Journal of Experimental Marine Biology and Ecology 545 (2021) 151628

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Physical and electrical disturbance experiments uncover potential bottom fishing impacts on benthic ecosystem functioning

Justin C. Tiano [a,*], Emil De Borger [a], Sarah O'Flynn [a], Chiu H. Cheng [a,b,c], Dick van Oevelen [a], Karline Soetaert [a,b]

[a] Royal Netherlands Institute for Sea Research (NIOZ) and Utrecht University, Department of Estuarine and Delta Systems, PO box 140, 4400 AC Yerseke, the Netherlands
[b] Ghent University, Department of Biology, Marine Biology Section, Krijgslaan 281/S8, 9000 Ghent, Belgium
[c] Wageningen Marine Research, Wageningen University and Research, PO Box 77, 4400AB, Yerseke, the Netherlands

ARTICLE INFO

Keywords:
Electrolysis
Resuspension
Biogeochemistry
Ecosystem functioning
Oxygen dynamics
Bottom trawling

ABSTRACT

Both physical and electrical impacts have been linked to North Sea fisheries activity. This study evaluates how these effects can influence marine ecological functioning by assessing their consequences on benthic pelagic coupling. Experiments were conducted on sediment microcosms taken from 9 North Sea and 2 Eastern Scheldt locations. Samples were subjected to physical disturbances by mechanically stirring the sediment surface or electrical stimulation with exposure to high frequency pulsed bipolar or direct currents. Electrical exposure times of 3 and 120-s were used to simulate *in situ* exposure times related to sole (*Solea solea*) and razor clam (*Ensis spp.*) electric fisheries respectively. Water column oxygen rapidly declined after sediment resuspension, inducing an immediate uptake ranging from 0.55 to 22 mmol oxygen per m^{-2} of sediment disturbed. Mechanical disturbances released the equivalent of up to 94 and 101 h of natural ammonium and silicate effluxes respectively. Fresh organic material significantly predicted the magnitude of mechanical-induced oxygen, ammonium, phosphate and silicate changes. No biogeochemical effects from bipolar (3 s or 120 s) or 3-s direct current exposures were detected. However, significant changes were induced by 120-s exposures to direct currents due to electrolysis and ionic drift. This lowered the water column pH by 1–1.3 units and caused the appearance of iron oxides on the sediment surface, resulting in the equivalent of 25–28 h of sedimentary phosphate removal. Our findings demonstrate that prolonged (+1 min) exposure to high frequency pulsed direct currents can cause electrochemical effects in the marine environment, with implications for phosphorus cycling. Nevertheless, bi-directional pulsed currents used in flatfish pulse trawling and AC waveforms featured in *Ensis* electrofishing, seem to severely limit these effects. Mechanical disturbance, on the other hand, causes a much greater effect on benthic pelagic coupling, the extent of which depends on sediment grain size, organic matter content, and the time of the year when the impact occurs.

1. Introduction

Research on functional ecosystem dynamics help link together structural components in marine ecology (Yvon-Durocher and Allen, 2012; Bell, 2019). For example, the cycling of nutrients in the seafloor is the sum of biological, chemical and physical processes, the results of which can alter oxygen and primary production in the water column (Fisher et al., 1982; Murphy et al., 2000) thereby affecting the functioning (transfer of energy, nutrient regeneration/sequestration *etc.*) of marine ecosystems. The sedimentary release and/or removal of nutrients, such as nitrogen and phosphorus, help control pelagic primary production and influence marine ecosystems through bottom up effects (Slomp et al., 1996; Soetaert and Middelburg, 2009). The removal of nutrients by sediments buffers marine systems against the formation of low oxygen zones, which often result from nutrient overloading combined with water column stratification (Weston et al., 2008; van der Molen et al., 2013). Anthropogenic activities can alter the provision of benthic ecosystem services by modifying sedimentary habitats. Bottom disturbance created by fisheries, for example, can change benthic nutrient concentrations (van de Velde et al., 2018; Tiano et al., 2019)

* Corresponding author.
E-mail address: Justin.Tiano@nioz.nl (J.C. Tiano).

https://doi.org/10.1016/j.jembe.2021.151628
Received 1 December 2020; Received in revised form 28 May 2021; Accepted 30 August 2021
Available online 3 September 2021

potentially impacting primary production (Dounas et al., 2007) and affecting benthic-pelagic coupling in marine ecosystems (Graf, 1989).

Disturbance-induced sediment resuspension causes the rapid fluxes of solutes from the sediment to the overlying water through the direct release of nutrient-rich porewater, and increased desorption and mineralization processes in the water column (Dounas et al., 2007; Couceiro et al., 2013; Tiano et al., 2019). The influx and degradation of organic matter drives benthic nutrient cycles and produces bioavailable compounds (Soetaert et al., 1996). Silt and clay content is positively correlated with organic matter and enhanced mineralization (De Borger et al., 2021a). Muddy organic-rich habitats are therefore, more likely to be at a higher risk from disturbance-induced biogeochemical changes compared to sandy, organic-poor environments.

Benthic disturbance in the North Sea is often associated with beam trawl fisheries and occurs mainly in sandy habitats with a smaller percentage of fishing effort focused on muddy areas (Rijnsdorp et al., 2020). Ecological concerns over the effects of North Sea bottom trawls have existed since their inception in the late middle ages (Collins, 1887; de Groot, 1984), however, the use of electricity in North Sea fisheries, and their potential to create electrolysis-induced biogeochemical changes, brought additional concerns to this topic (Soetaert et al., 2015; Haasnoot et al., 2016; Kraan et al., 2020).

Flatfish trawlers have used electricity to immobilize dover sole (*Solea solea*), facilitating their capture in oncoming nets (Fig. 1; Soetaert et al., 2015). This method uses rapid pulses of alternating polarities called 'pulsed bipolar currents' (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 (Breen et al., 2011; Woolmer et al., 2011; Murray et al., 2016; Fox et al., 2019). This technique has featured both continuous alternating (AC) and direct (DC) currents (Breen et al., 2011; Woolmer et al., 2011; Murray et al., 2016). As prolonged exposure (> 30 s) to electricity is necessary to gain an appropriate response from *Ensis spp.*, sediments can be exposed to electricity for well over a minute using this method (Stewart, 1977; Breen et al., 2011; Woolmer et al., 2011; Murray et al., 2016). In comparison, sediments exposed to electricity by flatfish pulse trawlers are affected for only 1–2 s (Soetaert et al., 2015; de Haan et al., 2016; Desender et al., 2016). Electric fields from pulse trawlers can easily penetrate water-logged marine sediment (> 20 cm; de Haan and Burggraaf, 2018). Consequently, electricity from these gears will affect a 3-dimensional area that surpasses the mechanical gear penetration into the seabed (Fig. 1). Electricity and microbial-mediated electrogenic processes have been linked with changes to marine biogeochemical characteristics (Nielsen et al., 2010; Goreau, 2012; Rao et al., 2016; van de Velde et al., 2016) and concerns have been reported over the possible chemical effects of electrotrawling on sedimentary habitats (Soetaert et al., 2015).

This study uses an experimental approach to explore functional ecological characteristics while evaluating anthropogenic-related impacts on benthic pelagic coupling. We focus on the release/consumption of bioavailable nutrients, which relate directly to bottom up ecological functioning (production potential) and the availability of oxygen required for the aerobic respiration. The null hypotheses of this study include: (1) electrical and mechanical disturbances have no effect on benthic biogeochemical parameters, (2) organic matter and grain size have no influence on the magnitude of disturbance-induced biogeochemical changes, and (3) mechanical disturbance has no effect on sediment grain sizes and/or organic matter in the sediment column. These hypotheses were tested with microcosm experiments used to simulate both mechanical and electrical effects seen in certain North Sea fisheries.

2. Materials and methods

2.1. Study area

Benthic sediment samples were collected from nine locations in the North Sea and two locations from the Dutch Eastern Scheldt (Fig. 2). North Sea stations feature names indicating the research vessel used for their sample collection ('Tridens' = TD1, TD2, TD3; 'Pelagia' = PG1, PG2, PG3, PG4, PG5, PG6) with station numbers corresponding to their order of collection. Eastern Scheldt stations (ES1 and ES2) are named to specify that they were located in the former estuary (it is now completely marine; Fig. 2). Sediments from the most northerly stations (PG3 and PG4) were silty with a median grain size (D50) under 62.5 μm. Stations PG1, PG5, PG6 and ES2 were defined as 'very fine sand' (D50 = 62.5–125 μm) habitats. Fine sand (125–250 μm) characterized stations TD1, TD2, PG2 and ES1. Station TD3 had the coarsest sediment with D50 sizes that ranged between medium (250–500 μm) and coarse (500–1000 μm) sand. PG3 and PG4 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 (ES1 and ES2) stations were

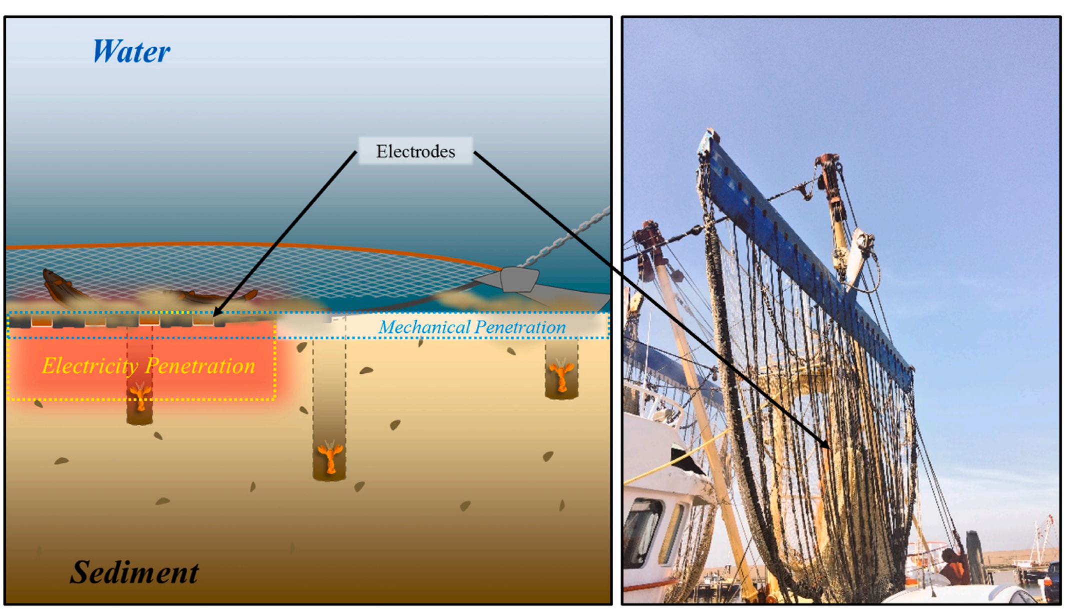

Fig. 1. Conceptual figure of a pulse trawl showing electrical and mechanical penetration into the seabed (*left*). Image of an HFK PulseWing gear (*right*).

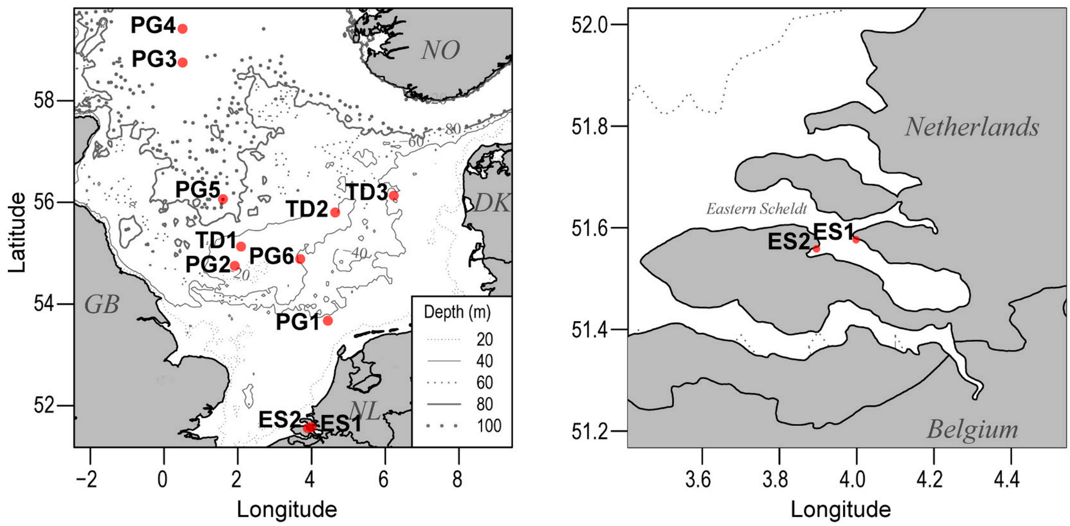

Fig. 2. Map of station locations. Numbers show the locations of North Sea and Eastern Scheldt stations (*left*). Close-up of Eastern Scheldt locations (*right*).

Table 1
Sampling date, coordinates and average environmental parameters between stations for depth (m), median grain size (D50; μm) % organic carbon (OC), 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}, positive = out of sediment). Nutrient flux measurements represent rates taken before experimental perturbations.

Station	Date	Position (N,E)	Depth	D50	OC	Chl *a*	Density	Biomass	Fluxes (mmol m^{-2} d^{-1})					
									O_2	NH_4^+	NO_2^-	NO_3^-	PO_4^{3-}	$Si(OH)_4$
TD1	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
TD2	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
TD3	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
PG1	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
PG2	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
PG3	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
PG4	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
PG5	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
PG6	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
ES1[a]	04/10/2018	51° 34.6, 3° 59.9	0.0	138.2	0.1	4.1	0[a]	0[a]	−15.6	2.60	0.29	−0.15	−0.09	0.34
ES2[a]	10/10/2018	51° 33.5, 3° 53.7	0.0	75.5	0.6	10.7	0[a]	0[a]	−15.9	3.99	0.48	−0.54	−0.05	1.12

[a] Sediments at stations ES1 and ES2 were sieved of macrofauna prior to experimental measurements.

located in the intertidal zone (~0 m).

2.2. 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 TD1–3 were visited with the RV Tridens in August–September 2017. The RV Pelagia was used to collect samples from station PG1 in November 2017 and from stations PG2-PG6 in May 2018. Box cores were subsampled using cylindrical PVC incubation cores (14.5 cm diameter × 30 cm height). For stations ES1 and ES2, incubation cores of the same dimensions were used to collect sediment directly from intertidal flats in the Eastern Scheldt in October 2018. To control for unpredictable faunal responses to the 2-min electrical exposures featured only at Eastern Scheldt stations (see Section 2.4.2: 'Electrical disturbance treatments'), their sediments 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 Eastern Scheldt stations which received the longer (2 min) electrical exposure periods and not for North Sea stations where the faunal response to electricity was thought to be less consequential due to their lower exposure time (3 s).

Cores containing sediment and overlying water from stations TD1–TD3 and PG2-6 were placed in water baths inside a climate controlled (12 °C) chamber on board the research vessels for 6 h prior to the first incubation (Table 2). For station PG1, samples were transported from Texel, Netherlands to the NIOZ facility in Yerseke, Netherlands. ES1 and ES2 samples were transported from the Eastern Scheldt intertidal flats (Netherlands) to the NIOZ facility (transport = ~5 h for station PG1, ~1 h for Eastern Scheldt stations). After arrival at the research institute, sediments from stations PG4, ES1 and ES2 were acclimatized for 48 h inside water baths within climate-controlled chambers, with the temperature representative of environmental conditions at the time of collection (12 °C for station PG1; 18 °C for Eastern Scheldt stations; Table 2). The longer acclimatization period allowed time for biogeochemical gradients to re-establish in the post-sieved sediments at stations ES1 and ES2 and for station PG1 sediments to re-adjust to constant conditions after exposure to fluctuating temperatures during transport.

2.3. Electrical parameters

To mimic electrical disturbance from pulse trawls and *Ensis* electrofishing gears, 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 characterized by a similar time gap between positive and negative pulses and is slightly easier to generate for electronic systems (Soetaert et al., 2019; Fig. 3, top left panel). Stations ES1 and ES2 included a pulsed direct current (PDC) treatment

Table 2
Number of cores per treatment for electrical (Bipolar, Direct) and mechanical (Mix) disturbance treatments and corresponding acclimatization periods (hours).

Station	Number of cores per treatment						Acclimatization time (h)
	Control	Mix	Bipolar	Direct	Bipolar	Direct	
		3 s			120 s		
TD1	1	–	3	–	–	–	
TD2	1	–	3	–	–	–	6
TD3	2	3	3	–	–	–	6
PG1	2	3	3	–	–	–	48
PG2	2	3	3	–	–	–	6
PG3	2	3	3	–	–	–	6
PG4	2	3	3	–	–	–	6
PG5	2	3	3	–	–	–	48
PG6	2	3	3	–	–	–	6
ES1	3	3	3	3	3[a]	3[a]	6
ES2	3	3	3	3	3[a]	3[a]	48

[a] 120-s electric disturbance treatments occurred 24 h after 3-s perturbations in the same (Bipolar/Direct) sediment incubation cores.

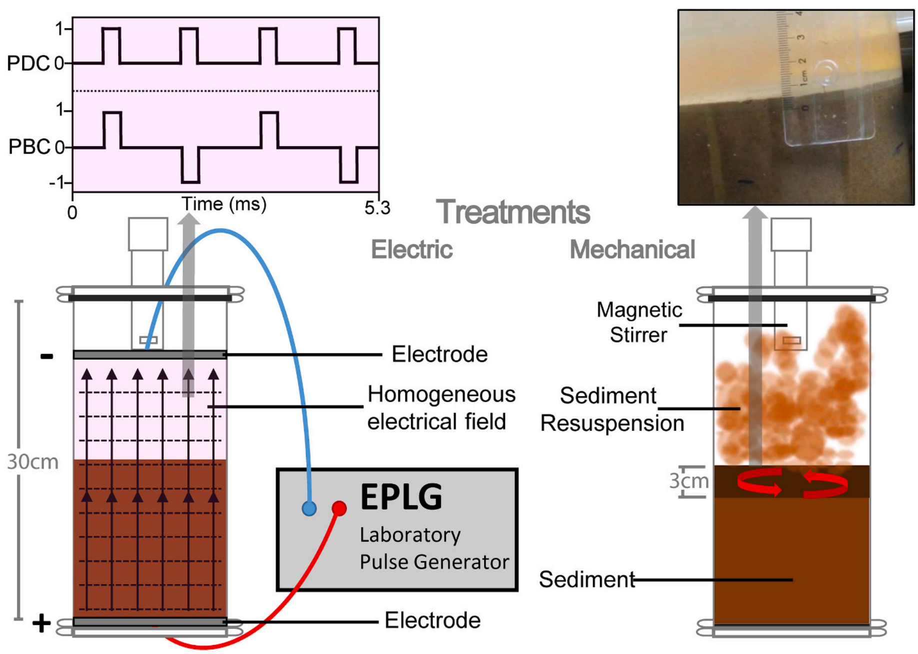

Fig. 3. Experimental setup: Electrical disturbance treatment setup showing the homogeneous electrical field between the electrodes with black arrows representing the pulsed flow of electrons and dashed lines representing equipotentials (zones with the same electrical potential; *left*). Characteristic positive pulses for pulsed direct current (PDC) treatments 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*).

characterized by unidirectional pulses (Fig. 3, 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 spp*. (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 bipolar waveforms displayed 40 positive and 40 negative pulses while all direct current pulses were positive (Fig. 3). For simplicity, we hereafter refer to our high frequency pulsed currents as 'Bipolar' to represent pulsed bipolar currents and 'Direct' to represent pulsed direct currents.

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; Fig. 3). A field strength of 200 V per meter (V m^{-1}) was created in the sediment and water column between the electrodes for Bipolar 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 Direct treatments to be more representative of *Ensis* electrofishing parameters (Fig. 3). 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).

The *ex situ* microcosms required differences from *in situ* electrofishing. Pulse trawls and *Ensis* electrofishing gears use cylindrical or wire shaped electrodes that run parallel to each other and create heterogeneous electric fields (Soetaert et al., 2015; Fig. 1). For exposure experiments in the laboratory, a homogenous electric field using flat electrodes is preferred in order to expose the whole sample to the same electric field strength (Soetaert et al., 2016; Boute et al., 2020). To obtain a homogenous electric field inside an incubation core while exposing the full sediment column, we oriented the electrodes vertically, with one electrode attached to the bottom of the core and the other suspended above the sediment (Fig. 3), whereas flatfish pulse trawls and *Ensis* electrofishing gears have horizontal oriented electrodes. Our experimental setup, nevertheless, allowed us to achieve our objectives of exploring the biogeochemical impacts of anthropogenic electric fields, while using electrical parameters seen in flatfish pulse trawl and *Ensis* electrofishing methods.

2.4. Experimental setup

To investigate the impact of electrical and mechanical disturbances, BACI (Before-After-Control-Impact) design experiments were conducted for all sampled locations. Figs. 3 and 4 help illustrate our somewhat complicated experimental design.

2.4.1. Mechanical disturbance treatments

Every station other than TD1 and TD2, received a mechanical disturbance treatment ('Mix'; Table 2). Logistic constraints onboard the RV Tridens limited the amount of samples taken for TD1 and TD2, which prevented the Mix treatment from taking place at those stations. To simulate trawl-induced mechanical mixing and sediment resuspension, a handheld electric mixer homogenized surface sediments inside incubation cores down to a depth of 3 cm (Fig. 3). Depestele et al. (2018) found average penetration depths of 1.8 and 4.1 cm for pulse trawls (PulseWing) and tickler chain SumWing trawls respectively, in the muddy sand sediments of the Frisian Front. Though penetration depths may vary between sediments and gear types, we maintained a consistent (3 cm) depth to compare results between all experimental samples. A 3-s 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 homogenize the total surface area of the sediment core.

2.4.2. Electrical disturbance treatments

All stations featured a Bipolar treatment while ES1 and ES2 received additional Direct current treatments (Table 2). For cores undergoing electrical exposure, an electrode was fitted to the bottom of the incubation core underneath the sediment column (Fig. 3). Upon opening the cores after pre-disturbance incubations (see Section 2.4.5: '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 (Fig. 3). In both flatfish pulse trawling and *Ensis* electrofishing, electrodes maintain physical contact with the sediment (Breen et al., 2011; Murray et al., 2016; Depestele et al., 2016; Depestele et al., 2018) allowing the penetration depth of the electrical field to exceed 20 cm into the sediment (de Haan and Burggraaf, 2018). Electrodes seen in flatfish pulse trawling range between 4 and 6 m in length (van Marlen et al., 2014; de Haan et al., 2016) and are towed at speeds of 2.3–2.6 m s^{-1} (4.5–5 knots; Poos et al., 2020) limiting the exposure time for a single point in the sediment to a few seconds at most. In comparison, electrodes for *Ensis* electrofishing are shorter (1–3 m) but are towed at much slower rates (1.5–3.3 m min^{-1}; Breen et al., 2011; Woolmer et al., 2011; Murray et al., 2016; Fox et al., 2019), which allow sediment exposure times of 18–120 s. We thus assigned exposure times of 3-s to represent electrical disturbance from flatfish pulse trawls ('3Bipolar' and '3Direct') while using 120-s exposure times ('120Bipolar' and '120Direct') to simulate sediment exposure periods found in the *Ensis* electrofishery (stations ES1 and ES2; Table 2). Maximal exposure times were used to assess the effects from 'severe' electrical disturbance from both methods. The *Ensis* electrofishing comparison was planned and implemented at a later stage in the study and were not included for North Sea stations.

2.4.3. 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 3Bipolar and 27 other cores were subjected to the Mix treatment.

For ES1 and ES2, all experimental cores were subjected to two rounds of disturbances 24 h apart (Fig. 4, *right panel*). This was conducted to observe possible differences between the first and second perturbations. Six experimental cores (separate from the Bipolar and Mix treatments) were used for the Direct current treatment with 3Direct occurring on day 2 and 120Direct on day 3 (Fig. 4; Table 2). The same procedure was carried out for Bipolar cores (3Bipolar and 120Bipolar). The 6 Mix cores at these stations were mechanically disturbed for 3-s on day 2 and day 3 to observe possible differences between first and second mechanical disturbance events (Fig. 4; Table 2).

2.4.4. 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

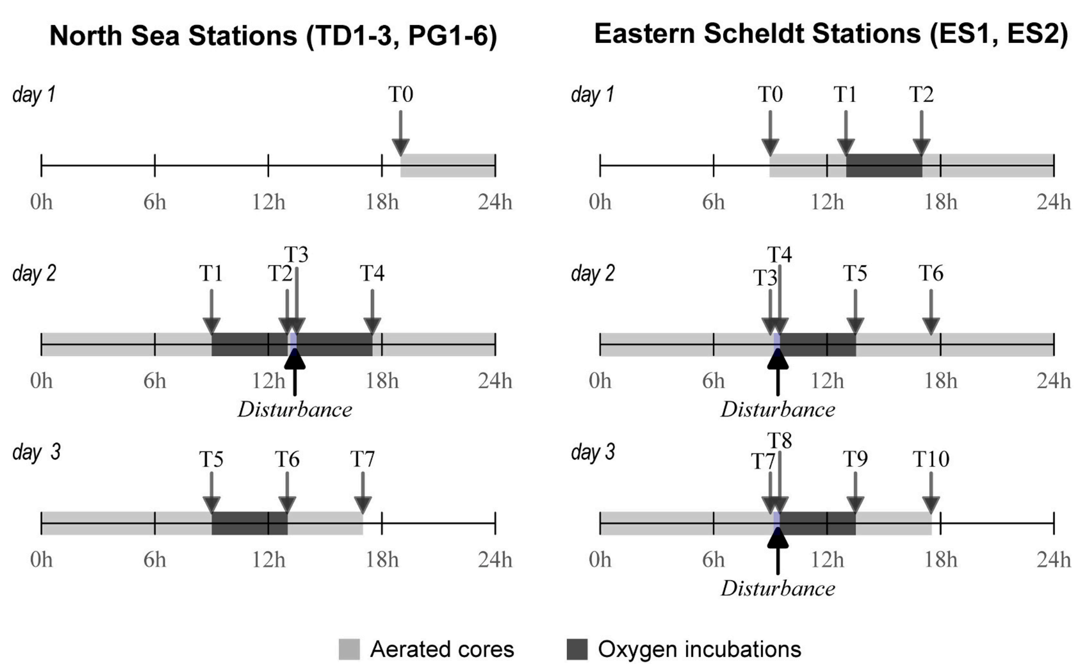

Fig. 4. General sampling scheme for stations North Sea stations (*left*) and stations Eastern Scheldt (*right*). Downward facing arrows represent water sample timesteps. Upward facing arrows represent disturbance times.

taken and stored in a polystyrene vial (Fig. 4). For North Sea stations, the overlying water in the cores was aerated overnight and a water sample (T1) was taken in the morning (Fig. 4, *left panel*). 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 s 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 (Fig. 3). Upon reopening the cores after the initial incubation, water samples were taken for nutrient analysis and the cores were aerated until O_2 saturation levels reached >95%. For Eastern Scheldt stations, pre-disturbance incubations occurred during the first day allowing additional water sampling timesteps for day 1 (Fig. 4, *right panel*).

2.4.5. Post-disturbance incubations

After pre-disturbance measurements, experimental cores were subjected to either electrical (3Bipolar, all stations; 3Direct, stations ES1 and ES2) or mechanical (Mix, all stations except TD1 and TD2; Table 2) treatments (day 2, Fig. 4). Immediately after the disturbance treatments, a water sample was taken and cores were sealed for a post-disturbance O_2 incubation (Fig. 4). Cores were reopened after 4 h and water samples were taken. On day 3, experimental cores underwent an additional oxygen incubation (North Sea stations) or a second round of experimental treatments (Eastern Scheldt stations; Fig. 4). For ES1 and ES2, samples subjected to electrical treatments underwent longer-term exposures (120Bipolar, 120Direct) 24 h after the first perturbations. Alongside, sediments used for mechanical disturbance received an additional 3-s Mix treatment 24 h after the original (Fig. 3). 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.

2.5. Core and sample processing

After the experimental treatments, incubation cores from North Sea stations 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 analyzer (Jodo et al., 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 ES1 and ES2 with a Radiometer PHM120 Acid-Base-Analyzer (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.

2.6. Sediment parameters

Data was collected for grain size characteristics for surface (0–5 cm) sediments at North Sea stations with a cut-off syringe (20 mL). Favorable logistics for Eastern Scheldt stations allowed 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. All samples were placed in a −20 °C freezer shortly after collection. Sediments 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 et al., 1986). Sediments from stations PG1–PG6 and ES1–ES2 were measured for organic carbon (OC), total nitrogen (TN) and chlorophyll (Chl *a*). An Interscience Flash 2000 organic element analyzer was used to determine OC and TN content. Acetone (90%) was used to extract Chl *a* pigments from freeze-dried sediments and analyzed using UV spectrophotometry (Ritchie, 2006).

2.7. Statistical analysis

Assumptions for parametric data (normal distribution/homogeneity of variances) were evaluated through a visual assessment of residuals. If the assumptions were not met, data underwent a $\log_e(x) + 1$ transformation prior to analyses. We used linear mixed models (LMM), using the R package: 'lme4' (Bates et al., 2015) to test if pH and solute (O_2, NH_4^+, NO_2^-, NO_3^-, PO_4^{3-} $Si(OH)_4$) concentrations in the overlying water of sediment cores were significantly different than in control sediments during the same period (under the null hypothesis of no differences between any disturbed or control treatments). To account for spatial differences between sample sites, a LMM was created using 'treatment' as a fixed variable and 'station' as a random variable. This was tested against another LMM that only contained the random variable (station) using a one-way analysis of variance (ANOVA). If a significant difference was found, pairwise tests between treatments were carried out using the estimated marginal means using the R-package: 'emmeans' (Lenth, 2019). For stations TD3, PG1–6, ES1 and ES2, similar methodology was used for results within each station using 'sample' as the random variable. Stations TD1 and TD2 were limited to only one control sample (LMM's were not possible) so significant differences were determined using a one-way ANOVA's and Tukey HSD pairwise tests. For Eastern Scheldt stations, LMM's were used to test whether resuspension from mechanical disturbance had any significant effects on grain size and organic matter in the upper sediment. Possible differences in solute concentrations from control cores during the perturbation sampling period (immediately before and after experimental disturbances) were investigated with LMM's using 'station' as a fixed factor and 'core' as the random factor.

To help account for the unbalanced experimental design while comparing effects between disturbed pH/solute concentrations, treatment effect sizes were estimated using the Hedges' g metric (R package: 'effsize') to incorporate small sample sizes (Grissom and Kim, 2005). Effect sizes were estimated between treatments across all stations. Hedges' g values were also estimated for treatments within stations TD3, PG1–6, ES1 and ES2. Single control samples in TD1 and TD2 prevented accurate effect size estimates within these sites, though their data contributed to the broad scale Hedges' g estimates that contained all stations.

To test the null hypothesis that variables related to organic matter (OC, TN, Chl *a*) and sediment grain size (Median grain size, Silt %, Very fine sand %) have no relationship with disturbance-induced changes to pH and/or solutes (O_2, NH_4^+, NO_2^-, NO_3^-, PO_4^{3-} $Si(OH)_4$), robust regressions were used using the R package: 'robustbase' (Maechler et al., 2020). 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 visualization were carried out using R (R Development Core Team, R, 2011).

3. Results

3.1. Natural biogeochemical fluxes

O_2 consumption before experimental treatments was highest at TD2, followed by ES1 and ES2 (Table 1, Supplementary Table S2). NH_4^+ effluxes were the highest in the Eastern Scheldt (>2.6 mmol m^{-2} d^{-1}, ES1) while all other stations averaged under 1.0 mmol m^{-2} d^{-1}. NO_3^- effluxes were the highest in the coarsest sediments at TD3 but displayed a negative flux (directed into the sediment) in the Eastern Scheldt. PO_4^{3-} exhibited a negative flux for 7 out of 11 locations and showed relatively low effluxes for stations TD1, PG2, PG4 and PG5. Natural $Si(OH)_4$ flux was highest at TD2 and lowest at PG2 which displayed low fluxes for all nutrients. Solutes in control cores measured before and after experiment perturbation periods, showed significantly lower PO_4^{3-} concentrations from ES1 compared to stations PG5 ($p < 0.01$) and PG6 ($p < 0.05$), though, no other significant differences were found.

3.2. Faunal parameters

Among North Sea stations, PG5 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 TD1 (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 among these stations with 81% of these individuals occurring at PG5. *Paramphinome jeffreysii* (bristle worms), was the second most abundant taxon and was found mainly in PG4 (51%) and PG5 (40%). PG4 had the highest species richness (24 taxa) followed by TD2 (22 taxa). Despite the variation in biomass and abundances of macrofauna between stations, no consistent or statistically significant relationships were found between faunal parameters and O_2 consumption or any other biogeochemical fluxes in this study ($p > 0.05$).

3.3. 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). Disturbed cores displayed a 'flattened' topography after resettling of the suspended sediments with a visible layer of fines on the surface of the cores (Fig. 3, *top right panel*). Sediment profiles from the Eastern Scheldt showed different responses to physical disturbance between the fine sand (ES1) and sandy mud (ES2) habitats. D50 became significantly lower at the surface (0–1 cm) after the Mix treatment (127.7 ± 2.6 μm) for ES1 compared to undisturbed control cores (137.6 ± 1.6 μm; $p < 0.001$; Fig. 5). Significantly higher OC (0.092 ± 0.003%; $p < 0.05$), TN (0.0150 ± 0.0002%; $p < 0.001$) and Chl *a* content (6.04 ± 0.74 μg g^{-1}; $p < 0.001$) were found in the mechanically mixed surface sediments of ES1 compared to control samples (0.076 ± 0.002 OC%, 0.0116 ± 0.0009 TN%; 4.12 ± 0.16 μg Chl *a* g^{-1}). For the sandy mud at ES2, no significant change was found between treatments 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; $p < 0.001$; Fig. 5). This shallow subsurface layer also displayed significantly lower Chl *a* (9.39 ± 1.32 μg g^{-1}), OC (0.44 ± 0.11%), and TN (0.053 ± 0.011%) content compared to control sediments (10.33 ± 1.24 μg Chl *a* g^{-1}; 0.61 ± 0.14 OC%; 0.068 ± 0.011 TN%; $p < 0.001$).

The Mix treatment created rapid changes in the absolute concentrations of O_2, NH_4^+, PO_4^{3-} and $Si(OH)_4$, in the overlying water, though the longer term (>8 h) fluxes did not change drastically (Fig. 6). Sediment resuspension quickly decreased water column O_2 concentrations at all stations where the treatment occurred except for station PG2 (Table 3). NH_4^+ was released from the sediment from stations sampled in autumn (TD3, PG1, ES1 and ES2), while there was a limited response

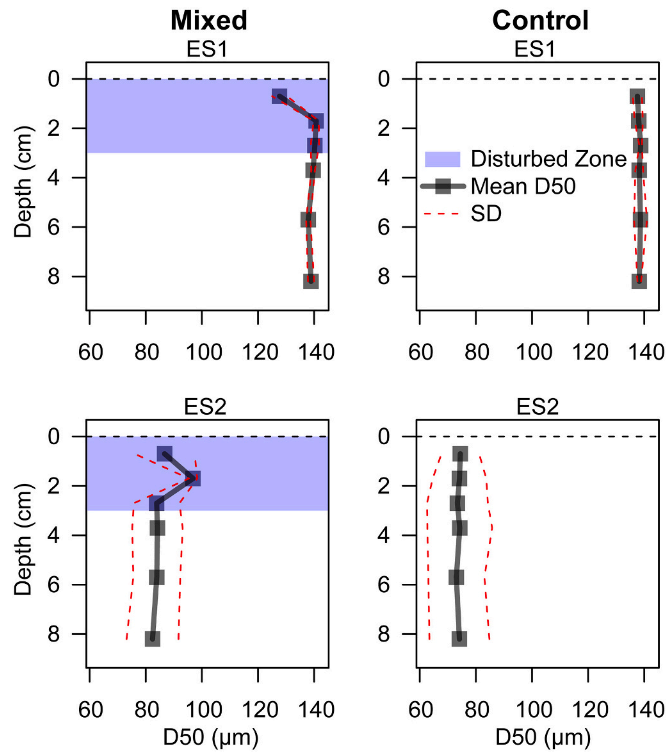

Fig. 5. Sediment median grain size (D50) profiles showing mechanically disturbed and control cores from Eastern Scheldt stations.

of NH_4^+ from stations sampled in spring (PG2-PG6; Table 3). The Mix treatment caused the release of PO_4^{3-} at all stations where it occurred except for PG2 and ES1. At station ES1 (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 (Fig. 6c). $Si(OH)_4$ was consistently released at all locations with mechanical perturbations (TD3, PG1-PG6, ES1-ES2). 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-} ($p < 0.01$) and $Si(OH)_4$ ($p < 0.001$) when compared with undisturbed control samples (Fig. 7). Sediment mixing also significantly decreased the pH at ES1 and ES2 (the only stations where pH was measured; $p < 0.001$; Fig. 8). Changes to absolute solute concentrations can be found in Supplementary Table S3.

When comparing effect sizes created from mechanical disturbances across all stations and treatments, $Si(OH)_4$ produced the highest Hedges' g value (2.3) while O_2 exhibited a strong negative response (Hedges' g: −1.47; Fig. 9). Mechanical disturbance showed the strongest effect size from O_2 at station ES1 (Hedges g: −6.4; Fig. 9; Supplementary Table S4).

Robust regressions 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 (PG1-PG6, ES1-ES2; $n = 24$), 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 Fig. 1). These relationships were all positive (higher Chl *a* led to larger disturbance-induced changes) with the exception of PO_4^{3-} which was inversely related to Chl *a*. 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 showing all positive relationships (TD3, PG1-PG6, ES1-ES2; $n = 27$; Supplementary Fig. 2). For disturbance-induced changes to pH (stations ES1 and ES2), Chl *a* explained 81% of the decrease caused from mechanical perturbations ($p < 0.001$; $n = 12$; Supplementary Fig. 3).

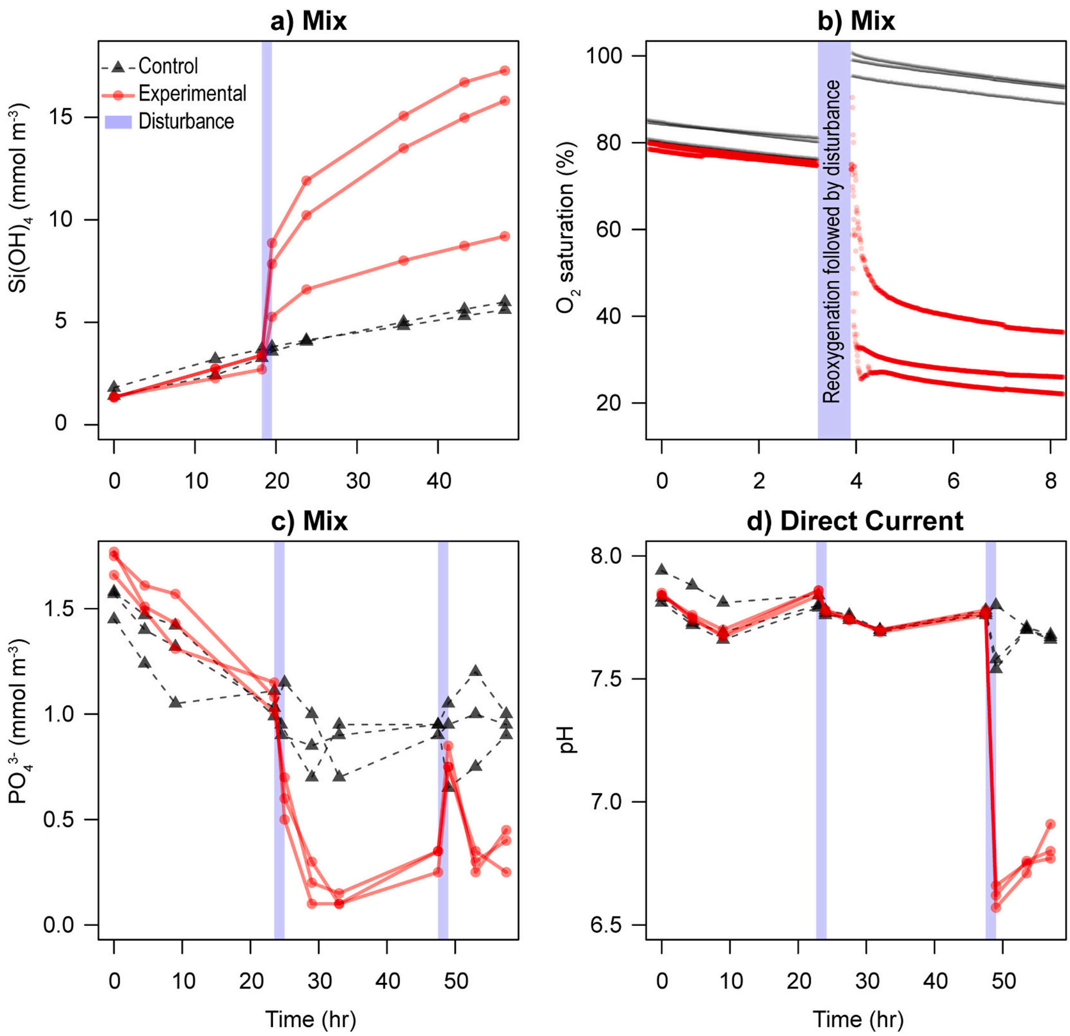

Fig. 6. Examples of perturbation-induced biogeochemical changes in the overlying water of incubation cores. Mechanical effects on silicate concentrations (a), oxygen saturation (b) and phosphate concentrations (c; showing 2 mixing events). The effect of direct current exposure on pH (d; 1st disturbance = 3 s, 2nd disturbance = 120 s).
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 high resolution optode technology used to measure oxygen concentrations.

3.4. 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: 'Electrical parameters'). Neither Bipolar treatment (3Bipolar and 120Bipolar) caused consistent changes to solute fluxes/concentrations or pH values. At station TD2, immediate NH_4^+ fluxes were significantly higher in Bipolar cores (+ 0.15 mmol m^{-2}) compared to controls ($p < 0.01$) though similar results were not replicated at other locations (Table 3). The only consistent effects from electrical perturbations came from cores subjected to 120Direct.

During 120Direct exposure, gas bubbles formed at the top electrode throughout the treatment period. An odor of chlorine was observed for 120Direct treated cores, which grew stronger with exposure time. Sediments exposed to 120Direct exhibited fluffy brown iron oxide particles forming on the sediment surface during the electrical exposure (Fig. 10). Values for pH and PO_4^{3-} were significantly lower after 120Direct compared to control cores ($p < 0.001$; Figs. 7 and 8; Table 3). While the 120Direct-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 (ES1) compared to sandy mud (ES2; $p < 0.01$; Table 3). Cores exposed to 120Direct also showed significantly lower NH_4^+ and NO_2^-concentrations compared to controls ($p < 0.05$; Fig. 6; Table 3).

When comparing effect sizes across all treatments, stations and parameters, 120Direct produced the largest Hedges' g values (in this case, negative values), which were found for pH (−8.3) and PO_4^{3-} (−3.2; Fig. 9). When comparing results within stations, 120Direct produced a strong negative effect for pH (−16.6) at ES2 and ES1 (−5.9; Supplementary Table S4).

3.5. 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 120Direct treatments (Table 4). On average, mechanical-induced oxygen consumption equaled 17.1 h of natural O_2 demand, with disturbances at ES2 equaling 33.1 h and PG2 equaling 2.4 h of natural fluxes. The perturbed NH_4^+ fluxes were equivalent to a natural flux lasting 3.8 (PG5) to 93.9 (PG6) hours. Natural Si$(OH)_4$ fluxes would have needed up to 101 h to attain the concentration change found at ES1 compared with 9.9 h at PG4. The 120Direct treatment caused rapid fluxes equivalent to 28 and 25.2 h of

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.

ST.	Treatment	Δ Solute concentration (mmol m^{-2}) and pH (m^{-2})						pH
		O_2	NH_4^+	NO_2^-	NO_3^-	PO_4^{3-}	$Si(OH)_4$	
TD1	3Bipolar	0.08	0.05	0	−0.06	0	0.03	–
TD2	3Bipolar	1.3	**0.15****	0	0.02	−0.03	−0.39	–
TD3	3Bipolar	−1.1	0.27	0	0.06	−0.02	0.08	–
	Mix	**−4.6***	0.32	0	0.18	**0.08****	**0.96*****	–
PG1	3Bipolar	0.13	0.05	0	0.02	0	0.09	–
	Mix	**−17***	**1.0*****	0	−0.09	**0.02****	**1.5****	–
PG2	3Bipolar	−0.21	−0.09	0	0.06	0	0	–
	Mix	−0.55	−0.08	0.02	−0.03	0	**0.02*****	–
PG3	3Bipolar	−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***	–
PG4	3Bipolar	0.42	0.66	0.12	−0.12	0	−0.26	–
	Mix	**−4.2***	−0.21	−0.06	0.20	**0.11*****	**0.66***	–
PG5	3Bipolar	0.21	−0.56	0.09	−0.36	−0.03	−0.59	–
	Mix	**−4.6***	0.06	−0.03	0	**0.23*****	**1.7*****	–
PG6	3Bipolar	−0.21	−0.02	0.02	0	0.03	−0.03	–
	Mix	**−14***	1.1	0	0.12	**0.11****	**1.9***	–
ES1	3Bipolar	0.45	0.44	0	−0.23	−0.02	−0.27	0
	3Direct	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
	120Bipolar	0.41	−0.18	0.02	−0.14	0.03	−0.27	0
	120Direct	1.48	0.17	−0.14	−0.29	−0.11	−0.3	**−0.15*****
ES2	3Bipolar	0.82	0.33	0.02	−0.17	−0.03	−0.14	−0.02
	3Direct	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***
	120Bipolar	0.37	0.08	0.09	0	−0.02	−0.05	−0.03
	120Direct	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 stations ES1 and ES2.

PO_4^{3-} uptake at ES1 and ES2 respectively. Natural flux equivalents to disturbed PO_4^{3-} fluxes 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-} (positive flux) from the sediments.

4. Discussion

A major concern of electrofisheries impacts are the potential biogeochemical effects imposed by these types of fisheries (Soetaert et al., 2015) and how this can affect functional ecosystem dynamics such as the transfer of organic matter, nutrients and energy. This study was aimed at filling some of the knowledge gaps on this topic. We, nonetheless, acknowledge that *ex situ* experiments are unable to fully replicate many important *in situ* conditions such as bottom currents and changing environmental conditions. Our results regarding the inhibition/limitation of biogeochemical impacts when using bipolar (and other alternating) currents can be directly applicable to any electrofishing technique. Other connections between our results and commercial bottom trawling, however, remain more suggestive due to the exploratory nature of this study.

Our experiments found consistent biogeochemical changes 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 an electrical current with alternating polarities (*i.e.* pulsed bipolar and alternating currents). In the following, we discuss the biogeochemical responses to mechanical disturbance and electrical exposure and how these effects can affect marine ecosystem functioning.

4.1. Mechanical effects

By extrapolating from our experimental results, we can estimate that mechanical disturbance from a North Sea trawler with two standard 12 m wide gears penetrating an average of 3 cm in the sediment, can cause the rapid release of 24 to 190 mol NH_4^+, 0.48 to 5.5 mol PO_4^{3-} and 0.5 to 50.4 mol of $Si(OH)_4$ for every km trawled while causing the consumption of 86.4 to 528 mol of O_2 from the water column. This can be compared to −12.5 to 95.8 mol NH_4^+, −2.2 to 0.96 mol PO_4^{3-} and 0.72 to 55.4 mol $Si(OH)_4$ naturally released by sediments along with the natural consumption of 129 to 604 mol O_2 in 24 h from an area of the same size.

We should, nonetheless, take into account the limitations associated with conducting mechanical disturbance experiments in closed systems. Perhaps most evident, we did not try to recreate bottom currents in our sediment cores, which would 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 situ*.

Mechanically perturbed cores in our study exhibited a layer of fine surface sediments after the particles resettled from resuspension (Fig. 3). This is similar to a field study where a layer of fines was visible on sediment profile images taken after *in situ* beam trawling (Tiano et al., 2020). This occurs because heavier particles are the first to resettle on the sediment water interface while finer grains can eventually sort themselves on the seabed surface. Sediment profiles taken after mechanical perturbations, however, show that the effect of mixing and resuspension on grain size characteristics depends on the type of sediment present. 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 (Fig. 5). 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). This is caused by the disturbance-induced winnowing of fine particles. Trawl-induced fining of sediments, however, was reported by Trimmer et al. (2005) in a

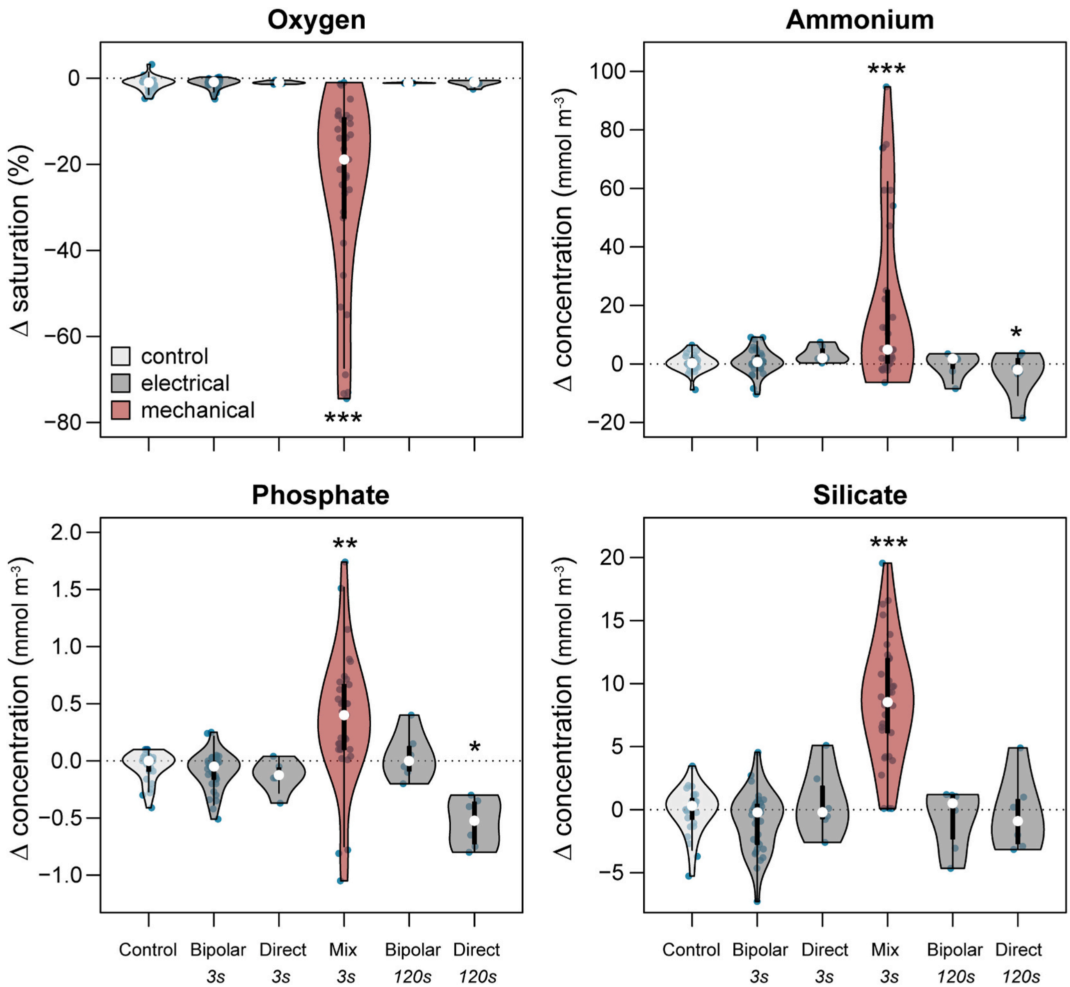

Fig. 7. Treatment-induced changes for oxygen saturation and ammonium, phosphate and silicate concentrations between experimental treatments in the water column of sediment cores. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$ significant differences compared to control samples.

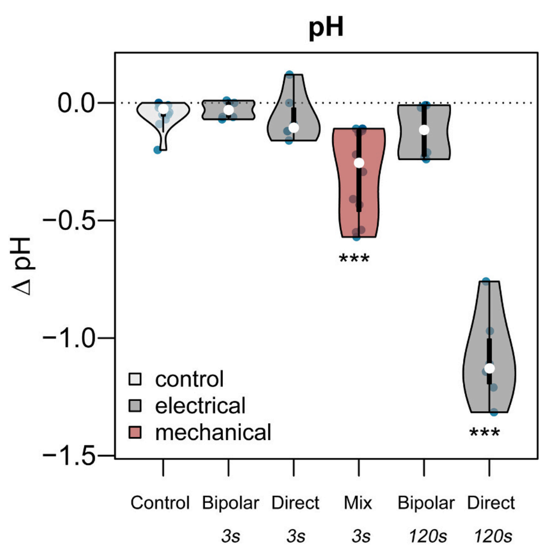

Fig. 8. Treatment-induced changes in water column pH found in sediment cores. Measurements for pH were only taken at stations ES1 and ES2. ***$p < 0.001$ significant differences compared to control samples.

relatively stable North Sea location (Outer Silver Pit) but not in a more dynamic area (Thames). Results from 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.

Our regressions provide evidence linking the magnitude of disturbance-induced solute changes to the amount of fresh organic material (Chl *a*) in the sediment. As the breakdown of organic matter leads to bioavailable nutrients, sediments with high Chl *a* concentrations often contain large amounts of porewater nutrients (De Borger et al., 2021a). Mechanical disturbance to productive, nutrient rich sediments will therefore, cause relatively large biogeochemical alterations. Fine sediments are more likely to contain higher concentrations of organic matter and nutrients compared to coarser grains (Virto et al., 2008; Bainbridge et al., 2012; De Borger et al., 2021a, 2021b). We found the percentage of very fine sands to be a reliable predictor of solute changes after sediment resuspension, likely due to their relationship with organic matter. However, no statistically significant relationships between silt and biogeochemical parameters, were found possibly due to low silt percentages in the majority of the sample sites (Table 1; Supplementary Table 1). Our results show that physical disturbance can concentrate fine-grained sediment and organic matter towards the sediment surface. This may explain the mechanism behind the higher organic matter concentrations found in trawled (surface) sediments reported in other studies (Polymenakou et al., 2005; Pusceddu et al., 2005; Palanques et al., 2014; Sciberras et al., 2016).

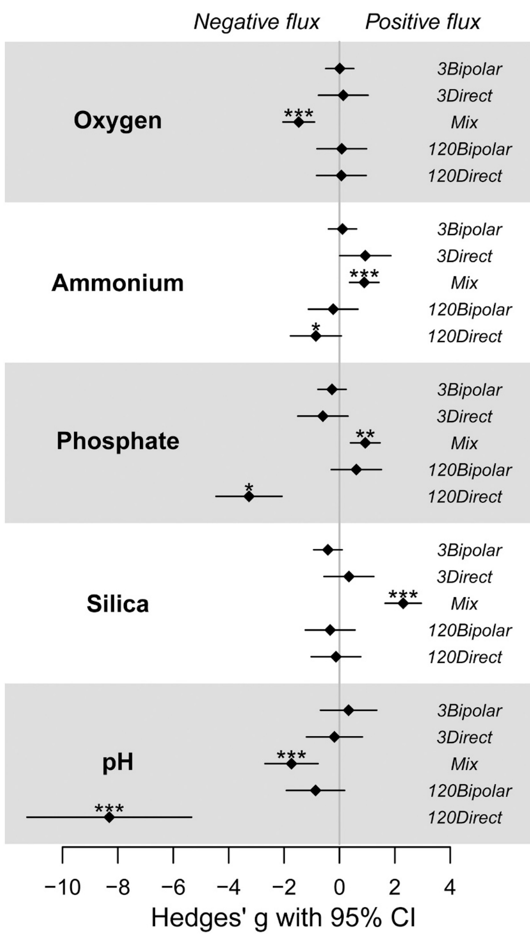

Fig. 9. Hedges' g effect sizes showing the relative effects of rapid solute changes across all treatments and stations for oxygen, ammonium, phosphate silica and pH. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$ significant differences compared to control samples.

We observed a seasonal effect on the amount of NH_4^+ released from mechanical disturbance that suggests a higher potential for disturbance-induced nutrient fluxes in autumn compared to spring. 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 PG2 (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 natural O_2, NO_3^- and $Si(OH)_4$ flux rates (Table 1, Supplementary Table 1). ES2 (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 natural fluxes across all solute parameters (Table 1).

Our results show that the nutrient exchange between the benthic and pelagic zones after a physical perturbation may 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-Rosell et al. (2012) found increases of 48 mmol m^{-3} and 6.9 mmol m^{-3} 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

Table 4
Time required for natural fluxes to equal perturbed fluxes for the Mix treatment (oxygen, ammonium, silicate) and for the 120-s direct current treatment (phosphate).

Stations	Time (h)			
	O_2	NH_4^+	$Si(OH)_4$	PO_4^{3-}
	Uptake	Release	Release	Uptake
	(Mix)	(Mix)	(Mix)	(120Direct)
TD3	12	20.4	76.8	–
PG1	32.6	NA	61.9	–
PG2	2.4	NA	12	–
PG3	7.8	6.9	21.6	–
PG4	9.5	NA	9.9	–
PG5	12.2	3.8	33	–
PG6	30.4	93.9	52	–
ES1	13.7	67.8	100.8	28
ES2	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). Direct treatments only occurred at stations ES1 and ES2.

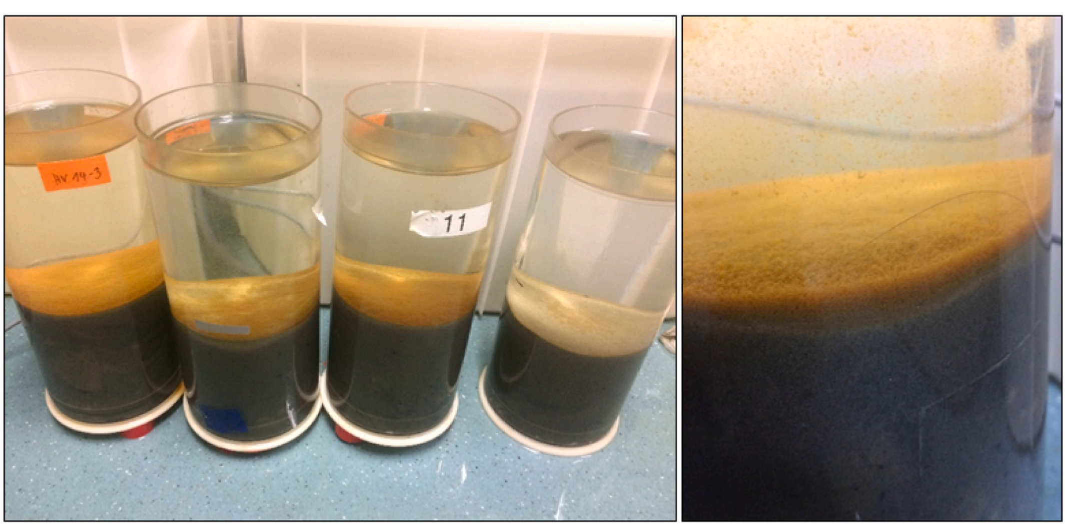

Fig. 10. Images of iron oxide formation in three cores exposed to pulsed direct currents next to one control core (*left*). A close-up view at newly formed iron oxides on the sediment surface and in the water column (*right*).

uptake of PO_4^{3-} found at station ES1 in our study. The first perturbation at ES1 likely oxidized a substantial amount of reduced iron during resuspension, causing the adsorption of PO_4^{3-} to iron oxides in the water column (Fig. 6c). Upon the second mechanical perturbation (24 h later), most of the iron in the upper sediments was probably oxidized, 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 (Fig. 6c). 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 Fig. 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 (PO_4^{3-} adsorbs to iron when oxidized), oxygen and organic matter (limits PO_4^{3-} adsorption to iron oxides; Weng et al., 2012; Sulu-Gambari et al., 2016).

Sediment resuspension causes the release of dissolved inorganic carbon from porewater (Almroth-Rosell et al., 2012), which lowers pH through the dissociation of carbon dioxide and release of protons (Soetaert et al., 2007). This coupled with a suite of chemical reoxidation reactions occurring in the water column after sediment resuspension, are the probable mechanisms driving the mechanical-induced reduction in pH found in our study (Soetaert et al., 2007). Water column pH affects the bioavailability of nutrients during resuspension by influencing adsorption/desorption processes, though the exact details of these effects are dependent on multiple factors such as redox conditions, sediment composition and buffering reactions (Soetaert et al., 2007; Wong and Yang, 1997; Niemistö et al., 2011).

4.2. Electrical effects

This study did not find any consistent biogeochemical effects concerning the pulsed bipolar currents used by the electrotrawl fishery for North Sea sole or for *Ensis* electrofishing using alternating currents. Sediment resuspension created from lowering the top electrode into the incubation core likely created the minor changes in NH_4^+ found for the Bipolar treatment at TD1 and TD2 (Table 3). Bipolar currents were used by Dutch flatfish trawl fishers 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 *Ensis* electrofishing, fishers have used continuous AC or DC currents (Breen et al., 2011; Woolmer et al., 2011; Murray et al., 2016). The 120Direct 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 needed to use 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. We, therefore, underestimated the duty cycle (percentage of time the current is flowing) while overestimating the field strength from *Ensis* electrofishing in our experiments. As Eastern Scheldt stations were subjected to 2-min electrical exposures, we stopped any indirect effects caused from electrically exposed 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 electrical fields on sediment biogeochemical parameters and not on sediment fauna. Many direct connections between our results and pulse trawling or Ensis electrofishing should therefore be interpreted with caution, however, our results suggesting the inhibition of geochemical effects from bipolar/alternating currents can be applied to any electrical field affecting the sediment.

One of the strongest effects we recorded from 120Direct 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 PO_4^{3-} compounds adsorbed onto in the overlying water (Sulu-Gambari et al., 2016; Rao et al., 2016). This phenomenon occurred because of the unidirectional current deployed in the 120Direct treatment caused the advective transport of porewater iron ions 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 pulsed bipolar currents seem to limit ionic drift, longer exposure to high frequency pulsed DC or continuous DC will cause the unidirectional movement of porewater ions in the sediment. This can lead to the transport of reduced iron towards the sediment surface and the subsequent binding to PO_4^{3-} in the water column. Our results suggest that 3 sec of a DC electrical field at 125 V m^{-1} is not enough to produce conspicuous changes to water column PO_4^3 while 2 min of the same stimulus can lead to a significant removal of bioavailable phosphorous. Ionic drift may also have affected nitrogen dynamics with the decreased NH_4^+ and NO_2^-in the water column of sediment cores after 120Direct, however, the exact mechanism causing these changes remains unclear.

Organic matter, silicates and pH play a strong role in the adsorption of PO_4^{3-} to iron oxides (Canfield et al., 2005; Weng et al., 2012; Jones et al., 2015). Between the two stations where 120Direct took place, significantly more water column PO_4^{3-} was removed in the station with lower sediment Chl *a* (a proxy for fresh organic material), OC content and $Si(OH)_4$ fluxes (Table 1). Organic matter and silicate compete with PO_4^{3-} for adsorption and can reduce the amount of iron bound phosphorus (Weng et al., 2012; Haynes and Zhou, 2018). As lower pH (4–6) can favor phosphorus-iron oxide binding (Weng et al., 2012) the decline in water column pH after 120Direct may have also helped facilitate this process. The electrolysis-induced decline in pH was the strongest effect seen in this study (Fig. 9, Supplementary Table S4). This may have been caused by the oxidation of iron, calcium or other metal ions (Soetaert et al., 2007) that fluxed to the sediment surface during ionic drift, or the production of hypochlorous acid (HOCl) due to the formation of chlorine gas (Cl_2) on the cathode and its subsequent reaction with water. The dynamics affecting pH can be complex but estimations of processes affecting changes in pH (and *vice versa*) are possible with an understanding of the net charges exchanged and buffering reactions that occur (Soetaert et al., 2007). With the buffering capacity of seawater, the changes in pH are expected to be much less detectable in an open (or *in situ*) system (Morgan et al., 2012), however, possible consequences to phosphorous dynamics may hold larger implications if DC electric fields (high frequency pulsed or continuous) are used in benthic habitats (Martins et al., 2014).

4.3. Implications

Our findings imply that electrochemical reactions from pulse trawling for sole and *Ensis* electrofishing using AC, are minimal due to their use of bi-directional currents. Biogeochemical effects are more likely, when using high frequency pulsed DC or continuous DC, which is more relevant for *Ensis* electrofishing only if DC is used. 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 electricity-induced adsorption of PO_4^{3-} (>25 h of PO_4^{3-} adsorbed within 2 min of pulsed direct currents; Table 4) confirms the possibility for electrodes to remove PO_4^{3-} from sedimentary habitats (Martins et al., 2014). Unintended phosphate removal may be a cause for concern if anthropogenic-induced electrolysis (electrofishing, faulty wiring on marine vessels, batteries in seawater *etc.*) causes changes to the natural phosphorus dynamics, though these effects may also buffer marine habitats against eutrophication (Martins et al., 2014). More research is necessary to show if these electrochemical effects are harmful (or helpful) 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 mechanical 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 h of natural sediment O_2 consumption (Table 4). Trawl-induced nutrient release from sediment resuspension is predicted to trigger primary production in the water column (Dounas et al., 2007). Mechanical bottom trawl disturbance can lower benthic mineralization (De Borger et al., 2021b; Tiano et al., 2019) and reduce denitrification (De Borger et al., 2021b; Ferguson et al., 2020; van der Molen et al., 2013). This can decrease sedimentary nutrient removal, thus lowering the buffering effect that marine sediments have against eutrophication. Furthermore, our demonstration of mechanically induced depletion of water column O_2, supports similar *in situ* observations 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., 2009; Almroth-Rosell et al., 2012) may create damaging additive effects on marine communities. Nevertheless, these effects are context dependent and contrasting findings such as trawl-induced increases in benthic mineralization (van de Velde et al., 2018) organic matter (Pusceddu et al., 2005; Palanques et al., 2014; Sciberras et al., 2016) and the lack of information regarding biogeochemical effects in the water column, highlight the need for further investigation on this topic.

Author contribution statement

The authors of this study hereby declare that the material presented in this manuscript is based on original research and has not been previously published or submitted elsewhere. All authors agree with the contents of the manuscript and its submission to the journal of Experimental Marine Biology and Ecology. None of the authors have any financial benefits or other conflicts of interest resulting from the publication of this manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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) as part of the Impact Assessment Pulsetrawl Fishery (IAPF) project (Grand/Award Number: 1300021172). 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 Parson-s'and Maria Balcelar Martinez from FUGRO for processing our macrofauna samples and sending us our data from the UK. We credit Pim Boute from Wageningen University for providing the oscilloscope and carrying out the measurements used to check our electrical parameters.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151628.

References

Almroth, E., Tengberg, A., Andersson, J.H., Pakhomova, S., 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. Cont. Shelf Res. 29 (5–6), 807–818. https://doi.org/10.1016/j.csr.2008.12.011.

Almroth-Rosell, E., Tengberg, A., Andersson, S., Apler, A., 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. J. Sea Res. 72, 38–48. https://doi.org/10.1016/j.seares.2012.04.012.

Bainbridge, Z.T., Wolanski, E., Álvarez-Romero, J.G., Lewis, S.E., Brodie, J.E., 2012. Fine sediment and nutrient dynamics related to particle size and floc formation in a Burdekin River flood plume, Australia. Mar. Pollut. Bull. 65 (4), 236–248. https://doi.org/10.1016/j.marpolbul.2012.01.043.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1) https://doi.org/10.18637/jss.v067.i01.

Bell, T., 2019. Next-generation experiments linking community structure and ecosystem functioning. Environ. Microbiol. Rep. 11 (1), 20–22. https://doi.org/10.1111/1758-2229.12711.

Boute, P.G., Soetaert, M., Reid Navarro, J.A., Lankheet, M.J., 2020. Effects of electrical pulse stimulation on behaviour and survival of marine benthic invertebrates. Front. Mar. Sci. 7, 592650. https://doi.org/10.3389/fmars.2020.592650.

Breen, M., Howell, T., Copland, P., 2011. A report on electrical fishing for razor clams (*Ensis sp.*) and its likely effects on the marine environment. Mar. Scotl. Sci. Rep. 375.

Burdorf, L.D.W., Tramper, A., Seitaj, D., Meire, L., Hidalgo-Martinez, S., Zetsche, E.-M., et al., 2016. Long-distance electron transport occurs globally in marine sediments. Biogeosci. Discuss. (September), 1–35. https://doi.org/10.5194/bg-2016-362.

Canfield, D.E., Kristensen, E., Thamdrup, B., 2005. Aquatic geomicrobiology. Adv. Mar. Biol. 48, 1–599. https://doi.org/10.1016/S0065-2881(05)48017-7.

Collins, J.W., 1887. The Beam-trawl Fishery of Great Britain, with notes on beam-trawling in other european countries, etc. Bull. U. S. Fish Comm. 19, 289–407.

Couceiro, F., Fones, G.R., Thompson, C.E.L., Statham, P.J., Sivyer, D.B., Parker, R., 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 (1–3), 37–52. https://doi.org/10.1007/s10533-012-9710-7.

De Borger, E., Braeckman, U., Soetaert, K., 2021a. Rapid organic matter cycling in North Sea sediments. Cont. Shelf Res. 214 (December), 104327. https://doi.org/10.1016/j.csr.2020.104327.

De Borger, E., Tiano, J., Braeckman, U., Rijnsdorp, A.D., Soetaert, K., 2021b. Impact of bottom trawling on sediment biogeochemistry: a modelling approach. Biogeosciences 18, 2539–2557. https://doi.org/10.5194/bg-18-2539-2021, 2021.

de Groot, S.J., 1984. The impact of bottom trawling on benthic fauna of the North-Sea. Ocean Manag. 9 (3–4), 177–190.

de Haan, D., Burggraaf, D., 2018. Field Strength Profile in and Above the Seabed as Reference to Pulse Trawl Fishing on Dover sole (*Solea solea*). Wageningen University and Research Report. C022/18.

de Haan, D., Fosseidengen, J.E., Fjelldal, P.G., Burggraaf, D., 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 J. Mar. Sci. 1–13. https://doi.org/10.1093/icesjms/fst176.

Depestele, J., Ivanovic, A., Degrendele, K., Esmaeili, M., Polet, H., Roche, M., O'Neil, F. G., 2016. Measuring and assessing the physical impact of beam trawling. ICES J. Mar. Sci. 73, i15–i26.

Depestele, J., Degrendele, K., Esmaeili, M., Ivanovi, A., Kröger, S., Neill, F.G.O., et al., 2018. Comparison of mechanical disturbance in soft sediments due to tickler-chain SumWing trawl vs. electro-fitted PulseWing trawl. ICES J. Mar. Sci. fsy124, 1–18. https://doi.org/10.1093/icesjms/fsy124.

Desender, M., Chiers, K., Polet, H., Verschueren, B., Saunders, J.H., Ampe, B., et al., 2016. Short-term effect of pulsed direct current on various species of adult fish and its implication in pulse trawling for brown shrimp in the North Sea. Fish. Res. 179 (February), 90–97. https://doi.org/10.1016/j.fishres.2016.02.018.

Dounas, C.G., Davies, I.M., Hayes, P.J., Arvanitidis, C.D., Koulouri, P.T., 2005. The effect of different types of otter trawl ground rope on benthic nutrient releases and sediment biogeochemistry. Benthic Habitats Eff. Fish. 41 (January), 539–544.

Dounas, C., Davies, I., Triantafyllou, G., Koulouri, P., Petihakis, G., Arvanitidis, C., et al., 2007. Large-scale impacts of bottom trawling on shelf primary productivity. Cont. Shelf Res. 27 (17), 2198–2210. https://doi.org/10.1016/j.csr.2007.05.006.

Ferguson, A.J.P., Oakes, J., Eyre, B.D., 2020. Bottom trawling reduces benthic denitrification and has the potential to influence the global nitrogen cycle. Limnol. Oceanogr. https://doi.org/10.1002/lol2.10150.

Fisher, T.R., Carlson, P.R., Barber, R.T., 1982. Sediment nutrient regeneration in three North Carolina estuaries. Estuar. Coast. Shelf Sci. 14 (1), 101–116. https://doi.org/10.1016/S0302-3524(82)80069-8.

Fox, C.J., McLay, A., Dickens, S., 2019. Development and application of electrofishing with towed video as a new survey method for razor clams (Ensis spp.). Fish. Res. 214 (January), 76–84. https://doi.org/10.1016/j.fishres.2019.01.027.
Goreau, T., 2012. Marine Electrolysis for Building Materials and environmental restoration. In: Electrolysis. InTech Publishing, Rijeka, Croatia, pp. 273–290. https://doi.org/10.5772/48783.
Graf, G., 1989. Benthic-Pelagic coupling in a deep-sea benthic community. Nature 341, 437–439.
Grissom, R., Kim, J., 2005. Effect Sizes for Research. Routledge, New York. https://doi.org/10.4324/9781410612915.
Haasnoot, T., Kraan, M., Bush, S.R., 2016. Fishing gear transitions: lessons from the Dutch flatfish pulse trawl. ICES J. Mar. Sci. 73 (4), 1235–1243. https://doi.org/10.1093/icesjms/fsw002.
Haynes, R., Zhou, Y., 2018. Competitive and noncompetitive adsorption of silicate and phosphate by two acid Si-deficient soils and their effects on P and Si extractability. Soil Sci. Plant Nutr. 64 (4), 535–541.
Jodo, M., Kawamoto, K., Tochimoto, M., Coverly, S.C., et al., 1992. Determination of nutrients in seawater by analysis rate and re- duced interference on segmented-flow analysis with higher ammonia. Journal of Automatic Chemistry 14, 163–167. https://doi.org/10.1155/S1463924692000300.
Jones, C., Nomosatryo, S., Crowe, S.A., Bjerrum, C.J., Canfield, D.E., 2015. Iron oxides, divalent cations, silica, and the early earth phosphorus crisis. Geology 43, 135–138.
Koller, M., Stahel, W.A., 2011. Sharpening Wald-type inference in robust regression for small samples. Comput. Stat. Data Anal. 55 (8), 2504–2515. https://doi.org/10.1016/j.csda.2011.02.014.
Kraan, M., Groeneveld, R., Pauwelussen, A., Haasnoot, T., Bush, S.R., 2020. Science, subsidies and the politics of the pulse trawl ban in the European Union. Mar. Policy 118 (August), 103975. https://doi.org/10.1016/j.marpol.2020.103975.
Lenth, R., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4. https://CRAN.R-project.org/package=emmeans.
Maechler, M., Rousseeuw, P., Croux, C., Todorov, V., Ruckstuhl, A., Salibian-Barrera, M., Verbeke, T., Koller, M., Conceicao, E.L., Anna di Palma, M., 2020. robustbase: Basic Robust Statistics. R package version 0.93-6.
Martins, G., Peixoto, L., Brito, A.G., Nogueira, R., 2014. Phosphorus-iron interaction in sediments: can an electrode minimize phosphorus release from sediments? Rev. Environ. Sci. Biotechnol. 13 (3), 265–275. https://doi.org/10.1007/s11157-014-9343-5.
McCave, I.N., Bryant, R.J., Cook, H.F., Coughanowr, C.A., 1986. Evaluation of a laser-difference-size analyzer for use with natural sediments. Res. Methods Papers 56, 561–564. https://doi.org/10.1306/212F89CC-2B24-11D7-8648000102C1865D.
Mengual, B., Cayocca, F., Le Hir, P., Draye, R., Laffargue, P., Vincent, B., Garlan, T., 2016. Influence of bottom trawling on sediment resuspension in the 'Grande-Vasière' area (Bay of Biscay, France). Ocean Dyn. 66 (9), 1181–1207. https://doi.org/10.1007/s10236-016-0974-7.
Morgan, B., Rate, A.W., Burton, E.D., 2012. Water chemistry and nutrient release during the resuspension of FeS-rich sediments in a eutrophic estuarine system. Sci. Total Environ. 432, 47–56. https://doi.org/10.1016/j.scitotenv.2012.05.065.
Murphy, A.E., Sageman, B.B., Hollander, D.J., Lyons, T.W., Brett, C.E., 2000. Black shale deposition and faunal overturn in the Devonian Appalachian basin: clastic starvation, seasonal water-column mixing, and efficient biolimiting nutrient recycling. Paleoceanography 15 (3), 280–291. https://doi.org/10.1029/1999PA000445.
Murray, F., Copland, P., Boulcott, P., Robertson, M., Bailey, N., 2016. Impacts of electrofishing for razor clams (Ensis spp.) on benthic fauna. Fish. Res. 174, 40–46. https://doi.org/10.1016/j.fishres.2015.08.028.
Nielsen, L.P., Risgaard-Petersen, N., 2015. Rethinking sediment biogeochemistry after the discovery of electric currents. Annu. Rev. Mar. Sci. 7 (1), 425–442. https://doi.org/10.1146/annurev-marine-010814-015708.
Nielsen, L.P., Risgaard-Petersen, N., Fossing, H., Christensen, P.B., Sayama, M., 2010. Electric currents couple spatially separated biogeochemical processes in marine sediment. Nature 463 (7284), 1071–1074. https://doi.org/10.1038/nature08790.
Niemistö, J., Holmroos, H., Horppila, J., 2011. Water pH and sediment resuspension regulating internal phosphorus loading in a shallow lake – field experiment on diurnal variation. J. Limnol. 70 (1), 3–10. https://doi.org/10.4081/jlimnol.2011.3.
Palanques, A., Puig, P., Guillén, J., Demestre, M., Martín, J., 2014. Effects of bottom trawling on the Ebro continental shelf sedimentary system (NW Mediterranean). Cont. Shelf Res. 72, 83–98. https://doi.org/10.1016/j.csr.2013.10.008.
Polymenakou, P.N., Pusceddu, A., Tselepides, A., Polychronaki, T., Giannakourou, A., Fiordelmondo, C., Danovaro, R., 2005. Benthic microbial abundance and activities in an intensively trawled ecosystem (Thermaikos Gulf, Aegean Sea). Cont. Shelf Res. 25 (19–20), 2570–2584. https://doi.org/10.1016/j.csr.2005.08.018.
Poos, J., Hintzen, N.T., van Rijssel, J.C., Rijnsdorp, A., 2020. Efficiency changes in bottom trawling for flatfish species as a result of the replacement of mechanical stimulation by electric stimulation. ICES J. Mar. Sci. (October) https://doi.org/10.1093/icesjms/fsaa126.
Pusceddu, A., Fiordelmondo, C., Polymenakou, P., Polychronaki, T., 2005. Effects of bottom trawling on the quantity and biochemical composition of organic matter in coastal marine sediments (Thermaikos Gulf, northwestern Aegean Sea). Cont. Shelf Res. 25, 2491–2505. https://doi.org/10.1016/j.csr.2005.08.013.
R Development Core Team, R, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vol. 1. https://doi.org/10.1007/978-3-540-74686-7.
Rao, A.M.F., Malkin, S.Y., Hidalgo-Martinez, S., Meysman, F.J.R., 2016. The impact of electrogenic sulfide oxidation on elemental cycling and solute fluxes in coastal sediment. Geochim. Cosmochim. Acta 172, 265–286. https://doi.org/10.1016/j.gca.2015.09.014.
Riemann, B., Hoffman, E., 1991. Ecological consequences of dredging and bottom tawling in the Limfjord, Denmark. Mar. Ecol. Prog. Ser. 69 (November 2015), 171–178. https://doi.org/10.3354/meps069171.
Rijnsdorp, A.D., Depestele, J., Eigaard, O.R., Hintzen, N.T., Ivanovic, A., Molenaar, P., van Kooten, T., 2020. Mitigating seafloor disturbance of bottom trawl fisheries for North Sea sole Solea solea by replacing mechanical with electrical stimulation. PLoS ONE 15 (11 November). https://doi.org/10.1371/journal.pone.0228528.
Risgaard-Petersen, N., Revil, A., Meister, P., Nielsen, L.P., 2012. Sulfur, iron-, and calcium cycling associated with natural electric currents running through marine sediment. Geochim. Cosmochim. Acta 92, 1–13. https://doi.org/10.1016/j.gca.2012.05.036.
Ritchie, R.J., 2006. Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents. Photosynth. Res. 89 (1), 27–41. https://doi.org/10.1007/s11120-006-9065-9.
Sciberras, M., Parker, R., Powell, C., Robertson, C., Kröger, S., Bolam, S., Geert Hiddink, J., 2016. Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. Limnol. Oceanogr. 61 (6), 2076–2089. https://doi.org/10.1002/lno.10354.
Slomp, C.P., Van der Gaast, S.J., Van Raaphorst, W., 1996. Phosphorus binding by poorly crystalline iron oxides in North Sea sediments. Mar. Chem. 52 (1), 55–73. https://doi.org/10.1016/0304-4203(95)00078-X.
Soetaert, K., Middelburg, J.J., 2009. Modeling eutrophication and oligotrophication of shallow-water marine systems: the importance of sediments under stratified and well-mixed conditions. Hydrobiologia 629 (1), 239–254. https://doi.org/10.1007/s10750-009-9777-x.
Soetaert, K., Herman, P.M.J., Middelburg, J.J., 1996. A model of early diagenetic processes from the shelf to abyssal depths. Geochim. Cosmochim. Acta 60 (6), 1019–1040.
Soetaert, K., Hofmann, A.F., Middelburg, J.J., Meysman, F.J.R., Greenwood, J., 2007. The effect of biogeochemical processes on pH. Mar. Chem. 105 (1–2), 30–51. https://doi.org/10.1016/j.marchem.2006.12.012.
Soetaert, M., Decostere, A., Polet, H., Verschueren, B., Chiers, K., 2015. Electrotrawling: a promising alternative fishing technique warranting further exploration. Fish Fish. 16 (1), 104–124. https://doi.org/10.1111/faf.12047.
Soetaert, M., Decostere, A., Verschueren, B., Saunders, J., Van Caelenberge, A., Puvanendran, V., et al., 2016. Side-effects of electrotrawling: exploring the safe operating space for Dover sole (*Solea solea* L.) and Atlantic cod (*Gadus morhua* L.). Fish. Res. 177 (November), 95–103. https://doi.org/10.1016/j.fishres.2016.01.019.
Soetaert, M., Boute, P.G., Beaumont, W.R.C., 2019. Guidelines for defining the use of electricity in marine electrotrawling. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsz122.
Stewart, P.A.M., 1977. A study of the response of flatfish (Pleuronectidae) to electrical stimulation. ICES J. Mar. Sci. 37 (2), 123–129. https://doi.org/10.1093/icesjms/37.2.123.
Sulu-Gambari, F., Seitaj, D., Meysman, F.J.R., Schauer, R., Polerecky, L., Slomp, C.P., 2016. Cable bacteria control iron-phosphorus dynamics in sediments of a coastal hypoxic basin. Environ. Sci. Technol. 50 (3), 1227–1233. https://doi.org/10.1021/acs.est.5b04369.
Tiano, J.C., Witbaard, R., Bergman, M.J.N., Van Rijswijk, P., Tramper, A., Van Oevelen, D., Soetaert, K., 2019. Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsz027.
Tiano, J.C., van der Reijden, K.J., O'Flynn, S., Beauchard, O., van der Ree, S., van der Wees, J., et al., 2020. Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front. Mar. Environ. Res. 159 (March), 104964. https://doi.org/10.1016/j.marenvres.2020.104964.
Trimmer, M., Petersen, J., Sivyer, D.B., Mills, C., Young, E., Parker, E.R., 2005. Impact of long-term benthic trawl disturbance on sediment sorting and biogeochemistry in the southern North Sea. Mar. Ecol. Prog. Ser. 298, 79–94. https://doi.org/10.3354/meps298079.
van de Velde, S., Lesven, L., Burdorf, L.D.W., Hidalgo-Martinez, S., Geelhoed, J.S., Van Rijswijk, P., Meysman, F.J.R., 2016. The impact of electrogenic sulfur oxidation on the biogeochemistry of coastal sediments: a field study. Geochim. Cosmochim. Acta 194, 211–232. https://doi.org/10.1016/j.gca.2016.08.038.
van de Velde, S., Van Lancker, V., Hidalgo-martinez, S., Berelson, W.M., 2018. Anthropogenic disturbance keeps the coastal seafloor biogeochemistry in a transient state. Sci. Rep. (December 2017), 1–10.
van der Molen, J., Aldridge, J.N., Coughlan, C., Parker, E.R., Stephens, D., Ruardij, P., 2013. Modelling marine ecosystem response to climate change and trawling in the North Sea. Biogeochemistry 113 (1–3), 213–236. https://doi.org/10.1007/s10533-012-9763-7.
van Marlen, B., Wiegerinck, J.A.M., van Os-Koomen, E., van Barneveld, E., 2014. Catch comparison of flatfish pulse trawls and a tickler chain beam trawl. Fish. Res. https://doi.org/10.1016/j.fishres.2013.11.007.
Virto, I., Barré, P., Chenu, C., 2008. Microaggregation and organic matter storage at the silt-size scale. Geoderma 146 (1–2), 326–335. https://doi.org/10.1016/j.geoderma.2008.05.021.
Weng, L., Van Riemsdijk, W.H., Hiemstra, T., 2012. Factors controlling phosphate interaction with iron oxides. J. Environ. Qual. 41 (3), 628–635. https://doi.org/10.2134/jeq2011.0250.
Weston, K., Fernand, L., Nicholls, J., Marca-Bell, A., Mills, D., Sivyer, D., Trimmer, M., 2008. Sedimentary and water column processes in the Oyster Grounds: a potentially hypoxic region of the North Sea. Mar. Environ. Res. 65 (3), 235–249. https://doi.org/10.1016/j.marenvres.2007.11.002.

Wong, J., Yang, C., 1997. The effect of pH and redox potential on the release of nutrients and heavy metals from a contaminated marine sediment. Toxicol. Environ. Chem. 62 (1–4), 1–10.

Woolmer, A., Maxwell, E., Lart, W., 2011. Effects of electrofishing for Ensis spp. on benthic macrofauna, epifauna and fish species. Salacia-Marine Research Report. Project (FIFG 57437).

Yvon-Durocher, G., Allen, A.P., 2012. Linking community size structure and ecosystem functioning using metabolic theory. Philos. Trans. R. Soc. B Biol. Sci. 367 (1605), 2998–3007. https://doi.org/10.1098/rstb.2012.0246.