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Short-term fate of seagrass and macroalgal detritus in *Arenicola marina* bioturbated sediments

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ABSTRACT: Seagrass meadows are globally important ecosystems for carbon (C) sequestration. However, bioturbation by benthic fauna can alter the distribution, degradation and overall preservation of C in the sediment. We performed a 4 wk laboratory experiment to investigate the short-term degradation and burial of 2 major C sources in bare sediments associated with seagrass ecosystems. Eelgrass *Zostera marina* and macroalgal (*Fucus vesiculosus*) detritus were amended in sediment with and without bioturbation by the common polychaete *Arenicola marina*. Bioturbation did not significantly affect the loss of eelgrass detritus (>0.5 mm), but caused a rapid burial of this material as a discrete layer (55% recovery) at sediment depths ranging from 8 to 14 cm. *A. marina* effects on macroalgal detritus were more pronounced, resulting, in total, in an 80% loss of macroalgal detritus by microbial degradation and worm ingestion. We conclude that *A. marina* bioturbation effectively buries eelgrass detritus into deep anoxic sediments, but we cannot confirm that this leads to enhanced C preservation in coastal ecosystems. In contrast, *A. marina* bioturbation significantly increases the degradation of macroalgal tissue, and it is unlikely that this detritus is a major source for permanent C burial.

KEY WORDS: Carbon degradation · Carbon burial · Lugworm · Bioturbation · *Zostera marina* · *Fucus vesiculosus*

1. INTRODUCTION

Coastal ecosystems including seagrass beds, saltmarshes, and mangrove forests are highly productive and sequester large amounts of organic carbon (C_{org}) in the sediment, serving an important role in the global carbon (C) cycle and climate change mitigation (Duarte et al. 2005, Fourqurean et al. 2012). Degradation and burial of C_{org} are key factors that control the storage of C in coastal ecosystems (Duarte et al. 2013). Aerobic microbial C_{org} degradation, which is constrained to the upper few mm of oxic sediment, is fast and efficient as it involves oxidised radicals with the ability to depolymerize relatively refractory organic molecules, such as lignin (Benner et al. 1984, Kristensen et al. 1995). Below the oxic sediment surface, microbial degradation is dominated by slower and less efficient anaerobic processes (Canfield 1994, Kristensen & Holmer 2001). Therefore, redox conditions and sediment burial have decisive implications on the degradation of C_{org}.

The C_{org} that is deposited in coastal seagrass ecosystems originates from various sources, including seagrass leaves, phytoplankton, macroalgae and terrestrial vegetation (Kennedy et al. 2010, Trevathan-Tackett et al. 2015). Seagrass detritus and vascular terrestrial plants rich in structural polymers (i.e. lignocellulose) are resistant to microbial degradation under anoxic conditions, and may persist in sediments (Trevathan-Tackett et al. 2015). Macroalgae (i.e. Fucales, Laminariales and Plocamiales) are other important primary producers in coastal ecosystems as they

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can contribute up to 50–75% of the stored C_{org} in eutrophic areas (Gacia et al. 2002, Kennedy et al. 2010, Hill et al. 2015, Krause-Jensen & Duarte 2016). Since macroalgal tissues are dominated by labile polysaccharides and lack structural polymers (i.e. lignin), they degrade at much higher rates compared with seagrass detritus (Kristensen 1994, Kristensen & Holmer 2001). Accordingly, seagrass detritus is usually a better source for long-term C_{org} burial than macroalgal detritus (Trevathan-Tackett et al. 2015).

Bioturbating benthic fauna are a natural component of coastal ecosystems. The role of bioturbation on sediment processes has long been recognised and is accepted as a key driving factor for biogeochemical processes in coastal and estuarine habitats (Wang et al. 2010, Kristensen et al. 2012). Large conveyer-belt feeding bioturbators, such as the polychaete *Arenicola marina* (hereafter referred to as '*Arenicola*'), are among the most common species occurring in sandy coastal temperate areas, such as intertidal flats, lagoons, semi-enclosed bays and fjords and often rapidly colonize empty spaces in the sediment inside or adjacent to eelgrass meadows (Philippart 1994, Valdemarsen et al. 2011, Govers et al. 2014). *Arenicola* is considered an ecosystem engineer due to its large capacity for both sediment particle-reworking and burrow ventilation (Kristensen et al. 2012). It significantly alters the sediment texture by selectively ingesting particles <1 mm and burying larger sizes down to ~10–40 cm depth, i.e. below the feeding funnel (Baumfalk 1979, Valdemarsen et al. 2011). Simultaneously, its intense burrow ventilation increases the oxygen availability in deep sediment layers, and inhibits anaerobic processes, such as sulphate reduction (Banta et al. 1999). However, few studies have reported in detail on how particle subduction and bioirrigation by *Arenicola* affect the fate of seagrass and macroalgal detritus recently buried at the sediment surface (Kristensen 2001).

In area-specific C budgets of coastal ecosystems, it is important that both bare and vegetated sediments are considered. Assessments for climate mitigation potential of marine environments are fundamentally based on the C_{org} content in the upper metre of the sediment, which is often extrapolated from 10–25 cm deep sediment cores (Fourqurean et al. 2012). This is the depth range potentially affected by *Arenicola* bioturbation. Therefore, it is critical to understand how *Arenicola* affects degradation and subduction of various C_{org} sources above and below its burial depth.

We investigated the effects of *Arenicola* bioturbation on the short-term fate of eelgrass *Zostera marina* and macroalgal (*Fucus vesiculosus*) detritus in sandy coastal sediments. This study had 2 goals: to examine the impact of *Arenicola* on (1) the degradation and (2) the burial of eelgrass and macroalgal detritus. We hypothesised that *Arenicola* bioturbation stimulates the degradation of macroalgal detritus to a higher extent than eelgrass detritus. Consequently, a higher fraction of eelgrass than macroalgal detritus would be buried deep into bioturbated sediments.

2. MATERIALS AND METHODS

2.1. Sediment and animal collection

Well-sorted sandy sediment with a median grain size of 210 µm and total 0.4% organic matter (loss on ignition) (Papaspyrou et al. 2007), and individuals of juvenile *Arenicola* were collected on separate days from Bregnør Bay in Odense Fjord, Denmark. The top-most sediment layer (~1 cm) was removed to ensure that highly labile benthic microalgae were excluded before sediment was sampled with a spade down to ~30 cm. Sediment was wet-sieved through a 0.5 mm mesh and homogenised on site. *Arenicola* juveniles were dug out of the sediment and recovered through careful sieving (1.0 mm mesh), and intact individuals were transferred to buckets for transport. In the laboratory, *Arenicola* individuals were acclimatized in Petri dishes containing seawater (salinity of 20) at 15°C for 36 h and then weighed. Only healthy juveniles of *Arenicola* (still active after the 36 h acclimation) were used in experiments.

2.2. Macrophyte collection

Eelgrass *Zostera marina* (hereafter referred to as '*Zostera*'), was collected at Enebærodde in the outer part of Odense Fjord, Denmark (Petersen et al. 2009). Green *Zostera* leaves were gathered from an eelgrass bed at approximately 1 m water depth and kept in seawater during transport back to the laboratory. Fronds of the brown alga *Fucus vesiculosus* (hereafter referred to as '*Fucus*') were harvested in the inner part of Odense Fjord. Leaves (*Zostera*) and fronds (*Fucus*) were gently cleaned of epiphytes, washed with distilled water and cut into ca. 15 mm long and 5 mm wide pieces. Subsequently, the macrophyte pieces were arranged into portions of 5 g wet weight (WW), each representing an experimental core as described below. Portions of mixed macrophyte detritus consisting of 2.5 g WW of each type were also prepared. Samples of the fresh macrophyte

material (both *Zostera* and *Fucus*) were stored initially for total C and nitrogen (N) analysis.

2.3. Characterisation of macrophyte detritus used for sediment amendment

Initial samples of *Zostera* and *Fucus* detritus (n = 5) were analysed for total C and N content, and wet weight to dry weight relationships (WW:DW). Approximately 2 g WW of each macrophyte was thoroughly washed in distilled water, blotted on paper tissue to remove excess water and weighed. Inorganic C from fouling animals, such as barnacles, bivalves and bryozoans, was not observed on the macrophyte samples. Samples were then dried at 60°C for 48 h and re-weighed to establish WW:DW. Dried and unacidified samples were ground using a clay mortar and pestle and analysed using a LECO TruSpec CN analyser.

2.4. Mesocosm experimental set-up

A 27 d laboratory experiment was set up to assess the effect of *Arenicola* bioturbation on the degradation and burial of *Zostera* and *Fucus* detritus in the sediment. A total of 8 experimental treatments with 3 replicates each were established, consisting of faunated (*Arenicola*) and defaunated (Control) sandy sediment cores, without enrichment (Non-amended) or enriched with eelgrass (*+Zostera*), macroalgae (*+Fucus*) or a mixture of eelgrass and macroalgal detritus (+Mix). Sediment cores were prepared by adding homogenised wet sediment into 24 acrylic (30 cm long, 8 cm inner diameter) core tubes, to a depth of 18 cm. Cores were left to compact overnight (approximately 16 h at 15°C). The following day, 60 g of the same homogenised wet sediment, corresponding to ~1 cm layer, was added to non-amended cores (n = 6). The three different batches of macrophyte detritus (5 g WW) were mixed with the wet homogenised sediment (60 g WW) and added to the remaining cores in a 1 cm thick layer to prepare the *+Zostera*, *+Fucus* and +Mix treatments. All cores were then left to settle for 4 h before an additional 3 cm layer of the wet homogenised sediment (180 g WW) was added on top, providing 22 cm of final sediment depth and the layer of macrophyte detritus located at 3–4 cm depth. This procedure prevented detritus loss by water currents and assured that all detritus in defaunated controls initially was buried in anoxic sediment. Each core was then topped up with seawater, and all 24 sediment cores were transferred to 4 seawater tanks (90 l capacity, salinity of 20) with water level 1 cm above the core rim. The cores were distributed in 4 tanks: 2 tanks with *Arenicola* cores and 2 tanks with defaunated cores. Each tank contained random, but not equal, core replicates from each of the 4 treatments. The cores with *Arenicola* were separated from defaunated cores to prevent migration of *Arenicola* to defaunated cores. Water was circulated below resuspension level using stirring magnets (1.5 cm long) fitted to the internal wall 2 cm below the upper rim of each core tube and driven by a central rotating external magnet (~60 rpm). Each tank held a total of 6 cores and was equipped with 2 air stones to aerate and mix the water. The set-up was kept at 15°C in the dark for the entire experimental period to restrict growth of benthic microalgae.

2.5. Flux measurements

Exchange of O_2, total CO_2 (TCO_2) and dissolved organic carbon (DOC) between the sediment and overlying water was determined by conducting flux incubations before (Day 0), and 1, 6, 13, 20, and 27 d after *Arenicola* was added to the sediment cores. Cores were left to compact for approximately 48 h before the first flux measurement was performed on Day 0. Right after the Day 0 flux measurements, 2 small-sized *Arenicola* individuals (0.28–0.56 g WW) were added to each faunated core (total of 0.6–0.7 g WW). The worms were allowed to construct burrows for 24 h before the second flux measurement was initiated on Day 1. During flux incubations, cores were sealed with gas-tight rubber bungs and water was mixed with continuous stirring as described in Section 2.4. Incubations were carried out for 2–3 h, and water O_2 concentration at the beginning and end of incubation was determined for individual cores using a fibreoptic O_2 dipping probe connected to a PreSens Microx 4 transmitter. Water samples were taken from each core using a 60 ml syringe connected to a silicon tube at the start and end of incubation to determine rates of O_2 uptake, TCO_2 production and DOC exchange. Start water samples were taken while the unsealed cores were submerged in the tanks. End water samples were taken after removing the cores from the tank one by one, opening the lid for O_2 measurement and subsequent water sampling, before placing the cores back to the tank. Subsamples for TCO_2 analysis were transferred to 3 ml gas-tight glass vials and preserved with saturated $HgCl_2$ (30 µl). Water

samples were stored in darkness at 4°C for <7 d and analysed for TCO_2 by flow injection (Hall & Aller 1992). Other subsamples for DOC analysis were transferred to 15 ml pre-combusted glass vials and stored at −20°C until analysis on a Shimadzu TOC-L total organic C analyser after acidification with 2 M HCl (pH <3) to remove TCO_2. The exchange of solutes between sediment and water was calculated as the difference between end and start concentrations assuming constant rates throughout incubations.

2.6. Sediment core slicing, worm recovery and macrophyte detritus extraction

Each sediment core was sliced on Day 27 of the mesocosm experiment. Individual cores were retrieved from the experimental set-up and sliced within 2 h. A water sample was collected before core slicing to establish overlying TCO_2, DOC and sulphate (SO_4^{2-}) concentrations in each of the 4 tanks. The remaining overlying water in the cores was syphoned off ca. 2 h after gently flattening conical faecal casts to ensure a distinct sediment surface before cores containing *Arenicola* were sliced. This procedure was done with minimal sediment resuspension. The accumulated faecal casts in cores containing *Arenicola* elevated the sediment surface by about 0.7 to 2.0 cm compared with the original surface. All sediment cores were then sliced by extruding and cutting the sediment elevation resulting from the faecal casts and the sediment in 1 cm intervals to 6 cm depth from the original surface, and in 2 cm intervals to 22 cm depth. Recovery of intact *Arenicola* was attempted, but most individuals were damaged due to the slicing procedure. Each slice was then gently homogenised with a metal spoon, and after manual recovery of all visible large pieces of macrophyte detritus, subsamples of every section were taken for porewater extraction (25 ml), as well as for evaluation of sediment characteristics (4 ml).

Two fractions of macrophyte detritus were recovered from the sediment at the end of the experiment: (1) large particulate organic carbon (POC, >0.5 mm) and (2) excess fine POC (<0.5 mm). This division was adopted since the recovered *Fucus* was broken into various sizes ranging from <0.5 to 15 mm, while *Zostera* detritus did not visually change in size (i.e. 15 mm). The remaining sediment from each slice and the subsample left after porewater extraction were sieved through a 0.5 mm mesh to assure that all large macrophyte fragments were collected. Together with the detritus recovered visually from subsamples, the detritus retained by the sieve was then washed in distilled water and dried at 60°C for 48 h for later POC >0.5 mm analysis, as described in Section 2.3. The material that passed the sieve was discarded. By assuming that the recovered detritus was homogeneously distributed in each slice, the recovered POC >0.5 mm was adjusted to the volume of full sediment slices by correcting for the sediment used for other purposes (i.e. sediment characteristics and porewater extraction). Any fine particulate fractions derived from macrophyte material (POC <0.5 mm) that was not accounted for in the sieving procedure was assessed using the total sediment C_{org} (= inherent C_{org} + POC <0.5 mm), analysed in separate non-sieved sediment subsamples free of large particles as described in the section below. The excess fine C_{org} representing POC <0.5 mm was calculated as the difference between the depth-integrated C_{org} in amended (+*Zostera*, +*Fucus* and +Mix) and non-amended cores (inherent C_{org}) in sediments with and without *Arenicola*.

2.7. Sediment characteristics

Sediment dry density, water content and porosity of each slice were determined by weighing 4 ml sediment free of visible detritus particles before and after drying at 60°C for 48 h. Dried subsamples (0.5 g each) were collected for C_{org} determination, ground with a mortar and pestle, acidified by fumigation and re-dried according to Komada et al. (2008). The dried sediment samples may have contained a few large particles that were not removed manually. This might underestimate the excess fine $C_{org,}$ (POC <0.5 mm) fraction in +*Fucus*, but should not affect the results in +*Zostera* treatments. The C_{org} content of each sediment sample was measured using a CN analyser as previously described, and converted to µmol cm^{-3} using the C molar mass and the sediment dry density (Lavery et al. 2013). Selected sediment intervals from non-amended and control treatments (0–2, 3–6, 8–10 and 18–20 cm; including sediment accumulated on top of the original surface −2 to 0 cm from cores containing *Arenicola*) were analysed for median grain size using a Malvern Mastersizer 3000 particle size analyser.

2.8. Porewater analysis

Porewater was extracted by centrifuging ca. 25 ml wet sediment subsamples in double centrifuge tubes

containing GF/C filters for 10 min at 500 × *g*. Subsamples of the extracted porewater were fixed with saturated $HgCl_2$ (1:100 v/v) and stored for TCO_2 analysis as described in Section 2.5. The remaining porewater was stored in glass vials at −20°C for DOC and SO_4^{2-} analyses. Porewater DOC concentrations were measured on a Shimadzu TOC-5000 analyser. SO_4^{2-} concentrations were analysed using ion chromatography and standardised against chloride concentrations as described by Martin & Banta (1992).

2.9. Determination of *Arenicola* metabolism

The contribution of *Arenicola* respiration to TCO_2 and O_2 flux was determined in a separate experiment. One *Arenicola* individual weighing 0.2–0.4 g WW was transferred to each of 5 replicate 50 ml Winkler bottles filled with O_2 saturated seawater. Water samples for O_2 and TCO_2 were taken (as described in Section 2.5) at the start and end of 2 h incubation. Incubation bottles were held in darkness at a constant temperature (15°C) and salinity (20) throughout the experiment. Samples were analysed for O_2 and TCO_2 as described in Section 2.5.

2.10. Statistical analysis

The impact of *Arenicola* on the degradation of *Zostera* and *Fucus* was tested with separate 2-way ANOVAs on total detritus recovery (depth integrated) and flux data (time integrated). The addition of *Arenicola* (control and cores containing *Arenicola*), and macrophyte detritus (*+Zostera*, *+Fucus*, +Mix and Non-amended) were used as fixed independent factors. Levene's test for homogeneity of variance was performed on data prior to analysis. When appropriate, Tukey's post hoc test was used to establish variables with a significantly different interaction. All tests were performed at a significance level of $\alpha = 0.05$, using IBM SPSS Statistics (Ver. 22).

3. RESULTS

3.1. Visual observations

Upward movement of sediment as a result of *Arenicola* subsurface feeding and surface defecation added an average of 1.2 ± 0.5 cm (mean ± SD) sediment on the surface of faunated cores. There was a clear appearance of light-coloured oxidised burrow walls in all *Arenicola* cores, and the faecal material on the sediment surface was oxidised. In non-amended cores, the oxidised sediment layer extended approximately 2–3 mm from the surface and was met by a dark-coloured sediment band of iron sulphides, indicating that sulphide produced by sulphate reduction in sediments below diffused upwards, reacting with iron (Preisler et al. 2007). Control cores and especially cores containing macrophyte detritus developed small white patches on the surface within the first week, indicative of sulphide-oxidising bacteria. These were largely absent in cores containing *Arenicola*. A 100% recovery of the added *Arenicola* individuals was attained by the end of the 27 d mesocosm experiment, although most of them were too damaged by the slicing procedure to provide reliable final biomass values.

3.2. C and N content of macrophyte detritus

Sediments amended with eelgrass (*+Zostera*) received 5.4 mol C m^{-2} of *Zostera* C (33.4 ± 1.0% C of DW leaf material) while those amended with macroalgae (*+Fucus*) initially received 5.3 mol C m^{-2} of *Fucus* C (41.4 ± 3.0% C of DW frond material), and those with mixed macrophyte material (+Mix) received 2.7 mol C m^{-2} of *Zostera* C and 2.6 mol C m^{-2} of *Fucus* C. Before the experiment, C:N ratios of the 2 macrophyte tissues were 30.6 ± 1.3 for eelgrass and 21.6 ± 1.5 for macroalgae.

3.3. Recovery of large macrophyte detritus (POC >0.5 mm)

All macrophyte detritus in defaunated sediments was recovered from 0–5 cm sediment depth (Fig. 1), which was around the depth where it was originally placed (3–4 cm), with only slight vertical displacement in either direction. Sediment reworking by *Arenicola* radically altered the distribution of detritus in all faunated cores. Most *Zostera* detritus was recovered 4–10 cm deeper than the deposition depth, which was 8–14 cm below the original surface, while *Fucus* detritus was evenly distributed throughout the bioturbated sediment from the faecal casts at the top and down to 14 cm. The same pattern was observed when the 2 types of macrophyte detritus were added as a mixture to sediment containing *Arenicola*. *Zostera* detritus appeared visually almost unaltered compared to the initial state. Larger pieces of *Fucus* (>5 mm) were only found in defaunated cores, while

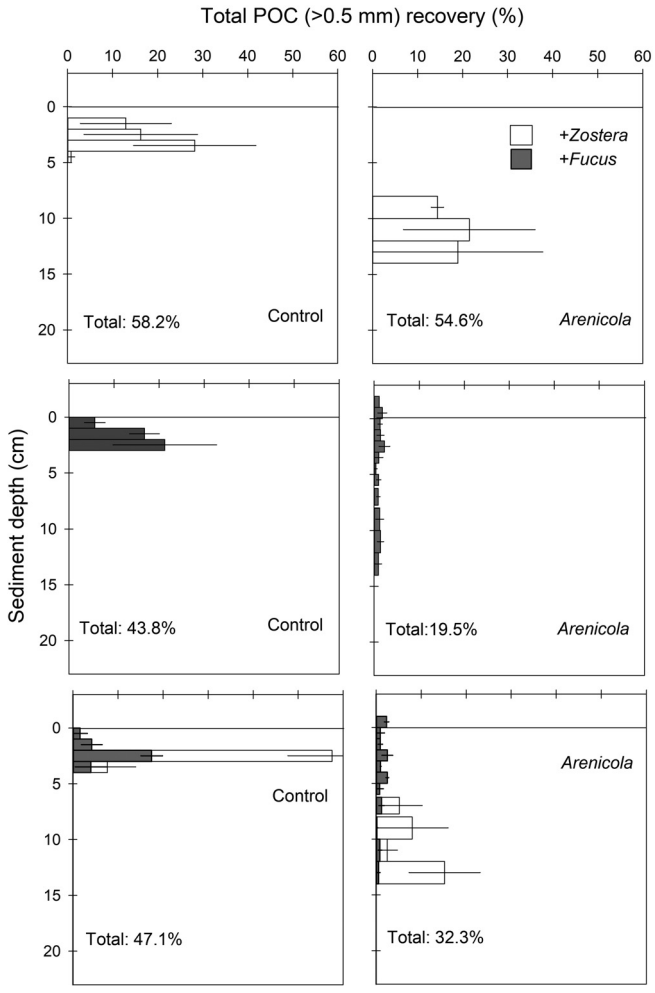

Fig. 1. Vertical profiles of large macrophyte detritus recovered (manually collected and retained on the sieve, particulate organic carbon [POC] >0.5 mm) in defaunated control and *Arenicola*-bioturbated sediment amended with eelgrass (+*Zostera*), macroalgae (+*Fucus*) and mixed (+Mix) macrophyte detritus. Recovered *Zostera* and *Fucus* material is represented by white and grey bars, respectively. The straight reference line (0 cm depth) indicates the original sediment surface depth. Initial position of macrophyte material was 3–4 cm depth. Error bars: SE (n = 3)

Fucus detritus was predominantly recovered as small particles (<5 mm) in cores containing *Arenicola*, suggesting maceration of *Fucus* detritus by the activities of *Arenicola*.

Overall, more *Zostera* detritus was recovered from the sediment than *Fucus* ($p < 0.001$; Fig. 1). Recovery of *Zostera* material was not significantly affected by the presence of either *Arenicola* ($p = 0.380$) or buried *Fucus* ($p = 0.672$). Recovery of *Fucus* was, however, significantly reduced by both the presence of buried *Zostera* ($p = 0.002$) and *Arenicola* ($p < 0.001$). In the presence of *Arenicola*, more than half (55%) of initially added *Zostera* detritus was found buried 8–14 cm into the sediment. Conversely, loss of *Fucus* (80%) was evident in sediment containing *Arenicola*. The total recovery varied from 47 to 32% in +Mix treatments without and with *Arenicola*, respectively. Of this, more *Zostera* (62–67%) and less *Fucus* (17–27%) detritus was recovered than in sediment containing only 1 type of detritus.

3.4. Sediment characteristics, C_{org} and excess fine C_{org} (POC <0.5 mm)

Dry sediment density varied from 1.36 to 1.54 g cm^{-3} and porosity ranged from 0.26 to 0.39 in all treatments. Control treatments had relatively homogeneous grain size distribution (median grain size 0.23–0.25 mm, Fig. 2) and silt+clay content (4.7–5.5%) at all depths. Treatments with *Arenicola* showed slightly lower grain size within the reworked sediment layer (0.20 mm from –2 to 10 cm depth) and 2-fold higher grain size (0.43 mm) in the 18–20 cm sediment depth zone. Accordingly, the silt+clay content in these treatments was highest in the top 0–2 cm layer (7.2%) followed by a gradual decrease below (from 6.2 to 1.5%) reaching the lowest level at 18–20 cm depth.

The sediment in all treatments had total C_{org} content varying from 0.1 to 0.3% of DW after removal of large macrophyte material. The treatment control +*Fucus* had higher levels of C_{org} (230–250 µmol C cm^{-3}) in the top 4 cm of the sediment, compared to all

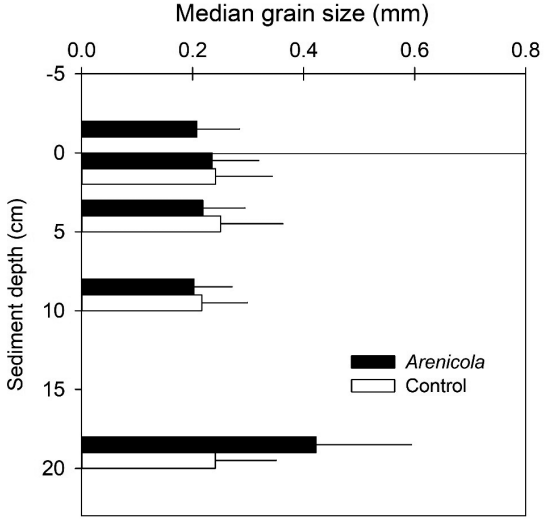

Fig. 2. Vertical profiles of median grain size (mm) of sediment collected from non-amended cores containing *Arenicola* and control sediment. The 0 cm depth line indicates the sediment–water interface. Error bars: SE (n =3)

layers below this depth (150–190 µmol C cm^{-3} C_{org}; Fig. 3). C_{org} within all other control treatments (non-amended and +*Zostera*) was relatively constant (150–180 µmol C cm^{-3}) at all sediment depths. Concentrations of C_{org} in all cores containing *Arenicola* were relatively high and variable (140–247 µmol C cm^{-3}) in the top 15 cm, but lower and less variable (80–130 µmol C cm^{-3}) in the bottom quarter (15–20 cm) of the sediment. Feeding activities by *Arenicola* therefore seemed to have transferred C_{org} in all cores from the bottom to the surface. In defaunated controls, the depth-integrated excess fine C_{org} (POC <0.5 mm) varied from 235 mmol m^{-2} in +*Zostera* to 2448 mmol m^{-2} in +*Fucus* treatments. In sediments with *Arenicola*, excess fine C_{org} was only found for +*Zostera* treatments (467 mmol m^{-2}).

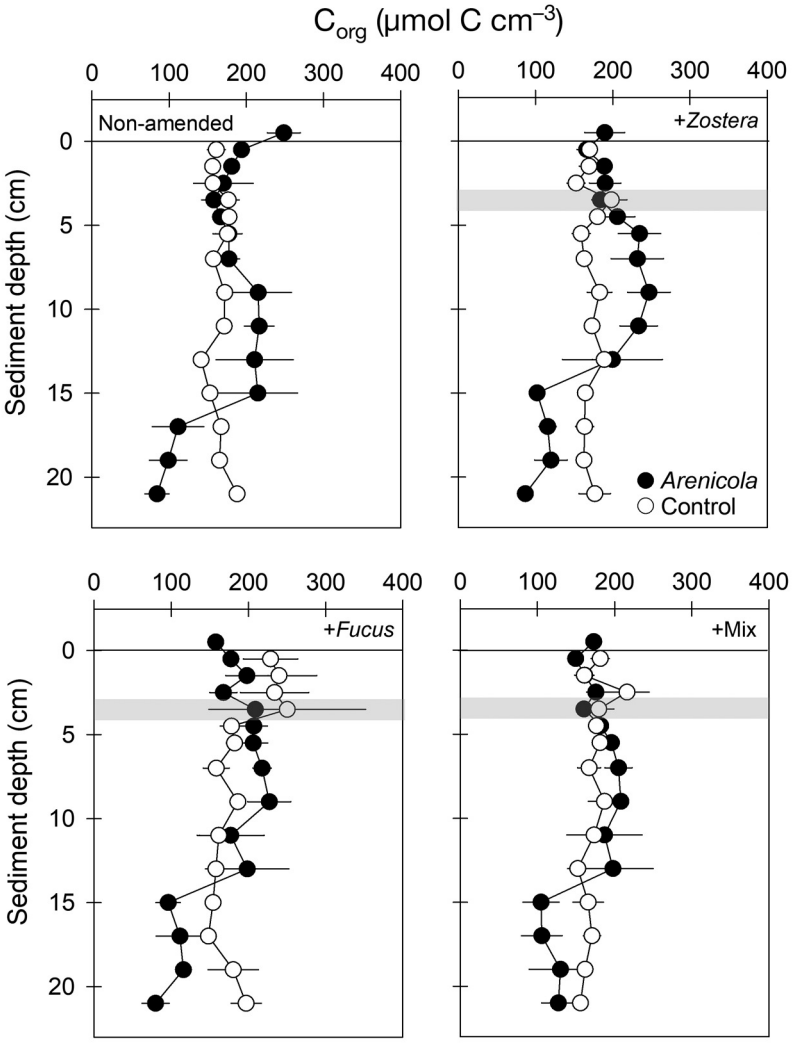

Fig. 3. Content of organic carbon (C_{org}) in sediments without enrichment (non-amended) and enriched with eelgrass (+*Zostera*), macroalgae (+*Fucus*) and mixed macrophyte material (+Mix) (= inherent C_{org} + particulate organic carbon [POC] <0.5 mm) after the removal of large macrophyte particles. The 2 curves in each graph show sediment cores with fauna (*Arenicola*; solid symbols) and without (Control; open symbols). The grey bar at 3–4 cm depth interval indicates the initial position of macrophyte enrichment. The solid horizontal line at 0 cm depth indicates the original sediment surface. Error bars: SE (n = 3)

3.5. Solute exchange

O_2 was consumed and TCO_2 released by all sediment cores (Fig. 4). O_2 uptake was almost identical initially (Day 0) at about 5–6 mmol m^{-2} d^{-1} in the non-amended and +*Zostera* treatments, while the +*Fucus* treatment showed 2- to 3-fold higher initial rates. *Arenicola* addition instantly increased the O_2 uptake by 4- to 10-fold in all treatments and more or less maintained those rates throughout the experiment. Therefore, the time-integrated O_2 uptake was significantly higher in all *Arenicola* treatments compared with defaunated controls ($p < 0.001$). In terms of macrophyte amendment, the O_2 uptake in *Arenicola* treatments was highest in +*Fucus* (54–68 mmol m^{-2} d^{-1}) followed by +Mix (44–59 mmol m^{-2} d^{-1}), non-amended (33–57 mmol m^{-2} d^{-1}) and +*Zostera* (33–44 mmol m^{-2} d^{-1}; $p < 0.001$).

Defaunated +*Fucus* treatments produced more TCO_2 initially (71 mmol m^{-2} d^{-1}) than all other sediments (1–12 mmol m^{-2} d^{-1}; Fig. 4). *Arenicola* bioturbation resulted in 5- to 30-fold increased TCO_2 release in all treatments immediately after the worms were introduced (Day 1). Subsequently, the TCO_2 release in treatments containing *Arenicola* decreased markedly throughout the experimental period, but remained significantly higher than in defaunated treatments ($p < 0.001$), except for amended treatments on the final date. TCO_2 release from sediment containing *Arenicola* was always higher when amended with *Fucus* (87–244 mmol m^{-2} d^{-1}) compared with +Mix (67–164 mmol m^{-2} d^{-1}), +*Zostera* (52–153 mmol m^{-2} d^{-1}) and non-amended treatments (51–239 mmol m^{-2} d^{-1}; $p < 0.001$).

DOC flux was variable throughout the experimental period, fluctuating in all treatments between release and uptake across the sediment–water interface (Fig. 4). DOC flux varied in all treatments between −17 and 60 mmol m^{-2} d^{-1}, with no clear trends over time.

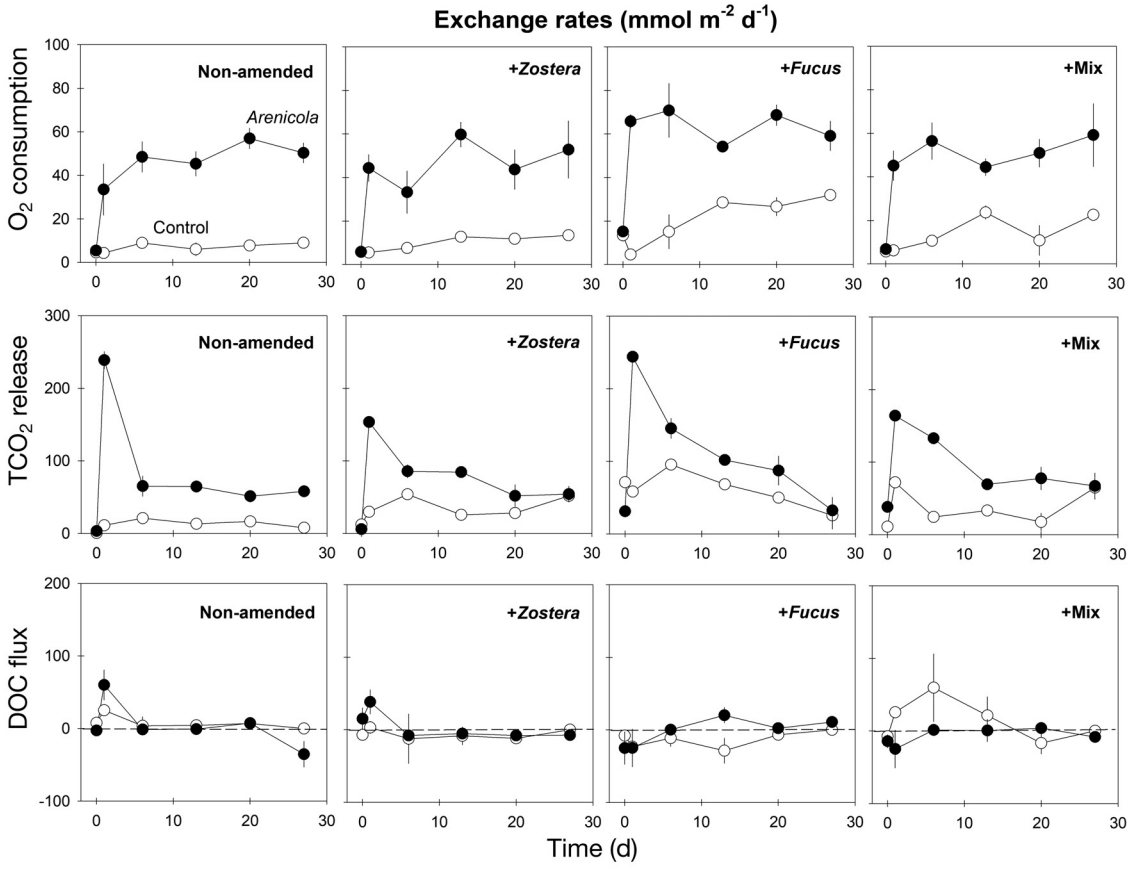

Fig. 4. Oxygen (O_2), total carbon dioxide (TCO_2) and dissolved organic carbon (DOC) exchange across the sediment–water interface over time (mmol m^{-2} d^{-1}) in sediments without enrichment (Non-amended), enriched with eelgrass (*+Zostera*), macroalgae (+ *Fucus*) and mixed macrophyte material (+Mix). The 2 curves in each graph show exchange rates in sediment with fauna (*Arenicola*; solid symbols) and without (Control; open symbols). Error bars: SE (n = 3)

3.6. Porewater profiles

Vertical distribution of porewater solutes was strongly influenced by the organic amendment and presence of *Arenicola* (Fig. 5). Defaunated sediment amended with macrophyte detritus displayed steep solute concentration gradients within the upper 10 cm of the sediment. TCO_2 in amended sediments increased from 3–9 mM near the sediment surface to 30–40 mM at 4–5 cm depth (highest in the *+Fucus* treatment) followed by constant or slightly decreasing levels below. DOC in amended sediments increased from 1–2 mM near the surface to 2–10 mM at 3–4 cm depth, followed by a rapid decrease to ~2 mM below. Highest DOC levels were recorded in the +*Fucus* treatment and lowest in the +*Zostera* treatment. SO_4^{2-} decreased from 10–15 mM near the sediment surface to 1–9 mM at 4 cm depth (lowest in the +Mix treatment) and returned almost to the surface level below 10 cm depth. Only TCO_2 changed markedly in defaunated sediment without macrophyte amendment, showing an increase with depth to ~20 mM. The flushing of porewater solutes by *Arenicola* ventilation straightened the profiles of any solute in all faunated treatments to such an extent that concentrations at any depth were not significantly different from that of the overlying water (Fig. 5).

3.7. *Arenicola* metabolism

Respiration by *Arenicola* resulted in a consumption of 60.6 ± 7.7 µmol O_2 g^{-1} d^{-1} and production of 90.0 ± 11.9 µmol TCO_2 g^{-1} d^{-1}. When extrapolated to the initial biomass (Table 1), *Arenicola* contributed with 7.8 ± 0.9 mmol m^{-2} d^{-1} to O_2 consumption and 11.5 ± 1.4 mmol m^{-2} d^{-1} to TCO_2 release. This represented 12–29% of the initial O_2 consumption and 5–8% of the initial TCO_2 release measured in faunated treat-

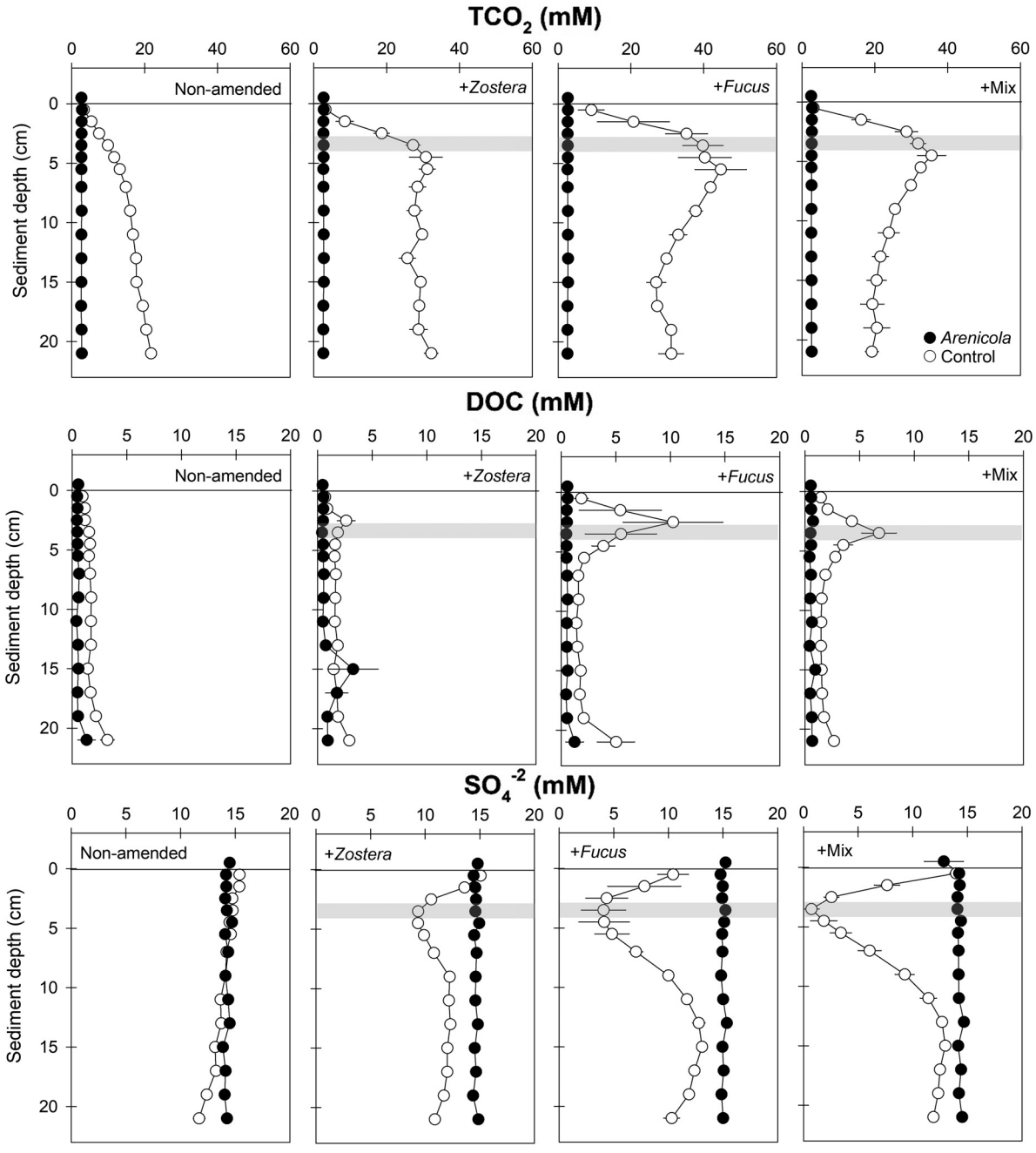

Fig. 5. Vertical porewater profiles of total carbon dioxide (TCO_2), dissolved organic carbon (DOC) and SO_4^{2-} in sediment cores without enrichment (non-amended), and with eelgrass (*+Zostera*), macroalgae (*+Fucus*) and mixed macrophyte material (+Mix). The 2 curves in each graph show profiles in sediment cores with fauna (*+Arenicola*; solid symbols) and without (Control; open symbols). The grey bar at 3–4 cm depth interval represents the initial burial depth of macrophyte material. The straight reference line (0 cm depth) represents the original sediment surface and values above it represent overlying water concentrations. Error bars: SE (n = 3)

ments. Due to lack of a final *Arenicola* biomass, it was assumed that these well-fed juveniles exhibited a 4% biomass growth during the experiment (De Wilde & Berghuis 1979). Final biomass was then estimated based on the initial biomass of intact individuals. Accordingly, the final contribution of *Arenicola* metabolism on Day 27 was 8.1 ± 1.0 mmol O_2 m^{-2} d^{-1} (14–30% of final O_2 consumption) and 12.0 ± 1.4 mmol TCO_2 m^{-2} d^{-1} (21–37% of final TCO_2 release).

Table 1. Initial and estimated final biomass of *Arenicola* in faunated treatments without (Non-amended) and with eelgrass (*+Zostera*), macroalgae (*+Fucus*) and mixed (+Mix) macrophyte detritus, and their calculated metabolic contributions to total carbon dioxide (TCO_2) and O_2 fluxes. Values represent mean ± SD (n = 5)

	Arenicola biomass (g m^{-2})		Contribution to O_2 (%)		Contribution to TCO_2 (%)	
	Initial	Final	Initial	Final	Initial	Final
Non-amended	132 ± 11	137 ± 12	29 ± 8	16 ± 1	5 ± 0	21 ± 2
+Zostera	124 ± 1	129 ± 1	18 ± 3	30 ± 15	8 ± 2	24 ± 5
+Fucus	131 ± 17	136 ± 17	12 ± 0	14 ± 1	5 ± 0	37 ± 20
+Mix	127 ± 2	132 ± 2	18 ± 2	15 ± 4	8 ± 2	21 ± 2

4. DISCUSSION

Seagrasses and macroalgae are recognised as important coastal C sinks contributing greatly to climate change mitigation (Mcleod et al. 2011, Fourqurean et al. 2012, Krause-Jensen & Duarte 2016). However, only a few studies have investigated the effects of bioturbation on the fate of detrital C in bare coastal sediments around seagrass ecosystems and macroalgal beds. In this study, we found that bioturbation by *Arenicola marina* affects the degradation and burial of 2 types of detritus differently. A large part of added *Zostera marina* detritus (55%) was buried almost intact in a distinct layer below 8 cm sediment depth, while within 4 wk, *Fucus vesiculosus* detritus was rapidly degraded by microbes or consumed and assimilated by the worms (80%). Both organic C sources typically constitute a large proportion of the C storage observed in sediments within and surrounding seagrass meadows (Gacia et al. 2002, Kennedy et al. 2010, Greiner et al. 2016). Therefore, the strong impact of bioturbators such as *Arenicola* must be considered when C burial and sequestration potential are investigated in coastal ecosystems.

4.1. *Arenicola* and the fate of *Zostera* and *Fucus* detritus

Arenicola is an upward conveyor feeder that is known to completely rework the top 6–40 cm of the sandy sediment it inhabits (Riisgaard & Banta 1998, Kristensen 2001, Valdemarsen et al. 2010). Accordingly, experimental sediment cores containing *Arenicola* are rapidly restructured due to the substantial sediment reworking. The strong grain size selectivity of *Arenicola* creates vertical stratification within the sediment (Baumfalk 1979, Wendelboe et al. 2013). It typically only ingests small particles < 0.5 mm (Andresen & Kristensen 2002) due to anatomical constraints of the mouth and pharynx. Larger particles such as coarse sand grains, gravel, shells and large organic debris are instead buried below the feeding depth, forming a graded bedding (Valdemarsen et al. 2011). The sorting capacity of *Arenicola* was also noticed in the present study, with 2-fold higher median grain size (0.43 mm) at 18–20 cm depth than in the upper 10 cm mixed layer (0.20 mm). This pattern was associated with a vertical stratification of silt+clay and C_{org}, exhibiting higher levels above than below 15 cm depth.

The physical reworking and active grain selection combined with intense bioirrigation by *Arenicola* affect the burial and subsequent degradation of *Zostera* and *Fucus* detritus differently. *Arenicola* is capable of efficient burial of *Zostera* detritus, as more than half of the deposited material at the end of our experiment was recovered in a discrete layer below 8–14 cm depth in the sediment. The mechanism of particle selection noticed for grain size and C_{org} can also explain the rapid burial of *Zostera* detritus, which apparently was not consumed by the worms but rather treated as large particles. This resulted in deposition of *Zostera* detritus at the base of the feeding funnel and thus burial below the bioturbation zone, as observed previously with plastic particles (Valdemarsen et al. 2011, Gebhardt & Forster 2018). In fact, the almost identical recovery in control cores suggests that *Zostera* detritus was buried fairly intact into the deep sediment, despite its exposure to the effects of bioirrigation in the experimental set-up. The burial of the lignocellulose fraction of seagrass tissues can therefore be markedly stimulated by *Arenicola* bioturbation (Godshalk & Wetzel 1978, Kristensen & Holmer 2001). However, we cannot confirm enhanced preservation of *Zostera* detritus by *Arenicola* in the deeper sediment zones observed here (8–14 cm) due to experimental constraints required for extended anoxic conditions such as time and sediment height.

The lower recovery of *Fucus* detritus and its homogeneous distribution within the bioturbated zone, on the other hand, was a consequence of microbial degradation, reworking and ingestion by *Arenicola*. It seems that tissue softening induced by degradation and combined with the extensive movement of sand grains by *Arenicola* resulted in maceration of the fragile *Fucus* detritus into smaller particles (Kristensen 1994, Lopes et al. 2011). The presence of *Fucus*

detritus in faecal casts in the −2 to 0 cm depth layer indicates that macroalgal detritus was ingested by the worms. The maceration, mixing and ingestion of labile *Fucus* detritus stimulated its degradation by increasing the relative surface area for microbial colonization and its exposure to oxic conditions (Aller 1994, Sun et al. 2002). This can explain the 30% higher degradation of *Fucus* detritus in bioturbated compared to defaunated treatments, which is comparable with previous studies reporting twice as fast degradation of *F. serratus* under oxic than anoxic sediment conditions (Kristensen & Mikkelsen 2003).

Arenicola individuals used in our experimental setup were small-sized juveniles (0.2–0.4 g WW ind.$^{-1}$) and added at a density of 400 ind. m^{-2} to simulate the typical juvenile abundance found in nature (Flach & Beukema 1994). Adult individuals with much higher biomass (4–10 g WW ind.$^{-1}$) are only found in abundances up to 80 ind. m^{-2} in coastal areas (Beukema & De Vlas 1979, Valdemarsen et al. 2011, Delefosse et al. 2012). Based on the initial and final burial depth of *Zostera* detritus, we roughly estimated that reworking rates in our cores were 1.4 cm^3 g^{-1} d^{-1}, which is lower than found previously for adult individuals (3–4 cm^3 g^{-1} d^{-1}, Valdemarsen et al. 2011). Reworking rates of *Arenicola* vary as a function of abundance and size of individuals, but environmental factors including temperature and food availability may also play a role. However, a model considering sediment reworking in relation to abundance and biomass indicates that a population consisting of many small individuals may have the same population burial effect as few larger individuals (Valdemarsen et al. 2011).

The losses of *Zostera* (42%) and *Fucus* (56%) detritus in defaunated treatments are probably caused by DOC leaching and by microbial excretion of exoenzymes and subsequent degradation and hydrolysis of labile components in the sediment (Kristensen 1994, Lopes et al. 2011). In fact, DOC production of the added detritus was clearly evident at the end of the experiment as elevated porewater DOC levels exactly where the macrophytes had been deposited. DOC was then probably consumed rapidly by the aerobic degradation processes near the sediment surface (Kristensen 2000). Otherwise, dominating anaerobic microbial processes were responsible for the degradation of both types of detritus in the absence of bioirrigation (Kristensen & Mikkelsen 2003). The significantly higher loss of *Fucus* than *Zostera* in the +Mix treatment suggests that addition of a reactive, labile source (*Fucus*) diverts microbial metabolism away from sources more resistant to degradation, such as refractory *Zostera* detritus (Canfield 1994, Zonneveld et al. 2010). This response is apparently the opposite of the microbial priming effect that has been observed in other studies (Kuzyakov et al. 2000, Thomson et al. 2019).

4.2. *Arenicola* and the transport and exchange fluxes of solutes

The drastically changed distribution of porewater solutes (TCO_2, SO_4^{2-} and DOC) in treatments with *Arenicola* indicates strong bioirrigation. The effect was distinct even in sediment immediately surrounding the *Zostera* and *Fucus* amended layer (0–5 cm), where accumulation (i.e. of TCO_2 and DOC) and depletion (i.e. of SO_4^{2-}) of solutes was substantial in defaunated sediment. Similar intense porewater flushing effect has been observed previously in sediments inhabited by *Arenicola* (Banta et al. 1999, Papaspyrou et al. 2007). The porewater transport caused by *Arenicola* ventilation was so powerful that solute concentrations in sediments containing *Arenicola* were completely uniform and comparable with overlying water levels. Thus, mineralisation products (TCO_2) generated within the sediment are quickly flushed to the overlying water by *Arenicola*, at the same time as electron acceptors, e.g. SO_4^{2-}, are replenished (Quintana et al. 2013).

The intense detritus burial and porewater transport in sediment influenced by *Arenicola* can explain the pattern of sediment–water TCO_2-effluxes. *Arenicola* induced high TCO_2 release in +*Fucus* treatments, which was initially more than 300% higher than the corresponding defaunated treatment, and decreased rapidly by about 50% (corrected for worm contribution) on Day 7 before reaching zero difference by the end of the experiment. The initial strong enhancement of microbial degradation was a consequence of high *Fucus* detritus lability (Kristensen 1994), combined with the intense particle reworking and bioirrigation. Thus, the *Fucus* detritus was exhausted much faster in the presence than absence of *Arenicola.* Although the rate of TCO_2 release observed initially in +*Zostera* and +Mix treatments with *Arenicola* was lower than in the +*Fucus* treatment, it was still more than 400% higher than the corresponding defaunated treatments. The worm stimulation in these treatments reached 100–200% on Day 14 before being reduced to zero at the end. Mechanisms other than changes in microbial stimulation contributed to the decline in this case. The rapid burial of *Zostera* detritus to deep sediment layers may have prevented aerobic microbial degradation, since TCO_2 release was reduced to levels of

defaunated treatments. In the non-amended treatment, the presence of *Arenicola* caused continuous high levels of inherent detritus degradation throughout the experiment as indicated by a steady 200–630% enhanced TCO_2 release compared to defaunated controls. A similar effect has been documented previously for *Arenicola* (Banta et al. 1999). The stimulatory effect of *Arenicola* is 2- to 4-fold higher than for other polychaetes, such as *Marenzelleria viridis* and *Nereis* (*Hediste*) *diversicolor*, in estuarine sandy sediments (Kristensen et al. 2014, Quintana et al. 2018). Therefore, the present results support the contention that *Arenicola* is an important ecosystem engineer when considering the processing of POC either by microbial degradation or burial in coastal sediments.

4.3. C budget

The loss of added particulate detritus (POC >0.5 mm) over the experimental period was considerable in all treatments, with lowest values for the +*Zostera* and highest for +*Fucus* treatments, and with the +Mix as intermediate (Table 2), which is comparable with the losses found in previous reports (Kristensen 1994). The presence of *Arenicola* enhanced the POC loss of *Fucus* detritus by 30%, while no difference in POC loss was evident between *Zostera* treatments and defaunated controls. The lost POC during degradation must be converted to DOC and TCO_2 (Kristensen 2000, Kristensen & Holmer 2001). The excess production of total dissolved C (TDC = DOC + TCO_2) in detritus-amended compared with non-amended treatments should therefore be consistent with POC loss and balance the C budget (Table 2). TDC production over the entire experiment was calculated as the sum of the TDC flux and TDC accumulated in the porewater (Table 2). The excess TDC production due to detritus addition can then be estimated by subtracting TDC generation in the non-amended treatments to deduct the degradation of inherent C_{org} (excess TDC = TDC in amended sediment − TDC in non-amended sediment). Unfortunately, excess TDC showed no clear pattern among treatments and with a deficit of C compared with the POC loss. The deficit (= POC loss [%] − excess TDC [%]) was most pronounced in *Arenicola* treatments, ranging from 30–48% of the initially added POC, while only 5–28% was missing in the defaunated treatments. The excess fine C_{org} (POC <0.5 mm, 235–2448 mmol m^{-2}) corresponding to the fine fraction of added detritus not captured by the sieving may partly explain this deficit. Other possible causes for the deficit include: (1) initial rapid pulses of TDC generated by *Arenicola* between incubations may not have been recorded within our time series; (2) assimilation and incorporation of detrital C into worm biomass was not measured due to worm damage during slicing; and (3) loss of fine particles due to water currents in the experimental set-up. Nevertheless, we can rely on the POC loss results and conclude that *Zostera* detritus is buried in anoxic sediment to a larger extent than *Fucus* detritus. The rapid burial of the *Zostera* detritus promoted by *Arenicola* to deeper sediments (i.e. 8–14 cm) may prevent resuspension and fast oxic degradation. Conversely, *Fucus* detritus is degraded rapidly in the presence of *Areni-*

Table 2. Carbon budgets (mmol m^{-2}) in control sediments, and sediments containing *Arenicola*, without (Non-amended) and with eelgrass (+*Zostera*), macroalgae (+*Fucus*) and mixed (+Mix) macrophyte detritus (particulate organic carbon [POC] >0.5 mm). Porewater accumulation (Δ PW) was calculated using depth-integrated total carbon dioxide (TCO_2) and dissolved organic carbon (DOC) concentrations at the beginning and end of the experiment. Time-integrated TCO_2 and DOC efflux were calculated as the sum of rates measured every week for a total of 27 d. *: negative fluxes indicate DOC consumption by the sediment; TDC: total dissolved carbon (sum of TCO_2 and DOC); na: non-applicable. Values represent mean ± SD (n = 3)

	Added POC (>0.5 mm)	Recovered POC (>0.5 mm)	POC loss	TCO_2 efflux	TCO_2 Δ PW	DOC efflux*	DOC Δ PW	TDC generation	POC loss (% of initial)	Excess TDC (% of initial)
Control										
Non-amended	na	na	na	408 ± 60	663 ± 18	−81 ± 120	37 ± 7	1027 ± 142	na	na
+*Zostera*	5411 ± 8	3162 ± 33	2249 ± 38	1142 ± 98	1337 ± 36	−51 ± 92	38 ± 4	2466 ± 198	42 ± 1	26 ± 4
+*Fucus*	5293 ± 20	2076 ± 242	3217 ± 258	1823 ± 133	1687 ± 100	384 ± 239	107 ± 31	4001 ± 442	61 ± 8	56 ± 8
+Mix	5326 ± 7	2507 ± 171	2819 ± 167	1147 ± 73	1164 ± 68	−17 ± 197	69 ± 6	2363 ± 165	53 ± 5	25 ± 3
Arenicola										
Non-amended	na	na	na	1992 ± 162	−127 ± 2	−175 ± 184	−38 ± 4	1652 ± 62	na	na
+*Zostera*	5426 ± 7	2974 ± 624	2452 ± 631	2347 ± 280	−131 ± 2	252 ± 89	−15 ± 14	2453 ± 310	45 ± 20	15 ± 6
+*Fucus*	5293 ± 20	1122 ± 82	4171 ± 78	3210 ± 307	−138 ± 3	287 ± 52	−39 ± 8	3320 ± 358	79 ± 3	32 ± 7
+Mix	5338 ± 3	1726 ± 335	3612 ± 334	2931 ± 173	−132 ± 6	151 ± 83	−38 ± 4	2912 ± 201	68 ± 11	24 ± 4

cola because of fragmentation within the bioturbation zone and lack of net burial.

4.4. Ecological implications

The results of this study have significant implications for the understanding of C cycling in bare and vegetated coastal ecosystems. It is demonstrated that bioturbating animals such as *Arenicola* may play a crucial role as they bury a large fraction of eelgrass detritus deep into the sediment, where it will likely be stored for long time. In this study, eelgrass detritus was buried to 8–14 cm depth by *Arenicola* juveniles, but it may travel even deeper down in areas with adult individuals having burrow depths up to 40 cm (Baumfalk 1979). Thus, the graded bedding effect of *Arenicola* feeding and reworking may contribute to C preservation by burial of *Zostera* detritus below the zone of porewater flushing. Macroalgal (i.e. *Fucus*) detritus, on the other hand, is rapidly lost though degradation, which is enhanced considerably by maceration through *Arenicola* activities. The fate of C_{org} in sediments is therefore highly source dependent and sensitive to the processing mechanisms induced by *Arenicola*, which confirms our hypothesis.

The well-studied estuary, Odense Fjord (Denmark), can provide evidence of the short-term impact of *Arenicola* bioturbation when extrapolated to the ecosystem scale (Petersen et al. 2009). The average *Zostera* biomass in the 62 km^2 fjord estimated based on 3% coverage is about 400 kg C yr^{-1} (Fyns Amt 2001, Carstensen et al. 2016). By assuming that 25% of eelgrass primary production is exported to bare sediments (Kennedy et al. 2010, Duarte & Krause-Jensen 2017), the results of our experiment indicate that *Arenicola* can bury 50 kg C yr^{-1} eelgrass detritus in the fjord. This burial rate is 25-fold higher than the annual C_{org} sequestration estimated for seagrass meadows in the area (Röhr et al. 2016), suggesting that bioturbation by selective deposit-feeders in unvegetated sediments may be important for the burial of C in coastal ecosystems. Other coastal processes such as sediment resuspension by winds and waves only mobilize material within the upper 2–3 cm sediment (Christiansen et al. 2006, Valdemarsen et al. 2010). Thus, if *Zostera* detritus is buried to depths below the bioturbated zone where conditions are fully anoxic, it is likely stored. Future studies evaluating sediment C storage associated with eelgrass beds should therefore account for the burial in bioturbated unvegetated sediments to achieve correct assessments of the C sink capacity of the entire coastal ecosystem.

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