effort are sometimes required. In the case of Chapter 4, a key objective was to determine differences between single and multiple hauls. Ultimately, we prioritised additional sampling in the multiple haul site, as although we expected small effect sizes in both experiments, we felt that the impacts of multiple hauls were more likely detectable, and more reflective of commercial fishing intensities.

6.2.3. Control sites

A major challenge for BACI experiments is finding a truly representative control site (Gray et al., 2006). As such, the lack of unfished reference areas in Europeans fishing grounds is known to impede our ability to detect fishing impacts (Engel and Kvitek 2008; Thrush and Dayton, 2002). By the mid 1990's there were widely documented changes to benthic fish and invertebrate communities across the North Sea (Frid et al., 2000). While comparisons with historical benthic community data has advanced our understanding of changes that have already occurred in the ecosystem (Bradshaw and Brands, 2002, Thurstan et al., 2010), they are unable to substitute as a reference state to appropriately compare fishing impact. Closing areas to trawling has been recommended to provide areas that can be used to accurately measure the impact of fishing in the future (Lindeboom, 1995). However, even now, roughly twenty-five years later, only ~ 40% of MPAs in Europe are not impacted by trawling (Dureuil et al., 2018). As a result, fishing impacts can only be measured against the remaining pockets of unfished seabed, some of which may not represent the habitats in the fishing grounds. The value of having closed areas as controls has been shown in Danish waters, where mussel dredging impacts were found to only be detectable when compared to long term unimpacted areas (McLaverty et al., 2020a).

Whilst the optimal experimental design would include unfished control sites, fishing studies without them are not redundant (Gray et al., 2006). The general paucity of unfished areas that are representative of fishing grounds is exemplified by some studies which consider 'unfished' conditions to be areas that have been unfished >10 (Sciberras et al. 2018). In many areas, this would only represent a fraction of the historical fishing impacts (Thurstan et al., 2010), and may explain the aforementioned low response of benthic fauna to fishing impacts in BACI studies (Section 1.3). In the case of our studies, the longest period since trawling was 9-years for the Danish seine study, followed by 4-years for the mussel dredge experiment, and 0-years for SOT. These represented the longest time periods possible in nearby comparable habitats. The recovery of benthic macrofauna from trawling, depends on the initial depletion rate as well as the habitat and taxa specific recovery rates (Sciberras et al., 2018). In general, well-sorted sandy habitats are considered the one of the least sensitive substrates to trawling (Bolam et al., 2014), owing to the inherently fast rates of species recovery. The faster recovery time in sand has also been suggested to be related to the size structure of benthic fauna, which is dominated by smaller taxa in sand (Querios et al., 2006). Given the sandy substrates in each of the case studies, the time since fishing in our experiments was likely sufficient to allow enough recovery of the community, with the exception of the SOT experiment.

6.2.4. Alternatives to BACI

An alternative approach to assess fishing impacts is done by comparing benthic communities across gradients of fishing intensity. Such studies have shown that benthic indicators are often negatively correlated with increasing fishing intensity (for example: Jennings et al., 2001; Tillin et al., 2006; Hiddink et al., 2006a; Querios et al., 2006; Engel and Kvitek 2008; McLaverty et al., 2020a,b). Unlike BACI experiments, which are carried out on small scales, gradient studies can evaluate fishing at a larger scales i.e. the scale of fisheries. Gradient studies can better capture dynamics such as recovery, which can be inhibited by a lack of recruitment potential caused by large-scale fishing impacts (Lambert et al., 2014). Similarly, the long-term or cumulative effects of trawling are more evident using these methods. However, these comparative approaches lack the specificity which is gained from more detailed small-scale experiments. Gradient studies cannot quantify the effects of individual fishing gear types (e.g. where multiple fisheries occur), the effect of specific gear components, the effect per single (and subsequent) gear pass, mortality rates of species and communities, and the immediate to short term effects of trawling. Each of these methods, BACI and gradient studies, have their respective strengths and weaknesses. However, given the type of information needed to properly evaluate the performance of new or modified fishing gears, particularly in comparison to conventional gear types, it would appear BACI-type approaches are better suited.

6.2.5. Alternative statistical approach

In Chapter 4, we followed the less commonly used methods of Conner et al (2016) and implemented a Bayesian framework to calculate BACI ratios, and probabilities of a fishing impact from Monte Carlo Markov Chain sampling (MCMC). There are many advantages of using this approach (detailed in Conner at al 2016) compared to more traditional approaches, despite the practicality of longer run times for models. A clear benefit was the interpretability of the results. MCMC be used to calculate BACI ratios (equivalent to percentage losses in other BACI studies), in addition to the posterior distribution. The posterior distribution allowed us to estimate the probability of a given effect size. As we generally did not observe large effects, we were interested in the probability of any negative effect (i.e. a decline relative to the control). These probabilities provided on a continuous scale are relatively informative, and arguably leaves the assessment of 'significance' to the reader's judgement. This is in comparison to frequentist approaches, where results falling outside of the 5% probability (as determined by the p-value), are categorically defined as scientifically unimportant (Muff et al., 2022). We also undertook multivariate community analysis using a Bayesian framework in an unconstrained ordination approach, and detected changes in individual species (Chapter 4). The advantage of this approach, in comparison to more traditional approaches (e.g. PERMANOVA), was the ability to perform model diagnostics, which allowed us to identify the most suitable model via model comparisons (WAIC/DIC). Further, the use of latent variables, instead of multivariate random effects, allowed us to fit joint models for the taxa in the community, while incorporating potential correlations between taxa.

6.2.6. Summary

There are many advantages of using a Before-After-Control-Impact design in evaluating fishing gear impacts to the seabed, but these approaches require caution in the interpretation of results. A lack of unfished control areas further accentuates the challenge. The most appropriate BACI design for a given situation will ultimately depend on aspects such as natural variation and resource availability. As BACI's represent the best method to accurately estimate fishing gear impacts on benthic macrofauna, it is recommended to focus on optimising the experimental design based on the given circumstances. Finally, evidence regarding fishing gear impacts require clarity of communication, in order to be understandable to a range of stakeholders. Statistical approaches such the MCMC, which provide both BACI ratios and associated posterior distribution probabilities, could be increasingly used in that regard.

6.3. Future perspectives

Trawling, and its impact on seabed habitats, remains topical and subject to much political debate (Kaiser et al., 2019). New nature restoration laws will soon come into force e.g. EU Biodiversity strategy for 2030, some of which will require EU member states to protect 20% of their natural habitats. These policies aim to halt biodiversity loss by focusing on restoring degraded habitats, and extending the network of protected areas (Hermoso et al., 2022). Efforts toward a more sustainable fishing industry have seen modified gears used to minimise by-catch (Kennelly et al., 2021) and to reduce fuel usage (Suuronen et al., 2012). The studies outlined in this thesis further contribute to research on the role of modified gears, by providing a new piece of the puzzle: the impact on benthic macrofauna.

Although modified and lightweight gears are already applied in Danish fisheries, there has remained a lack of quantitative information in regards the effects of these gears on benthic macrofauna. The Danish blue mussel fishery provides a good example of this, where a modified gear was introduced to comply with new fisheries management regulations. To abide with the Habitats and Birds Directives that underpin Natura 2000 designations, a mandatory switch to a new ‘lightweight’ mussel dredge was required for licenced vessels, along with on-board black-box vessel monitoring devices (Nielsen et al., 2021). The black-box records the footprint of the fishery and restricts the areal impact to 15% in each Natura 2000 site. While approaches such as the black box have undoubtedly improved the sustainability of the fishery, existing fisheries impact data were based on outdated assessments using conventional gear types (e.g. Dolmer et al., 1999). A key output of this thesis has therefore been the estimation of dredging impacts using the modified mussel dredge. Moving forward, these results can now be used in future annual Environmental Impact Assessments, which are currently required to estimate the potential impacts of the fisheries in each Natura 2000 areas (Nielsen et al., 2021). Given that the modified mussel dredge is used in a number of Natura 2000 sites across Denmark, this information can improve future management and ensure the fishery remains in line with nature conservation objectives.

The widespread adoption of an Ecosystem Approach to fisheries management has led to a need for data which are relevant across large special scales. Fisheries impacts data covering large areas often do not exist, or would be very costly to obtain. For this reason, new methods have been developed to enable trawling impacts to be assessed without the need for direct observations. This is done by combining data on seabed type, benthic recovery rates, and trawling intensity to estimate the Relative Seabed Status (RBS) of seabed habitats (Pitcher et al., 2017). RBS has been used in several recent studies to assess trawling impacts based on the longevity of benthic invertebrates (Hiddink et al., 2019), and to estimate the trawling impacts across diverse regions of the globe (Mazor et al., 2021). Furthermore, RBS is utilised by ICES to provide scientific advice to the European Commission (ICES, 2020), and will likely provide the basis of trawling impact management advice in the future. However, the calculation of RBS is reliant on gear specific benthic depletion rates (Pitcher et al., 2017), such as those presented in this thesis. Due to a lack of information on depletion rates for some less widely used gears (e.g. Danish seines) parameters from other gears are often applied. The same issue exists for habitat types, such as biogenic reefs (e.g. mussel beds), where parameters for their depletion and recovery rates are scarce (Pitcher et al., 2017). Accordingly, the new data provided in this thesis have the potential to improve estimates of RBS, and therefore improve estimates of the effects of trawling on large spatial scales.

The widespread adoption of an Ecosystem Approach to fisheries management has led to a need for data which are relevant across large special scales. Fisheries impacts data covering large areas often do not

exist, or would be very costly to obtain. For this reason, new methods have been developed to enable trawling impacts to be assessed without the need for direct observations. This is done by combining data on seabed type, benthic recovery rates, and trawling intensity to estimate the Relative Seabed Status (RBS) of seabed habitats (Pitcher et al., 2017). RBS has been used in several recent studies to assess trawling impacts based on the longevity of benthic invertebrates (Hiddink et al., 2019), and to estimate the trawling impacts across diverse regions of the globe (Mazor et al., 2017). Furthermore, RBS is utilised by ICES to provide scientific advice to the European Commission (ICES, 2020), and will likely provide the basis of trawling impact management advice in the future. However, the calculation of RBS is reliant on gear specific benthic depletion rates (Pitcher et al., 2017), such as those presented in this thesis. Due to a lack of information on depletion rates for some less widely used gears (e.g. Danish seines) parameters from other gears are often applied. The same issue exists for habitat types, such as biogenic reefs (e.g. mussel beds), where parameters for their depletion and recovery rates are scarce (Pitcher et al., 2017). Accordingly, the new data provided in this thesis have the potential to improve estimates of RBS, and therefore improve estimates of the effects of trawling on large spatial scales.

Given the ambition to improve seabed integrity at a European level, lightweight and modified gears could become more widely adopted to meet future conservation objectives. However, in addition to these benefits, lightweight and modified fishing gear have the potential to reduce carbon emissions from trawl fisheries. Marine sediments contain the largest pool of organic carbon on Earth, and are concentrated in coastal waters (Atwood et al., 2020), which also represent some of the most heavily fished areas (Eigaard et al., 2017). The remineralisation of carbon caused by trawling disturbance has the potential to contribute to increasing atmospheric CO2, while undisturbed sedimentary habitat could play an important role in carbon sequestration (Epstein and Roberts, 2022). Thus, as countries move forwards in their efforts to reduce their carbon footprint, fisheries have the potential to be penalised. As gear penetration depth is a key factor for the release of carbon from sediments, lightweight/modified gears with lower seabed contact may reduce sedimentary carbon remineralisation (Epstein and Roberts, 2022). Taking an example from Danish fisheries, the replacement of heavy and more damaging gears (e.g. beam trawls) with the lighter weight and low impact (e.g. Danish seines) would benefit both conservations objectives, as well as national ambitions of reaching net zero.

6.3.1. Conclusions

Gear modifications can only go part of the way to achieving more sustainable bottom trawl fisheries. This is as, by design, these gears interact with soft sediment habitats and result in varying degrees of damage to seabed ecosystems. However, the results of this thesis show that while some lightweight and modified gears do impact benthic macrofauna, the effects are often relatively small, and in some cases only impact specific species within a community. Modified gears may therefore not represent a ‘silver-bullet’ solution to improving the sustainability of bottom trawling, and are not recommended in place of e.g. spatial closures. Instead, the findings suggest that modified gears can provide a functional and low-impact alternative to a number of conventional gears. If these modified gears were to be more widely adopted, they have the potential to meet marine conservation objectives, reduce operational costs for fishermen, and shift the management of high impact fisheries towards a more fully integrated ecosystems approach.

References

Atwood, T.B., Witt, A., Mayorga, J., Hammill, E., Sala, E., 2020. Global Patterns in Marine Sediment Carbon Stocks. Front. Mar. Sci. 7, 1–9. https://doi.org/10.3389/fmars.2020.00165

Bergman, M.J.N., Van Santbrink, J.W., 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES J. Mar. Sci. 57, 1321–1331. https://doi.org/10.1006/jmsc.2000.0917

Bolam, S.G., Coggan, R.C., 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. https://doi.org/10.1016/j.seares.2013.05.003

Bradshaw, C., Veale, L.O., Brand, A.R., 2002. The role of scallop-dredge disturbance in long-term changes in Irish Sea benthic communities : a re-analysis of an historical dataset 47, 161–184. https://doi.org/10.1016/S1385-1101(02)00096-5

Bremner, J., Rogers, S.I., Frid, C.L.J., 2003. Assessing functional diversity in marine benthic ecosystems: A comparison of approaches. Mar. Ecol. Prog. Ser. 254, 11–25. https://doi.org/10.3354/meps254011

Brown, E.J., Finney, B., Dommisse, M., Hills, S., 2005. Effects of commercial otter trawling on the physical environment of the southeastern Bering Sea. Cont. Shelf Res. 25, 1281–1301. https://doi.org/10.1016/j.csr.2004.12.005

Conner, M.M., Saunders, W.C., Bouwes, N., Jordan, C., 2016. Evaluating impacts using a BACI design, ratios, and a Bayesian approach with a focus on restoration. Environ. Monit. Assess. 188. https://doi.org/10.1007/s10661-016-5526-6

Cook, R., Fariñas-Franco, J.M., Gell, F.R., Holt, R.H.F., Holt, T., Lindenbaum, C., Porter, J.S., Seed, R., Skates, L.R., Stringell, T.B., Sanderson, W.G., 2013. The Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A Dilemma for Evidence-Based Conservation. PLoS One 8, e69904. https://doi.org/10.1371/journal.pone.0069904

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. https://doi.org/10.1016/S0165-7836(98)00218-5

Drabsch, S.L., Tanner, J.E., Connell, S.D., 2001. Limited infaunal response to experimental trawling in previously untrawled areas. ICES J. Mar. Sci. 58, 1261–1271. https://doi.org/10.1006/jmsc.2001.1105

Dureuil, M., Boerder, K., Burnett, K.A., Froese, R., Worm, B., 2018. Elevated trawling inside protected areas undermines conservation outcomes in a global fishing hot spot. Science. 362, 1403–1407. https://doi.org/10.1126/science.aau0561

Eigaard, O.R., Bastardie, F., Breen, M., Dinesen, G.E., Hintzen, N.T., Laffargue, P., Mortensen, L.O., Nielsen, J.R., Nilsson, H.C., O'Neill, F.G., Polet, H., Reid, D.G., Sala, A., Sköld, M., Smith, C., Sørensen, T.K., Tully, O., Zengin, M., Rijnsdorp, A.D., 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. 73, i27–i43. https://doi.org/10.1093/icesjms/fsv099

Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G.E., Egekvist, J., Fock, H.O., Geitner, K., Gerritsen, H.D., González, M.M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J.R., Papadopoulou, N., Posen, P.E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C.J., Vanelslander, B., Rijnsdorp, A.D., 2017. The footprint of bottom trawling in European waters: Distribution, intensity, and seabed integrity. ICES J. Mar. Sci. 74, 847–865. https://doi.org/10.1093/icesjms/fsw194

Engel, J., Kvitek, R., 1998. Effects of Otter Trawling on a Benthic Community in Monterey Bay Nation. Conserv. Biol. 12, 1204–1214. https://www.jstor.org/stable/2989838

Epstein, G., Roberts, C.M., 2022. Identifying priority areas to manage mobile bottom fishing on seabed carbon in the UK. PLOS Clim. 1, e0000059. https://doi.org/10.1371/journal.pclm.0000059

FAO. 2022. Fishing Techniques. Danish seining. Technology Fact Sheets. Fisheries and Aquaculture Division [online]. Updated 2005-02-17

Frid, C.L.J., Clark, R.A., Hall, J.A., 1999. Long-term changes in the benthos on a heavily fished ground off the NE coast of England. Mar. Ecol. Prog. Ser. 188, 13–20. https://doi.org/10.3354/meps188013

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 Report.

Gray, J.S., Dayton, P., Thrush, S., Kaiser, M.J., 2006. On effects of trawling, benthos and sampling design. Mar. Pollut. Bull. 52, 840–843. https://doi.org/10.1016/j.marpolbul.2006.07.003

Green, R.H., 1979. Sampling design and statistical methods for environmental biologists. JWS, NY.

Hall-Spencer, J., Moore, P.G., 2000. Scallop dredging has profound, long-term impacts on maerl habitats. ICES J Mar Sci.57, 1407-1415. doi:10.1006/jmsc.2000.0918

Hermoso, V., Carvalho, S.B., Giakoumi, S., Goldsborough, D., Katsanevakis, S., Leontiou, S., Markantonatou, V., Rumes, B., Vogiatzakis, I.N., Yates, K.L., 2022. The EU Biodiversity Strategy for 2030: Opportunities and challenges on the path towards biodiversity recovery. Environ. Sci. Policy 127, 263–271. https://doi.org/10.1016/j.envsci.2021.10.028

Hewitt, J.E., Thrush, S.E., Cummings, V.J., 2001. Assessing environmental impacts: Effects of spatial and temporal variability at likely impact scales. Ecol. Appl. 11, 1502–1516. https://doi.org/https://doi.org/10.1890/1051-0761(2001)011[1502:AEIEOS]2.0.CO;2

Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E., Piet, G.J., 2006a. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Can. J. Fish. Aquat. Sci. 63, 721–736. https://doi.org/10.1139/f05-266

Hiddink J.G., Hutton, T., Jennings, S., Kaiser, M.J., 2006b. 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. doi:10.1016/j.icesjms.2006.02.006

Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proc. Natl. Acad. Sci. 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114

Hiddink, J.G., Jennings, S., Sciberras, M., Bolam, S.G., Cambiè, G., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Parma, A.M., Suuronen, P., Kaiser, M.J., Rijnsdorp, A.D., 2019. Assessing bottom trawling impacts based on the longevity of benthic invertebrates. J. Appl. Ecol. 56, 1075–1084. https://doi.org/10.1111/1365-2664.13278

Hiddink, J.G., Kaiser, M.J., Sciberras, M., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Parma, A.M., Suuronen, P., Rijnsdorp, A.D., Jennings, S., 2020. Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. J. Appl. Ecol. 57, 1199–1209. https://doi.org/10.1111/1365-2664.13617

Hinz, H., Prieto, V., Kaiser, M.J., 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecol. Appl. 19, 761–773. https://doi.org/10.1890/08-0351.1

Hoffmann, E., Dolmer, P., 2000. Effect of closed areas on distribution of fish and epibenthos. ICES J. Mar. Sci. 57, 1310–1314. https://doi.org/10.1006/jmsc.2000.0921

ICES. 2020. Working Group on Fisheries Benthic Impact and Trade-offs (WGFBIT; outputs from 2019 meeting). ICES Scientific Reports. 2:6. 101 pp. http://doi.org/10.17895/ices.pub.5955

Jacquemont, J., Blasiak, R., Le Cam, C., Le Gouellec, M., Claudet, J., 2022. Ocean conservation boosts climate change mitigation and adaptation. One Earth 5, 1126–1138. https://doi.org/10.1016/j.oneear.2022.09.002

Jennings, S., Pinnegar, J.K., Polunin, N.V.C., Warr, K.J., 2001. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. Mar. Ecol. Prog. Ser. 213, 127–142. https://doi.org/10.3354/meps213127

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. https://doi.org/10.3354/meps311001

Kaiser, M., Hormbrey, S., Booth, J.R., Hinz, H., Hiddink, J.G., 2018. Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. J. Appl. Ecol. 55, 1060–1070. https://doi.org/10.1111/1365-2664.13087

Kaiser, M.J., 2019. Recent advances in understanding the environmental footprint of trawling on the seabed. Can. J. Zool. 762, 755–762. https://doi.org/10.1139/cjz-2018-0248

Kennelly, S.J., Broadhurst, M.K., 2002. By-catch begone: Changes in the philosophy of fishing technology. Fish Fish. 3, 340–355. https://doi.org/10.1046/j.1467-2979.2002.00090.x

Lambert, G.I., Jennings, S., Kaiser, M.J., Davies, T.W., Hiddink, J.G., 2014. Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. J. Appl. Ecol. 51, 1326–1336. https://doi.org/10.1111/1365-2664.12277

Lambert, G.I., Murray, L.G., Hiddink, J.G., Hinz, H., Lincoln, H., Hold, N., Cambiè, G., Kaiser, M.J., 2017. Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance. Sci. Rep. 7, 5440. https://doi.org/10.1038/s41598-017-04715-4

Lindeboom, H.J., 1995. Protected areas in the North Sea: An absolute need for future marine research. Helgoländer Meeresuntersuchungen 49, 591–602. https://doi.org/10.1007/BF02368384

Mazor, T.K., Pitcher, C.R., Ellis, N., Rochester, W., Jennings, S., Hiddink, J.G., McConnaughey, R.A., Kaiser, M.J., Parma, A.M., Suuronen, P., Kangas, M., Hilborn, R., 2017. Trawl exposure and protection of seabed fauna at large spatial scales. Divers. Distrib. 23, 1280–1291. https://doi.org/10.1111/ddi.12622

McConnaughey, R.A., Hiddink, J.G., Jennings, S., Pitcher, C.R., Kaiser, M.J., Suuronen, P., Sciberras, M., Rijnsdorp, A.D., Collie, J.S., Mazor, T., Amoroso, R.O., Parma, A.M., Hilborn, R., 2020. Choosing best practices for managing impacts of trawl fishing on seabed habitats and biota. Fish Fish. 21, 319–337. https://doi.org/10.1111/faf.12431

McLaverty, C., Eigaard, O.R., Dinesen, G.E., Gislason, H., Kokkalis, A., Erichsen, A.C., Petersen, J.K., 2020a. High-resolution fisheries data reveal effects of bivalve dredging on benthic communities in stressed coastal systems. Mar. Ecol. Prog. Ser. 642, 21–38. https://doi.org/10.3354/meps13330

McLaverty, C., Eigaard, O.R., Gislason, H., Bastardie, F., Brooks, M.E., Jonsson, P., Lehmann, A., Dinesen, G.E., 2020b. 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

Muff, S., Nilsen, E.B., O'Hara, R.B., Nater, C.R., 2022. Rewriting results sections in the language of evidence. Trends Ecol. Evol. 37, 203–210. https://doi.org/10.1016/j.tree.2021.10.009

Nielsen, P., Nielsen, M.M., McLaverty, C., Kristensen, K., Geitner, K., Olsen, J., Saurel, C., Petersen, J.K., 2021. Management of bivalve fisheries in marine protected areas. Mar. Policy. 124, 104357 https://doi.org/10.1016/j.marpol.2020.104357

Noack, T., Frandsen, R.P., Wieland, K., Krag, L.A., Berg, F., Madsen, N., 2017. Fishing profiles of Danish seiners and bottom trawlers in relation to current EU management regulations. Fish. Manag. Ecol. 24, 436–445. https://doi.org/10.1111/fme.12244

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. https://doi.org/10.3354/meps07033

Pitcher, C.R., Burridge, C.Y., Wassenberg, T.J., Hill, B.J., Poiner, I.R., 2009. A large scale BACI experiment to test the effects of prawn trawling on seabed biota in a closed area of the Great Barrier Reef Marine Park, Australia. Fish. Res. 99, 168–183. https://doi.org/10.1016/j.fishres.2009.05.017

Pitcher, C.R., Ellis, N., Jennings, S., Hiddink, J.G., Mazor, T., Kaiser, M.J., Kangas, M.I., McConnaughey, R.A., Parma, A.M., Rijnsdorp, A.D., Suuronen, P., Collie, J.S., Amoroso, R., Hughes, K.M., Hilborn, R., 2017. Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. Methods Ecol. Evol. 8, 472–480. https://doi.org/10.1111/2041-210X.12705

Pitcher, C.R., Hiddink, J.G., Jennings, S., Collie, J., Parma, A.M., Amoroso, R., Mazor, T., Sciberras, M., McConnaughey, R.A., Rijnsdorp, A.D., Kaiser, M.J., Suuronen, P., Hilborn, R., 2022. Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. Proc. Natl. Acad. Sci. 119. https://doi.org/10.1073/pnas.2109449119

Prantoni, A.L., Lana, P.D.C., Sandrini-Neto, L., Filho, O.A.N., de Oliveira, V.M., 2013. An experimental evaluation of the short-term effects of trawling on infaunal assemblages of the coast off southern Brazil. J. Mar. Biol. Assoc. United Kingdom 93, 495–502. https://doi.org/10.1017/S002531541200029X

Queirós, A.M., Hiddink, J.G., Kaiser, M.J., 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. https://doi.org/10.1016/j.jembe.2006.03.001

Ragnarsson, S., Lindegarth, M., 2009. Testing hypotheses about temporary and persistent effects of otter trawling on infauna: changes in diversity rather than abundance. Mar. Ecol. Prog. Ser. 385, 51–64. https://doi.org/10.3354/meps08056

Reiss, H., Greenstreet, S.P.R., Sieben, K., Ehrich, S., Piet, G.J., Quirijns, F., Robinson, L., Wolff, W.J., 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. https://doi.org/10.3354/meps08243

Rijnsdorp, A.D., Bolam, S.G., Garcia, C., Hiddink, J.G., Hintzen, N.T., van Denderen, P.D., 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. https://doi.org/10.1002/eap.1731

Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish Fish. 19, 698–715. https://doi.org/10.1111/faf.12283

Sköld, M., Göransson, P., Jonsson, P., Bastardie, F., Blomqvist, M., Agrenius, S., Hiddink, J., Nilsson, H., Bartolino, V., 2018. Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. Mar. Ecol. Prog. Ser. 586, 41–55. https://doi.org/10.3354/meps12434

Smith, E.P., Orvos, D.R., Cairns Jr., J., 1993. Impact Assessment Using the Before-After-Control-Impact (BACI) Model: Concerns and Comments. Can. J. Fish. Aquat. Sci. 50, 627–637. https://doi.org/10.1139/f93-072

Suuronen, P., Chopin, F., Glass, C., Løkkeborg, S., Matsushita, Y., Queirolo, D., Rihan, D., 2012. Low impact and fuel efficient fishing - Looking beyond the horizon. Fish. Res. 119–120, 135–146. https://doi.org/10.1016/j.fishres.2011.12.009

Thrane, M., 2005. Energy Consumption in the Danish Fishery: Identification of Key Factors. J. Ind. Ecol. 8, 223–239. https://doi.org/10.1162/1088198041269427

Thrush, S.F., Dayton, P.K., 2002. Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annu. Rev. Ecol. Syst. 33, 449–473. https://doi.org/10.1146/annurev.ecolsys.33.010802.150515

Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A., 2006. Functional Role of Large Organisms in Intertidal Communities: Community Effects and Ecosystem Function. Ecosystems 9, 1029–1040. https://doi.org/10.1007/s10021-005-0068-8

Thurstan, R.H., Brockington, S., Roberts, C.M., 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat. Commun. 1, 15. https://doi.org/10.1038/ncomms1013

Tillin H.M, Hiddink J.G, Jennings S, Kaiser M.J, 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 284–286. https://doi.org/10.3354/meps318031

Tuck, I.D., Hall, S.J., Robertson, M.R., Armstrong, E., Basford, D.J., 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch 162, 227–242.

Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J. Exp. Mar. Bio. Ecol. 161, 145–178. https://doi.org/10.1016/0022-0981(92)90094-Q