



Impacts of bottom trawling on benthic biogeochemistry in muddy sediments: Removal of surface sediment using an experimental field study

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ARTICLE INFO

Keywords:

Baltic sea
Benthos
Environmental impact
Disturbance
macrofauna
Nutrient fluxes
Organic and dissolved inorganic carbon
Chlorophyll
water content

ABSTRACT

Experimental benthic dredging was conducted in an un-fished, muddy area in the Baltic Proper to mimic the impact of trawling by removing surface sediment, with a focus on benthic biogeochemical processes. Sediment cores were taken on the track and compared to undisturbed controls. Benthic fluxes were immediately affected and an upward shift in pore water DIC profiles was detected. The time needed for the sediment to readjust to a new biogeochemical state seemed to be nutrient-specific. Sediment properties (profiles of chlorophyll, organic carbon and water content) were found to change significantly. Macrofauna was removed completely by the dredge pointing out the potential loss of highly valuable functions that are associated with them. In the Baltic Sea, in areas which were previously the most heavily fished, the frequency of trawling may have left little time for readjustment and potentially kept the seabed in a permanent state of transient biogeochemical cycling.

1. Introduction

Anthropogenic stressors (e.g. fisheries, tourism or climate change) have long been recognized to have various negative impacts on marine sedimentary ecosystems (e.g. Bridger, 1970; Caddy, 1973). Bottom trawling is one of the most widespread and extensive sources of physical disturbance to soft-sediment benthic communities and habitats (Dayton et al., 1995; Jennings and Kaiser, 1998; Collie et al., 2000; Pauly et al., 2002; Kaiser et al., 2006; van Denderen et al., 2015; Oberle et al., 2016a). Industrial fishing occurs in >55% of the world's ocean (Kroodsmma et al., 2018) and bottom trawling accounts for > 25% of the global fisheries leaving a large spatial footprint (Eigaard et al., 2017; Amoroso et al., 2018; Watson and Tidd, 2018). In Europe, bottom trawling is estimated to disturb 79% of the coastal seabed (European Commission, 2020). The effects are diverse, reaching from increased resuspension and near-bottom turbidity caused by the scraping of the seafloor (Jones, 1992; Palanques et al., 2001; de Madron et al., 2005; Dellapenna et al., 2006; O'Neill and Summerbell, 2011; Bradshaw et al., 2012; Martín et al., 2014a; Mengual et al., 2016) to the alteration of the benthic habitat and damage, removal or changes of benthos (Craeymeersch et al., 1997; Jennings and Kaiser, 1998; Koslow et al., 2001; Kaiser et al., 2006; Queirós et al., 2006; Trimmer et al., 2005; Muthuvelu et al., 2013; van Denderen et al., 2015; Howarth et al., 2018; Sciberras

et al., 2018; Sköld et al., 2018) to distinct changes in ecosystem functioning (Larsen et al., 2005; Tillin et al., 2006; Pusceddu et al., 2014; Rijnsdorp et al., 2018). The magnitude of disturbance is context-dependent (e.g. Thrush and Dayton, 2002) and depends on sediment composition, topography, trawling speed, construction, and weight of trawling equipment (Gray and Elliott, 2009; O'Neill and Ivanović, 2016) as well as on the number and identity of benthic species, their biological traits, and ecological functions (De Juan et al., 2007; Hiddink et al., 2019).

Trawled sediments show higher degrees of mixing, erosion and grain-size sorting as well as organic carbon impoverishment as a consequence of the removal of surficial sediments (Mayer et al., 1991; Watling et al., 2001; Sánchez et al., 2009; Martín et al., 2014a). Since sediment properties and organic matter have an important role in the distribution of benthos (Sanders, 1958; Harkantra et al., 1982; Jayaraj et al., 2007; Gogina et al., 2017), species complexity, diversity, abundance, size and the productivity of benthic communities are also indirectly affected by trawling (Bergman and Hup, 1992; Ball et al., 2000; Collie et al., 2000; Frid et al., 2000; Duplisea et al., 2002; Jennings et al., 2002; Hinz et al., 2009; Thrush et al., 2015; Buhl-Mortensen et al., 2016; Sköld et al., 2018). Trawled areas are often dominated by small-bodied, opportunistic species with fast life histories to the detriment of large, long-lived organisms (Pitcher et al., 2000; Tillin et al., 2006; Olgard

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<https://doi.org/10.1016/j.marenvres.2021.105384>

Received 4 December 2020; Received in revised form 24 May 2021; Accepted 29 May 2021

Available online 6 June 2021

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et al., 2008; van Denderen et al., 2015). Generally, habitats with higher proportions of long-lived organisms are more sensitive to bottom trawling (Hiddink et al., 2019). The key to understanding the impact of trawling on ecosystem functioning is the relationship between the function of species and their vulnerability to trawling (Larsen et al., 2005). This selective forcing may change the trophic structure (Duffy, 2003; Wohlgemuth et al., 2016) and cause the loss of species interactions essential for nutrient dynamics (Chapin et al., 1997; Diaz and Cabido, 2001; Tilman, 2001; Solan et al., 2004; Gilbertson et al., 2012).

This shift has considerable implications on ecosystem processes and functions (Duplisea et al., 2001; Thrush and Dayton, 2002; Tillin et al., 2006). Essential ecosystem functions include biogeochemical processes such as remineralization of organic material, regeneration of nutrients and nutrient fluxes (e.g. Aller, 1982; Norling et al., 2007) that were found to change due to bottom trawling (Jennings and Kaiser, 1998; Pilskaln et al., 1998; Duplisea et al., 2001). Dissolved nutrients and organic matter (OM) are released from the sediment (Pilskaln et al., 1998; Falcão et al., 2003; van der Molen et al., 2013), and the remineralization of OM can be catalyzed through increased microbial activity (de Madron et al., 2005; Pusceddu et al., 2005b). Sediment oxygen consumption rates were found to decrease significantly (Riemann and Hoffmann, 1991; Tianio et al., 2019) and changes in the oxygen regime (Warnken et al., 2003) may influence the nitrogen cycle, as oxygen regulates both nitrification and denitrification (Rysgaard et al., 1994). The response of the biogeochemical processes to trawling is nutrient-specific and this has led to partly contrasting results. Ammonium effluxes were mainly found to increase due to trawling (Riemann and Hoffmann, 1991; Pilskaln et al., 1998; Duplisea et al., 2001; Falcão et al., 2003; Percival, 2004; van der Molen et al., 2013; Smith et al., 2016) while results with regard to NO_x - fluxes vary more, including both decreased NO_x - influxes (Smith et al., 2016) and increased effluxes (Falcão et al., 2003). Phosphate influxes were reported to decrease (van der Molen et al., 2013) or even changed to an efflux from the sediment (Percival, 2004; Duplisea et al., 2001; Falcão et al., 2003; Griffiths et al., 2017). These effects vary with sediment type (e.g. Sciberras et al., 2017); trawling increases surface concentrations of OM in cohesive sediments (i.e. mud with high clay content) (Palanques et al., 2014; Pusceddu et al., 2005a; Sciberras et al., 2016; Polymenakou et al., 2005), whereas no or only slight effects are reported for OM content and benthic community metabolism in non-cohesive (i.e. sandy) sediments (Hale et al., 2017; Tianio et al., 2019; Trimmer et al., 2005). Furthermore, the frequency of trawling plays a crucial role for the recovery potential of sediment biogeochemistry (van de Velde et al., 2018).

The Baltic Sea had been intensively fished for more than a century, mainly for Baltic cod. Maximum quotas – against scientific advice and regulations – were reached by the turn of the millennium, and have contributed to widespread degradation of the Baltic Sea ecosystem. Until today, there has not been much research conducted on the effects of bottom trawling in the Baltic Sea, although bottom trawling has occurred across ~15% of the entire Baltic Sea (ICES, 2019; estimates from 2018, excluding the Kattegat Sea area) and 80–100% of the seafloor is considered disturbed in some parts (e.g. southern Baltic Sea, Kattegat, Bornholm Basin) (HELCOM, 2018). As it is challenging to separate bottom trawling impacts from other environmental disturbances (Rumohr and Kujawski, 2000; Robinson and Frid, 2005), we conducted a controlled trawling event using a benthic dredge in a non-trawled area in the Baltic Sea. This dredge caused the removal of a few centimeters of surface sediment mimicking the action of the trawl doors of a small otter trawl, or the beam of a beam trawl. Divers took sediment cores exactly on the track where the surface sediment had been removed. Additional cores were taken a few meters away from the track as controls for comparison. The cores were used for analyses of sediment properties, vertical chlorophyll profiles, macrofauna composition, benthic fluxes across the sediment-water interface and profiles of dissolved inorganic carbon (DIC) in the pore waters.

In order to address the current knowledge gap on the biogeochemical effects of trawling on muddy Baltic sediments, we pursued two major objectives: 1) to quantify the biological and biogeochemical effects of trawling directly after the disturbance; and 2) to determine the potential for reestablishment of biogeochemical conditions in the sediment after one and two weeks, respectively. We hypothesized: i) surface dwelling macrofauna removal within the track; ii) nutrient-specific increased (NH_4^+ , PO_4^{3-}) or decreased (O_2 , NO_x) fluxes across the sediment-water interface; iii) a shift of pore water DIC profiles towards the sediment surface; and iv) readjustment of the sediment to a new biogeochemical state, i.e. to become similar to benthic fluxes and DIC profiles as at the control site.

2. Materials and methods

2.1. Study site

The study site was located at the mouth of the non-tidal estuary of Himmerfjärden in the Baltic Proper which is characterized by a surface area of 174 km² (Engqvist and Omstedt, 1992) and a permanent salinity gradient ranging from 5.5 in the inner part to 7.0 at the opening to the Baltic. Sampling took place just south of the town of Trosa and northeast of the island of Hänä (Fig. 1a). The area is a sheltered and undisturbed soft bottom habitat with a water depth of 12 m and a similar salinity to the open Baltic Proper.

2.2. Sampling

The field experiment took place on October 29, 2019. First, a CTD cast was taken at the chosen site of the dredging experiment to measure bottom water temperature (8.3 °C), salinity (6.5) and oxygen (11.23 mg/L O_2 , 99.8% O_2 saturation). Secondly, 30 min before dredging, two bottom water samples (c. 0.5 m.a.b) were taken with a 25 L Niskin bottle and reserved for the water exchange during the incubation experiments. A benthic dredge (Fig. 1b) was used to create a 200 m long track. It was towed in a SE to NW direction, from 58° 51.9678' N 017° 36.1487' E to 58° 52.0520' N 017° 36.0336' E, at a speed of ca. 0.65 knots. Water depth was around 12 m along the whole track. A buoy was deployed half way along the track with an offset of about 10m, to enable divers to access the track. Divers took 18 small sediment cores (inner diameter 4.6 cm, length 30 cm, sediment height c. 15 cm) directly in the centre of the track (further referred as 'IN' - cores), where sediment had been scraped away by the dredge. These cores were taken during two dives; the first 2 h after the dredging (in order to allow visibility to improve in the area) and the second 5 h afterwards (to allow for a suitable surface interval for the divers). The fauna collected in the dredge during the deployment (= c. 48 L sediment) was extracted from the sediment by sieving over 0.5 mm and 1 mm sieves and stored in 96% ethanol. This data provided background information about the benthic macrofauna communities as well as about the species affected by dredging.

A multicorer (K.U.M. Umwelt und Meerestechnik Kiel) fitted with four 4 acrylic tubes (inner diameter 9 cm, length 60 cm) was deployed seven times to take a total of 22 sediment cores approximately 10–20 m away from the track. From each of these larger cores, a smaller one was taken using the same type of acrylic tube of inner diameter 4.6 cm and length 30 cm (further referred to as 'OUT' - cores, sediment height approx. 15 cm) as used in the centre of the track. The overall total of 40 cores were filled to the brim with bottom water collected from the site, tightly sealed with rubber stoppers and placed in cool boxes with ice-packs and temperature loggers (HOBO Pendant® temperature/light 8K Data Logger) for immediate transport to Stockholm University (c. 2h drive).

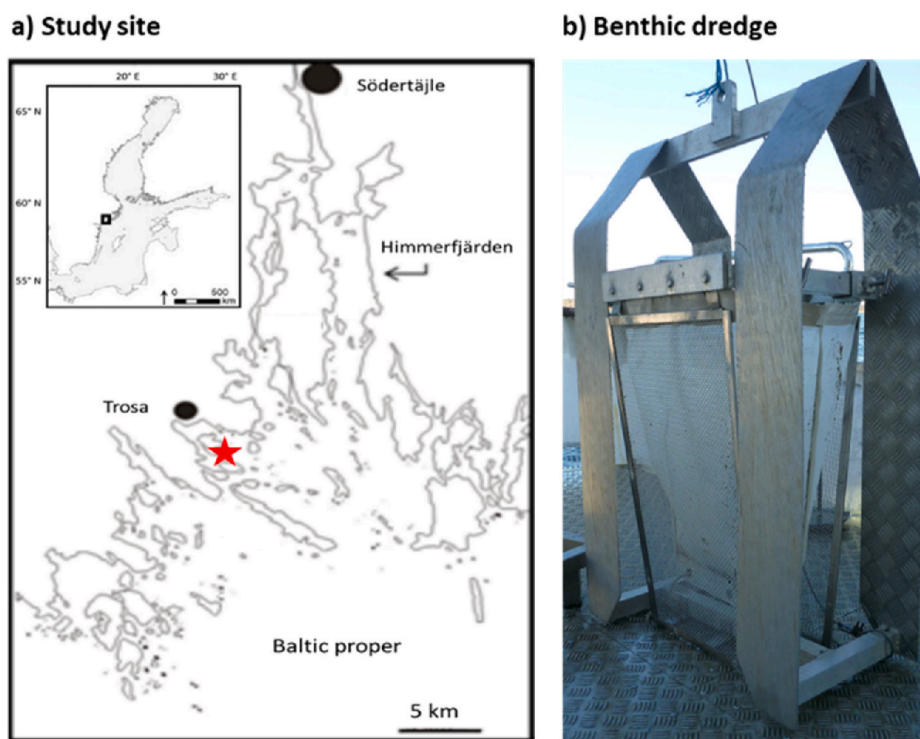


Fig. 1. a) Map of Himmerfjärden estuary showing the location of the experimental trawling (red star), b) Benthic dredge used to mimic bottom trawling. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.3. Laboratory analyses

At the university, the cores were placed in a dark climate chamber set to 6 °C. From each of the categories 'IN' and 'OUT', cores were randomly selected for different analyses: 1) benthic fluxes, 2) pore water DIC, 3) vertical chlorophyll (chl) profiles and 4) sediment properties. The incubation experiment for analysing the benthic fluxes was conducted three times; one day, c. 1 week and c. 2 weeks after dredging using the same cores. Cores for pore water and chlorophyll analyses were processed one day after dredging (t_{1-2} -cores, see Table 1) and c. 1 week later (t_{9-10} -cores, see Table 1). The exact number of cores used of for each analysis and for each time point is given in Table 1.

The overlying water in all incubation and pore water cores was removed and carefully replaced with bottom water from the site, avoiding suspension of the sediment. Magnetic stirrers were inserted into each one, half way between the sediment and water surface. The cores were then placed into a custom-built incubator with a central magnetic rotor, rotating at 60 rpm to drive the magnetic stirrers inside the cores. All other cores were placed in a rack in the same climate chamber. Temperature loggers were placed at four different places in the climate chamber to monitor temperature during the experiments. The

Table 1

Number of cores taken in the field during the trawling experiment inside ('IN') and outside ('OUT') the track and their selection for the different analyses.

	t_{1-2} (directly after trawling)		t_{9-10} (c. 1 week after trawling)		t_{16-17} (c. 2 weeks after trawling)	
	IN	OUT	IN	OUT	IN	OUT
incubation	3	6 ^b	3 ^a	6 ^a	3 ^a	6 ^a
pore water	3	3	3	3	0	0
chlorophyll	3	3	3	4	0	0
sediment properties	3	3	0	0	0	0
total n cores	18	22				

^a same cores as incubation cores t_{1-2} .

^b n = 5 for O₂.

overlying water was replaced again on days 3 and 6, half-replaced on day 7, and again fully replaced on days 10 and 13. Overlying water in the remaining cores (chlorophyll and sediment properties) was neither replaced nor stirred, but simply kept open in the dark climate chamber at 6 °C. Oxygen was monitored regularly and was on average 271 $\mu\text{mol/L}$, SD 21, n = 27 (= c. 73% saturation, SD 5.6).

2.3.1. Incubation

One to two days after dredging (t_1 - t_2), oxygen and nutrient ($\text{NO}_2^- + \text{NO}_3^-$, NH_4^+ , PO_4^{3-}) fluxes across the sediment-water interface were calculated by measuring changes in oxygen and nutrient concentrations in the overlying water of three 'IN' and six 'OUT' cores. The incubation time was set to approximately 24 h based on preliminary estimation of the oxygen consumption rates, to prevent O₂ concentrations decreasing below 30% of the initial value (Dalsgaard et al., 2000). First (t_1), a 10 mL water sample was taken from each incubation core using a plastic syringe and filtered through a 0.45 μm disposable filter into a 12 mL vial. These were frozen at -18 °C for later nutrient analyses. Secondly, the cores were topped up with site-collected bottom water and the oxygen concentration in the overlying water was measured using a mini-electrode (OX-500, Unisense). The oxygen mini-electrode was calibrated prior to the first measurement according to the manufacturer's instructions. The rubber stopper was placed firmly in each core, avoiding air bubbles. Duplicate 10 mL (0.45 μm -filtered) water samples were taken from the bottom water reserve tank for analysis of nutrients ($\text{NO}_2^- + \text{NO}_3^-$, NH_4^+ , PO_4^{3-}) and used to correct the initial concentrations of the nutrients after the water exchange. The same procedure was repeated in reverse order (i.e. first oxygen, then nutrients) the following day (t_2), approximately 24 h after the first measurements. This two-day incubation experiment was repeated again 9 to 10 (t_9 - t_{10}) as well as 16 to 17 (t_{16} - t_{17}) days after dredging to determine changes over time in benthic oxygen and nutrient fluxes. In the meantime, the cores were kept open in the climate chamber with the magnetic stirrers on and the water was exchanged as described above. Dissolved concentrations of ($\text{NO}_2^- + \text{NO}_3^-$)-N, NH_4^+ -N and PO_4^{3-} -P were determined on a

segmented flow autoanalyzer system (ALPKEM, Flow Solution IV). Precision varied depending on the concentration of the nutrient: NO_x ($\text{NO}_2^- + \text{NO}_3^-$): 0.3 $\mu\text{g/L}$ for 0.3–2 $\mu\text{g/L}$, 1.3 $\mu\text{g/L}$ for 2–20 $\mu\text{g/L}$ and 4% for >20 $\mu\text{g/L}$; NH_4^+ : 0.5 $\mu\text{g/L}$ for 0.5–3 $\mu\text{g/L}$, 1.7 $\mu\text{g/L}$ for 3–30 $\mu\text{g/L}$ and 5% for >30 $\mu\text{g/L}$; PO_4^{3-} : 0.5 $\mu\text{g/L}$ for 0.5–2 $\mu\text{g/L}$, 1.0 $\mu\text{g/L}$ for 2–25 $\mu\text{g/L}$ and 5% for >25 $\mu\text{g/L}$. After the final sampling on day 17, the sediment in the cores was sieved over a 0.5 mm and 1 mm sieve to retrieve the macrofauna which was then stored in 96% ethanol until taxonomic determination. The organisms were sorted, identified following the World Register of Marine Species WoRMS, counted and weighed (dry weights, dried at 60 °C for 24 h were used in the analyses).

Net fluxes ($\mu\text{mol/m}^2\text{d}$) of oxygen and all nutrients were calculated using the following equation:

$$\text{flux} = \frac{(C_f - C_i) \times V}{t \times A} \quad \text{Eq. (1)}$$

where C_f and C_i are the final and initial concentrations of the corresponding solute ($\mu\text{mol/L}$), V is the volume of the overlying water in the core (L), t is the incubation time (h) and A is the sediment surface of the incubation core (m^2).

2.3.2. Pore water

One day after dredging (t_1), three cores from each site ('IN'/'OUT') were sliced into 1 cm thick sections. The three slices from each depth layer were pooled into a 50 mL Falcon tube in order to obtain a sufficient amount of pore water. The samples were centrifuged at 4000 rpm for 8 min at 7 °C, the supernatant (i.e. pore water) was pipetted off, saved in 2 mL glass crimp-top vials with no headspace and stored in the fridge for later measurements of DIC profiles. This was repeated 10 days (t_{10}) after dredging with three additional cores from each site that had been held at 7 °C in the dark climate chamber to test for changes in the DIC profile over time within the sediment.

The DIC analyses were performed at the Department of Geological Sciences at Stockholm University a few days after sampling. 1 mL of pore water was transferred to a closed 12 mL He-flushed exetainer containing 100 μL concentrated 96% H_3PO_4 . 50 μL of the headspace gas were injected on SRI-8640 gas chromatograph with FID detector equipped with a post-column methanizer for reduction of CO_2 to CH_4 . CO_2 and naturally occurring CH_4 were separated on a 3 m Hayesep D column and a 1.5 m Hayesep pre-column. The system was calibrated using Linde gas standards with concentrations of 11.2, 100, and 1000 ppmv. In addition, a set of aqueous DIC standards in the concentration range 0.5 mmol/L to 10 mmol/L was prepared with a stock solution of 50 mmol/L sodium bicarbonate every two days for calibration of the methane peak.

2.3.3. Chlorophyll

Chlorophyll (chl) profiles in the sediment were determined to examine bioturbation activity (the rearrangement of particles by macrofauna). One day after dredging (t_1), three cores from each site ('IN'/'OUT') were sliced at 1 cm intervals, stored in zip-lock bags, and frozen at -18 °C. Three subsamples of 1 mL were subsequently taken from each thawed and homogenized sample and each mixed with 9 mL of 96% ethanol. The samples were left overnight in the fridge and chl analyzed the day after on a Shimadzu spectrophotometer at 663 and 750 nm following the method of HELCOM (1988). The process was repeated 10 days after dredging on additional cores from each treatment that had been kept at 7 °C without any treatment in the laboratory.

2.3.4. Sediment properties

For the characterization of the sediment properties, three cores from each site ('IN'/'OUT') were sliced at 1 cm intervals and frozen at -18 °C until further processing. A 5 mL subsample was taken from each slice, weighed (wet weight), dried at 60 °C for 24 h (for dry weight) and combusted at 500 °C for 4 h to obtain ash free dry weight. From the derived variables, water content (% by weight) and loss on ignition

(LOI) as a proxy for organic carbon (OC) were calculated.

2.3.5. Statistics

Statistical analyses were carried out using the software packages Statistica version 13.3.

In order to test differences between flux rates over time as well as within and outside the track, a two-way repeated measures ANOVA was performed on each set of benthic flux data (i.e. O_2 rate, NH_4^+ , PO_4^{3-} and NO_x - fluxes). The O_2 - flux data showed normal distribution and homogeneous variance, while the other fluxes showed non-normality and/or non-homogeneous variance for one or two of the time points. Various types of transformation were only able to improve some of the data, and non-parametric repeated measures ANOVA is unable to deal with multiple factors. Therefore, we chose to run the ANOVAs on the raw data, but to be cautious in our interpretation of the results.

3. Results

3.1. Dredge track

After the passage of the dredge, a clear track was visible as shown in Fig. 2. The tow of the dredge caused the removal of surface sediment that piled up irregularly on the sides. About 2.5–3 cm of surface sediment had been scraped away according to the depth of the track estimated by the divers.

3.2. Sediment properties

The vertical distribution of chl showed similar profiles for the two sampling sites ('IN' and 'OUT') and time points (directly and one week after dredging) (Fig. 3 a, b). In the top centimeter, chl concentrations differed between 'IN' and 'OUT' cores, but were similar at depth. During both time points, mean surface (0–1 cm) chl concentrations were lower inside the track (directly after dredging: $6.04 \pm 1.14 \mu\text{g/cm}^3$, one week after dredging: $6.31 \pm 0.53 \mu\text{g/cm}^3$) than outside (directly after dredging: $7.78 \pm 0.69 \mu\text{g/cm}^3$, one week after dredging: $9.8 \pm 1.41 \mu\text{g/cm}^3$) (Fig. 3 a). These results indicated that the surface layer of the sediment was removed by the dredge. Therefore, assuming that 2.5 cm of the surface sediment was removed along the track (corresponding to the depth of the track measured by the divers), the 'IN' profile was adjusted correspondingly (i.e. the concentration measured at 0–1 cm was set to 2.5 cm sediment depth, Fig. 3 a, b). As a result, the 'IN' profiles converged with the 'OUT' profiles both directly and one week after

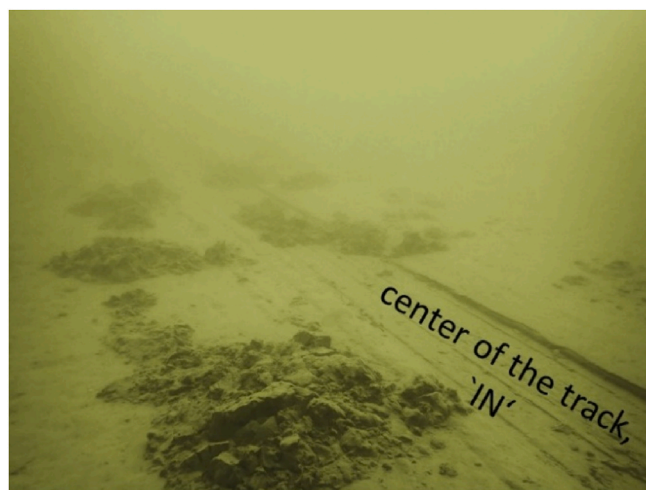


Fig. 2. Photo of the track caused by the benthic dredge. Note the centre of the track, where the surface sediment had been removed by the dredge. Here, 'IN' cores were taken by the divers.

trawling.

LOI (used as a proxy for OC content) in the ‘IN’ and ‘OUT’ cores differed throughout the sediment column with slightly lower concentrations inside the track (Fig. 3 c). The greatest difference was detected at the sediment surface (OC inside the track = $4.6 \pm 0.1\%$ compared to $8.5 \pm 1\%$ at the control site), suggesting the removal of an OC-rich surface layer by the dredge. However, when a similar depth adjustment of the profile was done as for the chl profiles, the match of ‘IN’ and ‘OUT’ profiles did not improve significantly.

Sediment water content indicated a similar profile both in- and outside the track with highest values at the sediment surface, an exponential decrease with depth, and constant values below 6 cm depth (Fig. 3 d, e). The profile displayed lower concentrations in cores that were taken inside the track. In the top centimeter, the water content of $83.4 \pm 1.1\%$ was lower at the control site (compared to water content = $79.3 \pm 2.4\%$ inside the track). The values decreased down to a depth of 6 cm, below which they became constant (71%). An adjustment of the ‘IN’ profiles based on the truncation effect caused by the removal of surface sediment as previously described for the chl profiles again resulted in significantly improved profile matches.

3.3. Macrofauna

A total number of 426 individuals with an overall biomass of 2.8 g (dw) were recovered in the dredge from the c. 200 m long track. Both in

the dredge as well as in the incubation cores, the benthic community consisted of three taxonomic groups: Oligochaeta, Chironomidae (neither determined to species level) and Bivalvia (only one species: *Limecola balthica*). In the dredge, oligochaetes contributed the most to the total abundance (77.2%), followed by *L. balthica* (12.4%) of which 49% were smaller than 1 cm in shell length, 43.5% had a length between 1 and 2 cm and 7.5% between 2 and 3 cm. Bivalves made up more than 99% of the macrofaunal biomass. A large difference was found in the abundance and biomass of macrofauna in the incubation cores. A mean abundance of 1504.3 ± 1247.8 organisms per m^2 (with a mean biomass of 0.17 ± 0.26 g dw per m^2) was found in the control cores taken parallel to the track, whereas no animals were detected in the cores taken in the centre of the track.

3.4. Sediment biogeochemistry

3.4.1. DIC concentration profiles

The DIC profiles at both sites (‘IN’ and ‘OUT’) were similar in shape, but the profile measured in the centre of the track (‘IN’) had higher concentrations in the upper 9 cm compared to the ‘OUT’ cores. Inside the track, the DIC value in the top cm, $2670 \mu\text{mol/L}$, and all concentrations measured deeper down in the sediment were higher than at the control site (top cm: $2070 \mu\text{mol/L}$) suggesting truncation of the ‘IN’ cores by the dredge.

One day after dredging (t_1), the DIC profiles of the ‘IN’ cores

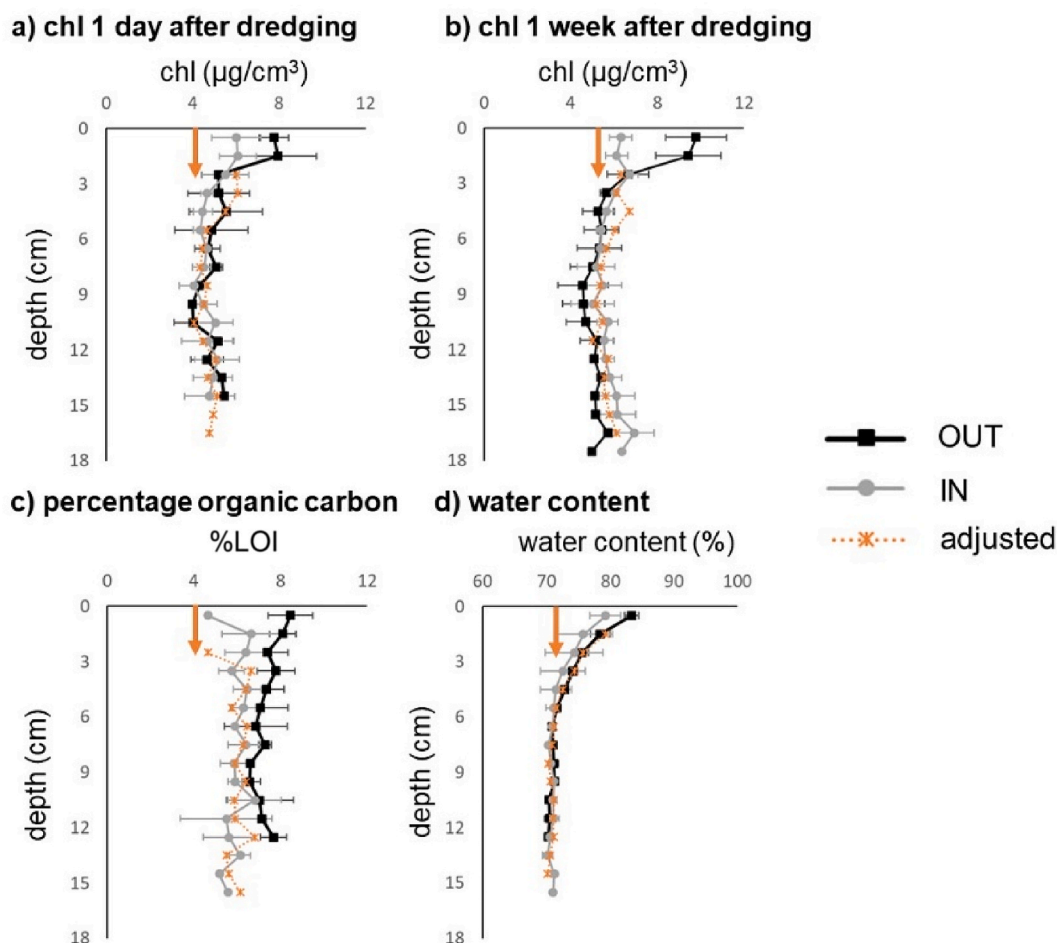


Fig. 3. Mean profiles of various sediment properties measured in cores taken inside (‘IN’, grey line with dots) and outside (‘OUT’, black line with squares) the track as well as adjusted ‘IN’ - profiles (orange line with crosses): a) profile of chlorophyll (chl) directly after dredging, b) profile of chlorophyll (chl) one week after dredging, c) profile of LOI (%) and d) profile of water content (%). Arrows demonstrate the downward shift of the ‘IN’ - profile to reflect how they would have looked before 2.5 cm sediment was removed from the surface (i.e. truncation effect). Number of cores used for mean profiles is given in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

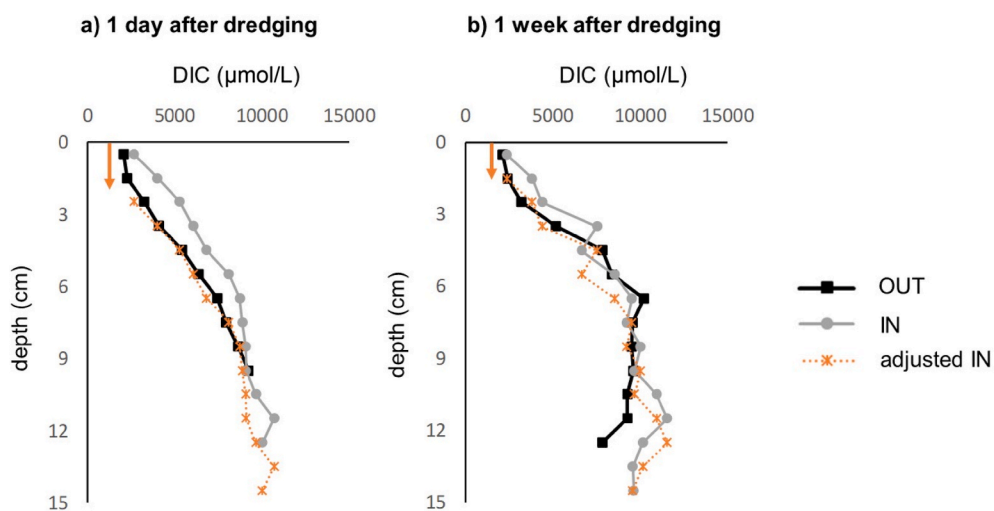


Fig. 4. DIC profiles in cores taken inside ('IN', grey line with dots) and outside ('OUT', black line with squares) the track as well as adjusted 'IN' - profiles (orange line with crosses) corresponding to the truncation effect: a) one day and b) one week after the dredging experiment. Arrows demonstrate the downward shift of the 'IN' - profile to reflect how they would have looked before 2.5 cm sediment was removed from the surface (i.e. truncation effect). DIC concentrations were derived from pooled pore water of three cores per site and time point. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

displayed convex upward shape with depth, whereas the 'OUT' cores had distinct concave-upward shape (Fig. 4 a). The former can be interpreted as indicating the combined effect of production and upward diffusion, whereas the latter points to mixing with bottom water by bioirrigation in the topmost 3 cm. As the sediment in the study area is generally not dredged or otherwise disturbed, the profile at the control site was regarded to reflect natural near-steady state conditions. For the 'IN'-cores, we infer a truncation effect in the pore water DIC profile due to the removal of surface sediment and, thus, increased surface DIC concentration (Fig. 4 a). The 'IN' profile was adjusted the same way as the 'IN' chl profile described above, considering the removal of 2.5 cm of surface sediments. As a result, both DIC profiles matched well indicating an apparent upward shift of the 2.5 cm deep sediment layers to the sediment surface in the 'IN' cores.

One week after dredging, a decrease in the uppermost DIC

concentration (top one cm) in the 'IN' cores compared to t_1 due to diffusion and mixing with bottom water was visible (Fig. 4 b). The difference in concentrations between 'IN' (DIC = 2380 $\mu\text{mol/L}$) and 'OUT' (DIC = 2140 $\mu\text{mol/L}$) was less pronounced than in t_1 . In addition, the DIC profiles were similar at both sites with only slightly higher concentrations inside the track. Again, the 'IN' profile was adjusted and resulted in the best match of both profiles when set to 1.5 cm. This suggests that the pore water DIC gradually established a new biogeochemical condition. Interestingly, the strong convex shape ('bulge') around 6 cm depth reflected a higher mineralization rate. This feature was more pronounced in the control cores.

3.4.2. Biogeochemical fluxes

Oxygen consumption rates were lower inside the track (rmANOVA; F(1, 6) = 14.4, $p = 0.009$) (Fig. 5 a). The difference between IN and OUT

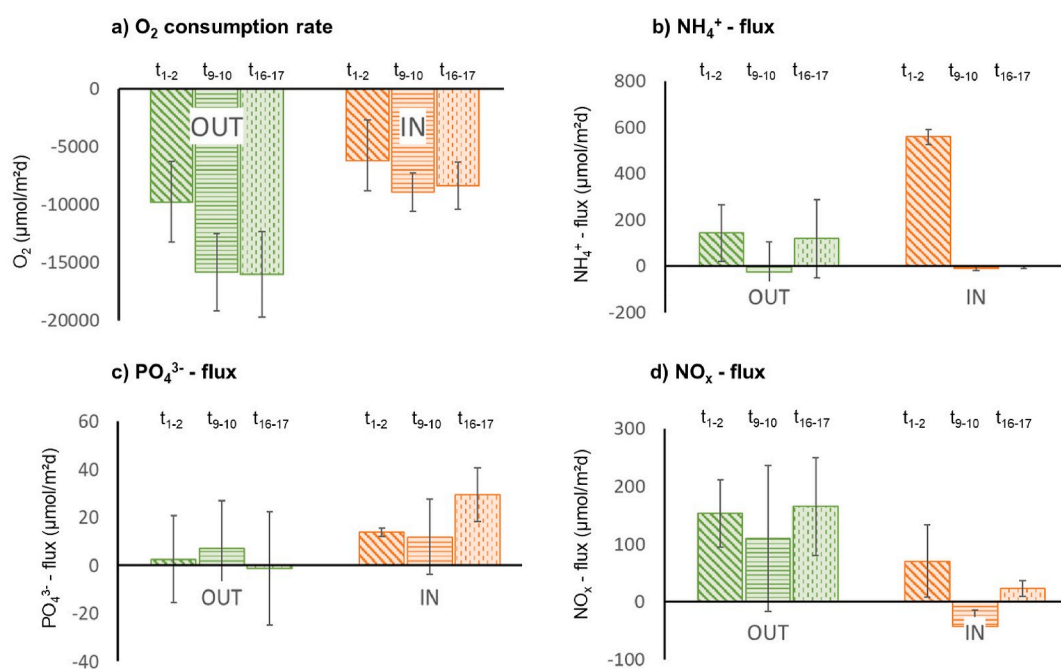


Fig. 5. Bar diagram presenting the benthic fluxes a) oxygen (O_2) consumption rate, b) ammonium (NH_4^+) - flux, c) phosphate (PO_4^{3-}) - flux and d) combined nitrate and nitrite (NO_x) - flux in the incubation cores that were taken outside ('OUT', green bars, $n = 6$, except for O_2 where $n = 5$) and inside ('IN' red bars, $n = 3$) the track. The fluxes were measured during the incubation experiment one day (t_{1-2}), one week (t_{9-10}) and two weeks (t_{16-17}) after the dredging. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

increased with time (rmANOVA; $F(2, 12) = 4.9, p = 0.03$), from a factor of 1.6 difference at t_{1-2} (O_2 rate 'IN': $6206.1 \pm 2620.9 \mu\text{mol}/\text{m}^2\text{d}$, 'OUT': $9757.9 \pm 3504.1 \mu\text{mol}/\text{m}^2\text{d}$) to $\times 1.9$ by t_{16-17} (O_2 rate 'IN': $8350.4 \pm 2041.1 \mu\text{mol}/\text{m}^2\text{d}$, 'OUT': $15,995.2 \pm 3677.3 \mu\text{mol}/\text{m}^2\text{d}$).

In the trawl track, there was a large efflux of NH_4^+ at t_{1-2} ($559.5 \pm 32.5 \mu\text{mol}/\text{m}^2\text{d}$; Fig. 5 b), but one and two weeks after dredging, NH_4^+ fluxes were negligible (t_{9-10} : $10.6 \pm 10.0 \mu\text{mol}/\text{m}^2\text{d}$, t_{16-17} : $4.8 \pm 3.5 \mu\text{mol}/\text{m}^2\text{d}$). Thus, there was a significant interaction between treatment and time (rmANOVA, $F(2, 14) = 12.0, p = 0.001$).

Mean PO_4^{3-} effluxes were higher in the 'IN' cores than the 'OUT' cores throughout the incubation, with the largest difference at t_{16-17} (IN: $29.4 \pm 11.2 \mu\text{mol}/\text{m}^2\text{d}$; OUT: $1.4 \pm 23.6 \mu\text{mol}/\text{m}^2\text{d}$) (Fig. 5 c). However, these differences were not statistically significant and there was no effect of time, presumably due to the high variability, especially at the control site.

Mean values of NO_x fluxes were lower inside the track than outside at all time points (IN: $17.1 \pm 60.4 \mu\text{mol}/\text{m}^2\text{d}$; OUT: $142.6 \pm 91.6 \mu\text{mol}/\text{m}^2\text{d}$; rmANOVA, $F(1, 7) = 10.1, p = 0.02$; Fig. 5 d).

Detailed information about the statistical outputs and mean biogeochemical fluxes for each treatment and time point are provided in the Supplementary Data.

4. Discussion

This controlled bottom trawling field experiment using a benthic dredge provided new insights into the immediate biological and biogeochemical effects of bottom trawling and the potential recovery of the sediment over the course of 2 weeks. The observed effects are not entirely applicable to all types of commercial bottom trawling but are rather more comparable to the action of the trawl doors of an otter trawl, or the beam of a beam trawl. Decreased chlorophyll, LOI (used as a proxy for OC) and water content in the surficial sediment indicated the removal of 2–3 cm of sediment, which was further supported by a decrease in macrofauna abundance, DIC profiles, and benthic fluxes of oxygen and nutrients.

4.1. Sediment properties

The decrease of surface LOI (proxy for OC) by 54% is in line with Pusceddu et al. (2014) who estimated that 60–100% of the OC input flux was removed daily by trawling within the La Fonera submarine canyon (northwestern Mediterranean Sea). Studies of longer-term effects imply that regular trawling may result in permanent decreases in OC through displacement and export of suspended sediment (Martín et al., 2014a; Paradis et al., 2019). Despite the shallow penetration of the gear in our study, a significant amount of food resources for the benthic organisms may therefore be removed, in line with other studies (Brylinsky et al., 1994; Martín et al., 2014a; Pusceddu et al., 2014; Tiano et al., 2019; De Borger et al., 2020).

The passage of trawling gear displaces and resuspends surface sediment with high water content (Palanques et al., 2001; Simpson and Watling, 2006), exposing deeper-buried sediment with lower water content at the sediment-water interface (Watling et al., 2001). This was confirmed by our experiment as indicated by the reduction of surface water content inside the track. This reduction was observed to a depth of 6 cm, matching the finding of Sparks-McConkey and Watling (2001) who also reported significant changes only in surface layers. Water content has implications for the benthic habitat, since benthic community composition is strongly influenced by the structure and properties of the sediment (e.g. grain size and porosity, Ellingsen, 2002). Trawling-induced changes in water content may lead to changes in sediment compaction and, thus, also in macrofauna community structure and benthic fluxes. We hypothesized that over time the macrofauna would rearrange the disturbed sediment by their bioturbating activity. However, since no organisms remained inside the track, this hypothesis could not be tested in our experiment. In a study with a less extreme

decrease in macrofauna, Tiano et al. (2019) reported that suspended silt particles were reintegrated in the upper sediment layers along with OC 75 h after experimental trawling and related this recovery to bioturbation when the organisms started to rebuild their burrows.

4.2. Macrofauna

As hypothesized, benthic organisms were removed from the sediment by the dredge inside the track in the present experiment. A high rate of removal and mortality of benthic macrofauna due to trawling has long been recognized (e.g. Bergman and Hup, 1992; Kaiser and Spencer, 1995; Ramsay et al., 1997; Lindeboom and de Groot, 1998; Jennings et al., 2001; Thrush and Dayton, 2002; Hiddink et al., 2017; van Denderen et al., 2020). However, especially the fate of the small oligochaetes at our study site was not entirely applicable to real bottom trawling conditions. In our experiment, all organisms seemed to be captured in the net of the dredge, which is in accordance with the 80% reduction in meiofauna abundance and the decrease in biodiversity by 50% in chronically trawled sediments reported by Pusceddu et al. (2014). However, as the mesh sizes of fishing nets are bigger, it may be argued that they would just be pushed through and be released after the passage of the nets. Smaller body-sized fauna can also simply get pushed aside due to physical displacement or pressure waves created by the trawl (Gilkinson et al., 1998). The reported ability of *L. balthica* to rebury itself within 17 min after displacement (McGreer, 1979) suggests a high chance of survival, an interpretation that is also strengthened by the study of Tulp et al. (2020), who classified this species as one of the least sensitive to the shrimp. On the other hand, bivalves are unable to actively avoid dredges and are, therefore, susceptible to damage from contact with hard parts of the fishing gear (Bergman and Hup, 1992).

The removal and/or long-term reduction in oligochaetes and *L. balthica* in our study area could have negative consequences for the ecosystem because of their ecological function. The presence of both taxonomic groups stimulates benthic biogeochemical processes by their bioturbating activities and oxygen consumption (Mermillod-Blondin et al., 2001; Michaud et al., 2006). Furthermore, the conveyor belt feeder *L. balthica* is an important player for non-local sediment mixing (Morys et al., 2017) as well as for ammonium and nitrate fluxes (see 4.3.3; Michaud et al., 2006).

4.3. Sediment biogeochemistry

The removal of surface sediment by dredging induced transient changes in sediment biogeochemical cycling with direct impacts on rates and pathways of nutrients and inorganic carbon across the sediment-water interface. The biogeochemical processes measured during our experiment presented the status of the sediment while readjusting to a new biogeochemical state. Since all macrofauna was removed inside the track, this readjustment was mainly driven by molecular diffusion rather than biological activity.

4.3.1. DIC profiles

As hypothesized, DIC profiles were truncated leading to transient higher surface sediment pore water concentrations after the passage of the dredge. The decrease in DIC concentration in the top centimeter within one week after trawling showed a gradual recovery driven by diffusion to the overlying water. The truncation of the DIC profile measured in the 'IN' cores was still visible after one week and indicated that the sediment had not reached a new steady state. van de Velde et al. (2018) suggested that pore water chemical composition may take as long as ~4 months to return to its initial steady-state conditions after an anthropogenic disturbance when surface sediment is removed. We expect the DIC profiles to readjust much faster since only 2.5 cm of surface sediment had been removed compared to the disturbance of down to 15 cm reported in van de Velde (2018). During this transition, DIC fluxes from the sediment are initially higher until they gradually

reach a new steady state gradient of DIC concentrations between sediment and overlying water. [van de Velde et al. \(2018\)](#) contended that a trawling frequency of 3 times per year would keep the seafloor in permanent transient state, i.e. a complete 'reset' of the pore-water geochemistry with near-constant concentrations in the upper sediment shortly after the disturbance, followed by gradual readjustment of the porewater DIC concentration in accordance to the rates of organic carbon mineralization and the bottom water DIC concentrations.

4.3.2. Oxygen consumption rate

The hypothesized decrease in total oxygen uptake due to the removal of surface sediment was supported by our experiment. Oxygen consumption rates represent the total (oxic and anoxic) metabolism by micro-, meio-, and macrofauna within the sediment as well as the chemical re-oxidation of reduced inorganic compounds, such as iron sulphides ([Glud, 2008](#)). The removal of the reactive surface sediment in which the abundances of microorganisms is high ([Watling et al., 2001](#)) and the fact that all macro-organisms had been removed by the dredge, most likely resulted in a decrease in biological activity and carbon mineralization ([Tiano et al., 2019](#)). The disturbed oxygen regime can have impacts on the N - cycle, as oxygen regulates nitrification and denitrification in benthic sediments ([Rysgaard et al., 1994](#)) as well as on the P - cycle, as oxygen regulates the release and retention of phosphate ([Sundby et al., 1992](#)).

4.3.3. Ammonium and nitrite and nitrate - fluxes

The hypothesized enhanced efflux of ammonium from the sediment was confirmed in the present study as indicated by the immediate release of ammonium measured after one day. The removal of surface sediment caused a shift to higher NH_4^+ concentrations at the sediment surface resulting in a readjustment of the pore water profile to reach a new steady state. NH_4^+ had the greatest flux from the sediment among all analyzed nutrients. [Tiano et al. \(2019\)](#) did not find a significant increase in ammonium fluxes, however, they reported an increase in pore water NH_4^+ in the top 3 cm of the sediment highlighting that the sediment was physically disturbed by tickler chain and PulseWing trawling. The adjustment towards a new biogeochemical state one week after the dredging in our study was faster than the time span of several months reported by [van der Velde et al. \(2018\)](#), however, in that study sediment disturbance was five times deeper. Calculations of the potential impact of trawling-induced fluxes by [Duplisea et al. \(2001\)](#) resulted in a pulsed release of ammonium from a single trawl passage that was 45 times higher than in an undisturbed sediment. In the present study, NH_4^+ flux was only 4 times higher inside the track.

[Hale et al. \(2017\)](#) pointed out that intensive trawling can result in a reduction of nitrate caused by increased denitrification, and a net loss as N_2 from the sediment ([Mayer et al., 1998](#); [Bertics et al., 2010](#); [Laverock et al., 2011](#)). As revealed by our incubations, the increased release of ammonium decreased the amount available for benthic nitrate production resulting in a reduced or even reversed NO_x - flux. Conversely, the presence of *L. balthica* in the control cores may have contributed to the net release of nitrate because their burrows are located within the still intact nitrification zone. In the burrows, the nitrate concentrations are higher than in the overlying water causing steeper concentration gradients at the sediment-water interface, and nitrate also gets flushed out during burrow ventilation ([Michaud et al., 2006](#)).

4.3.4. Phosphate - fluxes

Pore water concentration gradients near the sediment surface in undisturbed sediments under oxic bottom conditions are strongly influenced by the presence of a $\text{Fe}(\text{OH})_3$ layer with high phosphate sorption capacity. At steady state, under undisturbed oxygenated bottom water conditions, phosphate concentrations are commonly very low within the $\text{Fe}(\text{OH})_3$ layer owing to the strong adsorption of phosphate to iron hydroxides. In such sediments, the burial efficiency of inorganic phosphate, calculated as the proportion of buried phosphate relative to

the total influx of phosphate to the sediment, is significantly higher than under disturbed conditions, where a significant proportion of the sorptive $\text{Fe}(\text{OH})_3$ has been at least temporarily removed ([Froelich, 1988](#); [Sundby et al., 1992](#)).

Higher surface pore water concentrations of phosphate, due to the removal of surface sediment after truncation of the surface sediment by the dredge, reflect the exposure of deeper sediment layers where the iron hydroxide concentrations are lower, fewer sorption sites for phosphate exist, and pore water phosphate concentrations are higher. As a result, the burial efficiency of phosphate is at least temporarily lower and more phosphate was released from the sediment until surface pore water conditions have readjusted to the condition before the disturbance. Although the phosphate effluxes were not significantly enhanced compared to the control site, mean fluxes were higher in the track. Temporarily enhanced effluxes of phosphate were also reported by other studies, e.g. [Percival and Frid \(2000\)](#); [Duplisea et al. \(2001\)](#); [Viarioli et al. \(2003\)](#); [Percival \(2004\)](#); [Percival et al. \(2005\)](#); [de Madron et al. \(2005\)](#). [Percival and Frid \(2000\)](#) estimated trawling to increase the phosphate annual flux by 2.4% whereas we found an increase of 18% estimated from the mean fluxes one day after dredging. This suggests that the storage and recycling times of phosphate might be decreased in trawled sediments ([de Madron et al., 2005](#); [Percival et al., 2005](#)).

5. Conclusion and broader implications

Our study demonstrated the impact of a single dredge passage on the benthic habitat, as indicated by the significant reduction in surficial LOI (used as proxy for OC), chlorophyll, water content and DIC, the complete removal of macrofauna and the nutrient specific changes in benthic fluxes. These effects are drastic considering the relatively small disturbance caused by the dredge (i.e. 2.5 cm deep). In reality, trawl doors of otter trawls, for example, can penetrate up to 35 cm in muddy sediments. Our experimental approach is similar to the sweeps and bridles of otter trawls or to seine ropes that impact less than 2 cm of surface sediments ([Eigaard et al., 2016](#)). Overall, trawling can have different physical and biogeochemical effects on the seabed based on how the different parts of the gear interact with the seabed and different grades of impact ([Oberle et al., 2016b](#)). In our study, surface sediment was removed but sediments may, for example, also be overturned or completely mixed causing different impacts on sediment properties, macrofauna and benthic fluxes ([Martín et al., 2014b](#); [Oberle et al., 2016b](#); [De Borger et al., 2020](#)). Additionally, surface sediments that get resuspended due to trawling, will eventually deposit. The input of fine, organic rich material potentially close by the trawl track, will also modify natural conditions of the ecosystem. Thus, small-scale heterogeneity in different parts of the track and different distances to the track, as well as the time since the last disturbance ([Ferguson et al., 2020](#)) may partly explain the contrasting results reported in the literature. As already mentioned, a disturbance frequency of 3 times per year may keep the seafloor in a permanent transient biogeochemical state ([van de Velde et al., 2018](#)). It is, therefore, likely that commercially trawled Baltic Sea sediments rarely reach near steady state conditions, especially in areas with maximum bottom trawling intensities between 7 and 30 times per year ([HELCOM, 2017](#)). In regularly disturbed habitats, recovery rates for macrofauna are slow and range from 1.9 to 6.4 years ([Kaiser et al., 2006](#); [Hiddink et al., 2017](#)), depending on sediment type ([Hale et al., 2017](#)). On a long-term perspective, these areas exhibit reductions in the biomass of large, long-lived macrofauna ([Tillin et al., 2006](#); [van Denderen et al., 2015](#); [Rijnsdorp et al., 2018](#); [Hiddink et al., 2019](#)) to the advantage of small, opportunistic species with, however, lower bioturbation potential ([Solan et al., 2004](#); [Queirós et al., 2013](#)). Suspension and deposit feeders may also be indirectly affected by trawling since together with the reduction in OC and chl, the nutritional value of sedimentary organic matter was observed to decrease ([Bock and Miller, 1995](#); [Charles et al., 1995](#); [Sañé et al., 2013](#)) leading to a reduction of benthic food quality ([Watling et al., 2001](#)). However,

higher chl and/or OC concentrations were detected due to chronic trawling (Sciberras et al., 2016), which has been proposed to be an effect of reduced grazing activity caused by the loss of microorganisms and macrofauna and/or settling of resuspended particles (Watling et al., 2001; Bergman and Hup, 1992; Palanques et al., 2014). The potential change in biogeochemistry, food quality and macrofauna community composition, which, in turn, also impact biogeochemical processes, due to chronic disturbances of the seabed, may affect the productivity in the overlying waters (Conan et al., 1999) since NH_4^+ and PO_4^{3-} are necessary for phytoplankton growth (Karlson, 1989; L'HeGuen et al., 1996). Furthermore, trawling disturbs the redox structure of sediments and was found to cause a reduction in denitrification (Ferguson et al., 2020; De Borger et al., 2020) and an increase in nitrogen retention in the Baltic Sea ecosystem, potentially further contributing to Baltic Sea eutrophication.

The actual fate of the Baltic Sea ecosystem after many decades of heavy bottom trawling remains unclear since it is difficult to estimate long-term effects due to the lack of data. However, the crucial consequences determined in our small scale experiment and the fact that the Baltic Sea also suffers from other stressors (i.e. eutrophication, oxygen deficiency, pollution and climate change) suggests that impacts of bottom trawling on ecosystem services and on the recovery in the Baltic Sea could be more pronounced than in healthier marine ecosystems.

Author statement

Claudia Morys: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Volker Brüchert: Validation, Resources, Writing - Review & Editing, Clare Bradshaw: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing - Review & Editing, Supervision, Project administration, Funding acquisition

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.

Acknowledgement

This study was funded by the Swedish Research Council Formas (grant number: 2017-00866). We thank the team of the Askö laboratory as well as the divers Susanne Qvarfordt, Chiara d'Agata and Oskar Nyberg for successful field work. Additionally, we are grateful to Julia Steinbach and Henrik Sandberg for laboratory assistance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2021.105384>.

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