



# Low-frequency noise pollution impairs burrowing activities of marine benthic invertebrates<sup>☆</sup>

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## ABSTRACT

Sounds from human activities such as shipping and seismic surveys have been progressively invading natural soundscapes and pervading oceanic ambient sounds for decades. Benthic invertebrates are important ecosystem engineers that continually rework the sediment they live in. Here, we tested how low-frequency noise (LFN), a significant component of noise pollution, affects the sediment reworking activities of selected macrobenthic invertebrates. In a controlled laboratory setup, the effects of acute LFN exposure on the behavior of three abundant bioturbators on the North Atlantic coasts were explored for the first time by tracking their sediment reworking and bioirrigation activities in noisy and control environments via luminophore and sodium bromide (NaBr) tracers, respectively. The amphipod crustacean *Corophium volutator* was negatively affected by LFN, exhibiting lower bioturbation rates and shallower luminophore burial depths compared to controls. The effect of LFN on the polychaete *Arenicola marina* and the bivalve *Limecola balthica* remained inconclusive, although *A. marina* displayed greater variability in bioirrigation rates when exposed to LFN. Furthermore, a potential stress response was observed in *L. balthica* that could reduce bioturbation potential. Benthic macroinvertebrates may be in jeopardy along with the crucial ecosystem-maintaining services they provide. More research is urgently needed to understand, predict, and manage the impacts of anthropogenic noise pollution on marine fauna and their associated ecosystems.

## 1. Introduction

Countless marine animals rely on sound to survive, e.g. to detect predators, echolocation, navigation and communication with conspecifics (Leis et al., 2011; Montgomery et al., 2006; Slabbekoorn, 2010; Staaterman et al., 2010; Tolimieri et al., 2000). In recent decades, however, anthropogenic low-frequency noise has invaded natural soundscapes, pervading oceanic ambient sounds and potentially disrupting the biotic interactions. Low frequency noises (LFN) are sound waves with a frequency between 10 and 500 Hz (Carey and Evans, 2011). These sounds are emitted by many different sources, a major one of which being cargo ships. As marine traffic continues to grow, the LFN emitted by these large shipping vessels has become nearly ubiquitous throughout the world oceans. Offshore wind power is another major

contributor of LFN, which is also on the rise. Despite how much LFN is being emitted by anthropogenic activities, little is known about how this noise affects most groups of marine organisms.

Low frequency noise has been shown to modify call behavior (Foot et al., 2004; Lesage et al., 1999; Scheifele et al., 2005) and to decrease feeding efficiency (Soto et al., 2006) in marine mammals. Whales also actively avoid LFN, and as a result have been displaced from key feeding and breeding grounds (Jones et al., 1994; McCauley et al., 2003a; Stone and Tasker, 2006). In fish, impairment of hearing (McCauley et al., 2003b; Popper et al., 2005), startle and alarm responses (Fewtrell and McCauley, 2012; Pearson et al., 1992), and altered swim depths (Chapman and Hawkins, 1969; Fewtrell and McCauley, 2012; Slotte et al., 2004) have been observed when exposed to LFN. Acoustic courtship behavior and spawning in certain fish were also disrupted (de

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Jong et al., 2018a; de Jong et al., 2018b). Some studies have even attributed decreases in abundances and catch rates to the retardation of senses and the avoidance behavior induced by LFN (Engås et al., 1996; Pearson et al., 1992).

Research is very scarce, however, when it comes to the effect of LFN on benthic invertebrates. Animals such as clams and worms continually disrupt and rework the sediment they live in or on by burrowing, feeding, ventilating, and defecating. Thus, they play a pivotal part in influencing local sediment dynamics, maintaining biogeochemical cycles, and promoting the remineralization of organic matter. These bioturbators and bioirrigators effectively modulate resource exchange between the different layers of benthic sediment and at the seafloor-water interface, classifying them as ecosystem engineers (Aller, 1994; Aller and Cochran, 2019; Wrede et al., 2018). A pioneering study by Solan et al. (2016) showed that anthropogenic noise repressed the bioturbating behaviors of the Norwegian lobster *Nephrops norvegicus*, a megabenthic burrowing decapod crustacean and *Ruditapes philippinarum*, a burrowing bivalve. Still, little is known about possible effects on the vast majority of macrobenthic invertebrates.

This current study explored for the first time how LFN affects the behavior of three bioturbators abundantly present in the North Atlantic: the amphipod crustacean *Corophium volutator*, the polychaete *Arenicola marina*, and the bivalve *Limecola balthica*, helping fill the knowledge gap by providing urgently needed data. We tested how bioturbation and bioirrigation were affected by LFN in a controlled laboratory setup, highlighting first cause-effect relationships and thus allowing for broader conclusions on possible implications for marine benthic ecosystems.

## 2. Materials & methods

### 2.1. Animal and sediment sampling

Individuals of *Corophium volutator* were collected from an intertidal mudflat in Bremerhaven, Germany (53°32'20.2"N; 8°34'33.5"E, observed field density of 4444 ind./m<sup>2</sup>) while individuals of *Arenicola marina* (observed density of 111 ind./m<sup>2</sup>) and *Limecola balthica* (observed density of 778 ind./m<sup>2</sup>) were sampled in the intertidal zone of the Wadden Sea in Dorum, Germany (53°44'25.7"N; 8°30'34.8"E). The animals were immediately transported to the lab and were then randomly selected and distributed across the cores (experimental units; see further details in *General experimental settings*). After an initial checkup for injured individuals, polychaetes and bivalves that had remained on the sediment surface after 1 h (i.e. that did not burrow) were replaced. All animals successfully burrowed within cores were left to acclimate for 24 h.

Sediment was sampled two days prior to experiments during low tide from the same sites in the respective habitats of each species. For the trial with *C. volutator*, sediment (0.166 mm average mode grain size) was sieved through a 500 µm mesh size sieve, removing large animals and particles from the fine sediment. For the experiments with *A. marina* and *L. balthica*, sediment (0.113 mm average mode grain size) was sieved through a 1 mm mesh size sieve. The sediments were then filled into the cores to an approximate height of 18 cm and left overnight to settle. Excess water was drained the next day and the sediment was redistributed so that the sediment height of every core was within 1 cm of each other. The top 3 cm of sediment in each core were re-suspended, homogenized with the transplants, and allowed to resettle again.

A key difference between the sediments from the two sites was that sediment from Dorum formed a thick layer of fine silt that rested atop the sediment surface when allowed to settle overnight after resuspension. The layer was liquid-like in its penetrability and once disturbed permeated throughout the water column, significantly increasing turbidity. This was expected to interfere with the activity of the lumiphore tracers, therefore most of the silt was removed by lifting the core, vigorously swirling the unsettled contents, then pouring them out

immediately. The sediment in each core was then rebalanced and homogenized as previously described.

### 2.2. General experimental settings

Cylindrical cores were constructed from plexiglass (650 mm height, 240 mm diameter). One end of the core was left open, while the other was plugged and sealed with a plexiglass plate. Each core had a small inlet hole at a height of 22 cm and an outlet hole 5 cm under the upper rim of the core, allowing for a constant seawater flow (approximately 600 mL per minute). Filtered seawater was used from the facilities at the Alfred Wegener Institute in Bremerhaven, Germany. Squares of foam rubber mats (300 × 300 × 40 mm) were placed under each core; the mats reduced conduction of ambient low-frequency noise from the room to the cores (Fig. 1). The experiments were run under constant laboratory conditions (average temperature of 20 ± 1 °C simulating the North Sea summer range; 12 h light: 12 h darkness). Prior to the experiment, the air circulation and conditioning systems of the room were turned off to further reduce ambient low-frequency noise. The number of animals then put in each core was matched to each species' observed density in the field (200 *C. volutator*, 5 *A. marina*, and 35 *L. balthica*).

### 2.3. Low-frequency noise treatment and core noise monitoring

So-called “noise eggs,” essentially ovoid dry boxes with mobile vibrators, were built following the specifications of de Jong et al. (2017). However, diverging from the original design, two VARTA 2600 mAh rechargeable batteries were used in parallel per egg; the batteries were nickel-metal hydride (NiMH) cells and therefore provided a stable 1.2 V for most of their discharge life. A flat discharge curve is crucial as consistent frequencies are desired and the frequencies produced by the vibrator are modulated by the voltage it receives. The dominant low frequencies produced by the eggs while submerged in a core ranged from 100 to 200 Hz. Frequencies in the 2k-20k Hz range were also observed at comparatively lower sound pressure levels, possibly products of the interaction between the sounds produced and the properties of the core. Noise from treatment cores leaking into control cores was not a concern as the noise produced by the noise egg attenuates quickly and is not powerful enough to conduct through multiple materials and vibration sinks. However, there was a peak at approximately 50 Hz that appeared at varying sound pressure levels (SPL) in both noise and control conditions; this is not a frequency the noise egg is known to produce and was likely due to ambient noise from the climate room and neighboring machinery. Since the control was not truly silent, the term

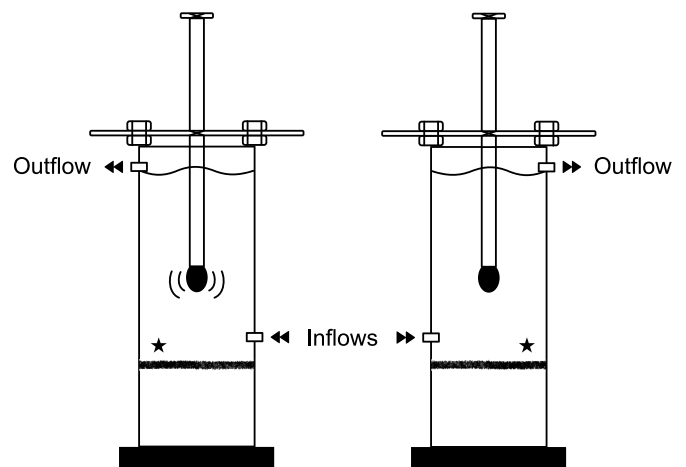


Fig. 1. Illustration of a core pair setup. The black lines directly below the inflows indicate the sediment surface. The stars indicate hydrophone positions during monitoring.

“noise” will henceforth mean “added noise” when regarding the current study.

Each noise egg was attached to a PVC pipe that was fastened to two parallel sticks perpendicular to the pipe. This was considered as a noise egg unit (hereafter NEU). A single NEU was submerged in each core, weighed down by small Ziploc bags filled with dry sand. The positions of the sandbags were adjusted so that the bags also rested on the rim of the core (when the NEUs were deployed) and thus mitigated the conduction of vibrations from the noise egg to the core walls (Fig. 1).

A fast Fourier transform (FFT) graph was produced daily to monitor the frequencies generated by the NEUs. Frequencies in cores were monitored using an Aquarian Scientific AS-1 hydrophone suspended 2 cm above the sediment surface. The hydrophone was paired with a PA-4 preamplifier (+26 dB) connected to a Zoom UAC-2 audio interface. The interface powered both components using 48 V phantom power. The UAC-2 itself was powered via USB by an unplugged laptop to avoid ground loop interference, and its output was analyzed live using ARTA software ([www.artalabs.hr](http://www.artalabs.hr)).

To generate an FFT graph in ARTA, the “Fr. response 2Ch” function was used with the following settings: Generator = External, Input = Left/R, Fs (sampling frequency, Hz) = 44,100, FFT = 4096. The hydrophone sensitivity provided by the manufacturer (0.0501187 mV/Pa) was entered manually into the “Audio Devices Setup” window. The averaging function was set to “Linear” to measure the dominant frequencies perceived by the hydrophone over a 100-s period. The Y-axis (dB) range was standardized for comparison between graphs (Fig. S1).

A power spectral density (PSD) graph (Fig. 2) was generated for a more accurate comparison of the signals. Recorded sounds of 10 s length were analyzed in R (3.5.1) (R Core Team, 2018) using the PAMGuide code (Merchant et al., 2015) using the following settings: Fs(Hz) = 44,100 and Window = Hann 50% for SPL and Fs(Hz) = 44,100, Window = Hann 50%, and Average = 1 s for PSD. The correction factor for calibration was calculated using technical specifications provided by the hydrophone manufacturer, the gain values from the pre-amplifier and audio interface, and the zero-to-peak voltage of the audio interface.

Our study was, however, limited by the inability to measure particle motion due to the lack of specialized sensors and the inherent difficulty of doing so in small spaces such as our cores (Hawkins and Popper, 2017; Martin et al., 2016; Roberts et al., 2016).

## 2.4. Experimental setup and data collection

### 2.4.1. Experimental setup

Five replicate core pairs were implemented; each pair of cores (one experimental core + one control core) shared a constantly oxygenated water circulation system (68 L total volume). The NEUs were inserted

and only the noise egg of the treatment core (Fig. 1, left) was turned on while that of the control core (Fig. 1, right) remained unpowered (without batteries). The inflows of each core pair were connected to the same water pump in a shared water tank. After the 24 h acclimatization of the animals, the experiment was started by inserting the NEUs. Further, 50 g of luminophores, or sand particles that glow under UV light, from Partrac (green, fluorescent, paramagnetic, 80–250  $\mu\text{m}$ ) were added to each core as a tracer for bioturbation activity.

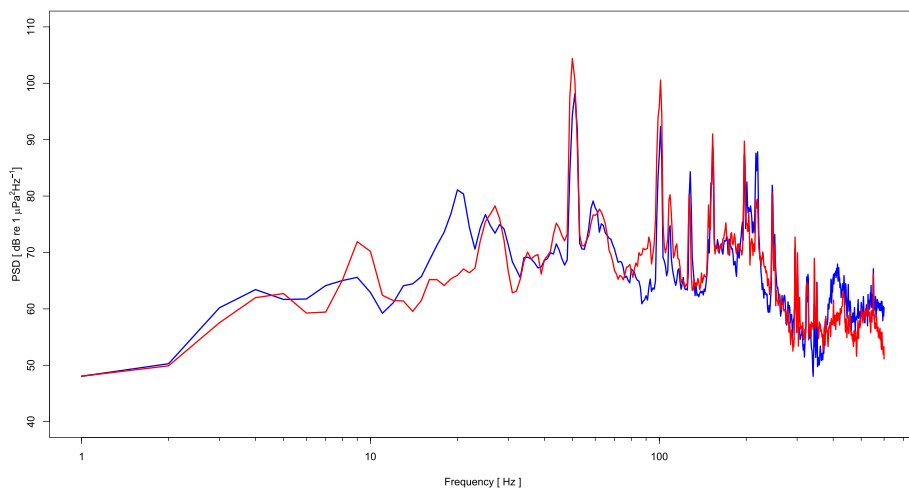
The experiment was left to run for six days. Sediment reworking and bioirrigation measurements were taken on the final day (see sections below for details) before terminating the experiment. All animals were then retrieved from the cores and the ash-free dry weight was determined for each core.

### 2.4.2. Sediment reworking measurement

A tripod-mounted Sony a6000 camera with a Sigma 30 mm f/1.4 prime lens was used for core photography. Frontal photos of the cores were taken on the last day of the experiment to track sediment reworking via luminophore movement. The backsides were also photographed after breaking down the water systems. All RAWs were imported into Adobe Lightroom CC, had their exposure boosted (+2.00) to ensure luminophore visibility and lens distortion corrected, then exported as full-size JPGs (6000  $\times$  4000 pixels, scale approximately 148 pixels/cm). The water column in each shot was painted over in Affinity Photo with the color #FD039B to define the sediment surface and removed using a custom plugin for ImageJ (1.53a). The plugin also equalized the sediment surface and adjusted the sediment column accordingly so that luminophore depths became comparable. After luminophores were identified via color thresholding and colored black while all else was colored white, a vertical profile of the particle distribution was plotted (Fig. S2). Sediment slicing was initially considered in case of wall effects, but wall effects are usually negligible when comparing the sediment reworking rates produced by both methods (Wrede et al., 2019). In addition, the reliance of sediment slicing on even sediment surfaces and the susceptibility of the sediment to displacement during slicing or organism extraction rendered the method infeasible for the current experiment.

### 2.4.3. Bioirrigation measurement

Water systems were unplugged and the inflow tubes of all cores were clipped shut and hung up to stop water exchange between cores on the final day. All water columns were then homogenized and 5 mL of water just beneath the surface were immediately drawn using single-use syringes and pumped through 0.45  $\mu\text{m}$  filters into storage tubes for an ambient measurement. After adding bromide tracers to bring the NaBr concentration in each core to 1.6 mM (3.35 g NaBr for *A. marina*, 3.13 g



**Fig. 2.** Power spectral density (PSD) comparison of the control (blue) and noise (red) treatment conditions. The lines represent the root mean square level (RMS). Higher dB values indicate higher sound intensity; since the dB scale is logarithmic, a 10 dB increase translates to a 10-fold increase in power. An example from live-monitoring with a more defined difference between noise and control conditions is provided in Fig. S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

NaBr for *L. balthica*), this sampling process was repeated immediately, then every hour for 6 h for the *A. marina* run (every other hour for the *L. balthica* run). The bioirrigation samples were then analyzed with wavelength scans in a DR 6000 UV VIS spectrophotometer and the results deconvoluted using a custom Matlab (R2020) script. Unfortunately, we could not measure bioirrigation for *C. volutator* as we did not have the technical opportunity at the time.

## 2.5. Data processing

### 2.5.1. Bioturbation coefficient

The relative luminophore concentrations were calculated for each depth increment in every core with the following formula:

$$\text{Relative lumis at depth} = \frac{\text{lumis at depth}}{\Sigma(\text{lumis})} * 100 \quad (1)$$

These values along with their respective depths were analyzed using a non-linear regression with the formula from Crank (1975):

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

where  $C(x,t)$  = the calculated relative luminophore concentration,  $N$  = the initial luminophore input,  $D_b$  = the bioturbation coefficient, and  $t$  = the time in days out of a year. This coefficient is a common measure for bioturbation rate (Wrede et al., 2017) and assumes that sediment movement by sediment reworking activity is purely diffusive. Two coefficients were obtained per core: one for the front side and another for the backside.

### 2.5.2. Luminophore burial depth

The mean luminophore burial depth (Mean LBD) was obtained by multiplying the relative luminophore values by their respective depths, then summing the products:

$$\text{Mean LBD} = \Sigma(\text{relative lumis at depth} * \text{depth}) \quad (3)$$

The max luminophore burial depth was determined visually by picking out the deepest feasible deposit in each photo, then dividing its depth (px) by the scale (px/cm) used for that photo in ImageJ:

$$\text{Max LBD} = \frac{\text{depth in pixels}}{\text{scale}} \quad (4)$$

### 2.5.3. Non-locality index

Non-local transport (NLT) is the non-diffusive and thus faster downward mixing of surface particles which the diffusion-based bioturbation coefficient does not account for. The non-locality index (NLI) indicates the extent of NLT and was calculated using the bioturbation coefficients ( $D_b$ ) and log-transformed profile data ( $D_b^n$ ) (Fernandes et al., 2006) as:

$$NLI = \frac{|D_b^n - D_b|}{\sqrt{D_b^n * D_b}} \quad (5)$$

To calculate  $D_b^n$ , natural logs of the relative luminophores at depth were first taken as:

$$y = \ln(\text{relative lumis at depth} + 1) \quad (6)$$

where the +1 kept resulting values positive. These values were then processed using the same non-linear regression as the diffusion-based bioturbation coefficient calculations to yield  $D_b^n$ .

Two NLI values were determined for every core (one for each side). An NLI >0 meant that NLT occurred, while an NLI = 0 meant that no or negligible NLT occurred. These values were not intended to replace the bioturbation coefficients calculated using the diffusive model of Crank (1975), but to provide more information regarding the sediment reworking done.

### 2.5.4. Bioirrigation rate

For the *A. marina* experiment, measurements from hours 0 to 6 (7 total) were checked for outliers using Grubbs' detection method. This was not done for the *L. balthica* experiment because there were only four measurements per core, and the Grubbs' outlier detection method employed by the calculator is prone to producing false positives when  $N \leq 6$  (Adikaram et al., 2015).

A linear regression was performed for every core using the measurements from hours 0 to 6. The  $Q$ , or the bioirrigation activity in each core, was determined using:

$$Q = \frac{V_{ow}}{C_{T_0} - C_{T_{ref}}} * \frac{dC_{T_0}}{dt} \quad (7)$$

where  $V_{ow}$  is the volume of the overlying water column,  $C_{T_0}$  is the  $Br^-$  concentration at  $T_0$ ,  $C_{T_{ref}}$  is the ambient  $Br^-$  concentration, and  $C_{T_0}/dt$  is the slope of the linear regressions (De Smet et al., 2016). The bioirrigation rate was then calculated with

$$BI = \frac{Q}{\text{surface area of core}} \quad (8)$$

## 2.6. Statistical analyses

Kolmogorov-Smirnov tests were performed on the calculated bioturbation and bioirrigation rates, mean and max LBDs, and NLI values to check for normality. In a few cases, the normality assumption was not met. However, the selected tests (linear mixed model and Wilcoxon matched-pairs signed rank test) were robust against non-normal distributions. F-tests were also performed to check for equal variances; all data met this assumption.

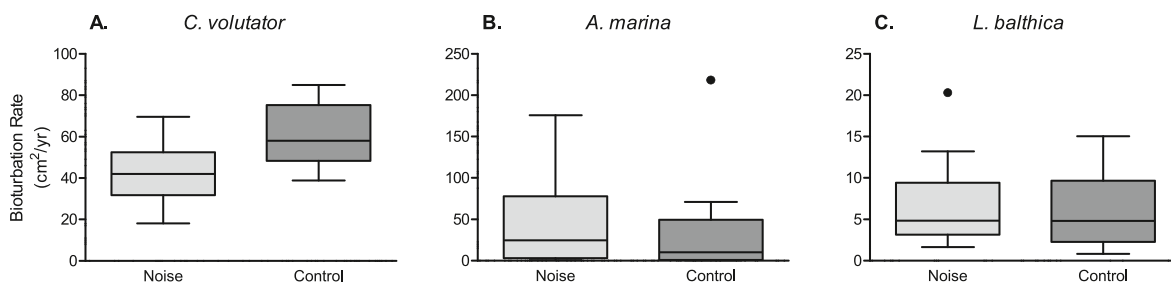
Statistical analyses for all values other than bioirrigation rates were done in R Studio (1.1.456) using R (3.5.1) (R Core Team, 2018). One linear mixed effect model was performed per parameter for every experiment using the R package *lme4* (Bates et al., 2015) to illustrate the relationship between the parameter in question and noise (treatment). In essence, every parameter was treated as a function of noise and the random effect of cores. A likelihood ratio test was then performed between every model and its respective null model (model without treatment) to obtain P-values that indicated whether the relationship between the parameter and noise was significant. All analyses were performed at a 95% confidence level.

Wilcoxon matched-pairs signed rank tests were performed in GraphPad Prism (5.03) to test for significant differences in bioirrigation rates between experimental and control cores. One test was performed per experiment; as with the mixed models, analyses were done at a 95% confidence level.

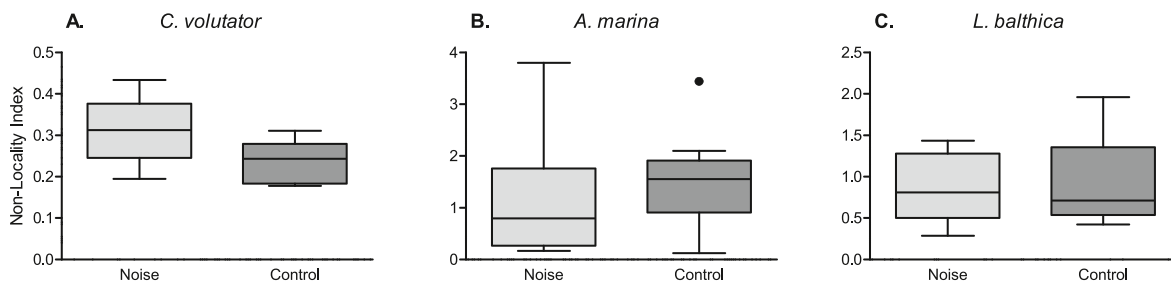
## 3. Results

### 3.1. Bioturbation rate

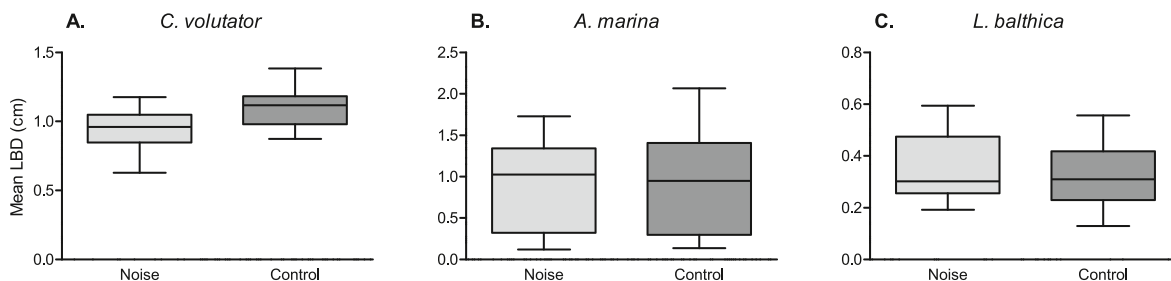
In the presence of noise, *Corophium volutator* reworked sediment significantly less than in the absence of noise ( $\chi^2(1) = 4.7974$ ,  $p = 0.0285$ ). The *C. volutator* individuals in noise cores reworked sediment at a mean rate of  $42.24 \text{ cm}^2/\text{yr}$  with a standard deviation of  $15.20 \text{ cm}^2/\text{yr}$  while those in control cores reworked sediment at a rate of  $60.42 \pm 14.96 \text{ cm}^2/\text{yr}$  (Fig. 3, A). In contrast, the rate at which *Arenicola marina* and *Limecola balthica* reworked sediment in the presence of noise did not differ significantly from control cores (Fig. 3B and C). There was, however, an increase in variability when *A. marina* was exposed to noise: individuals in noise cores reworked sediment at a mean rate of  $44.94 \pm 55.92 \text{ cm}^2/\text{yr}$  while those in control cores reworked sediment at a rate of  $37.75 \pm 67.46 \text{ cm}^2/\text{yr}$  (Fig. 3, B).



**Fig. 3.** Bioturbation rates ( $\text{cm}^2/\text{yr}$ ) of *C. volutator*, *A. marina*, and *L. balthica* after six days under noise and control conditions. The median, first and third quartiles, along with the minimum and maximum are shown. Outliers, or values that fall outside the Tukey fences, are represented by dots.



**Fig. 4.** Non-locality indices for *C. volutator*, *A. marina*, and *L. balthica* after six days under noise and control conditions. Higher NLIs indicate more non-local transport. The median, first and third quartiles, along with the minimum and maximum are shown. Outliers, or values that fall outside the Tukey fences, are represented by dots.



**Fig. 5.** Mean luminophore burial depths (cm) of *C. volutator*, *A. marina*, and *L. balthica* after six days under noise and control conditions. The median, first and third quartiles, along with the minimum and maximum are shown.

### 3.2. Non-locality index

The noise treatment had a significant effect on the non-locality index (NLI) of *C. volutator* ( $\chi^2(1) = 4.1407$ ,  $p = 0.0419$ ). In the presence of noise, *C. volutator* produced higher NLI ( $0.3109 \pm 0.07435$ ) than those in the absence of noise ( $0.2367 \pm 0.04890$ ) (Fig. 4, A). The noise treatment had no effect on the NLI of *A. marina* ( $\chi^2(1) = 0.7193$ ,  $p = 0.3964$ ) although there was again an increase in variability. The *A. marina* in noise cores yielded a mean NLI of  $1.151 \pm 1.163$  while those in control cores yielded a mean NLI of  $1.539 \pm 0.9075$  (Fig. 4, B). The NLI of *L. balthica* was also unaffected by the noise treatment ( $\chi^2(1) = 0.1211$ ,  $p = 0.7278$ ) (Fig. 4, C).

### 3.3. Mean luminophore burial depth

The noise treatment had a significant effect on the mean luminophore burial depth (LBD) ( $\chi^2(1) = 4.1796$ ,  $p = 0.0409$ ) of *C. volutator*. In the presence of noise, the amphipods buried luminophores on average less deep than in the absence of noise. Individuals in noise cores buried luminophores to an average mean depth of  $0.9434 \pm 0.1569$  cm while those in control cores buried luminophores to an average mean depth of  $1.104 \pm 0.1467$  cm (Fig. 5, A). In contrast, neither the mean

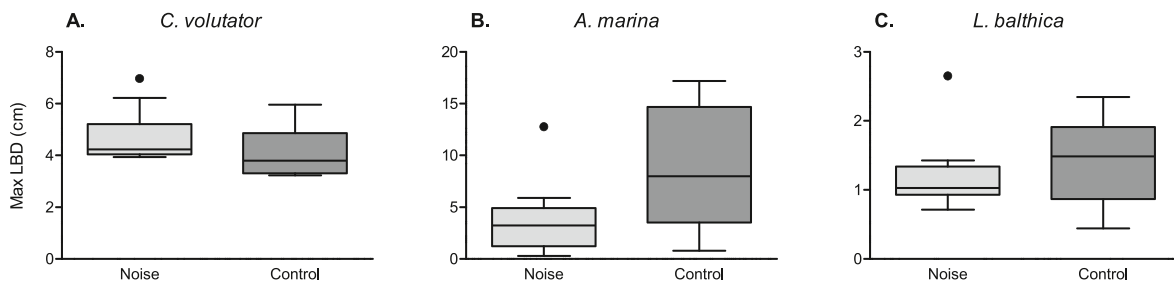
luminophore burial depths of *A. marina* ( $\chi^2(1) = 0.0104$ ,  $p = 0.9188$ ) nor those of *L. balthica* ( $\chi^2(1) = 0.166$ ,  $p = 0.6837$ ) were affected by the noise treatment (Fig. 5B and C).

### 3.4. Max luminophore burial depth

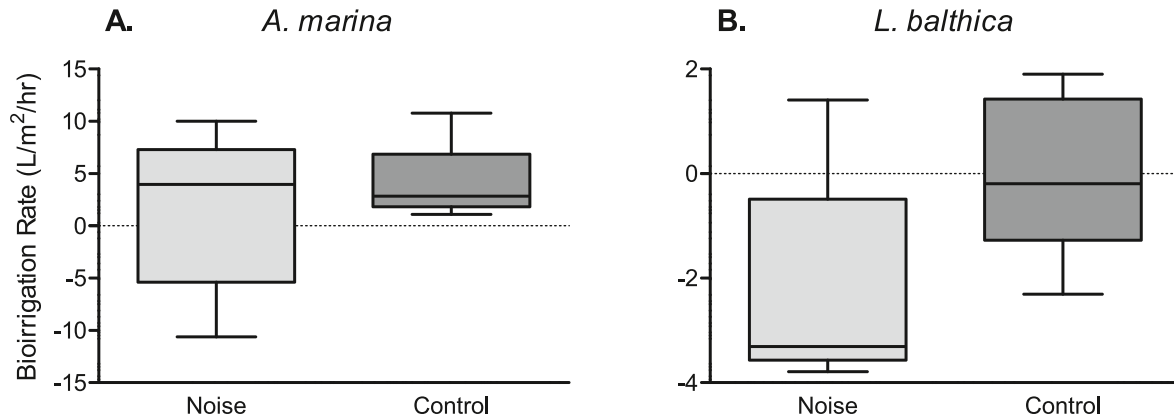
There were no significant differences in the maximum luminophore burial depths in the presence of noise compared to the controls in *C. volutator* ( $\chi^2(1) = 1.5949$ ,  $p = 0.2066$ ), *A. marina* ( $\chi^2(1) = 3.7118$ ,  $p = 0.0540$ ), and *L. balthica* ( $\chi^2(1) = 0.3143$ ,  $p = 0.5751$ ). Nevertheless, there were noticeable changes in the maximum luminophore burial depths of *A. marina*: individuals in noise cores buried luminophores to an average max depth of only  $3.846 \pm 3.592$  cm whereas those in control cores buried luminophores to an average max depth of  $8.649 \pm 5.567$  cm (Fig. 6).

### 3.5. Bioirrigation

There were no significant differences in the rates at which *A. marina* bioirrigated in the presence of noise compared to the controls ( $p(\text{exact}) = 0.8125$ ). However, the mean bioirrigation rate in noise cores displayed much greater variation ( $1.56 \pm 7.70$   $\text{L}/\text{m}^2/\text{hr}$ ) than that in



**Fig. 6.** Max luminophore burial depths (cm) of *C. volutator*, *A. marina*, and *L. balthica* after six days under noise and control conditions. The median, first and third quartiles, along with the minimum and maximum are shown. Outliers, or values that fall outside the Tukey fences, are represented by dots.



**Fig. 7.** Bioirrigation rates ( $L/m^2/hr$ ) of *A. marina* and *L. balthica* after six days under noise and control conditions. The median, first and third quartiles, along with the minimum and maximum are shown.

control cores ( $4.05 \pm 3.85 L/m^2/hr$ ). The bioirrigation rates ranged from  $-10.6$  to  $10.0 L/m^2/hr$  in the noise cores and from  $1.11$  to  $10.8 L/m^2/hr$  in the control cores (Fig. 7, A).

There were also no significant differences in the rates at which *L. balthica* bioirrigated in the presence of noise compared to the controls ( $p(\text{exact}) = 0.1875$ ). The mean bioirrigation rate in noise cores displayed great variation with  $-2.28 \pm 2.13 L/m^2/hr$  while that in control cores was  $0.0226 \pm 1.58 L/m^2/hr$ . The bioirrigation rates ranged from  $-3.79$  to  $1.41 L/m^2/hr$  in the noise cores and from  $-2.31$  to  $1.90 L/m^2/hr$  in the control cores (Fig. 7, B).

For a summary of all parameters measured across all species and treatments, please refer to Tables S1 and S2 in the supplementary materials.

## 4. Discussion

### 4.1. Burial depths and sediment reworking

*Corophium volutator* exposed to acute low frequency noise (LFN) buried luminophores on average less deep than those from the control group. However, the maximum depth to which both groups buried luminophores was not affected. In contrast, LFN did not seem to significantly affect how deep *Arenicola marina* and *Limecola balthica* buried, both on average and at maximum. Though not directly comparable, a different setup showed that the introduction of anthropogenic noise sources repressed burrowing behavior in the Norwegian lobster *Nephrops norvegicus* - one of the most commercially important crustaceans (Solan et al., 2016). The average maximum depth to which *N. norvegicus* redistributed sediment particles was reduced in the presence of noise, regardless of if the noise was continuous (shipping lane) or impulsive (wind farm pile-driving). This contrasts with the results of the current study, with the small amphipod crustacean *C. volutator* burying

particles to the same maximum depth in both the presence and absence of LFN. However, the mean depth to which *N. norvegicus* buried was unaffected by noise, a result that again contradicts that regarding *C. volutator*. The mean and maximum burial depths of the bivalve *Ruditapes philippinarum* have been shown to be unaffected by noise (Solan et al., 2016), which corroborates the findings of the current study regarding the burial depths of *L. balthica*. This suggests that adult bivalves may be robust against LFN.

Burrowing activity has a great chance of being hidden if the burrowers are small and the population density is not high enough to guarantee uniform animal distribution across the sediment surface in aquaria. Although our setups mimicked the natural density in the field, most of the individuals of *A. marina* and *L. balthica* did not burrow at the core walls but instead near the center where activity was not monitored. The calculated mean and maximum burial depths of both species thus deviated greatly from established values in literature due to skewing by cores with little to no visible activity at the walls (Cadée, 1976; Michaud et al., 2005). Naturally, this lack of visible activity also impacted the bioturbation rate ( $D_b$ ) and non-locality index (NLI), the calculations of which rely on luminophore particle displacement. If the results are taken at face value, then LFN ostensibly did not affect the sediment reworking and non-local transport (NLT) activities of *A. marina* and *L. balthica*. However, this most likely represents an underestimation and any direct implications drawn from this must be regarded with caution.

Individuals of *R. philippinarum* were shown to reduce their relocation activities and lie on the sediment with their valves closed instead of burrowing when exposed to anthropogenic noise (Solan et al., 2016). A similar behavior was observed in *L. balthica* in our study: a few individuals in most of the cores were observed to be either half-buried or fully exposed on the sediment surface with their valves closed. These individuals were initially assumed deceased, but closer inspection from the second day onward revealed that a few were actively foraging using

their siphons. Six of seven individuals that did not burrow into the sediment and were confirmed alive were in noise cores. Unfortunately, these observations were only meant to be general notes during daily maintenance and thus no further behavioral responses can be extrapolated from them.

No research has been done thus far on the effects of LFN on polychaetes (or even annelids for that matter), but the presence of statocysts in *A. marina* may provide some first indication as to how LFN might impact these worms (Wells, 1950). The statocysts of different cephalopod species have been shown to get damaged severely by LFN (André et al., 2011). While statocysts vary in structure between taxa, setae and their supporting cells are reliably present and appear to be sensitive to LFN. The statocysts in *A. marina* might be affected in a similar way when exposed to LFN, though not necessarily to the same degree. The statocysts are used by *A. marina* for orientation and guidance when burrowing (Buddenbrock, 1912) so if these structures were to be compromised, the ability of the worm to burrow (and thus rework sediment) would be as well.

*Corophium volutator* reworked sediment significantly less in the presence of low-frequency noise (LFN) than in the absence of. In addition, higher NLI were observed in cores with LFN than in those without. These responses strongly suggest that the sediment mixing capacity of *C. volutator* is reduced when exposed to LFN, especially when the reduced mean particle burial depths are also considered. This is evidence of how LFN affects the sediment reworking behavior of an amphipod ecosystem engineer.

*Corophium volutator* suspension feeds at high tide by generating a current with their pleopods and deposit feeds at low tide by scraping the sediment surface with their antennae, then wafting the food into mouth parts using the same current (Meadows and Reid, 1966). These behaviors induce the transport and mixing of sediment in and around the burrow. Shore crabs (*Carcinus maenas*) were shown to suspend feeding when ship noise was played (Wale et al., 2013), which might explain why bioturbation rates were reduced if this response holds true in *C. volutator*. Although sound perception in amphipods is largely unknown, it is also possible that amphipods perceive LFN as vibrations via structures such as a lateral line organ or sensory setae (Beermann et al., 2015; Platvoet et al., 2007), which could be used to detect the presence of potential predators. When predators were nearby during low tide, *C. volutator* retreated deeper into its burrow and spent more time there (MacDonald et al., 2014) instead of being active near the opening of the burrow. Although predator detection was not attributed to a specific mechanism, MacDonald et al. (2014) acknowledged that *C. volutator* may detect changes in substratum pressure. Interestingly, the same study also showed that while *C. volutator* did dwell deeper down, the burrow depths did not change. This contrasts with the results produced by the setup of the current study if the particle burial depth does correlate with burrow depth. Shore crabs in the study by Wale et al. (2013) also took longer to flee from simulated predator attacks while exposed to ship noise. More recently, young-of-the-year lobsters exposed to 3 h of constant low-frequency noise using the same source were shown to spend less time hiding in the presence of predators (e.g. shore crabs) and more time exploring (Leiva et al., 2021). Loss of antipredator behaviors, when considered together with the possibly reduced mean burrow depths in the current study may suggest potentially elevated predation rates upon *C. volutator* as a consequence of LFN exposure and thus reduced overall sediment reworking. This scenario would be dire since amphipods such as *C. volutator* have been shown to only contribute meaningfully to sediment reworking when abundant (De Backer et al., 2011). However, the ship noise in the setup by Wale et al. (2013) was employed over minutes and not days like in the current study; habituation to LFN by animals may be possible (Carroll et al., 2017; Day et al., 2020) depending on intensity, duration, frequency, and many other factors. The mortality of *C. volutator* was not affected by LFN, therefore the reduction in bioturbation rates and mean luminophore burial depth cannot be attributed to a loss of experimental animals in the treatments

(Table S2).

The current experiment did not simulate tidal rhythms even though intertidal species were used and thus our results should be considered accordingly. However, there are several bioturbation studies where intertidal or facultative intertidal species were submerged for the entire duration without issue (Fernandes et al., 2006; Mermillod-Blondin et al., 2004; Näkki et al., 2017; Solan et al., 2016). Another factor to consider is that the sides of the cores were not covered for visual assessment purposes and were thus exposed to ambient light during the daylight hours. The presence of in-depth light and how that may affect natural processes raises the possibility that an artefact cannot be ruled out. The effect of LFN on the organisms and how that may affect the quality of the shared water was also not factored into the design; while the possibility of an undetected effect cannot be discounted, all core pairs were subject to the same conditions and nevertheless produced the results presented.

#### 4.2. Bioirrigation

Low frequency noise did not seem to affect how much *A. marina* and *L. balthica* bioirrigated. Intriguingly, the bioirrigation rates in the presence of LFN varied much more than those in control conditions, especially in the case of *A. marina* where the variance differed by a factor of two. *Arenicola marina* exhibited all positive bioirrigation rates in the absence of noise and a mix of positive and negative rates in the presence of noise. Negative rates were also exhibited by *L. balthica*, but under both experimental conditions. These rates are theoretically impossible as “reverse irrigation” does not exist; negative rates are likely due to the irrigation effect being too small and thus shadowed by measurement noise from differing samples and the spectrometer analysis.

The burrowing bivalve *R. philippinarum* was shown to bioirrigate the least under continuous noise (shipping lane) and the most in the absence of anthropogenic noise (Solan et al., 2016). The oyster *Magallana gigas* also showed lower ventilation and valve activity rates when exposed to a cargo ship noise playback (Charifi et al., 2018). The results for *R. philippinarum* and *M. gigas* suggest that *L. balthica* might follow a similar trend if given a setup with similar relative proportions; the much larger overlying water column (and tracer ppm) in the current setup combined with the small body size and relatively low density of *L. balthica* may have hindered the detection of minor differences in tracer concentration. The depth at which *L. balthica* bioirrigates coincides with the sediment nitrification zone (Michaud et al., 2006), making the bivalve a facilitator of the nitrogen cycle. If the anti-burrowing behavior observed is indeed induced by LFN, not only might the sediment reworking contribution of *L. balthica* decrease and its mortality increase from elevated predation rates, but the biogeochemical cycling of the ecosystem may be reshaped in uncertain ways as well.

The irrigation behavior of *A. marina*, achieved through peristaltic movements of the body, has also been shown to be spontaneous and not reflexive. Decreasing the oxygen content of the surrounding water or pinning down the worm outside its burrow (which should cause significant stress) did not modify the clockwork-like bouts of irrigation (Wells, 1949). This means that even if *A. marina* is stressed by LFN, its ventilation of the burrow should remain constant. The amount of water pumped in each irrigation outburst, however, increased if the worm encountered oxygenated water after being deprived of oxygen (Wells, 1949). If LFN were to induce severe enough hyperventilation in *A. marina* to regularly deoxygenate the burrow water before the next irrigation bout, then the bioirrigation rate might increase simply due to the increase in volume pumped.

#### 5. Conclusions

Low frequency noise negatively affected the amphipod crustacean *C. volutator* while its effect on the polychaete *A. marina* and the bivalve *L. balthica* remained statistically inconclusive. However, the increase in sediment reworking and bioirrigation variability in *A. marina* and the

observed anti-burrowing behavior of *L. balthica* under noise conditions may be early indications of possible effects and provide bases for further experimentation. All three species are abundant bioturbators and bio-irrigators in their respective ecosystems, especially in the cases of *C. volutator* and *A. marina* where they are dominant species in terms of abundance and biomass, respectively (Beukema, 1974; De Backer et al., 2011). Such species often, proportionate to their high population densities, contribute the most to sediment reworking (De Backer et al., 2011; Gerino et al., 2007; Mugnai et al., 2003) and therefore density declines due to LFN might have major consequences for ecosystem functioning (Solan et al., 2004). In fact, the activity of the *A. marina* is regarded as a major reason why sandy tidal flats dominate the Wadden Sea (Volkenborn et al., 2007). The potential impairment of animal burrowing abilities by LFN might result in shallower sediment reworking depths and even increased mortality if feeding efficiency is affected. Such impacts may facilitate an ecosystem regime shift into an alternative stable state, the reversal of which is often extremely difficult if not effectively impossible due to hysteresis (Beisner et al., 2003). Perhaps of more acute relevance, however, are offshore wind farms and the constant LFN along with the additional surface area for biomass they contribute. If benthic organisms in wind farms react similarly to those in the current study to LFN, then the impaired biogeochemical cycling might be unable to keep step with the increased biomass production and result in eutrophication and sediment-type shifts in these areas. Therefore, it is of utmost importance to rapidly gain a better understanding of how LFN affects key species in our increasingly loud oceans to foresee and prevent scenarios like these.

#### Author statement

Sheng V. Wang – Conceptualization, methodology, investigation, data curation, formal analysis, writing – original draft, writing – review & editing. Alexa Wrede – Methodology, data curation, formal analysis, writing – review & editing. Nelly Tremblay – Methodology, writing – review & editing. Jan Beermann – Conceptualization, resources, methodology, data curation, formal analysis, writing – review & editing, supervision.

#### 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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