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The interplay of temperature and algal enrichment intensifies bioturbation of the intertidal amphipod *Corophium volutator*

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ABSTRACT

Bioturbation is a central transport process for ecosystem functioning, especially in large soft sediment habitats like the Wadden Sea. The amphipod *C. volutator* is a dominant bioturbator in the Wadden Sea, due to its great abundance and almost continuous particle movement. Expedition or loss of its bioturbation activity could thus hold ramifications for ecosystem functioning within sediments, like carbon sequestration and nutrient recycling. Here we test the effect that temperature and organic enrichment have on the bioturbation of *C. volutator*; two prevalent abiotic factors in the Corophiid's habitat that have fluctuated over recent decades, and are expected to change in the future. In-situ experiments were conducted under 8 and 15 °C, with varying levels (0 g, 0.1 g, and 0.2 g) of powdered *Ulva compressa* enriching cores containing *C. volutator*. We found a significant interaction effect of temperature and organic enrichment on the bioturbation rate of the amphipod, with bioturbation only increasing with added organic enrichment at 15 °C. Further, a threshold within our experiments was also reached under 15 °C, where the amphipod ceased to expedite bioturbation under higher organic enrichment. This upper limit on this dominant bioturbation imposed with organic enrichment emphasizes the sensitivity of *C. volutator*. Our findings reveal bioturbation can be limited by temperature in colder months, and opposingly, limited by organic enrichment under warmer conditions. In future Wadden Sea scenarios where temperature is predicted to be warmer and winters milder, enhanced bioturbation activity by *C. volutator* could prove crucial in continued ecosystem functions.

1. Introduction

Bioturbation is a central ecosystem process that is shared amongst many species across aquatic and terrestrial environments. Principally, bioturbation is the reworking of sediment particles by fauna (Kristensen et al., 2012) and plays a pivotal role in marine soft sediment environments (Lohrer et al., 2004; Solan et al., 2008; Teal et al., 2008). Marine bioturbating fauna can rework sediments through activities such as feeding, as well as burrow creation and ventilation (Kristensen et al., 2012). The movement of sediment and water particles on account of faunal bioturbation can have profound influences on ecosystem processes. For example, bioturbation can stabilize or destabilize sediments (Ciutat et al., 2006; Graf and Rosenberg, 1997; Grant and Daborn, 1994), affect movement of microphytobenthos and cysts or resting stages (Giangrande et al., 2002; Reise, 2002), and enhance preservation and burial of organic matter in deeper sediment layers, increasing the amount of food available in the sediment (Braeckman et al., 2011; Zhang et al., 2019). Faunal ventilation activities also enhance sediment oxygenation (Forster et al., 1999; Forster and Graf, 1995), thereby promoting nutrient cycling when strong concentration gradients between sediments and porewater are encountered (Kristensen, 2000; Wenzhöfer and Glud, 2004), facilitating nutrient effluxes and stimulating remineralization rates (Braeckman et al., 2014; Wrede et al., 2017). In turn, ecosystem functions are supported, namely biogeochemical cycling, primary production and overall bentho-pelagic coupling (Biles et al., 2002; Kristensen et al., 2012; Lohrer et al., 2004). Due to this unique role of bioturbation in these biological, chemical, and physical processes at any sediment-water interface, bioturbators can be classed as ecosystem engineers (Meysman et al., 2006).

The expansive mudflats of the Wadden Sea, one of the largest marine

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intertidal soft-bottom environments in the world (Reise et al., 2010), are a prime example of where bioturbation is central to ecosystem functioning. The Wadden Sea has high benthic biodiversity (Reise et al., 2010; Reise et al., 1994), and bioturbation contributes to the renowned high productivity and bentho-pelagic coupling observed in the Wadden Sea mudflats (Asmus and Asmus, 1998; van Beusekom et al., 1999; Volkenborn et al., 2007b; Volkenborn et al., 2007a). Nevertheless, as the Wadden Sea is bordered by 3 heavily industrialized countries, it is also subject to many anthropogenic stressors (Lotze et al., 2005). These include, but are not limited to, rising sea temperatures (Beukema and Dekker, 2020a, 2020b), and eutrophication, causing the rise and proliferation of opportunistic algal species, such as *Ulva* (Kolbe et al., 1995; Reise and Siebert, 1994).

Within the last 50 years, the Wadden Sea has experienced an increase in monthly mean temperatures by around 2 °C (Beukema and Dekker, 2020b; Beukema and Dekker, 2020a; van Aken, 2008) and various models depict further rises (Schrum et al., 2016; and references therein). Additionally, increasing organic and nutrient loads can cause propagations of green algal blooms (Valiela et al., 1997), which were most prevalent in the Wadden Sea in the 1990's (Kolbe et al., 1995; Reise and Siebert, 1994; Schories et al., 1997). In selected sub-regions of the Wadden Sea 60% of the tidal flats were completely covered by algal mats made up of *Ulva* species (Kolbe et al., 1995). Despite some reduction and regulation of nutrient discharges since, all inner coastal waters of the German Bight, thus including the Wadden Sea, have recently been classed as a ‘problem area’, indicating substantial eutrophication effects (Brockmann et al., 2018), and *Ulva* is still noted across Wadden Sea areas (Geertz-Hansen et al., 1993; Kamermans et al., 1998; Rossi, 2006; Steinhagen et al., 2019b). Once algal detritus is buried into sediment it can cause disjunct distributions of small enriched patches (Kamermans et al., 1998), directly impacting the habitat of any infauna.

Corophium volutator (Pallas, 1766) is an infaunal amphipod crustacean inhabiting the intertidal Wadden Sea, where it can reach abundances of up to 100,000 m^2 (Flach, 1992). It is a crucial prey item for many species (Horn et al., 2020; Mccurdy et al., 2005), and builds U-shaped burrows 2–4 cm deep in the sediment, where it can switch between deposit and suspension feeding (Riisgård and Schotge, 2007). This amphipod utilises either its antennae to draw detritus from the sediment surface to the entrance burrow, or its pleopods to create a directed current of water, which is subsequently filtered with the gnathopods (Icely and Nott, 1985). The strong bioturbation activity with constant movement of small particles over short distances, qualifies *C. volutator* as a biodiffusor (Kristensen et al., 2012). The high densities of this tiny crustacean make it a pivotal component of the Wadden Sea ecosystem.

In light of the ongoing and predicted abiotic changes in the Wadden Sea, *C. volutator* and its dominant bioturbation will indubitably be affected. An optimum temperature for its bioturbation has not been elucidated, although *C. volutator* is known to prefer temperatures between 15 and 20 °C (Meadows and Ruagh, 1981). Additionally, the impacts of algal enrichment on its bioturbation are still largely unknown. Algae mats have detrimental effects on *Corophium* abundance (Bolam et al., 2000; Hull, 1987; Rossi, 2006), and filaments of algae have been suggested to interfere with the pleopods of *C. volutator* (Hellou et al., 2005; Raffaelli et al., 1991), yet *C. volutator* has shown a much more variable response to enrichment by reason of opportunistic algal species. Due to these conflicting responses (i.e., positive thermotaxis towards temperatures between 15 and 20 °C, thus probable comfortable bioturbation, against the excluding effects of *Ulva* mats), more experimental evidence is required to elucidate *C. volutators'* bioturbation response.

It has been demonstrated that other bioturbating species display varying sediment reworking responses to both temperature and organic enrichment. For example, the polychaete ragworm *Hediste diversicolor* (Müller, 1766) has demonstrated positive movement towards *Ulva* enriched patches (Godbold et al., 2011). Higher levels of sediment reworking and deeper bioturbation by *H. diversicolor* occurs in lower levels of algal enrichment (Murray et al., 2017), and foraging of *H. diversicolor* is also enhanced up until 23 °C (Lambert et al., 1992). Similarly, the spatangoid bioturbator *Echinocardium cordatum* (Pennant, 1777) has been shown to enhance benthic remineralization rates and sediment oxygen uptake in the presence of organic enrichment (Osinga et al., 1995); and another spatangoid bioturbator, *Brissopsis lyrifera* (Forbes, 1841), increased its burrowing at higher temperatures (Hollertz and Duchêne, 2001). Since *C. volutator* is such a dominant part of the mudflat community, these varying burrowing responses to organic enrichment and temperature could thus imply a change in functional composition under these changing parameters, and support the fact that empirical information is needed for understanding potential responses of *C. volutator* to both temperature and enrichment rises.

Accordingly, here we tested how bioturbation of *C. volutator* is influenced by the combined effects of temperature and algal enrichment - two main abiotic drivers in the Wadden Sea. Based on the temperature preference of *C. volutator*, and the noted exclusions from heavy algal mats, it is hypothesized that *C. volutator* will have lower bioturbation rates in the presence of *Ulva*, yet bioturbation will be stronger under higher temperature alone. As these two abiotic factors directly impact the Wadden Sea area *C. volutator* inhabits, findings here will hold direct implications for any ecosystem functions their bioturbation facilitates.

2. Materials and methods

2.1. Sediment and seawater preparation

Seawater for the experiment was collected from the German Bight near Helgoland. The seawater was filtered in a 5 μm polypropylene filter, and thermally pasteurized (PALUX Touch ‘n’ Steam Basic 611, PALUX AG, Bad Mergentheim; 99 °C 4 h). The treated seawater was stored in either an 8 or 15 °C climate chamber, to maintain temperature until its addition to sediment cores.

Surficial sediment (0.233 mm average mode grain size) was collected from a Wadden Sea site off Bremerhaven, Germany (53°32′18.1”N, 8°34′30.4″E) at low tide in May 2020. Sieving was preferred over other techniques to remove fauna, as it has the least effect on the sediment microbial community (Stocum and Plante, 2006). The sieved sediment (mesh size 500 μm) was then transported back to the climate chambers, where it was divided and stored in either an 8 or 15 °C climate chamber. A temperature of 8 °C was initially used as that was the mean temperature of the Wadden Sea waters during the May field sampling (Martens and van Beusekom, 2008); and was increased to 15 °C for the second temperature treatment as this temperature is the average temperature of the Wadden Sea for the warmer months from May until September (van Aken, 2008). Sediments were left standing for 24 h following collection to allow the sediment, including the fine fraction, to settle. Seawater was then decanted from the top of the sediment trays. Treated seawater (8 or 15 °C according to temperature treatment, 33 psu) was added into the sediment storage trays, and the sediment homogenised by stirring it thoroughly. After another 24 h allowing the sediment to settle again in the trays, the treated seawater was decanted. The prepared sediment was then distributed evenly across incubation cores (Plexiglas: 10 cm diameter, 30 cm height), to a height of 15 cm (± 1 cm). The incubation cores were filled with treated seawater, homogenised to a slurry, and once more left for 24 h to settle. The treated seawater was then siphoned off, to get rid of any nutrients that may have been released from the sediment in the set up, and then filled with the final addition of treated seawater (1 L, 8 or 15 °C, salinity of 33 psu).

2.2. Algae and animal preparation

Thalli of the green macroalga *Ulva compressa* (Linnaeus, 1753) were collected from an intertidal mudflat in List on the island of Sylt (55°01′08.2”N 8°26′22.5″E). The species classification of *U. compressa* was not genetically determined, as a large population of *U. compressa* is knowingly present at the collection site (Steinhagen et al., 2019a) and within the Wadden Sea there is strong interconnectivity between *Ulva* populations (Steinhagen et al., 2019a; Steinhagen et al., 2019b). The algae used in this study were thus assumed to be *U. compressa* (hereafter referred to as "*Ulva*"). The *Ulva* fronds were transferred overnight to Bremerhaven, rinsed in the treated seawater, dried out in an oven (50 °C for 5 h; (Beermann and Boos, 2015)), and then ground with a mortar and pestle. The crushed *Ulva* was subsequently sieved through a 500 μm sieve to ensure a standardized powder.

Adult specimens of *C. volutator*, measuring between 5 and 8 mm (Mills and Fish, 1980), were manually collected from the same site as the sediment, in the mid-intertidal zone of the shore, and distributed into small storage aquaria. Each aquarium was stocked with 50 individuals. The animal storage aquaria were kept in the same order of their collection for addition to the sediment cores. In the lab, the animals were divided evenly between the two respective temperature treatments, and transferred from the small storage aquaria immediately into the climate chambers, which were already at their elected temperatures. All *C. volutator* individuals were subsequently transferred into a large tray of treated seawater (at each respective temperature), where 33 individuals (4177 ind/m^2) were randomly chosen and placed into each incubation core. An aeration stone (Tetratec AS 40, 40 × 25 mm) was added into each core, to ensure proper oxygenation and also water circulation throughout the experiment, without causing resuspension.

2.3. *Experimental set-up*

Ulva powder was added to the cores under 3 treatment levels (0 g, 0.1 g, 0.2 g), with the highest treatment level (0.2 g) being equivalent to 126 g m^{-2} in the field (Dyson et al., 2007; Kolbe et al., 1995; Raffaelli, 2000). This maximum was chosen because preliminary experiments had demonstrated that additions above 0.25 g cause anoxia and mortality, which is also concurrent with other studies (Bulling et al., 2008; Raffaelli, 2000). Throughout the course of the experiment, the cores were carefully checked for any signs of anoxic conditions (e.g., formation of black patches, H_2S odour). Four replicates (cores) were conducted per treatment level under two different temperature scenarios (8 and 15 °C) resulting in the total number of 24 experimental cores (Fig. S2).

Animals were left to acclimate in cores for 24 h, before a homogenised suspension of luminophores (fluorescently dyed sand) were added (4 g pink colour, 60 μm, 4 g green colour, 80–250 μm; Partrac Ltd. UK) by pouring a small homogenate (15 mL) of seawater and luminophores in an even layer across the sediment surface. The experiment was then monitored for any signs of anoxia, and ran for 5 days under a 12 h light: 12 h darkness scheme.

Sediment reworking was measured on day 6 by sediment profile imaging (see below). While slicing sediment cores to retrieve luminophores has been previously utilised to reduce wall effects (Maire et al., 2008), it has also been experimentally shown that differences in bioturbation between both methods are insignificant (Wrede et al., 2019). Further, slicing lessens spatial accuracy of the bioturbation measure, and sediment profile imaging as used here was preferable for looking at overall patterns of sediment reworking (Wrede et al., 2019).

After the bioturbation measurements were complete, the sediment cores were sieved out through a 500 μm sieve, and mortality of the animals was counted. Thereafter, animals were stored in ethanol (70%), and the biomass (wet mass, dry mass, and ash free dry mass) was measured.

2.4. *Quantification of bioturbation*

Photos were taken using a blacklight (Phillips, TL-D 18 W BLB 1SL) to illuminate the core sediment columns and luminophores. Photos of each side of the core were taken from a set distance (Camera: Nikon D800; 50 mm, f 7.1, exposure 2.0 s, ISO 1000). All images taken were cut to the same size with the image analysis software Image J (1.52a) (https://imagej.nih.gov/ij/index.html). The overlying water column within the images was then manually coloured with a chosen uniform marking colour (RGB: 253, 003, 155) in the program Gimp (2.10.20) (https://www.gimp.org/). ImageJ recognized this coloured water column through a custom-made plugin, which furthermore removes the coloured water column and smooths the sediment surface (Fig. S1). This custom-made plugin created a co-ordinate system, with the sediment-water interface as an 'x axis', and the vertical sediment column the 'y axis'.

The illuminated luminophores within the images were then identified using the threshold function of ImageJ (Hue: 1–255, Saturation 80–250, Brightness 80–255), and the image was converted to black and white, with black pixels representing the luminophores (Fig. S1). Each black pixel was counted within a pixel row, and transformed into a profile of luminophore distribution and depth.

Through a non-linear regression analysis using the 1D diffusion model proposed by Crank (1975), the bioturbation rate (D_b) was calculated (performed using Graph Pad Prism 5, GraphPad Software Inc.). This model can be applied for conservative tracers such as the luminophores where no sedimentation occurs, represented in the following formula from Crank (1975):

$$C(x,t) = \frac{N}{\sqrt{\pi D_b t}}\, exp\left(\frac{-x^2}{4D_b t}\right)$$

where $C(x,t)$ is the normalized tracer concentration relative to the initial input, x depth, N is the initial luminophore input, t is time, and D_b the biodiffusion coefficient, which is a measure for the bioturbation rate (Crank, 1975; Maire et al., 2007). This model assumes that luminophores are spread in an even layer at the sediment water interface.

The initial luminophore concentration N was estimated from the thickness (cm) of the first layer of luminophore pixels from the luminophore profile data. N was equal to 0.4.

Using this model, D_b was estimated by a non-linear regression fitted to the vertical profile of the luminophores, using the sum of least squares.

Non-local particle transport was also calculated with a non-locality index (NLI), using the log-transformed luminophore tracer concentrations. This metric provides supplementary information regarding the type of sediment reworking behaviour that was conducted. The NLI gives more weight to lower particle concentrations, by incorporating uninterrupted faster downward particle transport (Fernandes et al., 2006), as opposed to solely random short diffusive particle movement. This metric complements the information gained from Crank's wholly diffusive model.

The NLI utilises the bioturbation rate of actual tracer concentration ($C(x,t)$), and the bioturbation rate from log-transformed tracer concentration ($\log(C(x,t))$) (Fernandes et al., 2006). The NLI is as follows:

$$NLI = \frac{\left|{D_b}^{log} - D_b\right|}{\sqrt{{D_b}^{log} \times D_b}}$$

If NLI = 0, the bioturbation rate of log-transformed tracer concentrations and the standard tracer concentrations are equal, demonstrating no non-local (non-diffusive) transport; for example, steady diffusive particle mixing. On the other hand, when the NLI > 0, non-local transport of particles has occurred, where particles have perhaps fallen directly into an animals' burrow.

The mean weighted luminophore burial depth (Lum_{mean}) was calculated by multiplying the luminophore burial depth (cm) by the luminophore concentration at each depth.

The maximum luminophore burial depth (Lum_{max}) was measured from the core images as the distance (cm) between the sediment surface and the deepest luminophore.

2.5. Statistical analysis

For each variable describing the sediment reworking, (D_b, Lum_{mean}, Lum_{max}, and NLI), and amphipod dry biomass, a 2-way ANOVA ($\alpha = 0.05$) was performed using the 'aov' function from the R Package 'stats' (R Core Team, 2020). 'Temperature' and the '*Ulva* enrichment level' were fixed factors, with factor levels set at either 8 or 15 °C for 'temperature', or 0 g, 0.1 g, or 0.2 g for '*Ulva* enrichment'. The best model was chosen based upon AIC, where the lowest AIC signifies the best model fit (Field et al., 2012). Before conducting the 2-way ANOVA, data was subject to a Shapiro-Wilk test to assess normality, and Levene's test to test for equal variances. D_b and Lum_{mean} data were subsequently log-transformed to achieve normality, and passed the afore-mentioned tests. Tukey's multiple comparison test was utilised for post-hoc analysis using the "emmeans" package (Lenth et al., 2020).

3. Results

Typical burrowing of *C. volutator* was apparent from small holes seen on the surface of the sediment and along the sediment-wall interface within all cores. Lighter coloured brown sediment was observed along the outside of burrows irrigated by *C. volutator*. Whilst there were no small black anoxic sediment patches observed in the 8 °C experimental cores, a few were observed under 15 °C. No dead specimens were found during the experiment, and there was no significant difference of amphipod dry biomass (g) between core treatments (Table S2).

The analysis of the amphipod's bioturbation rate revealed a significant interaction between temperature and organic enrichment (Table 1). The bioturbation rates were substantially higher in the 15 °C treatment and displayed a significant effect of organic enrichment; in fact, the median bioturbation rates for cores in 15 °C with 0.1 g and 0.2 g of *Ulva* enrichment were virtually identical, (55.33 and 53.29 cm^2yr^{-1}, respectively; $p = 0.9587$, Fig. 1), and clearly higher than in the treatment where no *Ulva* powder had been added ($p = 0.0011$, $p = 0.0002$, respectively). Contrastingly, no differences between organic enrichment within the 8 °C treatment could be detected (each $p > 0.05$).

Conversely, the non–local transport (NLI) carried out by *C. volutator* displayed no significant interaction between temperature and organic enrichment (Table 1), as well as no effect of organic enrichment (Table 1). Nevertheless, temperature again affected the animals' response (Table 1), with higher NLI values at 8 °C than at 15 °C (Fig. 1).

Table 1
Results of 2-way ANOVA on the measured bioturbation parameters under temperature and *Ulva* enrichment. Significant values ($p < 0.05$) are in bold.

Factors and interaction for each variable	df	Mean sq.	F	*p*
Bioturbation				
Temperature	1	2.1112	143.4415	**<0.0001**
Ulva enrichment	2	0.1916	13.0181	**0.0003**
Temperature x *Ulva* enrichment	2	0.1370	9.30991	**0.0017**
Residuals	18	0.0147		
Non local index				
Temperature	1	0.1947	43.857	**<0.0001**
Ulva enrichment	2	0.0003	0.0591	0.9428
Temperature x *Ulva* enrichment	2	0.0090	2.0321	0.1601
Residuals	18	0.0044		
Mean weighted luminophore burial depth				
Temperature	1	0.1961	24.7959	**<0.0001**
Ulva enrichment	2	0.0165	2.0917	0.1525
Temperature x *Ulva* enrichment	2	0.0302	3.8229	**0.0413**
Residuals	18	0.0079		
Maximum luminophore burial depth				
Temperature	1	3.5427	25.2928	**<0.0001**
Ulva enrichment	2	0.1234	0.8807	0.4316
Temperature x *Ulva* enrichment	2	0.3649	2.6052	0.1015
Residuals	18	0.1401		

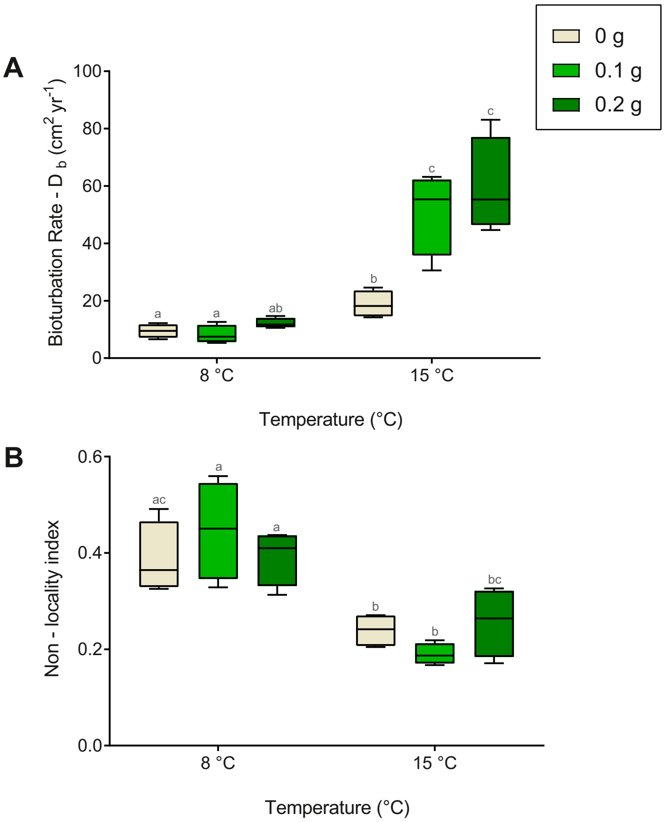

Fig. 1. Bioturbation rate (A) (cm^2yr^{-1}); (B) non-locality index of *C. volutator* under 8 and 15 °C climate chambers and differing levels of *Ulva* organic enrichment (legend). The boxes show the lower and upper quartiles, lines indicate the median, while the whiskers extend to the maximum and minimum values. Significant differences between groups due to temperature and enrichment effects are displayed by different letters above the boxplots ($p < 0.05$).

For the maximum luminophore burial depth, there was no significant interaction between temperature and organic enrichment (Table 1). Yet temperature alone had a significant effect (Table 1), with the maximum luminophore burial depth deeper within 15 °C. Within both temperature treatments, the burial response did not change across any level of organic enrichment (Table 1, Fig. 2).

There was a significant interaction between temperature and organic enrichment for the mean luminophore burial depth (Table 1). The mean luminophore burial depth conducted by *C. volutator* similarly reflected the bioturbation rates, with *C. volutator* in the 15 °C + *Ulva* treatments, burying slightly deeper than in other treatment combinations, however again, there was no acute difference between all organic enrichment levels within 15 °C (each $p > 0.05$, Fig. 2).

4. Discussion

Bioturbation rates measured here in this study at 15 °C are amongst some of the highest recorded for *C. volutator* at similar temperatures. Mermillod-Blondin et al. (2005, 2004), for instance, measured mixing rates of around 2.19 cm^2yr^{-1}, while de Backer et al. (2011) recorded bioturbation rates of around 1.46 cm^2yr^{-1} from much higher densities of *C. volutator*. Increased rates in this study likely have come from the full submersion of *C. volutator* for the entirety of the experiment, compared to the tidal regime used in de Backer et al. (2011), as the amphipod is inactive for up to 70% of emersion time (de Backer et al., 2010). Furthermore, the previous mentioned studies have measured *C. volutator* bioturbation by slicing sediment cores, as opposed to the sediment profile imaging technique used here. On the other hand, bioturbation rates of around 60 cm^2yr^{-1} for *C. volutator* measured by Wang et al.

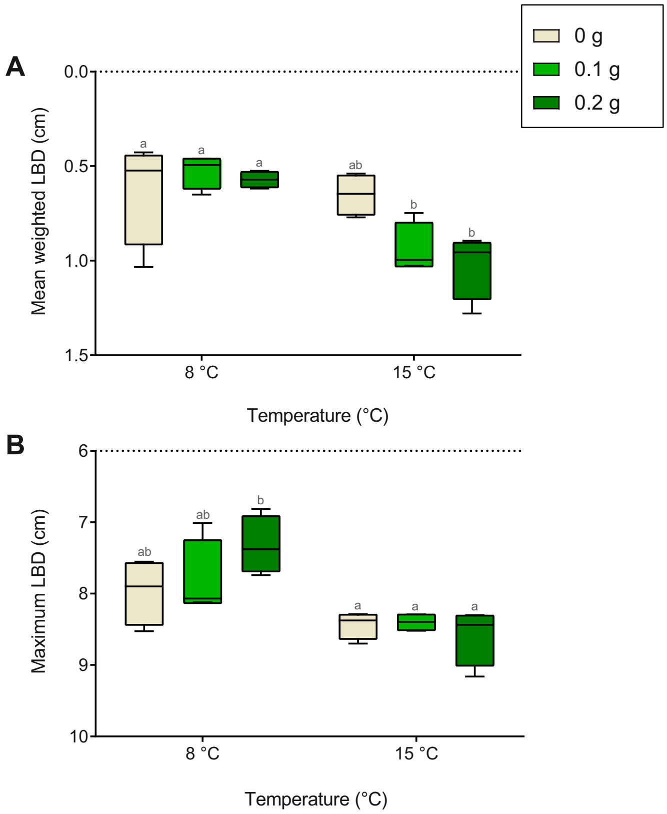

Fig. 2. Mean (A) and maximum (B) luminophore burial depths (LBD; cm) of *C. volutator* under 8 and 15 °C climate chambers and differing levels of *Ulva* organic enrichment (legend). Note the reversed scales, and dotted line representing a hypothetical sediment surface. The boxes show the lower and upper quartiles, lines indicate the median, while the whiskers extend to the maximum and minimum values. Significant differences between groups due to temperature and enrichment effects are displayed by different letters above the boxplots ($p < 0.05$).

(2022) at 20 °C, are in line with rates in this experiment. Wang et al. (2022) utilised similar densities and comparable sediment profile imaging, thereby supporting our findings. Thus, even though high bioturbation rates measured here nevertheless reflect the dominant bioturbation activity of *C. volutator*, disparate rates compared to other studies likely resulted from a combination of both differing bioturbation models used, and submersion for the duration of the experiment. Still, these disparities do not prevent interpretations of the relative differences amongst treatments within the limits of this experiment, which is focused on the interaction between both temperature and algal enrichment. Additionally, *C. volutator* conducts strong diffusive transport (de Backer et al., 2010; Meadows and Reid, 1966), and is consequently very well suited to the classic diffusional model used in this experiment. Cranks' model emphasizes larger luminophore concentrations at the sediment surface (Fernandes et al., 2006) thus fits the concentration data closer to the surface the best. Hence, it is suited for species sediment reworking at the sediment-water interface (< 5 cm), such as *C. volutator*.

For this reason, the observed increase in non-local particle transport observed at 8 °C is likely only a result of bioturbation by *C. volutator* not reaching its true diffusive state, as postulated in Crank's model (Crank, 1975), rather than the *Corophium* actually moving particles in a fast uninterrupted linear way. This increase in NLI under 8 °C could have arisen from weaker bioturbation under 8 °C compared to the 15 °C, resulting in the NLI index picking up higher levels of direct particle transport. This could occur, for example, when a luminophore tracer would fall from the sediment surface straight to the bottom of a burrow, instead of an isotropic random manner (Fernandes et al., 2006). Furthermore, minimal or non-existent non-local transport by *C. volutator* has also been reported in previous studies (Mermillod-Blondin et al., 2005; Mermillod-Blondin et al., 2004).

The lower bioturbation conducted by *C. volutator* under 8 °C follows expectations. Lower temperatures correspond with lower bioturbation rates across many bioturbating species (Berkenbusch and Rowden, 1999; Gimazane, 1972; Maire et al., 2007; Ouellette et al., 2004; Przeslawski et al., 2009; Retraubun et al., 1996; White et al., 1987). This is in line with the fact that invertebrates can curtail activity to reduce metabolic demands and their energy needs (Clarke and Fraser, 2004; Gillooly et al., 2001), while metabolic rates and respiration increase exponentially with temperature (Gillooly et al., 2001; Kleiber, 1932). Temperatures between 15 and 20 °C have already been shown to enhance activity of *C. volutator* (Meadows and Ruagh, 1981). Considering the bioturbation conducted by *C. volutator* is a direct result of its burrowing and feeding activities (Limia and Raffaelli, 1997; Meadows and Reid, 1966), it could be expected that their bioturbation rates here probably rose concomitantly with the increase in burrowing and feeding at this optimum temperature.

Additionally, algal enrichment led to a clear increase in the bioturbation rate of *Corophium* only at the higher temperature. Veritably, warmer temperatures leading up to, during, and following summer, such as 15 °C, have been shown to exacerbate the degradation of organic algal material (Conover et al., 2016; Hanisak, 1993; Paalme et al., 2002). This can create lethal anoxic patches which outright exclude the amphipod (Neira and Rackemann, 1996; Raffaelli, 2000), or opposingly, could provide important food resources for infauna (Kihslinger and Woodin, 2000; Rossi and Underwood, 2002). While a number of small black anoxic patches were observed in sediment cores under 15 °C, the latter theory of algal enrichment acting as a food resource is supported by our data. Our results clearly indicate enhanced sediment movement via antennae and gnathopods once *Ulva* was added. Although bioturbation can result from burrow building activities, this stark increase suggests that *Ulva* addition, or even decomposition, can stimulate grazing in *C. volutator*, within their comfortable temperature range. Thus, it could be speculated that the interaction of elevated temperature and algal enrichment possibly enhanced the amphipods bioturbation rate through a strong increase in foraging.

The noted increase in bioturbation from the interaction of algal enrichment and temperature at 15 °C was only apparent between cores that had either been enriched, or not. Typically, *C. volutator* feeds almost continuously (Icely and Nott, 1985; Møller and Riisgård, 2006; Riisgård and Schotge, 2007), with a gut clearance time of 0.06–0.4 h (Icely and Nott, 1985). Higher algal enrichment levels would therefore facilitate even more bioturbation. However, the enrichment levels of our experiment already seemed to have reached limiting concentrations for *C. volutator*. This meant that the *Ulva* added was either at, or above, a concentration at which ingestion rates are physiologically and mechanically repressed (Lehman, 1976), highlighting a short stretch that *Ulva* could act as a food source. Furthermore, *Ulva* concentrations above 0.25 g caused anoxia and mortality for *C. volutator* after 3 days in preliminary experiments. Thus, while the interaction of algal enrichment and temperature initially expedited the bioturbation rate, the algal enrichment essentially further acted as an upper limit to bioturbation of *C. volutator* within the bounds of our experiment. The sensitivity of *C. volutator* has been previously observed as per densities and colonisation levels (Ford et al., 1999; Hull, 1987; Rossi, 2006), and the observed stagnation of bioturbation in higher levels of enrichment here emphasize the narrow activity range of *C. volutator*. Now, this observed sensitivity can also be extended to its bioturbation activity.

Indeed, many amphipods are known to consume *Ulva* spp. (Crawley and Hyndes, 2007; Geertz-Hansen et al., 1993; Kamermans et al., 2002; Martin, 1966), especially due to *Ulva*'s palatability and limited chemical defences (Goecker and Kåll, 2003; Hay and Fenical, 1988). In its natural habitat, *C. volutator* imposes strong grazing pressures on benthic diatom populations (Gerdol and Hughes, 1994; Hagerthey et al., 2002), and consumes bacteria, flocks, and organic detritus on sediment grains (Murdoch et al., 1986). *Ulva* mats, in turn, have been shown to exclude *C. volutator* (Hull, 1987; Raffaelli, 2000). This has been attributed to the filamentous structure of many *Ulva* spp. interfering with the movement of the amphipod's pleopods (Raffaelli et al., 1991), which thus significantly hinders its bioturbation ability. Despite this known sensitivity, *C. volutator* evidently bioturbated amongst the algal enrichment in our experiment. Therefore, besides physical interference by filamentous blades, once broken down, our results show their bioturbation and hypothesized feeding can be bolstered in a similar way to other bioturbating species. As for some other bioturbator examples, the polychaete *Hediste diversicolor* (Müller, 1776) increased its bioturbation at moderate levels of *Ulva* enrichment (which would be equivalent to using 0.6 g in this experiment considering aquaria size; (Murray et al., 2017)). Correspondingly, both *H. diversicolor* and *Peringia ulvae* (Pennant, 1777) have also demonstrated positive movement towards *Ulva* enriched patches (Godbold et al., 2011).

Amplified bioturbation from the interaction of temperature and algal enrichment holds larger ramifications for bioturbation activity in the Wadden Sea. During the winter months, temperatures can certainly fall to 8 °C and below (Reuter et al., 2009; van Aken, 2008). Even if there is sufficient organic material for *Corophium* to graze upon during colder periods, our results suggest that they will likely not elevate their bioturbation. Notwithstanding, average sea surface temperatures in the Wadden Sea have risen over the past decades, which can mainly be attributed to milder winters (Beukema and Dekker, 2020a; Reuter et al., 2009; Wiltshire et al., 2010). During these warmer periods, temperature alongside algal enrichment would cause *C. volutator* to expedite its bioturbation activity and algal enrichment could become an increasingly important food source. There is a fine line, however, between conducive effects of algal enrichment to bioturbation, and limiting effects with ensuing reducing conditions. Nevertheless, increases in bioturbation from foraging or burrowing activities could aid in mitigating negative effects observed from increased enrichment observed on the coast. Faunal grazing pressure can for instance, match or supersede algal growth rate (Andersson et al., 2009; Geertz-Hansen et al., 1993), and laboratory experiments involving the gammarid amphipod *Gammarus locusta* (Linneaus, 1758) have demonstrated the potential of amphipods to halt destructive algal blooms (Andersson et al., 2009). Moreover, the large abundance of *C. volutator*, and consequent large bioturbation coverage over Wadden Sea mudflats, underlines the amphipods' huge potential to oxidize great surface areas of sediment, thereby facilitating aerobic reactions. This ability has been observed in other microcosm experiments with amphipod crustaceans, such as *Monoporeia affinis* (Lindström, 1855) increasing oxidation of surface sediment layers, and denitrification-nitrification coupling (Tuominen et al., 1999). The key here for *C. volutator* is its' density, as it has been experimentally demonstrated that only high densities play a large role in particle transport and thus organic matter processing (de Backer et al., 2011). Thus, together with ubiquitous abundance, higher bioturbation rates, and ability to maintain oxic surface sediments, *C. volutator* may then be able to repress eutrophication effects in upcoming warmer temperatures in the Wadden Sea. However, even though we demonstrated that *C. volutator* can indeed bioturbate amongst algal enrichment, there was a threshold observed under 0.2 g *Ulva* enrichment levels where negative effects of algal enrichment could commence and bioturbation cease to aid in mitigating possible eutrophic effects.

Moreover, higher bioturbation rates due to higher temperatures and greater availability of organic matter could provide more consumable carbon deeper into the sediment, while simultaneously reducing the penetration depth of oxidants like oxygen and nitrate (Wallenius et al., 2021). In turn, sulfate reduction activity and methanogensis are fostered (Borges et al., 2016). The observation of black spots of iron sulphide precipitate in the 15 °C core treatments support this deduction.

That being the case, the functional response of *C. volutator*'s bioturbation could be further elucidated using finer increments of algae and higher increments of temperature in further investigations. Additionally, these experiments could be conducted in mesocosm or field environments where phenomena such as tides are present, in order to mirror the natural environment more closely. Given the predicted temperature rises in the Wadden Sea, and documented relationship between temperature and decomposition rates, the upper limit to *C. volutator*'s bioturbation posed by algal enrichment should also act as incentive to continue to work towards dropping and monitoring the ongoing enrichment of coastal areas.

Author contributions

EF, AW, and JB conceived and designed the experiment. EF performed the experiment and analysed the data. EF wrote the original paper with contributions from all co-authors, and all approved the submitted version.

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Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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