



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

Justin C. Tiano^{1,2,*}, Rob Witbaard¹, Magda J. N. Bergman³, Pieter van Rijswijk¹, Anton Tramper¹, Dick van Oevelen¹, and Karline Soetaert^{1,2}

¹Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research (NIOZ), Utrecht University, P.O. Box 140, 4401 NT Yerseke, Korringaweg 7, The Netherlands

²Marine Biology Section, Department of Biology, Ghent University, Krijgslaan 281/S8, 9000 Ghent, Belgium

³Department of Ocean Systems, Royal Netherlands Institute for Sea Research (NIOZ), Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

*Corresponding author: tel: + 31 113 577 495; e-mail: justin.tiano@nioz.nl.

Tiano, J. C., Witbaard, R., Bergman, M. J. N., van Rijswijk, P., Tramper, A., van Oevelen, D., and Soetaert, K. Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsz060.

Received 18 January 2019; revised 4 March 2019; accepted 5 March 2019.

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 prominent alterations than PulseWing trawling on benthic biogeochemical processes.

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

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 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, 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 homogenization 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 O₂ consumption and increased concentrations of dissolved inorganic carbon, 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; Olsford *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 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, 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 PulseWing trawl gears on benthic biogeochemistry. 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.

Material and methods

Study site

Experimental fishing and sampling were carried out within a 1 km 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 (OC) percentage between 0.28 and 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 to 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 were used to estimate the likelihood of bottom trawl disturbance within 1 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, OC/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 h) and longer-term effects >24 h in the case of the tickler chain trawler.

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 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,

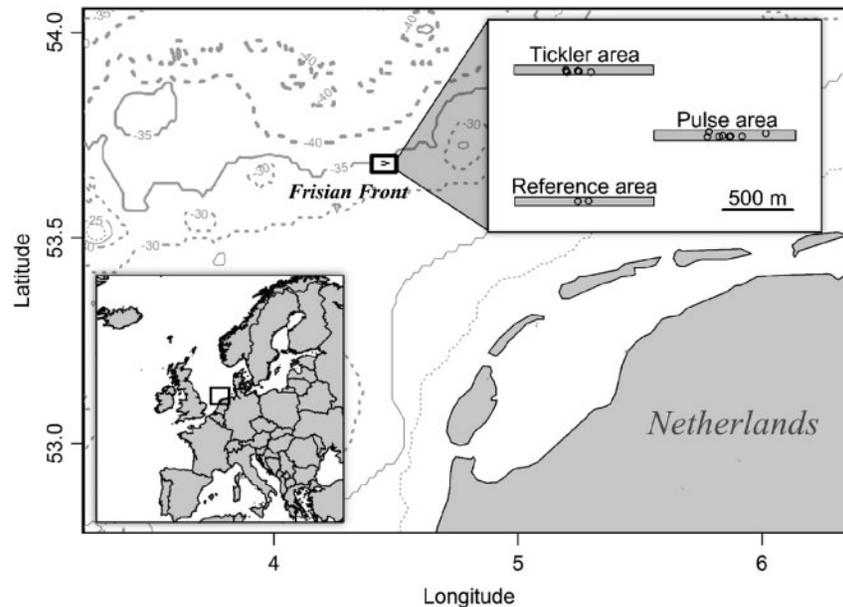


Figure 1. Map of the study site. The inset shows the positions of the experimental areas and box cores taken from the tickler treatment to the north, the pulse treatment to the east, and the reference area in the south.

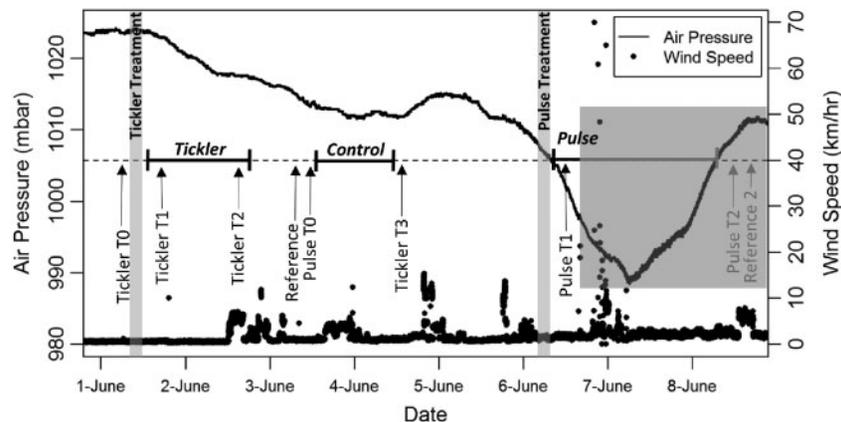


Figure 2. Sequence of events and weather conditions. Box core sediment samples (arrows), *in situ* lander deployments (brackets) and experimental fishing treatments (shaded columns) are shown. Samples taken in the shaded region on the right were not included in the analysis due to storm-induced sediment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

both vessels conducted seven 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 150–200% within the middle portion of the treatment areas (modelled after the procedures conducted in Bergman and van Santbrink, 2000; Depestele *et al.*, 2016).

We initially aimed for a full 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).

Experimental fishing

On 1 June 2017 (8 h 30–10 h) 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 6 June 2017 (7 h 30–10 h). 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. 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 (4–8 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. Tickler samples were taken 1 h 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 h 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). OC was measured by removing carbonate from the total carbon (TC) concentration (with 0.1N HCl) and calculating the difference (Nieuwenhuize *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 micro-profiling 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 homogeneous 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, three replicate profiles were taken from different areas of the sediment. For each profile, readings were taken at 100- μm intervals, starting $\sim 10\,000\ \mu\text{m}$ (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 to record oxygen consumption until a clear linear relationship was observed. The oxygen concentration during the incubation period was measured with optode sensors (FireSting O_2 , Pyroscience) using a measurement interval of 30 s. 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 ($\text{mmol m}^{-2} \text{d}^{-1}$) 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 h 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; Witbaard *et al.*, 2000; Duineveld *et al.*, 2004) 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 three measurement chambers enclosing a surface area of 144 cm². 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 s 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 was 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 were normally distributed and/or displayed homogeneity of variances. If assumptions for parametric testing were violated, data were normalized using a log-transformation. Differences in water depth, biogeochemical parameters (benthic O₂ 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 among 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, 2014).

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, $p > 0.05$). In addition, untrawled sediment from tickler T0, pulse T0, and reference box core samples did not show significant differences between O₂/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

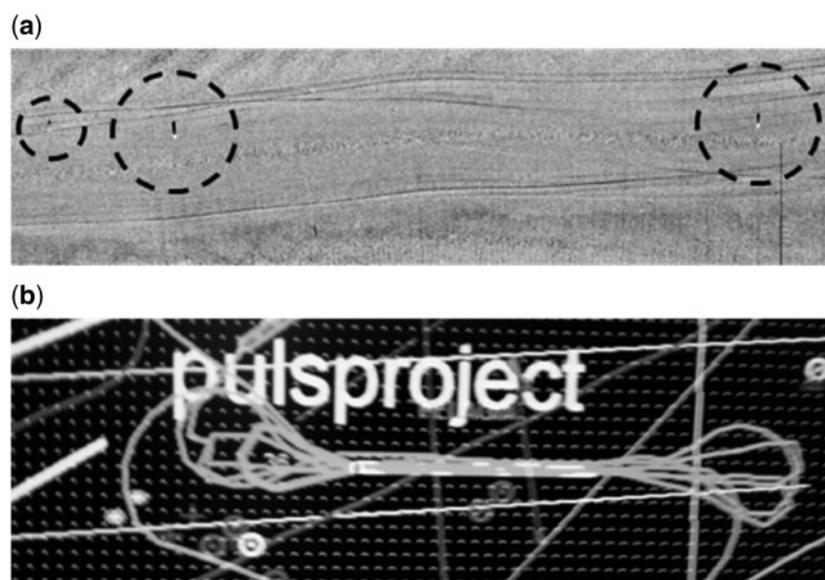


Figure 3. (a) A side-scan sonar image of the tickler trawled area. In addition to the evidence of bottom disturbance, images of two benthic ALBEX landers and an additional oxygen sensing lander can be seen within the disturbed portion of the seafloor. Image courtesy of Leo Koop. (b) Tracking of PulseWing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

possibility (0.25–1.25 h fished) of pulse trawling conducted in part of the reference area.

Our personal observations confirmed that both tickler chain and PulseWing commercial trawlers made seven 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 Automatic Identification System from the RV Pelagia.

Effect of the PulseWing on sediment plume dynamics

The turbidity sensor on the mooring logged a notable increase in the 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 4a). 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 4b). 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.

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 ($20.46 \pm 2.85\%$ silt) displayed significantly smaller mean silt (<63 μm) fractions compared to control ($33.06 \pm 7.33\%$ silt; HSD, $p < 0.001$) sediments (Figure 5a). Fine sand (62.5–125 μm) fractions in tickler T2 ($44.59 \pm 2.48\%$ fine sand) were significantly higher than control ($36.37 \pm 3.96\%$ fine sand; HSD, $p < 0.05$; Figure 5b) samples. For D10 values (10% of the sample particles are smaller than this value), both tickler T1 ($9.21 \pm 1.21 \mu\text{m}$) and tickler T2 ($12.13 \pm 1.42 \mu\text{m}$) were significantly higher than control ($6.78 \pm 1.26 \mu\text{m}$; HSD, $p < 0.05$, $p < 0.0001$) samples showing coarsening after beam trawl fishing (tickler T1/T2), followed by the re-establishment of ambient sediment characteristics (tickler T3; Figure 5d).

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

Chlorophyll *a* in surface sediments

Figure 6 displays the differences between average 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 $3.01 \pm 0.68 \mu\text{g chl } a \text{ g}^{-1}$, while fished samples decreased to $0.51 \pm 0.17 \mu\text{g chl } a \text{ g}^{-1}$ for tickler T1 and $1.76 \pm 0.91 \mu\text{g chl } a \text{ g}^{-1}$ for pulse T1. The acute impact from both fishing methods caused a significant decrease in surface chl *a* compared to the control areas, however, the effect of the tickler chain trawl (tickler T1; HSD, $p < 0.0001$) was more pronounced than

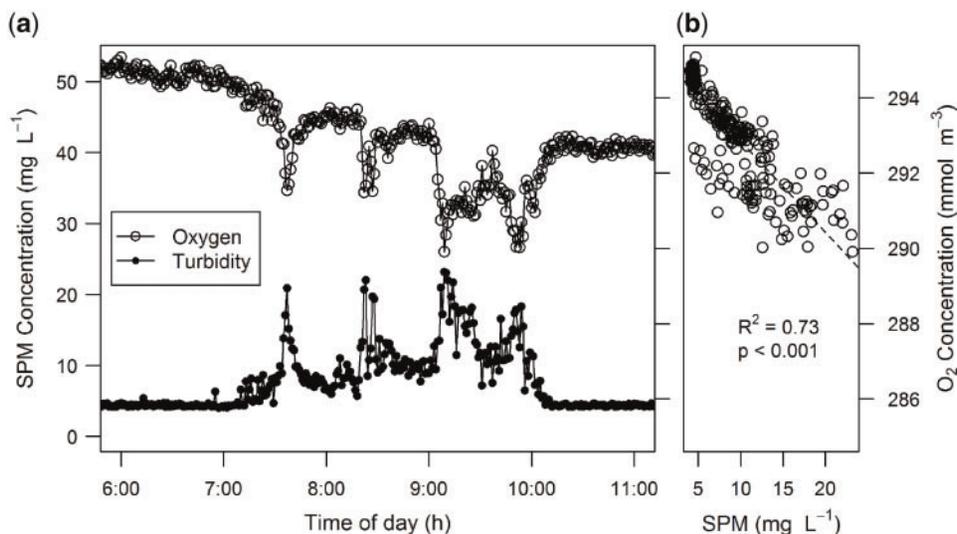


Figure 4. (a) PulseWing facilitated resuspension effects on SPM (mg l⁻¹) and O₂ (mmol m⁻³) concentrations. Data were taken from 3.5 m above the sediment surface. (b) The relationship between SPM (x-axis) and O₂ concentration (y-axis) in the water column during pulse fishing.

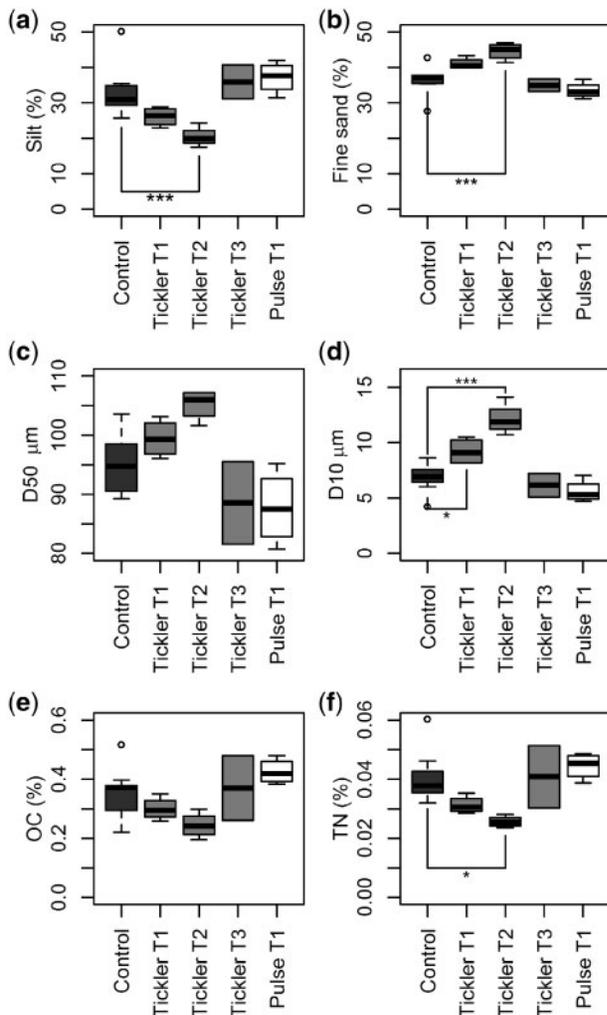


Figure 5. Surface sediment characteristics from control ($n = 9$), tickler T1 ($n = 4$), tickler T2 ($n = 2$), tickler T3 ($n = 3$), and pulse T1 ($n = 7$) samples: (a) % silt ($<63 \mu\text{m}$), (b) % fine sand ($63\text{--}125 \mu\text{m}$), (c) D50 = median grain size (μm), (d) D10 = diameter at which 10% of particles in the sample are smaller (μm), (e) % OC, and (f) % TN.

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 ($0.71 \pm 0.29 \mu\text{g chl } a \text{ g}^{-1}$, HSD, $p < 0.001$). Compared to tickler T2, tickler T3 samples showed an increase (though not significantly different from T1 or T2) in chl a content at $1.50 \pm 0.61 \mu\text{g chl } a \text{ g}^{-1}$, though this was still significantly lower than control samples (HSD, $p < 0.05$).

Fishing effects on oxygen and nutrients

Porewater NH_4^+ profiles in control samples exhibited a depth gradient with $<15 \mu\text{mol l}^{-1}$ at the surface that steadily increased down to $40 \mu\text{mol}$ 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 to control samples (Table 1). Tickler T1 samples in particular, displayed a homogenous depth profile for NH_4^+ which extended to 10 cm (Figure 7a). Pulse T1 NH_4^+ concentrations

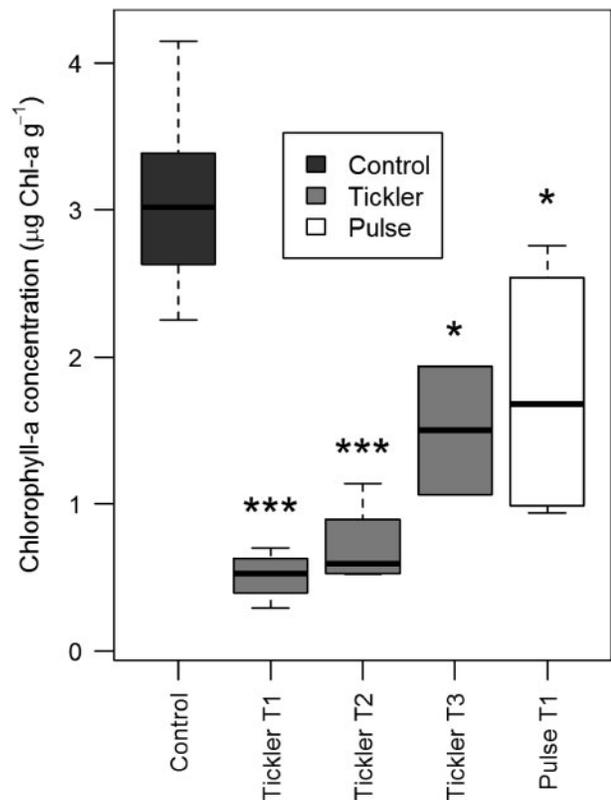


Figure 6. Surface chlorophyll a concentrations in control ($n = 9$), tickler T1 ($n = 4$), tickler T2 ($n = 4$), tickler T3 ($n = 2$), and pulse T1 ($n = 4$) sediments. * $p < 0.05$; *** $p < 0.001$ significant differences compared to control samples.

peak at 5 cm in the sediment while NH_4^+ in the control samples seem to increase past 10 cm (Figure 7b). No other significant differences were found between porewater nutrients in this study.

The average OPD after tickler chain trawling (tickler T1) was $3.78 \pm 0.73 \text{ mm}$. In comparison, pulse T1 cores had an OPD of $3.17 \pm 1.81 \text{ mm}$. These were both deeper than the OPD's found in the control cores which measured $2.25 \pm 0.56 \text{ mm}$ 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 ($2.97 \text{ mm} \pm 0.93$; 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 9a). *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 9b, Table 2).

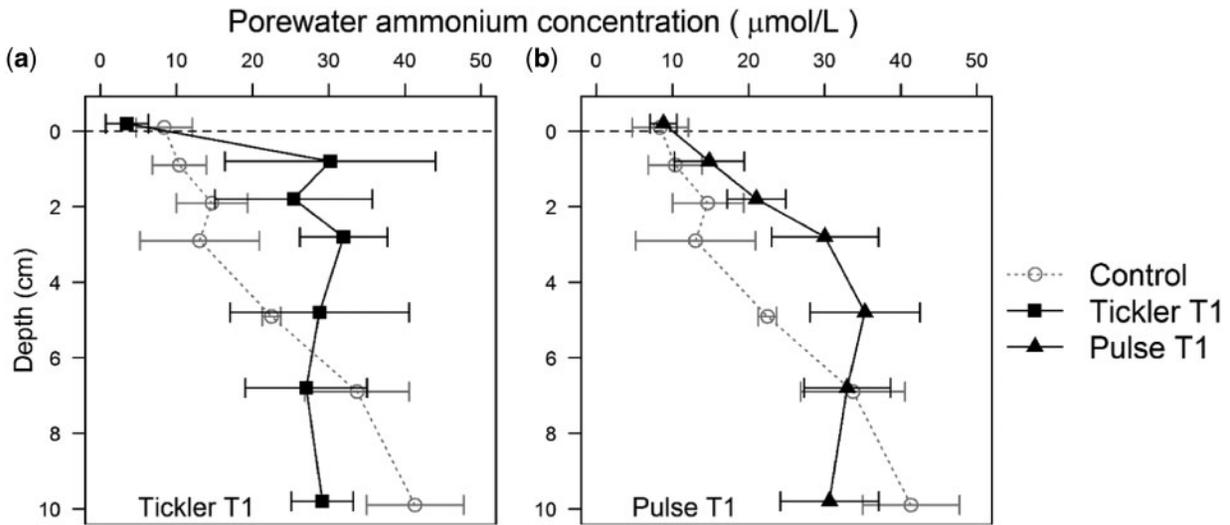


Figure 7. Porewater NH_4^+ concentrations comparing (a) tickler T1 and (b) pulse T1 with control (untrowled) samples.

Table 1. Porewater nutrient concentrations in the upper 3 cm ($\mu\text{mol l}^{-1}$).

	NH_4^+ Mean \pm SD	NO_x Mean \pm SD	PO_4^{3-} Mean \pm SD	SiO_2 Mean \pm SD	<i>n</i>
Control	13.85 \pm 7.64	2.94 \pm 5.64	0.46 \pm 0.31	85.48 \pm 19.16	15
Tickler T1	26.97 \pm 9.27**	2.52 \pm 1.85	0.53 \pm 0.34	80.00 \pm 23.46	6
Tickler T2	18.24 \pm 3.55	2.55 \pm 1.60	0.72 \pm 0.19	69.40 \pm 14.63	6
Pulse T1	21.96 \pm 8.10*	1.58 \pm 0.42	0.62 \pm 0.27	80.53 \pm 12.78	12

No porewater samples were collected for tickler T3.

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

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 were, therefore, used only from the lander which showed a range of flux data comparable to historical information from the Frisian Front.

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 characterized 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. 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 4a). 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 in silt, chlorophyll, and OC 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 5a–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: (i) the smallest sediment fraction (silt) is winnowed and reallocated away from the trawl track, while (ii) the heavier sand fractions resettled or remained on the trawl track

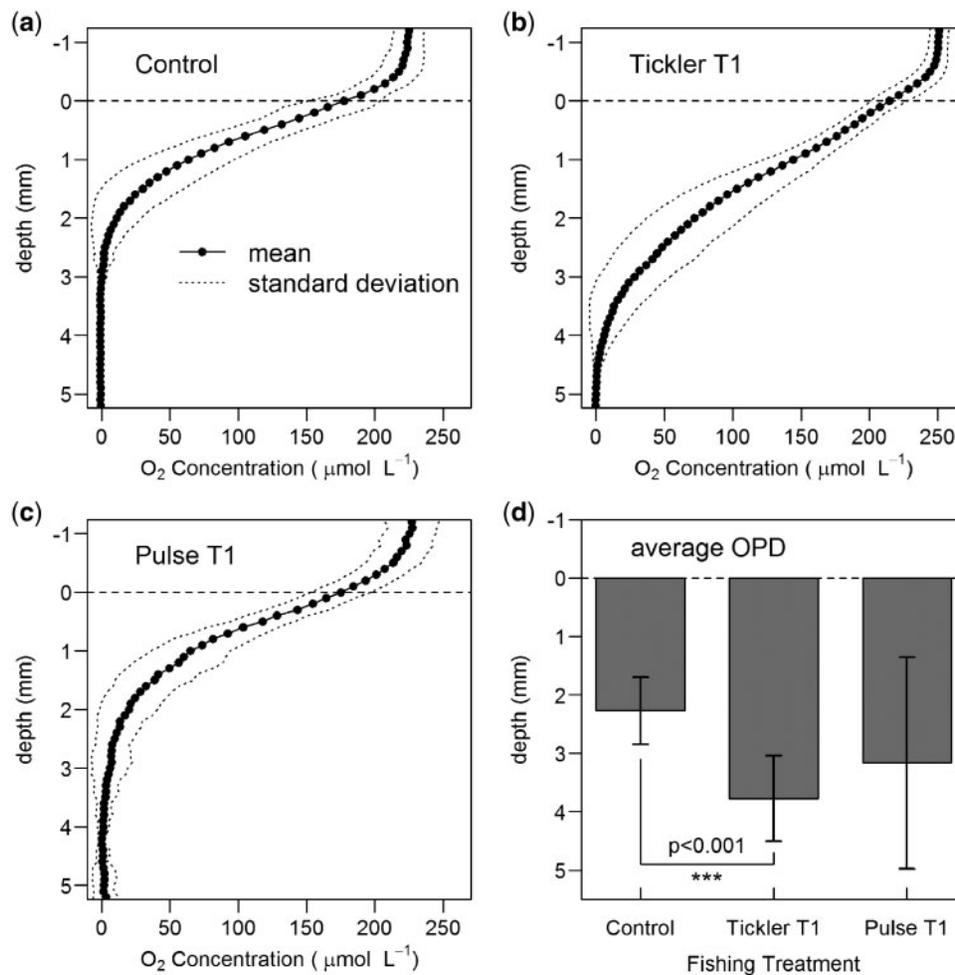


Figure 8. Oxygen microprofiles for (a) control, (b) tickler T1, and (c) pulse T1 areas. (d) Average O₂ penetration depth (mm) and standard deviation from each treatment.

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 with 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 (Figures 5f and 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 *U. deltaura* and *C. 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 4 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

Table 2. Benthic oxygen and nutrient fluxes ($\text{mmol m}^{-2} \text{d}^{-1}$) from on-board incubations and *in situ* lander deployments.

	O_2 Mean \pm SD	NH_4^+ Mean \pm SD	NO_x Mean \pm SD	PO_4^{3-} Mean \pm SD	Si(OH)_4 Mean \pm SD	<i>n</i>
<i>On-board incubations</i>						
Control	-17.78 ± 3.07	0.25 ± 0.34	0.106 ± 0.03	-0.003 ± 0.02	1.43 ± 0.37	9
Tickler T1	$-10.46 \pm 1.50^{***}$	0.35 ± 0.41	0.095 ± 0.02	0.001 ± 0.01	1.10 ± 0.41	4
Tickler T2	$-9.23 \pm 2.14^*$	0.10 ± 0.13	0.097 ± 0.02	0.001 ± 0.01	0.70 ± 0.36	2
Tickler T3	$-10.51 \pm 1.96^*$	n.d.	n.d.	n.d.	n.d.	3
Pulse T1	$-11.93 \pm 4.02^*$	0.28 ± 0.25	0.108 ± 0.02	0.002 ± 0.01	1.30 ± 0.52	7
<i>In situ incubations</i>						
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	$0.088 \pm 0.02^*$	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

n.d., No data; O_2 "fluxes" are denoted as negative.

Bold = significantly different from control samples.

* $p < 0.05$; *** $p < 0.001$.

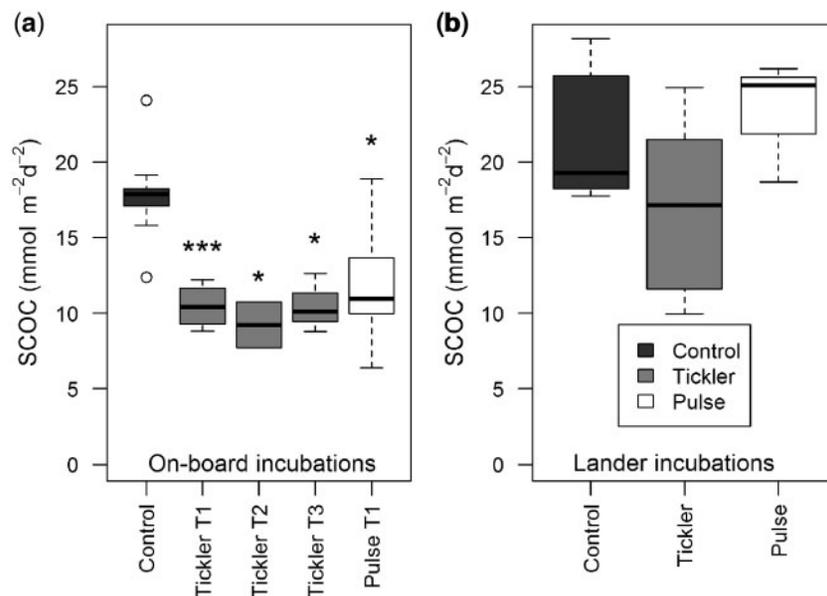


Figure 9. SCOC comparison between *ex situ* and *in situ* incubations. (a) SCOC in on-board measurements taken from box cores in control (untrawled), tickler T1 (6 h after impact), tickler T2 (30 h after impact), tickler T3 (75 h after impact), and pulse T1 (3.5 h after impact) sediment samples. (b)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

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 vs. 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 homogenized 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 homogenization 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 to control samples (Figure 8). These

results are supported by Allen and Clarke's (2007) prediction of a deeper sediment oxic layer following bottom trawl disturbance.

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 $5 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$ during winter months to its peak in August at around $50 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$ (van Raaphorst *et al.*, 1992; Nedwell *et al.*, 1993; Upton *et al.*, 1993; Boon and Duineveld, 1998; Boon *et al.*, 1998). From the month of June, O_2 consumption ranges between 15 and $36 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$ (Upton *et al.*, 1993; Boon and Duineveld, 1998; Boon *et al.*, 1998), which is comparable to 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 mineralization 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 aforementioned 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 TC mineralization rates after anthropogenic caused mixing in OC 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 OC, 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 ($0.10\text{--}0.61 \text{ mmol m}^{-2} \text{ d}^{-1}$) 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 to $1.7 \text{ mmol m}^{-2} \text{ d}^{-1}$) 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 $0.3 \text{ mmol m}^{-2} \text{ d}^{-1}$ in summer, however, van Raaphorst *et al.* (1992) found that NO_x fluxes in June remained closer to $0.1 \text{ mmol m}^{-2} \text{ d}^{-1}$ 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 to 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 occurring 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 to 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 to truly isolate the mechanical and electrical 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 reoxidized 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 to 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.

Acknowledgements

We thank the crews of the fishing vessels HD 29 and UK 227 for their cooperation and participation in this study as well as the crew of the RV Pelagia for providing the means to collect the data for this study. We express our gratitude to the NIOZ analytical lab for processing nutrient and sediment samples and also thank the various PhD students for helping with sample collection during this field expedition. VMS data aiding in the planning and assessment of this research was provided through Wageningen Marine Research and analysed by Niels Hintzen and Karin van der Reijden.

Funding

The research was made possible by the European Maritime and Fisheries Fund (EMFF), and the Netherlands Ministry of Agriculture Nature and Food Quality (LNV) (Grand/Award Number: 1300021172). This article does not necessarily reflect the view of European Commission or the Netherlands Ministries and does not anticipate the Commission/Dutch government's future policy in this area.

References

- Allen, J. I., and Clarke, K. R. 2007. Effects of demersal trawling on ecosystem functioning in the North Sea: a modelling study. *Marine Ecology Progress Series*, 336: 63–75.
- Almroth, E., Tengberg, A., Andersson, J. H., Pakhomova, S., and Hall, P. O. J. 2009. Effects of resuspension on benthic fluxes of oxygen, nutrients, dissolved inorganic carbon, iron and manganese in the Gulf of Finland, Baltic Sea. *Continental Shelf Research*, 29: 807–818.
- Almroth-Rosell, E., Tengberg, A., Andersson, S., Apler, A., and Hall, P. O. J. 2012. Effects of simulated natural and massive resuspension on benthic oxygen, nutrient and dissolved inorganic carbon fluxes in Loch Creran, Scotland. *Journal of Sea Research*, 72: 38–48.
- Batsleer, J., Rijnsdorp, A. D., Hamon, K. G., van Overzee, H. M. J., and Poos, J. J. 2016. Mixed fisheries management: is the ban on discarding likely to promote more selective and fuel efficient fishing in the Dutch flatfish fishery? *Fisheries Research*, 174: 118–128.
- Bergman, M. J. N., and Hup, M. 1992. Direct effects of beam trawling on macrofauna in a sandy sediment in the southern North Sea. *ICES Journal of Marine Science*, 49: 5–11.
- Bergman, M. J. N., and van Santbrink J., W. 2000. Mortality in mega-faunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. *ICES Journal of Marine Science*, 57: 1321–1331.
- Boon, A. R., and Duineveld, G. C. A. 1996. Phytopigments and fatty acids as molecular markers for the quality of near-bottom particulate organic matter in the North Sea. *Journal of Sea Research*, 35: 279–291.
- Boon, A. R., and Duineveld, G. C. A. 1998. Chlorophyll *a* as a marker for bioturbation and carbon flux in southern and central North Sea sediments. *Marine Ecology Progress Series*, 162: 33–43.
- Boon, A. R., Duineveld, G. C. A., Berghuis, E. M., and Van Der Weele, J. A. 1998. Relationships between benthic activity and the annual phytopigment cycle in near-bottom water and sediments in the southern North Sea. *Estuarine, Coastal and Shelf Science*, 46: 1–13.
- Bradshaw, C., Tjensvoll, I., Sköld, M., Allan, I. J., Molvaer, J., Magnusson, J., Naes, K. *et al.* 2012. Bottom trawling resuspends sediment and releases bioavailable contaminants in a polluted fjord. *Environmental Pollution*, 170: 232–241.
- Brylinsky, M., Gibson, J., and Gordon, D. C. Jr. 1994. Impacts of flounder trawls on the intertidal habitat and community of the Minas Basin, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 650–661.
- Collins, J. W. 1887. The beam-trawl fishery of Great Britain, with notes on beam-trawling in other European countries, etc. *Bulletin of the United States Fish Commission*, 19: 289–407.
- Couceiro, F., Fones, G. R., Thompson, C. E. L., Statham, P. J., Sivyver, D. B., Parker, R., Kelly-Gerrey, B. A. *et al.* 2013. Impact of resuspension of cohesive sediments at the Oyster Grounds (North Sea) on nutrient exchange across the sediment–water interface. *Biogeochemistry*, 113: 37–52.
- Dauwe, B., Herman, P. M. J., and Heip, C. H. R. 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Marine Ecology Progress Series*, 173: 67–83.
- De Backer, A., Van Hoey, G., Coates, D., Vanaverbeke, J., and Hostens, K. 2014. Similar diversity-disturbance responses to different physical impacts: three cases of small-scale biodiversity increase in the Belgian part of the North Sea. *Marine Pollution Bulletin*, 84: 251–262.
- de Haan, D., Fosseidengen, J. E., Fjellidal, P. G., Burggraaf, D., and Rijnsdorp, A. D. 2016. Pulse trawl fishing: characteristics of the electrical stimulation and the effect on behaviour and injuries of Atlantic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 73: 1557–1569.
- Depestele, J., Degrendele, K., Esmaili, M., Ivanovi, A., Kro, S., Neill, F. G. O., Parker, R. *et al.* 2018. Comparison of mechanical disturbance in soft sediments due to tickler-chain SumWing trawl vs. electro-fitted PulseWing trawl. *ICES Journal of Marine Science*, 76: 312–329.
- Depestele, J., Ivanovic, A., Degrendele, K., Esmaili, M., Polet, H., Roche, M., Summerbell, K. *et al.* 2016. Measuring and assessing the physical impact of beam trawling. *ICES Journal of Marine Science*, 73: i15–26.
- Dewicke, A., Rottiers, V., Mees, J., and Vincx, M. 2002. Evidence for an enriched hyperbenthic fauna in the Frisian front (North Sea). *Journal of Sea Research*, 47: 121–139.
- Dickens, G. R., Koelling, M., Smith, D. C., and Schnieders, L. 2007. Rhizon sampling of pore waters on scientific drilling expeditions: an example from the IODP expedition 302, Arctic Coring Expedition (ACEX). *Scientific Drilling*, 4: 22–25.
- Dounas, C., Davies, I., Triantafyllou, G., Koulouri, P., Petihakis, G., Arvanitidis, C., Sourlatzis, G. *et al.* 2007. Large-scale impacts of bottom trawling on shelf primary productivity. *Continental Shelf Research*, 27: 2198–2210.

- Dounas, C. G. 2006. A new apparatus for the direct measurement of the effects of otter trawling on benthic nutrient releases. *Journal of Experimental Marine Biology and Ecology*, 339: 251–259.
- Duineveld, G. C. A., and Boon, A. 2002. Short-term variations in the fluxes and composition of seston in near-bottom traps in the southern North Sea. *Helgoland Marine Research*, 56: 140–148.
- Duineveld, G. C. A., De Wilde, P. A. W. J., and Kok, A. 1990. A synopsis of the macrobenthic assemblages and benthic ETS activity in the Dutch sector of the North Sea. *Netherlands Journal of Sea Research*, 26: 125–138.
- Duineveld, G. C. A., Lavaleye, M. S. S., and Berghuis, E. M. 2004. Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). *Marine Ecology Progress Series*, 277: 13–23.
- Duplisea, D. E., Jennings, S., Malcolm, S. J., Parker, R., and Sivyer, D. B. 2001. Modelling potential impacts of bottom trawl fisheries on soft sediment biogeochemistry in the North Sea. *Geochemical Transactions*, 2: 112.
- Eigaard, O. R., Bastardie, F., Breen, M., Dinesen, G. E., Hintzen, N. T., Laffargue, P., Mortensen, L. O. *et al.* 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES Journal of Marine Science*, 73: i27–43.
- Gehlen, M., Malschaert, H., and van Raaphorst, W. R. 1995. Spatial and temporal variability of benthic silica fluxes in the southeastern North Sea. *Continental Shelf Research*, 15: 1675–1696.
- Gundersen, J. K., and Jorgensen, B. B. 1990. Microstructure of diffusive boundary layers and the oxygen uptake of the sea floor. *Nature*, 345: 604–607.
- Haasnoot, T., Kraan, M., and Bush, S. R. 2016. Fishing gear transitions: lessons from the Dutch flatfish pulse trawl. *ICES Journal of Marine Science*, 73: 1235–1243.
- Hiddink, J. G., Jennings, S., Sciberras, M., Szostek, C. L., Hughes, K. M., Ellis, N., Rijnsdorp, A. D. *et al.* 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 114: 8301–8306.
- Jodo, M., Kawamoto, K., Tochimoto, M., and Coverly, S. C. 1992. Determination of nutrients in seawater by analysis rate and reduced interference on segmented-flow analysis with higher ammonia. *Journal of Automatic Chemistry*, 14: 163–167.
- Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C. V., Somerfield, P. J., and Karakassis, I. 2006. Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*, 311: 1–14.
- Kaiser, M. J., Collie, J. S., Hall, S. J., Jennings, S., and Poiner, I. R. 2002. Modification of marine habitats by trawling activities: prognosis and solutions. *Fish and Fisheries*, 3: 114–136.
- Lohse, L., Malschaert, J. F. P., Slomp, C. P., Helder, W., and van Raaphorst, W. 1995. Sediment–water fluxes of inorganic nitrogen compounds along the transport route of organic matter in the North Sea. *Ophelia*, 41: 173–197.
- McCave, I. N., Bryant, R. J., Cook, H. F., and Coughanowr, C. A. 1986. Evaluation of a laser-diffraction-size analyzer for use with natural sediments. *Research Methods Papers*, 56: 561–564.
- Mengual, B., Cayocca, F., Le Hir, P., Draye, R., Laffargue, P., Vincent, B., and Garlan, T. 2016. Influence of bottom trawling on sediment resuspension in the ‘Grande-Vasière’ area (Bay of Biscay, France). *Ocean Dynamics*, 66: 1181–1207.
- Nedwell, D. B., Parkes, R. J., Upton, A. C., and Assinder, D. J. 1993. Seasonal fluxes across the sediment–water interface, and processes within sediments. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 343: 519–529.
- Nieuwenhuize, J., Maas, Y. E. M., and Middelburg, J. J. 1994. Rapid analysis of organic carbon and nitrogen in particulate materials. *Marine Chemistry*, 45: 217–224.
- Olsgard, F., Schaanning, M. T., Widdicombe, S., Kendall, M. A., and Austen, M. C. 2008. Effects of bottom trawling on ecosystem functioning. *Journal of Experimental Marine Biology and Ecology*, 366: 123–133.
- O’Neil, F. G., and Ivanovic, A. 2016. The physical impact of towed demersal fishing gears on soft sediments. *ICES Journal of Marine Science*, 73: i5–14.
- Otto, L., Zimmerman, J. T. E., Furnes, G. K., Mork, M., Saetre, R., and Becker, G. 1990. Review of the physical oceanography of the North Sea. *Netherlands Journal of Sea Research*, 26: 261–238.
- Palanques, A., Puig, P., Guillén, J., Demestre, M., and Martín, J. 2014. Effects of bottom trawling on the Ebro continental shelf sedimentary system (NW Mediterranean). *Continental Shelf Research*, 72: 83–98.
- Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., and Danovaro, R. 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 8861–8866.
- Pusceddu, A., Fiordelmondo, C., Polymenakou, P., Polychronaki, T., Tselepidis, A., and Danovaro, R. 2005. Effects of bottom trawling on the quantity and biochemical composition of organic matter in coastal marine sediments (Thermaikos Gulf, northwestern Aegean Sea). *Continental Shelf Research*, 25: 2491–2505.
- Queirós, A. M., Hiddink, J. G., Kaiser, M. J., and Hinz, H. 2006. Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. *Journal of Experimental Marine Biology and Ecology*, 335: 91–103.
- R Core Team 2014. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Revsbech, N. P. 1989. An oxygen microsensor with a guard cathode. *Limnology and Oceanography*, 34: 474–478.
- Riemann, B., and Hoffman, E. 1991. Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. *Marine Ecology Progress Series*, 69: 171–178.
- Rowden, A. A., and Jones, M. B. 1995. The burrow structure of the mud shrimp *Callinassa subterranea* (Decapoda: Thalassinidea) from the north sea. *Journal of Natural History*, 29: 1155–1165.
- Rowden, A. A., Jones, M. B., and Morris, A. W. 1998. The role of *Callinassa subterranea* (Montagu) (Thalassinidea) in sediment resuspension in the North Sea. *Continental Shelf Research*, 18: 1365–1380.
- Sciberras, M., Hiddink, J. G., Jennings, S., Szostek, C., Hughes, K. M., Kneafsey, B., Clarke, L. J. *et al.* 2018. Response of benthic fauna to experimental bottom fishing: a global meta-analysis. *Fish and Fisheries*, 19: 698–715.
- Sciberras, M., Parker, R., Powell, C., Robertson, C., Kröger, S., Bolam, S., and Hiddink, J. 2016. Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. *Limnology and Oceanography*, 61: 2076–2089.
- Seeberg-Elverfeldt, J., Schluter, M., Feseker, T., and Kolling, M. 2005. Rhizon sampling of porewaters near the sediment–water interface of aquatic systems. *Limnology and Oceanography: Methods*, 3: 361–371.
- Shotbolt, L. 2010. Pore water sampling from lake and estuary sediments using Rhizon samplers. *Journal of Paleolimnology*, 44: 695–700.
- Slomp, C. P., Malschaert, J. F. P., Lohse, L., and van Raaphorst, W. 1997. Iron and manganese cycling in different sedimentary environments on the North Sea continental margin. *Continental Shelf Research*, 17: 1083–1117.
- Soetaert, M., Decostere, A., Polet, H., Verschuere, B., and Chiers, K. 2015. Electrotrawling: a promising alternative fishing technique warranting further exploration. *Fish and Fisheries*, 16: 104–124.

- Soetaert, M., De Haan, D., Verschueren, B., Decostere, A., Puvanendran, V., Saunders, J., Polet, H. *et al.* 2016. Atlantic cod show a highly variable sensitivity to electric-induced spinal injuries. *Marine and Coastal Fisheries*, 8: 412–424.
- Sys, K., Poos, J. J., Meensel, J. V., Polet, H., and Buysse, J. 2016. Competitive interactions between two fishing fleets in the North Sea. *ICES Journal of Marine Science*, 73: 1485–1491.
- Tanner, J. E. 2003. The influence of prawn trawling on sessile benthic assemblages in Gulf St. Vincent, South Australia. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 517–526.
- Trimmer, M., Petersen, J., Sivyer, D. B., Mills, C., Young, E., and Parker, E. R. 2005. Impact of long-term benthic trawl disturbance on sediment sorting and biogeochemistry in the southern North Sea. *Marine Ecology Progress Series*, 298: 79–94.
- Upton, A. C., Nedwell, D. B., Parkes, R. J., and Harvey, S. M. 1993. Seasonal benthic microbial activity in the southern North Sea—Oxygen uptake and sulphate reduction. *Marine Ecology Progress Series*, 101: 273–282.
- van Denderen, P. D., Hintzen, N. T., Rijnsdorp, A. D., Ruardij, P., and van Kooten, T. 2014. Habitat-specific effects of fishing disturbance on benthic species richness in marine soft sediments. *Ecosystems*, 17: 1216–1226.
- van der Reijden, K. J., Molenaar, P., Chen, C., Uhlmann, S. S., Goudswaard, P. C., and van Marlen, B. 2017. Survival of under-sized plaice (*Pleuronectes platessa*), sole (*Solea solea*), and dab (*Limanda limanda*) in North Sea pulse-trawl fisheries. *ICES Journal of Marine Science*, 74: 1672–1680.
- van de Velde, S., Van Lancker, V., Hidalgo-Martinez, S., Berelson, W. M., and Meysman, F. J. R. 2018. Anthropogenic disturbance keeps the coastal seafloor biogeochemistry in a transient state. *Scientific Reports*, 8: 5582.
- van Marlen, B., Wiegerinck, J. A. M., van Os-Koomen, E., and van Barneveld, E. 2014. Catch comparison of flatfish pulse trawls and a tickler chain beam trawl. *Fisheries Research*, 151: 57–69.
- van Raaphorst, W., Kloosterhuis, H. T., Berghuis, E. M., Gieles, A. J. M., Malschaert, J. F. P., and van Noort, G. J. 1992. Nitrogen cycling in two types of sediments of the Southern North sea (Frisian front, broad fourteens): field data and mesocosm results. *Netherlands Journal of Sea Research*, 28: 293–316.
- Virto, I., Barré, P., and Chenu, C. 2008. Microaggregation and organic matter storage at the silt-size scale. *Geoderma*, 146: 326–335.
- Warnken, K. W., Gill, G. A., Dellapenna, T. M., Lehman, R. D., Harper, D. E., and Allison, M. A. 2003. The effects of shrimp trawling on sediment oxygen consumption and the fluxes of trace metals and nutrients from estuarine sediments. *Estuarine, Coastal and Shelf Science*, 57: 25–42.
- Watling, L., Findlay, R. H., Mayer, L. M., and Schick, D. F. 2001. Impact of a scallop drag on the sediment chemistry, microbiota, and faunal assemblages of a shallow subtidal marine benthic community. *Journal of Sea Research*, 46: 309–324.
- Witbaard, R., and Duineveld, G. C. A. 1989. Some aspects of the biology and ecology of the burrowing shrimp callinassa subterranea (Montagu) (Thalassinidea) from the southern north sea. *Sarsia*, 74: 209–219.
- Witbaard, R., Duineveld, G. C. A., Van Der Weele, J. A., Berghuis, E. M., and Reyss, J. P. 2000. The benthic response to the seasonal deposition of phytopigments at the Porcupine Abyssal Plain in the North East Atlantic. *Journal of Sea Research*, 43: 15–31.
- Zapata, M., Rodríguez, F., and Garrido, J.L., 2000. Separation of chlorophylls and carotenoids from marine phytoplankton: a new HPLC method using a reversed phase C8 column and pyridine-containing mobile phases. *Marine Ecology Progress Series*, 195: 29–45.

Handling editor: Steven Degraer