Bottom fishery impact generates tracer peaks easily confused with bioturbation traces in marine sediments

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Abstract. In the process of reworking sediments and thus shaping biogeochemical processes, marine bottom dwelling animals

10   are thought to play a pivotal role in many benthic environments. Bioturbation (particle reworking) includes downward transport of particles into the sediment as a major process and is sometimes detected as sub-surface maxima (peaks) of specific particulate substances (tracers). ~~This aspect of bioturbation (particle reworking) is often partitioned into short distance local and non-local transport acting over relatively longer distances~~ Here we document that sub-surface peaks, such as those typically attributed to biological particle transport in sediments, may equally be generated by otter boards in bottom trawling fishery.

15   Boards can generate tracer peaks whereby they scoop sediment from the surface, flip it over and deposit it onto the adjacent sea floor. These peaks are indistinguishable from those ~~(presumably)~~ generated by benthic fauna burying surface material at sediment depth. ~~in a process whereby.~~ We demonstrate this for the particle tracer chlorophyll a in silty sand from the Western Baltic Sea with fauna that generally does not burrow deep in a global comparison. Our inability to distinguish the driving processes generating the peaks indicates limits to our understanding of magnitude and spatial extend of bioturbation traces in

20   this environment. It also poses a problem to the assessment of fishery resource use and benthic processes. However, based on natural fauna abundance, behavioural information and fishery intensity data, we identify macrofauna and not otter boards as the dominant cause for peaks at the sites investigated here. ~~However, we can clearly identify macrofauna and not otter boards as the cause for peaks at the sites investigated here.~~

1 Introduction

Bottom trawling introduces anthropogenic disturbance to the seafloor. Research addressing different aspects of this activity is accumulating for it causes partial destruction of benthic habitats and its biota (Sparks-McConkey and Watling, 2001; Watling and Norse, 1998), alters sediment structure both physically and in ~~their~~ its granulometry (Oberle et al., 2016a; Bradshaw et al.,

2012, 2021), suspends finer grain sizes from the bulk sediment and may affect contaminant deposits (Oberle et al., 2016b).

30 Trawling affects ecosystem functions such as carbon storage (Epstein et al~~.~~., 202~~1~~2) and sediment integrity (de Juan et al., 2015) and ~~also~~ additionally interacts with other pressures on the benthic ecosystem such as contaminant deposits or hypoxia (Oberle et al., 2016b; Bunke et al., 2019; van Denderen et al., 202~~1~~2).

Investigations aiming to detect and quantify the effects of fishing gear at the seafloor face the difficulty that patterns may also stem from disturbances, natural or anthropogenic, other than trawling (Bunke et al., 2019). ~~While investigations aim to detect~~

35 ~~and quantify the effects of fishing gear at the seafloor there are at least two (major) difficulties. First, patterns showing the potential impact on sediments may in some cases also stem from disturbances, natural or anthropogenic, other than trawling (Bunke et al., 2019).~~ Deep reaching storms, particle reworking by bioturbating fauna, construction and dredging activity leave traces of disturbance at the seafloor as well.

~~L~~Localization ~~Secondly, localisation~~ of the impact on the sea floor and sampling also poses a major problem. Both

40 usually take place with limited spatial precision, which is why a majority of studies rel~~ies~~y on statistically capturing average effects in areas of certain trawling intensities. ~~The latter also have a "fuzzy" delineation characterized by~~ Measures such as swept area ~~surface~~ratio (SAR) of fishing intensity remain inaccurate in that they ~~measures~~average ~~such as~~ bottom trawls over long periods (per year or per quarter) and relate the impact to comparatively large areas (several km²) ~~(bt yr⁻¹ or swept area ratio (SAR). The scenarios presented by Oberle and co-workers (2016b) nicely demonstrate this latter difficulty. Their scenario~~

45 ~~2 of a trawling board cutting into the ground can be detected only when sampling takes place precisely at the impacted site (showing oil derivatives buried by the board in Oberle et al., 2016b). The other three scenarios rely on combining several measures and deduction of the overall motions of particles during mixing of the sediment usually by repeated trawling impacts.~~. However, the damage to the surface sediment by otter boards may be local. ~~S~~studies investigating the change of vertical distribution of sediment constituents demonstrate that an effect of trawling can be the removal of surface sediment and

50 considerable alterations of matter concentrations and processes in this sediment surface layer (Mestdagh et al., 2018~~; Morys et al., 2021~~; van de Velde et al., 2018; Morys et al., 2021). In an experimental dredge trawl Morys et al. (2021) found that sediment excavated to 2.5-3 cm depth piled up irregularly on the sides of the track.

Particle reworking by bioturbating organisms is an important aspect of transport for substances at and just below the sediment-water interface ~~(SWI)~~. While specific motions associated to their way of life (burrow construction, feeding, defecation~~…~~)

55 move particles in all spatial directions, at vastly different time intervals and over very different distances at any one time, the macroscopic pattern of the sum of these individual reworking events is mostly dealt with in simplified ways. A common differentiation describes numerous and small ("local") transport steps as an erratic, non-directional mixing process (analogous to diffusion) and observes "non-local" transports when directional transport over longer distances takes place and creates ~~concentration~~ peaks in vertical concentration profiles of particles in the sediment (e.g. chlorophyll used as a particle tracer).

60 The interpretation of peaks in ~~experimental~~ stable tracer distributions (glass beads, luminophores) or ~~natural~~ decaying tracer distributions (radioisotopes, chlorophyll) as signs of non-local transport is widespread (Wheatcroft et al., 1994; Blair et al., 1996; Meysman et al., 2003; Morys et al., 2016, 2017; Oberle et al., 2016b~~; Wheatcroft et al., 1994~~). Peaks are observed

regardless of ~~the~~ persistence ~~of the in the stable~~ tracers used, in stable ~~or~~ tracers or tracers ~~"age" (decay time, degradation)~~that decay with time. Natural decay of the tracer chlorophyll allows to "look back in time"~~,~~ ~~depending on the decay constant, by~~ for ~~about 70~~100 - 150 days ~~(two half-lives at 0.02 d^{-1}) with the~~when its peak concentration ~~declining~~ has declined to 25 % of its original value. Decay thus determines whether a peak will remain visible or if the event merges into the overall mixing which is usually dealt with as diffusion analogue. Chlorophyll as a particle tracer can therefore show relatively recent events of particle mixing only. Compiling data on the frequency of use and geographic coverage of studies employing different tracers, Solan et al. (2019) showed that next to radioisotopes the naturally occurring chlorophyll a molecule (Chl-a) is commonly used.

Transport of particles in sediments potentially always implies changes in availability, concentration or distribution of food (organic particles), contaminants and oxidising agents such as iron oxides, with potential effects on carbon burial and inorganic nutrient release, including potential feed-back of these rate changes on bioturbating macrofauna (Epstein et al., 2022; de Borger et al., 2020~~2~~; van Denderen et al., 2024~~2~~)~~.~~ It additionally affects dissolved electron acceptor distribution~~;~~ as concomitant fluid movement is inevitable. This fosters the interest in bioturbation as an important regulator for bacterial activity and diagenesis (Aller, 2014). ~~The Western Baltic Sea also harbours seafloors among the most intensively trawled areas of the world (Amoroso et al., 2018).~~

In the framework of research on impacts of trawling in the Fehmarn Belt area (FB), ~~western~~ Western Baltic Sea (Fig. 1) (https://www.io-warnemuende.de/dam-mgf-baltic-sea-home.html) we measured the depth distribution of Chl-a in order to study bioturbation. The Western Baltic Sea also harbours seafloors among the most intensively trawled areas of the world (Amoroso et al., 2018). Trawling ~~can may be massive considerable~~ in this area ~~and as~~ tracks ~~show demonstrating~~showing ~~the impact~~ in this area have been thoroughly analyzed (Schönke et al., 2022) and their ~~have been thoroughly analyzed~~ biogeochemical signals interpreted by ~~by (Schönke et al., (2022~~Rooze et al. (2024). Chlorophyll ~~P~~peaks detected ~~in area of investigation~~here are usually attributed to *Arctica islandica*, the dominant reworking bivalve, or other biota of the community. ~~However, intense trawling raises the question of an alternative origin of the peaks.~~

The ~~Iceland clam~~ocean quahog, ~~-~~*Arctica islandica*, ~~is the longest-lived non-colonial animal known to science (Wanamaker et al., 2008). It commonly inhabits depths between 10 and 280 m in fine-grained muddy sand (Ridgway and Richardson, 2011). As a suspension feeder, it feeds on phytoplankton and~~ lives just below the sediment surface, from where it maintains contact with seawater via its short siphon (Winter, 1969). *A. islandica* is classified as a surface biodiffusor (also: surficial modifier/biodiffusor; Queirós et al. 2013) based on its surface dwelling activity. Its activity causes constant and random local transport of particles over short distances in the uppermost centimetres of the sediment (Kristensen et al., 2012; Queirós et al., 2013). ~~However, the~~The species also shows a behaviour known as "survival by metabolic suppression" induced by hypoxia, when it burrows to deeper horizons. Therefore, the ~~Iceland clam~~ocean quahog is also considered a "downward conveyor" that translocates particles to depth by non-local transport (Kristensen et al., 2012; Morys et al., 2017)~~. . In a 1999 benthic study, a wide distribution of the organism was found at depths ranging from 15.6 m to 29.6 m. Mean abundance was 91 ind./m² with a AFDM ash-free dry mass biomass of 15 g/m².~~ In Mecklenburg Bay, *A. islandica* accounts for up to 99% of the biomass representing the most important species below the halocline (Morys et al., 2017~~; Zettler et al., 2001~~).

However, intense trawling raises the question of an alternative origin of the peaks. Previous studies (Oberle et al., 2016b), UW-video evidence, and a possible analogy to terrestrial soil turnover during ploughing triggered the idea of surface sediment subduction by otter boards. To our knowledge there is no evidence of this transport process in the literature.

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Anticipating sediment displacement similar to Morys et al. (2021) we conducted an *ex situ* experiment to mimic otter board effects at the sediment- water interface and compared it to field. We subsequently performed an *in situ* experiment with trawling and immediate targeted sampling by scuba divers. Our aims were to i) mimic the genesis of altered Chl-a peaks distributions experimentally, ii) compare these with peaks found in the field and potentially originating from commercial

105 trawling effects and finally iii) to discuss the likelihood and consequences of confusion of these peaks with those generated by bioturbation.

2 Material and Methods

We performed experiments *ex situ* in a mesocosm and *in situ* by setting trawl marks to provide proof of principle of mechanisms operating. We investigated the changes of particle distribution brought about by the mechanic impact of otter trawling.

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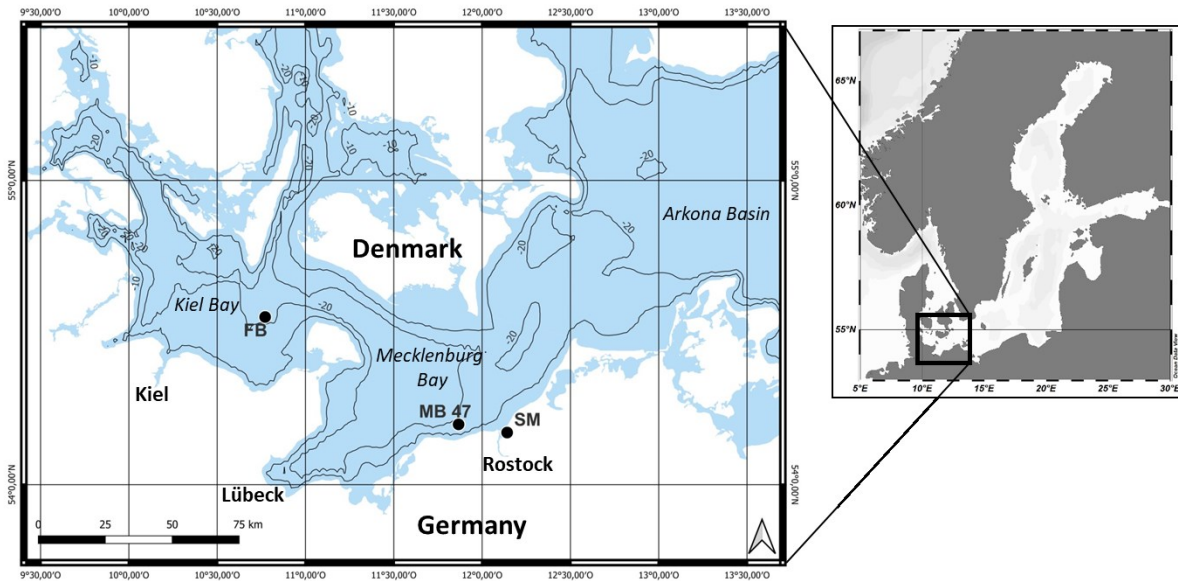
Figure 1: Locations in the Western Baltic Sea where (1) random sampling revealed sub-surface tracer peaks in the field (FB), (2) an *in situ* trawling experiment was performed (MB 47) and (3) sediment was retrieved for an *ex situ* mesocosm experiment (SM).

4

Ex situ experiment

In April 2021 we simulated the mechanical trawling impact at a small scale in a mesocosm using a shovel and a rake. The mesocosm consisted of a circular aquarium (0.8 m diameter, 1 m height) which had been filled 3 month before with sandy sediment to reconstruct a ~~natural,~~ horizontally homogeneous, vertically declining Chl-a distribution. The lowest sediment layer consisted of 15 cm sieved sand (0.5 mm) that had been stored in the dark for > 3 months. This was overlain by 8 cm freshly sieved sediment from ~~a~~ the field site Schnatermann ~~close by~~ (S~~M, ee figure~~Fig. 1~~, Schnatermann (SM)~~) that had been removed from 2 – 10 cm depth, excluding the upper 2 cm surface layer sediment with much microphytobenthos at this shallow location (SM, 0.5 m water depth). Finally, the uppermost layer in the mesocosm contained 2 cm of sieved surface material from that field site harboring a rich microphytobenthos community. The upper 10 cm of sediment consisted of silty fine sand (m.d. 190 µm) ~~with C_{org}~~ similar to the sediment at the *in situ* experimental site ~~(unpublished data)~~. The mesocosm stood outside the university buildings at ambient light and temperature (temperature range 2 to 16 °C) and was covered by 15 cm of water (10 psu).

On April 8 2021, we manipulated the surface sediment with a shovel (~8 cm wide) and a rake according to the scheme in figure 2. We decided to excavate sediment keeping a defined geometry of depth and width when removing sediment rather than some plough-like tool which we found difficult to implement. In fact, we are not sure about the exact mechanism and geometry of sediment removal and its deposition on the adjacent sediment by an otter board, therefore the method used in the mesocosm is a surrogate and not necessarily the same as the physical process that might be active *in situ*. We excavated sediment with a flat rectangular shovel, scoop by scoop to about 4 cm depth from the surface (track leading along sediment core position 6 – 10) and deposited it upside down to the left onto the adjacent sediment surface (from position 11 – 15). The resulting "furrow" and "mound" of about 40 cm length showed a surface topography with wave-like cross section as shown in figure 2 (dashed line). We also pulled a rake through the sediment along the core positions 1 – 5 mixing the sediment to ~ 2 cm depth while slowly moving up and down. This is to mimic the impact of the trawl net with its footrope ~~ground rope~~ ("net"). Immediately after the manipulation sampling started with five 36 mm inner diameter acrylic cores ~~were sampled~~taken in rows along each of the structures created (cores 1 – 15), ~~while~~ and controls ~~were~~ randomly placed across the unaffected area (positions 16 – 20).
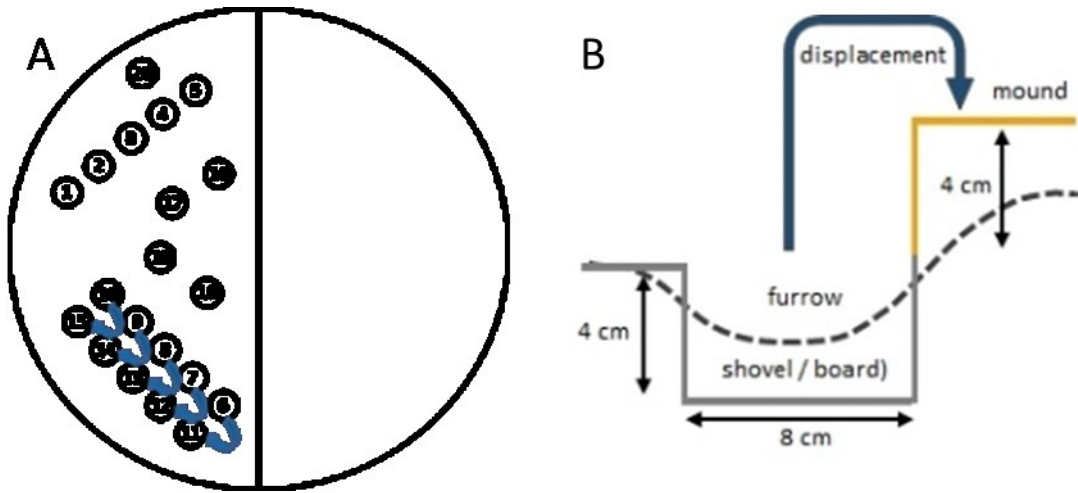
Figure 2: A: Sampling scheme on the left side of the mesocosm; a corresponding experiment on the right side including bioturbating organisms is not addressed here. Cores 1 – 5 net, 6 – 10 furrow, 11 – 15 mound, and cores 16 – 20 controls. <u>Arrows indicate sediment removal and deposition.</u> B: Schematic of sediment excavation. Dashed line indicates final surface topography.

In situ experiment

On the 19th of June 2021 a small otter trawl typical for the area was performed at 20 m water depth at approximately 54°12'N and 11°52'E (MB 47) by RV "Solea", while RV "Limanda" and further research vessels conducted a series of associated measurements and sampling (Fig. 1). The site at 20.3 m depth is inhabited by *Arctica islandica* (46 Ind. m^{-2}) in much the same way as the investigation area Fehmarn Belt (s. below). Sediments consisted of silty fine sand (m.d. 180 µm; C$_{org}$ 0.9 % dw).

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Scuba divers sampled the net area (effect of footrope) in one trawl track and . Ccontrol cores were taken in the recently untrawled vicinity that same day. Five 36 mm inner diameter cores were taken randomly ~~in an area of~~within 1 m² ~~each~~in both areas. On a second trawl track sampling by scuba diving occurred from furrow and mound areas. Here cores were inserted along the axis of the shallow furrow carved by the otter board (~~Fig~~Fig. 3). Material excavated by the board lay in irregular piles on the outer rim of the furrow. Cores were inserted along the highest ridge of these piles parallel to the direction of the furrow.
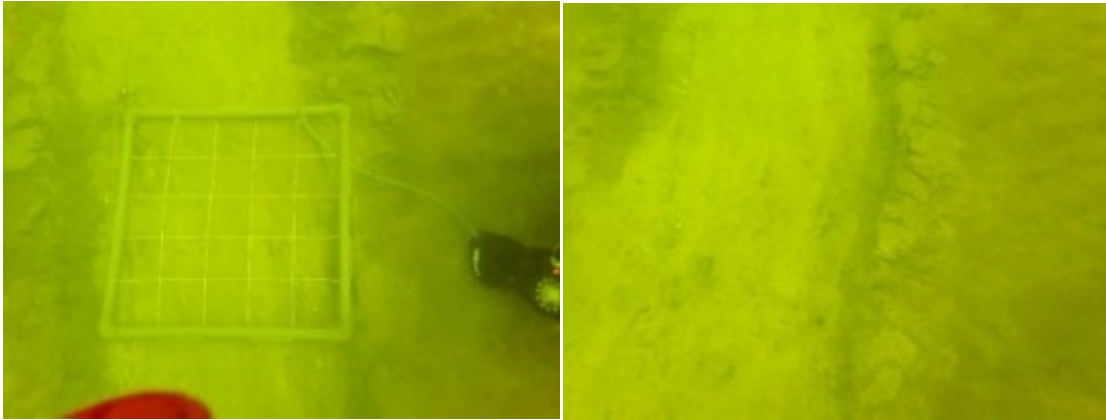

Figure 3: UW photographs of otter board track visible as light sediment with a depth of approximately 4 cm (counting square: 50 cm width). The material displaced from the furrow is visible as mound with transversal cracks on the right hand side of the lighter furrow (right photo). Photographs curtesy of H. Pielenz.

Field data

In the Fehmarn Belt area random sampling by multiple corer (MUC) was performed in 2020 and subsequent years for Chl-a depth distribution to describe the bioturbation activity. Cores (10 cm diameter) were sliced, ~~at the same intervals as below; the 10 cm diameter sl~~slices~~ices were~~ homogenized~~mixed~~ and samples treated as described below~~was reported below~~.

The site is characterized by muddy fine sand (median diameter 50 µm; C_{org} 5.5 % dw) (Gogina and Feldens, 2020) and is dominated by *A. islandica* (43 Ind. m^{-2}). Sampling of the benthic macrofauna was performed using a van Veen grab (75 kg, sieve lid) with a sampling area of 0.1 m² and sieving (0.5 mm) on 30 grab hauls. Samples were preserved with 4% formaldehyde seawater solution ~~in sea water mixture~~.

Processing

Processing took place within three hours after core retrieval. Sediment was carefully extruded from the tube and cut in intervals of 0.5 cm to 2 cm depth, followed by 1 cm slices to 8 cm and 2 cm slices to a final depth of 12 cm. Layers were homogenized with spatula in Petri dishes. One cm^3 of sediment was subsampled using a cut syringe and placed in a centrifuge tube for storage at -18 °C. For pigment extraction samples were thawed, mixed with 8 ml > 96% denatured ethanol (WALTER-CMP) and vortexed for 5 s. They were then extracted in the dark at ~7 °C for 22 - 24 hours with one additional mixing step several hours into the extraction. Prior to the measurement samples were centrifuged at 2000 rpm for 4 minutes. Chlorophyll fluorescence was measured (Trilogy, module CHLA, Turner Designs), with additional acidification prior to the determination of phaeopigments (50 μL 1 N HCl). Chl-a concentrations (μg cm^{-3}) were calculated from raw fluorescence values following JGOFS Report 19 (1994). We calibrated the fluorimeter using a spectrophotometrically determined standard curve.

Rates of Chl-a decay required for modelling particle reworking (Sun et al., 1991) were obtained by incubating (7 °C) surface sediment in the dark in re-sealable containers. During 35 days, three parallel samples were removed at different time intervals and treated as described above. From the temporal decline of Chl-a concentration a pseudo-first order constant, k_d, was calculated.

Modelling data

The distribution of chlorophyll concentrations with depth was used to infer rates of transport, separating local from non-local transport. Soetaert et al. (1996) derived a hierarchical model family consisting of six models of increasingly complex biological transport. The simplest model describes the tracer distribution without mixing by organisms and only depending on decay and sediment accumulation. In model 2 diffusive mixing is included (D_b [cm^2 y^{-1}]). Starting from model 3, all subsequent models include 'non-local' transport of tracer from the sediment surface to depth with increasingly complexity (injection, J, and ingestion, r). There is no benefit in trying to differentiate between models of higher complexity (models 3, 4, 4a and 5), since fitting results seemingly differ owing to some horizontal heterogeneity in our data. Also, we lack observations that would allow to differentiate mechanisms like particle injection in physical sediment turnover and compare it to model results. Therefore, we grouped theall fits of non-local models into a category "non-local" and do not interpret them further. Here we will group the non-local terms, injection (J) and ingestion (r), from models 3, 4 and 4a and not interpret them further. A level of p ≤& 0.05 was used for statistical significance in modelling (see Soetaert et al., 1996 for details).

3 Results

205 The two experiments provided similar displacement of surface sediment onto the adjacent seafloor. The effect of removal was visible ~~by eye~~ as surface topography, however only with a small vertical displacement of the sediment-water interface. Peaks found in our *ex situ* experiment were made by shovelling sediment and consciously depositing it upside down onto the adjacent sediment. This created peaks ~~which on average display a peak concentrating of 20 µg Chl a cm^{-3}~~ at 1.25 cm depth on average. After shovelling, the sediment visibly slid to both sides of the newly formed mound, but particularly into the furrow. The

210 relatively narrow furrow compared to the excavation depth (4 cm) might have promoted this sliding effect compared to the field experiment with a wider furrow. ~~After shovelling, the sediment visibly slid to both sides of the newly formed mound, but particularly into the furrow. The relatively narrow furrow compared to the excavation depth (4 cm) might have promoted this sliding effect compared to the field experiment with a wider furrow.~~ The Chl-a profiles imply that an overall net deposition of 1 - 1.5 cm remained. The peak concentration (Fig. 4, upper panel) declines upwards and downwards at similar rates and

215 approaches the background of about 8 µg cm^{-3} at 3.5 cm depth. This is 2.25 cm below the original sediment water interface and corresponds well to concentrations in control and net areas below 2 cm. Concentrations in the upper one cm of the furrow are surprisingly high on average. This may be a result of sediment sliding back from the mounds.

The pattern in the *in situ* experiment is the same as *ex situ* despite very different levels of concentrations. In the field experiment,~~we cannot rule out bioturbation traces or older trawling tracks that were no longer visible at the site when diving~~

220 the impact by the ground net remains undetectable as net profiles resemble controls closely. Surface mean concentrations of 4 µg cm^{-3} decline quickly with depth. Furrow surface concentrations are somewhat lower than controls and indicate a net decapping effect of ~~≤~~about 1 cm in the ~~field~~*in situ* experiment. The peak at 1.25 cm depth in the mound resembles that in the *ex situ* experiment. With 6 µg cm^{-3} its average concentration is higher than z~~=~~ = 0 concentrations in the controls and may indicate some sorting mechanism active. Morys et al. (2021) described surface sediment removal by dredging with very similar

225 patterns in the furrow zone.

~~Overall, the generating mechanism and the effect of this type of trawling board on the particle tracer profile appear clear.~~

~~In the *ex situ* experiment freshly piled up sediment from the mound slid back into the adjacent furrow leaving a vertical difference of about 2 cm between furrow and mound. In the field the furrow was somewhat deeper (~ 4 cm).~~ Overall, the

230 generating mechanism and the effect of this type of otter board on the particle tracer profile appear clear. The displaced sediment generated a peak in the vertical profile of particulate chlorophyll in both experiments. The profile shape indicates that the peaks result from the fact that the sediment material was flipped over. Maximum surface concentrations of two interfaces meet at depth of about 1.25 cm (Fig. 4). This generates a pronounced signal of sediment movement. A much higher concentration close to the sediment surface in the *ex situ* experiment than at the *in situ* site ~~results~~ resulted from the sediments

235 rich in microphytobenthos sampled in preparation of our experiment from a shallow local site.
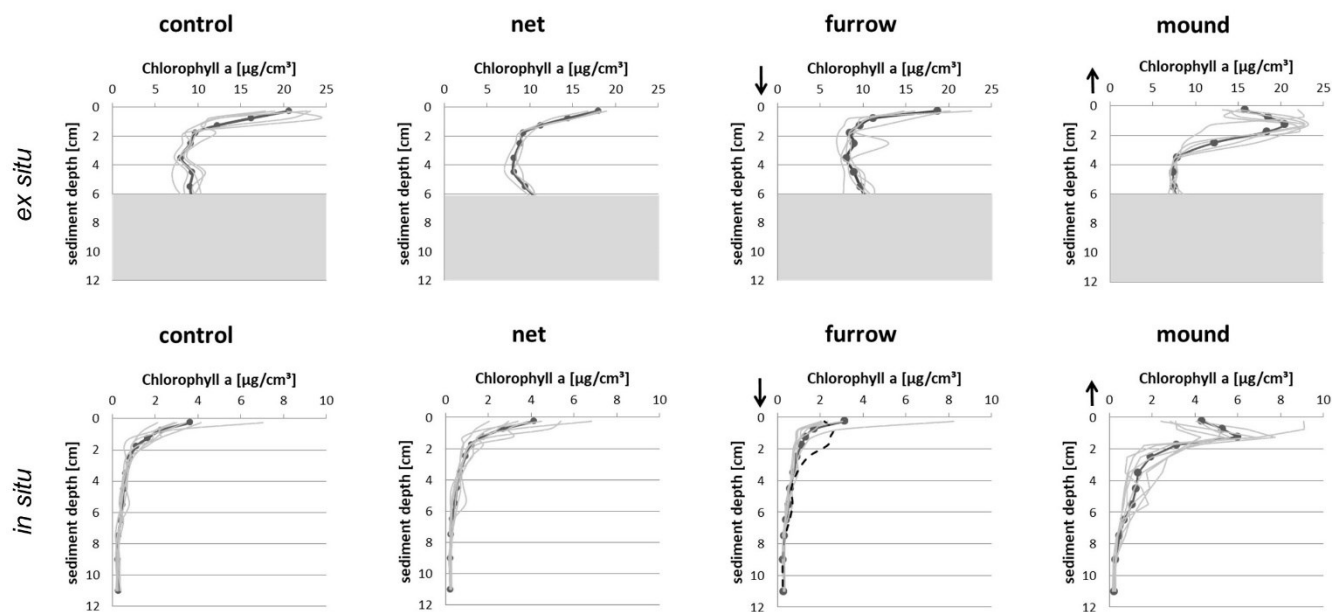
Fig<u>ure</u> 4: Averaged (bold) and individual Chl-a tracer profiles (grey) for both *ex situ* (upper row) and *in situ* experiments (lower row). Dashed line in lower furrow panel represents one core sampled with an individual of *Arctica islandica* found at 2 cm depth. Arrows indicate that the topography of the sediment water interface was shifted relative to control or net areas by approximately 1 ~~1.5~~ 1.5 cm: down in the furrow and up in the mound area. Shaded area<u>s</u> in upper panels indicate~~s elevated~~ pigment levels not relevant to the present discussion ~~but generated by mishandling during preparation of the experiment~~.

<u>Field data in Fehmarn Belt showed peaks of different maximum concentration and depth in</u> ~~In Fehmarn Belt~~ 7 out of 11 profiles randomly sampled ~~showed peaks of different maximum concentration and depth~~. Figure 5 depicts three examples and one profile without peak. Most peaks <u>were</u> positioned within the top 2 cm of the sediment with the exception of one single peak at 3 – 5 cm shown in ~~Fig.~~<u>figure</u> 5. ~~These~~ <u>Such</u> peaks are commonly interpreted as signs of non-local transport resulting from faunal activity.
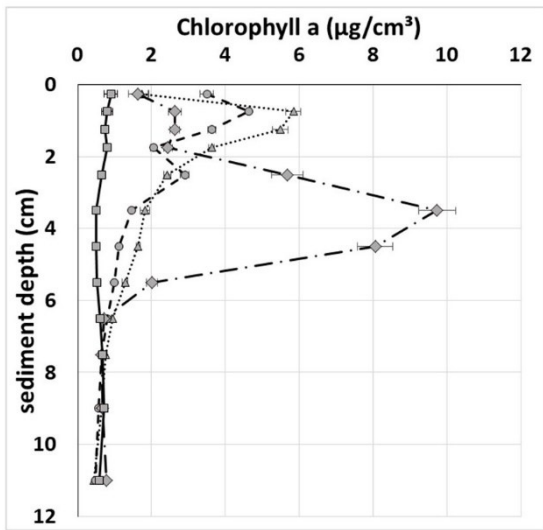
Figure 5: Examples of peaks detected in Fehmarn Belt during random sampling by multiple corer.

We compiled the qualitative information on non-local ~~and~~ versus local reworking retrieved from mixing.exe by giving the number of best fits in each category (Table 1). The overview includes three field sites with muddy sediment or silty fine sands. Peaks are a frequent feature in sediments from Mecklenburg Bay and Fehmarn Belt when sampled randomly from ships. Without explicitly targeting specific features produced by demersal fishery gear (~~–~~net, mounds or furrows~~,~~) – 32 to 64% of samples depicted peaks. In the two experiments where trawl features were specifically sampled, peaks were most abundant in mound areas (70 – 80%). Samples from furrows displayed comparatively many profiles without any mixing, however they also showed local and non-local mixing at roughly equal numbers. Net areas and control areas ~~are~~ were similar in that they ~~are~~ were dominated by local mixing in the trawl experiment. ~~In the *ex situ* experiment, depth below 6 cm showed artefacts in tracer distribution generated during preparation of the experiment. This may have consequences for the modelling results, therefore respective~~The *ex situ* control and net values in table 1 should be considered with caution because of inconsistencies in tracer distribution below 6 cm.~~.~~

Table ~~.~~1: Compilation of results from targeted sampling in the two experiments, highlighting local versus non-local transport as interpreted using the software mixing.exe (Soetaert et al., 1996). ~~Numbers of depth-profiles modelled in e~~Each column shows the numbers of depth-profiles modelled and column 'non-local' in brackets ~~the~~ percentage of non-local modelling results ~~shown in brackets are depicted~~ shown in brackets. ~~For comparison~~ Our own results randomly obtained ~~results~~ in the Fehmarn Belt area in 2020 and data reported by Morys et al.~~,~~ (2016) from Mecklenburg Bay ~~(Morys et al., 2016)~~ are ~~reported~~provided for comparison.

	local (Db)	non-local (J; r)	no mixing
Field Trawl Experiment			
control (n=7)	6	1 (14)	0
net (n=7)	6	1 (14)	0
furrow (n=7)	3	2 (28)	2
mound (n=7)	2	5 (71)	0
Ex situ Experiment			
control (n=5)	2	3 (60)	0
net (n=3)	0	3 (100)	0
furrow (n=5)	1	1 (20)	3
mound (n=5)	1	4 (80)	0
Fehmarn Belt 2020, unpublished own data (7 of 11)	3	7 (64)	1
Mecklenburg Bight, Morys et al. (2016) (7 of 22)	10	7 (32)	5

	local (Db)	non-local (J; r)	no mixing
In situ Experiment			
control (n=7)	6	1 (14)	0
net (n=7)	6	1 (14)	0
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control (n=5)	2	3 (60)	0
net (n=3)	0	3 (100)	0
furrow (n=5)	1	1 (20)	3
mound (n=5)	1	4 (80)	0
Field data			
Fehmarn Belt 2020, unpublished own data (7 of 11)	3	7 (64)	1
Mecklenburg Bay, Morys et al. (2016) (7 of 22)	10	7 (32)	5

4 Discussion

Two experimental approaches to sediment reworking by otter board trawling showed largely identical results. Both simulated *ex situ* sediment reworking using a shovel as surrogate and targeted sampling of *in situ* otter board marks revealed the same pattern of sub-surface peaks. This leads us to conclude, at least qualitatively, that the mechanism acting is the same. ThisIt may indicateindicates., too, that while scraping the sediment the otter board reverses a sediment slab more than it pushes

~~sediment aside.~~ -Deposition of part of the excavated surface sediment onto the adjacent sediment-water interface generates concentration peaks of the particle tracer Chl-a. These peaks resemble those of <u>biogenic</u> origin in non-local bioturbation.

285   This similarity poses a problem in areas like Fehmarn Belt where Chl-a peaks in the vertical sediment profile may stem from bioturbating infauna or fishery gear ~~on the seafloor~~. The uncertain origin of the observed peaks may affect the assessment of ~~for instance the~~ bioturbation intensity<u>, since peaks may only indicate sediment perturbation in general and not necessarily that owed to macrofauna at the seafloor</u>. Similarly, addressing quantitative aspects of otter board disruption of the seafloor may be difficult.

290   ~~Peaks found in our *ex situ* experiment were made by shovelling sediment and consciously depositing it upside down onto the adjacent sediment. This created peaks which on average display a peak concentrating of 20 µg Chl-a cm⁻³ at 1.25 cm depth. After shovelling, the sediment visibly slid to both sides of the newly formed mound, but particularly into the furrow. The relatively narrow furrow compared to the excavation depth (4 cm) might have promoted this sliding effect compared to the field experiment with a wider furrow. The Chl-a profiles imply that a net deposition of 1 cm remained. The concentration (Fig.~~
295   ~~4) declines upwards and downwards at similar rates and approaches the background of about 8 µg cm⁻³ at 3.5 cm depth. This is 2.25 cm below the original sediment water interface and corresponds well to concentrations in control and net areas below 2 cm. Concentrations in the upper one cm of the furrow are surprisingly high on average. This may be a result of sediment sliding back from the mounds.~~

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300   ~~experiment, we cannot rule out bioturbation traces or older trawling tracks that were no longer visible at the site when diving. The impact by the ground net remains undetectable. Surface mean concentrations of 4 µg cm⁻³ decline quickly with depth. Furrow surface concentrations are somewhat lower than controls and correspond to a net decapping effect of ≤ 1.5 cm in the field. The peak at 1.25 cm depth in the mound resembles that in the *ex situ* experiment. With 6 µg cm⁻³ its average concentration is higher than z=0 concentrations in the controls and may indicate some sorting mechanism active. Morys et al. (2021)~~
305   ~~described surface sediment removal by dredging with very similar patterns in the furrow zone. Overall, the generating mechanism and the effect of this type of trawling board on the particle tracer profile appear clear.~~

There are more or less pronounced additional peaks visible in ~~many~~ <u>some individual *in situ*</u> ~~of the~~ profiles ~~and panels (*in situ*: net, furrow, mound; *ex situ*: net, furrow, mound).~~ <u>Based on the decay of Chl-a tracer with time we are certain that any previous trawling event that may have generated the peak would be older than 3- 4 months. It would therefore not interfere with our</u>
310   <u>interpretation of the relocation of fresh surface particle tracer. However, we found an *A. islandica* individual of 2 cm length at the peak depth</u> ~~In~~ <u>in the sediment core from which we obtained</u> the profile highlighted in the *in situ* furrow (Fig. 4)<u>,</u>. ~~however, we found an *A. islandica* individual of 2 cm length at the peak depth~~<u>;</u> ~~;~~ <u>in</u> view of the core diameter (36 mm) we attribute this peak directly to the activity of this animal. Patchiness in concentrations in horizontal and vertical direction is obvious in both field and *ex situ* data. ~~Inappropriate mixing in the *ex situ* experiment and older traces of organisms or trawling in the *in situ*~~
315   ~~data may be responsible.~~ This is a reminder that there may always be peaks left without known origin, and that averaging <u>of replicate profiles</u> is advisable.

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We regularly encountered Chl-a peaks in Fehmarn Belt~~.~~ where MUC-sampling ~~here~~ was random~~.~~ ~~S~~ ~~that is the position of any tube on the MUC can only be as precise as 1 m (using Ultra-Short Base Line (USBL) acoustic positioning). Also we cannot intentionally core any structure generated by fishing gear or animal siphons of *A. islandica*. In~~till~~ ~~Fehmarn Belt,~~ 7 of 11

320 randomly cored locations displayed peaks at depths comparable to our experimentally generated peaks (Tab. 1; Fig~~s~~. 4, 5~~))~~. ~~One peak differed in concentration and depth.~~ . These peaks cannot be assigned to either ~~fishing~~ trawling or bioturbation with any certainty.

Below we will pursue the questions 1) if this problem is unique to our area of investigation in Fehmarn Belt, 2) which ~~consequences~~ implications it may have ~~in~~ for our understanding of the ecosystem and 3) if there are ways to resolve it?

325

Unique~~ness~~ness to our area of investigation

It is not clear if the problem of indistinguishable peaks exists in other ~~fishing~~trawling areas of the oceans, too. ~~We suspect that the origin of peaks in a given area can only be inferred if the bioturbating organisms, the gear used and intensity of fishing are known.~~ In the areas investigated here~~,~~ *A. islandica* is the benthic organism dominant in biomass (Zettler et al.~~,~~ 2001) and

330 is thought responsible for reworking of sediments (Morys et al., 2016, 2017). The area is also among the most heavily trawled in the North Sea and Baltic Sea region (Amoroso et al., 2018). We are not aware of a similar comparison of trawling effects and bioturbation effects in the literature.

In general, both transport phenomena, biological non-local reworking and physical ~~trawling~~ impact of the otter boards, will move sediment particles ~~the same~~in a similar way, at least on a relatively co~~a~~aurse scale of centimeters as employed here.

335 Decapping by trawling is described by Morys et al. (2021) and Bradshaw et al. (2021) who reported the removal of the top sediment layer in an artificial furrow in the Baltic off southern Sweden.~~Specifically, and applicable to the data presented here, . The underlying processes – particularly of bioturbation – may involve smaller steps of individual particle displacement that blend into seemingly diffusive transport (Meysman et al., 2003), but this is irrelevant to the observations made here.~~ While their report is based on direct observation and measured vertical distributions of sediment parameters~~ary material~~, several

340 indirect reports from other seas show that this decapping effect seems to be ~~a common~~ a feature observed in other trawling areas (Oberle et al., 2016b; Tiano et al., 2019; Depestele et al., 2019; Morys et al. 2021). However, the observation of a peak generated ~~, possibly~~ during the process of decapping, as in the present paper~~however~~, has not been reported by any of the previous authors.

~~Oberle could not be certain if they sampled the effect of a board. But they inferred this by "modelling".~~Oberle et al. (2016b)

345 attribute mixing of sediments by trawl boards on the Iberian shelf as deep as 35 cm into the sediment. They deciphered trawling effects on sediments off the Iberian west coast by combining lithological information, traces from recent oil pollution and highly resolved spatial information on bottom trawling. ~~Oberle~~ These authors could not be certain ~~if they~~to exactly ~~sampl~~ed the sediment site where an effect of a board would be visible.~~,~~ The authors suggested five scenarios of impact ~~B~~b. ~~But they inferred~~ investigated an area with~~where~~ conditions allowing to draw conclusions based on different lines of evidence. ~~this by~~

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350 ~~"modelling". Without information as closely related spatially targeted as our sampling by scuba divers, the authors suggested five scenarios of impact.~~ Scenario 2 is the one mirroring our turnover of surface sediment. The former sediment surface is buried and tracer appears at 18 cm rather than at 6 cm, the usual mixing depth by animals and currents ~~at the site~~in the area. ~~Here~~At the Iberian site~~,~~ the large difference in depth makes a differentiation between shallow biogenic ~~(shallow)~~peaks and deep peaks generated by fishing boards ~~(deep)~~ possible.

355 ~~As~~Contrary to the situation found by Oberle et al. (2016b), the peaks of Chl-a are undistinguishable when~~long as~~ two co-occurring mechanisms of transport generate t~~e~~hem ~~the~~ at similar ~~depth to which~~depths ~~the transports affect the sediment are comparable and both mechanisms co-occur, they may generate undistinguishable peaks in the depth distribution~~. Morys et al. (~~2016,~~ 2017) used a pairwise comparison of the fauna present and the occurrence of a peak within the same sediment core to convincingly argue for the animals causing that peak. The authors found positive correlations in 40-70% of the 22 investigated

360 profiles including locations in close proximity (Mecklenburg Bay) to both our field sites. This is compelling evidence for biogenic origin of peaks. While there is little direct proof of a cause-effect relation of biological peak generation in the literature, there is no doubt that some benthos does generate peaks by non-local transport mechanism (e.g. Blair et al., 1996). ~~The pattern of particle tracers generated by ground trawling, however, may depend on gear and sediment type. Nets are reported to mix surface sediments and reduce chl a content in the top centimeter (Tiano et al. 2019; Oberle et al. 2016b). Depestele et

365 al. (2019) working at a south-western Frisian Front site in the North Sea found that trawling may affect particle size distribution down to 2-4 cm depth. They also suggested that this trawling caused injection of finer particles into the sediment at about 4 cm depth, while winnowing the top surface sediment due to a combined mechanism of sediment removal (decapping) and mixing. The trawling gear used in their study is much larger than the gear used in ours. In our data there is no visible decapping effect in the net area, possibly because of the smaller size gear employed. Mixing may be the only correct approach in

370 biogeochemical modelling here in contrast to de Borger et al. (2021) who used a combination of erosion and mixing effect to infer consequences for carbon mineralisation and N-cycling modelling North Sea sites. Additionally the simulated and real impact profiles in net areas were indistinguishable from respective controls in our study. This implies that sediment mixing appears to be quasi random and similar in both cases. We thus conclude that these net impacts are not detectable in Chl a depth distributions.~~

375 ~~Our data indicate the mechanism of excavation and reversed deposition of Chl a containing particulate material. This mechanism is generating a peak similar to the biogenic peaks found by Morys et al. (2016, 2017) in close proximity to both our field sites (Mecklenburg Bay).~~ We suspect that the origin of peaks in a given area can only be inferred if ~~the~~ bioturbating organisms, ~~the~~ gear used and intensity of ~~fishing~~trawling are known.

380 **Implications** ~~Consequences~~

The most notable consequence of indistinguishable peaks is likely that bioturbation studies may be suspected to overestimate the biogenic reworking effect. We will argue below (Ways to ~~resolve) that~~resolve) that this is not the case in Fehmarn Belt,

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however, this issue ~~might needs~~ might need observation in other areas where trawling and bioturbation are prominent. ~~Increasingly studies employ bioturbation potentials, indices to capture the effects of bioturbating macrofauna in maps for instance in the discussion of ecosystem functions … (…, …). These indices are calculated from biomass, abundance and … numbers … for traits of benthic organisms.~~ If some peaks were indicating trawling and not non-local reworking, ~~the~~our concept of how the seafloor is reworked ~~term … in the corresponding calculations~~ might need reassessment.

Effects within the sediment may be visible when heavy gear is used. In the Fehmarn Belt area fishing gear is comparatively light. ~~And so on~~

We did not detect changes in Chl-a distribution in the net area as the simulated and real impact profiles in net areas were indistinguishable from respective controls in our study. Nets are reported to mix surface sediments and reduce Chl-a content in the top centimeter (Oberle et al., 2016b; Tiano et al., 2019~~; Oberle et al. 2016b~~). Depestele et al., (2019) working at a south-western Frisian Front site in the North Sea found that trawling may affect particle size distribution down to 2-4 cm depth. They also suggested that this trawling caused injection of finer particles into the sediment at about 4 cm depth, while winnowing the top surface sediment due to a combined mechanism of sediment removal (decapping) and mixing. While we cannot exclude similar winnowing or injection in our data, their role is likely small judging from the similarity to control depth profiles of Chl-a. Biological mixing of particles, reworking (Kristensen et al., 2012), and bioresuspension (Graf and Rosenberg, 1997) may generate the same profile in control sediment as seen in the net area. In our data there is no visible decapping effect in the net area, possibly because of the smaller size gear employed. Trawling gear referred to by Depestele et al. (2019) and used in the North Sea is in general much larger than the gear used in our study and in Fehmarn Belt. We thus conclude that the net impact is not detectable in our Chl-a depth distributions and mixing appears to be quasi random and similar to controls.

While otter boards may generate peaks and tracer profiles that resemble those of bioturbating fauna, the mechanisms of particle transport differ considerably and imply different consequences. Removing and overthrowing sediment as by scouring otter boards, ~~ ~~can burry animals, a process which does not usually happen during bioturbation. Particularly smaller surface-dwelling benthos (cumacea, ophiurids) and meiofauna may not be able to escape from a slap of sediment deposited above them. Larger burrowers like *A. islandica* have the ability to escape, depending on the height of deposits above the original sediment surface (Bromley 1996, Powilleit et al., 2009). Some fauna may be excavated from the sediment or damaged during board passage and become available for predators and scavengers. Reports on the shift of functional groups~~/~~ towards smaller size and possibly opportunistic fauna caused by bottom trawling support this (Sparks-McConkey and Watling, 2001; Hiddink et al., 2019). As demonstrated by Mestdagh et al. (2018), particle reworking, possibly as a consequence of an escape reaction, and bioirrigation may mitigate effects of trawling.

Reversal of the top sediment will also affect sediment biogeochemistry, since it changes chemical gradients close to the sediment-water interface completely. In the troughs decapping locally exposes anoxic sediments to oxygenated overlying water. While oxygen consumption was not measured, it conceivably may increase when the board exposes high concentrations of reduced dissolved substances in the furrow or when reactive organic matter such as chlorophyll is buried in the mound. It

may decrease, however, with less reactive sediment exposed in the furrow or with the reversed sediment slap forming the mound surface (Tiano et al., 2019, 2022). Van de Velde et al. (2018) simulated and measured complete homogenisation of a 15 cm surface layer due to mixing by trawling nets as well as dumping of a homogeneous 15 cm layer on top of an existing sediment. They found pronounced enhanced mineralisation dominated by anaerobic pathways and effects on manganese cycling as a consequence of both scenarios. Based on samples from the experiment we report here, Röser et al. (2022) suggest that the coupled Fe-Mn-P cycle reacts very sensitively, as expressed by altered porewater gradients, indicating Mn enrichment in the mound area and Mn loss in the furrow. A disruption of the steady-state biogeochemical distribution is apparent in both furrow and mound areas, although our setting differs considerably from more massive gear trawling impacts discussed for the North Sea (van de Velde et al., (2018; Tiano et al,. 2019) both in sediment height (~5 cm versus 15 cm) and mechanism (decapping/turnover versus mixing).

The present investigation cannot further explore organic carbon fate after such trawling impacts (Epstein et al., 2022) since we did not generate corresponding data. Transient redox reactions in the sediment initiated by trawling (Bradshaw et al., 2021; Morys et al., 2021; Tiano et al., 2019), however, may differ considerably from redox oscillating know to occur during bioturbation (Forster et al., 1996, Aller et al., 2014, Gilbert et al., 2016). Redox oscillations as they occur along burrows of infauna are considered a drivers for differences in chemical speciation, element cycling and priming processes associated with bacterial carbon cycling. Their occurrence is intrinsically linked to a spatial diffusion geometry associated with burrows and biogenic structures (Aller 1994). Since the physics and geometry of an otter board impact on the sea floor is vastly different, we anticipate that its effects on diageneses in fact differ substantially from bioturbation effects.

Another aspect relates to the differences in bottom areas impacted by trawling and bioturbation. An otter board affects a comparatively large area (50 cm wide and many meters long in our case), while bioturbation most often acts locally and affects the immediate surrounding. A special and particular case exists in assemblies of conveyor belt feeding fauna, such as Arenicola marina. As a population these bioturbations affect extended large areas of sediment (Volkenborn and Reise, 2006) despite local bioturbation effects (Gebhardt and Forster, 2018). …

In conclusion, we argue that we need to know if peaks indicate trawling or bioturbation, because their effects on biota and the way they affect geochemical processes differ substantially.

As one consequence, resuspension associated with bottom trawling impacts the ecosystem (Bradshaw, 2012). Effects within the sediment, as another consequence, may be visible when heavy gear is used. Oberle et al. (2016b) deciphered trawling effects on sediments off the Iberian west coast by combining lithological information, traces from recent oil pollution and highly resolved spatial information on bottom trawling. Without information as closely targeted as out sampling by scuba divers, the authors suggested five scenarios of impact. Scenario 2 is the one mirroring our turnover of surface sediment. The former sediment surface is buried and tracer appears at 18 cm rather than 6 cm, the usual mixing depth by animals and currents at the site. Here, the large difference in depth makes a differentiation between biogenic (shallow) and fishing boards (deep) possible. Oberle et al. (2016b) attribute mixing of sediments by trawl boards on the Iberian shelf to 35 cm sediment.

~~In the Fehmarn Belt area fishing gear is comparatively light. While peaks and tracer profiles look very much alike, their genesis implies different consequences. Removing and overthrowing sediment can burry animals, a process which does not usually happen during bioturbation. Particularly smaller surface dwelling benthos (cumacea, ophiurids) may not be able to escape from a slap of sediment deposited above them. Larger burrowers like *A. islandica* have the ability to escape, depending on the~~

455 ~~height of deposits above the original sediment surface (Bromley 1996, Powilleit and Kleine 2009).Some fauna may be excavated from the sediment or damaged during board passage and become available for predators and scavengers. Reports on the shift of functional groups/ towards smaller size and possibly opportunistic fauna caused by bottom trawling support this (Sparks McConkey and Watling, 2001; Hiddink et al. 2019).~~

~~Reversal of the top sediment may affect sediment biogeochemistry, since it changes chemical gradients completely close to~~

460 ~~the sediment water interface at the mounds. In the troughs decapping exposes anoxic sediments to oxygenated overlying water. Transient states of solute fluxes and r redox reactions in the sediment (Bradshaw et al. 2021; Morys et al. 2021; Tiano et al., 2019). On the other hand, bioturbation may also lead to non-steady-state situations (Aller 2014~~

Ways to resolve?

465 ~~Tracer peaks generated by non-local transport of particles appear differently depending on tracer half life. The slower a decay the longer peaks will persist. Thus, repeated events of transport produce peaks at different depth merging as new peaks emerge while the oldest still remain (^{210}Pb). We determined the half life of the chlorophyll as 50 d, effectively making peaks visible for about 1050 days. During this time peak concretions would drop to 25 % and start to fade into background noise.~~

~~Strictly speaking, local and non local are end-members of a continuum of transport steps from smaller to larger step sizes~~

470 ~~(Meysman et al., 2003; Schiffers et al., 2011). Following current understanding smaller and more frequent steps as described by the Einstein-Smoluchowski relation are the essential steps in diffusive mixing. These cannot be resolved with the course vertical resolution we apply, though methods exist to do so (Schiffers et al., 2011). Our comparatively large steps on the order of centimeters, with presumably longer resting times, should not be as frequent and, therefore, should be longer visible. This is where half life and step size together point to a certain persistence of peaks, particularly in shorter lived tracers.~~

475 In our Fehmarn Belt data set, we cannot assign a single peak with any certainty to biological or physical reworking. Can knowledge of the environment ~~and probability~~ help to resolve ~~the~~ this issue, since differences in peak generation likely indicate different effects in the ecosystem? ~~are unlikely to show up in tracer half life or tracer type? In our Fehmarn Belt data set, we cannot assign a single peak with any certainty to biological or physical reworking.~~ We may obtain some certainty about the origin of peaks~~arrive at a conclusion~~ by employing ~~some~~ generalized information on faunal abundance and behavior as well

480 as trawling intensity as outlined below.

Fehmarn Belt is amongst the areas with very high fishing intensity globally (Amoroso et al. 2018). The International Council for the Exploration of the Sea (ICES) assesses trawling effort as SAR$_{subsurface}$, swept area ratio below 2 cm sediment depth (v. Dorrien, pers. communication/2023 project report; ICES database: https://doi.org/10.17895/ ices.data.20310255.v3; Eigaard

et al., 2016) with 0.1 per quarter or 10% of an area ~~in~~within three months. This number relates strictly to mobile bottom-contacting gear and includes specific information regarding gear and vessel size, but lacks high spatial resolution. In order to relate this information to our data~~Here,~~ we averaged 4 areas (size: 5.6 x 3.2 km area, i.e. 17.9 km²) from April - June 2020 overlapping with the research area in Fehmarn Belt in which we sampled and detected peaks in June 2020. Although it is difficult to relate this information to the very nature of physical scouring effects and their spatial distribution on the seafloor, it is the best information available. With SAR$_{subsurface}$ we can imagine that otter boards affect below surface sediment in 10 % of the area within this quarter (April - June 2020). ~~We can equally imagine that the probability of an otter board generating a peak is 0.1 for every m^{-2} in three months or 0.4 m^{-2} yr^{-1} if homogeneously spaced.~~

~~Alternativ Text:~~ We can equally imagine this as a probability: otter boards potentially generate peaks in 0.1 m² on every m² within three months or 0.4 m^{-2} yr^{-1} if homogeneously spaced.

On the other hand, *A. islandica* are likely to move daily. Their abundance in Fehmarn Belt amounts to around 40 individuals m^{-2}. The animals ~~move during hypoxia induced burial, but otherwise~~usually stay close to the sediment surface because of their short siphon. They move the shells when gaping and closing in response to threat by demersal predators and food supply for filter-feeding. Ballesta-Artero et al. (2017) demonstrated that gaping activity in these bivalves changes seasonally with food supply, but shows a minimum of 1-2 gaping events per month during lowest activity in winter. The authors could not determine the frequency of gaping during high activity phases, but it is certainly higher. We assume that shell movement during gaping is a mechanism allowing surface material including C~~e~~hl-a pigments to slide along the shell into deeper sediment layers (anywhere to 4 cm depth, the size of Arctica-individuals). Forty individuals could produce at least 40 transport events per month or 480 m^{-2} yr^{-1}. The numbers calculated suggest 3 orders of magnitude higher frequencies for biogenic non-local transport (480 versus 0.4 m^{-2} yr^{-1}).

The spatial aspects of the particle transport events discussed above are particularly difficult to assess, since patchy occurrence of *A. islandica* and clustering of trawl tracks (Schönke et al., 2022) are frequent~~ly observed~~. Mound width and thus the area showing peaks generated by otter boards, likely depends on sediment type, steepness of the mounds and is additionally altered by the "bumpy" and discontinuous character of sediment deposition along the furrow (Morys et al., 2021). Despite this, with similar assumptions as above, and with more uncertainty we estimate that ~~Arctica~~ *islandica* rework sediment on 0.94 m² yr^{-1} (5 cm diameter circle around one animal, i.e. 19.6 cm² reworked multiplied by 480 m^{-2} = 0.94 m²). This is a larger area than the area disturbed by otter boards (0.1 m²). ~~The numbers calculated suggest 3 orders of magnitude higher frequencies for biogenic non-local transport (480 m^{-2} yr^{-1} versus 0.4 m^{-2} yr^{-1}).~~

Thus, w~~W~~e consider it conservatively safe to assume that the majority of peaks detected in Fehmarn Belt stem from *A. islandica* active on a daily scale. Bioturbation by *A. islandica* in Fehmarn Belt should thus ~~constitute~~be the more frequent ~~the dominant~~ particle reworking process ~~and outnumber the~~when compared to otter board sediment reworking. Therefore, we may continue to interpret chlorophyll peaks as bioturbation traces in this area. Researchers in other areas of the oceans impacted by bottom trawling may perform similar estimates of the likelihood of trawling and bioturbation traces as shown here, if information on trawling intensity and abundance of major bioturbating fauna is available.

While we feel confident to say that we generally look at bioturbation when we find peaks, this does not imply that the effects of bottom trawling in our area are not important or may be visible in other data. ~~(paper Rooze et al 2024).~~ The present result does not withstand impacts which we cannot measure using the particle tracer Chl-a, such as on fauna mortality, sediment resuspension or remobilization of reduced sediment components. Furthermore, we cannot elucidate with the present data the biological and biogeochemical effects associated. Particularly the spatial magnitude of both bioturbation and trawling need better quantification for such a comparison.

520 Future exclusion of fishery in the area will provide a test field in which the persistence of peaks may be tested and their origin

525 confirmed.

Data availability

Data are presently not available from a data repository, because it seems unnecessary for the review process or for the readers
530 to access depth profiles of chlorophyll. Figures 4 and 5 include the data necessary to validate the conclusions made in this manuscript. Data are available from the corresponding author. If necessary, however, we will supply the data in a repository with doi in due time.

Author contributions

All authors provided data and contributed to writing this manuscript. CR, JL and LP sampled and measured in the experiments,
535 MP and SF in the field data. SF and MP provided the concept and most of the figures, SF and MP wrote the manuscript.

Competing interests

The contact author has declared that none of the authors has any competing interests

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