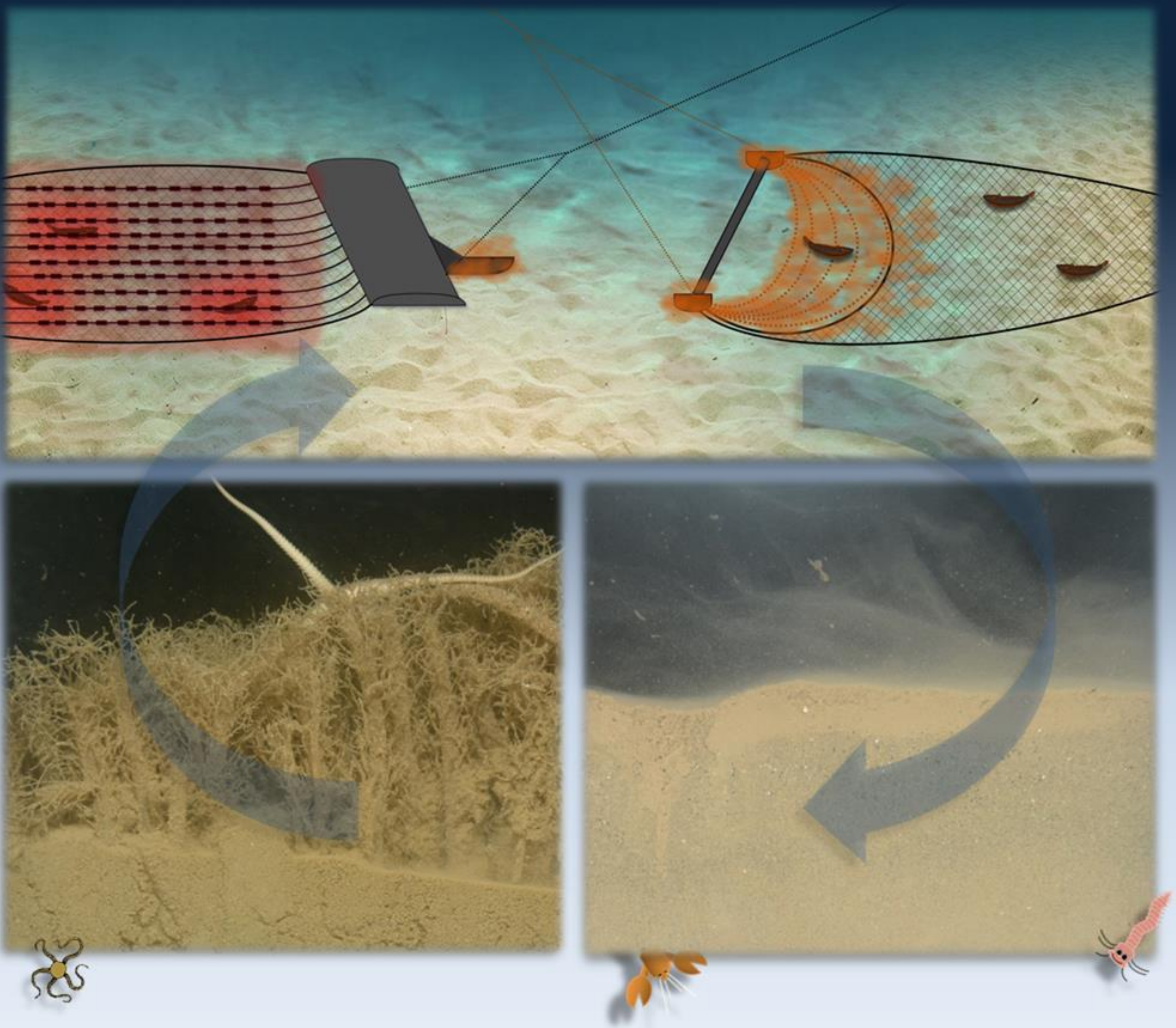
Evaluating the consequences of bottom trawling on benthic pelagic coupling and ecosystem functioning



GHENT UNIVERSITY

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NIOZ

Evaluating the consequences of bottom trawling on benthic pelagic coupling and ecosystem functioning

by Justin C. Tiano

“Being realistic is the most common path to mediocrity.” – Will Smith

Tiano J. C. (2020)

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Evaluating the consequences of bottom trawling on benthic pelagic coupling and ecosystem functioning

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SUMMARY

Bottom trawling can cause severe alterations on benthic ecosystems, however, we are just beginning to understand how these disturbances can affect biogeochemical functioning and benthic pelagic coupling. The cycling of carbon, oxygen and nutrients regulate the existence of Earth's ecosystems but can also be significantly affected by the organisms living in these habitats. As trawling has a direct impact on both biogeochemical and organismal parameters, the net effect on benthic pelagic coupling can be complex and difficult to predict.

European waters exhibit some of the highest levels of trawling on Earth (Amoroso et al., 2018). Bottom trawling in the North Sea, as well as opposition against it, has been occurring for well over 600 years (Collins, 1887). In recent times, novel 'electric pulse' fishing methods, occurring in the North Sea, have been steeped in controversy concerning their unstudied ecosystem effects (Kraan et al., 2020). This PhD aims to uncover some of the mysteries behind bottom trawl-induced effects on benthic pelagic coupling and to discover the potential effects of electric pulse trawls on biogeochemistry and ecosystem functioning.

The research in this thesis begins with a large-scale field study conducted to compare the *in situ* impacts of electric pulse and traditionally used tickler chain beam trawl techniques (**Chapter 2**). This study was conducted in the Frisian Front region of the North Sea in collaboration with professional fishermen to produce intensively trawled areas. Here, we discovered that acute trawling could significantly reduce the benthic mineralization of organic matter (OM) while reallocating some of the metabolic activity into the water column. This was accompanied with a deepening of the sedimentary oxic layer suggesting lower levels of biological activity for these sediments due to decreased OM content and possibly reduced microbial densities caused by the trawl-induced removal of surficial sediment. Reduced benthic metabolism after trawling was attributed to a steep decline in labile OM on surface sediments, also implying lower food availability for benthic organisms. Although both fishing methods caused significant biogeochemical alterations, an overall reduced impact could been seen in pulse trawls versus traditional methods.

Chapter 3 takes data from the same field campaign as chapter 2, this time investigating the effects of bottom trawls on benthic ecological communities and physical changes. Acoustic and optical techniques revealed a flattening of the seabed and a reduction of burrow holes made by benthic organisms. A severe decline in epibenthos and juvenile taxa after trawling was accompanied with increases of the deep burrowing mud shrimps, *Callianassa subterranea*. These results suggest that while organisms residing near the sediment surface were removed by bottom trawling, fauna that had escaped trawling in deep burrows will spend more time close to the sediment surface, possibly fixing damaged/buried burrow entrances, after trawling impact. Historical information shows a regime shift occurring in the Frisian Front, which was once home to high abundances of shallow burrowing brittle stars (*Amphiura filiformis*) but is now a *C. subterranea* dominated habitat (Amaro, 2005). Our results suggest that trawling may have facilitated this shift in species. Unlike the previous study (chapter 2), here our results did not detect a differential effect of pulse or conventional beam trawls implying that they can have similar effects on benthic communities in soft sediments.

To better understand the biogeochemical effects from mechanical-induced sediment resuspension and potential electrolysis, **Chapter 4** simulated these disturbances in controlled mesocosms. Sediments were taken from 9 North Sea and 2 Easter Scheldt locations and received either mechanical mixing perturbations in the surface layers (to represent physical disturbances from trawling), or electrical exposures of 3 or 120 seconds from pulsed bipolar currents (PBC) or pulsed direct currents (PDC). Mechanical disturbances released the equivalent of 90+ hours of natural nutrient effluxes in some sediments, while rapidly depleting water column oxygen. Electrolysis was only detected in sediments exposed to 120 seconds of PDC. This treatment caused the electric-induced movement of porewater ions creating the formation of iron oxides on the sediment surface, subsequently binding to phosphorus in the water column. Mechanical and PDC-induced alterations to solute concentrations were linked with labile OM content, sediment grain size, and time of year when sediments were collected. These results suggest that PBC employed by the pulse trawling used for flatfish is not likely to generate biogeochemical effects while direct currents, which have been employed in *Ensis* electrofishing, may affect marine phosphorus dynamics. Furthermore, our findings show that mechanical disturbance will have a higher biogeochemical impact in the late summer/early autumn, in soft sediments rich with labile OM.

Chapter 5 documents a study, which combined physical, biogeochemical and ecological data collection techniques, resulting in one of the most comprehensive acute effects focused bottom trawling studies to date. We worked with professional fishermen to create multiple trawled treatment areas in the dynamic coastal waters of the Vlakte van de Raan, in habitats dominated by *Lanice conchilega* reefs. Here we detected significant declines of 46% and 57% in sediment oxygen consumption from pulse and tickler chain beam trawls respectively, which was attributed to a decrease in faunal-mediated biogeochemical functioning. Trawling also decoupled relationships between *L. conchilega* and abundances of other macrofauna, oxygen consumption, sediment characteristics, and nitrate fluxes. Our study shows that biogenic habitats are vulnerable to ecological and biogeochemical changes from trawling, even in dynamic sandy areas where disturbance effects are expected to be lower. Pulse trawls showed more inconsistent effects compared to beam trawls, leading to a lower average impact, though these methods can sometimes create equal levels of disturbance.

The research in this thesis concludes with a discussion on the applied and fundamental implications of the research carried out during this PhD (**Chapter 6**). Our findings show a slightly reduced direct impact from pulse versus beam trawls, though significant effects can be expected from both gear types. We found that pulse trawls do not elicit a significant electrochemical response and have a slightly lower effect on biogeochemical parameters compared to conventional methods due to less mechanical disturbance. In light of other research, however, the main benefit of pulse trawls compared to tickler chain beam trawls has less to do with any decreased direct environmental impact but rather with the efficiency of pulse trawl gears, which leads to less time at sea and a reduced ecological footprint (Rijnsdorp et al., 2020). While we can ascertain if certain gears produce greater biogeochemical effects than others, we still have only a limited understanding of the larger scale (fundamental) implications of these effects. Our findings of lower mineralization may create consequences related to reduced nutrient cycling of sedimentary habitats. More research is necessary to understand the consequences of bottom trawling on holistic ecosystem processes including benthic pelagic coupling, but the work conducted during this PhD was able to uncover some important information that contributes to a more complete understanding of this topic.

The final section in this thesis (**Appendix**) reports on some future research plans aiming to build upon the work conducted during this PhD. This section is adapted from an accepted grant proposal, written to continue research on trawl-induced ecosystem effects. Our objective is to facilitate and scientifically validate the use of environmentally friendly fishing techniques by creating a type of practical application that can be used to predict the long-term effects of using certain gears. We plan on expanding preexisting computational models to predict the effects of different trawl gears on benthic pelagic coupling and biology. Using scaled down physical models of fishing gears, in collaboration with a local non-profit, we will quantify mechanical effects of different types of bottom gears to be used in the computational models. Predictions will be verified by carrying out laboratory experiments with sediments from representative North Sea areas. The work conducted during this PhD has opened the door to n , Pleuronectes platessaew questions that we aim to tackle in this upcoming research.

SAMENVATTING

Bodemtrawls kunnen ernstige veranderingen in benthische ecosystemen veroorzaken, maar we beginnen nu pas te begrijpen hoe deze verstoringen het biogeochemisch functioneren en de benthisch-pelagische koppeling kunnen beïnvloeden. De cyclus van koolstof, zuurstof en voedingsstoffen reguleert het bestaan van de ecosystemen op aarde, en kan aanzienlijk worden beïnvloed door organismen die in deze habitats leven (Braeckman et al., 2010). Aangezien trawlen een directe invloed heeft op zowel biogeochemische parameters als de bodemgemeenschap, kan het netto-effect op de bentisch-pelagische koppeling complex en moeilijk te voorspellen zijn.

Europese wateren vertonen enkele van de hoogste trawlintensiteiten op aarde (Amoroso et al., 2018). Bodemtrawlvisserij op de Noordzee, en de oppositie daartegen, vindt al meer dan 600 jaar plaats (Collins, 1887). Recent zijn er in de Noordzee nieuwe visserijmethoden voor 'elektrisch pulsvissen' ontwikkeld, die controversieel zijn vanwege hun ongekende ecosysteemeffecten (Kraan et al., 2020). Dit doctoraat heeft als doel enkele van de mysteries van de door bodemtrawl veroorzaakte effecten op de benthisch-pelagische koppeling te ontdekken, en de potentiële effecten van elektrische pulstrawls op de biogeochemie en het functioneren van ecosystemen bloot te leggen.

Het onderzoek in dit proefschrift begint met een grootschalige veldstudie die is uitgevoerd om de *in situ* effecten van elektrische pulsen en traditioneel gebruikte wekkerketting-trawltechnieken te vergelijken (**Hoofdstuk 2)**. Deze studie is uitgevoerd in het Friese Frontgebied van de Noordzee in samenwerking met professionele vissers om intensief geteisterde gebieden na te bootsen. Hier ontdekten we dat trawlvisserij de benthische mineralisatie van organisch materiaal (OM) onmiddellijk aanzienlijk kan verminderen, terwijl een deel van de metabole activiteit verplaatst wordt naar de waterkolom. Dit ging gepaard met een verdieping van de zuurstofrijke laag in het sediment, wat wijst op een lagere biologische activiteit in deze sedimenten. Een verminderd bentisch metabolisme na de trawlvisserij werd toegeschreven aan een sterke daling van de labiele OM in sedimenten aan het oppervlak, wat ook een lagere voedselbeschikbaarheid impliceert voor bentische organismen. Hoewel beide vismethoden aanzienlijke biogeochemische veranderingen veroorzaakten, was er in het algemeen een verminderde impact te zien bij pulskorren versus traditionele methoden.

Hoofdstuk 3 gebruikt gegevens van dezelfde veldcampagne als hoofdstuk 2, dit keer om de effecten van bodemtrawls op benthische ecologische gemeenschappen en fysieke veranderingen te onderzoeken. Akoestische en optische technieken onthulden een afvlakking van de zeebodem en een vermindering van holen gemaakt door bentische organismen. Een ernstige achteruitgang van epibenthos en juveniele taxa na de trawlvisserij ging gepaard met toenames van diep gravende moddergarnalen, *Callianassa subterranea*. Deze resultaten suggereren dat organismen in de buurt van het sedimentoppervlak verwijderd worden door bodemtrawls, en dat dieper levende fauna zich na een bodemtrawl dichter bij het oppervlak bevindt, mogelijks om beschadigde holen en gangen te herstellen. Historische informatie toont een verschuiving van de soortencompositie op het Friese Front, dat ooit de thuisbasis was van grote hoeveelheden ondiepe gravende brokkelsterren (*Amphiura filiformis*), maar nu door *C. subterranea* gedomineerd wordt (Amaro, 2005). Onze resultaten suggereren dat trawlen deze verschuiving in soorten mogelijks vergemakkelijkt heeft. In tegenstelling tot de vorige studie (hoofdstuk 2), vertoonden onze resultaten hier geen verschil tussen de effecten van puls- of conventionele boomkorren, wat suggereert dat ze vergelijkbare effecten kunnen hebben op bentische gemeenschappen in zachte sedimenten.

Om de biogeochemische effecten van mechanisch geïnduceerde sedimentresuspensie en potentiële elektrolyse beter te begrijpen, simuleerden we deze verstoringen in gecontroleerde mesokosmossen (**Hoofdstuk 4)**. Sedimentenmonsters werden genomen op 9 locaties in de Noordzee en 2 in de Oosterschelde, en werden mechanisch verzameld in de oppervlaktelagen (om fysieke verstoringen door trawlvisserij na te bootsen), of blootgesteld aan elektrische pulsen van 3 of 120 seconden door gepulseerde bipolaire stromen (PBC) of gepulseerde directe stromen (PDC). Mechanische storingen gaven in sommige sedimenten het equivalent van meer dan 90 uur aan natuurlijke nutriëntenafvoer vrij, terwijl zuurstof in de waterkolom snel uitgeput raakte. Elektrolyse werd alleen gedetecteerd in sedimenten die waren blootgesteld aan 120 seconden PDC. De PDC behandeling veroorzaakte de elektrogene beweging van poriewaterionen, waardoor ijzeroxiden aan het sedimentoppervlak werden gevormd die vervolgens aan fosfor in de waterkolom bonden. Mechanische en PDC-geïnduceerde veranderingen in opgeloste concentraties waren gekoppeld aan het labiel OM-gehalte, de korrelgrootte van sediment en de tijd van het jaar waarin sedimenten werden verzameld. Deze resultaten suggereren dat PBC die wordt gebruikt door de pulsvisserij naar platvissen waarschijnlijk geen biogeochemische effecten zal genereren, terwijl directe stromen, die bij Ensis-elektrovissen (messchelpen) worden gebruikt, de dynamiek van marien fosfor kunnen beïnvloeden. Mesheften laten onze bevindingen zien dat mechanische verstoring een hogere biogeochemische impact zal hebben in de late zomer / vroege herfst, in zachte sedimenten die rijk zijn aan labiel OM.

Hoofdstuk 5 documenteert een studie waarin fysische, biogeochemische en ecologische technieken voor het verzamelen van gegevens werden gecombineerd, met als resultaat een van de meest uitgebreide onderzoeken naar de acute effecten van bodemtrawls tot nu toe. We hebben met professionele vissers samengewerkt om meerdere trawlgebieden te creëren in de dynamische kustwateren van de Vlakte van de Raan, in habitats die worden gedomineerd door *Lanice conchilega*-riffen. Hier ontdekten we significante afnames van 46% en 57% in het zuurstofverbruik in sediment door respectievelijk puls- en wekkerkettingtrawls, wat werd toegeschreven aan een afname in door de fauna veroorzaakte biogeochemische werking. De trawlvisserij ontkoppelde ook de relaties tussen *L. conchilega* en de overvloed aan andere macrofauna , zuurstofverbruik, sedimentkenmerken en nitraatstromen. Onze studie toont aan dat biogene habitats kwetsbaar zijn voor nitraatuitwisselingen biogeochemische veranderingen door sleepnetten, zelfs in dynamische zandgebieden waar de verwachtte verstoringseffecten lager zijn. Pulstrawls leidden tot meer inconsistente effecten in vergelijking met boomkorren, met een lagere gemiddelde impact als gevolg, hoewel deze methoden soms gelijke verstoringsniveaus veroorzaakten.

Dit proefschrift wordt afgesloten met een discussie over de toegepaste en fundamentele implicaties van het onderzoek dat tijdens dit doctoraat is uitgevoerd (**Hoofdstuk 6**). Onze bevindingen laten een licht verminderde directe impact zien van puls- versus boomkorren, hoewel van beide vistuigen aanzienlijke effecten worden verwacht. We ontdekten dat pulskorren geen significante elektrochemische respons opwekken, en een iets lager effect hebben op biogeochemische parameters in vergelijking met conventionele methoden, met als hoofdreden de verminderde mechanische verstoring. Gezien de resultaten van ander onderzoek, lijkt het belangrijkste voordeel van pulskorren in vergelijking met wekkerkettingtrawls echter minder te maken hebben met directe ecosysteemeffecten, maar eerder met de efficiëntie van pulskorren, wat leidt tot minder tijd op zee en een kleinere ecologische voetafdruk (Rijnsdorp et al., 2020). Hoewel we kunnen nagaan of bepaalde toestellen grotere biogeochemische effecten produceren dan anderen, hebben we nog maar een beperkt inzicht in de fundamentele implicaties van deze effecten op grotere schaal. Onze bevindingen van een lagere mineralisatie kunnen leiden tot een verminderde cyclering van nutriënten in sedimentaire habitats. Meer onderzoek is nodig om de gevolgen van bodemtrawls op de holistische ecosysteemprocessen waaronder benthisch-pelagische koppeling te begrijpen, maar het werk dat tijdens dit doctoraat werd verricht, heeft belangrijke informatie blootgelegd die bijdraagt tot een completer begrip van dit onderwerp.

Het laatste deel van dit proefschrift (bijlage) rapporteert over enkele toekomstige onderzoeksplannen die erop gericht zijn voort te bouwen op het werk dat tijdens dit doctoraat is verricht. Dit gedeelte is een aangepaste versie van een geaccepteerd subsidievoorstel, geschreven om het onderzoek naar door sleepnetten veroorzaakte ecosysteemeffecten voort te zetten.Ons doel is om het gebruik van milieuvriendelijke vistechnieken te vergemakkelijken en wetenschappelijk te valideren door een praktische toepassing te creëren die gebruikt kan worden om de langetermijneffecten van het gebruik van bepaalde vistuigen te voorspellen. We zijn van plan om verder te bouwen op reeds bestaande rekenmodellen, om zo de effecten van verschillende vistuigen op de benthisch-pelagische koppeling en de biologie te voorspellen. Met behulp van geschaalde fysieke modellen van vistuigen, in samenwerking met een lokale non-profitorganisatie, zullen we de mechanische effecten van verschillende soorten vistuigen voor de computermodellen kwantificeren. Voorspellingen zullen geverifieerd worden door laboratoriumexperimenten uit te voeren met sedimenten uit representatieve Noordzeegebieden. Het werk dat tijdens dit doctoraat is verricht, heeft de deur geopend naar nieuwe vragen die we in dit aanstaande onderzoek willen beantwoorden.

Chapter 1 General Introduction

Bottom trawling, biogeochemistry and pulse fishing

PulseWing Trawl (Harlingen, NL)

Photo: Justin Tiano

Trawling is the act of towing a net through the water in order to capture aquatic species for sale or consumption. Bottom trawling involves dragging a net along the seafloor and is commonly thought of as one of the most destructive activities for marine habitats (Watling, 2005). Despite this, a high global demand for seafood production persists. The interactions between human activity and ecosystem dynamics can be very complex and are incompletely understood. Proper science based fisheries management is, therefore, vital for the conservation and longevity of many threatened marine habitats. The research found within this PhD thesis explores different ways that bottom trawling affects benthic ecosystems. In general, it focuses on broad scale functional aspects related to the coupling of benthic and pelagic processes, the cycling of nutrients and the abundance of keystone benthic species. A point of emphasis in this research is the assessment of the effects of the relatively novel, marine electric pulse fisheries compared to their conventional alternatives (Soetaert et al., 2015). Policy makers and environmental managers may use our work to make informed decisions regarding fisheries management. At the same time, much of this research remains fundamental in nature and investigates several unexplored topics in marine science. This chapter begins by discussing the historically disturbed context of North Sea habitats. It then provides an overview of the research pertaining to bottom trawls and their effects on benthic biota and biogeochemistry, followed by an introduction to North Sea electrotrawls. We end this chapter with the objectives and the structure of this PhD thesis.

CHANGE IN THE NORTH SEA: A HISTRORICAL PERSPECTIVE

In terms of human disturbance, the North Sea is one of the most heavily impacted areas in the world (Halpern et al., 2010). Anthropogenic stressors such as offshore development and shipping traffic add to its continually changing marine environment. Climate change has and continues to alter the distribution of North Sea fish (Dulvy et a., 2008) and benthos populations (Hiddink et al., 2015) and it is predicted to cause direct (van der Molen et al., 2012) and indirect consequences to benthic pelagic coupling (Kirby et al., 2007). Multiple factors, including bottom trawling and changes to benthic community composition, have been linked with increased sediment resuspension in North Sea and have led to significant declines in water clarity within the past century (Amaro et al., 2007; Capuzzo et al., 2015). Sixty-three percent of all North Sea sediments are trawled between 1 and >10 times per year (Eigaard et al., 2016).

The trawl induced mortality and removal of benthic organisms is a potential driver of structural changes to macrobenthos communities and regime shifts in the southern North Sea (Reise et al., 1989; Frid et al., 2000; van Nes et al., 2007). Historical bottom trawl effort is suspected to have played a role in the decline of hard substrates, large boulders and oyster reefs that were once a common occurrence in the North Sea according to 19th and early 20th century documents (Coolen, 2017). It is possible that a sizable portion of the North Sea is now experiencing a trawl induced alternative stable state (Kaiser et al. 2000). Despite the environmental consequences of bottom trawl activity, many fishermen are quick to point out that their methods are not unlike that of terrestrial farmers.

ECOSYSTEM EFFECTS OF BOTTOM FISHING

Bottom fishing has been a consistent practice in the North Sea since the late middle ages (de Groot, 1984). Resistance against the use of beam trawls has also persisted throughout its history with protests dating back to 1376 (Collins, 1887). Concerns over the environmental consequences of beam trawling included fears of its ability to reduce the abundance of immature fish and degrade once productive fishing grounds (Collins, 1887). Contrary to modern times, distinguished scientists of the late 19th century were known to make claims that humans could not possibly influence fish stocks from the sea (Collins, 1887). We now know, of course, that this is not true (Buhl-mortensen et al., 2016) but we also realize that the effects of bottom fishing are complex and context dependent.

Trawl effects on the benthic community

There has been extensive research on the impacts of trawling on benthic faunal communities (Kaiser et al., 2006; Hiddink et al., 2017; Sciberras et al., 2018). A general decrease in abundance, biodiversity and biomass is a common occurrence after direct trawling impacts (Bergman and Hup 1992; Thrush et al., 1998; Pranovi et al., 2000; Kenchington et al., 2011; Hixon et al, 2007; Hinz et al., 2009; Fariñas-Franco et al., 2018; **Figure 1**) though these effects vary depending on fishing gear, penetration into the seabed and habitat type (Hinz et al., 2012; Grabowski et al., 2014; Sciberras et al., 2018). Generally, heavier gears or ones which disturb the sediment at greater depths (i.e. hydraulic dredges) create more severe and longer lasting impacts on benthic ecosystems (Hiddink et al., 2017; Depestele et al., 2018). Trawling has a flattening effect on sedimentary benthic environments (Schwinghamer et al., 2010;

O'Neill et al., 2013) and has a proportionally greater effect on large epifauna residing at or near the sediment surface compared to deep burrowing organisms (Kaiser et al., 2000; Tillin et al., 2006; Romano et al., 2016; **Figure 1**).

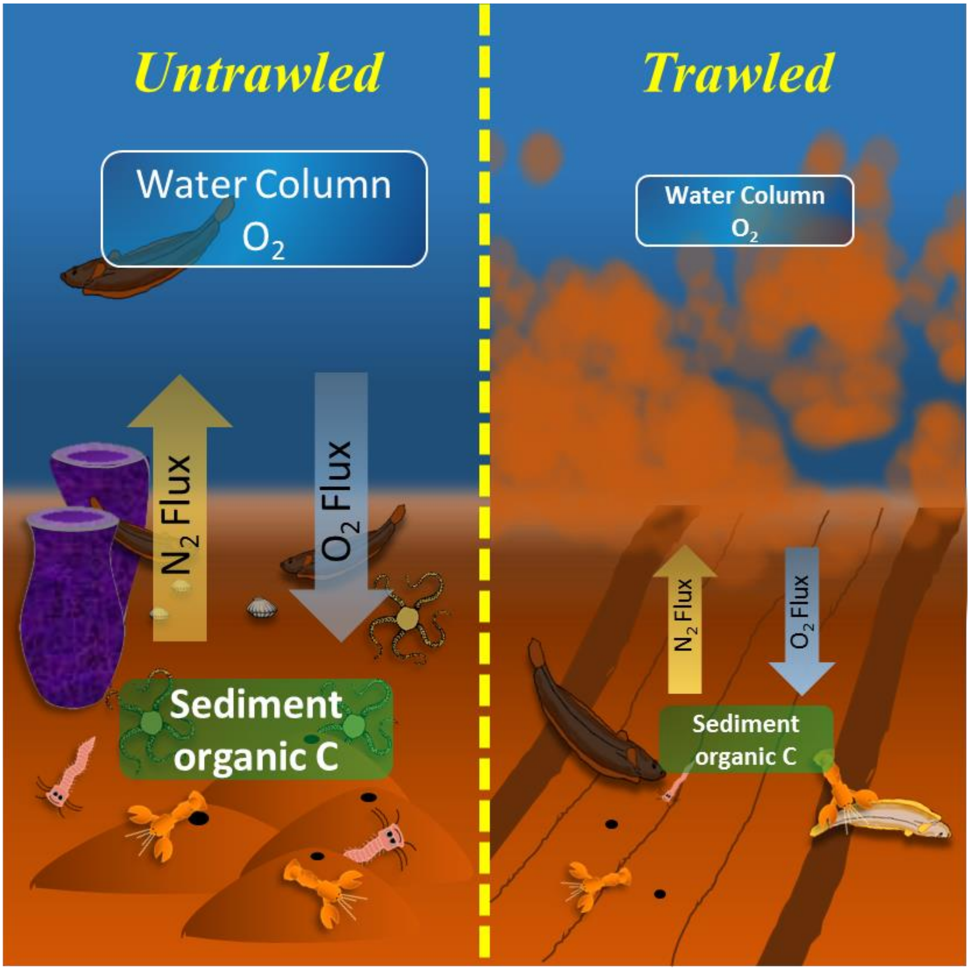

Figure 1. Schematic example of untrawled vs. trawled ecosystem dynamics. Arrows represent fluxes of nitrogen (N_2) and oxygen (O_2) from the sediment before and after trawling (not to be confused with trawl-induced instantaneous fluxes). The arrow sizes represent the strength of the fluxes. The text box sizes represent the relative concentrations of oxygen in the water column and organic carbon in the sediment.

Bottom disturbance is clearly disadvantageous for many species, however, it can also create a competitive advantage for trawl resistant animals (Sköld et al., 2018; **Figure 1**). Several studies have demonstrated increases in the biomass or abundances of certain benthic fauna in response to trawling (Tanner et al., 1998; Tillin et al., 2006; van Denderen et al., 2016; Sciberras et al., 2016). Reasons for this include competitive release or the trawl-induced removal of predators allowing the proliferation of prey species (Sköld et al., 2018). Moderate levels of trawling have been linked with increased production of smaller macrobenthos (Jennings et al., 2001; Tillin et al., 2006) and better physiological conditions in certain fish (Mangano et al., 2017). Bottom up effects are created from the trawl-induced mortality of benthic organisms and can benefit to benthivorous fish (van Denderen et al., 2013) and scavenging macrobenthos (Kaiser and Spencer 1994; **Figure 1**).

Discards and unearthed macrobenthos caused from bottom fishing gears, create an easily accessible food source for scavengers (Groenewold and Fonds 2000). This effect is also known to attract cetaceans (Couperus 1994; Fertl and Leatherwood 1997), birds and seals (Ryan and Moloney 1988) that benefit from the concentrated food source but may also end up as bycatch themselves (Du Fresne et al., 2007). Trawling has been related to lower trophic levels in certain fish suggesting a shift in foraging behavior towards scavenging for benthos exposed from trawling (Shephard and 2014; **Figure 1**). Disturbance from bottom trawls seems to facilitate unique ecosystem dynamics with scavenging benthos, which are attracted to the trawl activity (Kaiser and Spencer 1994; Schwinghamer et al., 2010), falling prey to opportunistic fish species that are also exploiting the trawl-induced food source (Kaiser and Spencer 1994). Fishermen are often of the opinion that their trawl activity leads to more fish. They may be correct in that trawling seems to benefit certain mobile predators (including commercially important species like *Pleuronectes platessa*) and scavengers (Groenewold and Fonds 2000; Mangano et al., 2017) and can facilitate the proliferation of small and fast growing organisms (prey for opportunistic predators) (Tillin et al., 2006; Sköld et al., 2018) but this comes at the expense of biodiversity and creates simplified food webs (Tillin et al., 2006).

Trawl effects on biogeochemistry

Compared to effects on faunal parameters, relatively little is known about the impact of bottom fishing on biogeochemical cycles. This PhD focuses heavily on the effects of bottom trawling on sediment biogeochemistry and how this connects to benthic pelagic coupling. Due to the knowledge gaps related to this topic, there is still much left to discover but the following summarizes what we know about this subject so far.

All bottom trawling and dredging gears have, by nature, some degree of contact with the seafloor. Ground ropes are located at the net opening and ensure the capture of target organisms by maintaining constant contact with the sediment, leaving little opportunities to escape underneath the net. The net itself can be a source of friction with the seabed, though other aspects of bottom trawl gears such as tickler chains (electrodes in pulse fishing gear), beam trawl shoes and otter trawl doors are considered to exert the heaviest impacts on the sediment (Eigaard et al. 2016). This physical impact penetrates and homogenizes subsurface layers and mobilizes sediment into the water column (O'Neill et al. 2013; Depestele et al., 2018). Tickler chains can penetrate the seabed up to 10 cm in soft sediments though there is variation between gear components, sediment type, and towing speed (Eigaard et al. 2016). Trawl induced sediment resuspension (even from just the ground rope) can cause significant releases of nutrients and organic material from surface sediments (Dounas et al., 2005; **Figure 1**).

Sediment resuspension caused from trawling or storm induced currents can have similar effects on organic material in the water column (Paerl et al., 2001; Pusceddu et al., 2005) though the wider scale impact of wave induced sediment mobilization is predicted to have a markedly larger effect on the export of suspended sediment (Ferre et al., 2008). Trawling can cause decreases in the labile fraction of organic material in the water column (Pusceddu et al., 2005) and surface sediments (Sañé et al., 2013), which can come from the resuspension of refractory organic material (Pusceddu et al., 2015). Trawl induced-pulses of nutrients released into the water column are predicted to temporarily enhance primary production (Pilskaln et al., 1998; Dounas et al., 2007), though reductions in the potential food quality (decrease in bioavailable carbon in resuspension) of suspended organic material may create negative consequences for suspension feeders (Pusceddu et al., 2005). In the Frisian Front, trawling has been linked with changes in species composition, implying increased faunal induced sediment erosion (Amaro et al., 2007; van Nes et al., 2007). Namely, there is evidence that the increase in trawl resistant deep burrowing mud shrimps such as *Callianassa subterrenea* may have increased sediment erodibility (Amaro et al., 2007) possibly creating a positive feedback loop that can lead to more mobilized sediment (Capuzzo et al., 2015).

Increased turbidity can cause reduced oxygen concentrations in the water column (Almroth et al., 2009; Almroth-Rosell et al., 2012; Couceiro et al., 2013). Storm induced turbidity can differ from trawling effects in that wave mixing can increase oxygen concentrations even with high SPM concentrations (Greenwood et al., 2010). Trawling, on the other hand, shifts the mineralization of organic material from the benthic to the pelagic zone causing rapid declines in water column oxygen levels (Riemann and Hoffmann 1991). As low oxygen zones are predicted to increase with climate change (Weston et al., 2008; Meire et al., 2013; van der Molen et al., 2013), direct bottom trawling likely enhances the risk of near bed hypoxia.

Benthic biogeochemical impacts of bottom fishing can vary depending on sediment type, organic matter input/content, macrofaunal species assemblage and temporal factors. The mixing of benthic sediment layers results in the homogenization of porewater nutrients (van de Velde et al., 2018). This can increase or decrease the fluxes of nutrients depending on how it influences diffusive gradients between the sediment and the overlying water (Warnken et al., 2003). Porewater nutrients will re-establish steady state gradients through time, however, so this effect will hinge on when the disturbance occurred as well as the amounts of nutrients in the sediments (van der Molen et al., 2013; van de Velde et al., 2018). Trawling is predicted to reduce sedimentary nitrogen removal by decreasing porewater nitrate concentrations (van der Molen et al., 2013) and removing sections of the sediment that maximize denitrification (Ferguson et al., 2020; **Figure 1**). Biogeochemical processes like denitrification are often linked with benthic faunal abundance and activity (Hale et al., 2017; Sciberras et al., 2017). Knowledge of benthic community responses to disturbance is thus, integral to gaining a comprehensive understanding of how trawling alters biogeochemical dynamics (Olsgard et al., 2008; Hale et al., 2017).

The removal of surficial fauna may lead to higher amounts of infaunal organisms which can lead to varying degrees of faunal induced particle reworking (bioturbation) or active transport of overlying water into the sediment (bioirrigation) (Olsgard et al., 2008; Hale et al., 2017). Olsgard et al., (2008) linked bioirrigating species with increased sedimentary uptake of dissolved inorganic nitrogen (DIN) while bioturbators led to the release of DIN. Duplisea et al., (2001) predicted that the presence of macrofauna limits the amounts of available carbon in a system and allows trawl-disturbed systems to more easily reach dynamic steady states. Simulations with high trawl disturbance were characterized by enhanced carbon fluxes from anoxic to oxic metabolic pathways, which took the system out of equilibrium (Duplisea et al., 2001). Trawl induced mortality to carbon concentrating suspension feeders is expected to significantly increase the biogeochemical impact of trawling by expanding the oxygenated layer in the sediment (Allen and Clarke 2007). Conversely, the removal of bioirrigators from trawling activity may also lead to a reduction in the oxic layer in sediment patches where irrigation activity has ceased.

Sediment community oxygen consumption (SCOC) includes aerobic respiration (microbial/meiofaunal/macrofaunal), anaerobic re-oxidation of reduced substances and nitrification processes and can be used as a proxy total sediment mineralization of organic material (Stratmann et al., 2019). The amount of fresh (labile) organic material enhances benthic mineralization rates by providing a food source with high nutritional quality for benthic microbes and fauna (Paradis et al., 2019). There are, however, some contrasting findings regarding what happens to sedimentary organic material and benthic mineralization rates after trawling.

The acute effect of benthic trawling and dredging reduces sedimentary chl *a* (a proxy for labile organic matter) content from surficial sediments in the tracks of the gears (Mayer et al., 1991; Brylinsky et al., 1994; Watling et al., 2001; Pusceddu et al., 2014; **Figure 1**). Organic matter content has a strong association with silt/clay particles (Virto et al., 2008). Upon disturbance, much of the sedimentary organic fraction is resuspended and winnowed away with the fine sediments, leaving coarse grains on the sediment surface (Brown et al., 2005; Mengual et al., 2016). Reduced levels of fresh organic material, thereby decreases SCOC and increases the oxygen penetration depth, which can signify a decline in benthic metabolism (Gundersen and Jorgensen, 1990; **Figure 1**).

Several studies, however, find seemingly the opposite effect with increased benthic mineralization rates and enhanced production of chl *a* or organic matter content (Polymenakou et al., 2005; Pusceddu et al., 2005; Palanques et al., 2014; Sciberras et al., 2016; van de Velde et al., 2018; Paradis et al., 2019). Trawling has been connected with increased microbial activity leading to faster carbon degradation rates (Polymenakou et al., 2005). Reasons for increased sedimentary organic carbon percentages include the uplift of refractory organic fractions from trawl induced sediment reworking, the settling of resuspended silt particles depositing organic content, and/or lower levels of macrofaunal grazing activity (Pusceddu et al., 2005; Palanques et al., 2014). Additionally, increases for benthic mineralization may come from the mechanical mixing of labile and refractory organic fractions which causes a ‘priming’ effect enhancing mineralization rates or the exposure of previously anoxic organic material to aerobic conditions (van Nugteren et al., 2009; van de Velde et al., 2018).

It is possible that these two seemingly separate schools of thought, between 1) the trawl induced decrease of organic material and benthic mineralization versus 2) the fishing related increase in the same parameters, are both correct. Differences probably lie between characteristics in different study sites, the temporal relationship between trawling and biogeochemical impacts (short vs long-term impact) and the types of studies which were conducted (i.e. collecting samples within recently trawled tracks vs. sampling in areas known for areas of high trawling intensity). Trimmer et al., (2005) linked increased trawling activity to the fining of sediments (and possibly increased benthic production) in a relatively stable North Sea location (Outer Silver Pit) but did not find the same effects of trawling in an area of much higher natural disturbance (Thames). This adds to the argument that some biogeochemical/physical trawl effects can be specific to the different ecosystems. Whichever the case, this highlights the fact that there is still much room for discovery within this field of study.

Factors contributing to ecosystem vulnerability

Bottom fishing induced changes to biological communities, biogeochemistry and physical sediment features are expected to be higher in muddy vs sandy benthic habitats (Kaiser et al., 2002; Bolam et al., 2013; Sciberras et al., 2016; Rijnsdorp et al., 2020). Muddy sediments tend to have more organic material (Virto et al., 2008), higher densities of sensitive fauna (Bolam et al., 2013) and are susceptible to deeper levels of gear penetration than coarser grained habitats (Depestele et al., 2016; Depestele et al., 2018). Habitats with three-dimensional biogenic structures can be particularly vulnerable regardless of substrate (Grabowski et al., 2014) and are associated with longer recovery periods (Kaiser et al., 2002). Higher temperatures and water column stratification are predicted to exacerbate the effects of trawling on biogeochemical parameters, as the potential change in biogechemically active sediments will be enhanced (van der Molen et al., 2013). Finally, benthic impacts will differ according to the type of bottom gears deployed (Rijnsdorp et al., 2020). The depth of seabed penetration is a reliable predictor of benthic faunal depletion (Hiddink et al., 2017). Studies have found the greatest bottom fishing impacts coming from hydraulic dredges, scallop dredges, beam trawls, and otter trawls (though the effect is wider) in this general order, while the lowest impacts come from static (non-towed) methods such as gillnets and traps (Grabowski et al., 2014; Hiddink et al., 2017). An interesting development in the North Sea, (and one of the main topics of this PhD research), has been the introduction and potential impacts of electric pulse trawling, much of which was unknown prior to the start of the research included this thesis.

THE INTRODUCTION OF MARINE ELECTROTRAWLS IN THE NORTH SEA

The use of electricity as a method to catch fish started to gain widespread use in the 1950's as a scientific fish community sampling technique in freshwater habitats (Vibert, 1963, Soetaert et al., 2015). Marine electrotrawls for shrimp were used in China until their ban in 2001 where a lack of regulations (no quota or electrical restrictions) led to the collapse of this fishery, eventually leading to its prohibition (Yu et al., 2007). In the North Sea, electric bottom fishing for brown shrimp (*Crangon crangon*), dover sole (*Solea solea*) and razor clams (*Ensis spp.*) have been employed as experimental methods (Soetaert et al., 2015; **Figure 2**). Despite promising results regarding the use of electrofishing methods as a more environmentally friendly alternative to conventional techniques, marine electrofishing garnered much controversy leading to a decision by the European Parliament in 2019 to ban their use in Europe (Kraan et al., 2020).

Conventional bottom trawl methods for harvesting shrimp and flatfish employ the use of heavy chains and bobbins, used to mechanically stimulate target species off the sediment and into the net (**Figure 2**). Hydraulic dredges, traditionally used to catch razor clams, flush the sediment with hydro jets and are thought to be one of the most impactful bottom fishing gears available (Grabowski et al., 2014; Hiddink et al., 2017). Pulses of electricity are used for experimental electric trawling in *C. crangon* (low frequency direct currents) and *S. solea* (high frequency bi-polar currents) fisheries, to either startle (*C. crangon*) or immobilize (*S. solea*) target species, allowing their capture in oncoming bottom nets (Desender, 2018; Soetaert et al., 2019; Verschueren et al., 2019; **Figure 2**). Electrofishing for *Ensis spp.* involves towing slow moving electrodes employing continuous alternating (AC) or direct (DC) currents which disturb clams out of their burrows to be collected by divers (Woolmer et al., 2011; Murray et al., 2016; **Figure 2**). Advantages attributed to the electric fishing include lower bycatch rates (van Marlen et al., 2014; Verschueren et al., 2019), less mechanical disturbance (Depestele et al., 2016; Depestele et al., 2018), higher efficiency (Rijnsdorp et al., 2020) and lower fuel consumption (van Marlen et al., 2014).

Figure 2. Comparison between a traditional tickler chain rigged beam trawl (top left) and an electric PulseWing trawl (top right) which are both used to fish for North Sea dover sole (*Solea solea*). Electrodes and gear used to stimulate and catch razor clams, *Ensis spp.* (bottom left) and a 'Hovercran' electric trawler used to catch brown shrimp, *Crangon crangon* (bottom right).

Beam trawl photo by Justin Tiano. PulseWing and Hovercran trawl photos adapted from Soetaert et al., (2015). Electric razor clam trawl photo from Breen et al., (2011).

In recent years, a significant amount of scientific information has been collected about the effects of pulse trawls on physiological responses of target and non-target species, ecosystem effects of gears and fleet dynamics, and societal impacts (ICES, 2018, 2019, 2020). Elecrofishing has long been associated with spinal injuries in certain fish (McMichael, 1993) and pulse fishing for sole has been no exception, with injury rates in cod ranging from 0 – 70 % (de Haan et al., 2016; Soetaert et al., 2016a). This outcome seems to disproportionately affect larger cod, however, other fish experimented on, have not shared the same susceptibility to injuries (de Haan et al., 2016; Soetaert et al., 2016b; Soetaert et al., 2018). In the end, these injuries are probably negligible on the ecosystem scale, as all captured cod will suffer the same fate as other landed fish.

The effects of pulse trawls on non-target benthos was of particular concern as the consequences may lead to unintended bottom up effects and the associated electricity has been shown to penetrate the sediment (de Haan and Burggraaf 2018). Nevertheless, to date, no research on any of the 25+ species of benthos studied have shown any direct mortality from electrical exposure used in North Sea experimental electrofisheries (Smaal and Brummelhuis 2005; van Marlen et al., 2009; Woolmer et al., 2011; Soetaert et al., 2015; Murray et al., 2016; Soetaert et al., ICES, 2020; Boute et al., *in revision*). This suggests that the majority of pulse trawl induced effects on benthic communities will come solely from mechanical disturbance.

Depestele et al., (2016) and Depestele et al., (2018) reported a reduced average effect from pulse trawls on seabed bathymetry, roughness, and penetration depth. A lessened mechanical effect of pulse trawls, compared to the traditionally used tickler chain beam trawls, is expected as the gears are lighter and maintain less constant contact with the seabed compared to their conventional counterpart (Depestele et al., 2018). Ground ropes, nets, and electrodes can still cause significant levels of mechanical disturbance but these effects tend to be more variable than that of traditional beam trawling. Pulse trawl induced effects on benthic biogeochemical parameters, however, was a large knowledge gap at the beginning of this PhD research, and concerns persisted over the possibility of electrolysis induced release of toxic compounds (Soetaert et al., 2015).

Electrical fields generated by cable bacteria, occur naturally in the marine environment and can create significant effects on sediment biogeochemistry (Nielsen et al., 2010). These microbes create a flow of electrons that drive a process called ‘ionic drift’, which mobilizes ions in relation to their polarity (Risgaard-Petersen et al., 2012). This process can have a profound effect on phosphorus dynamics as reduced sedimentary iron is transported to the surface and removes available phosphorus from the water column when the iron gets oxidized (Sulu-Gambari et al., 2016). Similar effects from anthropogenic electrical activity are possible (Martins et al., 2014) but at the start of this PhD, the possibility for pulse trawl induced electrolysis was still largely unknown.

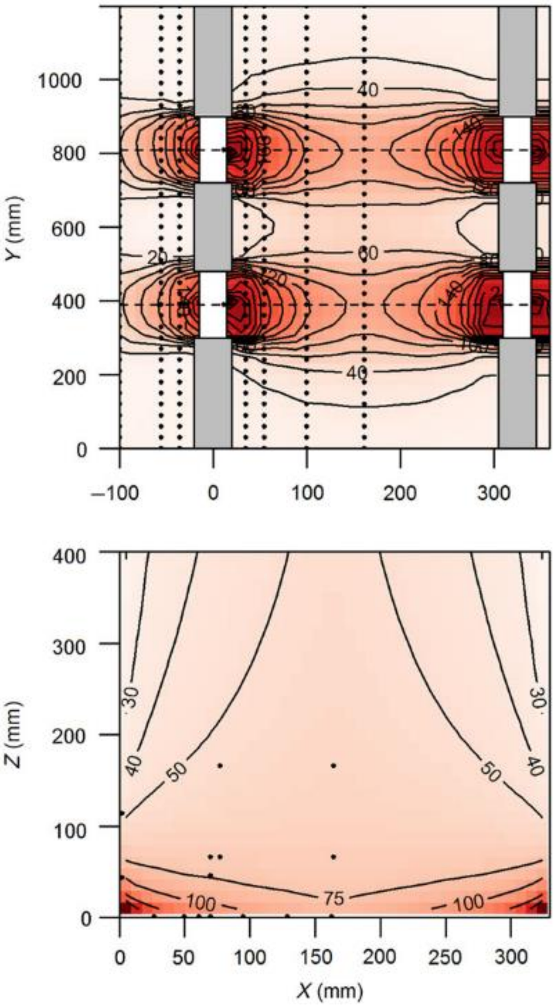

Figure 3. (Top) A horizontal view of the peak field strength (mm scale) of the heterogenous electrical field generated from a flatfish pulse trawler using Delmeco electrodes (only two electrode pairs shown). White parts show electrical conductors while grey parts show isolators. (Bottom) The view of electric field strength in the vertical plane above two electrodes. Measurements are indicated with the black dots (bottom figure only). Contour lines represent peak field strengths (volts/meter). Adapted from de Haan et al., (2016).

PHD THESIS OBJECTIVES

Benthic faunal activity and sediment biogeochemical processes are strongly coupled (Braeckman et al., 2010). Areas of high primary production are often sites full of commercially important species and higher levels of fishing effort (van Denderen et al., 2014). The interplay between direct disturbance effects, macrofaunal community functioning and biogeochemical dynamics needs to be analyzed and sometimes isolated to gain a better understanding of trawl effects on benthic pelagic coupling. The following research chapters assess these topics individually (**Chapters 2 – 4**) and comprehensively (**Chapter 5**).

This research was conducted as one of the work packages from the Impact Assessment Pulsetrawl Fishery (IAPF) project funded by the European Maritime and Fisheries Fund (EMFF) and the Netherlands Ministry of Agriculture Nature and Food Quality (LNV). The main objective for this project was to assess the long-term impact of the commercial application of pulse trawls in the North Sea flatfish fishery. This particular work package aimed to assess the effect of pulse trawls on the functioning and biogeochemistry of benthic ecosystems in relation to conventional methods.

Research questions

In the broadest sense, the central question driving this PhD was:

- *What is the effect of pulse trawling on the functioning and biogeochemistry of benthic ecosystems?*

This question is addressed in all of the research chapters of this thesis. In order to place these effects in a proper context, the benthic impacts of pulse trawls need to be compared with their closest alternative. Therefore, the first research question needed to be followed up with:

- *What is the differential impact between pulse trawls and conventional tickler chain trawls?*

Chapter 2, **Chapter 3**, and **Chapter 5** investigate this topic with *in situ* studies in collaboration with professional pulse and beam trawlers.

With the uncertainties surrounding the biogeochemical effects of electricity, **Chapter 4** explores the question:

- *How do electric fields affect benthic biogeochemical processes?*

As pulse trawls also exhibit physical disturbance, **Chapter 4** follows up the previous question is with:

- ❖ *What are the direct mechanical effects of trawl-induced sediment resuspension?*

The following research uses a combination of large-scale field manipulation studies and experiments in controlled laboratory settings, to assess the effects of pulse and beam trawls on benthic ecosystem dynamics and benthic pelagic coupling.

PHD THESIS STRUCTURE

Chapters 2 and 3 in this thesis report results from an *in situ* trawl disturbance study in the offshore muddy sands of the Frisian Front. These studies report the effects of pulse and beam trawls on benthic biogeochemical functioning and community dynamics. Chapter 4 uses a controlled experimental approach to isolate the direct effects of electricity and mechanical disturbance on sediments from multiple North Sea habitats. Chapter 5 details a comprehensive field study exploring the effects of electric pulse and beam trawling on physical, biogeochemical and ecological functioning in a dynamic coastal habitat, namely, the Vlakte van de Raan.

In **Chapter 2**, we worked with the Dutch fishing industry to experimentally trawl two areas in the Frisian Front region of the North Sea. Professional fishermen produced intensive bottom trawl effects with a standard tickler chain beam trawler and with an electro-fitted PulseWing trawler. This study used a combination of *in situ* benthic landers and on board benthic sediment incubation methods to measure the biogeochemical fluxes from the sediment water interface in pre-trawled, trawled, and reference areas. The direct coupling of benthic disturbance to water column oxygen and suspended particulate matter (SPM) concentrations was assessed during pulse trawling with an *in situ* mooring.

Chapter 3 follows up on Chapter 2 by assessing trawl effects on the benthic community, based on sediment profile imagery, high definition video transects, and side scan sonar information gathered in the same research campaign. This study uses a biological trait and multivariate approach to investigate the effects of pulse and beam trawls, on taxa with different functional roles, to see if there is a differential response in certain species. The addition of visual and acoustic techniques provided multiple perspectives of bottom trawl impacts on broad and detailed scales.

Chapter 4 documents a study exploring the potential effects of electricity and physical disturbance on benthic biogeochemical fluxes. This study used sediment from nine North Sea and two Eastern Scheldt locations. We took a measured experimental approach to isolate possible impacts from electrical pulses and demonstrate what kind of parameters are needed to generate a biogeochemical response. At the same time, these results were compared with mechanically impacted sediments in controlled microcosms. Experimentally induced changes to nutrient and oxygen levels (released into or consumed from the overlying water), were put into context by relating them to the natural fluxes of nutrients in the same sediments.

Chapter 5 reports the most comprehensive study in this thesis and documents a large scale *in situ* assessment of eurocutter pulse and beam trawls in a coastal environment dominated by biogenic reefs. Here, we took a similar approach to chapters 2 and 3 in creating experimentally trawled sites (working with professional fishermen), however, a different experimental design was required to capture trawl effects in the dynamic and highly variable habitat of the Vlakte van de Raan (located 10 km off the Dutch coast). This study assessed bottom trawl effects on physical, geochemical, and ecological parameters by combining information from the water column, seabed bathymetry and backscatter, sediment profile imagery, biogeochemical fluxes, porewater nutrients, sediment features, and benthic community characteristics.

After the general discussion chapter, we look at ways to build upon this PhD research in the **Appendix (Outlook to the Future)**. This section is adapted from an accepted research proposal expanding on the work conducted in this PhD. A logical next step from the acute experimental studies would be to upscale these effects through predictive modelling. The proposed research uses a combination of experimental and modelling techniques to predict biogeochemical and ecological effects of trawling on broad spatio-temporal scales. The end product from this work aims to be a computational application that the fishing industry and the public may use to scientifically validate environmentally friendly fishing gears.

Chapter 2

Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling

ICES Journal of Marine Science (2019)

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Benthic Lander deployment (Frisian Front)

Photo: Karline Soetaert

Abstract

Research on the environmental impacts of bottom fishing gears has focused mainly on structural characteristics of benthic habitats such as faunal composition and the physical features of the seafloor. This study focuses more on functional characteristics by addressing the biogeochemical consequences associated with tickler chain beam trawl and electric PulseWing trawl gears. In June 2017, professional fishermen trawled experimental transects with both types of gears in the Frisian Front area of the North Sea. Box core sediment samples and *in-situ* landers were used to evaluate biogeochemical fluxes and sediment characteristics in untrawled and trawled areas (samples taken 3.5 – 70 h after fishing). A reduction of sedimentary chlorophyll *a* was observed, which was larger following tickler chain (83%) compared to PulseWing trawling (43%). This displacement of surface material caused significant decreases in the sediment oxygen consumption in tickler chain (41%) and PulseWing trawled samples (33%) along with a deeper penetration of oxygen in the sediment (tickler chain: 3.78 mm, PulseWing: 3.17 mm) compared to untrawled areas (2.27 mm). Our research implies that bottom trawl disturbance can lead to immediate declines in benthic community metabolism, with tickler chain trawling exhibiting more prominant alterations than PulseWing trawling on benthic biogeochemical processes.

Keywords: biogeochemistry, ecosystem functioning, oxygen dynamics, nutrients, beam trawling, pulse trawling, organic carbon, Frisian Front

INTRODUCTION

Concerns over the ecological impacts of bottom trawl fishing have dated back since its inception in the 14th century (Collins, 1887). This form of fishing has since gained widespread use and we find ourselves asking the same questions about its environmental effects as during its commencement. Current worldwide criticism of bottom trawling and the introduction of the experimental method of "electric pulse fishing" in the North Sea, once again brings this topic to the limelight. We have knowledge about the effects of bottom trawls on many structural aspects of benthic environments, including the mortality of benthic organisms (Bergman and van Santbrink, 2000; Kaiser *et al*., 2006; Hiddink *et al*., 2017; Sciberras *et al*., 2018) and the mechanical impacts on seabed bathymetry (Depestele *et al*., 2016; Eigaard *et al*., 2016; O'Neil and Ivanovic, 2016). However, only limited information is available about factors which affect the explicit functioning of benthic ecosystems. The role of biogeochemical functioning, in particular, remains a neglected topic in fisheries impact studies (Kaiser *et al*., 2002; Olsgard et al., 2008). Furthermore, no research has been conducted on the potential side-effects of electric pulse trawling on geochemical fluxes (Soetaert *et al*., 2015).

Traditional beam trawls, rigged with tickler chains or chain matrices, scrape the seabed in order to mechanically stimulate and catch flatfish. This can lead to a direct release of nutrients from the sediments which can enhance primary production in the water column (Duplisea *et al*., 2001; Dounas *et al*., 2006; Dounas *et al*., 2007; Couceiro *et al*., 2013) and may also release contaminated material if present (Bradshaw *et al*., 2012). Benthic trawling has been linked to reduced oxygen concentrations in the water column (Riemann and Hoffman, 1991), the homogenisation of benthic nutrient profiles (van de Velde *et al*., 2018) and alterations of the sediment redox layer (Depestele *et al*., 2018). Sediment resuspension produced by trawling activity has been associated with enhanced bottom water O_2 consumption and increased concentrations of dissolved inorganic carbon (DIC), ammonium and silicate (Almroth et al., 2009; Almroth-Rosell et al., 2012). The potential for towed gears to remove and kill benthic fauna (Bergman and Hup, 1992; Bergman and van Santbrink, 2000) can indirectly alter benthic ecosystem functioning with the loss of important bioturbators and/or ecosystem engineers (Duplisea *et al*., 2001; Olsgard *et al*., 2008). Bottom trawling, dredging or other types of human disturbance has been linked to both the fining (Trimmer *et al*., 2005; De Backer *et al*., 2014) and coarsening of the bottom material (Palanques *et al*., 2014; Mengual et al., 2016; Depestele *et al*., 2018), both of which can induce changes to the whole benthic community (De Backer *et al.*, 2014).

The controversial introduction of electric (flatfish) pulse trawling changed the behaviour and activity of fishermen in the North Sea (Sys *et al.*, 2016). With this method, tickler chains are being replaced by electrodes to electrically stimulate flatfish out of the sediment. Reduced fuel consumption (up to 50%) from lower towing speeds/decreased drag through the seafloor (van Marlen *et al.*, 2014), reductions and increased survivorship of discards (van Marlen *et al.*, 2014; Batsleer *et al.*, 2016; van der Reijden *et al.*, 2017) provided evidence for pulse fishing as an environmentally friendly alternative to traditional tickler chain beam trawling. Its popularity amongst the Dutch fishing fleet (Haasnoot *et al.*, 2016), however, was met with international criticism due to increased competition between fishermen (Sys *et al.*, 2016) and ecological concerns over animal welfare (de Haan *et al.*, 2016; Soetaert *et al.*, 2016). Compared to traditional tickler chain trawl gears, pulse trawls show reduced alterations to seabed bathymetry (Depestele *et al.*, 2016; Depestele *et al.*, 2018). It may be speculated that the reduced mechanical disturbance will also lead to a lower impact on benthic biogeochemistry. Nonetheless, concrete knowledge about the potentially negative side-effects of pulse trawling on characteristics such as sediment community metabolism and benthic pelagic coupling is lacking. Further research in these areas is therefore needed to fully understand the environmental effects of different bottom trawl gears.

Our research investigates the impact of both conventional (tickler chain) beam trawl and electric pulse trawl gears on benthic biogeochemistry. The model of pulse trawl used in this study is the HFK “PulseWing” which is used to capture flatfish. Along with the mechanical effects from PulseWing and tickler chain trawling, Depestele *et al*. (2018) explored changes in biogeochemical redox conditions associated with the two methods. Here we build upon this knowledge and present the first study with pulse trawling focusing on benthic metabolism and nutrient cycles.

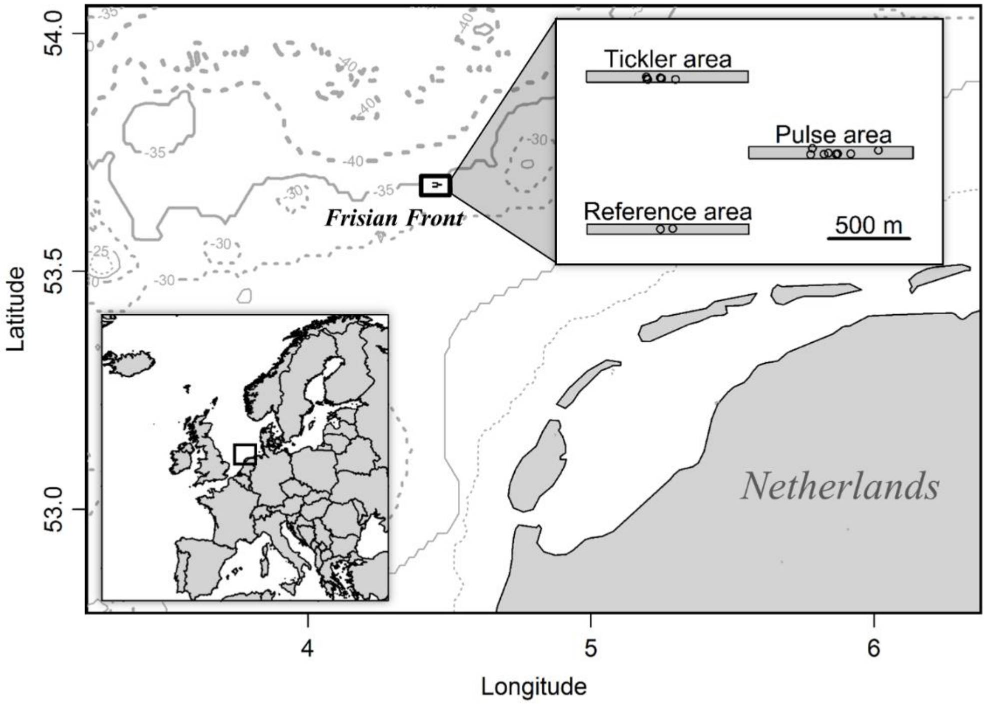

Figure 1. Map of the study site. The inset shows the positions of the experimental areas and box cores taken from the tickler treatment to the north, the pulse treatment to the east and the reference area in the south.

MATERIALS AND METHODS

Study site

Experimental fishing and sampling were carried out within a one kilometre radius of 53.6816° N and 4.4565° E at a water depth of 34 m in the area of the North Sea known as the Frisian Front (**Figure 1**). This area provided a promising location for our study due in part to its high productivity and homogeneity. The Frisian Front is a transitional zone between coarser sandy sediments in the Southern Bight to the south and the siltier Oyster Grounds to the north. It exhibits fine muddy sand with an organic carbon percentage between 0.28-1.0 (Upton *et al.*, 1993; Gehlen *et al.*, 1995; Lohse *et al.*, 1995; Slomp *et al.*, 1997; Boon and Duineveld, 1998). These sediments are subject to faunal induced mixing with the presence of deep burrowing organisms such as *Callianassa subterranea* and *Upogebia deltaura* (Rowden *et al.*, 1998; Dewicke *et* *al.*, 2002). Compared with adjacent North Sea habitats, the Frisian Front exhibits a high influx of chlorophyll *a* (Chl *a*) to the sediments (Boon and Duineveld 1998). This is caused when water masses from the north and south converge and slow down when they meet in this transitional zone (Otto *et al.*, 1990) which allows the settlement of fine grained organic material from the water column (Boon and Duineveld 1998). The result is a biologically enriched area relatively high in benthic biomass (Dauwe *et al*., 1998; Dewicke *et al*, 2002; Duineveld and Boon, 2002) and metabolic activity (Duineveld *et al*., 1990). Moreover, areas with these characteristics (muddy sediment/high biomass) are known to be more vulnerable to trawling activity than sandy dynamic habitats as soft sediment allows deeper penetration of bottom fishing gears and are generally in areas with low tidal/wave action (Duplisea *et al*., 2001; Kaiser *et al*., 2006; Queirós *et al*., 2006, Allen and Clarke, 2007; Sciberras *et al*., 2016). These environmental conditions paired with the extensive historical data on the site made the Frisian Front an ideal location to measure the impact of bottom trawl fishing. Vessel monitoring system (VMS) data was used to estimate the likelihood of bottom trawl disturbance within one year prior to the study using the method shown in van Denderen *et al*., (2014).

Experimental design

To experimentally determine the biogeochemical impact of tickler chain and PulseWing trawl gears, commercial trawlers were instructed to fish specified areas in the Frisian Front. Benthic samples were collected before and after fishing and at a nearby reference location (**Figures 1 and 2**). Intact sediment samples were brought on-board to obtain information on Chl *a*, particle size, organic carbon/nitrogen, oxygen microprofiles, porewater nutrients and oxygen/nutrient fluxes under controlled conditions while *in-situ* data for benthic fluxes and water column parameters was also obtained to capture information in a more natural setting. We looked at short-term effects (<24 hr) and longer-term effects >24 hr in the case of the tickler chain trawler (a storm prevented additional sampling after pulse trawling).

Two rectangular 80 m by 1000 m treatment areas were specified for experimental fishing by either beam trawl (“tickler”) or pulse trawl (“pulse”) gears. A non-fished reference area was chosen south of the treatment areas (**Figure 1**). The areas were spaced 400 m apart and aligned parallel but not directly adjacent to each other in order to minimize interference from resuspended sediment caused from the experimental trawling (**Figure 1**). To ensure full “coverage” of the seafloor being fished in the treatment areas, both vessels conducted 7 trawl passes in parallel yet slightly overlapping trajectories over the treatment areas. Given the widths and the space between the trawl gears, this led to a fishing intensity of 150 to 200% within the middle portion of the treatment areas (modelled after the procedures conducted in Bergman and van Santbrink, 2000 and Depestele *et al*., 2016).

We originally aimed for a full BACI (Before-After-Control-Impact) design to allow the comparison of trawled experimental areas and an untrawled reference area before and after the tickler chain and PulseWing fishing disturbances. Due to unforeseen logistic constraints and a severe summer storm which took place at the end of the campaign, a complete balanced design using all experimental equipment (i.e. *in-situ* mooring/landers, box cores) could not be achieved. Our untrawled "control" samples, therefore, come from the experimental trawl areas before the fishing disturbance (T0) as well as one sampling period in an adjacent reference area. The storm, which took place during the afternoon of 6 June 2017, modified the surface sediment due to storm-induced sediment resuspension and mixing. Hence, we decided to discard all samples taken after the storm event (**Figure 2**).

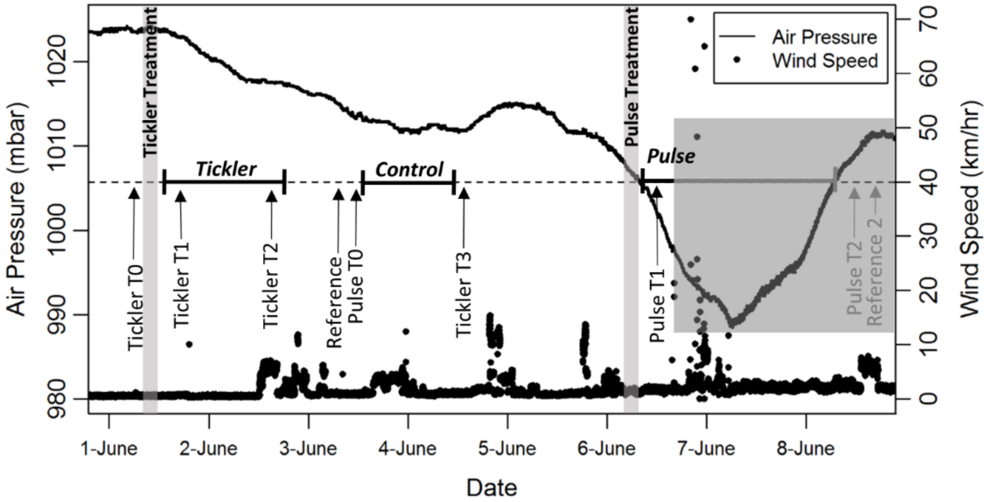

Figure 2. Sequence of events and weather conditions. Box core sediment samples (arrows), *in-situ* lander deployments (brackets) and experimental fishing treatments (shaded columns) are shown. Samples taken in the shaded region on the right were not included in the analysis due to storm induced sediment disturbance.

Experimental fishing

On the 1st of June 2017 (8h30 – 10h) the tickler treatment was carried out by the HD 29 commercial vessel which towed its gear at ~ 6 knots. Conventional 12 m wide beam trawl gears (a shoe located at both ends of the beam) were towed at both sides of the ship, each rigged with 8 tickler chains and 10 net ticklers. Following the experimental fishing, a side-scan sonar was used to observe changes in bathymetry caused from tickler chain trawling.

The pulse treatment was carried out by the UK 227 commercial vessel on the 6th of June 2017 (7h30 – 10h). This vessel trawled at a speed of ~ 5 knots and towed a 12 m wide "HFK PulseWing" at either side of the boat. With the PulseWing, the traditional beam is replaced with an aero foil shaped 'wing' without shoes at the ends but with one "nose" located in the middle of the front section of the gear. The wing creates lift as it is towed through the water similar to an aeroplane wing. The nose controls the angle of attack and the gear will exert force onto the sediment when the nose faces downward. It is designed to skim above the seabed with a standard beam trawl net behind it. To stimulate the flatfish from the seabed, the tickler chains are replaced by electrodes which use a pulsed bi-polar current. This type of alternating current is used to minimize the effects of electrolysis which would cause corrosion of the electrodes (H.K. Woolthuis, designer of HFK PulseWing, pers. comm). Each pulse wing gear was rigged with 28 electrodes lined up parallel to the fishing direction (0.42 m apart) and worked with a voltage of 50 V at the electrodes at 80 pulses per second. More details on the fishing gears and electric parameters used, can be found in van Marlen *et al*., (2014) and de Haan *et al*., (2016).

Data collection

Water column plume dynamics

To investigate the effect of PulseWing trawling on the water column characteristics, a mooring was deployed (4 to 8 June 2018) 100 m north of the experimental area. The location of the mooring was chosen based on the predicted direction of the current during the experimental fishing operation. The mooring was equipped with an Aanderaa SeaGuard recorder, suspended at 3.5 m above the sediment (29 m depth) which featured a turbidity sensor which measured suspended particulate matter (SPM), an oxygen optode and doppler current sensor. The logistic and time constraints mentioned earlier did not allow for the planned deployment of this mooring during tickler chain trawling.

Box core sampling

All sampling equipment was deployed from the R.V. *Pelagia*. A cylindrical NIOZ box corer with an internal diameter of 30 cm and a height of 55 cm, collected intact sediment samples up to 40 cm deep into the seafloor. Samples from the tickler treatment area were taken one hour before fishing (T0: 2 deployments, 2 replicates per core, 4 incubations) and 6 h (T1: 2 deployments, 2 replicates per box core, 4 incubations), 30 h (T2: 2 deployments, 1 replicate per box core, 2 incubations) and 75 h (T3: 3 deployments 1 replicate per box core, 3 incubations; no nutrient flux samples or porewater nutrients taken) after trawl disturbance (**Figure 2**). In the pulse treatment area, samples were taken 3 days before trawling (T0: 3 deployments, 1 replicate per box core, 3 incubations) and 3.5 hours after trawling (T1: 4 deployments, 2 replicates for 3 box cores and 1 replicate for 1 of the box core, 7 incubations). For the untrawled control variable, the T0 samples from tickler and pulse areas were combined with additional data (2 deployments, 1 replicate per box core, 2 incubations) taken from the reference area on 3 June 2017.

Dry sediment parameters and chlorophyll a

All sediment samples were freeze dried and sieved (1 mm) prior to analysis. Laser diffraction was used to measure particle size analysis (PSA) parameters with a Malvern Mastersizer 2000 (McCave *et al.*, 1986). Organic carbon (OC), was measured by removing carbonate from the total carbon (TC) concentration (with 0.1N HCl) and calculating the difference (McCave *et al.*, 1994). TC, OC and total nitrogen (TN) content were determined using an Interscience Flash 2000 organic element analyser. Samples for chl *a* analysis were collected from the top 1 cm of sediment from each box core and were immediately placed in a -80 °C freezer for storage. Sediment phytopigments were extracted with acetone and measured using HPLC methods (Zapata *et al.*, 2000). Subsamples for carbon/nitrogen (C/N) and PSA were taken with 3.5 cm diameter sediment cores and were sliced at 2.5 cm intervals down to 12.5 cm.

On-board measurements: Benthic profiles and fluxes

From the box cores, “incubation” sediment cores (14 cm diameter) with overlying water were subsampled for oxygen microprofiling and subsequent oxygen consumption/nutrient flux incubations (hereafter referred to as “on-board incubations” to distinguish between *in-situ* lander incubations). During the on-board incubations, overlying water in the cores was continuously mixed with a central stirring mechanism which ensured homogenous concentrations of nutrients and O_2 but without resuspending the sediment. All incubations were run in a climate-controlled chamber which maintained a constant temperature of 12°C representative of the *in-situ* bottom water.

Clark-type O_2 micro-electrodes (50 µm tip diameter, Unisense) were used to make oxygen-depth profiles in the cores immediately after collection (Revsbech, 1989). In each incubation core, 3 replicate profiles were taken from different areas of the sediment. For each profile, readings were taken at 100-µm intervals, starting approximately 10000 µm (10 mm) above the sediment water interface (100% O_2 saturation) to the depth in the sediment at which all oxygen was depleted (i.e. the oxygen penetration depth [OPD]). A two-point calibration was conducted prior to measurements using 100% and 0% oxygen saturated seawater to represent water column and anoxic O_2 concentrations respectively.

The incubation cores used for oxygen profiling were subsequently placed in a 12°C water bath to obtain sediment oxygen and nutrient flux estimations in dark conditions. Cores were sealed for up to 12 h in order to record oxygen consumption until a clear linear relationship was observed. The oxygen concentration during the incubation period was measured with optode sensors (FireStingO2, Pyroscience) using a measurement interval of 30 seconds. Oxygen and nutrient flux measurements occurred concurrently although at the end of the oxygen incubation, the cores were opened, re-aerated and kept for an additional 24-36 h to continue sample collection for nutrient flux measurements. Ammonium (NH_4^+), nitrogen oxides (NO_x), phosphate (PO_4^{3-}) and silicate (SiO_2) fluxes (mmol m^{-2} d^{-1}) were determined by fitting a linear regression over the concentration change in the overlying water over time and multiplying the regression coefficient with the height of the water column. For this regression, water samples were taken at 0, 8, 16, 22, 36, and 48 hours after the start of the incubation with a syringe and filtered (0.45 µm) into a 10 mL polystyrene vial for nutrient analysis (NH_4^+, NO_x, PO_4^{3-} and SiO_2) and stored frozen (-20°C). Upon thawing, samples were analysed by a SEAL QuAAtro segmented flow analyser (Jodo *et al.*, 1992). If the fitted regression was not statistically significant (Pearson correlation, $p > 0.05$), it was interpreted as a zero flux.

Box cores were further subsampled for porewater nutrients using 10 cm diameter sub-cores with vertical sampling ports. These were used in combination with rhizon samplers (Rhizosphere Research Products) to collect water samples at 0, 1, 2, 3, 5, 7, and 10 cm depth (Seeberg-Elverfeldt *et al.*, 2005; Dickens *et al.*, 2007; Shotbolt, 2010). Porewater nutrients were stored and analysed using the same methods as the incubation water samples.

In-situ SCOC and nutrient fluxes

To gather information from an untrawled location, two Autonomous Landers for Biological Experiments (ALBEX; Duineveld *et al.*, 2004; Witbaard *et al.*, 2000) were positioned inside the pulse treatment area on 4 June 2017 before fishing as the control deployment. To measure fishing effects, these were deployed in tickler (1 June 2017) and pulse (6 June 2017) trawled areas within 3 h after fishing concluded. The landers were used to obtain *in-situ* rates of oxygen and nutrient fluxes from the sediment. The exact position inside the tickler trawled area was verified by using a side scan sonar (Kongsberg PULSAR) which was used in conjunction with the Kongsberg EM302m MBES (Multibeam Echosounder) mounted on the RV Pelagia (**Figure 3**).

Each lander held 3 measurement chambers enclosing a surface area of 144 cm^2. For deployment, the landers were carefully lowered on a cable until they reached the seafloor. After descent, each measurement chamber was autonomously driven into the sediment by a hydraulic mechanism. The *in-situ* incubations lasted 5 h and began shortly after deployment, though the landers were retrieved between 20 and 48 h after deployment depending on the sampling schedule.

The decrease in oxygen concentration in the headspace of each chamber was measured every 30 seconds using JFE-ALEC rinko optodes. Water in the chamber was stirred with a magnetic stirrer mounted to the lid. At pre-set time intervals, a 30 mL water sample was taken from the headspace of each chamber. At the first (and last) sampling moment, a simultaneous sample from the outside water was taken. In this way a sequence of water samples were taken. Upon retrieval, water samples were immediately frozen and analysed similar to the other nutrient samples.

Data analysis and statistics

Shapiro-Wilk and Levene’s tests were conducted to determine if data was normally distributed and/or displayed homogeneity of variances. If assumptions for parametric testing were violated, data was normalised using a log-transformation. Differences in water depth, biogeochemical parameters (benthic O_2 and nutrient fluxes, OPD, Chl *a*, porewater nutrients, OC, TN), and sediment characteristics (% silt, % fine sand, D50, D10) between T0 samples from the tickler chain, PulseWing and reference areas (i.e. untrawled areas) were tested for by applying a one-way analysis of variance (ANOVA). A one-way ANOVA was used to investigate significant differences in biogeochemical and sediment parameters between tickler T1, tickler T2, tickler T3, pulse T1 and untrawled samples. If significant differences were detected by the ANOVA, a Tukey HSD post hoc test was applied to perform pairwise comparisons between specific treatments. To quantify the relationship between water column oxygen and SPM concentrations, a linear regression was performed. All statistical analyses were performed using R (R Core Team, 2013).

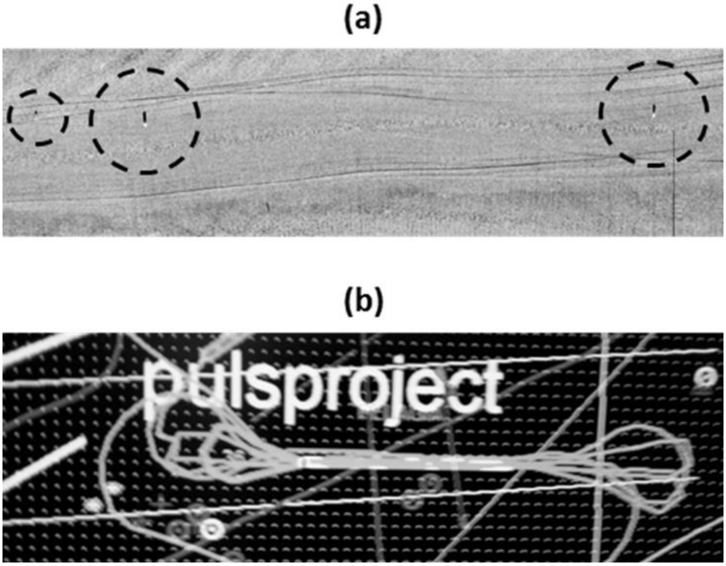

Figure 3. (**a**) A side-scan sonar image of the tickler trawled area. In addition to the evidence of bottom disturbance, images of 2 benthic ALBEX landers and an additional oxygen sensing lander can be seen within the disturbed portion of the seafloor. Image courtesy of Leo Koop. (**b**) Tracking of PulseWing trawl coordinates showing the path taken by the fisherman while fishing the experimental (pulse) area.

RESULTS

Study site characteristics

Data from the echosounder showed no significant differences in water depth between sample locations in tickler, pulse, or reference areas (ANOVA, $p > 0.05$). Additionally, untrawled sediment from tickler T0, pulse T0 and reference box core samples did not show significant differences between O_2/nutrient fluxes, porewater nutrients, chl *a*, OC, TN, measurements or grain size characteristics (ANOVA, $p > 0.05$). Therefore, for the rest of the analyses, data from the T0 (pulse and tickler) and reference samples were pooled to act as the control treatment representing the untrawled situation. Estimates of trawl disturbance using VMS data suggested that in the year leading up to the study, the fishing effort within the treatment areas was minimal with little to no beam trawling occurring, however, the analysis also suggested a possibility (0.25 – 1.25 h fished) of pulse trawling conducted in a small section of the reference area. All sampled areas were assumed to be relatively undisturbed.

Our personal observations confirmed that both tickler chain and PulseWing commercial trawlers made 7 trawl passes through the designated treatment areas. The effect of tickler chain trawling was also verified by using side-scan sonar, which showed the mechanically disturbed seabed across the planned treatment area (**Figure 3**). Furthermore, the sonar images revealed that the benthic landers were placed inside the disturbed area (**Figure 3**). Unfavourable weather conditions prevented us from using the side scan sonar following PulseWing trawling. As a result, we relied on the visual tracking of the pulse trawler using its AIS (Automatic Identification System) from the RV Pelagia.

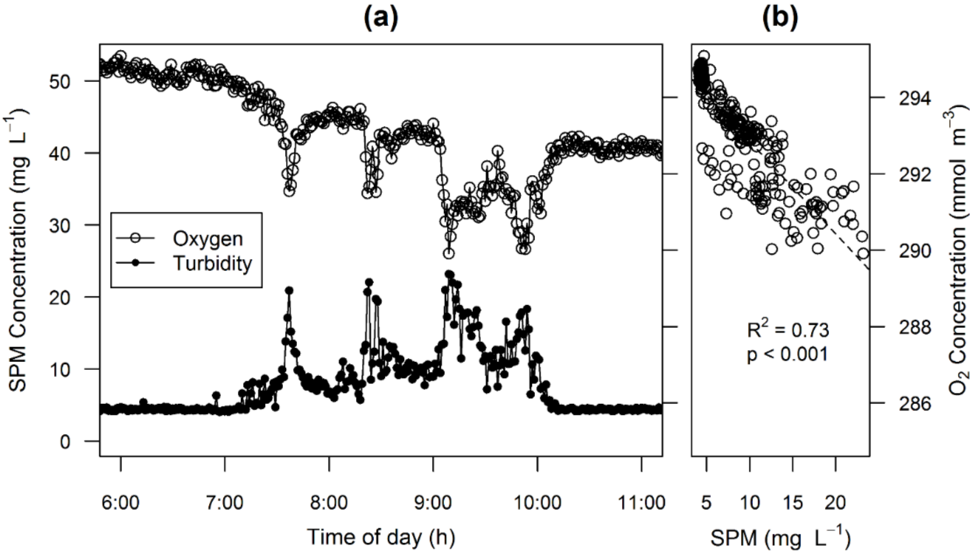

Figure 4. (**a**) PulseWing facilitated resuspension effects on SPM (mg L^{-1}) and O_2 (mmol m^{-3}) concentrations. Data was taken from 3.5 m above the sediment surface. (**b**) The relationship between SPM (x-axis) and O_2 concentration (y-axis) in the water column during pulse fishing.

Effect of the PulseWing on sediment plume dynamics

The turbidity sensor on the mooring logged a notable increase in the suspended particulate matter (SPM) concentration, including distinct peaks with each passage of the PulseWing trawl (**Figure 4**). SPM concentrations ranged from 4.0 to 23.2 mg L^{-1} and increased rapidly whenever the pulse trawler passed through its designated treatment area. The peaks in SPM coincided with dips in the dissolved oxygen concentration (**Figure 4**a). Linear regression analysis showed that 73% of the variation in oxygen concentration was accounted for by the variations in turbidity during experimental pulse fishing demonstrating an inverse relationship ($p < 0.001$; **Figure 4**b). Data from the SeaGuard showed that at the time of trawling, the current was northward and in the direction of the mooring and with a current velocity between 3 and 15 cm s^{-1}.

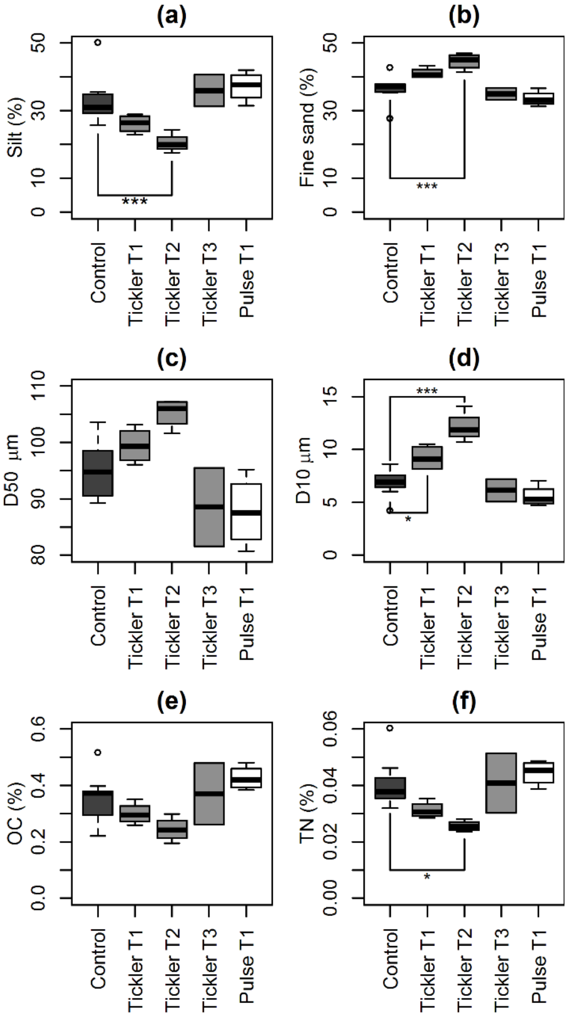

Figure 5. Surface sediment characteristics from control (*n* = 9), tickler T1 (*n* = 4), tickler T2 (*n* = 2), tickler T3 (*n* = 3) and pulse T1 (*n* = 7) samples: (**a**) % silt (<63 µm), (**b**) % fine sand

(63-125 µm), (**c**) D50 = median grainsize (µm), (**d**) D10 = diameter at which 10% of particles in the sample are smaller (µm), (**e**) % organic carbon, (**f**) % total nitrogen.

Fishing effects on sediment characteristics

Physical sediment parameters

Box core sediment samples collected after beam trawling (tickler T1, tickler T2) exhibited a fluffy layer of fine sand at the surface which was not present in control samples. Tickler samples also appeared visibly “flatter” in topography, while control samples displayed superficial sand ripples. These characteristics (finer sediment layer/flat topography) were present in some but not all sediment samples taken after pulse trawling (pulse T1).

As deeper sediment layers (2.5 – 12.5 cm) did not exhibit any significant differences for physical sediment characteristics between treatments (ANOVA, $p > 0.05$), the following documents the changes found in the upper sediment layers (0 – 2.5 cm) which displayed evidence of trawl-induced alterations. Tickler T2 (20.46 ± 2.85 % silt) displayed significantly smaller mean silt (<63 µm) fractions compared to control (33.06 ± 7.33 % silt; HSD, $p < 0.001$) sediments (**Figure 5**a). Fine sand (62.5-125 µm) fractions in tickler T2 (44.59 ± 2.48 % fine sand) were significantly higher than control (36.37 ± 3.96 % fine sand; HSD, $p < 0.05$; **Figure 5**b) samples. For D10 values (10% of the sample particles are smaller than this value), both tickler T1 (9.21 ± 1.21 µm) and tickler T2 (12.13 ± 1.42 µm) were significantly higher than control (6.78 ± 1.26 µm; HSD, $p < 0.05$, $p < 0.0001$) samples showing coarsening after beam trawl fishing (tickler T1/T2), followed by the reestablishment of ambient sediment characteristics (tickler T3; **Figure 5**d).

Figure 5e and **5**f display organic carbon and total nitrogen in surface sediments (0 – 2.5 cm). OC and TN trended similarly to the silt content although the average organic carbon in surface sediments was not significantly different between the control and trawled samples (ANOVA, $p > 0.05$). Total nitrogen content in these sediments was significantly lower in tickler T2 (0.026 ± 0.002 % TN) samples compared with control (0.041±0.009 % TN; HSD, $p < 0.05$) values (**Figure 5**f).

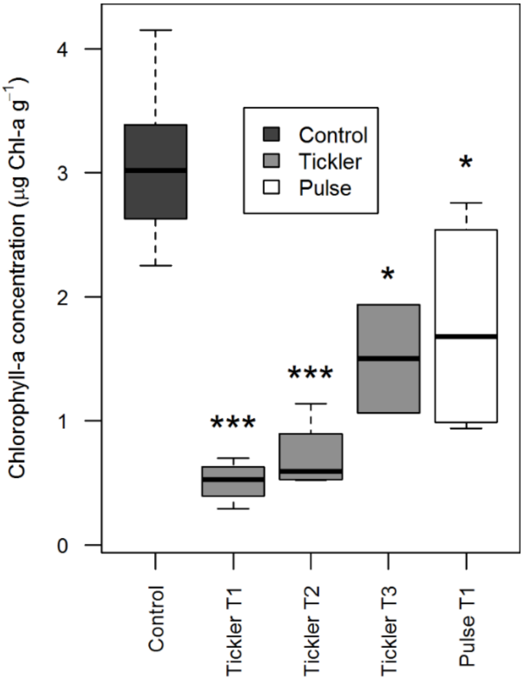

Figure 6. Surface chlorophyll-*a* concentrations in control (*n* = 9), tickler T1 (*n* = 4), tickler T2 (*n* = 4), tickler T3 (*n* = 2) and pulse T1 (*n* = 4) sediments. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$ significant differences compared to control samples.

Chlorophyll-a in surface sediments

Figure 6 displays the differences between levels of surface chlorophyll *a* amongst control, tickler T1, tickler T2, tickler T3 and pulse T1 treatments. Control samples had an average chl *a* concentration of 3.01 ± 0.68 µg chl *a* g^{-1}, while fished samples decreased to 0.51 ± 0.17 µg chl *a* g^{-1} for tickler T1 and 1.76 ± 0.91 µg chl *a* g^{-1} for pulse T1. The acute impact from both fishing methods caused a significant decrease in surface chl *a* compared with the control areas, however, the effect of the tickler chain trawl (tickler T1; HSD, $p < 0.0001$) was more pronounced than the effects of the PulseWing trawl (pulse T1; HSD, $p < 0.05$; **Figure 6**). Surface chl *a* in tickler T2 samples remained significantly lower than in control samples (0.71 ± 0.29 µg chl *a* g^{-1}, HSD, $p < 0.001$). Compared to tickler T2, tickler T3 samples showed an increase (though not significantly different than T1 or T2) in chl *a* content at 1.50 ± 0.61 µg chl *a* g^{-1}, though this was still significantly lower than control samples (HSD, $p < 0.05$).

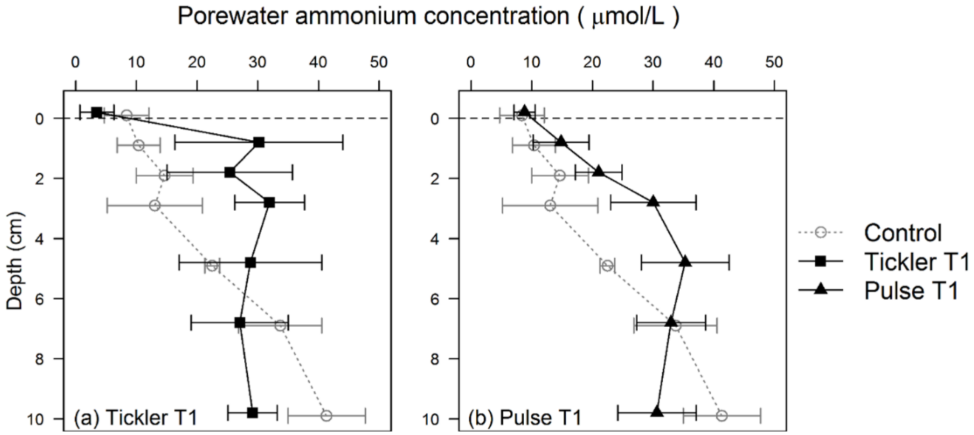

Figure 7. Porewater NH_4^+ concentrations comparing (**a**) tickler T1 and (**b**) pulse T1 with control (untrawled) samples

Table 1. Porewater nutrient concentrations in the upper 3 cm (µmol/L). No porewater samples were collected for tickler T3.

	NH_4^+ mean ± sd	NO_x mean ± sd	PO_4^{3-} mean ± sd	SiO_2 mean ± sd	*N*
Control	13.85±7.64	2.94±5.64	0.46±0.31	85.48±19.16	15
Tickler T1	**26.97±9.27****	2.52±1.85	0.53±0.34	80.00±23.46	6
Tickler T2	18.24±3.55	2.55±1.60	0.72±0.19	69.40±14.63	6
Pulse T1	**21.96±8.10***	**1.58±0.42**	**0.62±0.27**	**80.53±12.78**	**12**

Bold = significantly different from control samples. $^*p < 0.05$; $^{**}p < 0.01$

Fishing effects on oxygen and nutrients

Porewater NH_4^+ profiles in control samples exhibited a depth gradient with <15 µmol L^{-1} at the surface that steadily increased down to 40 µmol at 10 cm depth (**Figure 7**). Following tickler and pulse trawling, average NH_4^+ concentrations in the upper 3 cm of the box cores were significantly elevated for tickler T1 (HSD, $p < 0.01$) and pulse T1 (HSD, $p < 0.05$) treatments compared with control samples (**Table 1**). Tickler T1 samples in particular, displayed a homogenous depth profile for NH_4^+ which extended to 10 cm (**Figure 7**a). Pulse T1 NH_4^+ concentrations peak at 5 cm in the sediment while NH_4^+ in the control samples seem to increase past 10 cm (**Figure 7**b). No other significant differences were found between porewater nutrients in this study.

The average oxygen penetration depth after tickler chain trawling (tickler T1) was 3.78 ± 0.73 mm. In comparison, pulse T1 cores had an oxygen penetration depth of 3.17 ± 1.81 mm. These were both deeper than the OPD's found in the control cores which measured 2.25 ± 0.56 mm though the difference was only significant between the control and tickler T1 treatments (HSD, $p < 0.001$; **Figure 8**). Accurate OPD measurements for tickler T2 could not be obtained, because of variability created from macrofaunal burrows near the sediment water interface. However, the OPD in tickler T3 samples were not significantly deeper than control profiles (2.97 mm ± 0.93; HSD, $p < 0.05$).

Table 2 shows the average O_2 and nutrient flux values between on-board and *in-situ* incubations (note: O_2 "fluxes" in the Table are denoted as negative to be consistent with the nutrient flux data, while in-text O_2 "consumption" data are positive by definition). Sediment community oxygen consumption (SCOC) was significantly higher in the control incubations compared to both tickler T1 (HSD, $p < 0.001$) and pulse T1 (HSD, $p < 0.05$) treatments (**Table 2**, **Figure 9**). SCOC in tickler T2 and T3 samples remained significantly lower than the control (HSD, $p < 0.05$) measurements (**Table 2**, **Figure 9**a). *In-situ* oxygen consumption measured by the ALBEX landers was lowest after tickler chain trawling, and highest after PulseWing trawling though the differences were not significant (**Figure 9**b, **Table 2**).

Table 2. Benthic oxygen and nutrient fluxes (mmol m^{-2} $d^{-1)}$ from on-board incubations and in-situ lander deployments. n.d. = no data, O_2 “fluxes” are denoted as negative.

On-board incubations	O_2 mean ± sd	**NH_4^+** mean ± sd	**NO_x** mean ± sd	**PO_4^{3-}** mean ± sd	**$Si(OH)_4$** mean ± sd	*N*
Control	-17.78±3.07	0.25±0.34	0.106±0.03	-0.003±0.02	1.43±0.37	9
Tickler T1	**-10.46±1.50*****	0.35±0.41	0.095±0.02	0.001±0.01	1.10±0.41	4
Tickler T2	**-9.23±2.14***	0.10±0.13	0.097±0.02	0.001±0.01	0.70±0.36	2
Tickler T3	**-10.51±1.96***	n.d.	n.d.	n.d.	n.d.	3
Pulse T1	**-11.93±4.02***	0.28±0.25	0.108±0.02	0.002±0.01	1.30±0.52	7
In-situ incubations	O_2 mean ± sd	NH_4^+ mean ± sd	NO_x mean ± sd	PO_4^{3-} mean ± sd	$Si(OH)_4$ mean ± sd	*n*
Control	-21.40±4.45	0.39±0.29	0.177±0.05	0.071±0.03	2.85±1.04	6
Tickler	-17.01±6.36	0.61±0.55	**0.088±0.02***	0.076±0.04	2.22±0.84	6
Pulse	**-23.30±4.05**	**0.17±0.12**	**0.089±0.06**	**0.047±0.02**	**3.78±0.98**	**3**

Bold = significantly different from control samples. $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

Nutrient fluxes from the on-board incubation cores showed no significant differences between fished or control treatments (ANOVA, $p > 0.05$, **Table 2**). *In-situ* incubations yielded lower NO_x fluxes after tickler chain and PulseWing trawling compared to the control deployment which was statistically significant for the tickler treatment (HSD, $p < 0.05$, **Table 2**). No other significant differences were found in nutrient fluxes between control, tickler or pulse lander deployments, however, *in-situ* estimates for PO_4^{3-} and SiO_2 fluxes were markedly higher than in the on-board incubations (**Table 2**). It is noted that data from only one of the landers could be used after PulseWing trawling. Storm induced water currents created a build-up of sediment which partially buried the incubation chambers of one of the landers (which was evidenced upon retrieval) and seemed to create irregular measurements. Data was, therefore, used only from the lander which showed a range of flux data comparable to historical information from the Frisian Front.

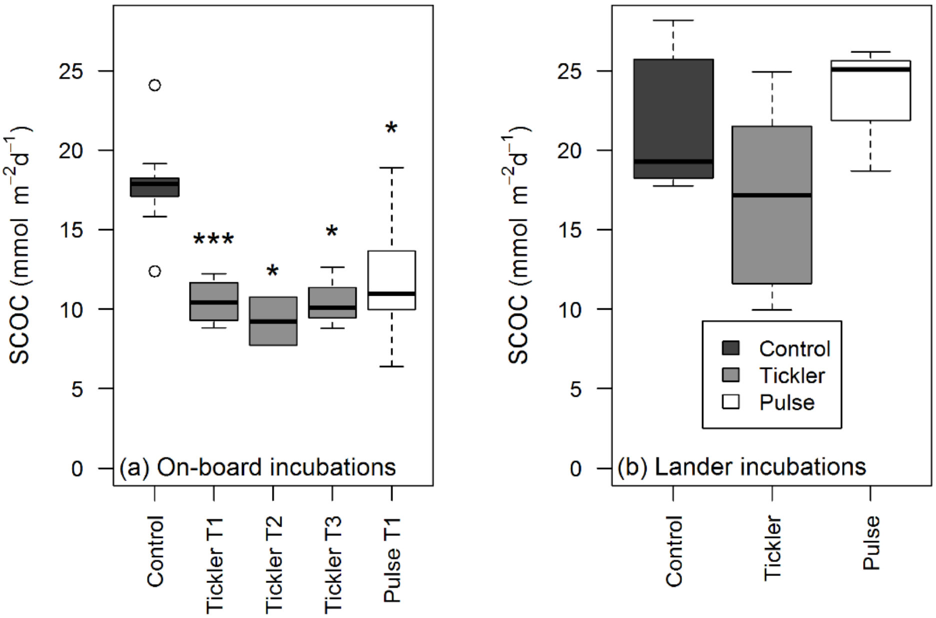

Figure 9. Sediment community oxygen consumption (SCOC) comparison between *ex situ* and *in situ* incubations. (**a**) SCOC in on-board measurements taken from box cores in control (untrawled), tickler T1 (6 h after impact), tickler T2 (30 h after impact), tickler T3 (75 h after impact), and pulse T1 (3.5 h after impact) sediment samples. (**b**) O_2 consumption measured from *in-situ* ALBEX landers for control (untrawled), tickler (1 h after impact), and pulse (1 h after impact) deployments. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$ significant differences compared to control samples.

Discussion

In this study we compared the effects of conventional tickler chain and electric PulseWing trawling on benthic biogeochemical functioning and water column processes in the Frisian Front, an area located 50 km off the Dutch Coast characterised by fine sandy sediments. Despite unfortunate methodological constraints, we were able to effectively capture and assess the acute effects of bottom trawl activity on the biogeochemical functioning of North Sea sediments. In particular, our results show that trawling resulted in clear differences between chl *a* (labile organic material), and oxygen dynamics in trawled and untrawled sediments. It is also important to point out that additional samples collected for the pulse T1 sampling timestep may have created additional variablility to the results. Here, we discuss the effect of bottom fishing on water column properties, followed by sedimentary organic and inorganic solid particles, to end with the impact on benthic oxygen and nutrient dynamics.

Effects in the water column

The mooring, deployed during PulseWing trawling, showed increased turbidity after each pass of the fishing vessel (**Figure 4**), indicating resuspension of sediments to the overlying water. This data supports the findings of Depestele *et al*., (2016) who recorded sediment resuspension from both tickler chain and pulse trawled gears. Concurrent with the increased turbidity, we observed prominent drops in water column oxygen concentrations (**Figure 4**a). A similar decrease in water column O_2 was documented by Riemann and Hoffman, (1991) after mussel dredging in the Limfjord. The release of low oxygenated porewater and reoxidation of reduced substances resuspended from the sediment may be the primary cause for the increased water column O_2 uptake (Almroth et al., 2009; Almroth-Rosell et al., 2012).

The sediment data are consistent with these water column observations. The decrease of silt, chlorophyll and organic carbon in the upper sediment layers after fishing suggests resuspension of these substances to the water column. Furthermore, the reduction in sediment oxygen uptake that we found after fishing suggests that part of the metabolic activity, due to removal of labile organic matter and loss of reduced compounds, is displaced from the sediment to the overlying water.

Removal of surficial sediment

We observed an overall coarsening in surface sediments due to beam trawl activity (**Figure 5**a-d), which is in agreement with Depestele *et al*., (2018), Mengual *et al*., (2016) and Palanques *et al*., (2014). The appearance of finer particles on the sediment surface after tickler chain trawling, however, suggests that two processes are occurring: 1) the smallest sediment fraction (silt) is winnowed and reallocated away from the trawl track, while 2) the heavier sand fractions resettled or remained on the trawl track leaving finer particles (but not the finest silt fraction) sorted on the surface with heavier particles underneath. As sedimentary organic matter and nitrogen are strongly associated to the abundance of silt and clay (Virto *et al.*, 2008), the winnowing of the upper silt fraction led to significant decreases in TN and labile organic material as shown in our chl *a* results. Tickler T3 samples showed reintegration of silt particles in the upper sediment layers along with the restoration of TN and chl *a* values towards levels found in control samples (**Figure 5**f, **Figure 6**). This relatively fast “recovery” of sediment parameters may have occurred through the deposition of previously resuspended particles and/or bioturbation activity as infaunal organisms such as *Upogebia deltaura* and *Callianassa subterranea* rebuild their burrows after disturbance and are known to expel large amounts of sediments from depth (Rowden *et al*., 1998).

Our study was conducted after the spring bloom (April/May), which provides an annual influx of chl *a* from the water column onto the sediment surface of the Frisian Front (Boon and Duineveld, 1996; Boon *et al.*, 1998). Both trawl types induced large reductions of sediment chl *a* (83% - tickler T1, 45% - pulse T1; **Figure 6**), implying that trawling physically removed the top sediment layer along with the labile organic material within it, lowering benthic food quality (Watling *et al*., 2001). The observed reductions in chl *a* are in agreement with Brylinsky *et al*, (1994) and Watling *et al*., (2001), who documented significant losses of phytopigments shortly after towing bottom trawl gears in shallow (<15 m) sediments. The loss of chl *a* is expected if an acute mechanical stressor, such as bottom trawling, is able to displace the surface sediment, however, longer-term effects on sediment phytopigments and organic material may vary.

Several studies in shallow shelf environments (10 – 70 m) have linked bottom trawling to increased sediment chl *a* and/or OC (Pusceddu *et al*., 2005; Palanques *et al*., 2014; Sciberras *et al*., 2016). Yet some evidence suggests that this may be a long-term side effect of trawling and not an acute response. In the Bay of Fundy, Brylinsky *et al*, (1994) detected an increase in sediment chl *a* occurring 80 days after an initial depletion of phytopigments caused from experimental trawling. Similarly, near the coast of Maine (USA), Watling *et al*., (2001) observed an 88% decline in chl *a* from the sediment surface immediately after scallop dredging, but reported only a 4% difference in chl *a* from disturbed and adjacent areas four months after disturbance. Enhanced OC and chl *a* production after bottom trawl disturbance may come as a delayed response due to the loss of microbial (Watling *et al*., 2001) or macrofaunal (Bergman and Hup, 1992; Bergman and van Santbrink, 2000; Tanner, 2003; Olsgard *et al.,* 2008) biomass leading to reduced grazing activity and/or the eventual settling of silt particles (Palanques *et al*., 2014). It is noted that Pusceddu *et al*., (2014), who sampled chronically trawled versus untrawled deep sea sediments (500 – 2000 m), reported reduced chl *a* and OC concentrations due to bottom trawling. However, deep sea environments lack the biological and physical mechanisms to recover quickly from disturbance, thus leaving OC and pigment levels in their depleted state for longer periods of time.

Effect on biogeochemical profiles and fluxes

The significant increase in porewater NH_4^+ after tickler chain and PulseWing trawling (tickler T1/pulse T1) in the top 3 cm sediment suggest a physical disturbance in the upper sediment layer (**Table 1**, **Figure 7**). The homogenised NH_4^+ profile in tickler T1 and shallower peak in NH_4^+ concentration in pulse T1 compared to control samples may reflect the removal of the upper sediment layer, the homogenisation of the sediment column, increased ammonification due to the mixing of organic material or a combination of these factors. As it can take several months for NH_4^+ to reach a new steady state after sediment disturbance (van de Velde *et al.*, 2018), these altered profiles probably show transient effects. Oxygen, in contrast will more quickly reach its steady state in the sediment.

Decreased labile organic material and the removal of reduced compounds will lower SCOC and increase O_2 concentrations in the sediment, thereby increasing the OPD (Gundersen and Jorgensen, 1990). Our results demonstrate this pattern as fishing disturbance led to deeper OPD's in addition to the reduction in SCOC (**Figures 8** and **9**) and chl *a* (**Figure 6**). The OPD's in our study were 40% deeper in the tickler T1 and 29% deeper in pulse profiles in comparison with control samples (**Figure 8**). These results are supported by Allen and Clarke, (2007)'s prediction of a deeper sediment oxic layer following bottom trawl disturbance.

Sediment community oxygen consumption (SCOC) can be used as a measure for total (oxic and anoxic) sediment metabolism, as it represents the collective respiration of microbial, meiofaunal and macrofaunal communities residing in the sediment, as well as chemical reoxidation processes of reduced compounds (Glud 2008). Historical data from the Frisian Front shows seasonal variation in O_2 consumption from 5 mmol O_2 m^{-2} d^{-1} during winter months to its peak in August at around 50 mmol O_2 m^{-2} d^{-1} (van Raaphorst *et al.*, 1992; Nedwell, *et al.*, 1993; Upton *et al.*, 1993; Boon *et al.*, 1998; Boon and Duineveld, 1998). From the month of June, O_2 consumption ranges between 15 to 36 mmol O_2 m^{-2} d^{-1} (Upton *et al.*, 1993; Boon *et al.*, 1998; Boon and Duineveld, 1998), which is comparable with the SCOC rates from our study before trawling.

Although the differences in O_2 consumption from the *in-situ* lander incubations were not statistically significant, the results are complimentary to the data from our on-board incubations, implying that fishing with tickler chains is more likely to cause reductions in SCOC than PulseWing trawling. The reduction of SCOC rates and deepening of the OPD after trawl disturbance is consistent with the removal of the reactive top layer of sediment, as demonstrated by the loss in chlorophyll and organic matter. This top layer typically also holds high abundances of microbial (Watling *et al.*, 2001) and macrofaunal (Dauwe *et al.*, 1998) organisms. Thus, removal of this layer likely decreased the overall biological activity and carbon mineralisation in these sediments. It may be possible for trawl induced faunal mortality to enhance SCOC through increased bacterial degradation, however, this effect was not detected in our study.

To our knowledge, we are the first to report significantly decreased SCOC rates and increased O_2 penetration in marine sediments following bottom trawling. Trimmer *et al*., (2005) found no significant changes in oxygen uptake between trawled (various bottom gear types) and untrawled sandy sediments in the southern North Sea. Sciberras *et al*., (2016) did not find a significant effect of bottomfishing (scallop dredge/otter trawl) on OPD in sandy and muddy sediments in the Irish Sea. Our bottom trawl assessment differs from the aformentioned studies in that we measured acute and short-term impacts which allowed us greater spatial and temporal control over the trawl disturbance and subsequent sample collection. In the soft sediments of Galveston Bay Texas, Warnken *et al*., (2003) conducted an acute experimental study on shrimp trawling and found no significant effect from fishing in their oxygen flux measurements. The most pronounced results in our study, however, came from beam trawl gears rigged with tickler chains which undoubtedly cause greater disturbance to the seafloor compared to lighter shrimp trawls. Our results also contrast with the findings of van de Velde *et al*., (2018) who reported a drastic increase in total carbon mineralisation rates after anthropogenic caused mixing in organic carbon rich muddy sediments off the coast of Belgium. The increase was attributed to the re-exposure of previously buried organic material to oxic conditions. The sediments in their study, however, are extremely eutrophic and therefore not representative for most North Sea sediments. In comparison, Frisian Front sediments are less metabolically active, contain significantly less organic carbon, and have much higher macrofaunal activity. Nutrient fluxes measured in sediment cores and *in-situ* were quite variable both in the control and trawled areas. The ammonium fluxes (0.10 – 0.61 mmol m^{-2} d^{-1}) were lower than the maximum summertime values recorded in previous studies, but were well within the range of annual fluctuations in NH_4^+ flux (-0.1 – 1.7 mmol m^{-2} d^{-1}) in this area (van Raaphorst *et al*., 1992; Nedwell, *et al*., 1993; Lohse *et al*., 1995). NO_x fluxes in the Frisian Front can reach a value around 0.3 mmol m^{-2} d^{-1} in summer, however, van Raaphorst *et al*. (1992) found that NO_x fluxes in June remained closer to 0.1 mmol m^{-2} d^{-1} which is comparable to the fluxes found in our study (**Table 2**). Whereas the NH_4^+ fluxes between treatments in our study were not significantly different, we found a 50% decrease between *in-situ* lander NO_x fluxes from control and tickler trawled incubations. The Frisian Front exhibits distinct porewater NO_x maxima near the sediment surface (Lohse *et al*., 1995), which is consistent with the nitrate fluxing out of the sediment (**Table 2**). The removal of the top sediment layer may have weakened the diffusive gradient between NO_x and the overlying water, therefore reducing fluxes from the sediment.

In-situ lander flux estimates were consistently higher for oxygen, phosphate and silicate compared with on-board incubations (**Table 2**). Cores used for the on-board incubations held 22 cm of sediment at most, and so the fluxes recorded in the on-board incubation cores, measure the results of processes occuring within this space. The *in-situ* landers have no such limitation and measure fluxes over a deeper sediment layer. Bioturbating infauna in the North Sea are known to contribute to significant releases of silicate from the sediment (Olsgard *et al.*, 2008). A prominent mud shrimp in the Frisian Front, *C. subterranea*, has burrows extending down to 81 cm, and water in its burrows can hold higher concentrations of phosphate and ammonium compared to the overlying water (Witbaard and Duineveld, 1989, Rowden and Jones, 1995). Macrofaunal burrows were frequently seen in our sediment samples, several of which extended beyond the bottom of the incubation cores. We therefore infer that processes occurring deep in the sediment are the primary cause for the discrepancy in fluxes measured in our in-situ landers compared with the on-board incubations, where the former includes the impact of deep dwelling organisms, and the latter does not. Wave-induced advective transport may have also played a role in our *in-situ* lander results if waves were able to pump burrow water into the measurement chambers. The impermeable muddy sand in the Frisian Front, however, would prevent this process from occurring through advective porewater transport.

While this study was able to compare the net biogeochemical impact from electric pulse trawl and tickler chain beam trawl techniques, there remains questions about the effects of the electricity itself. The impact of electric pulses on macrofauna (burrowing infauna in particular which may avoid any mechanical impact) may have indirect biogeochemical consequences if their functioning is affected. Further research is necessary in order to truly isolate the mechanical and physical effects associated with pulse trawling.

Implications

Previous research has shown that different bottom gear types can cause variable effects on benthic fauna (Kaiser *et al.*, 2006; Hiddink *et al.*, 2017; Sciberras *et al.*, 2018). Moreover, severe bottom trawling may potentially induce long-term impacts on benthic biogeochemical cycles in certain sediments (Pusceddu *et al.*, 2014; van de Velde *et al.*, 2018). Our study adds the ability for bottom trawl gears to slow down overall benthic metabolism, at a time scale of several days at the least. The lowering of benthic oxygen consumption and the simultaneous increase in oxygen demand from the water column, provides evidence that trawling displaces part of the benthic activity into the overlying water. This can limit the amount of carbon burial in trawled sediments as reduced substances become reoxidised and released back into the pelagic environment. Given the scope of bottom trawl fishing, this may have widespread implications for carbon mineralization and nutrient cycling with possible consequences to global climate dynamics. Concurrently, the significant loss of labile organic matter (in the form of chl *a*) from the sediments after trawl disturbance and consequent lowering of the food quality may affect benthic lifeforms on longer time scales.

Finally, this study demonstrated the greater impact of tickler chain beam trawl gears on biogeochemical functioning when compared with PulseWing trawling. Information gained from this research has implications for bottom trawl fisheries management and provides concrete evidence linking lower mechanical disturbance in fishing gears to a reduced impact on benthic marine ecosystems.

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Chapter 3

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

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Sieving macrofauna before a North Sea storm (Frisian Front)

Photo: Karline Soetaert

Abstract

In this study, we analysed the benthic effects of two *in situ* fisheries disturbance experiments using a combination of side-scan sonar, high definition underwater video, sediment profile imagery, and box core sampling techniques after conventional beam trawling and box core sampling after electric pulse trawling in a southern North Sea habitat. Acoustic and optical methods visualised the morphological changes induced by experimental beam trawling, showing the flattening and homogenisation of surface sediments. Video transects found a 94% decrease in epibenthos in beam trawled sediments compared to an untrawled control site and a 74% decrease in untrawled sediments of the same transect. Box core samples taken 5.5 h, 29 h and 75 h after beam trawling detected a downward trend in infaunal densities (T0: 7698, T1: 3963, T2: 2566, T3: 1213 individuals per m^2) and taxon richness (T0: 22.7, T1: 17.2, T2: 13.5, T3: 7.3 taxa per sample) that continued after the initial impact with small-bodied and juvenile taxa being especially prone to depletion. Pulse trawled samples showed similar levels of macrofauna depletion between pre-trawled and recently trawled samples, though, unfavourable weather conditions prevented further sampling (T0: 8206, T1: 3721). Data from shallow sediment samples showed trawl resilience in large mud shrimps and evidence of their upward movement towards the sediment surface after disturbance. Both trawl gears induced significant changes to infaunal communities, however, no differential effect between the two gears. This shows that pulse trawl gears can induce similar effects to beam trawls on benthic communities in soft sediments. Our results also suggest that in the Frisian Front, trawling favours the survival of deep burrowers while removing surficial macrofauna.

Keywords: Benthic ecology, biodiversity, sediment profile imagery, underwater video, side-scan sonar, beam trawling, pulse trawling

INTRODUCTION

Bottom fishing has been a controversial practice since its origins in the thirteenth century (de Groot, 1984). Historical records of the North Sea show maps of biogenic reefs and harder substrates which were present before the arrival of extensive bottom trawling (Coolen, 2017). It is also believed that soft sediment habitats and macrobenthic communities in the southern North Sea have been shaped by anthropogenic processes including beam trawling (Capuzzo et al., 2015; van Nes et al., 2007). The exact causes of these changes, however, can be difficult to pinpoint and are location specific. Furthermore, fishermen argue that their methods are comparable to farming on land which creates similar if not greater effects to terrestrial habitats. In order to better manage and mitigate bottom trawling effects on benthic ecosystems, it is essential to gain a detailed understanding of their biotic and abiotic impacts on marine habitats.

Beam trawling removes benthic organisms (Hiddink et al., 2017; Sciberras et al., 2018) and can affect the stability of a system through cascading food web modifications (Shephard et al., 2010, Shephard et al., 2014). Studies have shown increased vulnerability for large-bodied invertebrate epifauna to bottom trawl disturbance, while burrowing fauna may show more resilience (Thrush et al., 1998; Tillin et al., 2006, O’Neill et al., 2013). Trawling can also expose previously buried benthos leaving them at a higher risk for predation (Kaiser and Spencer, 1994; Groenewold and Fonds, 2000; Schwinghamer et al., 2010). Several methods are available to evaluate the effects of bottom trawl disturbance on benthic communities. The majority of trawl assessment studies base their findings on the physical collection of benthos from benthic grab and core samplers and/or bottom trawls/dredges. Compared with single point benthic samplers, towed video imagery allows greater spatial coverage of the seafloor, it has the potential to record changes to seabed morphology and benthic communities, and has also been suggested as an alternative to trawl surveys (Ayma et al., 2016; Damveld et al., 2018; McIntyre, et al., 2015; Smith et al., 2007). Acoustic techniques, such as side-scan sonar, provide an even broader perspective of seabed bathymetry and have been used extensively in trawl impact studies (Graham et al., 2004). The use of sediment profile imagery (SPI) for impact assessments allows the observation of subsurface redox conditions and can be used to derive indices describing benthic habitat quality (Birchenough et al., 2006; Mulsow et al., 2006; Teal et al., 2010). Each of the aforementioned techniques has its advantages and limitations; however, the use of these methods in conjunction with each other may help gain a more complete assessment of anthropogenic disturbance (Birchenough et al., 2006).

The primary objective of this study is to combine acoustic, optical, and sediment extraction methods, to provide a comprehensive assessment of bottom trawl disturbance in the Frisian Front. In the same study site, Tiano et al. (2019) reported differences in benthic biogeochemical effects created from electric pulse trawl and tickler chain beam trawling. While beam trawls regularly use chains to physically dig flatfish out of the sediment, pulse trawls use electric stimulation to perform the same task leading to lower gear penetration depths (Depestele et al., 2018). The secondary objective of this study is to follow up on Tiano et al. (2019) by comparing differences in macrobenthos composition before and after an experimental disturbance by beam and pulse trawls.

MATERIALS AND METHODS

Study area: Frisian front

All sampling and experimental trawling was conducted in the area of the North Sea known as the Frisian Front between 53.6861°N, 4.4414°E and 53.6814°N, 4.4719°E, at a water depth of ~ 34 m (**Figure 1**). The experimental area exhibited muddy sand with a median grain size averaging 92.6 µm and an organic matter percentage of 0.35 % (Tiano et al., 2019). This relatively homogenous sedimentary environment hosts diverse and abundant benthic faunal assemblages (Dauwe et al., 1998; Dewicke et al., 2002; Duineveld and Boon, 2002). The high productivity in the Frisian Front arises as water currents from the north and south converge and decelerate, allowing the deposition of organic matter (Boon and Duineveld, 1998; Otto et al., 1990). Evidence suggests that this area has undergone a phase shift in recent decades, from a habitat dominated by the shallow burrowing brittlestar *Amphiura filiformis* to one which now supports high individual densities of the deep burrowing mud shrimp *Callianassa subterranea* (Amaro, 2005; van Nes et al., 2007). Although bottom trawl activities occur regularly in the Frisian Front, vessel monitoring system (VMS) analysis from Tiano et al. (2019) which was used to estimate fishing intensity, suggested that the probability of trawling in the experimental area within the prior year was minimal.

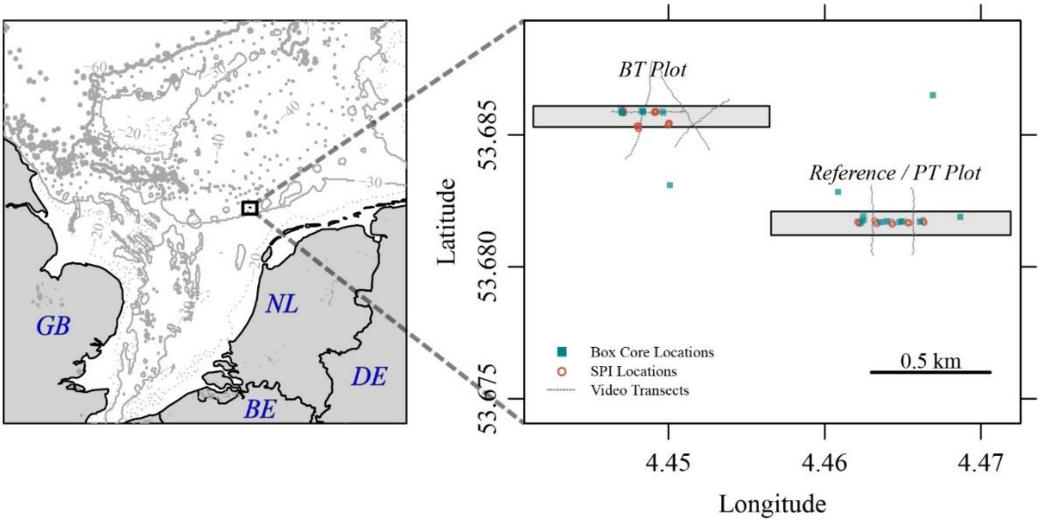


Figure 1. Location of field experiment and data collection in the North Sea (left). Sample locations and experimental fishing areas: beam trawl (BT) plot, PulseWing trawl (PT) plot (right). For video transects and sediment profile imagery (SPI) data collection, the PT plot was used as an untrawled reference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

Experimental design

Experimental trawling was conducted in June 2017, with one vessel equipped with traditional tickler-chain beam trawls and the other with electric PulseWing trawls (**Table 1**). The vessels carried out beam trawling (BT) and pulse trawling (PT) treatments by making 7 parallel trawled passes through designated BT and PT plots (**Figure 1**). More details about the gear configuration and experimental trawling procedure can be found in Tiano et al. (2019).

A before-after-control-impact (BACI) design experiment was originally planned for both fishing methods. However, logistic constraints (sampling before BT was limited due to a late vessel replacement and early arrival of BT fishers) and inclement weather (a storm occurring shortly after PT) prevented this. As a result, a control-impact design was used for SPI and video transect data using BT impacted sediments, compared with untrawled sediments in and around the PT plot (prior to PT disturbance; **Table 1**). For macrofauna collection, a before-after design was used to collect most of the data for both BT and PT in their designated plots (**Table 1**). As a

Table 1.
Information collected for the beam trawl (BT) and pulse trawl (PT) experiments. Shallow cores represent samples taken from ~15-20 cm in the sediment with incubation cores. Deep cores represent samples taken from ~30-40 cm in the sediment with standard box cores.

Beam Trawling (1 June 2017, 8:30 – 11:30)

	Date	Start Time	Location	Impact
Side-Scan Sonar				
Sonar Survey	2 June 2017	10:27	BT Plot	*Trawled*
Sonar Survey	3 June 2017	20:59	BT Plot	*Trawled*
High Definition Hopper Camera				
Video Transect	2 June 2017	14:42	BT Plot	*Trawled*
Video Transect	3 June 2017	16:21	PT Plot (before trawling)	*Untrawled*
Video Transect	4 June 2017	16:41	BT Plot	*Trawled*
Sediment profile imagery (SPI)				
SPI images	1 June 2017	13:44	BT Plot	*Trawled*
SPI images	4 June 2017	9:00	PT Plot (before trawling)	*Untrawled*
Macrofauna collection (box corer)				
T0: - *3 shallow cores*	1 June 2017	8:08	BT Plot	*Untrawled*
T1: - *3 shallow cores,* - *2 deep cores*	1 June 2017	17:02	BT Plot	*Trawled*
T2: - *2 shallow cores*	2 June 2017	16:38	BT Plot	*Trawled*
T3: - *3 shallow cores*	4 June 2017	14:27	BT Plot	*Trawled*
Ref (Reference): - *3 deep cores*	4 June 2017	15:01	Outside of BT and PT plots	*Untrawled*

Table 2. *Continued*

Pulse Trawling (6 June 2017, 7:30 – 10:00)				
	Date	Start Time	Location	Impact
Macrofauna collection (box corer)				
P0:	*3 June 2017*	10:16	PT Plot	*Untrawled*
- 3 shallow cores				
- 5 deep cores				
P1:	*6 June 2017*	11:36	PT Plot	*Trawled*
- 7 shallow cores				
- 4 deep cores				

proper before-after comparison was lacking for certain BT impacted samples (see section: *2.3.4* for "deep cores" reference treatment) additional untrawled sediments were collected adjacent to BT and PT plots for comparison (control-impact design; **Table 1**). All experimental equipment was deployed from the RV "Pelagia" (Royal NIOZ).

Data collection

Side-scan sonar

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

HD Video transects

Video footage of the seabed was collected using the downward facing HD NIOZ (Netherlands Institute for Sea Research, Texel) hopper camera, as described in Damveld et al. (2018). The frame comprised a HD video camera, a light, and 2 lasers that were placed 30 cm apart for scaling. Its height above the seabed was kept constant by adjusting the length of the towing cable, based on video live-view. During video operations, the vessel had a speed of ± 0.1 m/s. Video transects were carried out ~ 27 h and ~ 50 h after BT (**Table 1**). At the BT plot, these transects covered both trawled and untrawled sections (**Figure 1**). Transects over sediments in the PT plot prior to trawling disturbance were used as an untrawled reference area. For the three treatments (untrawled, ~ 27 h, ~ 50 h), 2 transects of ± 200 m were performed. Video stills were automatically created for every second. For analysis, subsequent stills were selected with a 15 s interval to prevent spatial overlap. If a still was not usable, the previous or following still was selected. All still-analyses were performed by two independently working observers, to minimize potential observer-bias. For each selected still, the observed surface was determined from the laser points in ImageJ version 1.52a (Schneider et al., 2012; Schindelin et al., 2012), any epibenthos present was identified to the lowest taxonomic level possible and epibenthos density (number of organisms per m^2) was calculated. Further analysis was restricted to the area in between the laser points (**Figure 2e**). All epifauna burrow entrances (holes) in the seabed were marked, and total surface area was determined to calculate hole density (number holes per m^2), average hole size, and hole coverage (% hole surface relative to seabed surface). Location of each still was determined by an interpolation of the vessels' GPS position, which was recorded every 30 seconds. Subsequently, for individual transects in the BT plot, all stills were classified as "trawled" or "non-trawled" depending on its GPS position in relation to the trawled sediments inside and the untrawled areas directly outside the plot (**Figure 1**). Comparisons were made between stills in the untrawled reference transects (all of which were "non-trawled") and "trawled" stills from ~27 h and ~50 h time steps. For further analysis of post-trawled sediments (~27 h and ~50 h), "non-trawled" stills were compared with the "trawled" stills for the individual transects at the BT plot. Six video transects were performed, resulting in 1178 stills which were analysed by two independent observers.

For each parameter of interest (hole density, hole size, hole coverage, epibenthos density), six linear mixed effect models were created using the *lmer*-function in the lme4-package (Bates, et al., 2015) from the open source software R (R core, 2019). Model 1a and 1b were based on data from observer 1, whereas model 2a and 2b were based on data from observer 2. Model 3a and 3b were based on all values, and included 'observer' as a random explanatory variable. Models 'a' contained the full model, in which the parameter was tested against the time step (fixed) and transect (random). Models 'b' only contained the random parameter transect. For each set of models, the a-model was tested against the b-model with a one-way ANOVA to test for significance. When the average model (3a) was significant, the estimated marginal means were calculated for the time step factor with the *emmeans*-function from the emmeans R-package (Lenth 2019) and the three time steps were compared.

Comparisons of trawled and non-trawled stills between time steps were performed by a similar methodology.

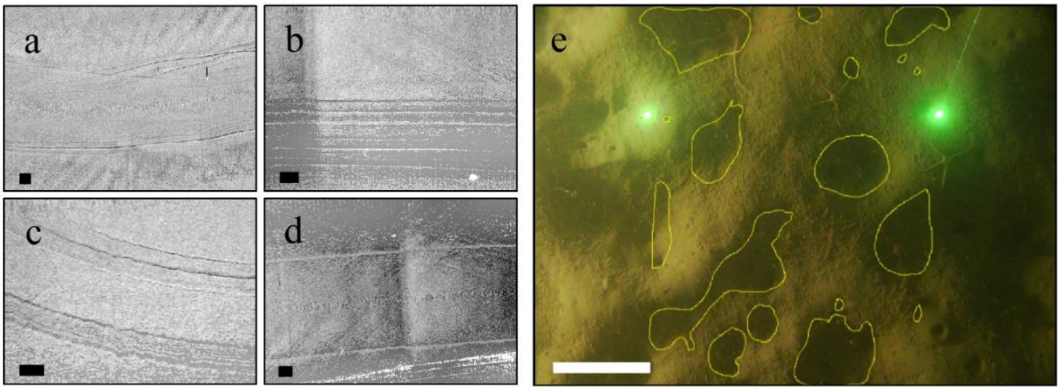


Figure 2. Side-scan sonar (a – d; scale bar = 10 m) and high definition underwater video imagery (e; scale bar = 0.1 m). Sinusoidal waveforms on the seabed adjacent to flattened beam trawled sediment (a). Several furrows in beam trawled sediment after multiple trawl passes (b). Two parallel trawl tracks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

Sediment Profile Imagery (SPI)

The subsurface structure of the seabed was studied using a Sediment Profile Imagery (SPI) camera (Ocean Imaging Systems, North Falmouth, MA, USA) made available by the Flanders Marine Institute (VLIZ), which was deployed ~ 2 h after BT in the trawled area and in an untrawled reference area (**Table 1**). The SPI camera consists of a galvanized frame that is lowered to the seabed. There, a prism protrudes in the seafloor, enabling the built-in camera to photograph a vertical section of the seabed (see Rhoads and Cande, (1971) for the principle of the SPI). For all images, the Benthic Habitat Quality index (BHQi) was determined, based on surficial structures, sub-surficial structures, and average Redox Potential Discontinuity (aRPD) depth (Nilsson and Rosenberg, 1997; Shumchenia and King, 2010). In addition, penetration depth was measured, as well as the thickness of the fine-sediment layer at the top of the seabed. All photos were analysed in ImageJ (Schneider et al., 2012; Schindelin et al., 2012), using the dimensions of the prism frame (14 x 25 cm) as scale. Differences in BHQi, RPD-depth and fine-sediment layer thickness before and after trawling were determined with Wilcoxon signed-rank tests.

Macrofauna collection

A round NIOZ box corer with a height of 55 cm and an internal diameter of 30 cm was used to collect benthic sediment samples both inside and outside experimentally trawled plots (**Figure 1**). Twenty-three cores (14 cm diameter x 30 cm height) were subsampled from box cores and incubated to derive oxygen and nutrient fluxes for a biogeochemical focused study (Tiano et al. 2019; **Table 1**). After the incubations, the cores were sieved and processed for the analysis of species communities. An additional fourteen intact box cores were taken and sieved (1 mm) specifically for macrofaunal collection (**Table 1**).

We hereafter refer to the incubation cores as "shallow cores" and the intact box cores as "deep cores" to reflect the infaunal communities found in the samples. For the BT treatments, box core samples were taken 0.5 h before (T0; 4 shallow cores), 5.5 h after (T1; 4 shallow cores, 2 deep cores), 29 h after (T2; 2 shallow cores), and 75 h after (T3, 3 shallow cores) trawl disturbance. For the PT treatments, the box corer was deployed 3 days before (P0; 3 shallow cores, 5 deep cores) and 3.5 h after (P1; 7 shallow cores, 4 deep cores) trawling. Deep cores were only taken for T1, P0, and P1 treatments due to logistic and time constraints limiting the number of data collection methods available (see section *2.2*). To facilitate further comparisons with undisturbed samples, deep cores were taken at adjacent locations to serve as an additional untrawled "reference" treatment (Ref; 3 deep cores; **Figure 1**, **Table 1**).

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

Macrofauna found in the box cores were grouped amongst five biological traits: burrowing depth, body length, body mass, fragility, and motility. Each trait was subdivided into modalities describing trait-based characteristics. Twenty-one different modalities were identified among the five selected traits (**Supplementary Table 1**). Infaunal densities and biomasses were compared between different treatments (T0, T1, T2, T3, P0, P1, Ref).

Univariate ecological characteristics and biological traits were analysed using a one-way ANOVA using the different treatment timeteps as a grouping factor. Shapiro-Wilk and Levene's tests were conducted to determine if data met the parametric assumptions of normal distributions and/or homogeneity of variances. If the assumptions were not met, a *log* transformation was performed to normalize the data prior to analysis. Pairwise Tukey HSD post hoc tests were applied upon detection of significant differences by the ANOVA. Effects on community composition were explored and tested by means of Between Class Analysis (BCA) on *log*-transformed organism densities (Dolédec and Chessel, 1987) from the “ade4” package (Dray and Dufour, 2007). Monte-Carlo tests with 999 permutations were carried out to see if trawling significantly affected benthic faunal assemblages (Heo and Gabriel, 1997).

All statistical analysis and data visualization were performed using the R software (R Development Core Team, 2019).

RESULTS

Sonar

Images from side-scan sonar revealed a visible bathymetrical disturbance in the BT plot (**Figure 2**). BT impacted sediments were flattened compared to adjacent untrawled areas. In addition, noticeable furrows were observed in the trawled areas (**Figure 2**b, **2**c). Sinusoidal waveforms created from water movement were detected in the untrawled sediments adjacent to the BT plot, though the surrounding seabed did not show drastic differences in water depth (33.8 ± 0.6 m). Although analysis of VMS data suggested little to no bottom trawling within a year prior to the experimental trawling in the specified sites (Tiano et al., 2019), old trawl tracks were observed intersecting the experimentally trawled sediments within 0.5 km of some sampling locations (**Figure 2**d).

Video Transects

Compared with information from the side-scan sonar, the trawl marks and furrows were less conspicuous in the downward facing video images. Biogenic mounds produced from bioturbating macroinvertebrates were visible in all sediments though the seabed was noticeably flatter within the trawled area. Data differed slightly between the two observers but was consistent among all stills and did not affect patterns observed between transects (**Figure 3**). A drastic difference in epibenthos density was detected between trawled sediments from video transects covering the BT plot (0.6 ± 1.4 ind m^{-2} after 27 h, $p < 0.001$; 1.7 ± 3.1 ind m^{-2} after 50 h, $p < 0.001$) and transects covering the untrawled reference location (10.8 ± 8.9 ind m^{-2}; **Figure 3**c). Brittle stars (*Amphiura filiformis*), heart urchins (*Echinocardium cordatum*) and

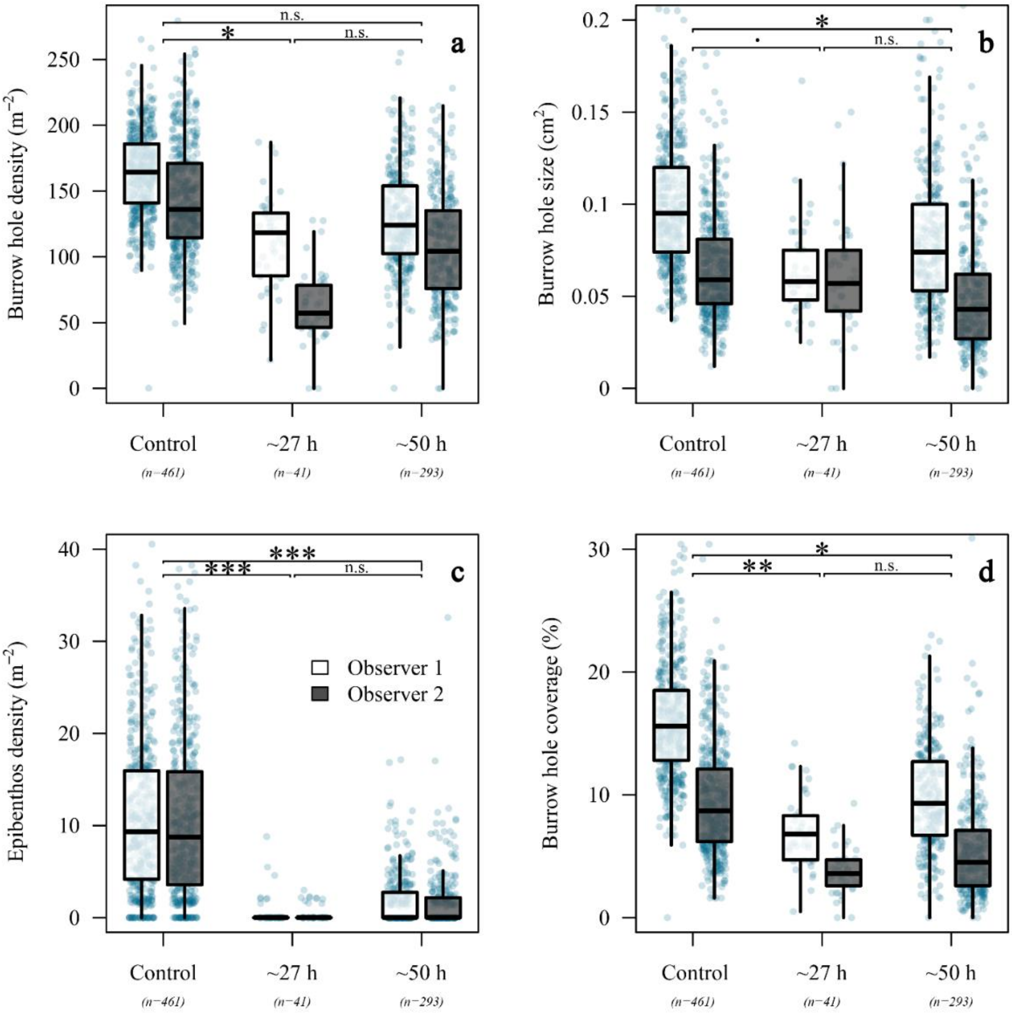


Figure 3. The effects of beam trawling on burrow hole density per m^2 (a), burrow hole size (b), epibenthos density per m^2 (c), and burrow hole coverage (d) from an untrawled control area, and areas covered twenty-seven (~27 h) and fifty (~50 h) hours after trawling. Only trawled stills are included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

annelid worms (Polychaeta) were amongst the macrofauna observed on the sediment surface. Burrow holes present in trawled sediments were smaller and hence, covered significantly less area (**Figure 3**b, **3**d). Individual transects conducted over the BT plot also yielded significant differences between 'trawled' and 'non-trawled' video stills for all parameters (epibenthos, hole density, % hole coverage, hole size) 27 h after trawling and for epibenthos and % hole coverage 50 h after trawling (**Supplementary Table 2**).

SPI Camera

A total of 59 SPI photos were taken. Of these, 13 photos were classified invalid, due to the seabed surface being invisible as the prism had protruded too deep. The SPI photos that were retained had a penetration depth of 17.2 ± 2.88 cm (mean ± SD). Infauna was observed in 72% of beam trawled images and 61% of untrawled images. SPI images from the BT impacted area displayed mechanically stirred sediments, showing a layer of lighter coloured fine sediment on a flattened surface (**Supplementary Figure 1**). In contrast, images from the untrawled area showed a non-uniform sediment surface consisting of biogenic mounds and/or sand ripples.

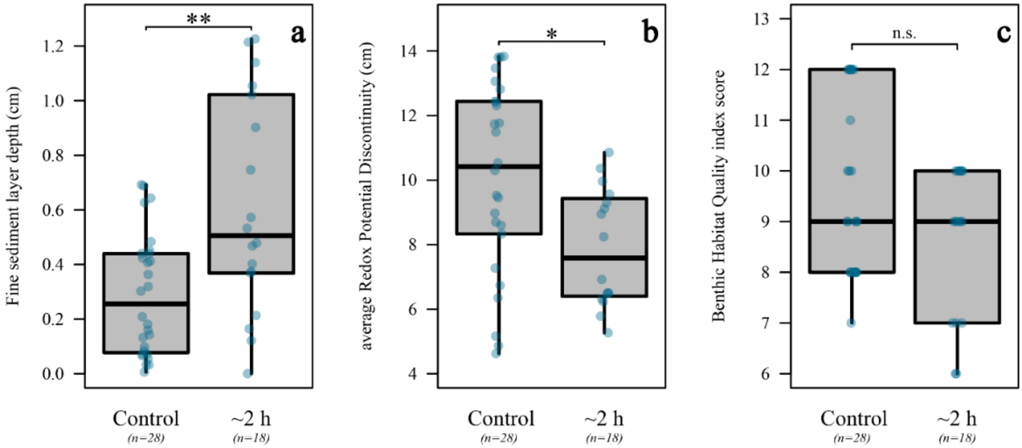


Figure 4. Fine sediment layer thickness (a), average Redox Potential Discontinuity (b) and Benthic Habitat Quality index score (c) for the untrawled control and areas beam trawled within 2 hours (~ 2h), based on sediment profile imagery (SPI). n.s. = not significant; * = *p*-value below 0.05; ** = *p*-value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

Compared with the BT impacted images, the untrawled reference images showed a significantly thinner layer of fine sediments ($p < 0.01$) and a significantly deeper aRPD ($p < 0.05$; **Figure 4**). BHQi did not differ significantly between beam trawled and untrawled areas ($p > 0.05$).

Macrofauna

In total, 121 taxa were identified in the shallow cores and deep core sediment samples used in this study. Both shallow cores and deep cores were dominated numerically by juvenile white furrow shell *Abra alba*, juvenile Ophiuroidea, and adult brittle star (*A. filiformis*) individuals. In particular, the aforementioned juveniles were present (in relatively large quantities) in all samples except for T3 shallow cores (**Supplementary Table 3**). In total, juveniles contributed to 54% and 55% of macrofauna in shallow and deep cores respectively.

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

Effects on general community descriptors

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

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

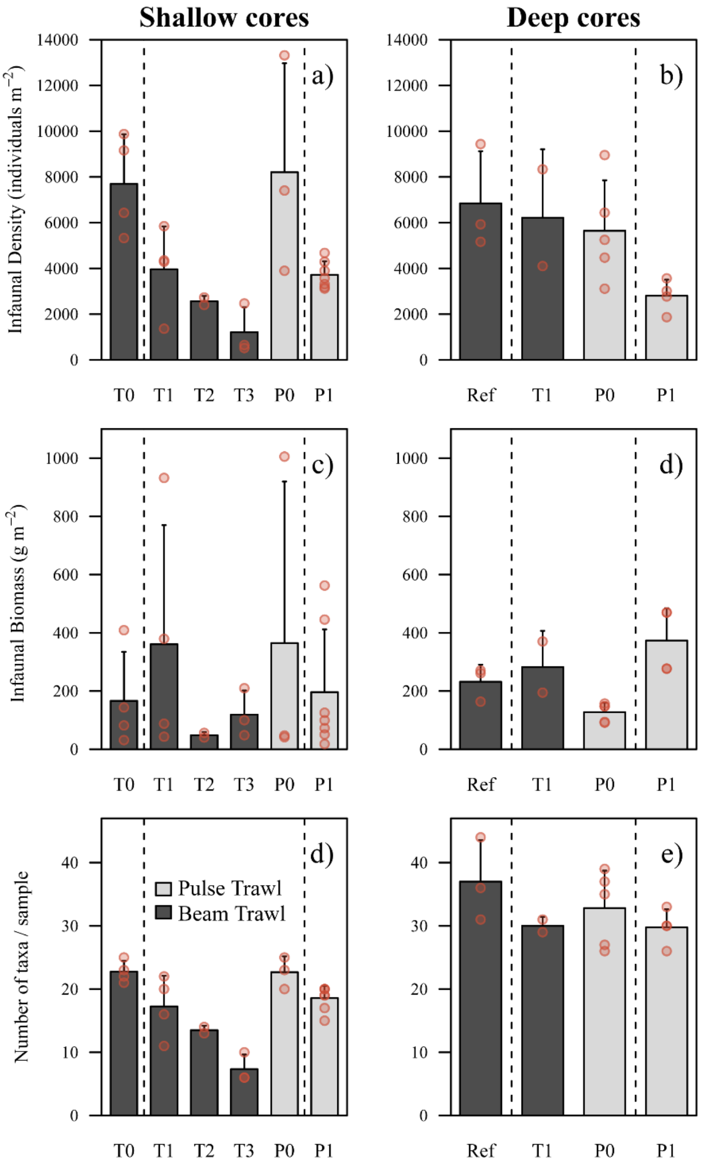


Figure 5. Univariate ecological data collected in shallow cores (a, c, d) and deep cores (b, d, e). Dashed lines indicate the experimental fishing occurrences. Organism densities (individuals per m^2; a, b), infaunal biomass (grams wet weight per m^2; c, d) and taxon richness (number of taxa per sample;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

between trawled and untrawled samples were similar for other univariate parameters ($p > 0.05$, **Figure 5**).

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

Effects on community structure

BCA on shallow and deep cores revealed prominent trawling effects (**Figure 6**). On shallow cores, the effect accounted for 43 % of compositional community variation ($p < 0.001$). Most of the trawling effect was expressed on axis 1, with a gradual ordination of both T and P temporal treatments (**Figure 6**a), characterised by a persistence of *C. subterranea*, in trawled sediments opposed to most other taxon responses (**Figure 6**b). Axis 2 represented differences in treatments T1 and P1, characterised by *Phoronida*, and juvenile *Spatangoida* for the former, and *Amphiura filiformis*, *Lumbrineris cyngulata*, *Oxydromus flexuosus*, *Nucula nitidosa*, and adult *Abra alba* for the latter. On deep cores, the trawling effect accounted for 33.5 % of compositional community variation ($p < 0.01$). Axis 1 mainly separated P1 with the other treatments, while axis 2 slightly isolated P0 from the other treatments (**Figure 6**c). P0 was characterised by strong covariances between juvenile *A. alba* and the polychaetes *Diplocirrus glaucus* and *Scalibregma inflatum* , whereas the reference and T1 samples were more characterised by juveniles of Ophiuroidea and Echinoidea, *Eudorella truncatula,* and *Kurtiella bidentata*. Only three taxa were characteristic of the P1 treatment: *Mediomastus fragilis*, Atherospio and *Parexogone hebes* (**Figure 6**d). **Supplementary Table 4** shows the taxa with the highest and lowest ordination scores for axes 1 and 2 from the BCA analysis for the shallow cores and deep cores.

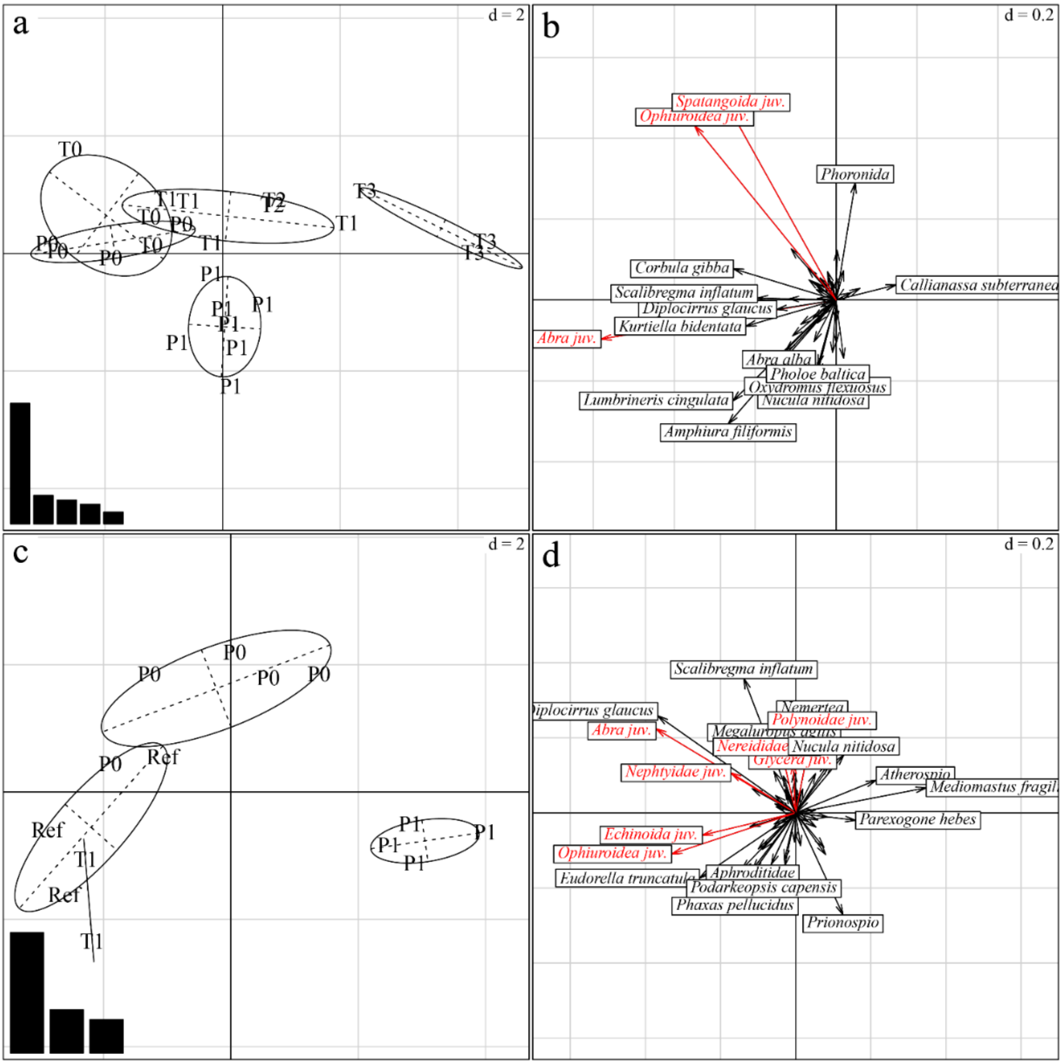


Figure 6. Between-class analysis (BCA) of trawling effects on benthic community structure for shallow cores (top) and deep cores (bottom) including taxon projections (b, d) and associated eigenvalue diagrams showing relative amounts of variation in each axis (a and c bottom left). The first and second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

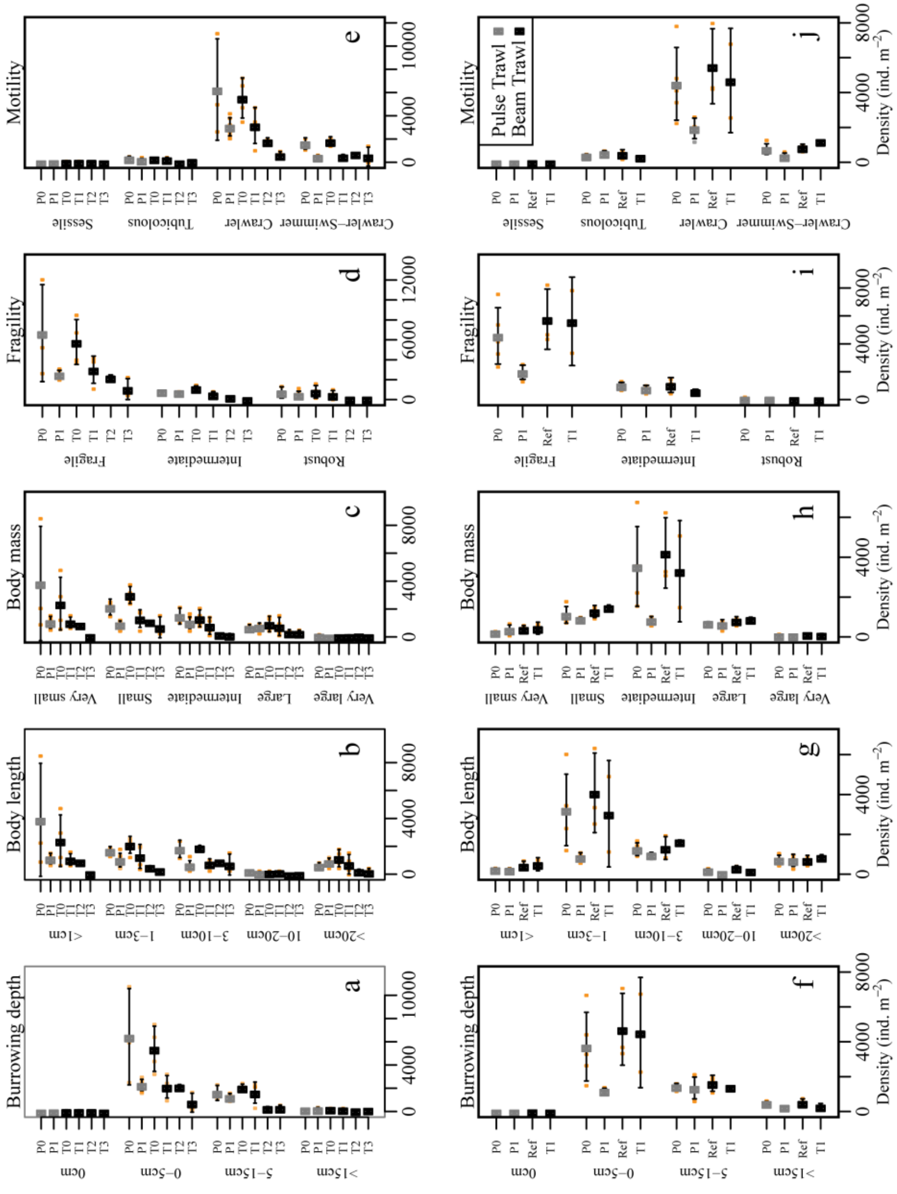


Figure 7. Densities of taxa (individuals per m^2) representing biological traits (burrowing depth, body length, body mass, fragility and mobility) from shallow cores (a – e) and deep cores (f – j). Open symbols represent the pulse trawl treatment while closed symbols represent the beam trawl treatment.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

Treatment effects on biological traits

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

DISCUSSION

It is important to note that the 'untrawled' areas in this study are not necessarily indicative of a pristine marine ecosystem. Hundreds of years of bottom trawling (~150 years intensive) and other types of anthropogenic disturbance in the North Sea make it virtually impossible to find habitats reflecting historical conditions unaffected by human activity (Robinson and Frid, 2008; Coolen, 2017). The findings of this study are, therefore, conservative and the effects of bottom trawling are potentially much greater in pristine habitats (Jones, 1992).

This study achieved our primary objective by using a multi-faceted approach to gain detailed information of bottom trawl effects in the Frisian Front. In spite of uncontrollable logistic constraints which did not allow the use of sonar, SPI, and video after the pulse trawl experiment, we were able to assess the trawling impact on infaunal communities from both beam trawl and pulse trawl fishing methods, which was sufficient for our secondary objective. Better meteorological conditions led to a more comprehensive assessment of BT disturbance. Our results suggest that trawling simplifies the benthic food web by reducing the number of epifaunal organisms and shallow burrowers, in line with the postulated notion of trawl-induced regime shifts occurring in the southern North Sea (Capuzzo et al., 2015; van Nes et al., 2007). The following discusses the results on physical, biological and biogeochemical parameters as interpreted through optical, acoustic and traditional approaches to bottom trawl assessment.

Effect on sediment morphology

The combination of acoustic and optical methods allows the observation of trawl-induced physical changes on different spatial scales. The broad perspective achieved from the side-scan sonar is used to observe the greater extent of trawling impacts (Humborstad et al., 2004; Lucchetti and Sala, 2012; Schwinghamer et al., 2010; Smith et al., 2007). In our study, the sonar information suggested the flattening and homogenisation of the seafloor, and trawl-induced furrows and other three dimensional features were clearly visible in the sonar images. On the other hand, the downward facing video data, gave a higher level of spatial resolution which was vital for assessing biological features (Damveld et al., 2018). SPI information confirmed the flattening effect shown in the sonar analysis by providing details on the surface and subsurface sediment characteristics. Our SPI data differs slightly from Depestele et al., (2018; who conducted a trawl experiment in a nearby site) in that our images featured a distinct layer of fines on the surface of BT impacted sediments (**Supplementary Figure 1**). This is likely due to the shorter time interval between trawling and SPI data collection in our study (~ 2 h) as the longer time frame (~ 12 h) seen in Depestele et al. (2018) may have allowed the removal of the deposited fine material by tidal currents.

Effect on benthic macrofaunal communities

It was decided to keep juvenile taxa in the analysis as they contributed to a substantial proportion of all collected samples (**Supplementary Table 3**). When conducting our BCA without juveniles, the trawling effect accounted for 7.6% less variance in shallow cores and 1.3% less in deep cores compared to the full dataset. As trawling only disturbs the surficial sediment layers (Depestele et al., 2018; Mengual et al., 2016; Palanques et al., 2014; Tiano et al., 2019), its effect on the macrofauna community was more visible in shallow versus deep samples. In particular, the T1 deep core samples showed no strong evidence of trawl disturbance. This may be due to limited representation (2 samples), possibly sampling in areas missed by the BT gear (in the space between the two gears), a dilution effect from having a deeper sample with more unaffected taxa or a combination of these factors (**Figure 6**c).

Nevertheless, we found lower macrofaunal densities and diversity in 5 out of 6 trawled treatments (T1, T2, T3, P1 shallow cores; P1 deep cores) confirming a pattern seen in numerous trawl impact studies using macrofaunal collection methods (Fariñas-Franco et al., 2018; Pranovi et al., 2000; Sciberras et al., 2018). Video technology in trawl impact studies have documented similar decreases in observed epibenthos (Buhl-Mortensen et al., 2016; Collie et al., 2000; Engel and Kvitek, 1998;

Schwinghamer et al., 2010; Smith et al., 2007, 2000; Thrush et al., 1998). We observed a prominent (94 %) reduction in epibenthos between trawled sediments and an untrawled transect 500 m away. Perhaps more telling was the 74% decrease in epibenthos found between trawled and untrawled areas of the same transect. Fauna found in these areas, however, may have been subject to trawl-induced sediment deposition as evidenced by our SPI camera images (**Supplementary Figure 1**). Nevertheless, to our knowledge, this is the first study to record trawl-induced decreases of this magnitude using underwater video. This effect was supported by the reduction of infaunal species densities found in the sediment samples.

Species residing on or near the sediment surface, such as newly settled juvenile infauna, are particularly vulnerable to trawl disturbances. The BCA for both the shallow and the deep cores, linked juvenile *A. alba* and juvenile Ophiuroidea within the top three taxa most affected by trawl disturbance (**Figure 6**, **Supplementary Table 4**). The presence or absence of trawling during important breeding seasons can have significant effects on juvenile survival (Abdul Jaleel et al., 2015). The idea of a regime shift induced by trawling in the Frisian Front from epifauna to burrowing infauna (Amaro, 2005; van Nes et al., 2007) is supported by this study; particularly if the trawling disturbed juvenile settlement during a critical recruitment period.

On the other end of the spectrum, it is generally accepted that older and larger invertebrates show higher vulnerability to trawl disturbance (Thrush et al., 1998; Tillin et al., 2006). This, however, appears contradictory to our findings of increased bottom trawl resilience in certain large macrofauna. This atypical response is driven by the community composition in the Frisian Front and is not expected to hold true in other habitats. High densities of mud shrimps *C. subterranea* and *U. deltaura* in the Frisian Front help explain this phenomenon. These species could have evaded the direct trawl impact in their deeper burrows. Increases in the average weight of individuals from trawled vs. untrawled samples, suggest that smaller taxa were displaced (leaving behind the larger deeper dwelling organisms) and were thus more heavily affected by trawling at our experimental location.

Larger-sized taxa can dilute trawl-induced impacts on community biomass (Hinz et al., 2009) and likely led to the inconsistent patterns in biomass found between treatments in this study. *C. subterranea,* was observed in higher densities in trawled shallow cores where it significantly contributed to the community biomass, (**Figure 6**). This increase may have been caused from the upward movement of the mud shrimps towards the sediment water interface in order to rebuild collapsed burrow entrances. Evidence from our video transect data supports this hypothesis. After an initial trawl-induced reduction in burrow hole density, the subsequent increase from

27 to 50 h after trawling implies the reconstruction of macrofaunal burrow entrances by surviving taxa.

This study did not find evidence of recovery for total macrofaunal densities and taxon richness in BT impacted sediments in the time frame of the investigation. After the initial BT impact (T1), values continued to decline up to 75 h (T3) after disturbance (**Figure 5**a**, 5**e). This prolonged decrease might be explained by increased predation as trawling can create an exploitable food source for benthivores by unearthing damaged macrobenthos, (van Denderen et al., 2013; Groenewold and Fonds, 2000; Mangano et al., 2017). Likewise, benthos found in T1 samples may have already been dead upon collection owing their continued depletion from the area by tidal currents.

Biogeochemical effects

While the effects of trawling on biogeochemistry in these sediments were assessed in Tiano et al. (2019), the present study is able to add new information to this discussion. Tiano et al. (2019) found decreased sediment oxygen demand in trawled sediments. Based on the same samples, the present study did not detect significant patterns for community biomass between treatments and sometimes recorded a higher biomass in trawled sediment samples (**Figure 5**). This suggests that the changed sediment oxygen dynamics in this location may be governed more from microbial patterns than from macrofaunal respiration.

Oxygen penetration and sediment mixing from faunal or anthropogenic sources are factors which influence benthic redox conditions (Teal et al., 2010). The vertical colour change (from light to dark) indicating the aRPD depth, is used as a proxy for sediment oxidation depth (Rhoads and Cande, 1971). Impact assessment studies have linked shallower aRPD depths to increased sediment oxygen demand as this will limit the oxidation of the sediment by reducing the O_2 penetration depth (Badino et al., 2004; Mulsow et al., 2006; Wildish et al., 2003). The trawl-induced reduction of the aRPD found in this study, thus, appeared in contradiction with the increased thickness of the oxic layer and decreased benthic oxygen demand, found in Tiano et al. (2019). Whereas oxygen profiles readjust quickly to altered oxygen consumption rates, it is likely that the aRPD needed a prolonged period in order to re-establish itself to new oxic conditions after disturbance. A visible aRPD is dependent on the amounts of particulate iron oxides in the sediment and has been shown by Depestele et al., (2018) to take over 48 h to re-establish after tickler chain trawling. While the oxygen penetration depth in the Frisian Front is a few millimetres deep (Tiano et al., 2019), the depth of oxidised sediment as shown by the aRPD in this study was found at over

10 cm in untrawled sediments (Figure 4). As the aRPD is often linked with faunal-mediated sediment reworking bringing oxidised sediments to greater depths, the aRPD recovery period may depend on bioturbation to re-establish the iron oxide gradient (Teal et al., 2010).

Implications

Although hampered by logistic constraints, this study allowed some comparison between the impact of two bottom gears (BT and PT) on benthic infauna. Tiano et al. (2019) found a smaller impact from pulse trawls compared to beam trawls on sediment chlorophyll a concentrations and benthic oxygen consumption. On the same samples, we recorded significant effects from both bottom gears on infaunal community composition. Nonetheless, we were not able to properly distinguish whether one method had a larger impact than the other. Bergman and Meesters, (2020) found a lower impact for PT compared to BT when sampling benthic megafauna. Our study, however, focused mostly on smaller as well as deeper dwelling infauna, thereby observing trawl effects on a different species community. Although pulse trawl gears have been linked with lower mechanical disturbance (Depestele et al., 2018, 2016; Tiano et al., 2019) and bycatch rates (van der Reijden et al., 2017; van Marlen, et al., 2014) compared to BT gears, our results show that their direct impact on benthic infaunal communities can be comparable to that of BT in soft sediment ecosystems.

The use of multiple techniques presented a variety of perspectives on which to measure the impact of bottom trawling gears. Sonar and video transect data coupled with more detailed SPI and box core information showed that BT flattens the top layer of sediment while significantly displacing epibenthos and smaller shallow burrowing species. Densities and biomass of deep burrowing taxa seemed relatively unaffected, although some species were probably impacted indirectly. Our study provides evidence of trawl induced behavioural changes prompting burrowing organisms to move closer to the sediment water interface potentially increasing their vulnerability to predation. Collapsed burrow entrances likely hinder burrow ventilation (Witbaard and Duineveld, 1989) and add an increased energetic cost upon the reconstruction of these structures (Rowden and Jones, 1995). The loss of juvenile infauna after both beam and pulse trawling may have implications for the recruitment success of benthic invertebrates.

In light of these findings, we can speculate that trawling in the Frisian Front favoured the proliferation of deep burrowing species while limiting the recruitment and abundances of macrofauna at or closer to the sediment surface. This possibility was mentioned as a potential trigger behind the shift from an *A. filiformis* to a *C.*

subterranea dominated benthic community in the Frisian Front (Amaro, 2005; van Nes et al., 2007). Here we provide experimental results supporting this proposed mechanism, adding details on how human activities can affect benthic ecosystems.

Acknowledgements

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

Supplementary material for: Chapter 3

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

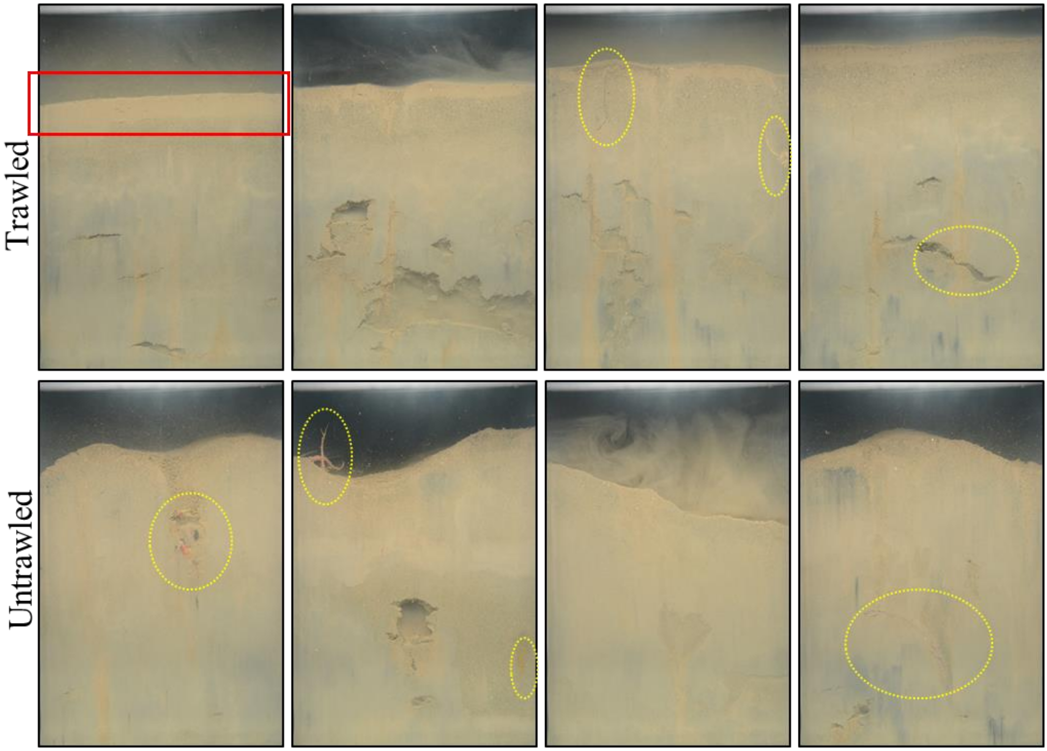


Figure S1. An assortment of sediment profile images (SPI) displaying beam trawled sediment (top) compared with images from an untrawled reference area (bottom). The red box highlights the characteristic fine sediment layer found in beam trawled images. Infauna from the images are circled in yellow.

Table S1
Biological traits and modalities

Biological Trait	Modality
Burrowing Depth	0 cm
	0 – 5 cm
	5 – 15 cm
	> 15 cm
Burrowing Depth	< 1 cm
	1 – 3 cm
	3 – 10 cm
	10 – 20 cm
	> 20 cm
Body Mass	Very small
	Small
	Intermediate
	Large
	Very Large
Fragility	Fragile
	Intermediate
	Robust
Motility	Sessile
	Tuberculous
	Crawler
	Crawler – Swimmer

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

Parameter	Time step	Disturbance	Observer 1	Observer 2	*n*	p-value
Epibenthos Density	~ 27 h	*Trawled*	0.70 ± 1.79	0.51 ± 0.9	41	**<0.0001**
		Untrawled	2.28 ± 4.42	2.46 ± 5.1	288	
	~ 50 h	*Trawled*	1.91 ± 2.95	1.59 ± 3.2	293	
		Untrawled	3.80 ± 6.44	2.19 ± 4.2	95	**<0.0001**
Hole Density	~ 27 h	*Trawled*	112.2 ± 36.3	62.6 ± 27.6	41	**<0.0001**
		Untrawled	112.3 ± 40.1	80.4 ± 31.3	288	
	~ 50 h	*Trawled*	128.8 ± 37.8	109.2 ± 52.6	293	0.68
		Untrawled	131.0 ± 31.6	133.2 ± 202.4	95	
Hole Size	~ 27 h	*Trawled*	0.0006 ± 0.0003	0.0006 ± 0.0003	41	**0.002**
		Untrawled	0.0009 ± 0.0004	0.0007 ± 0.0004	288	
	~ 50 h	*Trawled*	0.0008 ± 0.0004	0.0008 ± 0.0004	293	0.67
		Untrawled	0.0005 ± 0.0004	0.0006 ± 0.0003	95	
Hole coverage	~ 27 h	*Trawled*	0.07 ± 0.03	0.04 ± 0.02	41	**<0.0001**
		Untrawled	0.10 ± 0.04	0.05 ± 0.04	288	
	~ 50 h	*Trawled*	0.10 ± 0.04	0.05 ± 0.04	293	**0.005**
		Untrawled	0.10 ± 0.04	0.08 ± 0.12	95	

Table S3
Mean individual densities of juvenile *Abra alba* and Ophiuroidea per sample per m^2

Station	Shallow cores	
	Abra juv.	*Ophiuroidea juv.*
P0	3683.0	1126.6
P1	993.5	241.4
T0	2161.1	1462.4
T1	942.4	357.5
T2	844.9	649.9
T3	0	433.3

Station	Deep cores	
	Abra juv.	*Ophiuroidea juv.*
P0	2700.6	382.2
P1	396.3	127.4
Ref	3543.3	509.5
T1	2809.6	990.8

Table S4.
Top five highest and lowest ordination scores for taxa for Axis 1 (x-axis) and Axis 2 (y-axis) from the Between-Class Analysis (BCA) from shallow subcore and deep boxcores. Scores correspond to the location of the different treatments (T0, T1, T2, T3, P0, P1, Ref) in the BCA ordination plots.

Shallow cores

Taxa with *lowest* ordination scores	**Axis 1**	Taxa with *highest* ordination scores	**Axis 1**
Abra alba juveniles*	-0.58	*Callianassa subterranea*	0.15
Ophiuroidea juveniles*	-0.35	*Gyge branchialis*	0.06
Amphiura filiformis	-0.27	Phoronida	0.05
Spatangoida juveniles*	-0.26	Bopyroidea	0.04
Lumbrineris cingulata	-0.25	*Ione thoracica*	0.04

Taxa with *lowest* ordination scores	**Axis 2**	Taxa with *highest* ordination scores	**Axis 2**
Amphiura filiformis	-0.31	Spatangoida juveniles*	0.47
Lumbrineris cingulata	-0.25	Ophiuroidea juveniles*	0.43
Nucula nitidosa	-0.21	Phoronida	0.29
Oxydromus flexuosus	-0.18	*Tellimya ferruginosa*	0.13
Pholoe baltica	-0.16	*Corystes cassivelaunus* juveniles*	0.12

Deep cores

Taxa with *lowest* ordination scores	**Axis 1**	Taxa with *highest* ordination scores	**Axis 1**
Abra alba juveniles*	-0.37	*Mediomastus fragilis*	0.35
Diplocirrus glaucus	-0.37	Atherospio	0.21
Ophiuroidea juveniles*	-0.33	*Parexogone hebes*	0.16
Eudorella truncatula	-0.257	*Nucula nitidosa*	0.13
Echinoida juveniles*	-0.25	Prionospio	0.13

Taxa with *lowest* ordination scores	**Axis 2**	Taxa with *highest* ordination scores	**Axis 2**
Prionospio	-0.27	*Scalibregma inflatum*	0.36
Phaxas pellucidus	-0.22	*Diplocirrus glaucus*	0.26
Podarkeopsis capensis	-0.18	*Abra alba* juveniles*	0.22
Eudorella truncatula	-0.17	Nemertea	0.21
Aphroditidae	-0.15	Polynoidae juveniles*	0.21

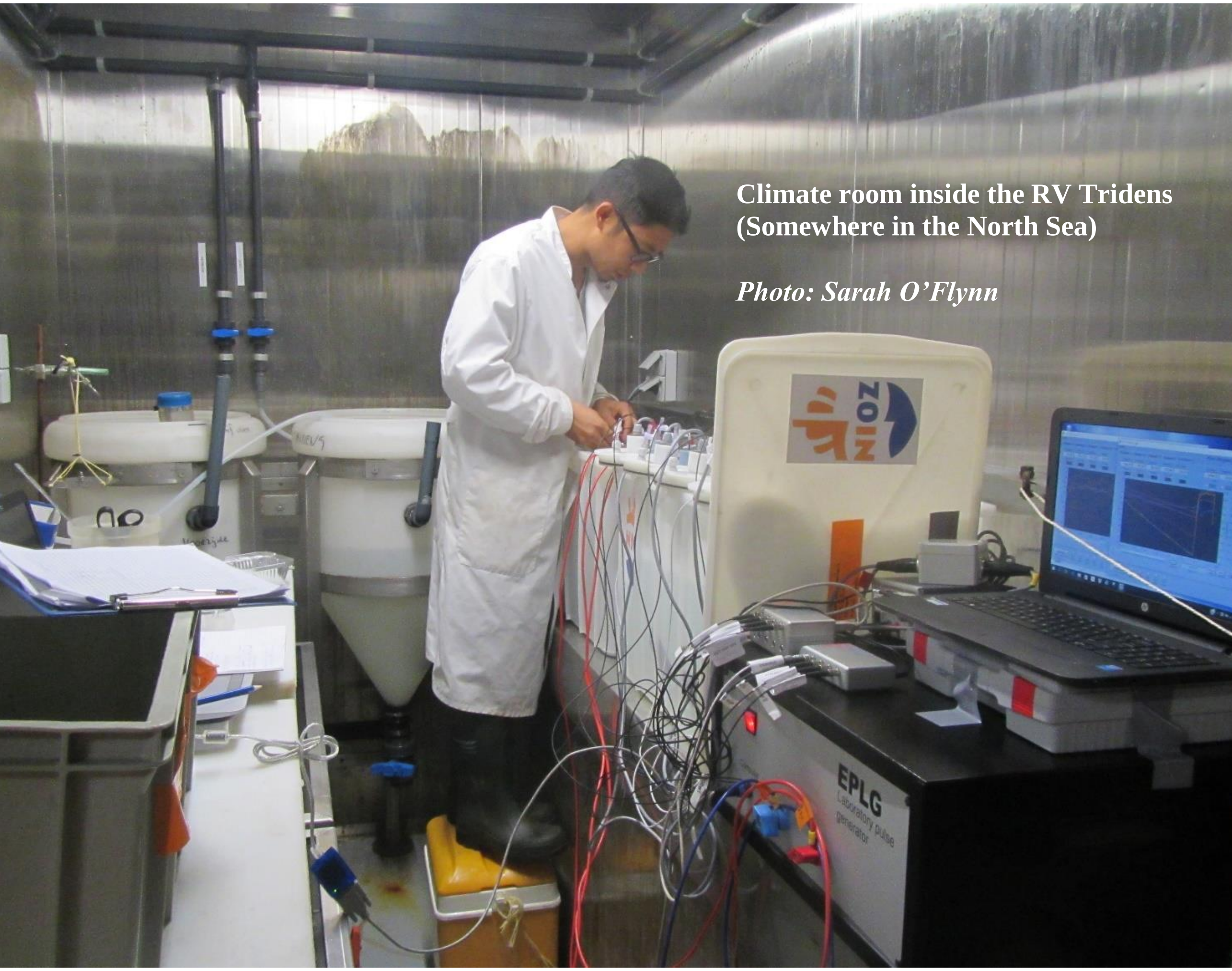
* indicates juvenile taxa

Chapter 4

Impacts of anthropogenic sediment mixing and electrical perturbations on sediment biogeochemistry

Submitted

Justin C. Tiano, Emil De Borger, Sarah O’Flynn, Chiu H. Cheng, Dick van Oevelen, Karline Soetaert



Climate room inside the RV Tridens (Somewhere in the North Sea)

Photo: Sarah O’Flynn

Abstract

This study experimentally isolated the physical and electrical stimuli used in marine electro fisheries to evaluate their impact on biogeochemistry and nutrient cycling of the seafloor and bottom water. Experiments were conducted on sediment samples taken from 9 North Sea and 2 Eastern Scheldt locations. Samples were subjected to either physical stress by mechanically stirring the sediment surface or electrical stimulation with exposure to high frequency pulsed bipolar (PBC) or direct (PDC) currents. Electrical exposure times of 3 and 120-seconds were used to simulate in situ exposure times related to sole (*Solea solea*) and razor clam (*Ensis spp.*) electric fisheries respectively. Physical stress caused a rapid decline in water column oxygen of the incubation cores, inducing an immediate uptake ranging from 0.55 to 22 mmol oxygen per m^{-2} of sediment resuspended. Mechanical perturbations directly released the equivalent of up to 94 and 101 hours of natural ammonium and silicate effluxes respectively. Fresh organic material and sediment grain size significantly predicted the magnitude of mechanical-induced oxygen, ammonium, phosphate and silicate changes. No effects of PBC (3s or 120s) or 3-second PDC exposure on oxygen or nutrient fluxes were detected. However, significant changes to these parameters were induced by 120-second exposures to PDC due to electrolysis and ionic drift. This led to lower water column pH (1-1.2) and the appearance of iron oxides on the sediment surface, resulting in the equivalent of 25.2-28 hours of sedimentary phosphate removal. Our findings demonstrate that prolonged (+1 min) high frequency PDC or continuous direct currents can cause electrochemical effects in the marine environment, with implications for phosphorus cycling. Nevertheless, bi-directional pulsed currents employed in flatfish pulse trawling and AC currents commonly used in the *Ensis* electrofishery, severely limit this effect. Mechanical disturbance, on the other hand, causes a much greater impact on benthic pelagic coupling, the extent of which depends on sediment grain size, organic matter content, and the time of the year when it occurs.

Keywords: Electrofishing, pulse trawling, mechanical disturbance, biogeochemistry, ecosystem functioning, oxygen dynamics, benthic impacts

INTRODUCTION

In addition to the electricity generated through electrophysiological adaptations by organisms such as the electric eel (*Electrophorus electricus*), electric fields take place naturally in marine environments and are occur in sediments with electrogenic microbial organisms (Burdorf et al., 2016). The electrical activity produced by these organisms can induce significant biogeochemical changes to benthic ecosystems and can alter sedimentary nutrient dynamics (Rao et al., 2016; Sulu-Gambari et al., 2016). Humans also use electrolysis to manipulate biogeochemistry for activities such as the production of chemical compounds, the removal of organic carbon from wastewater, and the precipitation of minerals for coral reef restoration (Peixoto et al., 2013; Goreau, 2012). Not much is known, however, about the unintended environmental impacts of anthropogenic electrolysis in the marine environment (Soetaert et al., 2015).

In recent years, fishermen have been experimenting with electrical methods used to exploit commercially important species in the North Sea (Soetaert et al., 2015; Haasnoot et al., 2016). While electric fishing methods have been widely used (mainly for scientific purposes) since the 1950’s (Vibert, 1963), the large-scale introduction of electric pulse trawling in Europe created much controversy due to its perceived negative impact on marine ecosystems (Kraan et al., 2020). When applied for catching common sole (*Solea solea*), electrodes are used to immobilize flatfish, allowing their capture in a net that drags along the seabed (Soetaert et al., 2015). This method typically uses rapid pulses of alternating polarities called pulsed bipolar currents (PBC; Soetaert et al., 2019). Another electrofishing method uses slow moving electrodes to stimulate razor clams (*Ensis spp.*) out of their burrows, permitting their collection by divers (Murray et al., 2016). Fishermen using this technique have employed both continuous alternating (AC) and direct (DC) currents (Woolmer et al., 2011; Murray et al., 2016). While exposure time of a given point on the seafloor is just over 1 second for a pulse trawl, sediments are exposed for over 1 minute using *Ensis* electrofishing methods. Apart from the animal welfare related risks, the potential consequences of electrolysis-induced chemical changes is a source of concern (Soetaert et al., 2015). As pulse trawl-induced electric fields easily penetrate the water-logged marine sediment (de Haan and Burggraaf 2018), a biogeochemical response may occur from both the seafloor and the water column. Electrical fields in the marine environment have been associated with changes to solute fluxes, and the mobilisation of porewater ions (Nielsen et al., 2010; Rao et al., 2016). Presently, however, there are only two published studies which include the biogeochemical effects from electric pulse trawling; neither of which separates electrical and mechanical impacts (Tiano et al., 2019; Depestele et al., 2018). It is not yet known if or how the electric fields from electrofishing methods affect biogeochemical processes.

Alongside the electrical disturbances, pulse trawling also causes sediment mixing and resuspension from the mechanical impact of their gear and bottom nets (Tiano et al., 2019). Disturbance-induced sediment resuspension causes the rapid fluxes of solutes through the direct release of nutrient rich porewater and increased desorption and mineralisation processes (Couceiro et al., 2013). Depestele et al., (2018) found a more variable but lower average seabed penetration from pulse trawls (1.8 cm) compared to standard tickler chain rigged trawls (4.1 cm). While the penetration of fishing gears has been linked to higher organism mortality (Hiddink et al., 2017), their effects on biogeochemical parameters are still understudied (Tiano et al., 2019).

This study aims to isolate the electric and mechanical effects from marine electrofishing methods on benthic pelagic coupling. We investigate if and how pulsed electric currents affect benthic biogeochemistry and nutrient cycling and identify which electrical parameters are necessary to generate such a response. Alongside, we determine the factors, such as sediment grain size and/or organic matter content, that best predict the magnitude of biogeochemical changes caused by disturbances. While providing new information about mechanical-induced sediment resuspension, our study is the first to document biogeochemical effects from electrical exposure by marine electrofishing.

MATERIALS AND METHODS

Study Area

Benthic sediment samples were collected from 9 locations in the North Sea (stations 1-9) and two locations from the Dutch Eastern Scheldt (stations 10-11, **Figure 1**). Sediments from stations 6 and 7 were silty with a median grain size (D50) under 62.5 µm. Sediment from stations 4, 8, 9 and 11 were defined as ‘very fine sand’ (D50 = 62.5-125 µm). Fine sand (125-250 µm) characterised stations 1, 2, 5 and 10. Station 3 had the coarsest sediment with D50 sizes that ranged between medium (250-500 µm) and coarse (500-1000 µm) sand. Stations 6 and 7 were taken from the greatest water depths (144 and 132 m) while the depths of other North Sea stations ranged between 26 and 77 m (**Table 1**). Eastern Scheldt stations (10 – 11) were collected from the intertidal zone.

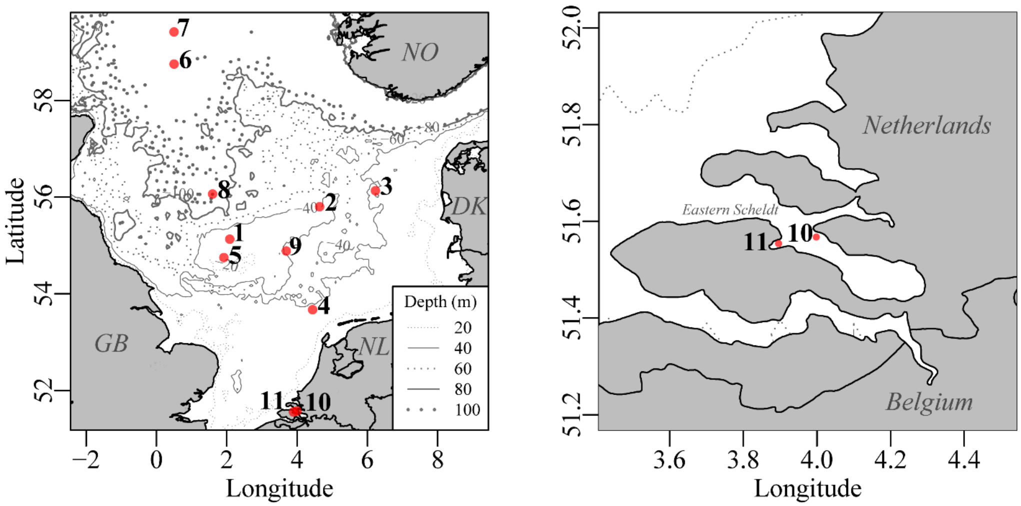


Figure 1. Red dots show the locations of stations 1-11 in the North Sea (left). Close-up of Eastern Scheldt locations (red dots) for stations 10 and 11 (right).

Sample collection

Intact sediments from North Sea stations were collected using a NIOZ box corer with an internal diameter of 32 cm and a height of 55 cm. Stations 1-3 were visited with the RV Tridens in August-September 2017. The RV Pelagia was used to collect samples from station 4 in November 2017 and from stations 5-9 in May 2018. Box core sediment samples were subsampled using cylindrical PVC incubation cores (14.5 cm diameter x 30 cm height). Using incubation cores of the same dimensions, we collected sediment from intertidal locations in the Eastern Scheldt estuary for stations 10 and 11 in October 2018. To control for unpredictable faunal responses to the 2-minute electrical exposures featured only at stations 10 and 11 (see section: *Electrical disturbance treatments*), sediments from the Eastern Scheldt stations were sieved (1 mm) and reconstituted to remove macrofauna (also for non-electrocuted cores to maintain consistency) prior to experimental measurements (**Table 1**). This was only conducted for stations which received the longer (2 minute) electrical exposure periods and not for the other stations (1 – 9) where the faunal response to electricity was thought to be less consequential due to their lower exposure time (3 seconds).

Cores containing sediment and overlying water from stations 1-3 and 5-9 were placed in water baths inside a climate controlled (12°C) chamber on board the research

Table 1.
Sampling date, coordinates and average environmental parameters between stations for depth (m), median grain size (D50; µm) % organic carbon, sediment chlorophyll *a* content (µg g^{-1}), macrofauna densities (individuals m^{-2}), macrofaunal biomass (grams wet weight m-^{2}), and biogeochemical fluxes (mmol m^{-2} d^{-1}). Nutrient flux measurements represent rates taken before experimental perturbations.

									Fluxes (mmol m^2 d^{-1})					
ST	Date	Position (N,E)	Depth	D50	OC	Chl *a*	Density	Biomass	O_2	NH_4^+	NO_2^-	NO_3^-	PO_4^{3-}	$Si(OH)_4$
1	30/08/2017	55° 7.8, 2° 5.1	34.3	240.5	-	-	504	1.2	-9.1	0.06	0.001	0.06	0.01	0.05
2	07/09/2017	55° 48.1, 4° 38.5	42.5	173.5	-	-	4387	48.8	-25.2	0.99	0.02	0.19	-0.04	2.31
3	09/09/2017	56° 7.9, 6° 13.8	42.4	475.2	-	-	2288	6.4	-9.3	0.37	-0.07	0.51	-0.04	0.34
4	08/11/2017	53° 40.3, 4° 26.5	34.0	87.9	0.4	2.8	1261	38.4	-12.7	<-0.01	-0.04	0.08	<-0.01	0.57
5	25/05/2018	54° 45, 1° 55	26.8	216.9	0.1	0.7	1677	10.3	-5.4	0.70	0.1	0.01	0.01	0.03
6	27/05/2018	58° 45.1, 0° 30.1	144.6	24.7	1.1	1.1	1092	15.5	-11.1	-0.52	-0.1	0.36	<-0.01	1.22
7	30/05/2018	59° 25, 0° 29	132.6	55.1	0.6	0.4	4991	214	-10.6	0.06	-0.1	0.48	0.04	1.62
8	01/06/2018	56° 3.9, 1° 35.8	77.5	212.9	0.2	0.3	7591	66.5	-9.1	0.38	0.06	0.34	0.02	1.22
9	03/06/2018	54° 53.1, 3° 41.6	41.2	124.6	0.2	0.8	858	7.3	-11.3	0.28	0.03	0.21	-0.03	0.90
10*	04/10/2018	51° 34.6, 3° 59.9	0.0	138.2	0.1	4.1	0*	0*	-15.6	2.60	0.29	-0.15	-0.09	0.34
11*	10/10/2018	51° 33.5, 3° 53.7	0.0	75.5	0.6	10.7	0*	0*	-15.9	3.99	0.48	-0.54	-0.05	1.12

*sediment at intertidal stations 10 and 11 were sieved of macrofauna prior to experimental measurements vessels for 6 h prior to the first incubation. For station 4, samples were transported from Texel, Netherlands to the NIOZ facility in Yerseke, Netherlands. For stations 10 and 11 samples were transported from the Eastern Scheldt intertidal flats (Netherlands) to the NIOZ facility (transport = ~5 h for station 4, ~1 h for stations 10 and 11). After arrival at the research institute, sediments from stations 4, 10 and 11 were acclimatised for 48 h inside buffer tanks within climate-controlled chambers, with the temperature representative of environmental conditions at the time of collection (12°C for station 4; 18°C for stations 10, 11). The longer acclimatisation period allowed time for biogeochemical gradients to re-establish in the post-sieved sediments at stations 10 and 11 and for station 4 sediments to re-adjust to constant conditions after exposure to fluctuating temperatures during transport.

Electrical parameters used

Sediment from all stations were subjected to a pulsed bipolar current (PBC) treatment, exhibiting both positive and negative electric pulses. Bipolar pulsed waveforms are similar to pulsed alternating currents (PAC), however, with PAC the reversal of pulses is almost immediate while PBC is characterised by a similar time gap between positive and negative pulses and is slightly easier to generate for electronic systems (Soetaert et al., 2019; **Figure 2**, top left panel). Stations 10 and 11 included a pulsed direct current (PDC) treatment characterised by unidirectional pulses (**Figure 2**, top left panel). High frequency PDC is generally avoided as it causes corrosion of the electrodes but continuous DC has been used with electrofishing for the bivalve *Ensis* (Woolmer et al., 2011). Square shaped pulses exhibiting a width (PW) of 0.33 ms, were used for both PBC and PDC waveforms. PBC treatments featured a frequency of 40 Hz (40 unique pulse cycles per second) while PDC treatments exhibited an 80 Hz frequency (Soetaert et al., 2019). To clarify, both waveforms presented 80 pulses per second but the PBC pulse displayed 40 positive and 40 negative pulses while all PDC pulses were positive (**Figure 2**).

For each core exposed to electrical currents, two plate-shaped stainless steel electrodes were used to generate a homogenous electric field (Soetaert et al., 2016; Soetaert et al., 2019; **Figure 2**). A field strength of 200 volts per meter (V m^{-1}) was created in the sediment and water column between the electrodes for PBC treatments to represent the electrical field close to the electrode from a flatfish pulse trawler. The weakest possible field strength allowed by our pulse generator for electrodes 20 cm apart (125 V m^{-1}) was used for PDC treatments to be more representative of *Ensis* electrofishing parameters (**Figure 2**). All electrical perturbations were carried out using a laboratory pulse generator (EPLG bvba, Belgium) using 2 m by 6 mm^2 wires which extended directly from the generator to the electrodes. To check for any loss in voltage from the generator to the electrodes, the exact electrical parameters were checked using an oscilloscope (DSO5014A, Agilent Technologies).

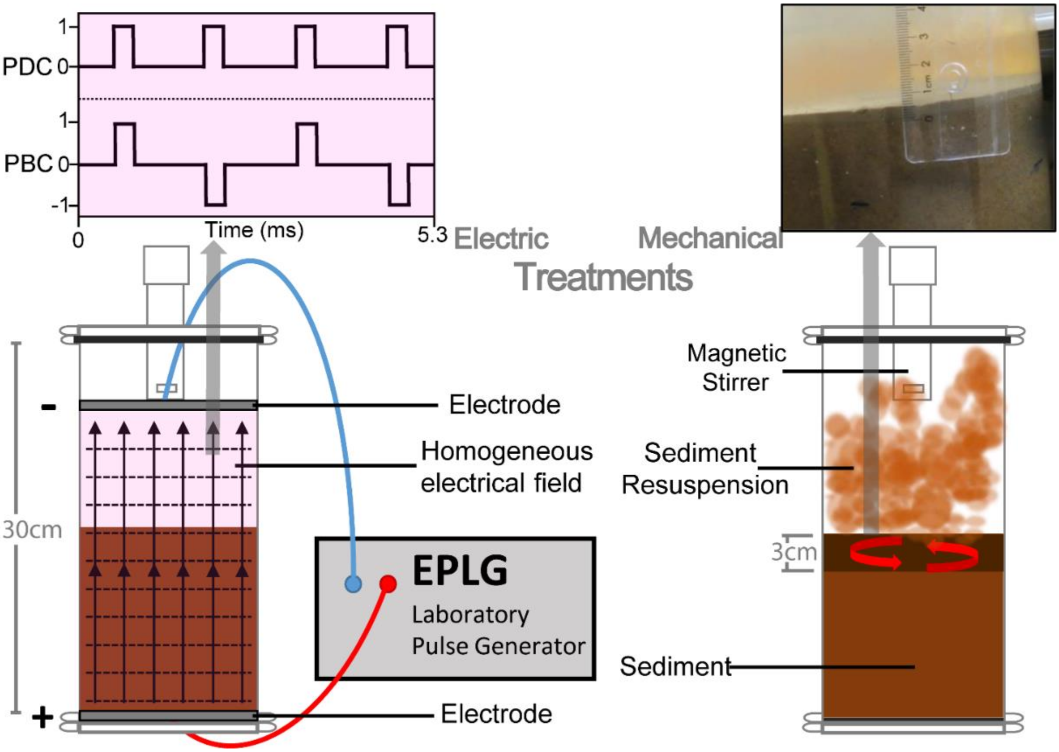


Figure 2. Experimental setup: Electrical disturbance treatment setup showing the homogeneous electrical field between the electrodes with black arrows representing the pulsed flow of electrons and dashed lines representing equipotentials (zones with the same electrical potential; *left*). Characteristic positive pulses for pulsed direct current treatments (PDC) and alternating positive and negative pulses for the pulsed bipolar treatments (PBC; *top left*). Mechanical disturbance treatment (*right*) with example of sediment-water interface after disturbance (*top right*).

Experimental setup

To investigate the impact of electrical and mechanical disturbances, BACI (Before-After-Control-Impact) design experiments were conducted for all sampled locations. **Figure 2** and **Figure 3** help illustrate our somewhat complicated experimental design.

Mechanical disturbance treatments

Stations 3 to 11 received a mechanical disturbance treatment (‘Mix’; **Table 2**). Logistic constraints onboard the RV Tridens limited the amount of samples taken for stations 1 and 2, which prevented the Mix treatment from taking place at those stations. To simulate trawl-induced mechanical mixing and sediment resuspension, a handheld electric mixer homogenised surface sediments inside incubation cores down to a depth of 3 cm (**Figure 2**). A 3-second perturbation period is slightly higher than the *in situ* disturbance time needed for a bottom trawl gear to pass over a given point in the sediment at 5 knots (~ 1.4 s; de Haan et al., 2016). This slight overestimate, however, was necessary for the mixer to homogenise the total surface area of the sediment core.

Electrical disturbance treatments

Stations 1 – 11 featured a PBC treatment while stations 10 and 11 received additional PDC treatments (**Table 2**). For cores undergoing electrical exposure, an electrode was fitted to the bottom of the incubation core underneath the sediment column (during sediment collection; **Figure 2**). Upon opening the cores after pre-disturbance incubations (see section: *Post-disturbance incubations*), a second electrode was lowered into the water column of the incubation core and suspended 20 cm above the first electrode before the electrical perturbation was applied (**Figure 2**). Similar to mechanical disturbance, 3-second electrical perturbations represented trawl exposed (pulse trawl in this case) sediments (‘3sPBC’ and ‘3sPDC’) while 120-second exposure times (‘120sPBC’ and ‘120sPDC’) were used to simulate the exposure periods found in the *Ensis* electrofishery for stations 10 and 11 (Murray et al., 2016). The longer exposure times and Ensis electrofishery comparison were planned and implemented at a later stage in the study and were not included for stations 1 – 9.

Division of cores for experimental treatments

For individual treatments, three experimental cores and a single undisturbed control core were used per location sampled (**Table 2**). In total, data from 22 undisturbed control cores were compared with cores from experimental treatments. Thirty-three cores were exposed to 3sPBC and 27 other cores were subjected to the Mix treatment.

For stations 10 and 11, all experimental cores were subjected to two rounds of disturbances 24 h apart (**Figure 3**, *right*). This was conducted to observe possible differences between the first and second perturbations. Six experimental cores

Table 2.
Number of incubation cores for each station.

Station	Number of cores per treatment
1	3 PBC, 1 Control
2	3 PBC, 1 Control
3	3 PBC, 3 Mix, 2 Controls
4	3 PBC, 3 Mix, 2 Controls
5	3 PBC, 3 Mix, 2 Controls
6	3 PBC, 3 Mix, 2 Controls
7	3 PBC, 3 Mix, 2 Controls
8	3 PBC, 3 Mix, 2 Controls
9	3 PBC, 3 Mix, 2 Controls
10	3 PBC, 3 PDC, 3 Mix, 3 Controls
11	3 PBC, 3 PDC, 3 Mix, 3 Controls

(separate from the PBC and Mix treatments) were used for 3sPDC and 120sPDC exposures conducted on the following day (**Figure 3**; **Table 2**). The same procedure was carried out for PBC cores (3sPBC and 120sPBC). The 6 Mix cores at these stations were mechanically disturbed for 3-seconds on both perturbation days (*DAY 2 and 3*; **Figure 3**) to observe possible differences between first and second mechanical disturbance events (**Figure 3**; **Table 2**).

Pre-disturbance incubations

Prior to the first incubation, overlying water was carefully added to each core before an initial (T0) 10 mL water sample for nutrients was taken and stored in a polystyrene vial (**Figure 3**). For stations 1-9, the overlying water in the cores was aerated overnight and a water sample (T1) was taken in the morning (**Figure 3**, left). The cores were subsequently sealed from air contact and a 4 h 'oxygen incubation' was conducted to measure natural oxygen fluxes before experimental perturbations. Oxygen concentrations in the overlying water were measured at an interval of 30 seconds with optode sensors (FireStingO_2, Pyroscience). Core lids were fitted with a stirring mechanism that ensured homogenous concentrations of nutrients and O_2 in the overlying water of the sediment cores (**Figure 2**). Upon reopening the cores after

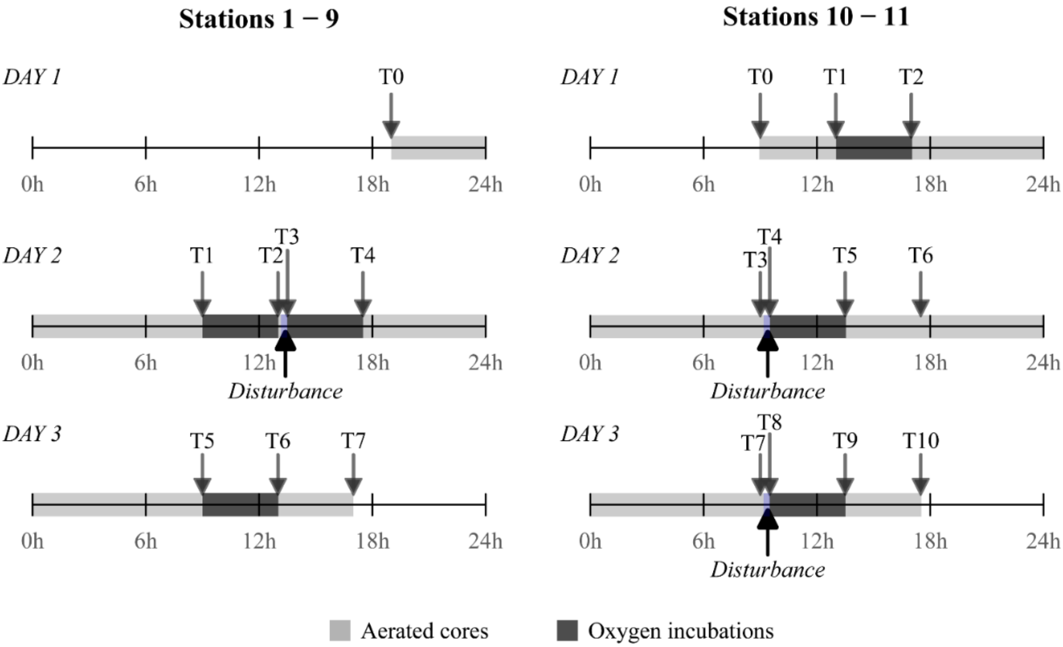


Figure 3. General sampling scheme for stations 1-9 (left) and stations 10-11 (right). Downward facing arrows arrows represent water sample timesteps. Upward facing arrows represent disturbance times.

the initial incubation, water samples were taken for nutrient analysis and the cores were aerated until O_2 saturation levels reached >95 percent. For stations 10-11, pre-disturbance incubations occurred during the first day allowing additional water sampling timesteps for *DAY 1* (**Figure 3**, *right*).

Post-disturbance incubations

After pre-disturbance measurements, experimental cores were subjected to either electrical (3sPBC, stations 1 – 11; 3sPDC, stations 10 and 11) or mechanical (Mix, stations 3 – 11) treatments (Fig 3, *DAY 2*). Immediately after the disturbance treatments, a water sample was taken and cores were sealed for a post-disturbance O_2 incubation (**Figure 3**). Cores were reopened after 4 h and water samples were taken. On *DAY 3*, experimental cores underwent an additional oxygen incubation (stations 1-9) or a second round of experimental treatments (stations 10 and 11; **Figure 3**). For stations 10 and 11, sediments were exposed to 120sPBC, 120sPDC and a second Mix treatment 24 h after the first perturbations. Oxygen and nutrient measurements continued, as previously described, for 8 h after the second perturbations. Control cores were subject to the same sampling/oxygen incubation schedule without the disturbance events.

Core and sample processing

After the experimental treatments, incubation cores from stations 1-9 were rinsed over a 1 mm mesh sieve to collect macrofauna and assess their contribution towards sediment fluxes. Faunal samples were preserved in 4% formalin seawater prior to analysis. Individual macrofauna were sorted and identified (lowest possible taxon) before obtaining measurements for biomass (blotted wet weights) and macrobenthos densities.

All water samples were filtered (0.45 µm mesh) and were frozen (-20°C) in 10 mL vials prior to analysis. After thawing, a SEAL QuAAtro segmented flow analyser (Jodo 1992) was used to determine inorganic nutrient concentrations. Oxygen (O_2), ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), phosphate (PO_4^{3-}) and silicate ($Si(OH)_4$) fluxes were estimated by fitting a regression of the concentration change over time, and then multiplying with the height of the overlying water column to convert to aerial fluxes in mmol (or absolute pH changes) m^{-2} d^{-1}. Solute fluxes were measured by separate regressions of the data before and after perturbations. The pH values in the overlying water of the incubation cores were measured for stations 10 and 11 with a Radiometer PHM120 Acid-Base-Analyser (electrode VWRJJ113). Treatment-induced changes in solute concentrations and pH were estimated as the difference between pre and post disturbance values.

To calculate the natural flux equivalents of the treatment-induced concentration changes (ex. treatment caused the equivalent of 20 h of natural O_2 fluxes), the treatment-induced concentration change was divided by the 'natural flux' (fluxes measured before perturbation treatments) of the sediments.

Sediment parameters

Data was collected for grain size characteristics for surface (0-5 cm) sediments in stations 1 – 9 with a cut-off syringe (20 mL). Favourable logistics for experiments using samples from stations 10 and 11 allowed for a more thorough analysis of sediment characteristics. For these stations, smaller cores (3.5 cm diameter) were used to subsample sediment from incubation cores at the end of the experiments. From these subcores, vertical sediment slices (0-1, 1-2, 2-3, 3-5, 5-7, 7-10 cm) were collected for particle size analysis. Samples were placed in a -20°C freezer shortly after collection. All samples were freeze dried and run through a 1 mm sieve prior to analysis. A Malvern Mastersizer 2000 was used for particle size analysis via laser diffraction (McCave, 1986). Sediments from stations 4 – 11 were measured for organic carbon (OC), total nitrogen (TN) and chlorophyll (chl a). An Interscience Flash 2000 organic element analyser was used to determine OC and TN content. Acetone (90 %) was used to extract Chl a pigments from freeze-dried sediments and analysed using UV spectrophotometry (Ritchie, 2006).

Statistical Analysis

Measurements taken before disturbance were assumed to be the most representative for the natural in-situ situation as environmental conditions in the sediment cores may change temporally even with acclimatization periods. After disturbances, experimental cores were compared with control cores. Biogeochemical flux rates measured before disturbances were compared with disturbance-induced changes to absolute solute concentrations to estimate the time needed for natural fluxes to equal the instant perturbed fluxes. The assumptions for parametric data (normal distribution/homogeneity of variances) were tested for with Shapiro-Wilk (normality) and Levene’s tests (homogeneity). Data were log-transformed, to improve on violations of the assumptions if needed. Significant differences for pH/solute (O_2, NH_4^+, NO_2^-, NO_3^-, PO_4^{3-} $Si(OH)_4$) fluxes and treatment-induced concentration changes were determined using a one way analysis or variance (ANOVA) to compare differences in the means between treatment groups (control, PBC, PDC, Mix). If a significant difference was found, Tukey HSD tests were conducted to evaluate pairwise comparisons. Robust regressions were used to investigate the relationship between sediment parameters (grain size, OC, TN, Chl a) and changing pH/solute concentrations and fluxes. This type of regression places lower weights on outliers and is less affected by violations of linear regression assumptions (Koller and Stahel 2011). All statistical analyses and data visualisation were carried out using R (R Core Team 2014).

RESULTS

Natural biogeochemical fluxes

O_2 consumption before experimental treatments was highest at station 2, followed by the intertidal stations 10 and 11 (**Table 1**). NH_4^+ effluxes were the highest in the intertidal (>2.6 mmol m^{-2} d^{-1}) while all other stations averaged under 1.0 mmol m^{-2} d^{-1}. NO_3^- effluxes were the highest in the coarsest sediments (station 3) but displayed a negative flux (directed into the sediment) at intertidal locations. PO_4^{3-} exhibited a negative flux for 7 out of 11 locations and showed small effluxes for stations 1, 5, 7

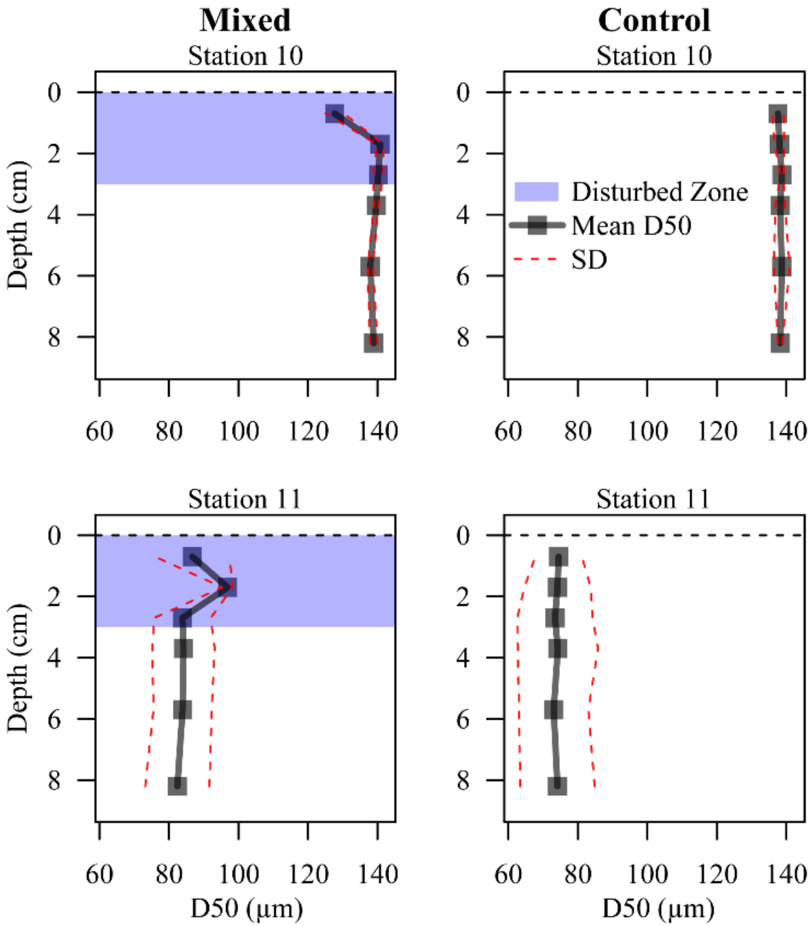


Figure 4. Sediment median grain size (D50) profiles showing mechanically disturbed and control cores from stations 10 and 11.

and 8. Natural $Si(OH)_4$ flux was highest at station 2 and lowest at station 5 which displayed low fluxes for all nutrients.

Faunal parameters

Among the non-sieved stations (1-9), station 8 held the highest average macrofauna densities (mean ± SD = 7591±2081 individuals m^{-2}) and biomass (66.5±64.7 g wet weight m^{-2}), while the lowest values came from station 1 (504±98 individuals m^{-2}; 1.2±0.7 g wet weight m^{-2}; **Table 1**). Juvenile Spatangoida (heart urchins) was the most dominant macrofauna taxon found amongst these stations with

Table 3.
Changes in average solute concentrations in the overlying water (per sediment m^2), between stations (ST) from before to after electrical and mechanical perturbation treatments.

		Δ Solute concentration (mmol m^{-2}) and pH (m^{-2})						
ST.	Treatment	O_2	NH_4^+	NO_2^-	NO_3^-	PO_4^{3-}	$Si(OH)_4$	pH
1	3sPBC	-0.08	**0.05***	0	**-0.06***	0	0.03	-
2	3sPBC	-1.3	**0.15****	0	0.02	-0.03	-0.39	-
3	3sPBC	-1.1	0.27	0	0.06	-0.02	0.08	-
	Mix	**-4.6****	0.32	0	0.18	**0.08***	**0.96****	-
4	3sPBC	-0.13	0.05	0	0.02	0	0.09	-
	Mix	**-17***	**1.0****	0	-0.09	**0.02***	**1.5***	-
5	3sPBC	-0.21	-0.09	0	0.06	0	0	-
	Mix	-0.55	-0.08	0.02	-0.03	0	**0.02****	-
6	3sPBC	-0.3	0.14	0.03	-0.11	-0.02	-0.11	-
	Mix	**-3.6****	-0.15	-0.17	0.60	**0.09****	**1.1****	-
7	3sPBC	-0.42	0.66	0.12	-0.12	0	-0.26	-
	Mix	**-4.2***	-0.21	-0.06	0.20	**0.11***	**0.66***	-
8	3sPBC	-0.21	-0.56	0.09	-0.36	-0.03	-0.59	-
	Mix	**-4.6*****	0.06	-0.03	0	**0.23****	**1.7*****	-
9	3sPBC	-0.21	-0.02	0.02	0	0.03	-0.03	-
	Mix	**-14***	1.1	0	0.12	**0.11***	**1.9***	-
10	3sPBC	-0.45	0.44	0	-0.23	-0.02	-0.27	0
	3sPDC	-0.3	0.42	0.03	-0.12	-0.05	-0.2	0
	Mix	**-8.9*****	**7.3*****	-0.03	-0.36	-0.03	**1.3****	-0.02
	120sPBC	-0.41	-0.18	0.02	-0.14	0.03	-0.27	0
	120sPDC	-1.48	0.17	-0.14	-0.29	**-0.11***	-0.3	**-0.15*****
11	3sPBC	-0.82	0.33	0.02	-0.17	-0.03	-0.14	-0.02
	3sPDC	-0.45	0.56	0.08	0.23	-0.02	0.39	-0.02
	Mix	**-22*****	**7.9*****	0	0.03	**0.02***	**2.1****	**-0.08*****
	120sPBC	-0.37	0.08	0.09	0	-0.02	-0.05	-0.03
	120sPDC	-0.19	-1.1	**-0.27*****	0.26	**-0.05****	0.2	**-0.18*****

Bold = significantly different compared to control samples. $*p < 0.05$; $**p < 0.01$; $***p < 0.001$
pH measurements were only taken for sites 10 and 11

81% of these individuals occurring at station 8. *Paramphinome jeffreysii* (bristle worms), was the second most abundant taxon and was found mainly in stations 7 (51%) and 8 (40%). Station 7 had the highest species richness (24 taxa) followed by station 2 (22 taxa). Despite the variation in biomass and abundances of macrofauna between stations, no consistent relationships were found between faunal parameters and O_2 consumption or any other biogeochemical flux.

Mechanical perturbations

The Mix treatment created turbidity in the overlying water which lasted from a few hours to several days depending on the observed grain size of the sediments (muddy = longer resuspension time, sandy = shorter resuspension time; J Tiano, pers. obs). Disturbed cores displayed a ‘flattened’ topography after resettling of the suspended sediments with a visible layer of fines on the surface of the cores (**Figure 2**, *top right panel*). Sediment profiles taken at stations 10 and 11 showed different responses to physical disturbance between the fine sand (station 10) and sandy mud (station 11) habitats. D50 became significantly lower at the surface (0-1 cm) after the Mix treatment (127.7±2.6 µm) for station 10 compared to undisturbed control cores (137.6±1.6 µm; $p < 0.001$; **Figure 4**). Significantly higher TN (0.0150±0.0002 TN%) and chl *a* content (6.04±0.74 µg chl *a* g^{-1}) were found in the mechanically mixed surface sediments of station 10 compared to control samples (0.0116±0.0009 TN%; 4.12±0.16 µg chl *a* g^{-1}; $p < 0.01$). For the sandy mud at station 11, no significant change was found at the surface layers (0-1 cm; $p > 0.05$) but the Mix treatment caused a significant increase in mean D50 for shallow subsurface (1-2 cm depth) sediment slices (86.3±8.6 µm) compared to controls (73.9±8.4 µm; $p < 0.01$; **Figure 4**). This shallow subsurface layer also displayed significantly lower chl *a* (9.39±1.32 µg chl *a* g^{-1}; $p < 0.05$), OC (0.44±0.11 OC%; $p < 0.01$), and TN (0.053±0.011 TN%; $p < 0.01$) content compared to control sediments (10.33±1.24 µg chl *a* g^{-1}; 0.61±0.14 OC%; 0.068±0.011 TN%).

Mechanical perturbations altered solute fluxes in some cores, however, this effect was not consistent between or within locations ($p > 0.05$; **Table 3**). In most cases, the Mix treatment created rapid changes in the absolute concentrations of O_2, NH_4^+, PO_4^{3-} and $Si(OH)_4$, though the longer term (>8 h) fluxes did not change drastically (**Figure 5**). Physical mixing quickly decreased O_2 concentrations in all stations where the treatment occurred except for station 5 (**Table 3**). NH_4^+ was released from the sediment from stations sampled in autumn (stations 3, 4, 10 and 11), while there was a limited response of NH_4^+ from stations sampled in spring (stations 5-9; **Table 3**). The Mix treatment caused the release of PO_4^{3-} at all stations where it occurred except for stations 5 and 10. At station 10 (which included a second Mix treatment) the first perturbation created a strong influx of PO_4^{3-} while the second perturbation released PO_4^{3-} to the overlying water (**Figure 5c**). $Si(OH)_4$ was consistently released at all locations with mechanical perturbations (stations 3-11). When evaluating all stations combined, the Mix treatment caused significant declines in water column O_2 ($p < 0.001$) and significant increases for NH_4^+ ($p < 0.001$), PO_4^{3-} ($p < 0.05$) and $Si(OH)_4$

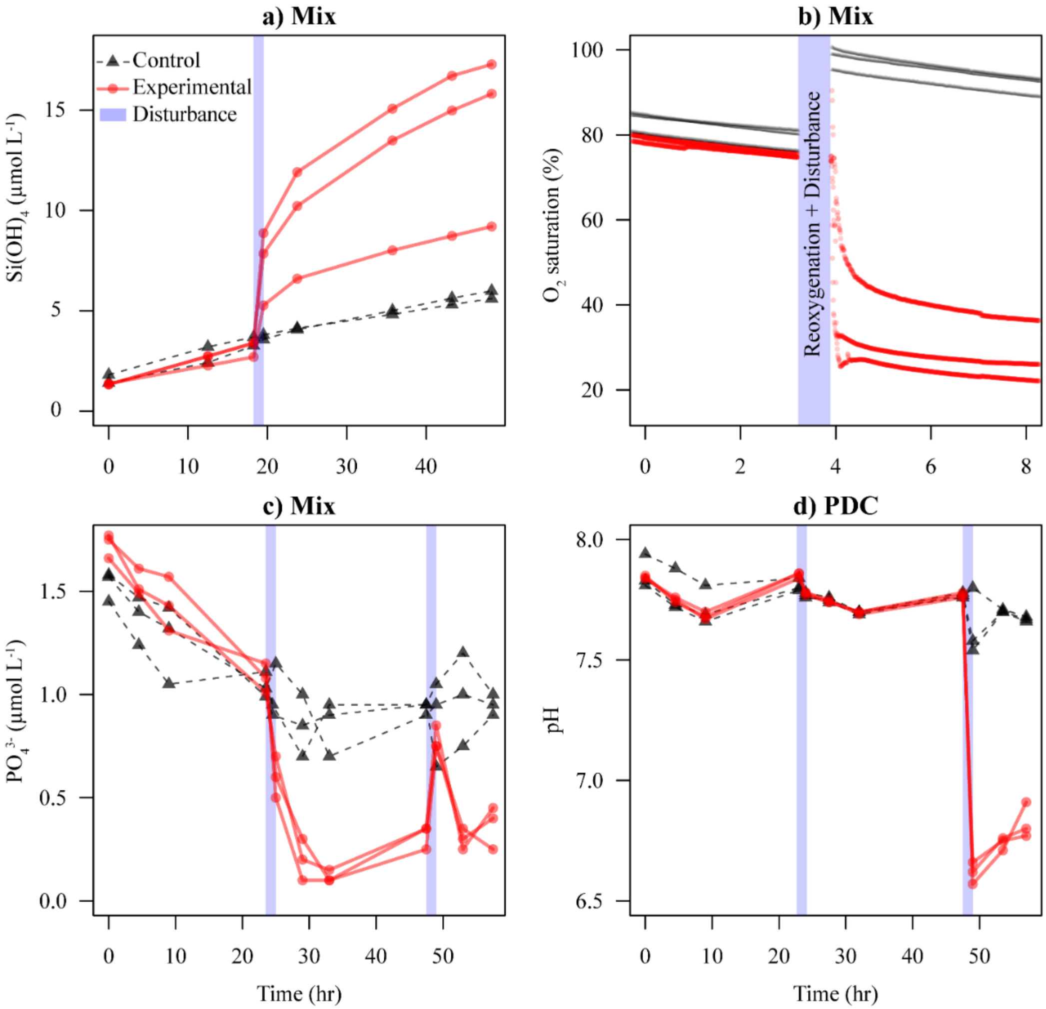


Figure 5. Examples of perturbation-induced biogeochemical changes in the overlying water of incubation cores. Mechanical effects on silicate concentrations (a), oxygen saturation (b) and phosphate concentrations (c; showing 2 mixing events). The effect of PDC exposure on pH (d; 1st disturbance = 3 seconds, 2nd disturbance = 120 seconds).

Note. In panel (b) the shorter time scale makes the reoxygenation + disturbance event appear wider than in the other panels. The resolution of data points here is also much higher than in the other panels because of the optode technology used to measure oxygen.

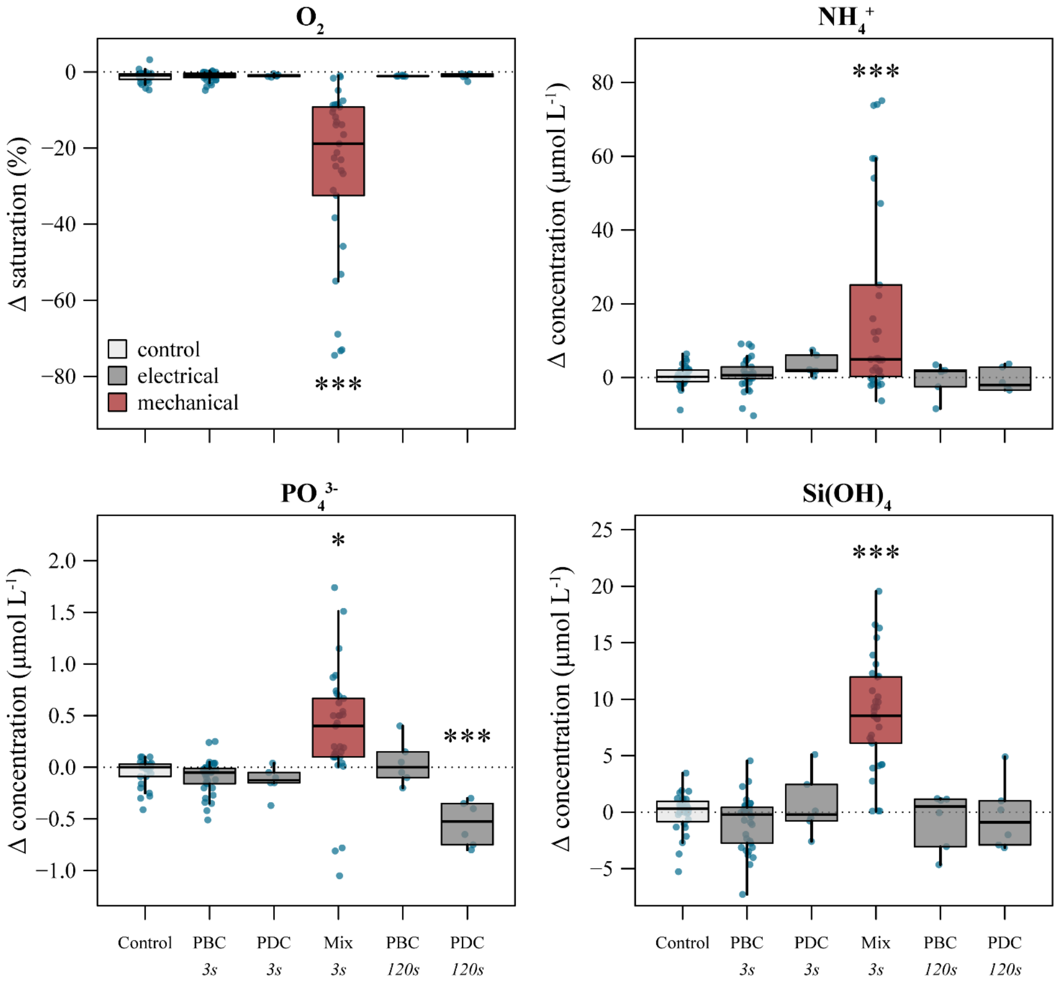


Figure 6. Treatment-induced changes for oxygen saturation and ammonium, phosphate and silicate concentrations between experimental treatments in sediment cores.

($p < 0.001$) when compared with undisturbed control samples (**Figure 6**). Sediment mixing also decreased the pH at stations 10 and 11 (only stations where pH was measured) though this was not statistically significant ($p = 0.07$; **Figure 7**). Changes to absolute solute concentrations can be found in **Supplementary Table 2**.

Robust regressions, using the R package: 'robustbase' (Maechler et al., 2020) on the percentage of very fine sand (62.5–125 µm) and sediment chl *a* content, significantly predicted the magnitude of mechanically-induced concentration changes in solutes: O_2, NH_4^+, PO_4^{3-} and $Si(OH)_4$. At locations where chl *a* was measured (stations 4 – 11; $n = 24$), this variable explained 86 % of O_2 ($p < 0.001$), 22 % of PO_4^{3-} ($p < 0.01$), and 21 % of $Si(OH)_4$ ($p < 0.01$) variation (**Supplementary Figure 1**). The percentage of very fine sand significantly predicted 45 % of O_2 ($p < 0.01$), 30 % of NH_4^+ ($p < 0.01$), and 17 % of $Si(OH)_4$ ($p < 0.05$) concentration changes from the Mix treatment (stations 3-11; $n = 27$; **Supplementary Figure 2**). For pH (stations 10 and 11), chl *a* explained 81% of the decrease caused from mechanical perturbations ($p < 0.001$; $n = 12$; **Supplementary Figure 3**).

Electrical perturbations

Oscilloscope measurements showed a negligible drop in voltage from the generator to the electrodes (electricity may lose voltage as it travels through the wires) confirming the 200 and 125 V m^{-1} field strengths and other electrical parameters used for these experiments (section 2.3). Neither PBC treatment (3sPBC and 120sPBC) caused consistent changes to solute fluxes/concentrations or pH values. NH_4^+ flux was significantly different in PBC cores compared to controls for stations 1 and 2, and NO_3^- flux was significantly different at station 1, though similar results were not replicated at other locations (Table 3). The only consistent effects was a decrease in pH and PO_4^{3-} from the water column in cores subjected to 120sPDC (stations 10 and 11).

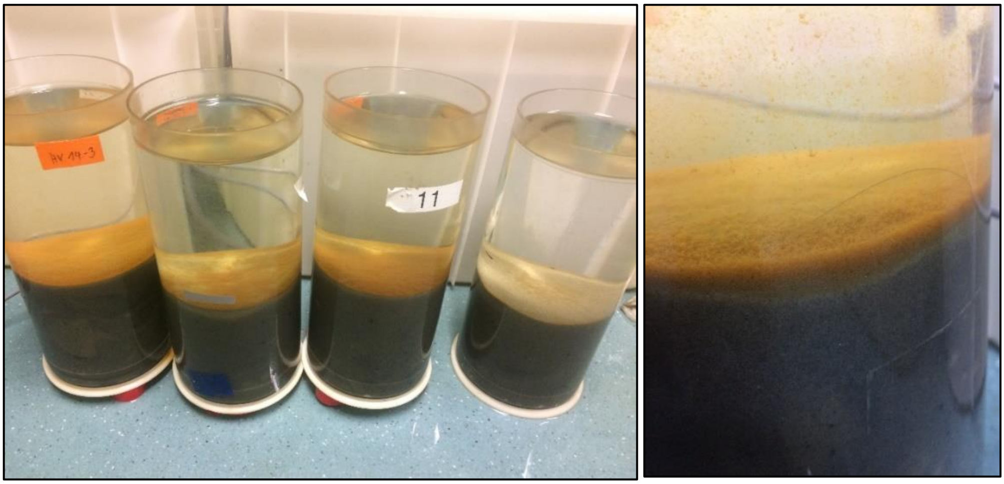


Figure 8. Photos of iron oxide formation in three PDC exposed cores next to one control core (*left*). A closer look at newly formed iron oxides on the sediment surface and in the water column (*right*).

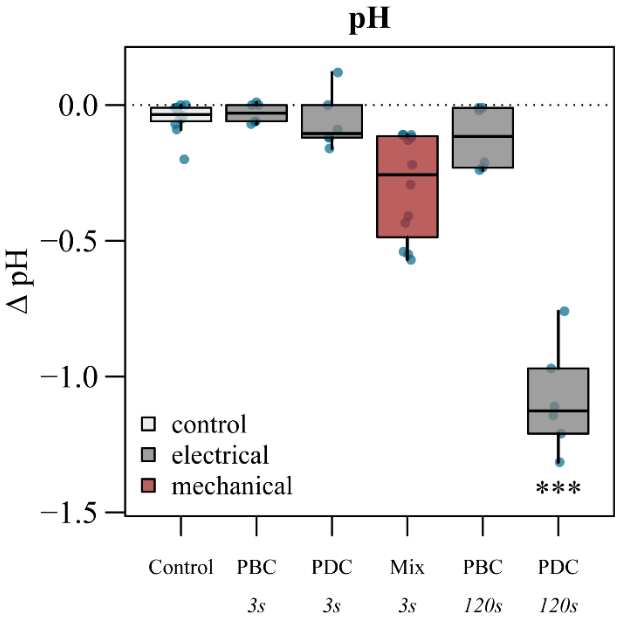


Figure 7. Changes in pH between treatments in sediment cores. Measurements for pH were only taken at stations 10 and 11.

During 120sPDC exposure, gas bubbles formed at the top electrode throughout the treatment period. An odour of chlorine was observed for 120sPDC treated cores, which grew stronger with exposure time. Sediments exposed to 120sPDC exhibited fluffy brown iron oxide particles forming on the sediment surface during the electrical exposure (**Figure 8**). Values for pH and PO_4^{3-} were significantly lower after 120sPDC compared to control cores ($p < 0.001$; **Figure 6** and **7**; **Table 3**). While the 120sPDC-induced changes in pH did not differ between the two stations, the removal of water column PO_4^{3-} was significantly higher in fine sand (station 10) compared to sandy mud (station 11; $p < 0.01$; **Table 3**).

Perturbed fluxes and natural flux equivalents

The amount of hours required for natural solute release to equal the perturbation-induced solute release, was calculated for O_2, NH_4^+, $Si(OH)_4$ for the Mix treatment, and also for PO_4^{3-} for 120sPDC treatments (**Table 4**). On average, mechanically-induced oxygen consumption equalled 17.1 hours of natural O_2 demand, with disturbances at station 11 equalling 33.1 h and station 5 equalling 2.4 h of natural

Table 4.
Time required for natural fluxes to equal perturbed fluxes for the Mix treatment (oxygen, ammonium, silicates) and for the 120-second PDC treatment (phosphates).

Stations	Time (h)			
	O_2 Uptake (Mix)	NH_4^+ Release (Mix)	$Si(OH)_4$ Release (Mix)	PO_4^{3-} Uptake (120sPDC)
3	12	20.4	76.8	-
4	32.6	NA	61.9	-
5	2.4	NA	12	-
6	7.8	6.9	21.6	-
7	9.5	NA	9.9	-
8	12.2	3.8	33	-
9	30.4	93.9	52	-
10	13.7	67.8	100.8	28
11	33.1	47.7	45.8	25.2

Note. Natural flux equivalents to treatment-induced NH_4^+ releases (efflux) cannot be calculated with negative (influx) natural fluxes (NA values given).
PDC treatments only occurred at stations 10 and 11

fluxes. The perturbed NH_4^+ fluxes were equivalent to a natural flux lasting 3.8 (station 8) to 93.9 (station 9) hours. Natural $Si(OH)_4$ fluxes would have needed up to 101 h to attain the concentration change found at station 10 compared with 9.9 h at station 7. The 120sPDC treatment caused rapid fluxes equivalent to 28 and 25.2 h of PO_4^{3-} uptake at stations 10 and 11 respectively. PO_4^{3-} values were not calculated for the Mix treatment as most (7 out of 11) natural fluxes were negative while the mechanical perturbations released PO_4^{3-} from the sediments.

DISCUSSION

A major concern of electrofisheries impacts is the possible biogeochemical effects imposed by these types of fisheries (Soetaert et al., 2015). This study was aimed at filling some of these knowledge gaps on this topic. We found consistent biogeochemical patterns related to mechanical-induced sediment resuspension, while identifying parameters to help explain the magnitude of these effects. We also demonstrate that a type of direct current (high frequency pulsed or continuous DC) is required to create consistent and measurable biogeochemical changes from electrical fields and that these effects are limited when using a current with alternating polarities (i.e. PBC and AC). In the following, we discuss the biogeochemical responses to mechanical disturbance and electrical exposure.

Mechanical Effects

There are a number of limitations associated with mechanical disturbance in a closed system. Perhaps most importantly, we did not try to recreate bottom currents in our sediment cores, which can cause the rapid diffusion of resuspended solutes particles in field settings. Despite this, we were able to simulate effects such as rapid oxygen depletion and nutrient releases, which have been observed in various in situ trawl studies (Riemann and Hoffman, 1991; Dounas et al., 2005; Dounas et al., 2007; Tiano et al., 2019). Our experimental setup allowed us to measure the net effect of sediment resuspension, which would be undoubtedly diluted if conducted in field settings. There may have also been acclimatization issues with possible differences between in situ and laboratory temperatures. The perturbation effects, which were the most important for our study, however, were less likely to be affected by differing temperatures than longer-term flux measurements. These short-term effects are heavily influenced by the nutrients in the porewater, which are at least somewhat buffered from the outside environmental conditions.

Mechanically perturbed cores showed a layer of fine sediments on the surface, which is similar to a field study where this fine layer was visible on sediment profile images taken after *in situ* beam trawling (**Figure 2**; Tiano et al. 2020). Our sediment profiles taken after mechanical perturbations show that the effect of mixing and resuspension on grain size characteristics depends on the type of sediment present. Trawl-induced coarsening of the upper sediments has been reported in several *in situ* studies (Palanques et al., 2014; Mengual et al., 2016; Depestele et al., 2018; Tiano et al., 2019). Bottom disturbance can cause a winnowing of finer particles after impact. Trawl-induced fining of sediments, however, was reported by Trimmer et al., (2005) in a relatively stable North Sea location (Outer Silver Pit) but not in a more dynamic area (Thames). Our study found both fining and coarsening in the upper sediment layers after sediment resuspension from fine sand and sandy mud respectively, supporting the variable results found in other studies (**Figure 4**). Nonetheless, disturbance effects on particle sizes found in our study may be more indicative of low disturbance habitats as no advective currents were created inside our sediment cores, resulting in sediment sorting without current-induced winnowing.

The magnitude of disturbance-induced solute changes correlates well with the amount of fresh organic material (chl *a*) in the sediment. Smaller grain sizes are more likely to contain higher concentrations of organic material and nutrients compared to coarser grains (Virto et al., 2008; Bainbridge et al., 2012). We also found the percentage of very fine sands to be a reliable predictor of solute changes after sediment resuspension as they increased the potential for biogeochemical alterations. We did not find statistically significant relationships between silt and biogeochemical parameters, possibly due to low silt percentages in the majority of the sample sites (**Table 1**; **Supplementary Table 1**). These broad relationships may be used scale up our findings to larger geographical areas.

We observed a seasonal effect on the amount of NH_4^+ released from mechanical disturbance. Stations sampled in spring 2018 showed no significant releases of NH_4^+ (**Table 3**). Dounas et al., (2007) also found lower levels of inorganic nitrogen released from trawl disturbance in winter-spring compared to the summer-autumn months. The build-up of inorganic nitrogen over the summer and autumn may help explain the lack of NH_4^+ release in the spring sampling locations found in our study. Data from station 5 (collected in spring), in particular, showed only minor effects from mechanical disturbance (**Table 3**). This station displayed the lowest OC and TN values as well as the lowest O_2, NO_3^- and Si(OH)4 flux rates (**Table 1**, **Supplementary Table 1**). Station 11 (collected in autumn), in contrast, showed the greatest response from mechanical disturbance and also exhibited the highest levels of chl *a* content, and generally strong fluxes across all solute parameters (**Table 1**). Our results suggest that mechanical disturbance will have greater effects in biogeochemically active sediments and will vary depending on the time of the year (higher at end of summer/autumn), fresh organic matter input and sediment grain size.

Our results show that nutrient exchange between the benthic and pelagic zones depend on the type of nutrient, on sediment characteristics and on the number of disturbances. After intense sediment resuspension events created in the incubation chambers of *in situ* landers, Almroth-Rossell et al., (2012) found increases of 48 µmol L^{-1} and 6.9 µmol L^{-1} in the absolute concentrations of NH_4^+ and $Si(OH)_4$ immediately after disturbance, which are within range of the values found in our study (**Supplementary Table 2**). Their observed decrease of water column PO_4^{3-} after disturbance was consistent with the mechanical-induced (1st perturbation) sedimentary uptake of PO_4^{3-} found at station 10 in our study. The first perturbation at station 10 likely oxidised a substantial amount of reduced iron during resuspension, causing the adsorption of PO_4^{3-} to iron oxides in the water column (**Figure 5c**). Upon the second mechanical perturbation, 24 h later, most of the iron in the upper sediments was probably oxidised, therefore, not allowing sufficient phosphorus-iron binding to create the same effect. Instead, the greater amounts of PO_4^{3-} in the sediments were temporarily released into the overlying water (**Figure 5c**). We observed a significant release of PO_4^{3-} in 7 out of the 8 locations where mechanical disturbance took place (**Table 3**). Furthermore, we detected an inverse relationship between PO_4^{3-} and sedimentary chl *a* content (**Supplementary Figure 1**). Our results are consistent with Couceiro et al., (2013) who found increased water column PO_4^{3-} and $Si(OH)_4$ in sediment resuspension experiments, and Riemann and Hoffman (1991) who found increased NH_4^+ and decreased O_2 in the water column after bottom trawling and dredging. While certain solutes show consistent effects from disturbance (NH_4^+, $Si(OH)_4$: efflux; O_2 : influx), disturbance effects of PO_4^{3-} will vary with iron (adsorbs to PO_4^{3-} when oxidised), oxygen and organic matter (limits PO_4^{3-} adsorption to iron oxides; Weng et al., 2012; Sulu-Gambari et al., 2016).

While trawl-induced changes to organic material (Brylinsky et al., 1994; Watling et al., 2001; Puscuddu et al., 2005; Palanques et al., 2014; Puscuddu et al., 2014; Sciberras et al., 2016; Paradis et al., 2019;) and benthic mineralisation (Tiano et al., 2019, van de Velde et al., 2018) have been reported in previous studies, there is limited empirical evidence for a direct link between mechanical disturbance and long term changes in nutrient fluxes. Warnken et al., (2003) reported trawl-induced increases to NH_4^+ fluxes, Ferguson et al., (2020) revealed decreased N_2 fluxes after trawling events and Tiano et al. (2019) found lower O_2 consumption rates after bottom trawl disturbance. Nevertheless, other studies have shown inconclusive or weak effects from physical perturbations on non-instantaneous nutrient fluxes (Trimmer et al., 2005; Almroth et al., 2009; Olsgard et al., 2009; Almroth-Rossel et al., 2012; Tiano et al., 2019). The measurement of instant or rapid trawl-induced fluxes may be a more indicative of *in situ* trawl impacts on nutrient dynamics (Riemann and Hoffmann 1991; Dounas et al., 2007; Almroth-Rosell et al., 2012; Palanques et al., 2014). Nonetheless, intermittent trawl-induced pulses (versus long term flux alterations) of nutrients and sediment into the water column can create an additive impact to the direct physical modifications and removal of organisms due to bottom trawling, and may lead to profound changes in benthic ecosystems (Piskaln et al., 1998).

Electrical effects

This study did not find any consistent biogeochemical effects concerning the pulsed bi-polar currents (PBC) used by the electrotrawl fishery for North Sea sole. Sediment resuspension created from lowering the top electrode into the incubation core likely created the minor changes in NH_4^+ and NO_3^- found for the PBC treatment at stations 1 and 2 (Table 3). PBC currents were used in the sole fishery to minimize the effect of electrolysis, which would corrode the electrodes after repeated use (H. K. Woolthuis, designer of HFK PulseWing, pers. comm.). The alternating polarity of pulses limits the unidirectional movement of ions and decreases the likelihood for significant electrochemical effects. For the *Ensis* electrofishery, fishers have used continuous AC or DC currents (Woolmer et al., 2011; Murray et al., 2016). The 120sPDC treatment in our study, which caused significant effects, is an approximation of the parameters used for *Ensis* electric fishing but there are notable differences.

The pulse generator used in this study did not have the ability to create continuous currents (we maintained the high frequency pulsed currents). We also used a stronger electrical field (125 V m^{-1}) than what is typical for *Ensis* fishing (50 V m^{-1}) due to the size limitation of our sediment cores (30 cm max electrode distance) and minimum currents (25 V) allowed by our generator. Therefore, we underestimated the duty cycle (percentage of time the current is flowing) while overestimating the field strength from *Ensis* electrofishing in our experiments. We also oriented our electrodes vertically which was needed to create a homogenous electrical field and expose the full 15 cm sediment column. Marine sediment does not provide a barrier to the electrical fields produced from pulse trawls which have been found to penetrate over 20 cm into the sediment (de Haan and Burggraaf, 2018). As stations 10 and 11 were subjected to 120-second electrical exposures, we stopped any indirect effects caused from electrically overexposed macrofauna, by removing them from the cores before the start of the experiments. This was deemed necessary, as our goal was to measure the direct effects of anthropogenic electrical fields on sediment biogeochemical parameters and not on sediment fauna.

One of the strongest biogeochemical effects we recorded from 120sPDC was the removal of water column PO_4^{3-}. This occurred because of the rapid electric field-induced precipitation of iron oxides on the sediment surface, which adsorped onto PO_4^{3-} compounds in the overlying water (Sulu-Gambari et al., 2016; Rao et al., 2016). This phenomenon occurred because of the unidirectional current deployed in the prolonged PDC treatment caused the advective transport of porewater iron to the sediment surface. This is a process known as 'ionic drift' which occurs naturally in bacteria-mediated electric fields found in various marine sediments (Nielsen and Risgaard-Petersen, 2015; Burdorf et al., 2016). Ionic drift transports porewater nutrients such as Fe^{2+}, Ca^{2+} and SO_4^{2-}, in relation to their polarity and that of the electric field (Risgaard-Petersen et al., 2012; van de Velde et al., 2016). While the rapid back and forth pulses found in high frequency PBC seem to limit ionic drift, longer exposure to high frequency PDC or continuous DC will cause the unidirectional movement of porewater ions in the sediment. The results of which, may lead to the mobilisation of reduced iron and subsequent adsorption to of PO_4^{3-} from the water column.

The presence of organic material and pH plays a strong role in the adsorption of PO_4^{3-} to iron oxides (Canfield et al., 2005; Weng et al., 2012). Between the two stations where 120sPDC took place, significantly more water column PO_4^{3-} was removed in the station with less sediment chl *a* (a proxy for fresh organic material) and OC content. Organic matter competes with PO_4^{3-} for adsorption and can reduce the amount of iron bound phosphorus (Weng et al., 2012). As lower pH (4-6) can favour phosphorus-iron oxide binding (Weng et al., 2012) the decline in water column pH after 120sPDC exposure may have also helped facilitate this process. The electrolysis-induced decline in pH may have been caused by the formation of chlorine gas (Cl_2) on the cathode. The chlorine can react with water (H_2O) to create hypochlorous acid (HOCl), thus reducing the water column pH. With the buffering capacity of seawater, the changes in pH are expected to be much less detectable in an open system, however, possible consequences to phosphorous dynamics may hold larger implications if DC electric fields (high frequency pulsed or continuous) are used in benthic habitats.

Implications

Our findings imply that electrochemical reactions from pulse trawling used for sole are minimal due to its use of PBC. Biogeochemical effects are more likely, when using PDC or continuous DC, which is more relevant for *Ensis* electrofishing. It is not yet clear, however, if these changes are damaging to marine habitats. Potentially harmful Cl_2 is formed during marine electrolysis, however, Cl_2 seems to be neutralized quickly in marine environments (Goreau, 2012). On manmade marine structures created from electrolysis (by stimulating calcium carbonate formation), several observations have been made of organisms residing in close proximity to where the Cl_2 is produced (Goreau, 2012). The PDC-induced adsorption of PO_4^{3-} (>25 hours of

PO_4^{3-} adsorbed in 2 min of PDC; **Table 4**) confirms the possibility for electrodes to inhibit PO_4^{3-} release from sediments (Martins et al., 2014), though this effect may be buffered in areas with high sedimentary organic material. Unintended phosphate removal may be a cause for concern if electrical activities cause changes to the natural phosphorus dynamics. More research is necessary to show if these electrochemical effects are harmful to benthic ecosystems.

We can conclude, nevertheless, that the mechanical impact from electro trawls (or any other bottom fishing technique) is more likely to cause potentially harmful alterations to benthic pelagic coupling compared to the effect of electricity. We found that a 3 second disturbance to the top 3 cm of sediment, typical for bottom trawling gears (Depestele et al., 2018), can release the equivalent of several days' worth of natural NH_4^+ and $Si(OH)_4$ fluxes from the sediments while consuming up to 33 hours of natural sediment O_2 consumption (**Table 4**). Trawl-induced releases of nutrients are predicted to trigger primary production in the water column (Dounas et al., 2007). Bottom trawling can lower the mineralisation of organic material in the sediment (Tiano et al., 2019) and reduce denitrification (Ferguson et al., 2020), consequently slowing down the natural rates of nutrient recycling. This lowers the buffering effect that marine sediments can have against eutrophication. Additionally, our demonstration of mechanically induced depletion of water column O_2, supports similar *in situ* observations after trawl disturbance in which trawl-induced resuspension caused a rapid uptake of water column oxygen (Riemann and Hoffman 1991; Tiano et al., 2019). The increased risk of eutrophication coupled with the mechanical-induced depletion of water column O_2 levels (Almroth et al, 2010, Almroth et al., 2012) may create damaging additive effects on marine communities.

This study was able to identify the solutes that are most likely to be affected by direct mechanical impacts, while connecting the magnitude of these effects to the amounts of fresh organic material, sediment grain size and time of the year. This information can be used to upscale the biogeochemical effects of bottom trawling and sediment resuspension. Understanding these dynamics can help mitigate the anthropogenic impacts in vulnerable marine ecosystems.

Acknowledgements

This research was made possible by the Netherlands Ministry of Agriculture Nature and Food Quality (LNV) and the European Maritime and Fisheries Fund (EMFF). We thank the crews of the RV Tridens and RV Pelagia for helping us collect samples from multiple areas in the North Sea. We also thank Matt Parsons'and Maria Balcelar Martinez from FUGRO for processing our macrofauna samples and sending us our data from the UK.

Supplementary Material for: Chapter 4

Impacts of anthropogenic sediment mixing and electrical perturbations on sediment biogeochemistry

Table S1.

Total nitrogen (%TN), carbon to nitrogen ratio (C:N) and particle size parameters: % silt (<63 m), % very fine sand (62.5-125 μm), % fine sand (125-250 μm), % medium sand (0.25-0.5 mm), % coarse sand (0.5–1 mm), diameter (μm) at which 10% of particles in the sample are smaller (D10), diameter (μm) at which 90% of particles in the sample are smaller (D90).

Station	TN	C:N	Silt	Very fine sand	Fine sand	Medium sand	Coarse sand	D10	D90
1	-	-	0.0	0.7	54.8	44.3	0.3	166.0	347
2	-	-	9.1	13.4	59.9	17.5	0.0	77.1	283
3	-	-	2.5	0.3	7.8	43.0	46.3	252.0	818
4	0.04	10.3	36.5	34.4	27.8	1.5	0.0	5.8	179
5	0.01	6.6	0.0	3.8	62.7	33.3	0.1	143.0	328
6	0.14	9.0	88.2	11.0	0.68	0.36	0.0	4.3	67.2
7	0.08	9.3	55.8	34.2	10.3	0.0	1.0	7.0	126
8	0.03	9.2	9.3	6.4	48.3	34.9	0.0	64.2	363
9	0.03	8.6	14.5	35.7	46.5	3.2	0.0	17.9	206
10	0.01	7.3	0.2	36.9	61.1	1.8	0.0	94.4	202
11	0.07	10.3	42.3	34.9	22.3	0.7	0.0	6.8	164

Table S2.
Changes in absolute mean solute concentrations after electrical and mix perturbations in µmol L^{-1}

		Δ Solute concentration (µmol L^{-1}) and pH						
Station	Tr.	O_2	NH_4^+	NO_2	NO_3	PO_4^{3-}	$Si(OH)_4$	pH
1	Control	-0.8	-0.5	0	0.2	0	0	-
	3s PBC	-0.6	**0.3***	0	**-0.4***	0	0.2	-
2	Control	-2.2	-0.7	0	-0.1	-0.1	0.2	-
	3s PBC	-8.4	**1.0****	0	0.1	-0.2	-2.6	-
3	Control	-5.1	0.1	0	0.2	0	0.6	-
	3s PBC	-7.6	1.8	0	0.4	-0.1	0.5	-
	Mix	**-31****	2.1	0	1.2	**0.5***	**6.4*****	-
4	Control	-7	0.1	0.2	0.1	0	0.9	-
	3s PBC	-0.8	0.3	0	0.1	0	0.6	-
	Mix	**-115***	**6.8****	0	-0.6	**0.1***	**9.8***	-
5	Control	-0.6	-2	0	-0.1	0	0	-
	3s PBC	-1.4	-0.6	0	0.4	0	0	-
	Mix	-3.6	-0.5	0.1	-0.2	0	**0.1****	-
6	Control	-1.1	4.8	0.5	2.5	0	0.2	-
	3s PBC	-2	0.9	0.2	-0.7	-0.1	-0.7	-
	Mix	**-24****	-1	-1.1	4	**0.6****	**7.2****	-
7	Control	-5.3	0.4	0.5	-0.4	-0.2	-2.4	-
	3s PBC	-2.8	4.4	0.8	-0.8	0	-1.7	-
	Mix	**-28***	-1.4	-0.4	1.3	**0.7***	**4.4***	-
8	Control	-2.5	0	-0.3	0.3	0	1.2	-
	3s PBC	-1.4	-3.7	0.6	-2.4	-0.2	-3.9	-
	Mix	**-31*****	0.4	-0.2	0	**1.5***	**11*****	-
9	Control	-2.8	4.1	0	0.9	-0.1	1.2	-
	3s PBC	-1.4	-0.1	0.1	0	0.2	-0.2	-
	Mix	**-95***	7.3	0	0.8	**0.7***	**13***	-
10	Control	-4	-0.4	0.1	-0.1	-0.1	-0.4	0
	3s PBC	-3	2.9	0	-1.5	-0.1	-1.8	0
	3s PDC	-2	2.8	0.2	-0.8	-0.3	-1.3	0
	Mix	**-59*****	**49*****	-0.2	-2.4	-0.2	**8.4****	-0.1
	120s PBC	-2.7	-1.2	0.1	-0.9	0.2	-1.8	0
	120s PDC	-9.8	1.1	-0.9	-1.9	**-0.7***	-2	**-1*****

Table S2. *Continued*

Station	Tr.	O_2	NH_4^+	NO_2	NO_3	PO_4^{3-}	$Si(OH)_4$	pH
11	Control	-3.9	0.1	0.5	-0.5	-0.1	-0.5	-0.1
	3s PBC	-5.5	2.2	0.1	-1.1	-0.4	-0.9	-0.1
	3s PDC	-3	3.7	0.5	1.5	-0.1	2.6	-0.1
	Mix	**-146*****	**53*****	0	0.2	0.1	**14****	**-0.5*****
	120s PBC	-2.5	0.5	0.6	0	-0.1	-0.3	-0.2
	120s PDC	-1.2	-7.5	**-1.8*****	1.7	0.4	1.3	**-1.2*****

Bold = significantly different compared to control samples. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$
pH measurements were only taken for sites 10 and 11

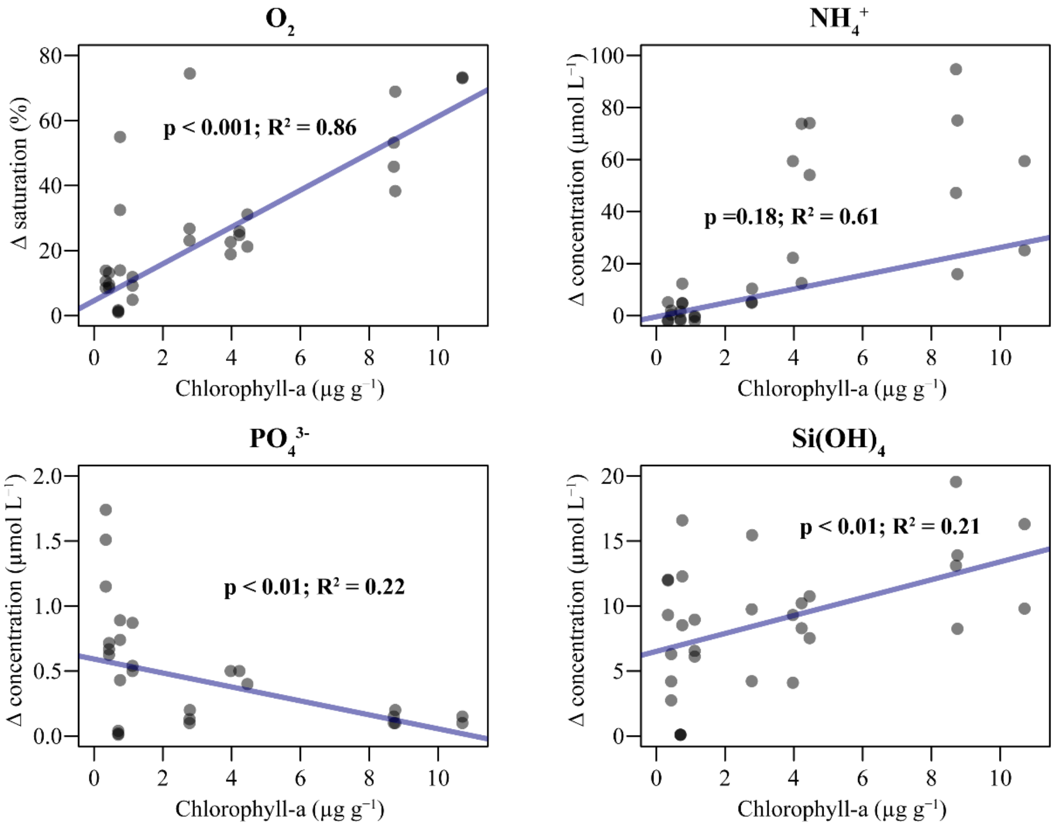


Figure S1. Robust regression analysis of mechanical-induced changes in solute concentrations in the overlying water of sediment cores versus chlorophyll-a (µg g^{-1}) content.

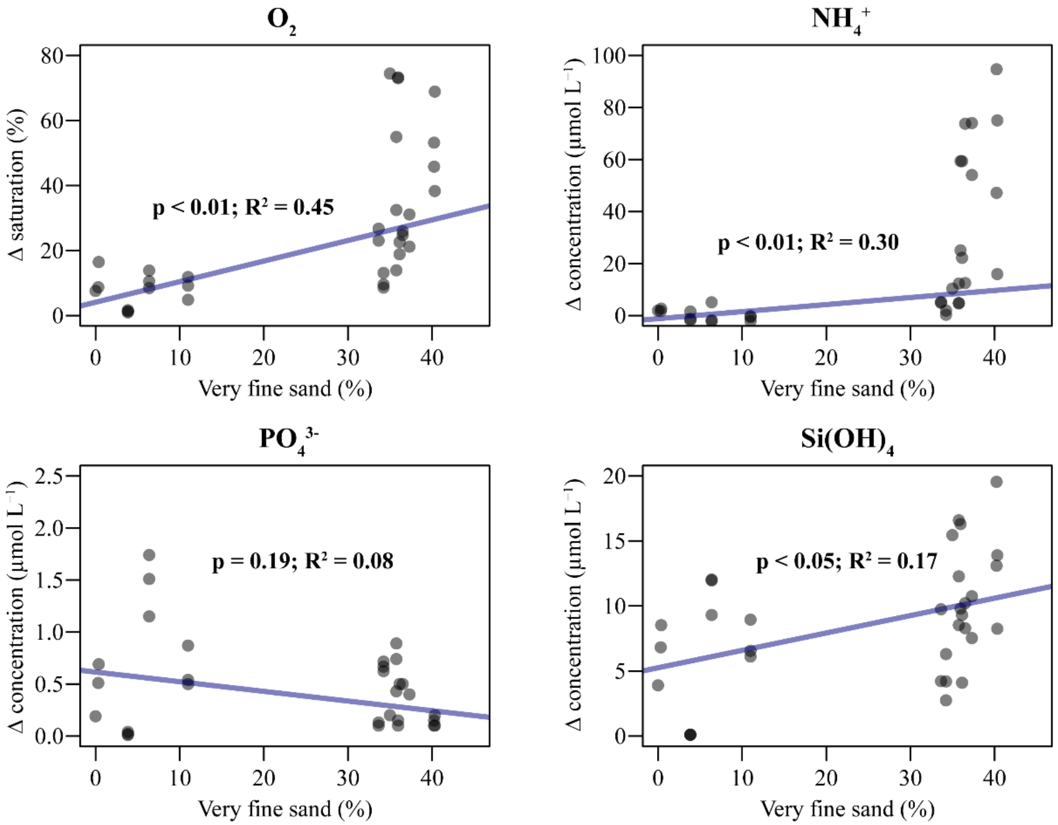


Figure S2. Robust regression analysis of mechanical-induced changes in solute concentrations in the overlying water of sediment cores versus very fine sand (62.5-125 µm) content.

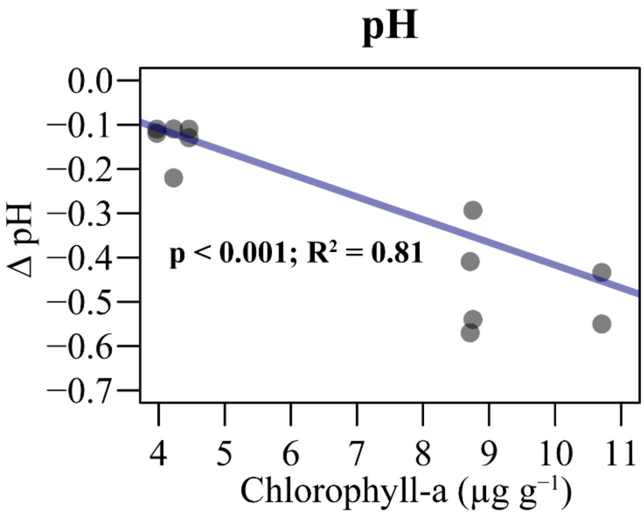


Figure S3. Robust regression analysis of mechanical-induced changes in pH in the overlying water of sediment cores versus chlorophyll-a (µg g^{-1}) content.

Chapter 5

Ecosystem impacts from electro-trawls and conventional beam trawls in subtidal Lanice conchilega reef communities

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Experimental pulse trawling (Vlakte van de Raan)

Photo: Justin Tiano

Abstract

Dynamic, sandy environments are generally more resilient to mechanical stress, however, biogenic reef habitats may provide an exception to this rule. This study explores the physical, biological and biogeochemical effects of electric pulse and tickler chain rigged beam trawls on a coastal ecosystem dominated by the tube building polychaete, *Lanice conchilega*. With a before-after-control-impact designed *in situ* study, we detected a ~1 cm bathymetric deepening after trawling associated with significant losses in benthic chlorophyll *a* caused from both fishing gears. Pulse and tickler chain trawls reduced sediment oxygen consumption by up to 46% and 57% respectively. A significant decrease in *L. conchilega* abundance was found after pulse trawling (72%), however, total macrobenthos densities were only significantly reduced after tickler chain beam trawling (52%). Significant relationships were found between *L. conchilega* densities and very fine sand fractions, oxygen and nitrate fluxes, densities of other species and species richness before but not after trawling. Our results indicate a variable but on average slightly reduced effect for pulse compared to tickler chain beam trawls on benthic community and biogeochemical characteristics. Moreover, both gears caused remarkably high alterations to absolute oxygen consumption rates, implying a loss in faunal mediated biogeochemical functioning. This study suggests that *L. conchilega* reefs may be less resilient to trawling than previously believed and should be considered when assessing habitat vulnerability.

Keywords: beam trawling, pulse trawling, *Lanice conchilega*, ecosystem functioning, biogenic reef, coastal habitat, biogeochemistry, benthic ecology

INTRODUCTION

Marine sediment ecosystems are important drivers for benthic pelagic coupling (Mermillod-Blondin and Rosenberg, 2006) and carbon mineralization (Seiter et al., 2005). Biogenic reef habitats in particular, such as those created by the tube-building polychaete, *Lanice conchilega*, are able to capture substantial amounts of organic carbon compared to adjacent sediments (De Smet et al., 2016) resulting in dense and biologically diverse benthic communities (Van Hoey et al., 2008). This species may be found in in various North Sea habitats but generally prefer shallow muddy and fine sands where it may exhibit densities upwards of 1,000 individuals per m^2 (Van Hoey et al., 2008). Bottom trawling activities are a common occurrence in North Sea *L. conchilega* dominated habitats (Rabaut, 2009) and present a considerable threat to biogenic reef ecosystems (Kaiser et al., 2002; Fariñas-Franco et al., 2018). Benthic community resilience to bottom trawl impacts have been linked to both *L. conchilega* reefs (Rabaut et al., 2008) and the dynamic sandy habitats they are often found in (Duplisea et al., 2001; Kaiser et al., 2006; Sciberras et al., 2016; Rijnsdorp et al., 2020a). Consequences of trawling on more holistic ecosystem processes such as benthic pelagic coupling , however, have not been thoroughly examined in these systems.

Bottom fishing affects carbon cycling by displacing bottom dwelling organisms (Bergman and Hup, 1992; Sciberras et al., 2018), removing sediment structures needed to maximize biogeochemical processes (Ferguson et al., 2020; Depestele et al., 2018), and resuspending fresh organic material from the sediment surface, resulting in reduced mineralization of organic carbon (Tiano et., al. 2019). In nutrient rich sediments, mechanical disturbance may temporarily increase carbon mineralization if refractory organic fractions are mixed with and reactivated by fresh organic matter (van de Velde et al., 2018). Trawl-induced mortality to benthic organisms can simplify benthic communities and can lead to a loss in functional diversity (Tillin et al., 2006; Tiano et al., 2020). The removal (significant or partial) of an abundant ecosystem engineer such as *L. conchilega* would likely have major impacts on biogeochemical and community dynamics.

The severity of bottom trawl impact depends on the size and type of fishing gear used and speed at which it drags over the seabed (Eigaard et al., 2016; Depestele et al., 2016; Depestele et al., 2018; Rijnsdorp et al,. 2020a, 2020b). In the southern North Sea, beam trawls rigged with tickler chains are used to mechanically stimulate flatfish up from the seafloor, facilitating their capture. The experimental alternative, ‘pulse trawls’, expose the seabed to electrical fields, causing the immobilization of target fish for oncoming bottom nets (Soetaert et al., 2015). Previous comparisons conducted in the Frisian Front, a relatively homogenous offshore habitat known for its high abundances and diversity of benthic organisms (Dauwe et al., 1998; Dewick et al., 2002), have found a reduced impact of pulse compared to tickler rigged trawls on physical and biogeochemical parameters (Depestele et al., 2018; Tiano et al. 2019) but a similar impact on benthic communities (Tiano et al., 2020). Dynamic nearshore habitats, in contrast, may provide a more challenging environment for detecting significant anthropogenic alterations.

Benthic habitats characterized by coarse sediment and high levels of natural disturbance, display more biogeochemical and ecological resilience to bottom fishing compared muddy and more hydrodynamically static ecosystems (Duplisea et al., 2001; Kaiser et al., 2002; Bolam et al., 2013; Sciberras et al., 2016; Rijnsdorp et al., 2020). Macrobenthos found in sandy, well-sorted sediments, tend to be less sensitive to trawl disturbance than in muddy poorly sorted habitats (Bolam et al., 2013). Communities dominated by three-dimensional biological features, such biogenic reefs, are an exception to this and can be vulnerable to trawl disturbance regardless of energy level or substrate type (Kaiser et al., 2002; Grabowski et al., 2014). *L. conchilega* reefs, however, might be more resilient to bottom trawling as individual tubeworms may escape the threat by retreating and into their burrows (Rabaut, 2009).

The current study uses a combination of water column, sonar, sediment profile imagery and boxcore sampling techniques to provide a comprehensive assessment of the physical, biological and biogeochemical effects from two types of bottom trawling in a biogenic reef habitat. Our main objective was to measure the acute ecosystem effects of electric pulse and tickler chain beam trawls in a high-energy coastal system using a before-after control-impact (BACI) design. More specifically, the high abundances of *Lanice conchilega* in the region, allowed us to quantify the effect of this species on ecological and biogeochemical parameters, and how this changes due to fishing disturbance.

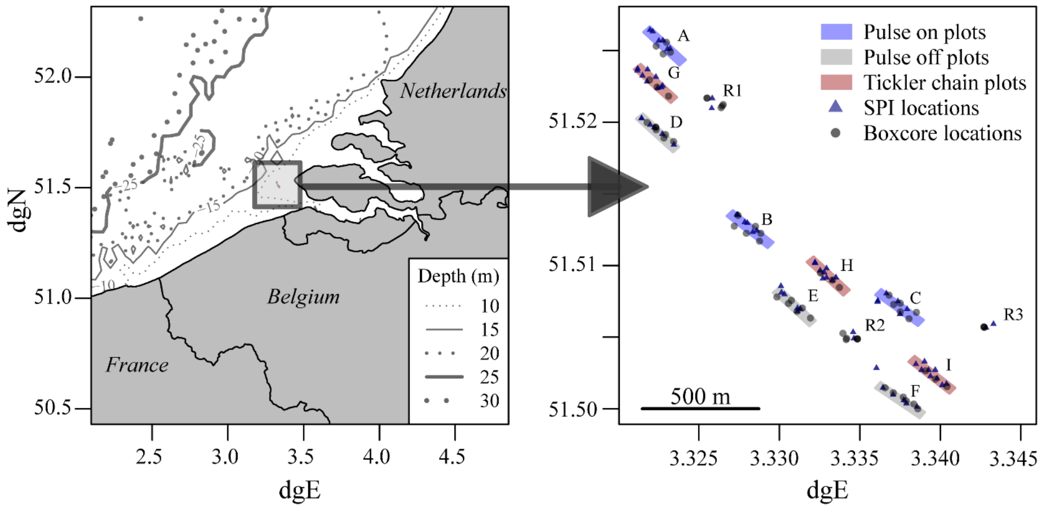


Figure 1. Geographic location of the study site (left). Experimental plots (A-G), reference stations (R1-R3), sediment profile imagery (SPI) locations, and boxcore sampling locations (right).

METHODS

Study area

This study took place in shallow subtidal waters (8 – 10 m depth), 10 km away from the Netherlands coast close to the Dutch and Belgian EEZ (exclusive economic zone) border (**Figure 1**). This region, known as the ‘Vlakte van de Raan’, is an area known for its subtidal sandbanks, which create a mosaic of habitat areas of varying ecological value (Degraer and Hostens, 2016, Pecceu et al. 2016). The experimental areas were characterized by ‘fine sand’ with an average median grain size of 200.5 µm and an average chlorophyll *a* content (0-10 cm depth) of 13.1 µg g^{-1} (**Figure S1**). The exact location for this study within the Vlakte van de Raan (**Figure 1**), was chosen due to its relatively low levels of bottom trawl disturbance (no flatfish or shrimp trawl disturbance in one year as verified with vessel monitoring data) and the high macrobenthic densities and biomass (Craeymeersch et al., 2006).

Experimental trawling design

The effects of acute fishing disturbance from pulse and tickler-chain beam trawls were evaluated in controlled experimental settings following a beyond BACI protocol (Underwood, 1992). Three experimental treatments were conducted: (1) tickler-chain beam trawling (hereafter called ‘Tickler’), (2) pulse trawling with and (3) without electricity turned on (hereafter called 'Pulse-ON' and 'Pulse-OFF' treatment). Each treatment was repeated three times in spatially separated areas (Pulse-ON = A, B, C; Pulse-OFF = D, E, F, Tickler = G, H, I), resulting in a total of nine experimental plots of 50 by 300 m (15 000 m² per plot; **Figure 1**). Individual plots were subdivided by three different sampling 'stations' representing the western, middle, and eastern portions of the plot. Three additional untrawled reference stations (R1, R2, R3) were chosen within the experimental area (**Figure 1**).

Pulse trawls (Delmaco) were deployed from the commercial fishing vessel (FV) 'TH6 Johanna Cornelia' (24 m) and tickler-chain trawls from the FV 'YE238 Geertruida' (22 m). The vessels were relatively small trawlers (<221 kW engine) and allowed to fish within 12 nm of the coast. Both pulse trawl (~1.1 tonne in air) and tickler-chain trawl (~2.4 tonne in air) gears measured 4 m in width and had one trawl shoe at either side of its beam. The fishing vessels made a total of six trawl passes over each experimental plot at a speed of ~5 kn (pulse) and ~6 kn (tickler). Experimental fishing with the pulse trawl was performed on 12 June 2018 between 4.30 and 11.30 AM UTC. Experimental fishing with the tickler-chain trawl was performed on 15 of June 2018 between 4.00 and 6.30 AM UTC. Sonar, sediment profile imagery and benthic sample information was collected before/after trawling and in the reference areas (**Figure 1**). Water column information was collected during trawling activity. All experimental equipment was deployed from the RV 'Simon Stevin' (Flanders Marine Institute).

Water column measurements

To measure turbidity during trawling events, the research vessel (RV) deployed an SBE 25plus Sealogger (CTD) with two optical backscatter point sensors (OBS) while suspended continuously at 5 m depth during experimental trawling activity. For each treatment plot measured (A, B, C, D, E, G, and H) the RV strategically positioned itself against the current and the ongoing trawling, ~80 m adjacent to the corresponding plots. Water was collected using Niskin bottles mounted on the CTD during Pulse-ON (plots B and C), Pulse-OFF (plots D and E), and Tickler (plots G and H) treatments. Information for suspended particulate matter (SPM), organic carbon (OC) and total nitrogen (TN) was obtained by running ~ 10 liters of collected water through precombusted GF/F filters (0.7 µm). Filters were dried at 60°C before being decarbonated with 0.1N HCl (Nieuwenhuize et al., 1994) and analyzed with an Interscience Flash 2000 elemental analyzer.

Bathymetry and Backscatter

Bathymetry and backscatter data were collected using a Kongsberg EM2040 single head multi-beam echo sounder (MBES) mounted on the RV (Depestele et al., 2018). While bathymetry data can tell us how sediment was deepened by trawling, backscatter (reflection of soundwaves) can give insight on if trawling changes affects sediment type of seabed roughness (Depestele et al., 2018). All data were collected with a MBES frequency of 300 kHz, a speed of 8 knots and at orientation parallel to the longest side of the experimental plots to avoid backscatter bias from the survey line directions (Lurton et al., 2018). Bathymetrical and backscatter data was collected before (T0) and after (T1) trawling. The RV followed the fishing vessel at an approximate distance of 300 m during one single haul in each of the experimental plots to register the bathymetrical data (T1). The fishing vessels continued trawling in the experimental plot and after six passes in each of the experimental plot, the RV collected MBES backscatter data within 12 hours (T2).

A high resolution (0.5 x 0.5 m) digital elevation model of the seabed was created from the MBES data using Qimera (QPS). Trawl tracks were located from the GPS-derived position of the vessel path and visual detection using backscatter and bathymetrical info. Transects of 12 m were positioned every 20 m along the trawl track in GIS software (N = 74 for Pulse-ON, N = 100 for Pulse-OFF and N = 94 for Tickler; **Supplementary Figure 1**). For the transects with visible trawl marks, the mean water depth was calculated for five locations inside and outside the trawl tracks. These measurements were based on the locations of the trawl track that were estimated from the MBES measurements at T1. The water depth was estimated at these same locations at T0. The difference between mean water depths inside and outside the track was used to assess if the trawl caused bathymetrical changes in the track.

A backscatter mosaic (1 x 1 m) was created in FMGeocoder Toolbox (QPS FMGT). Backscatter data was sampled by (1) using transects for comparison of T0 and T1 and (2) by using all backscatter data in each experimental plot. Values outside 1.5 times the interquartile range were removed as outliers (1.5% of all values). This resulted in a total number of backscatter values > 120,000 for each treatment and time interval (T0 and T2).

Sediment Profile Imagery

A Sediment Profile Imagery (SPI) camera (Ocean Imaging Systems, North Falmouth, MA, USA) was used to characterize surface and subsurface sediment features. Three replicate images were taken at each sampling station (3 stations per treatment plot; **Figure 1**). Images were taken in undisturbed sediments (T0) for the

Pulse-ON treatment plots on 7 June 2018. On 8 June 2018, images were taken for R1, R2 and Pulse-OFF (T0) plots. Images for two of the three Pulse-OFF T1 plots (D and F) were captured on 12 June 2018 1-2 h after trawling, though technical difficulties prevented further use of the SPI until the following day. The remaining T1 images for Pulse-ON and Pulse-OFF treatments captured on 13 June 2018 (19 – 21 h after trawling) followed by visits to the reference stations and Tickler (T0) plots. Tickler T1 images were captured on 15 June 2018, 1.5 – 3 h after beam trawling. Information for prism penetration depth (depth at which the camera is able to penetrate the sediment) and visual observations of fauna, sediment characteristics and oxidation were obtained using SpiArcBase (Romero-Ramires et al., 2013).

Benthic Samples

Benthic sediment samples were collected using cylindrical NIOZ box corers (50 cm height, 32 cm diameter; Netherlands Institute for Sea Research, Texel). For timesteps T0 and T1, three replicate box cores were taken inside individual treatment plots (western, center and eastern stations) and at reference stations (69 box cores total; **Figure 1**). During experimental fishing activity, box cores in trawled sediments were collected shortly after 6 trawling consecutive passes were made in each treatment plot (within 0.5 h after fishing), often while experimental fishing continued in the subsequent plot. On 11 June 2018, box cores were collected for T0 Pulse-ON and Pulse-OFF treatments and at reference stations R1 and R2. T1 samples for Pulse-ON and Pulse-OFF treatments were collected on 12 June 2018. Box cores for R1, R2 and R3 reference stations and T0 Tickler treatment plots were collected on 13 June 2018. Tickler T1 samples were collected on 15 June 2018.

Sediment Parameters

Box cores were subsampled for sediment at the western and eastern stations of each plot and for replicates 1 and 3 for reference stations. Sediment samples were subdivided at 0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-2.5, 2.5-3, 3-4, 4-5, 5-6, 6-8, 8-10 cm slices taken from 3.5 cm inner diameter subcores. All samples were stored in a -20 °C freezer before freeze-drying and sieving (1 mm) for particle analysis. Sediment grain sizes were obtained via laser diffraction using a Malvern Mastersizer 2000 (McCave et al., 1986). Chlorophyll *a* (chl *a*) pigments were extracted using acetone and analyzed with UV spectrophotometry (Ritchie, 2006).

Porewater nutrients

Two box cores were subsampled for porewater at western and eastern stations for each treatment plot and reference stations (replicates 1 and 3) with 10 cm diameter subcores with vertical sampling ports. Porewater was extracted at 0, 1, 2, 3, 5, 7 and 10 cm depth using rhizon samplers (Rhizophere Research Products; Seeberg-Elverfeldt et al., 2005; Dickens et al., 2007; Shobolt 2010). Porewater samples were added to 10 mL polystyrene vials and stored in -20 °C prior to analysis. To acquire nutrients, samples were thawed and analyzed using a SEAL QuAAtro segmented flow analyzer (Jodo et al., 1992) to determine concentrations of ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), phosphate (PO_4^{3-}), and silicate ($Si(OH)_4$).

Benthic biogeochemical fluxes

Incubation cores (15 cm inner diameter by 30 cm height) were collected from all box core samples (3x per treatment plot and reference station) with overlying water. These were subsequently placed in a water bath and left to incubate to obtain information on nutrient fluxes exchanging to and from the sediment and water column in dark conditions. Magnetic stirrers, fixed to the lid of incubation cores, ensured homogenized water column conditions. Incubation cores were sealed from air contact for 4 hours to measure rates of sediment community oxygen consumption (SCOC). During this period, oxygen concentrations were monitored every 30 s using optode sensors placed in the overlying water of the incubation cores (FireStingO_2, Pyroscience). At the end of the O_2 incubations, cores were re-opened and aerated to remain at above 90% O_2 saturation for the ongoing nutrient incubations. Ten mL water samples were collected at the overlying water of incubation cores at 0, 4, 8, 16 hour time intervals to obtain flux information on NH_4^+, NO_2^-, NO_3^-, PO_4^{3-}, and $Si(OH)_4$. Water samples for nutrient fluxes were stored and analyzed using the same methods described for porewater nutrients. Flux estimates were obtained by fitting linear regressions on nutrient concentrations changes over time and multiplying the regression coefficient with the height of the overlying water (Tiano et al., 2019).

Macrofauna collection

After the flux measurements, incubation cores were rinsed through a 1 mm sieve to collect the benthic macrofauna inside them. Faunal samples were preserved in 4% formalin seawater on board the vessel. Sorting and identification of preserved macrofauna samples took place at the Flanders Institute for Agricultural and Fisheries

Research (ILVO) to obtain measurements for taxon densities and biomass (blotted wet weights).

Statistical analysis

Water column

Differences between water column conditions (continuous CTD measurements and SPM filters) during Pulse-ON, Pulse-OFF and Tickler treatments were assessed with one way ANOVA's and Tukey HSD pairwise tests. Assumptions of normality and homogeneity of variances were verified using Shapiro-Wilk and Levene's tests. If parametric assumptions were violated, data underwent a log-transformation prior to analysis.

MBES information

Bathymetrical differences between water depths inside and outside the track locations $\Delta_{i,T,G}$ were calculated for each transect i at each time interval T (T0 = before and T1 = after trawling) for each trawl gear type G [Eq. 1]. A paired Wilcoxon signed-rank test was used to test if Delta-values were significantly different between T1 and T0 for each gear type. Significant positive Delta-values indicated that the water depth inside the trawl track was higher than outside the trawl track.

$$\Delta_{i,T,G} = (water\ depth_{outside} - water\ depth_{inside\ track\ location})_{i,T,G} \qquad \text{[Eq. 1]}$$

The indention I of each transect i was calculated by subtracting the delta value at T0 from the Delta-value at T1 [Eq. 2].

$$I_{i,G} = (\Delta_{T1} - \Delta_{T0})_{i,G} \qquad \text{[Eq. 2]}$$

A resulting positive value indicated a deepening of the trawl track. The indention of the trawl was compared between trawl types using a Kruskal-Wallis Rank sum Test.

Statistical differences in backscatter values were compared for the combination of time and trawl types using experimental plots as replicates in a Kruskal-Wallis Rank sum Test. The experimental plots were also compared using the Kruskal-Wallis Rank sum Test. A Dunn test with Benjamini-Hochberg method was applied for pairwise comparisons between sites.

SPI and benthic sample analysis

To account for spatial differences while examining changes caused from fishing treatments, linear mixed effects models (LMM) were used to investigate SPI penetration depth, sediment, porewater nutrient concentrations, biogeochemical flux and univariate ecological characteristics using the *lmer*-function in the R package: ‘lme4’ (Bates et al., 2015). For each treatment, a ‘model-a’ was created to include ‘timestep’ (T0 or T1) as a fixed variable and ‘station’ as a random variable to minimize spatial autocorrelation between different locations. A ‘model-b’ considered only the random variable (station). Model-a and model-b were tested against each other using a one-way ANOVA using the same procedure for managing normality assumptions as conducted for the water column data.

Impact of Lanice conchilega

Robust regression analysis, using the R package: ‘robustbase’ (Maechler et al., 2020), was conducted to investigate the effect of *L. conchilega* densities and biomass on physical, biogeochemical and faunal parameters in trawled and untrawled samples. This alternative to least squares techniques is an iterative analysis which down-weights the influence of outliers on regression coefficients and is less affected by violations of linear regression assumptions (Koller and Stahel 2011). To reduce possible bias from the spatial differences in *L. conchilega* densities/biomass between treatment plots, all pre-trawled and post-trawled data were pooled together for this analysis.

All data visualization and statistical analyses were carried out using R (R Core Team 2014).

RESULTS

Water column conditions during trawling

Turbidity measured by the OBS sensors detected significantly higher amounts of water column SPM concentrations during tickler chain trawling (mean ± standard deviation = 62.5±17.1 mg SPM L^{-1}, $p < 0.001$) compared to Pulse-ON (19.6±5.3 mg SPM L^{-1}) and Pulse-OFF treatments (13.3±5.8 mg SPM L^{-1}; **Figure 2**). SPM filters displayed higher average estimates of water column turbidity (Tickler = 100.6±18.7 mg SPM L^{-1}; Pulse-ON = 21.6±1.7 mg SPM L^{-1}, Pulse-OFF = 21.8±1.6 mg SPM L^{-1}) with significantly higher turbidity during the Tickler treatment compared to both pulse fishing treatments ($p < 0.01$). Higher SPM on the filters coincided with lower OC content (Tickler = 2.4±0.2 OC%; Pulse-ON = 3.6±0.1 OC%, Pulse-OFF = 4.3±0.6

OC%) and TN percentages (Tickler = 0.4±0.01 TN%; Pulse-ON = 0.7±0.2 TN%, Pulse-OFF = 0.6±0.05 TN%) with the Pulse-OFF treatment showing a significantly higher water column OC % compared to during tickler chain trawling ($p < 0.05$). Data from a 'Meetnet Vlaamse Banken' buoy (located in ~7 km south west of the experimental location) showed current speeds ranging from 0.08 to 1.21 m s^{-1} during pulse trawling and 0.23 to 0.85 m s^{-1} during tickler chain trawling. On the day before both pulse trawl treatments, water currents reached a maximum speed of 1.23 m s^{-1} compared to 1.5 m s^{-1} the day before the tickler treatment (**Supplementary Figure 2**).

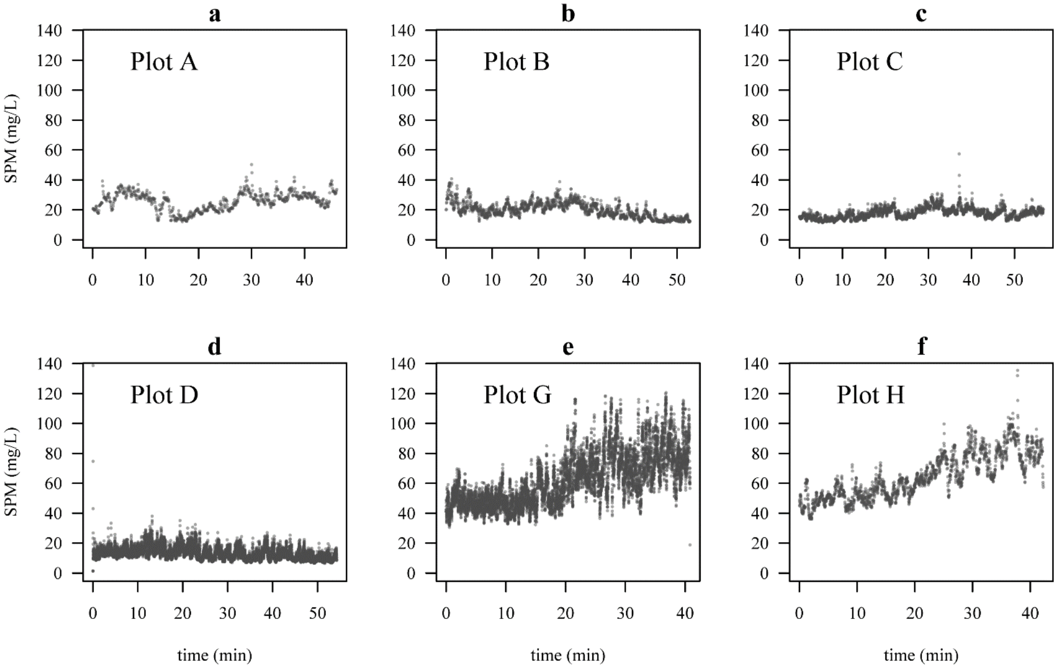


Figure 2. Water column turbidity during the time of trawling for Pulse-ON plots (a-c), Pulse-OFF plot (d) and Tickler plots (e-f).

Trawl effects on bathymetry

The locations inside the track were, on average, shallower before trawling (T0) than the locations outside the track (**Supplementary Figure 3**). The locations inside the track were deeper than the locations outside the track after trawling (T1). Delta-values were significantly different before and after trawling for each trawl type (Pulse-ON: $p < 0.05$, Pulse-OFF: $p < 0.001$, Tickler: $p < 0.001$), though the effect sizes were relatively small (Cohen's d estimates of -0.21, -0.30 and -0.29 for Pulse-ON, Pulse-

OFF and Tickler respectively). The track locations were deepened, on average, by 1 cm after trawling. The indention of the trawl track was not significantly different between treatments ($p > 0.05$), implying that the bathymetrical change due to pulse trawling (with or without electricity) and due to tickler-chain beam trawling was similar (**Table 1**).

Trawl effects on backscatter

The backscatter values at T1 were reduced for each of the trawl types, but the size of the reduction was < 2 dB, which may be considered as a threshold for the detection of trawl marks (Depestele et al., 2018; Roche et al., 2018). Backscatter delta-values were not significantly different before and after trawling for any of the trawl types ($p > 0.05$).

The backscatter values of the track locations in all treatments (after 1 trawl pass) exhibited reduced values though there was no statistical difference between the three trawl types ($p > 0.05$). Comparison of mean backscatter values over entire plots (after 6 trawl passes) showed dB values ranging between -26.64 and -25.40. The mean backscatter strength did not differ by more than 2 dB between the treatments at T0 and T1 and was not significantly different between any of the time-treatment interactions ($p > 0.05$; **Supplementary Table 1**). Backscatter values were not statistically different by experimental plots ($p > 0.05$; **Figure 3**), as confirmed by a post-hoc Dunn test with Benjamin-Hochberg correction on the p-values. Uncorrected p-values suggested that sites A and F were different, as indicated by significant pairwise differences ($p < 0.05$) between A and B, H and I, as well as pairwise differences between F and B, C, H and I (**Figure 3**).

Table 1.
Indention of the track locations (in cm)

Treatment	Time	mean	sd	Q25	median	Q75	n
Pulse-OFF	T1-T0	1.17	1.84	1.20	-0.03	2.50	88
Pulse-ON	T1-T0	0.99	3.92	1.00	-0.80	3.48	74
Tickler	T1-T0	1.11	2.74	1.10	-0.80	2.70	89

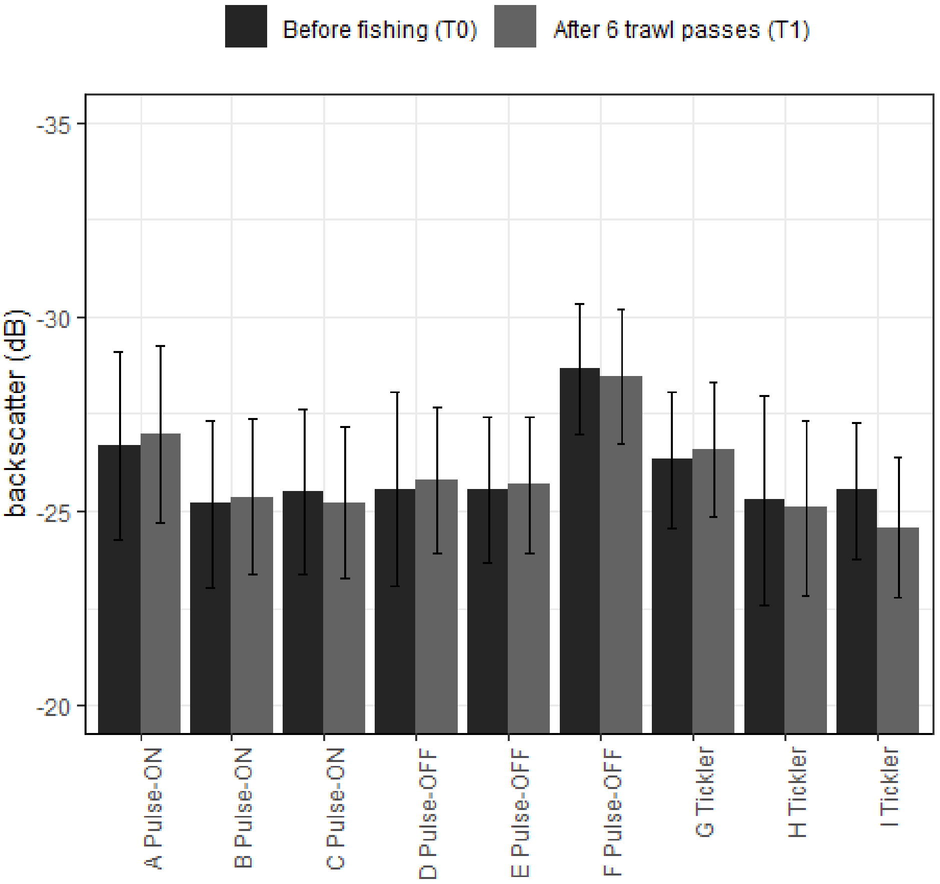


Figure 3. Mean backscatter values (dB) by experimental plot (before and after trawling) with the standard deviations.

Sediment profile image analysis

One hundred eighty SPI photos were captured between T0-T1 treatment plots and reference stations. *L. conchilega* tubeworms were identified in 72 % of images taken and were often associated with heterogeneous patterns of oxidized sediment (**Figure 4**b). Mechanical disturbance was evident in certain T1 images showing ‘flattened’ tubes and/or sediment (**Figure 4**c). Average penetration depth did not differ significantly between T0-T1 for fishing treatments but was deeper for all treatments after trawling (Tickler: T0 = 52.3±23 mm, T1: 67.4±41 mm; Pulse-ON: T0 = 48.2±18 mm, T1 = 48.9±12 mm; Pulse-OFF: T0 = 52.5±20 mm, T1 = 53.7±17 mm; $p > 0.05$).

Reference stations showed higher average penetration (Reference: 59.5±40 mm) compared to all except tickler T1 sediments.

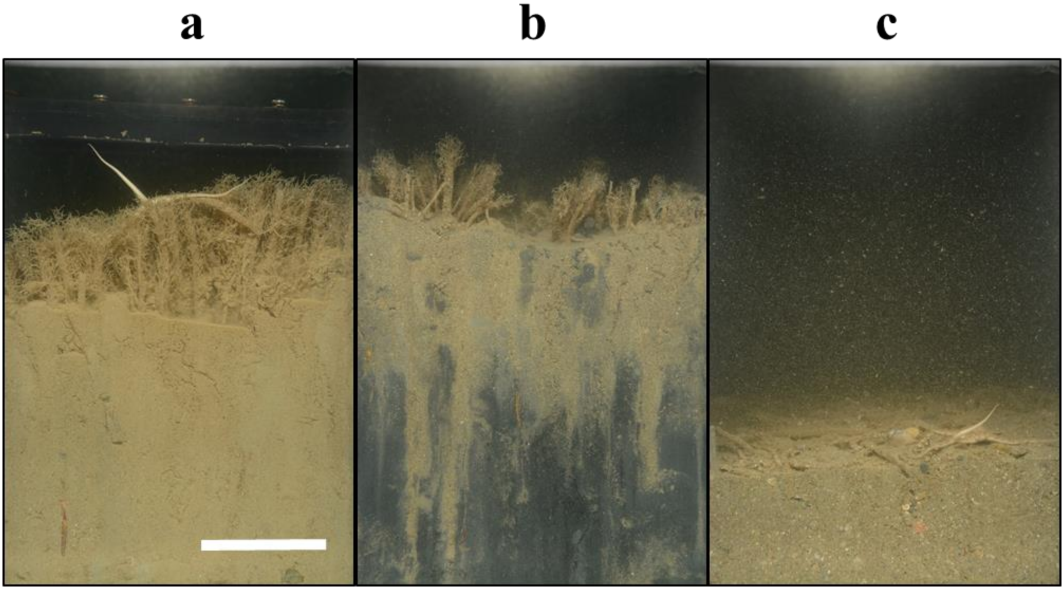


Figure 4. Sediment profile imagery showing a dense *Lanice conchilega* tubeworm reef (a), bioirrigation induced sediment oxidation (b) and evidence of trawl disturbance: flattened tubeworms and sediment (c). Scale bar = 5 cm.

Trawls effects on sediment parameters

Very fine sand fractions (62.5-125 µm) and chl *a* content in the sediment column (0-10 cm) were significantly lower in Tickler T1 compared to T0 samples ($p < 0.01$; **Table 2**). For the Pulse-ON treatment, significant differences were found when comparing T0-T1 silt fractions and chl *a* content ($p < 0.01$; **Table 2**). Surface sediment parameters (0 – 1 cm) showed significant increases in median grain size between T0-T1 for Tickler ($p < 0.01$) and Pulse-ON ($p < 0.05$) treatments. Larger grain sizes in surface sediment coincided with significantly smaller silt fractions (Tickler, $p < 0.001$; Pulse-ON, $p < 0.05$) and chl *a* content (Tickler, $p < 0.001$; Pulse-ON, $p < 0.05$) in the same sediments. Robust regression of chl *a* content versus silt percentages in the sediment column explained 92 % of variation. No significant differences in sediment parameters between T0-T1 were found in the Pulse-OFF treatment.

Table 2.
Results for T0-T1 between Tickler, Pulse-ON, and Pulse-OFF treatments (mean ± SD) for sediment parameters and porewater nutrient profiles ($\mu mol\ L^{-1}$).

	Tickler				Pulse-ON				Pulse-OFF			
Sediment	T0	n	T1	n	T0	n	T1	n	T0	n	T1	n
Very fine sand (%)	**10.5±4.3**	64	**9.2±4.5**	65	8.3±4.2	53	7.4±4.2	64	10.9±3.4	55	11.1±2.8	63
Chl *a* ($\mu g\ g^{-1}$)	**18.8±31.1**	64	**8.4±16.7**	65	**10.2±8.9**	53	**9.1±16.3**	64	12.1±16.1	55	18.7±30.2	63
Silt (%)	12.9±16.8	64	10.9±13.6	65	**8.4±6.6**	53	**7.7±12.0**	64	8.4±9.1	55	11.5±16.3	63
Median grain size (μm)	188.6±60.7	64	206.7±72.4	65	211.0±42.3	53	220.4±62.8	64	192.2±28.6	55	181.7±43.7	63

	Tickler				Pulse-ON				Pulse-OFF			
Porewater	T0	n	T1	n	T0	n	T1	n	T0	n	T1	n
NH_4^+	**25.6±16.7**	35	**47.1±37.9**	35	74.1±59.1	34	80.7±58.7	36	92.3±82.6	36	79.9±61.1	36
NO_3^-	**4.1±2.7**	35	**6.4±4.1**	35	13.9±20.2	34	6.1±8.2	36	**4.9±7.3**	36	**6.8±4.9**	36
PO_4^{3-}	7.6±5.8	35	8.7±9.0	35	**5.2±6.7**	34	**8.2±7.4**	36	**9.4±15.8**	36	**13.1±9.9**	36
$Si(OH)_4$	68.9±52.4	35	105.6±95.2	35	91.0±92.8	34	97.9±72.5	36	115.7±88.9	36	137.2±89.8	36

Bold signifies significant differences between T0 and T1.
Note. Large spatial variation accounted for statistically.

Trawl effects on biogeochemical fluxes and profiles

Average SCOC rates were significantly reduced between T0 (Tickler: 172±109 mmol $O_2\ m^{-2}\ d^{-1}$; Pulse-ON: 144±199 mmol $O_2\ m^{-2}\ d^{-1}$;) and T1 (Tickler: 74±40 mmol $O_2\ m^{-2}\ d^{-1}$; Pulse-ON: 78±89 mmol $O_2\ m^{-2}\ d^{-1}$) for Tickler ($p < 0.001$) and Pulse-ON ($p < 0.05$) but not for the Pulse-OFF treatment (T0 = 72±35 mmol $O_2\ m^{-2}\ d^{-1}$, T1 = 73±44 mmol $O_2\ m^{-2}\ d^{-1}$; **Figure 5**a). No other consistent or significant patterns were found for nutrient fluxes between T0-T1 fishing treatments ($p > 0.05$). Mean ammonium fluxes ranged from 0.5±0.3 mmol $NH_4^+\ m^{-2}\ d^{-1}$ at Pulse-OFF T0 to 1.6±1.6 mmol $NH_4^+\ m^{-2}\ d^{-1}$ at Tickler T1. Nitrate fluxes were highest at Pulse-ON T1 (0.02±0.02 mmol $NO_3^-\ m^{-2}\ d^{-1}$) and exhibited negative average fluxes for reference samples (-0.02±0.03 mmol NO_3^- m^{-2} d^{-1}). Effluxes of phosphate ranged from 0.01±0.03 mmol PO_4^{3-} m^{-2} d^{-1} (Pulse-ON T0) to 0.05±0.07 mmol PO_4^{3-} m^{-2} d^{-1} (Pulse-OFF T0). Silicate effluxes were lowest at Pulse-ON T0 (0.7±0.6 mmol $Si(OH)_4$ m^{-2} d^{-1}) and highest at Tickler T1 (1.7±0.7 mmol $Si(OH)_4$ m^{-2} d^{-1}).

Average porewater nitrate concentrations in the sediment column (0 – 10 cm) were significantly higher after trawling in Tickler and Pulse-OFF treatments compared to pre-trawled sediments (Tickler, $p < 0.01$; Pulse-OFF, $p < 0.01$; **Table 2**). Ammonium concentrations in the sediment significantly increased from T0 to T1 ($p < 0.01$) after Tickler trawling (**Table 2**). Average porewater phosphate concentrations were elevated after trawling for all experimental treatments but this was significant only in Pulse-ON ($p < 0.01$) and Pulse-OFF ($p < 0.001$; **Table 2**).

Trawl effects on macrofauna density and macrobenthos composition

Sixty-nine taxonomical groups were identified in this study with *L. conchilega* dominating benthic macrobenthos densities (54%). The bivalve, *Kurtiella bidentata*, and polychaetes, *Magelona spp.*, and *Eumida sanguinea* made up 13%, 4% and 3% of total macrofauna density respectively. Though they only contributed 1% of total macrobenthos density, the razor clam, *Ensis leei*, represented 45% of total biomass collected followed by *L. conchilega* (22%), *Spisula subtruncata* (bivalve, 14%), and *Echinocardium cordatum* (heart urchins, 4%).

Benthic macrofaunal densities decreased from T0 (Tickler: 11782±7360 ind m^{-2}; Pulse-ON: 9783±14072 ind m^{-2}; Pulse-OFF: 6241±5120 ind m^{-2}) to T1 (Tickler: 4949±3428 ind m^{-2}; Pulse-ON: 3336±3529 ind m^{-2}; Pulse-OFF: 5483±3623 ind m^{-2}) but were only significant after the Tickler treatment ($p < 0.05$; **Figure 5**b). Reference samples varied greatly but held the highest average densities from all the treatments (22659±15639 ind m^{-2}; **Figure 5**b).

Between different treatment groups, *L. conchilega* maintained the highest average densities in the reference stations (13225±9282 ind m^{-2}). *L. conchilega* densities experienced significant declines between T0 (5801±9352 ind m^{-2}) and T1 (1587±3022 ind m^{-2}) from the Pulse-ON treatment ($p < 0.05$) but not in the Pulse-OFF (T0 = 3081±3711 ind m^{-2}, T1 = 2251±3547 ind m^{-2}) or Tickler treatments (T0 = 5880±3838 ind m^{-2}, T1 = 2172±1913 ind m^{-2}). Amongst other abundant taxa, *Abra alba* (bivalve) density declined significantly after tickler chain trawling (T0 = 418±632 ind m^{-2}, T1 = 231±420 ind m^{-2}, $p < 0.05$) and *E. sanguinea* was significantly lower after the Pulse-ON treatment (T0 = 555±1315 ind m^{-2}, T1 = 93±195 ind m^{-2}, $p < 0.001$).

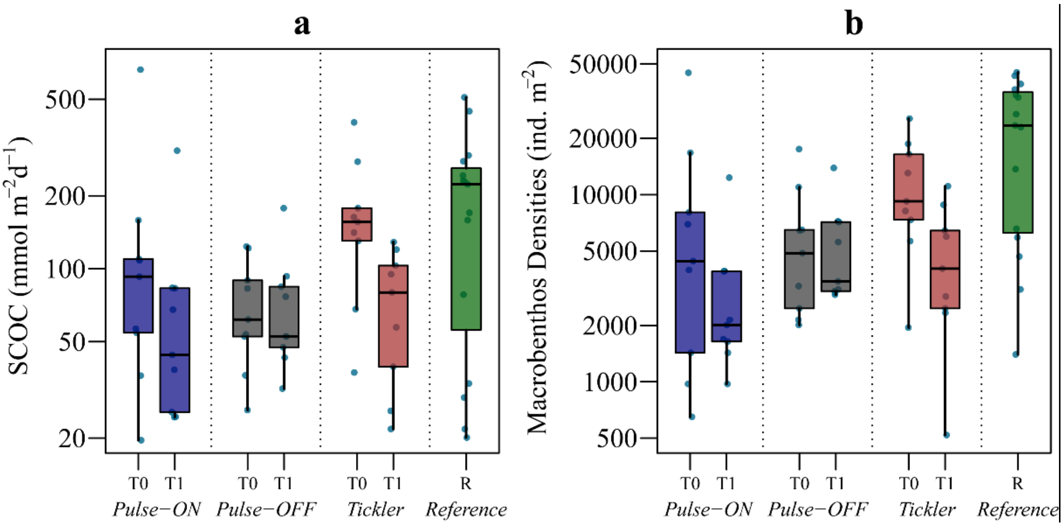


Figure 5. Oxygen consumption (a) and macrobenthos densities (b) measured from treatment plots before (T0) and after (T1) fishing and in reference stations. Y-axes are on a log-scale.

Effects of Lanice conchilega in trawled and untrawled sediments

L. conchilega was found in 68 out of 69 (98.5%) benthic sediment samples collected in this study. In pre-trawled sediments, *L. conchilega* density was explained 73% of variation in other taxon abundances (p < 0.001) and 27% of variation in species richness (p < 0.01) while no significant relationships were found for these parameters in trawled samples (p > 0.05; **Figure 6**, **Table 3**). Tubeworm densities were linked with smaller sediment grain sizes, explaining 33% of variability in the percentage of very fine sand (p < 0.05; **Table 3**) in pre-trawled samples, while this relationship was not found in trawled sediments.

L. conchilega biomass significantly predicted 88% of O_2 consumption (p < 0.001) and 22% of nitrate effluxes (p < 0.01) from undisturbed sediment. No significant relationships were found after trawling (**Figure 6**, **Table 2**).

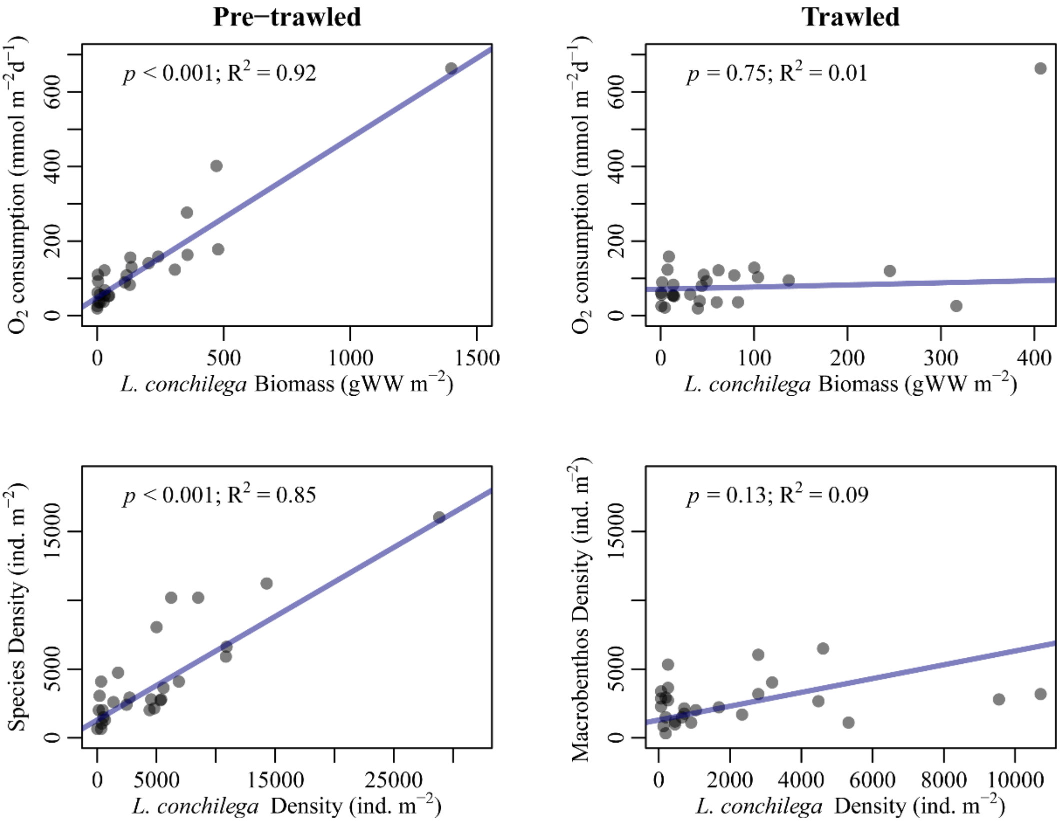


Figure 6. Robust regression analysis of oxygen consumption (mmol per m^2 per day) versus *Lanice conchilega* biomass (grams of wet weight per m^2) (top) and densities of other taxa versus *L. conchilega* densities (individuals per m^2) (bottom) in pre-trawled and trawled sediments. Note x-axis scales are different.

Table 3.
Robust regression coefficients (slope, p-value, multiple R-squared) showing the relationship of *Lanice conchilega* individual densities versus sedimentary and faunal parameters and *L. conchilega* biomass versus biogeochemical fluxes in trawled and untrawled sediments

	Parameter	*Untrawled*			*Trawled*		
		slope	*p*	R^2	*slope*	*p*	R^2
Sediment	Median grain size	-0.0012	0.29	0.07	-0.0068	0.18	0.11
	% Very fine sand	**0.0002**	**0.01**	**0.33**	0.0005	0.16	0.12
	% Silt	0.0003	0.25	0.08	0.0015	0.14	0.13
Fauna	Density of other taxa	**0.460**	**<0.001**	**0.85**	0.103	0.07	0.05
	Species richness	**0.0003**	**0.005**	**0.27**	0.0004	0.13	0.09
Fluxes	O_2 consumption	**0.427**	**<0.001**	**0.92**	0.056	0.75	0.01
	NO_3 flux	**<0.0001**	**0.002**	**0.21**	<-0.0001	0.82	0.01

Bolded values show significant relationships

DISCUSSION

Most data gathered in this study exhibited a large amount of spatial variability reflecting the dynamic nature of this coastal ecosystem (Degraer and Hostens, 2016; **Figure 3**). Despite the challenge of detecting disturbance effects in such a variable system, we were able to accomplish our objective of providing a comprehensive comparison of acute bottom trawling effects from pulse and tickler chain trawl gears. The dominance of *L. conchilega* in this habitat provided an additional opportunity to explore the effects of tubeworm abundance on environmental parameters in disturbed and undisturbed settings. Here, we discuss water column observations, trawl-induced changes to physical, biogeochemical, and ecological characteristics followed by the greater implications from these findings.

Our study also follows up on some similar research conducted in the Frisian Front region of the North Sea (Depestele et al., 2018, Tiano et al., 2019; Tiano et al., 2020). The offshore Frisian Front ecosystem (~60 km from the Dutch Coast), however, experiences much lower levels of tidal disturbance, exhibits smaller grain sizes, and holds completely different macrofaunal assemblages/biogeochemical characteristics compared to the Vlakte van de Raan (van Raaphorst et al., 1992; Dewicke et al., 2002;

Degraer and Hostens, 2016; Depestele et al., 2018). Furthermore, our study combines much of the methodology used in Depestele et al., (2018), Tiano et al., (2019) and Tiano et al., (2020), resulting in one of the most comprehensive bottom trawl studies to date. With only limited information available on the topic of trawl induced biogeochemical impacts, it is important to be able to compare disturbance effects with different ecosystem dynamics.

SPM during experimental trawling

The water column was 73-78% more turbid during tickler chain beam trawling compared to both pulse trawl treatments. As tickler chain trawls penetrate deeper into the sediment and tow at faster speeds compared to pulse trawls (Depestele et al., 2016; Depestele et al., 2018), they are predicted to mobilize more sediment (Rijnsdorp et al., 2020). However, due to the higher current speeds evident in the day prior to tickler chain trawling, we cannot be confident that this increased turbidity was the result from enhanced resuspension caused from bottom trawling alone. It is possible that trawling coupled with current induced resuspension enhanced SPM measurements during the Tickler treatment.

Our study found lower concentrations of sedimentary chl *a* after trawling suggesting that labile organic material was resuspended from the seafloor to the water column as seen in Tiano et al. (2019). SPM collected in our study, however, was inversely related to percentages of water column OC and TN. This may mean that organic matter and SPM in the water column were diluted with lower amounts of OC and TN in the resuspended sediment. Fettweis et al., (2006) attributed high turbidity in the Dutch/Belgian coastal zone, to low organic matter availability, with less cohesive particles forming a larger fraction of SPM.

Changes to the physical environment

A single trawl pass for all three treatments yielded a bathymetrical indentation ~ 1 cm in the sediment. Although neither pulse treatment (electricity on or off) was expected to deviate from each other, this study did not confirm the previous studies, which found greater bathymetrical effects with tickler chain beam trawling (Depestele et al. 2016; Depestele et al. 2018). This is likely due to softer sediments (smaller median grain sizes) in the aforementioned studies, compared to the Vlakte van de Raan. Backscatter data in our study produced similar results (after 1x and 6x trawl passes) between treatments, though spatial differences were detected in the northern and southernmost plots (**Figure 3**). Trawl marks in sandy seabeds typically reduce the backscatter value, causing more negative dB values (Roche et al., 2018). The backscatter values of the track locations in our study were consistently reduced, but the magnitude of the changes was, on average, too low to be considered as a substantial alteration in backscatter value due to trawling (Roche et al., 2018). Backscatter values can approximate sediment characteristics, but do not purely reflect sediment grain size and can be distorted by 'scatterers' such as shell debris and biogenic reefs, which may interfere with the acoustic signals. Additionally, sediment compaction in areas with high tubeworm densities may have also prevented the trawl gears from penetrating the seabed.

Tubeworm reefs in untrawled sediments were positively associated with smaller grain size fractions (**Figure 4**; **Table 3**). This pattern is commonly found with *L. conchilega* as high tube densities will slow down bottom current velocities leading to the settling of smaller particles (Van Hoey et al., 2008; De Smet et al., 2015; Foshtomi et al., 2018). Trawl induced coarsening of sediments found in *L. conchilega* dominated habitats may occur through both the resuspension and winnowing of finer grained particles from direct trawling impacts (Palanques et al., 2014; Mengual et al., 2016; Depestele et al., 2018; Tiano et al., 2019) and the alteration of sediment characteristics caused by the rapid extraction of tube structures from the seabed. With *L. conchilega*'s distinctive stabilizing effect on sediments (Rabaut et al., 2009), the additive impacts of direct trawling and decreased tube densities may lower sediment compaction as evidenced in the consistent (though statistically insignificant) increase in SPI penetration after trawl treatments (Tickler: 22%; Pulse-ON: 1.4%; Pulse-OFF: 2.3%).

This study generally found the largest alterations to sedimentary characteristics after the Tickler treatment followed by the Pulse-ON treatment with no significant effects detected after Pulse-OFF trawling. As electricity has no impact on physical sediment characteristics, the difference between the physical disturbances induced by Pulse-ON and Pulse-OFF treatments was unexpected and is attributed to the variable mechanical impact associated with pulse trawl gears (Depestele et al., 2018). Pulse trawl electrodes have the ability to penetrate the sediment but tend to 'bounce' off the seabed at erratic intervals while tickler chains maintain more consistent contact with the seafloor. This leads to a lower average penetration for pulse trawls compared to tickler chain trawls but with greater variability (Depestele et al., 2018).

Changes to biogeochemical characteristics

We detected significant declines in chl *a* from surface sediment (0-1 cm) of 63% and 37% after tickler chain and pulse trawling (Pulse-ON) respectively. These relative changes are lower than the chl *a* measured after tickler (83%) and pulse (43%)

trawling in the siltier Frisian Front sediments (Tiano et al., 2019). Sandy dynamic habitats, like the Vlakte van de Raan, exhibit more stress resilient characteristics and are generally less vulnerable to trawling impacts compared to muddier more static environments like the Frisian Front (Duplisea et al., 2001; Kaiser et al., 2006; Queirós et al., 2006; Allen and Clarke, 2007; Sciberras et al., 2016; Rijnsdorp et al., 2020). Moreover, this was demonstrated with the shallower bathymetrical change caused from trawl passes found in the current study compared to pulse and tickler chain trawling in the Frisian Front (Depestele et al., 2019).

This study, nonetheless, found stronger significant reductions in SCOC (Tickler: 57%, Pulse-ON: 46%) compared to Tiano et al., (2019; Tickler: 41%, Pulse: 33%) despite the lower mechanical impact. To put things in perspective, the absolute changes in SCOC rate (mmol m^{-2} d^{-1}) detected in the current study are 94% and 89% higher for tickler trawls and pulse trawls respectfully than the absolute changes found in Tiano et al., (2019). The relatively large changes in SCOC found in this study may be explained by the decrease in fauna such as *L. conchilega* which can be highly influential to SCOC and other biogeochemical fluxes (Braeckman et al., 2010). In addition to respiration, when *L. conchilega* (and other infauna) irrigate their burrows, they can drastically expand the surface area available for sediment-oxygen exchange (De Smet et al., 2016; Kristensen and Kostka, 2013), with major impacts to biogeochemical dynamics (Olsgard et al., 2008; Braeckman et al., 2010).

L. conchilega in untrawled sediments had a clear effect on O_2 and NO_3 fluxes, though these relationships disappeared after disturbance (**Figure 6**, **Table 3**). The change in these relationships probably came from a combination of reduced average tubeworm densities (consistently lower after trawling but only significant after the Pulse-ON treatment) and trawl-induced habitat alterations. These results support the assertion by Hale et al., (2017), that trawling decouples faunal-mediated biogeochemical processes.

The Pulse-ON treatment, which led to the biggest decrease (72%) and lowest *L. conchilega* densities after T1, was also the only experimental treatment that did not produce a significant increase in porewater nitrate concentrations. Previous research suggests a density dependent enhancement by *L. conchilega* on denitrification/nitrification processes (Aller, 1988; Braeckman et al., 2010; Foshtomi et al., 2018). Trawling has also been shown to decrease denitrification rates by altering the sediment layers that optimize denitrification (Ferguson et al., 2020). It is possible that both trawl disturbance and a loss (Pulse-ON) or retention (Pulse-OFF, Tickler) of functional species roles after trawling, played a role in the enhanced nitrate concentrations, though it is difficult to pinpoint the exact cause of this increase.

Benthic community observations

No studies have shown direct mortality to benthic species caused from electrical pulses used in experimental North Sea pulse fisheries (Polet et al., 2005; van Marlen et al., 2009; Soetaert et al., 2015; Soetaert et al., 2016; ICES, 2018, 2019, 2020; Boute et al., *in revision*). While electrical field strengths and adverse impacts from pulse stimulation have been linked to organisms with large body sizes (particularly in large cod; de Haan et al., 2016; Soetaert et al., 2016a, 2016b; Soetaert et al., ICES, 2020), there is currently no evidence for acute electrically induced injuries or mortality for benthos. Nonetheless, our study only found a significant decrease in *L. conchilega* densities with the Pulse-ON treatment. Electric stimulation used in the pulse trawl fishery is known to cause a 'muscle cramping' response in certain polychaetes (ICES, 2020). It is not known if *L. conchilega* cramps in response to electrical stimuli, though cramping may cause infauna to remain immobilized near the sediment surface in greater risk of physical removal (as opposed to escaping deeper into the sediment).

The Pulse-ON treatment also caused a significant decrease of *Eumida sanguinea*, a species closely associated to *L. conchilega* (Callaway, 2006; Rabaut et al., 2008) though other taxa, such as *Abra alba*, only showed notable decreases in response to tickler chain trawling. Nonetheless, when accounting for total macrobenthos densities, the only significant affect came from the Tickler treatment (58% decrease) reflecting the more consistent effect associated with tickler chain beam trawl gears (Depestele et al., 2018; Tiano et al., 2019). Pre-trawled habitats in this study linked *L. conchilega* to the densities of other taxa and species richness, though this relationship was no longer detected after experimental trawling (**Figure 6**, **Table 3**). This suggests that, although tubeworm densities were impacted to some extent, trawling disproportionally affected the corresponding taxa. Rabaut et al. (2008) reported changes to the intertidal *L. conchilega* reef community after beam trawling but not to the tubeworms themselves. Our research reflects some similar findings (with *E. sanguinea* in particular), however, the impact on tubeworm densities found in the current study suggests that *L. conchilega* may be less resilient to trawling than previously thought (Rabaut et al. 2008, Callaway et al., 2010).

Implications

This study found various effects from conventional tickler chain beam trawls and electric pulse trawl techniques. Though pulse trawls (and any other bottom fishing technique) can undoubtedly cause significant habitat damage, these effects tend to be quite variable (Tiano et al., 2019). The more consistent effect of tickler chain beam trawls are, on average, greater than that of pulse trawls as shown in the physical, geochemical, and species community level changes seen in this study, however, we also show that pulse trawls may be equally as damaging to certain benthos. Bergman and Meesters, (2020) found a smaller effect, of pulse trawls compared to beam trawls, on benthic megafauna in the North Sea Oyster Grounds area, while Tiano et al., (2020) found similar effects between the two gears on benthic infauna in the Frisian Front. It is likely that the lower average penetration depth of the lighter pulse trawl gears will be less damaging to many benthic communities compared to tickler chain rigged beam trawls (Hiddink et al., 2017; Depestele et al., 2018), however, this reduced effect is dependent on species assemblages and sediment type. Perhaps more importantly, there is evidence that the Dutch trawler fleet reduced its overall benthic impact when operating mainly with pulse trawls compared to periods when beam trawls were the primary gear used (Rijnsorp et al., 2020b; ICES, 2020). This is attributed to of the reduced amount of time at sea needed in order to reach their catch quotas when exploiting North Sea sole (*Solea solea*; Rijnsorp et al., 2020b; ICES, 2020).

The high SCOC values found at our experimental location imply that this community is an important site for carbon degradation (Stratmann et al., 2019). The trawl-induced declines in SCOC suggest that some disturbed locations in this community lost over half of its ability to mineralize organic material. This highlights the propensity for bottom trawling to reduce carbon cycling in marine sediments and shift the mineralization processes to the overlying water (Tiano et al., 2019). With enhanced mineralization rates in the water column (due to higher oxic conditions compared the sediment), this dynamic can lead to the removal of sedimentary carbon, increased nitrogen retention in the seabed (decreased denitrification), and a large-scale reallocation of benthic nutrients given the global scope of bottom fishing (Amoroso et al., 2018; Tiano et al., 2019; Ferguson et al., 2020).

Results in this study show that even highly dynamic coastal areas can be susceptible to significant trawl-induced changes depending on the type of benthic community present. Biogenic reef communities like the ones found in the Vlakte van de Raan, can be highly productive habitats with enhanced biogeochemical characteristics. With these features, the potential for disturbance-induced changes becomes greater if keystone species such as *L. conchilega* are affected. When assessing the vulnerability of marine habitats, environmental managers and policy makers need to consider abundant ecosystem engineers as they perform important ecological and biogeochemical functions.

Acknowledgements

We would like to thank the crews of the TH6 for YE238 for their excellent work and coordination in making multiple trawled areas. We are grateful to the crew of the Simon Stevin for helping us collect our data. We also thank the students working at ILVO who helped process our macrofauna samples. This work would not have been possible without the collaboration with the Flanders Marine Institute (VLIZ) who provided the RV Simon Stevin, along with the multiple data collection devices (multi-beam, CTD, SPI etc.). This research is partially funded by the European Maritime and Fisheries Fund (EMFF) and the Netherlands Ministry of Agriculture Nature and Food Quality (LNV).

Supplementary Materials for Chapter 5:

Ecosystem impacts from electric pulse and conventional beam trawls in subtidal Lanice conchilega reef communities

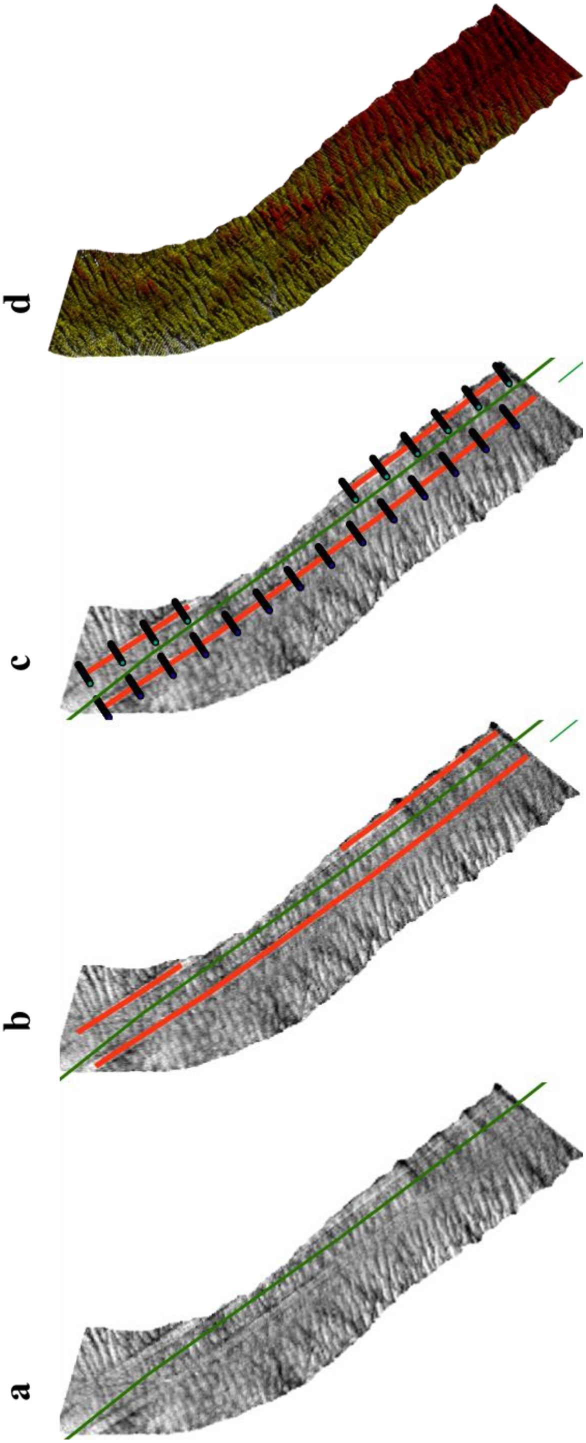


Figure S1. Identification of trawl tracks using backscatter (a-c) and bathymetry (d) imagery.

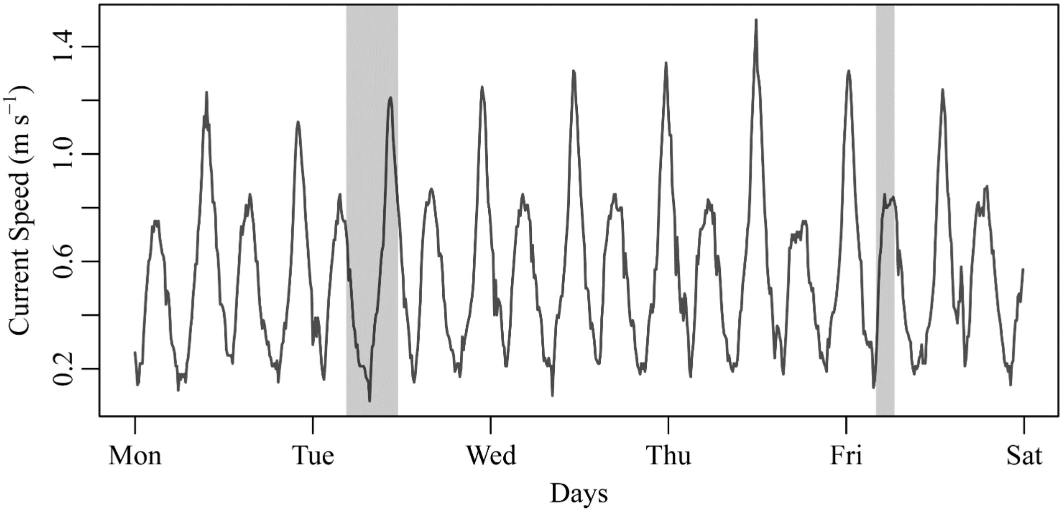


Figure S2. Water current speeds during the week of bottom trawl measurements. The shaded region on the left indicates the time of pulse trawling while the shaded region on the right indicates the time of beam trawling. This data was obtained from the “Scheur Wielingen” measuring station located in the Vlakte van de Raan.

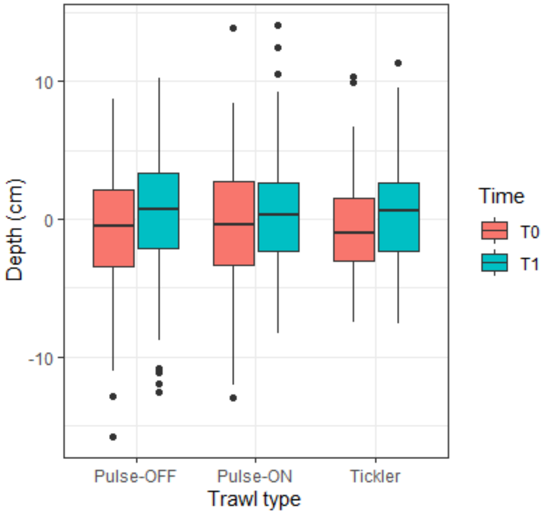


Figure S3. Bathymetrical changes. Delta-values give the differences in water depth outside and inside the location of the track before (T0) and after (T1) trawling

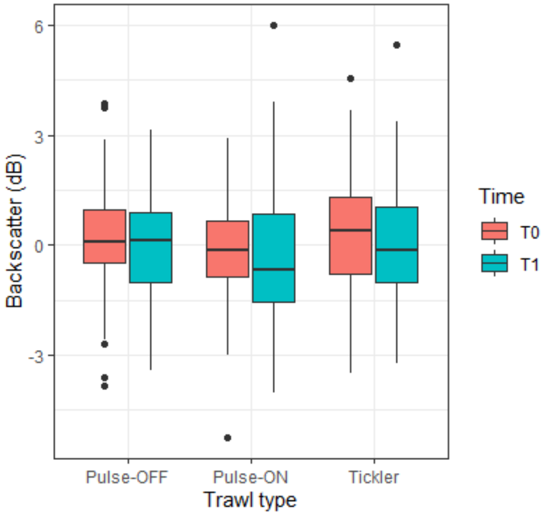


Fig S4. Changes in backscatter. Delta-values give the differences in backscatter outside and inside the location of the track before (T0) and after (T1) trawling.

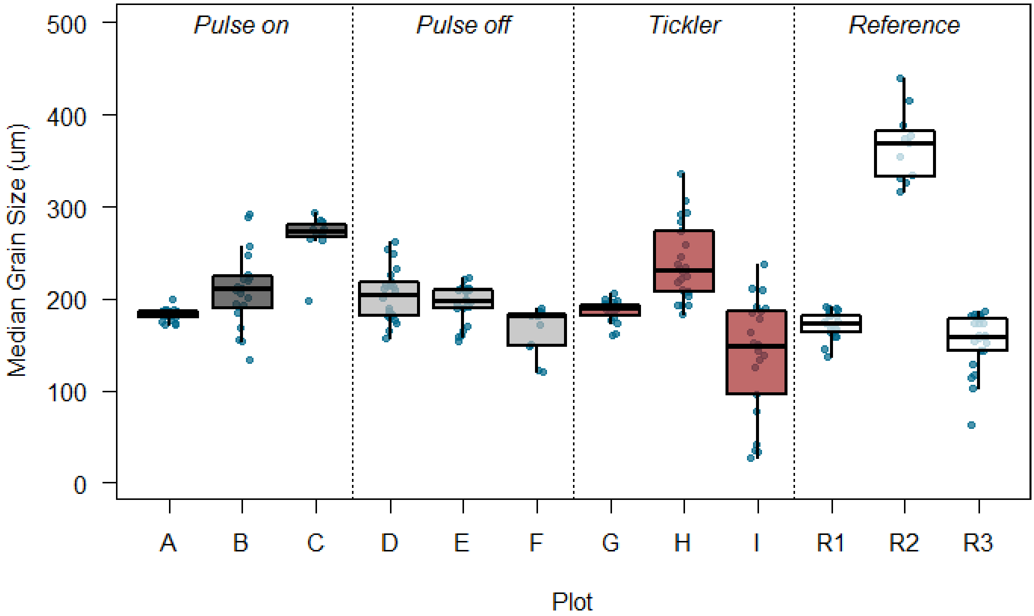


Figure S5. Median grain sizes found in T0 experimental (pulse on, pulse off, tickler) plots and reference locations.

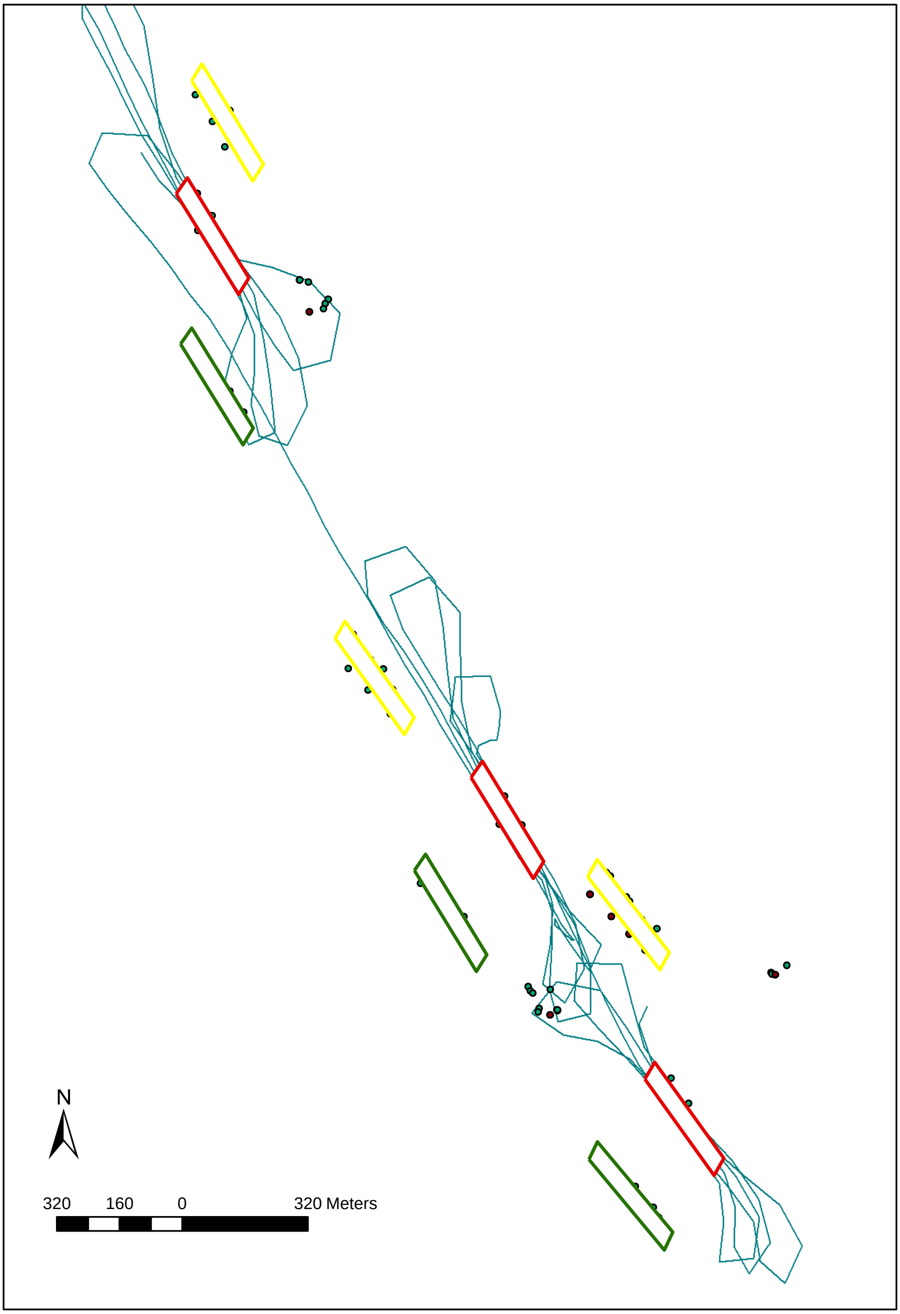


Figure S6. Beam trawl fishing paths through “tickler” treatment plots. Dots are SPI and boxcore sample locations.

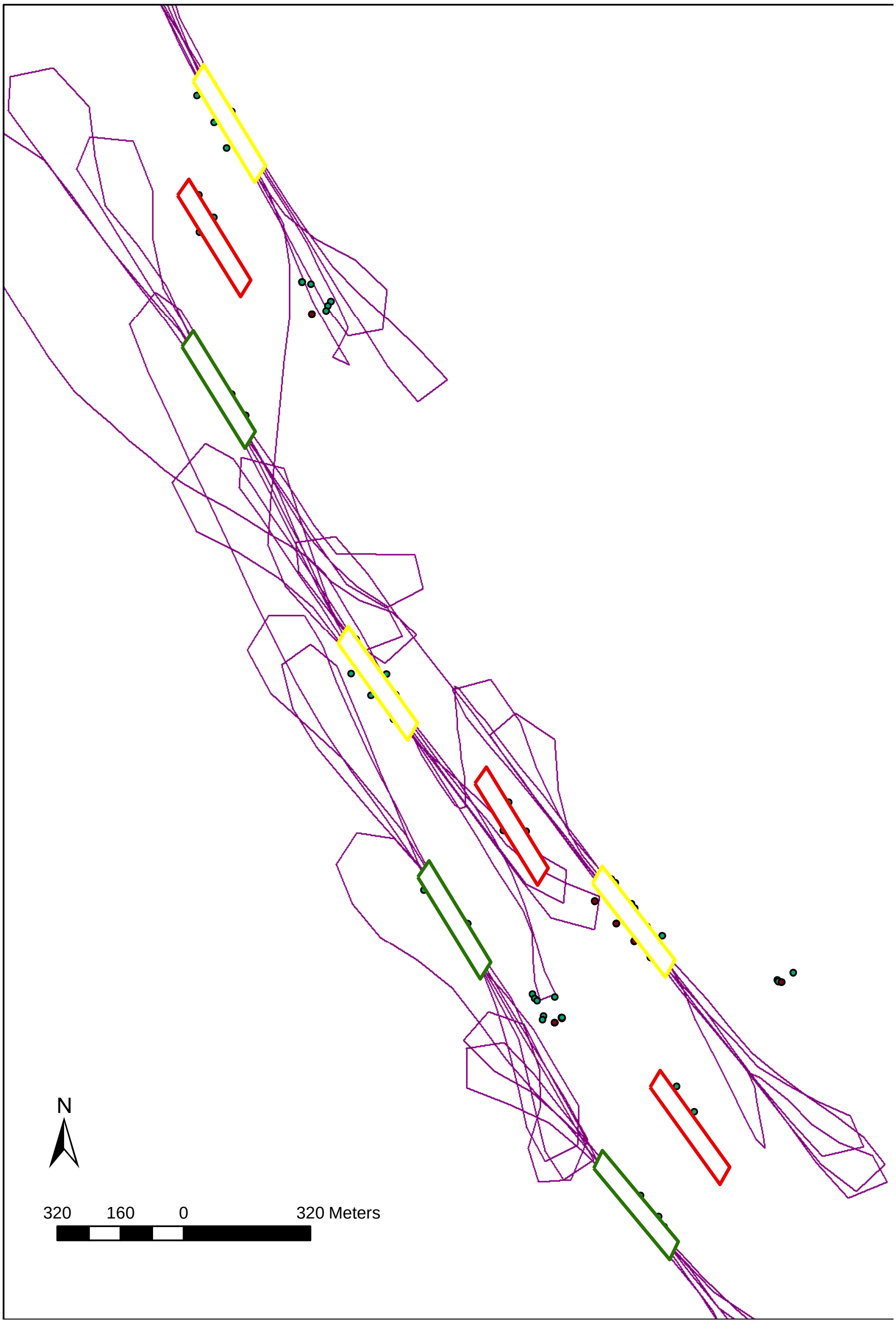


Figure S7. Pulse trawl fishing paths through “pulse on” and “pulse off” treatment plots. Dots are SPI and boxcore sample locations.

Table S1.
Backscatter changes following the one trawl pass (dB).

Treatment	Time	mean	sd	Q25	median	Q75	Q025	Q975	CI95	n
Pulse-OFF	T1-T0	-0.23	1.87	-0.30	-1.39	0.92	-3.49	3.31	6.81	88
Pulse-ON	T1-T0	-0.20	2.25	-0.47	-1.62	0.98	-4.00	4.58	8.58	74
Tickler	T1-T0	-0.30	2.09	-0.38	-1.70	1.31	-4.54	3.24	7.78	89

Table S2.
Comparison of backscatter statistics (dB) of the entire plot for each treatment (6 trawl passes)

Treatment	Time	mean	sd	Q25	median	Q75	Q025	Q975	CI95	n
Pulse-OFF	T0	-26.57	2.51	-28.43	-26.54	-24.65	-31.26	-21.50	9.76	156016
Pulse-OFF	T1	-26.64	2.20	-28.12	-26.54	-24.97	-30.95	-22.45	8.50	162561
Pulse-ON	T0	-25.74	2.30	-27.17	-25.60	-24.34	-30.32	-21.19	9.13	129962
Pulse-ON	T1	-25.83	2.22	-27.17	-25.91	-24.34	-30.32	-21.50	8.82	162605
Tickler	T0	-25.66	2.18	-27.17	-25.60	-24.34	-30.00	-21.19	8.81	147976
Tickler	T1	-25.40	2.12	-26.86	-25.44	-24.02	-29.53	-21.19	8.34	162578

Chapter 6 General Discussion

A scientific verdict on pulse trawling and further exploration of human impacts on biogeochemistry

RV Tridens Beam Trawl Survey
(Somewhere in the North Sea)

Photo: Justin Tiano

The work conducted during this PhD has often bridged gaps between applied and fundamental research. One of our main objectives was to investigate and assess the possible impact of electric pulse trawls, which at the time of writing, remains a politically charged topic. The information gained from exploring this subject can have immediate political and societal implications, as our results and recommendations are enough to facilitate scientifically informed decisions (ICES advice, 2020). On a broader scale, the impacts of anthropogenic disturbance on marine biogeochemical cycles and bentho-pelagic coupling, continues to be a relatively unexplored field of study. Because of this, we often delved into topics with little known baselines and contrasting results (ex. disturbance effects on organic matter [OM]). There is still much room for discovery on the topic of disturbance-induced biogeochemical changes, but we are happy to add our grains of salt to the sea of knowledge. This chapter begins by discussing what this work means for pulse trawling (applied implications) and for general anthropogenic impacts on marine biogeochemical cycling (fundamental implications).

WHAT THIS RESEARCH MEANS FOR PULSE TRAWLING

It is important to note that the majority of the research carried out during this PhD investigated the effects of pulse trawls for the Dutch sole fishery and not electrotrawls for brown shrimp (Desender, 2018) or electrofishing for razor clams (Murray et al., 2016). This PhD was conducted in the background of key political events surrounding the topic, including the EU parliamentary vote to ban marine electric fishing (Kraan et al., 2020) and the release of two ICES (International Council for the Exploration of the Sea) advice documents on the environmental impacts of pulse fishing (ICES, 2018; ICES, 2020). Throughout the media attention and contact from interest groups we received, our role was to remain separate from the politics to provide a neutral and unbiased assessment of pulse trawling. Nevertheless, to understand the implications of our work, it is important to know the greater context of the situation. Here, we discuss why these gears are controversial, where our findings fit in the pulse fishing story, what we can conclude based on the research conducted so far, and what needs further investigation.

Criticism and context

The use of marine electrotrawls in the North Sea has been met with widespread criticism from environmental groups and small-scale fishermen. Non-governmental organizations have remarked on the potential consequences of the novel bottom trawl gears on marine habitats as well as the (excessive) increase of Dutch pulse trawl permits (Le Manach et al., 2019). Pulse trawlers have a competitive advantage over small-scale fishermen and traditional beam trawlers when exploiting North Sea sole (Sys et al., 2016). In the Netherlands, the transition from conventional to pulse trawl gears benefited the fishermen that used them but led to negative economic consequences to foreign and domestic competitors (Haasnoot et al., 2016; Sys et al., 2016). Another source of criticism stemmed from the fact that pulse trawling gained widespread use amongst the Dutch trawler fleet before their environmental consequences could be fully evaluated.

We now know that the increased efficiency of pulse trawlers led to fishermen reaching their quotas earlier, thus spending less time at sea fishing for sole (Rijnsdorp et al., 2020b). This, along with slower towing speeds, is predicted to significantly reduce trawling impacts on benthic biomass, sediment resuspension, and overall footprint, in comparison with tickler chain beam trawlers (Rijnsdorp et al., 2020b). Lower fuel emissions, enhanced selectivity of target species (van Marlen et al., 2014; Batsleer et al., 2016) and higher rates of discard survival (van der Reijden et al., 2017), provide further evidence of improvement for pulse versus beam trawls. Depestele et al., (2018) showed that, on a scale of a few days, the redox conditions recover faster after pulse trawling compared to tickler chain trawling. As the visible sediment oxidized layer (aRPD) is often associated with bioturbation activity, this may also mean that the recovery of sediment faunal functioning may also take longer after beam trawling than after pulse trawling. The results of this PhD, however, suggest that, in terms of direct benthic impacts, pulse trawls offer only a moderate improvement compared conventional methods.

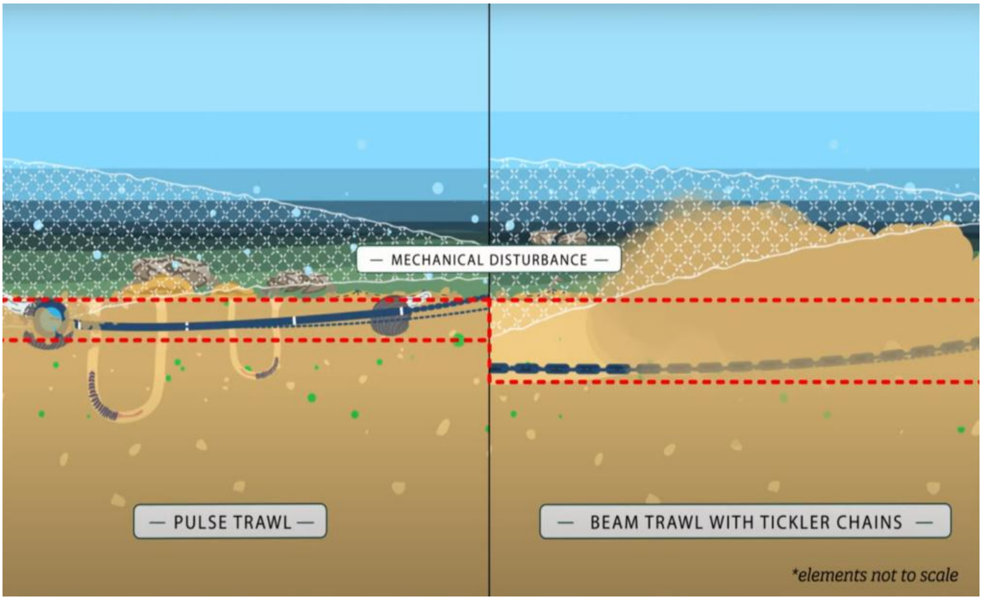


Figure 1. Screenshot from Wageningen Marine Research video on the "Effects of pulse fishing on the seafloor and benthos". Illustration shows mechanical penetration of pulse (left) versus tickler chain beam (right) trawls in the seabed. https://www.youtube.com/watch?v=pSjFQEBxjpc

Implications for pulse trawling from this PhD research

We can most likely conclude that the direct benthic impact of electrical stimulation from pulse trawls is minimal, therefore, linking the majority of its effects to mechanical disturbance (ICES, 2020, Boute et al., *in revision*; **Chapter 4**; **Figure 1**). With lower gear penetration into the seabed for pulse trawl gears compared to beam trawls (Depestele et al., 2016; Depestele et al., 2018), it is expected that the consequences on benthic communities will also be reduced (Hiddink et al., 2017; Bergman and Meesters, 2020; Rijnsdorp et al., 2020). Yet, the field data we collected in **Chapter 3** and **Chapter 5**, contained mixed results. Tiano et al., (2020/**Chapter 3**) found no detectable differences between the impacts of pulse trawls and beam trawls on benthic infaunal communities in the Frisian Front. The significant decrease from beam trawls, but not pulse trawls, on *total* community densities found in **Chapter 5**, suggests a greater, or rather, more consistent effect of tickler chain versus pulse trawlers on coastal *Lanice conchilega* reefs (though pulse trawls created a significant reduction in *L. conchilega* densities). When comparing bottom trawl effects on benthic megafauna in the Oyster Grounds, Bergman and Meesters, (2020) found a reduced effect of pulse compared to conventional tickler chain trawls. The varied results from these studies suggest that any reduced effect from pulse trawls on benthic communities is not consistent and is probably dependent on benthic species assemblages and sediment type.

In situ effects of pulse and beam trawls on biogeochemical parameters seen in **Chapter 2**, followed patterns of mechanical disturbance found in Depestele et al., (2018) showing significant but reduced effects from pulse trawls in the Frisian Front. **Chapter 5**, which incorporated the same methodology used in Depestele et al., (2018), did not find a detectable difference in the mechanical impact from the two gears but did find a greater biogeochemical effect from tickler chain beam trawls.

Our experimental results suggest a reduced biogeochemical impact from pulse trawls, however, De Borger et al., *under review* predicts that, on larger spatio-temporal scales (assuming a direct head to head comparison), effects on carbon and nitrogen cycling may end up being similar between both gears. This is due to the fresh OM (which drives sedimentary biogechemical processes) settling and concentrating on the sediment surface. Even light mechanical effects are able to resuspend the surface layer of fresh OM, displacing it and reducing most mineralization (degradation of OM) processes (Dounas et al., 2005; De Borger et al., *under review*). We speculate that due to the lower mechanical disturbance, the recovery time of biogeochemical characteristics from pulse versus beam trawl impact, can be moderately reduced (possibly differing by a few days between the impacts from both gears) but will take longer in biogeochemically active locations (**Chapter 4**; Depestele et al., 2018). When comparing head to head scenarios with long-term trawling simulations (with multiple events per year), however, this disparity seems to go away and the impact/recovery becomes similar between the two gear types (De Borger et al., *under review*).

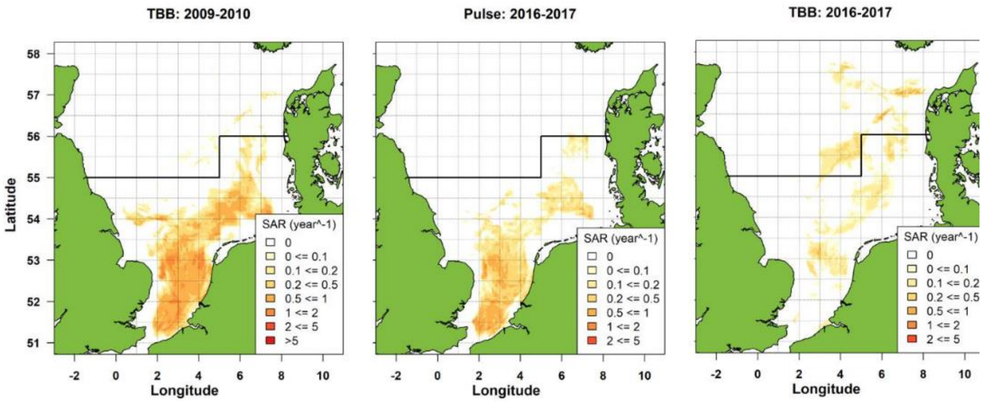


Figure 2. Spatial distribution of trawling intensity (annual swept area ratio SAR) of the total Dutch beam trawl fleet before (beam trawl = TBB 2009 – 2010) and after (Pulse 2016 – 2017 and TBB 2016 – 2017) the transition to pulse fishing. Figure from Rijnsdorp et al., 2020.

Conclusions and recommendations regarding pulse trawling

In terms of pulse trawling, some of the main conclusions we can draw from this PhD are:

1) Any direct biogeochemical response to pulse trawl-induced electricity is either undetectable or extremely limited due to the alternating (bi-polar) pulsed currents (**Chapter 4**).
2) Biogeochemical effects from pulse trawls are moderately reduced compared to beam trawls due to lower mechanical disturbance, at least on the short term (**Chapter 2**, **Chapter 5**).
3) The effects of Pulse trawls on benthic communities can be just as impactful as beam trawls but are not likely to be worse (**Chapter 3**). These effects are, however, more variable than that of beam trawls and can be comparatively smaller in certain habitats and communities (**Chapter 5**).

In light of what we now know about elecrotrawl gears, we can conclude that the main benefit to benthic ecosystems from pulse trawls does not come from a reduced level of direct bottom disturbance compared to traditional methods, but rather from their higher catch efficiency, which leads to a lower ecological footprint (Rijnsdorp et al., 2020; **Figure 2**). While decreased bycatch (van Marlen et al., 2014) and lower levels of mechanical disturbance (Depestele et al., 2016; Depestele et al., 2018) are an improvement upon traditional methods, less time needed at sea is, by far, the greatest benefit of pulse trawls on benthic marine ecosystems. Bottom trawls, by definition, have some form of contact with the seafloor, and evidence suggests that even minor levels of disturbance are enough to generate a significant biogeochemical response (Dounas et al., 2005; De Borger et al., *under review*). The strategies that we recommend to reduce fisheries impacts on the benthic environment come from either spatial or temporal management of bottom trawl efforts and/or from the transition to gears that can reduce spatio-temporal ecological footprints. As pulse trawls encompass the latter, and have the added advantages of higher selectivity, lower mechanical disturbance and reduced fuel use, it is only logical to recognize their advantage over tickler chain beam trawl gears. This is supported by the ICES Advice documents on pulse trawling from 2018 and 2020 that took into account research from this PhD thesis (ICES, 2018; ICES, 2020). The most recent advice concludes that pulse trawling poses fewer ecological and environmental risks to to North Sea habitats compared to conventional beam trawls (ICES, 2020).

Nevertheless, there is a level of disturbance associated with any bottom trawl gear and pulse trawls are not exempt from this. Opponents of pulse trawls who claim that these methods are more destructive to benthic ecosystems compared to small scale fishing techniques (long-lines/gillnets etc.) are correct with these assertions. If only small-scale methods are used and all types of bottom trawling was stopped, the impact to the benthic environment would probably be much lower. If, however, all Dutch trawlers were to transition back to traditional beam trawling (or another type of ineficient fishing gear), the ecological footprint from flatish trawling and risk of degradation to North Sea ecosystems may be greater than if pulse trawling were to continue (**Figure 2**).

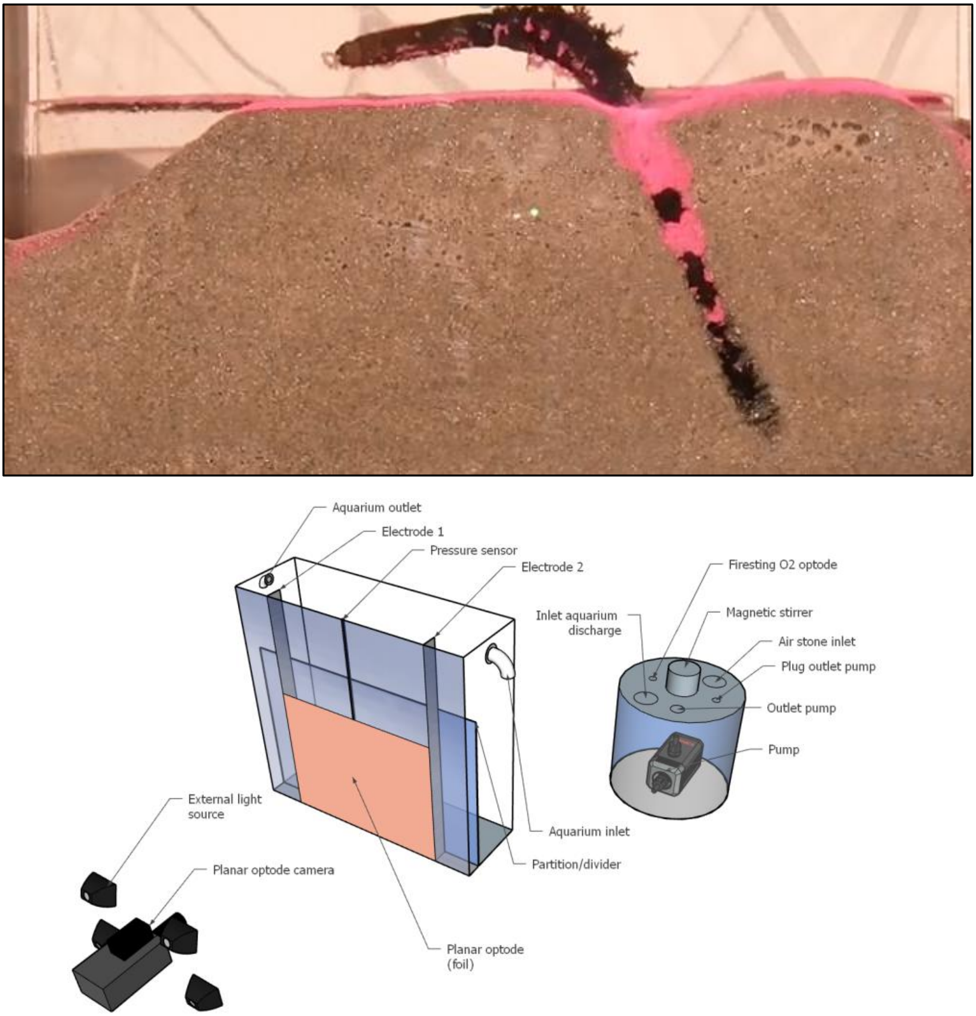


Figure 3. A lugworm (*Arenicola marina*) burrowing into the sediment in an aquarium to test its response to electrical stimulation. Pink luminophores were added to observe bioturbation activities (*top*). Experimental setup to measure faunal-mediated effects to oxygen from electrical stimulation (*bottom*).

Knowledge gaps and future work

The scope of this PhD did not encompass a detailed assessment of marine electric fishing methods used for shrimp or razor clams. Though we briefly experimented with electric razor clam exposure times and electrical parameters in **Chapter 4**, and found that pulse direct currents (PDC) may generate biogeochemical responses, we did not use a treatment with shrimp pulse parameters. Shrimp electrotrawls use low frequency

(5 Hz) unidirectional pulses, however, because of the low duty cycle (0.25%) used by shrimp pulse gears compared with high frequency pulse gears for sole (40 Hz; 2% duty cycle), shrimp pulse settings are not likely to generate a significant biogeochemical response even with PDC waveforms (de Haan et al., 2016; Desender et al., 2017). Unpublished laboratory experiments conducted during this PhD found decreases in pH in saltwater aquariums during 10 minutes of electrical exposure for high frequency (80 Hz) PDC but not from low frequency (5 Hz) PDC (shrimp pulse) or high frequency (40 Hz) pulsed bi-polar currents (PBC, sole pulse; see Soetaert et al., 2019 for details on electric pulse parameters). Though electrolysis effects from shrimp trawls have not been thoroughly researched, the electrical parameters they use are not expected to generate a biogeochemical response.

Perhaps the biggest knowledge gap that remains, when assessing electric pulse-induced biogeochemical effects, is the indirect effects of electrical exposure to faunal-mediated biogeochemical functioning. As macrofauna often exert profound effects to sediment biogeochemical dynamics (Braeckman et al., 2010), any potential impediment to their normal activities may affect local carbon and nutrient cycling. During this PhD, some work was started on the effects of electricity on *Arenicola marina*-mediated oxygen dynamics in the sediment (**Figure 3**). Preliminary findings suggested non-lethal effects of electric pulse exposure, which may temporarily affect bioirrigative functioning. More work is necessary in order to fully realize these results and to test if/how fisheries-induced electric exposure has a lasting effect on faunal-mediated biogeochemical processes.

Our knowledge of bottom fishing-induced effects on sediment biogeochemistry and benthic pelagic coupling, is not nearly as concrete as other fisheries related topics (*i.e.* effects on benthic communities). While we can make recommendations based on larger/smaller effects from certain types of fisheries, more research is needed to verify and understand the wider scale implications from these results. Longer-term impacts of fishing can be difficult to tease out from environmental factors (van Kooten et al., 2015). Nonetheless, researching challenging broad-scale topics is of particular importance for the conservation of benthic ecosystems. A logical next step to build upon this PhD research can be to upscale our findings through predictive modelling (**appendix**) and/or to and couple fishing intensity data (**Figure 2**) with biogeochemical information from select locations. Even with a ban on pulse trawling, future research outlined in the BFIAT (Bottom Fishing Impact Assessment Tool) project outlined in the **appendix** section of this thesis aims to allow predictions and comparisons of various types of bottom trawl gears by running scenarios of fishing gears with different sediment penetration depths. Initiatives such as this will allow us to continue our investigation of different innovative gears and hopefully demonstrate their true ecosystem effects to the public regardless of the political outcomes.

WHAT THIS RESEARCH MEANS FOR GENERAL ANTHROPOGENIC IMPACTS ON BIOGEOCHEMICAL CYCLES

There is only a limited amount of literature on the topic of biogeochemical effects caused by bottom trawl gears (much of which is summarized in **Chapter 1**). When reviewing contrasting results on topics such as the effects of bottom fishing on OM and/or benthic mineralization (increase/decrease), it is clear that we still have a narrow understanding of this subject. Trawl-induced changes to nutrient cycling may alter benthic pelagic coupling and can potentially lead to severe consequences to marine ecosystems through eutrophication (Dounas et al., 2007), low oxygen zones (Riemann and Hoffman, 1991), and long-term changes to benthic communities (Pilskaln et al., 1998). The possibility that trawling will consistently lead to these outcomes, however, is uncertain and can vary greatly depending on hydrodynamics, sediment characteristics, local primary production and other factors. In order to best mitigate the negative ecosystem effects of bottom trawling and other types of anthropogenic disturbances, we must increase our understanding of the topic through continued research. The following discusses the application of anthropogenic electrolysis in marine environments, possible reasons behind contrasting results from bottom trawl studies, and biogeochemical implications from this PhD research. Finally, we end this thesis by discussing the fundamental conclusions from this PhD and ideas about how to build upon this work.

Human-induced electrolysis

One of the topics we address in **Chapter 4** is the possibility of marine electrolysis caused by anthropogenic activities. In the case of electric fishing, any electrolysis occurring would be an unintentional consequence, thus, it is purposefully minimized with the use of PBC or alternating continuous currents (AC; Soetaert et al., 2019; **Chapter 4**). Humans do, however, use electrolysis to manipulate biogeochemistry on a regular basis. In addition to the industrial production of metals and chemical compounds, electrochemistry is used to treat of wastewater by removing organic carbon compounds (Chopra et al., 2011; Peixoto et al., 2013). In the marine environment, electrolysis has been used for coral reef restoration by causing the electrochemical-mediated precipitation of minerals, providing a suitable substrate for coral recruitment (Goreau, 2012).

It has been postulated that eutrophication can be mitigated by using electrodes to limit the release of sedimentary phosphorus (Martins et al., 2014). This involves a process similar to the microbial-induced electrogenic mobilization and dissolution of reduced iron, which occurs naturally in certain marine ecosystems (Sulu-Gambari et al., 2016). Our experiments in **Chapter 4** resulted in a similar effect, as two minutes of electric stimulation (high frequency PDC) to the sediment caused enough mobilized iron oxidation to remove the equivalent of 25-28 hours of natural sedimentary phosphate removal from the water column. Though the objectives of this PhD did not involve aquatic ecotechnology, our results support the notion of electrode-mediated phosphate removal as an ecotechnological method for managing nutrient dynamics (Martins et al., 2014). Concurrently, the unintended consequences of human-induced marine electrolysis (*ex.* the submersion of metals with differing electrical potentials into seawater) may inadvertently affect bentho-pelagic phosphorus coupling, though this effect will be lessened in sediments with high OM content (Weng et al., 2012; **Chapter 4**).

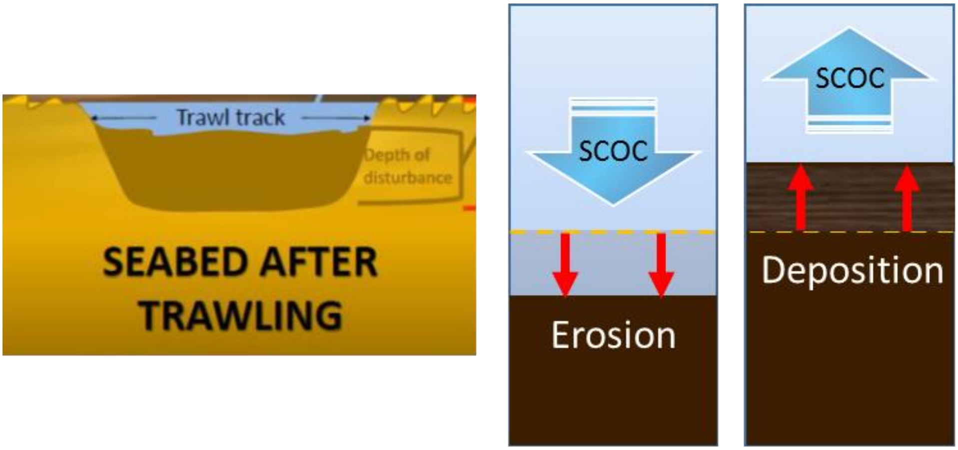


Figure 4. Concept of the direct effect from trawling on sediment erosion and homogenization (*left*) adapted from Depestele et al., (2018). How sediment oxygen consumption (SCOC) can be affected by erosion (decreased SCOC) and deposition (increased SCOC; *right*)

Resolving discrepancies between trawling, organic matter and benthic mineralization

The fate of OM and benthic mineralization in trawl disturbed sediments remains a mystery riddled with results that seem to contradict one another. Some studies on this topic have reported depleted OM coupled with lower benthic mineralization

(Mayer et al., 1991; Brylinsky et al., 1994; Watling et al., 2001; Pusceddu et al., 2014; **Chapter 2**; **Chapter 5**) while others observed the opposite effect (Polymenakou et al., 2005; Pusceddu et al., 2005; Palanques et al., 2014; Sciberras et al., 2016; van de Velde et al., 2018; Paradis et al., 2019). We, however, believe that the contrasting results on this topic may all be correct under differing circumstances.

The trawl-induced resuspension and subsequent winnowing of silt and clay particles lead to the upward coarsening of the sediment column (Mengual et al., 2016; Depestele et al., 2018). This provides a logical explanation for decreased concentrations of sedimentary OM, which are attached to fine particles (Virto et al., 2008; **Chapter 2**). Lower amounts of fresh OM on the sediment surface can lead to reduced benthic mineralization and vice versa (Paradis et al., 2019; **Chapter 2**; **Chapter 5**). However, the anthropogenic mixing of muddy sediments in particular, can also temporarily increase benthic metabolism with a conspicuous shift from anoxic to oxic mineralization pathways (van de Velde et al., 2018; De Borger et al., *under review*). The reactivation of refractory OM fractions, as they mix with labile OM from the sediment surface (OM priming), can also increase benthic mineralization rates (van Nugteren et al., 2009; van de Velde et al., 2018). Results from our field studies suggest that, after bottom trawling, fine sand and muddy sand habitats in the North Sea will experience a depletion of chl *a* from the sediment surface leading to lower benthic mineralization in directly impacted areas (**Chapter 2**; **Chapter 5**; **Figure 4**). Yet, habitats with differing hydrodynamics and/or sedimentary properties may not yield the same results.

In **Chapter 4**, we observed the aftermath of sediment resuspension events in a closed system. Rather than the upward coarsening exhibited in the trawled sediments of various other studies (Brown et al., 2005; Mengual et al., 2016; Depestele et al., 2018; Tiano et al,. 2019/**Chapter 2**; **Chapter 5**) smaller resuspended particles in a closed environment cannot be winnowed away by currents and thus, settle on the sediment surface with corresponding OM content (**Chapter 4**). In relatively static environments with little hydrodynamic movement, trawl-induced resuspension can lead to the fining of surface sediment layers (Trimmer et al., 2005). The deposition of silt/clay particles may reallocate and concentrate OM to the sediment surface after trawling, though, this effect is likely maximized in areas of low hydrodynamic energy (Trimmer et al., 2005; **Chapter 4**).

While sediment erosion can lower benthic mineralization, the deposition of fresh sediment and OM can have the opposite effect (Paradis et al., 2019; Tiano, *unpublished data*; **Chapter 2**, **Chapter 5**; **Figure 4**). The studies that connect trawling with enhanced OM/mineralization, tend to collect samples in areas either before and during regional trawling periods or they contrast habitats known for high and low trawl disturbance (Polymenakou et al., 2005; Pusceddu et al., 2005; Palanques et al., 2014; Sciberras et al., 2016). It is possible that these studies measure the depositional effect of trawling (regional effect) while the experiments that report reduced OM/mineralization are looking at the erosion effects found in the directly impacted areas (i.e. inside the trawl tracks) (Mayer et al., 1991; Brylinsky et al., 1994; Watling et al., 2001; Tiano et al,. 2019/**Chapter 2**; **Chapter 5**; **Figure 4**). Simultaneously, the effects of sediment transport on macrofauna can add complexity to these dynamics. Deposition can have a smothering effect on benthic macrofauna and if deposited sediment is not sufficienly enriched with OM, faunal mortality and subsequent loss in respiration can lead to decreased SCOC (Mestdaugh et al., 2018). There is still much left to discover in order to truly decipher the biogeochemical effects from trawl disturbance, however, as we continue our exploration of this topic, we are improving our understanding of anthropogenic effects on greater ecosystem processes.

Potential effects of reduced nutrient cycling

One important ecosystem service provided by marine sedimentary habitats is their propensity to remove nutrients, thus providing a buffer against eutrophication (Slomp et al., 1996; Soetaert and Middelburg, 2009). The experimental and modelling work that we have conducted on trawl-induced biogeochemical effects, imply that bottom trawling in the North Sea not only results in the release of porewater nutrients, but can lead to lower total mineralization rates and reduced amounts of carbon in the sediment (**Chapter 2**; **Chapter 4**; **Chapter 5**; De Borger et al., *under review*). In addition to affecting organic carbon mineralization, trawling is predicted to significantly reduce rates of benthic denitrification (van der Molen et al., 2013; Ferguson et al., 2020; De Borger et al., *under review*). These effects equate to a general reduction of sedimentary nutrient cycling and increased nutrients in the water column.

In addition to the increased risk of eutrophication, trawl-induced sediment resuspension can cause rapid reductions in water column oxygen levels (**Chapter 2**). The increased water column oxygen demand observed in **Chapter 2** was short-lived. This effect, however, can potentially trigger the increase of low oxygen zones in the bottom water, which occurs regularly in certain North Sea habitats (Weston et al., 2008; Greenwood et al., 2010; Almroth-Rosell et al., 2012). Reduced bottom oxygen levels in the North Sea are predicted to increase with climate change, enhancing the possibility of additive impacts (trawling + eutrophication + warm temperatures) on marine oxygen dynamics (Weston et al., 2008; van der Molen et al., 2013).

Sediment community oxygen consumption (SCOC) can be used as a proxy for total mineralization as it takes into account oxic and anoxic OM degradation processes (Stratmann et al., 2019). SCOC rates observed in, Chapter 2 and Chapter 5 show that acute trawling can decrease benthic mineralization rates from 33% to 57% in North Sea sediments. Eigaard et al., (2016) estimated that 63% of North Sea sediments are trawled between 1 and more than 10 times per year. It is possible that every year, large areas of the North Sea temporarily lose a significant amount of their carbon mineralization capacity due to trawl activity (Chapter 2; Chapter 5). The recovery of these habitats is governed by the arrival of new OM which stimulates carbon mineralization and nutrient cycling in the sediment (Paradis et al., 2019).

General conclusions and recommendations for future work

Given the historical levels of bottom trawling across the world's oceans, it is likely that trawling has played some role in global biogeochemical cycles. Though there is much room left to improve our understanding of these effects, this PhD has contributed some novel insights into trawl-induced biogeochemical impacts. Some of our main fundamental conclusions are:

1) Bottom trawling can lower benthic oxygen consumption and OM mineralization rates to over half of their pre-trawled levels (**Chapter 2**; **Chapter 5**).
2) Trawl disturbance can create a competitive advantage for deep burrowers over epifauna and shallow burrowers (**Chapter 3**).
3) The release of nutrients from physical disturbance is higher in late summer/autumn, when sediment grain sizes are smaller, and with sediments rich in fresh OM (**Chapter 4**).
4) The settling dynamics of resuspended sediment and OM will vary depending on grain size characteristics (**Chapter 4**).
5) Biogeochemical impacts from bottom trawls on biogenic communities can be remarkably higher than in pure sedimentary habitats (**Chapter 5**).

As trawl impacts on biogeochemical parameters seem to differ depending on the types of habitat, benthic assemblages and hydrodynamic regimes, more work is necessary to gain a mechanistic understanding as to why these variations occur. Experimental studies can be combined with modelled predictions to better understand the trawl-induced mixing, resuspension and deposition of organic particles. This is precisely the aim of the accepted BFIAT proposal detailed in the **appendix** section of this thesis. The BFIAT project will build on the work conducted in this PhD thesis to be able to predict ecosystem effects of different types of bottom trawling depending on their gear penetration depth in the sediment. It may also be a possibility that trawling has an indirect effect on benthic herbivory levels, potentially leading to higher sedimentary OM; a topic that may be explored through longer term *in situ* and *ex situ* experiments.

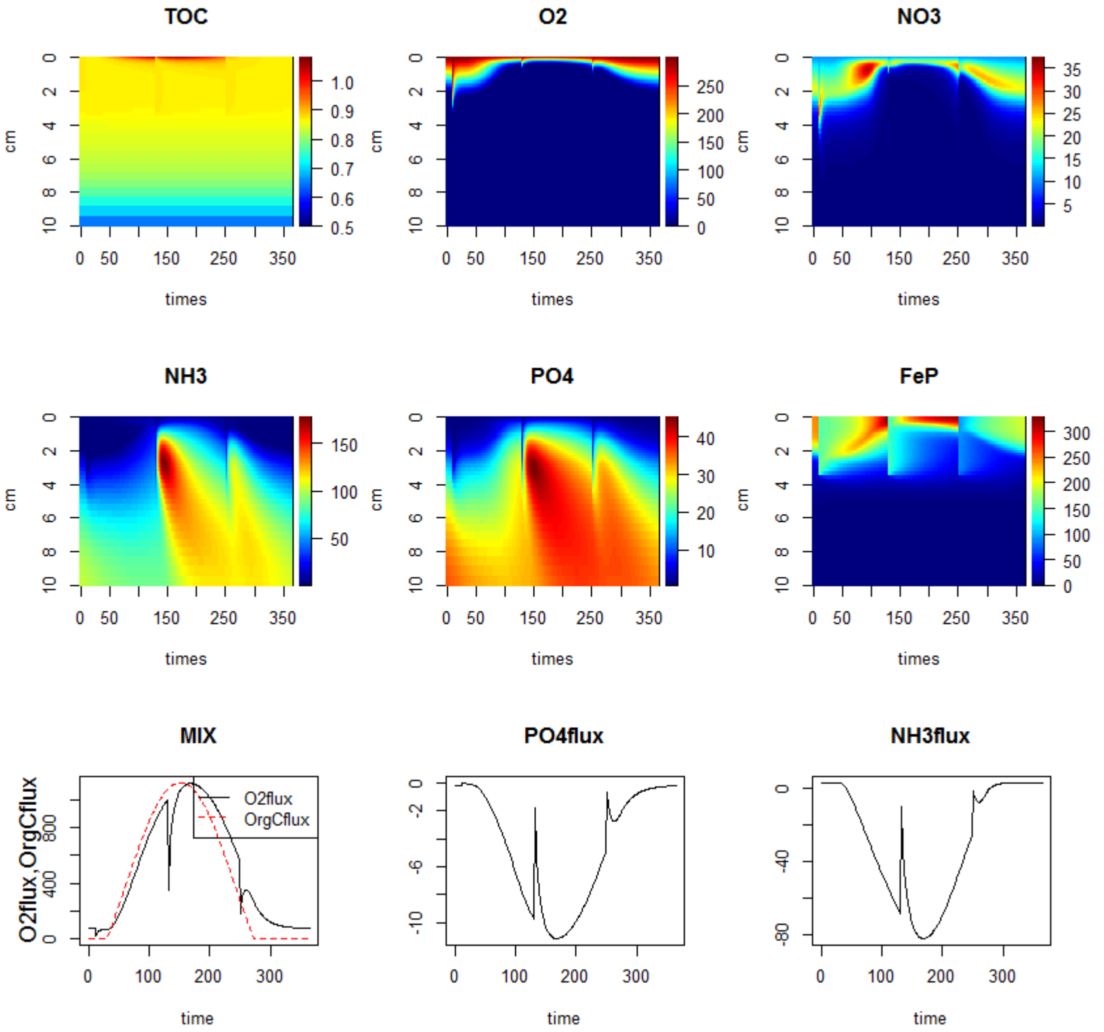
Our work is relevant to gain a better understanding of, not only bottom trawl impacts, but general disturbance effects on seabed habitats. While trawling can lead to severe local impacts, natural disturbance has a much broader effect and resuspends significantly more sediment than bottom trawling (Ferré et al., 2008). To put the effects of trawling into context, connections and comparisons must be made between natural and anthropogenic disturbances. It is important for us to deepen our fundamental knowledge of the potential changes to natural biogeochemical cycles, as long-term alterations will affect the survival of Earth’s many ecosystems.

Outlook to the Future

Bottom Fishing Impact Assessment Tool (BFIAT)

This section was adapted from an NWO (Netherlands Organisation for Scientific Research) grant proposal, which was submitted in February 2020 and accepted in May 2020.

Written and developed by: Karline Soetaert, Justin C. Tiano, Olivier Beauchard



Bottom Fishing Impact Assessment Tool (BFIAT)

Key words: Benthic impact assessment, scientific validation, predictive model, ecology, biogeochemistry, fisheries

Research Summary

Climate change has prompted a search for alternative, less fuel-consuming fishing gears, however, gaining public acceptance of alternative gears involves the scientific validation of their impacts on marine habitats. Traditional fishing impact assessments occur several years after the introduction of new fishing methods. Here, we propose a tool that can provide environmental impact information early in the gear design/development process. In the BFIAT proposal, we will create a practical computational tool to predict the environmental effects of different fishing gears on the marine carbon and nutrient cycles and on marine benthic life. The bottom effects will be derived from the physical impact of the fishing gears on the sediment (induced by the weight and penetration into the seabed). Using new experimental data and information from previous studies, we will expand on a mechanistic, predictive model describing sediment biogeochemistry to which we will add a biological component. In cooperation with the Visserij-innovatiecentrum, we shall quantify the physical effects of different gears, using their experimental fishing facility. We will then perform small-scale lab experiments to test the environmental consequences of these physical perturbations on the sediment biological and biogeochemical functioning. The yearly NIOZ monitoring campaigns will provide access to relevant areas in the North Sea to apply the predictive model in natural conditions. For the final course of action, we will develop a user-friendly (web-based) application using model results to project spatio-temporal bottom fishing effects.

The objective of BFIAT: to facilitate the introduction of new types of fisheries by providing a scientific basis for estimating their environmental footprints and by aiding in the selection of lower impact (alternative) fishing practices.

Scientific description

Research contents / Introduction

Sea floor ecosystem services

The sea floor provides many important ecosystem services. Benthic macrofauna (sediment inhabiting animals larger than 1 mm) are the main food source for demersal fish (Amara et al., 2001) and therefore support demersal fisheries. The feeding, respiration and movement of these animals also mixes and pumps oxygen into the sediment, which facilitates important biogeochemical functions such as nutrient release via benthic-pelagic coupling (Mermillod-Blondin and Rosenberg, 2006). The sedimentary release of nutrients fuels pelagic primary production and thus has an important impact on the system's productivity. Within the marine realm, sediments are also the main sites where reactive nitrogen (Soetaert and Middelburg, 2009) and phosphorus (Slomp et al., 1996) are removed, thus buffering marine habitats against eutrophication. Removal of nutrients from the marine system also prevents or reduces the extent of low oxygen zones, which often result from nutrient overloading combined with water column stratification. As their occurrence is predicted to increase in the North Sea (Weston et al., 2008), the buffering ability from the sediment is becoming increasingly important.

Over the last century, the use of bottom trawls and other mobile fishing gears have increased in intensity and geographic extent (Kroodsma et al., 2018). Through contact with the sea floor, these gears can significantly modify benthic habitats and their associated benthic communities (Kaiser et al., 2000), while removing target and non-target species (Kaiser et al., 2006). Sedimentary disturbance induced by fisheries can alter rates of nutrient cycling (Tiano et al., 2019) and primary production which can severely affect marine ecosystems (Graf, 1989). To date there is only limited information about the impact of fisheries on the marine nutrient cycles and carrying capacity, and on the impact of marine life as a whole.

Within the EU, the maintenance of a "Good Environmental Status" in the marine environment plays an important role. To comply with the EU Marine Strategy framework Directive (MSDF), several effects on the sea floor induced by physical disturbances need to be monitored. One concern is the spatial extent and distribution of physical disturbance, and how this affects benthic habitat types. A third criterion considers a.o. the typical species composition, and the absence of particularly sensitive or fragile species or of species providing a key function.

As the public interest about human impacts in our natural environment continues to grow, the dissemination of accurate information is essential. Scientists can facilitate this by enlightening the public about the (quantified) advantages from less impactful methods or by detecting added risks associated with exploitative techniques.

Detecting and quantifying bottom fishing effects - biogeochemistry

In the frame of the IAPF project, it has been shown that bottom fishing gears release nutrients into the pelagic environment, reduce the benthic metabolism and may lead to decreased rates of carbon burial (Tiano et al., 2019; **Figure 1**). Benthic trawling has been linked to lower oxygen concentrations in the water column (Riemann & Hoffman, 1991; Tiano et al., 2019), the homogenization of benthic nutrient profiles (van de Velde et al., 2018) and alterations of the sediment redox layer (Depestele et al., 2018; Tiano et al. *in review*). Reduced mechanical disturbance has been connected with a lower biogeochemical impact (Depestele et al., 2016; Depestele et al., 2018; Tiano et al., 2019). Lighter gears with smaller penetration depths are, therefore, less impactful on benthic pelagic coupling. Nevertheless, compared to trawl impact studies on biological parameters, knowledge on the biogeochemical impact of fishing is sparse (Kaiser et al., 2002; Soetaert et al., 2015).

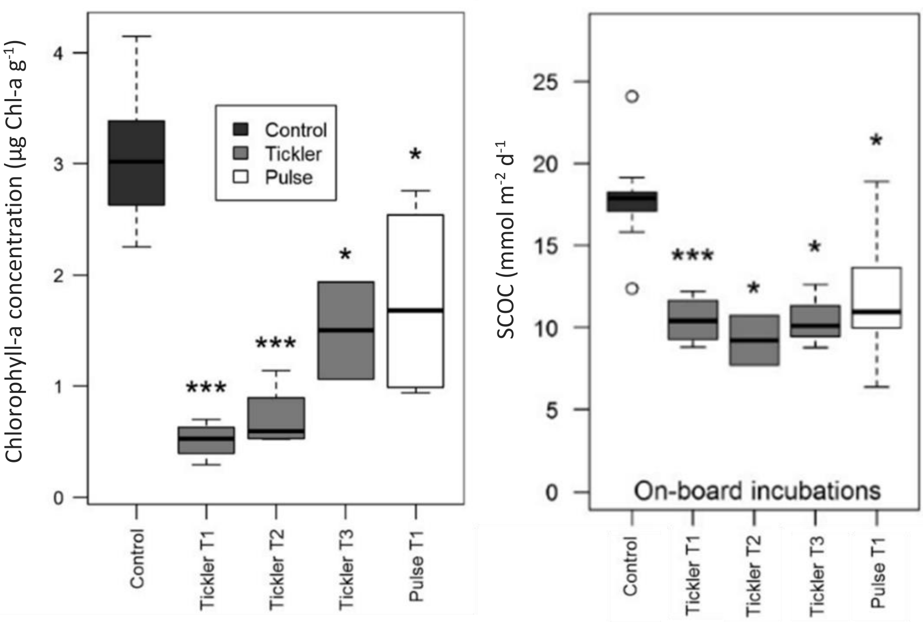


Figure 1. Biogeochemical impact from tickler chain beam trawls vs. electric pulse trawls for chlorophyll-a (left) and sediment community oxygen consumption (SCOC; right). **Figure** adapted from Tiano et al. 2019

Detecting and quantifying bottom fishing effects - biology

Past studies to assess the state of benthic communities focused on taxonomy, implying that all species are equally important. While species differ markedly in their responses to, and capacity to recover from changing environments, the exact mortality and recovery rates following disturbance are only available for a limited number of species. It is however possible to use trait-based information to estimate the responsiveness of species to physical disturbances (Beauchard et al., 2017).

In a recent work (ICES, 2018; Beauchard et al., *submitted*), it is argued that two components need to be considered to account for trawling effects: a "sensitivity" component, reflecting the instantaneous biomass depletion and a "recovery" component reflecting the longer term recolonization of the depleted habitat. These two features are linked to key characteristics of the species natural history: the sensitivity component depends on the organism's exposition to the trawling gear (body length, body fragility, burrowing depth), while the recovery component is associated to traits that account for reproductive success and offspring survival (e.g. age at maturity, reproductive life span, recolonization mode, etc.). The combination of these two components then defines the "vulnerability" of a species community to bottom fishing. Preliminary maps of these indicators in Dutch waters have been produced (**Figure 2**). An extension for the whole North Sea should be achieved in March 2020 (ICES WGBIODIV, 10-14th February 2020).

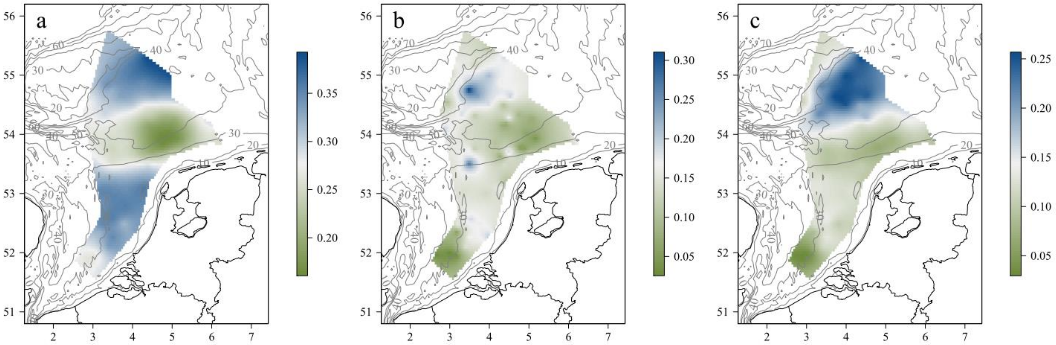


Figure 2. Interpolation maps of the sensitivity (a), recoverability (b) and vulnerability (c) components of benthic communities in the Dutch EEZ. High values express either high sensitivity, slow recovery or high vulnerability.

WHY BFIAT

Concerns over the ecological impact of bottom fishing have existed for hundreds of years (Collins, 1887; de Groot, 1984). A rise in fuel costs and criticism of environmental impacts led to the introduction of the electric pulse trawl in the North Sea (Soetaert et al., 2015). With this method, tickler chains (used to dig flatfish out of the sediment) were replaced by electrodes to (electrically) stimulate fish into oncoming nets. Reduced fuel consumption from lower towing speeds/decreased drag through the seafloor (van Marlen et al., 2014), reductions and increased survivorship of discards (van Marlen et al., 2014; Batsleer et al., 2016; van der Reijden et al., 2017) provided some evidence for pulse fishing as an environmentally friendly alternative to traditional tickler chain beam trawling. Its popularity amongst the Dutch fishing fleet (Haasnoot et al., 2016), however, was met with international criticism due to increased competition between fishermen (Sys et al., 2016) and ecological concerns over animal welfare (de Haan et al., 2016; Soetaert et al., 2016).

Although a fair amount of research has now been conducted on pulse fishing (ICES, 2019, Tiano et al., 2019; Bergman & Meesters, 2020), this method is now banned by the EU after millions of euros worth of investment. A perceived uncertainty over the environmental effects of pulse trawling was given as one of the reasons for its prohibition. This demonstrates that scientific information of environmental risks associated with new gears should be obtained at an early stage, in order to prevent or lessen the negative economic consequences following their introduction.

In BFIAT, we will quantify fisheries impacts by combining the assessment of biogeochemical ecosystem functioning with biological trait analysis of benthic communities in a comprehensive web-based tool that can be used by non-specialised personnel to make scientifically valid predictions on effects of fishing gears.

DESCRIPTION OF WORK.

The research is divided into 4 work packages starting with experimental techniques to be combined with modelling approaches.

WP1. DATA ACQUISITION

a. Physical disturbances

Research from the BENTHIS project has provided some information on how bottom trawl gears can affect different sediment types (Teal et al., 2014; Depestele et al., 2016; Depestele et al., 2018). For BFIAT, we plan to add to this knowledge by performing experiments using the large flume maintained by the Visserij-innovatiecentrum to quantify the physical effects of different gears on sediments. The use of coloured particles called “luminophores” can be used to observe the type (erosion, mixing etc.) and depth of disturbance caused by bottom fishing gears. This, and information from the BENTHIS studies will provide the input data to be used in WP1b.

<u>Deliverable</u>: perturbation depths for various fishing gears and weights

b. Biogeochemical effects.

In controlled laboratory settings, we will perform dedicated experiments characterising the biogeochemistry for sediments obtained from the field, before and after an artificial perturbation of the upper sediment layers, in accordance to the results obtained in WP1a.

The NIOZ recently acquired a comprehensive dataset of benthic biogeochemistry in the North Sea comprising of 20 stations, and spanning several benthic community types (**Figure 3**). Bottom trawl effects have been estimated for 11 stations. Within the BFIAT project, we will extend this dataset by participating in the yearly monitoring surveys to the North Sea with the NIOZ flagship PELAGIA. We will focus on marine habitats that are unsampled with respect to the sediment biogeochemistry.

<u>Deliverable</u>: biogeochemical characterisation of in situ sediments, with an experimental assessment of effects of physical disturbances.

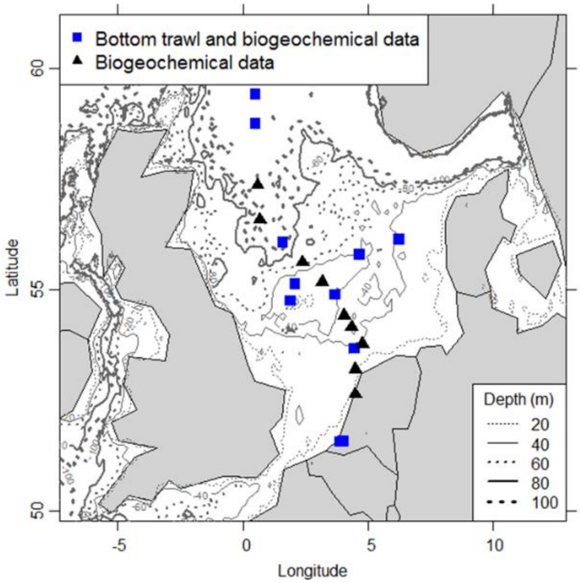


Figure 3. North Sea map showing stations with benthic biogeochemical information gathered by the NIOZ. Square symbols show stations where

WP2. BIOGEOCHEMICAL MODELLING

Traditionally, sediment biogeochemistry can be adequately described by so-called early diagenetic models (Soetaert et al., 2001). These are predictive, mechanistic models that represent the main sediment biogeochemical processes (mineralisation, nitrification, denitrification, etc.), the physical transport mechanisms (molecular diffusion, sediment accretion) and how they are impacted by benthic organisms (animal sediment mixing or bioturbation, animal pumping or bio-irrigation). The BFIAT project will make use of an existing biogeochemical model (Soetaert et al., 1996). This model has recently been extended with phosphorus dynamics (Ait Ballagh et al., 2020) and is being applied to the biogeochemical data gathered in the North Sea. The model has the ability to estimate the effects of sediment perturbations (sediment mixing, erosion) on the nutrient cycles, based on the nature and the depth of sediment disturbance. After further calibration of the model to the data (WP1), the model will be applied to forecast the effects of fisheries on key biogeochemical properties. A sensitivity analysis will be run to estimate the biogeochemical effects for combinations of gear type and benthic community classes.

Deliverables:

- A predictive model to assess the effect of physical disturbances on sediment biogeochemistry in different areas.
- Spatial and temporal predictions of bottom fishing impacts on benthic biogeochemistry.

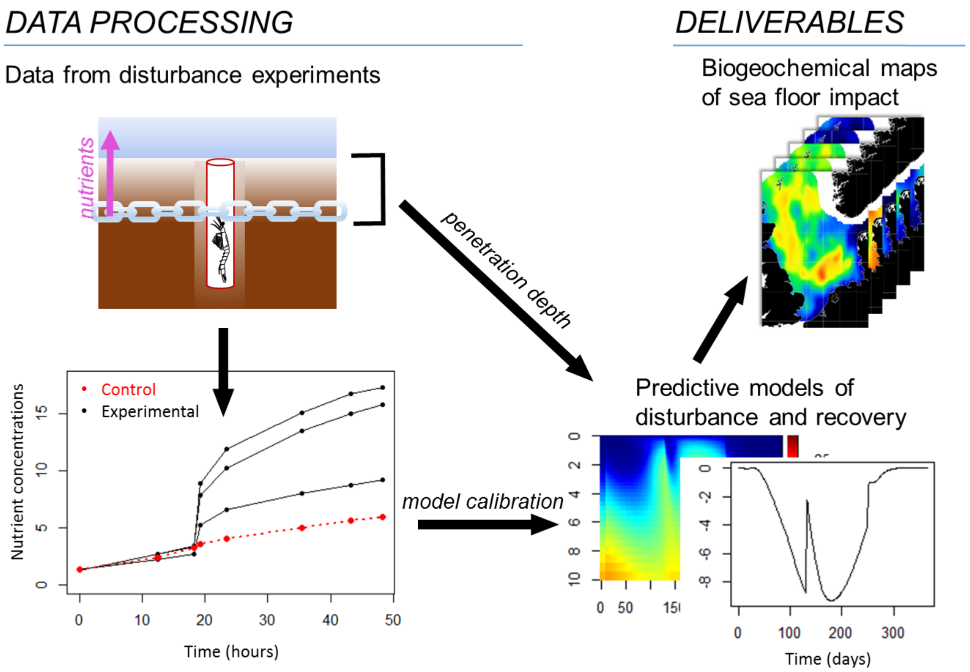


Figure 4. Conceptual illustration of WP1 experimental work on physical and biogeochemical effects (left) and WP2 model results with spatial and temporal predictions (right).

WP3. SPECIES COMMUNITY MODELLING

Benthic biology is traditionally modelled using habitat-suitability models from field data that statistically predict the spatial extent of occurrences of benthic species based on specific environmental parameters such as depth, sediment composition, maximal current velocity or primary productivity. For the BFIAT project, the studied response variables will be the biological traits, organism densities and biomass.

The NIOZ is currently working on a compilation of North Sea benthic species traits with respect to crucial ecosystem services such as biomass production, biogeochemistry and niche creation (O. Beauchard, 630 European species). This data set will enable the identification of areas that are vital for this particular ecosystem service. Combined with the (updated) maps of the vulnerability of areas to bottom trawling (see **Figure 2**) it will be possible to derive the effects of bottom trawling to the main ecosystem services. Care will be taken not to confound the relationship of trawling intensity with environmental gradients as fisheries impact, as fisheries concentrate in areas of highest benthic primary productivity. These confounding effects, rarely taken into account, will be circumvented by the use of variation partitioning (ICES, 2017).

We will develop a quantitative model to predict biomass removal and recovery as a function to the type of trawling gear, and that will make use of the biological traits of the benthos. A sensitivity analysis will be run to estimate the biomass depletion for combinations of gear type and community sensitivity classes.

Deliverables:

- A predictive model of benthic biomass depletion and recovery rate per gear type and benthic community sensitivity class.
- Spatial and temporal predictions of bottom fishing impacts on benthic communities.

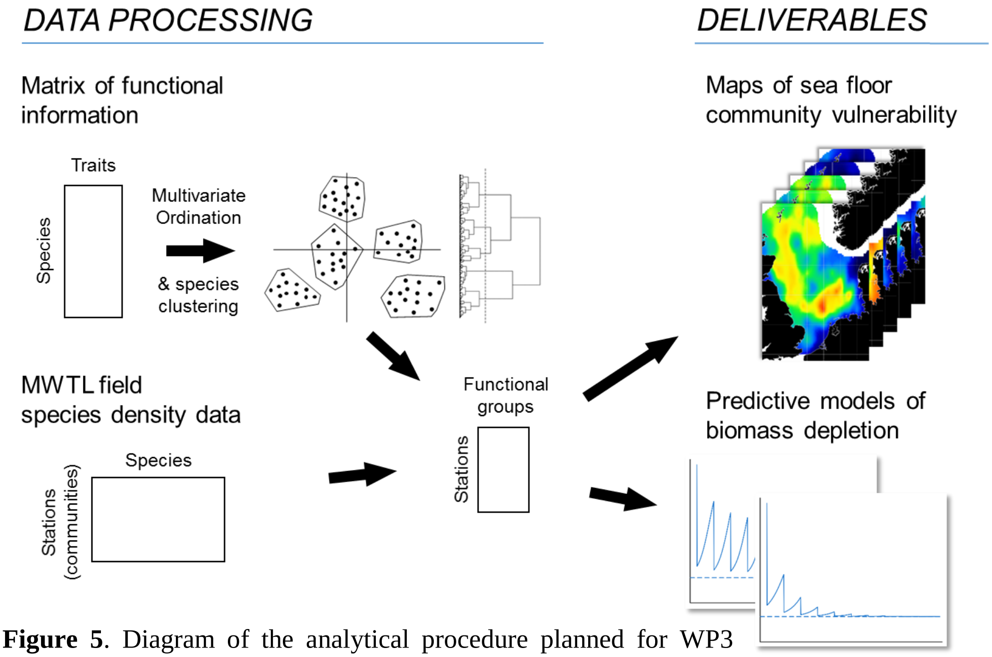


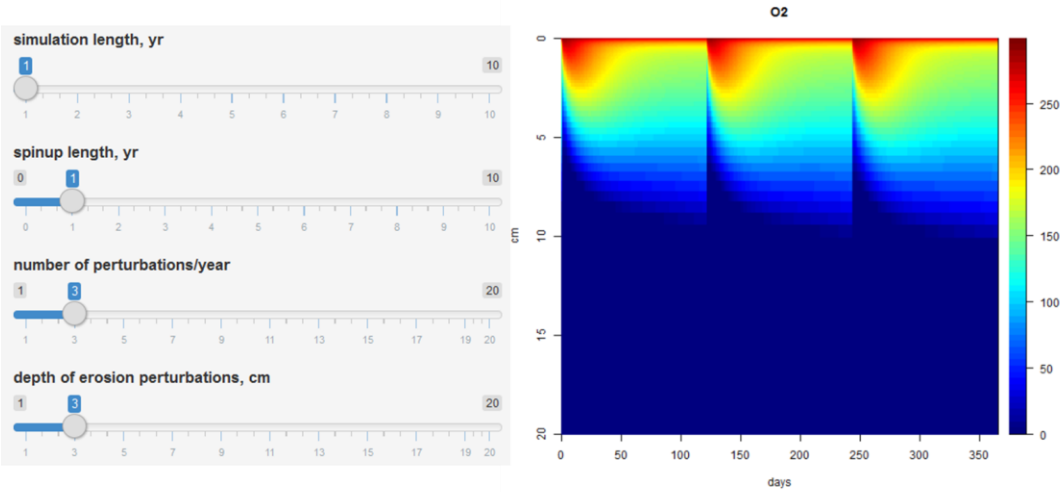
Figure 5. Diagram of the analytical procedure planned for WP3 which will map and predict how species communities respond to disturbances.

WP4. INTERACTIVE TOOL

The biogeochemical and biological models are implemented in R, which is well suited for creating web-based applications. The biogeochemical model is sufficiently fast to allow it being applied in web-based interactive tools (e.g. for a rudimentary version, see www.RforScience\OMEXDIA; **Figure 6**).

Deliverable:

- A web-based interface developed by the NIOZ to facilitate the application of BFIAT.



simulation length, yr: 1 (1–10)

spinup length, yr: 1 (0–10)

number of perturbations/year: 3 (1–20)

depth of erosion perturbations, cm: 3 (1–20)

Figure 6. Screenshot of the CNPDIA model (the model from which BFIAT will be expanded upon) predicting the response and recovery of oxygen concentrations inside the sediment. Three fisheries disturbance events are simulated throughout the year.

Utilisation plan

The problem and the proposed solution

One of the mistakes made during the introduction of electric pulse trawls was waiting too long to assess their environmental effects. After millions of euros invested into “pulse fishing”, this technique is now banned by the EU while the results of its environmental impacts continue to come out (Tiano et al., 2019). Lessons learnt from the introduction of pulse fishing has demonstrated that scientific information of environmental risks associated with new gears should be obtained at an earlier stage, so as to gain public acceptance of new methods. Furthermore, significantly damaging ecosystem impacts of alternative gears need to be known as soon as possible in order to make appropriate adjustments and minimise environmental impact.

At the NIOZ we are proposing a technique to provide scientific predictions *before* the large scale introduction of new fishing gears. This has the potential to give reliable evidence of the environmental improvements of alternative fishing methods and can potentially avert adverse economic consequences if unforeseen ecosystem impacts are greater than envisioned. Given the prolonged reality of the scientific publication process (may take several years after the development of any new technology), one of the advantages of our proposed research is that, upon completion of the BFIAT (approximately two years), non-scientists can gain insight on the potential impact of various fishing techniques just by using the application. Fishing gear developers, fishing industry representatives, NGO’s, policy makers, and environmental planners may be beneficiaries of BFIAT.

Uses of BFIAT include, amongst others:

a) Estimation of the environmental effects of alternative gears *before* their introduction.
b) Calculation of measureable changes between the effects of different gear types.
c) Prediction of the time of the year where bottom fishing impacts are highest.
d) Creation of predictive scenarios based on the type of fishing gear used in different areas.
e) Projections several years into the future of how different types of fishing may affect seafloor ecosystems.

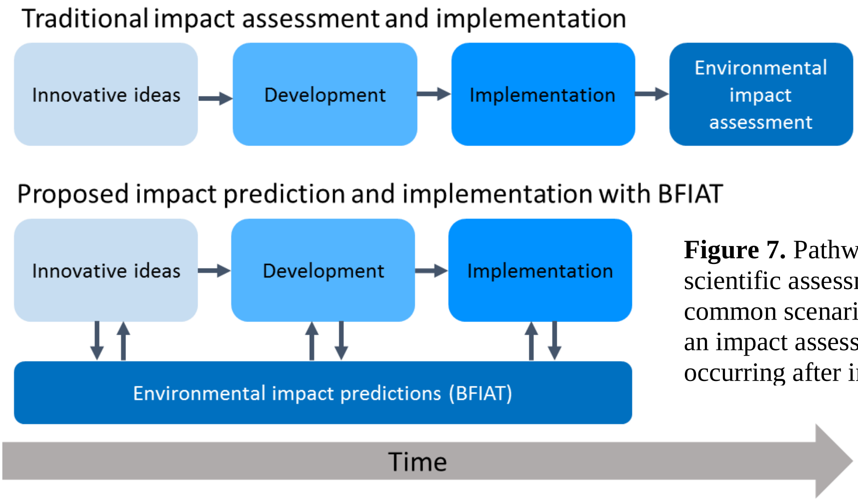


Figure 7. Pathways towards scientific assessment. Top: a common scenario with having an impact assessment occurring after implementation

Several end-users have expressed interest in the results from the BFIAT project.

"The Dutch Fishermen's Association sees the importance of the continued development of fishing gear to adapt to changing environmental circumstances and societal demands and needs. The Dutch Fishermen's Association sees the importance of a practical, scientifically justified computer tool to estimate the environmental effects of innovative fishing gears in various marine habitats, including different seabed types." -- **Nederlandse Vissersbond**

"The tool is highly topical in a time when fishing gear innovations are urgently needed by the Dutch demersal fishing industry. The primary, but not the only, driver is the total pulse fishing ban which is coming into force. This is an existential threat for a significant part of the industry, because reverting back to beam trawling with tickler chains doubles fuel expenditures. Various efforts are under way to develop alternative fuel-efficient gears, and these gears are expected to have a lower seafloor impact as a result of reduced hydrodynamic and / or bottom contact drag needed to achieve fuel savings. The tool which this proposal aims to develop will help the introduction of these gears by predicting seafloor impact outcomes without the need for full field trials, which may take a long time and a substantial investment. We expect the tool to be used for a variety of designs currently under development, for example in our EMFF project "OSW Selectiviteit & Overleving". -- **VisNed**

The **Visserij-innovatiecentrum** will collaborate with us through the use of their facilities where the effects of different gear types at various speeds can be assessed in large experimental tanks. A budget of 15,000 euros is allocated to this task.

Positioning of the project proposal

Uniqueness of the proposed project

- To our knowledge, we are the first to try to create a predictive bottom fishing assessment application which combines biogeochemical and species community data.
- One of the main purposes of BFIAT is to allow and encourage the active role of scientific impact assessments earlier in the gear design process (**Figure 7**). This will shorten the time needed to gain information about the environmental effects of alternative fishing gears while providing the ability to quantify improvements or reveal reasons to make adjustments.
- The addition of biological trait data will offer previously unknown information about the vulnerability of North Sea communities and can be important information for environmental managers and policy makers.

Embedding of the proposed project

The proposed research builds upon work conducted in the IAPF project. Empirical evidence gathered from this project provides a basis for the prediction and upscaling using modelling techniques. A mechanistic model has already been developed but in order to truly realise its potential, further work is necessary. Additional activity by the Soetaert lab group, such as the acquisition of North Sea porewater nutrient profiles and model fitting (conducted in the FaCE-It and SANDBOX projects), will reinforce the results of the final BFIAT model. Research conducted in the DISCLOSE project will lay a foundation for BFIAT's biological component by overlaying data on vulnerable ecological habitats. Data from species occurrences will be taken from the annual Rijkswaterstaat North Sea monitoring dataset. Vessel monitoring data (VMS) will be obtained in partnership with Wageningen Marine Resarch (WMR).

Cooperation with the Visserij-innovatiecentrum in addition to the continued partnership with VisNed and the Nederlandse Vissersbond (see Section 5), will allow for the direct involvement with the fishing sector. The new collaboration with Visserij-innovatiecentrum is particularly advantageous, as it will permit the experimentation with different gear technologies at their facilities.

Table 3. Links to relevant projects					
Name	*Involved Institutes*	*Biogeo-chemistry*	*Biology*	*Fishing impacts*	*Link with BFIAT*
IAPF link	NIOZ WUR WMR ILVO	x	x	x	Knowledge of biological and biogeochemical trawl impacts gained from experimental research. Preliminary predictive model developed.
FaCE-It link	NIOZ ILVO UGent	x	x	x	Biogeochemical profiles and model fitting from North Sea data. Collaboration with IAPF bottom trawl study.
DISCLOSE link	NIOZ TU Delft RUG		x	x	North Sea habitat maps to assess species communities. Collaboration with IAPF bottom trawl study.
SANDBOX link	NIOZ TU Delft UT	x	x		Biogeochemical profiles and model fitting from North Sea data.

Explanation for abbreviations and acronyms can be found in the final section

Abbreviations and acronyms

Terms	
BFIAT	Bottom Fishing Impact Assessment Tool
CNPDIA	Carbon Nitrogen and Phosphorus Dynamic model
NFU	Non-scientific personnel
NPO	Non profit organisation
SME	Small and mid-size enterprises
VMS	Vessel Monitoring System
Research Institutes	
ICES	International Council for the Exploration of the Sea
ILVO	Instituut voor Landbouw, Visserij en Voedengsonderzoek
NIOZ	Koninklijk Nederlands Instituut voor Zeeonderzoek
RUG	Rijksuniversiteit Groningen
TU Delft	Technische Universiteit Delft
UGent	Universiteit Gent
UT	Universiteit Twente
WMR	Wageningen Marine Research
WUR	Wageningen University & Research
Multi-year research projects	
BENTHIS	Benthic Ecosystem Fisheries Impact Studies
DISCLOSE	DIstribution, StruCture and functioning of LOw-resilience seafloor communities and habitats of the Dutch North SEa
FaCE-It	Functional biodiversity in a Changing sedimentary Environment
IAPF	Impact Assessment Pulsetrawl Fishery
SANDBOX	Smart and sustainable design for offshore operations in a sandy seabed

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Benthos collection (North Sea)

Photo: Justin Tiano

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Translation: *"From Justin"*
*"The Great Marine Biologist
and the Whale"*
(It's in 5 year old English)

Curriculum Vitae

About the author

As a child, Justin Tiano loved basketball, rap music, and marine biology (see drawing on the left). He was born in the Philippines but grew up in the western United States in California and Nevada. During his undergraduate studies, he decided to follow his childhood fascination about life under water and was given the opportunity to work in a limnology research laboratory. There, he learned more about aquatic ecology and biogeochemistry, which only sparked his interest even more. Despite his attraction to the sciences, he had a limiting belief that he was not smart enough to conduct a PhD, although it remained a dream of his. After a few years of travelling in Australia and New Zealand, he decided to do a masters degree in marine conservation to see if he really had what it takes to be a real scientist. During his fruitful but intensive masters studies in Wellington, New Zealand, he realized that a career in research was what he wanted for his life and with renewed confidence in himself, he decided to follow his passion and pursue a doctorate in marine or aquatic science. Also during that time, he got married to a really awesome French girl and they decided to move from New Zealand to Europe to be close to family, and for her to go back to her studies just as he did in New Zealand. After settling in the Netherlands, it was not easy for Justin to find a PhD position and he ended up working as a bartender in Amsterdam while continuing to apply to different positions. After several failed attempts, his dreams were finally realized and he was offered a PhD position at the Netherlands Institute for Sea Research (NIOZ). His PhD experience ended up being everything he could ever ask for. Filled with challenge, adventure, and even media experiences, Justin truly relished this time and loved his work. The topic of his research was the effects of bottom trawling on biogeochemistry and he became one of the few researchers assessing the controversial, electric pulse fishing method, which garnered much attention. At the moment, he is continuing his research on the effects of fishing and biogeochemistry as a postdoctoral researcher at the NIOZ and is thrilled to have fulfilled and to be able to continue his childhood dream of becoming a marine biologist.

Left: The cover of a 'book' I made when I was 5 years old, about a marine biologist and his whale.

Curriculum Vitae

Name:	Justin Christopher Tiano
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Nationality:	USA
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EDUCATION

Doctor of Philosophy (PhD), Marine Sciences **2016 - present**
Ghent University **Ghent, Belgium**

Thesis: *"Evaluating the consequences of bottom trawling on benthic pelagic coupling and ecosystem functioning"*

Master of Marine Conservation **2013-2014**
Victoria University of Wellington **Wellington, New Zealand**

Thesis: "*Spatial variation in diet composition of the Southern New Zealand Arrow Squid, Nototodarus sloanii, from the Chatham Rise and Campbell Plateau"*

Bachelor of Science **2006-2011**
University of Nevada **Reno, Nevada, USA**

PUBLICATIONS

Published peer reviewed articles

- Tiano J.C., S. O'flynn, K.J. van der Reijden, T. Ysebaert, K. Soetaert, (2020). Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front, *Marine Environmental Research,* 159, July 2020 104964. *doi.org/10.1016/j.marenvres.2020.104964*
- De Borger E., J. Tiano, U. Braeckman, T. Ysebaert, K. Soetaert, (2020). Biological and biogeochemical methods for estimating bioirrigation: a case study in the Oosterschelde estuary, *Biogeosciences,* 17, 1701-1715. *doi.org/10.5194/bg-17-1701-2020*
- Tiano J.C., R. Witbaard, M.J.N. Bergman, P. van Rijswijk, A. Tramper, D. van Oevelen, K. Soetaert (2019) Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling, *ICES Journal of Marine Science,* fsz060, *doi.org/10.1093/icesjms/fsz060*

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- Tiano J.C., E. De Borger, S. O'flynn, C. Cheng, K. Soetaert, Impacts of anthropogenic sediment mixing and electrical perturbations on sediment biogeochemistry, *submitted*
- Tiano J.C., J. Depestele, G. Van Hoey, J. Fernandes, P. van Rijswijk, K. Soetaert, Ecosystem impacts from electro-trawls and conventional beam trawls in subtidal Lanice conchilega reef communities, *in preparation*

Research Reports

- ICES. 2020. ICES Working Group on Electrical Trawling (WGELECTRA). ICES Scientific Reports. 2:37. 108 pp. http://doi.org/10.17895/ices.pub.6006
- Rijnsdorp, A. A. D., Boute, P., Tiano, J.C.., Lankheet, M., Soetaert, K., Beier, U., De Borger, E., Hintzen, N., Molenaar, P., Polet, H., Poos., J.J., Schram, E., Soetaert, M., van Oversee, H., van de Wolfshaar, K., van Kooten, T., (2020). The implications of a transition from tickler chain beam trawl to electric pulse trawl on the sustainability and ecosystem effects of the fishery for North Sea sole : an impact assessment. https://doi.org/https://doi.org/10.18174/519729
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CONFERENCE CONTRIBUTIONS

- Tiano J.C. (2019) 'Was it a good idea to mix trawling with electricity?', Oral Presentation: NIOZ Science Days, 14 November, Texel Netherlands.
- Tiano J.C., R. Witbaard, M. Bergman, P. van Rijswijk, A. Tramper, K. Soetaert (2018) 'Electric pulse fishing creates more variable biogeochemical effects than beam trawling', Oral Presentation: ICES Annual Science Conference, 25 September, Hamburg Germany.
- Tiano, J.C., A. Rijnsdorp, K. Soetaert. Is Electric Pulse Fishing Safer for the Environment? Poster Presentation: North Sea Open Science Conference; 7-10 November 2016; Ostend, Belgium.

RESEARCH GRANTS

Research towards Sustainable Fisheries-innovation project **May 2020**

Postdoctoral grant (2 years)
Netherlands Organisation for Scientific Research (NWO), Netherlands
Project name: “*Bottom Fishing Impact Assessment Tool (BFIAT)”*

OUTREACH AND MEDIA APPEARANCES

February 2020 Interview for News Article in “Science” - How trawling affects biogeochemistry

June 2019 TV interview for German news “Aktuelle Stunde” - Health of the North Sea

March 2019 TV interview for “Nieuwlicht” news program - Pulse fishing research and politics

August 2018 Outreach at mussel festival - Research at the NIOZ

May 2018 Interview for the Dutch “Financiel Dagblad” - Pulse fishing research

April 2018 TV interview for BBC One “Inside Out” - Pulse fishing controversy

January 2018 TV interview for “Omroep Zeeland” regional news - Pulse fishing research

January 2018 Interview for “Bionieuws” science magazine - Pulse fishing research

July 2017 Interview for “Nederlandse Visserbond” news letter – upcoming pulse fishing research

May 2017 Interview with “Resource” research magazine - Electric pulse fishing

Biogeochemical cycles control the existence of Earth's ecosystems, and while the effects of bottom trawling on ecological communities have been extensively studied, impacts on biogeochemistry remain a neglected topic in fisheries research. This PhD explores the relationship between bottom trawl disturbance, biogeochemical cycles and the coupling between benthic and pelagic zones. In particular, this research investigates the potential impact of novel electric "pulse" trawls compared with traditional methods.

FACULTY OF SCIENCES