Marine Pollution Bulletin 222 (2026) 118764

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Noisy waters affect feeding and metabolic enzyme activities of amphipod mesograzers

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ARTICLE INFO

Keywords:
Anthropogenic noise
Noise pollution
Marinogammarus marinus
Crustaceans
Habitat choice
Mitochondria

ABSTRACT

The consequences of the progressive intrusion of anthropogenic noise into natural oceanic soundscapes are largely unknown despite the fact that most metazoans utilize sound or vibration for intra- and interspecific interactions as well as orientation. Coastal ecosystems in particular can be characterized by a high level of human activity and thus anthropogenic noise sources. Here, we studied the impact of such noise on marine mesograzers, small invertebrates that play crucial ecological roles by controlling macrophyte growth while serving as key food sources for higher trophic levels in algae-dominated coastal ecosystems. The effect of added continuous low-frequency noise on the habitat choice, feeding rate, and metabolic enzyme activities of the amphipod mesograzer *Marinogammarus marinus* was tested in a controlled laboratory setting. While habitat choice appeared unaffected by the added noise, exposed animals exhibited reduced feeding performance as well as altered metabolic enzyme activities. If sustained, the physiological homeostasis of *M. marinus* and their role in the ecosystem may be jeopardized. The ever-rising sound levels in the oceans may thus have consequences for algae-dominated animal communities in coastal areas.

1. Introduction

The progressive intrusion of anthropogenic noise into natural oceanic soundscapes is an increasingly concerning matter. Many marine animals utilize sound or vibration for different kinds of intra- and interspecific interactions as well as orientation (Montgomery et al., 2006; Slabbekoorn, 2010; Tyack, 1998). The continued intensification of anthropogenic noise, especially in the low-frequency range (10–500 Hz according to Carey and Evans (2011)), threatens to disrupt these biological processes. This overall increase can be attributed primarily to growing commercial ship traffic, but also to energy production (e.g., wind farms, oil platforms) as well as offshore construction and ocean exploration (Duarte et al., 2021; Jalkanen et al., 2022; Possenti et al., 2024). Ships and offshore wind operations mainly emit steady and ongoing vibrations in the low-frequency range (i.e. “continuous” low-frequency noise (LFN)), while pile-driving and seismic surveys emit transient, often high-energy bursts of low-frequency vibrations (i.e. “impulsive” LFN) with rapid onset as well as decay. While anthropogenic noise pollution has been ongoing for decades, research of noise effects on marine life outside of marine vertebrates is still in its early stages. The implications of noise pollution for marine ecosystems are thus sparsely documented, although existing studies have indicated some interference with certain ecosystem functions (e.g., Solan et al., 2016; Wang et al., 2022).

Despite their ecological importance, the impact of underwater noise on most marine invertebrates remains largely unexplored. Marine mesograzers, for example, are small herbivorous invertebrates ($\leq$ 2.5 cm) that can control macrophyte growth by either directly grazing on the macrophytes and/or grazing on their epiphytes (Duffy and Hay, 2000; Machado et al., 2017; Reynolds et al., 2014). In addition, mesograzers such as amphipod crustaceans constitute an important food source for higher trophic levels (Moksnes et al., 2008; Paar et al., 2019). Stomach content analyses of fish predators off Swedish coasts, for example, showed that such herbivores can dominate the diets of several

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https://doi.org/10.1016/j.marpolbul.2025.118764
Received 3 March 2025; Received in revised form 15 September 2025; Accepted 22 September 2025

predator species such as the eelpout *Zoarces viviparus* and the corkwing wrasse *Symphodus melops* (Wennhage and Pihl, 2002). Mesograzers can thus be of pivotal importance for coastal ecosystems (e.g., Andersson et al., 2009; Reynolds et al., 2014).

Marine mesograzers have repeatedly been reported to be sensitive to a variety of stressors. Stress-related behavioral responses can include reduced feeding and dietary shifts (Ober et al., 2022; Pastorinho et al., 2011; Schram et al., 2015), increased avoidance behaviors and modified habitat choice (Beermann et al., 2018; Bibby et al., 2007; Boström and Mattila, 1999; Lasley-Rasher et al., 2011), altered locomotion and startle responses (Green-Ojo et al., 2024; Rogers et al., 1998), and adversely affected mating interactions (Borges et al., 2018; Pereira et al., 2023). Physiological responses include decreased immunocompetence (Roth et al., 2010; Wood et al., 2014), increased oxidative stress (Dellali et al., 2021; Queiroz et al., 2023), altered growth and molt rates (Cardoso et al., 2018; Green-Ojo et al., 2024), and even carry-over effects into successive generations (Borges et al., 2018; Lopes et al., 2019; Pereira et al., 2023). Most of these responses were in reaction to anthropogenic stressors such as ocean acidification and chemical pollutants as well as potentially stress-inducing factors such as temperature differences applied in laboratory settings. While the stress responses of small mesograzing crustaceans to noise pollution is largely unknown, a number of studies have investigated the effect of anthropogenic noise on larger crustaceans; the reported effects span from altered feeding (Azarm-Karnagh et al., 2023; Regnault and Lagardere, 1983), breeding (Sal Moyano et al., 2023), and locomotor activity (Snitman et al., 2022) to increased physiological stress, affecting respiration, excretion, protein production, DNA fragmentation, and oxidative stress (Filiciotto et al., 2016; Filiciotto et al., 2014; Regnault and Lagardere, 1983; Snitman et al., 2022).

Behavioral responses such as feeding and habitat choice are intuitive metrics given the ecological niche of mesograzers; however, understanding the molecular mechanisms that may correspond to these reactions is essential for a more complete picture. Molecular methods allow for the indirect assessment of parameters such as respiration that can be difficult to measure without affecting the treatment and, through extra handling, the organism and its behavior. Metabolic enzyme activities, in particular, can serve as sensitive indicators of physiological disruption under stress (Dahlhoff, 2004). In this context, the mitochondrion and the biochemistry within are of particular interest as mitochondria provide energy in a universal form required by most cellular processes via respiration. When the razor clam *Sinonovacula constricta* was exposed to anthropogenic noise in a laboratory setting, several genes related to glycolysis and the Krebs cycle, key metabolic pathways in the mitochondria, were down-regulated (Peng et al., 2016). Thus, in this current study, we focused on select enzymes integral to the different main processes involved in energy production in the mitochondria: citrate synthase (CS) of the Krebs cycle (aerobic pathway), complexes I, III, and IV of the electron transport system (aerobic pathway), and lactate dehydrogenase (LDH) of the anaerobic pathway.

The enzymatic system in the mitochondria carries out part of aerobic respiration by converting the products of glycolysis and pyruvate oxidation (the first two steps of aerobic respiration) into reducing intermediates, which are then used to generate energy in the form of adenosine triphosphate (ATP). This system consists primarily of the Krebs cycle and the electron transport system (ETS). The former is initiated by the enzyme CS and oxidizes nutrients to produce intermediates for the ETS as well as some ATP. The latter generates a proton gradient across the inner mitochondrial membrane through proton pumps; this gradient then drives the flow of protons through the ATP synthase complex to catalyze the conversion of adenosine diphosphate (ADP) to ATP. In hypoxic conditions (which can arise from tissue stress), anaerobic pathways may take over to sustain basal energy requirements. The enzyme LDH facilitates the conversion of pyruvate (a product of glycolysis) into lactate while concomitantly converting NADH to NAD+ (a product and reactant, respectively, of glycolysis). Since glycolysis also produces some ATP, LDH thus allows for the maintenance of energy production when oxygen levels are low. Maintaining the catalytic functions of all components in relation to each other is thus crucial.

When organisms are under stress, however, the synchrony of these activities may be disrupted. The ETS includes sites for the production of reactive oxygen species (ROS), in particular complex I and III and to an extent, complex II and IV (the latter of which is cytochrome *c* oxidase, or COX) (Hernansanz-Agustín and Enríquez, 2021; Sabharwal and Schumacker, 2014). While ROS such as superoxide and hydrogen peroxide are essential to many cellular pathways as signaling molecules, excessive ROS production and accumulation can have deleterious effects (e.g., cell death, tumor development) (Dan Dunn et al., 2015; Sabharwal and Schumacker, 2014). The main function of COX is to reduce oxygen to water, thereby keeping the number of free electrons available to partially reduce oxygen and form ROS in control. Thus, a deficiency or the impairment of COX can induce higher ROS production (Srinivasan and Avadhani, 2012); this is especially important when the metabolism, behavior, reproduction, and sensory functions of crustaceans are both directly and indirectly influenced by the periodic, energy-intensive shedding of the integument and the associated metabolite cycles during the molting process.

Here, we tested how anthropogenic continuous LFN affects a crustacean mesograzer – the gammarid amphipod *Marinogammarus marinus* (Leach, 1816). This species is abundantly found along eastern North Atlantic coasts on hard substrates with fucoid assemblages, where it is an effective herbivore of the brown macroalgae (Den Hartog, 1964; Martins et al., 2014; Pinkster and Broodbakker, 1980). We tested the effects of added continuous noise on feeding rate, habitat choice, and metabolic enzyme activities using a controlled laboratory setup to establish potential cause-effect relationships, allowing for conclusions on potential consequences for marine coastal ecosystems.

2. Materials and methods

2.1. Animal collection and general experimental settings

Approximately 1000 individuals of *Marinogammarus marinus* were collected in June 2023 from the intertidal zone of the northern beach of the island of Helgoland (German Bight, North Sea; 54°11′21.1"N, 7°53′00.6″E). The amphipods were immediately transported to the laboratory of the Biologische Anstalt Helgoland (Dummermuth et al., 2023), sorted, and then acclimated in a large tank under stable environmental conditions (15 °C, i.e. matching the field seawater temperature; 12 h light: 12 h darkness) with a constant supply of fresh *Fucus spiralis* (Linnaeus, 1753) and *Ascophyllum nodosum* (Linnaeus) (Le Jolis, 1863) for approximately one week until they were utilized in the experiment. Oxygen was supplied via an air stone and the seawater in the holding tank was changed twice per day.

2.2. Experimental setup

Twenty transparent plastic aquaria (32.3 × 17.8 × 18.5 cm; L x W x H) were filled with 6 L of continuously aerated filtered seawater. A single ceramic tile (10 × 10 cm; L x W) was placed in the same corner of each tank and propped up on one side by a small rock to form a shelter (Fig. 1). Rectangles of vibration-reducing pads were positioned under each tank to reduce the conduction of ambient vibrations and vibrations to and from neighboring tanks. Water temperature was monitored constantly to ensure identical conditions across all tanks, and noise treatments (sound pressure and frequencies) were measured at the beginning and end of each experimental run but verified daily.

2.3. Low-frequency noise treatment and monitoring

"Noise eggs," or waterproof dive eggs containing a small vibration

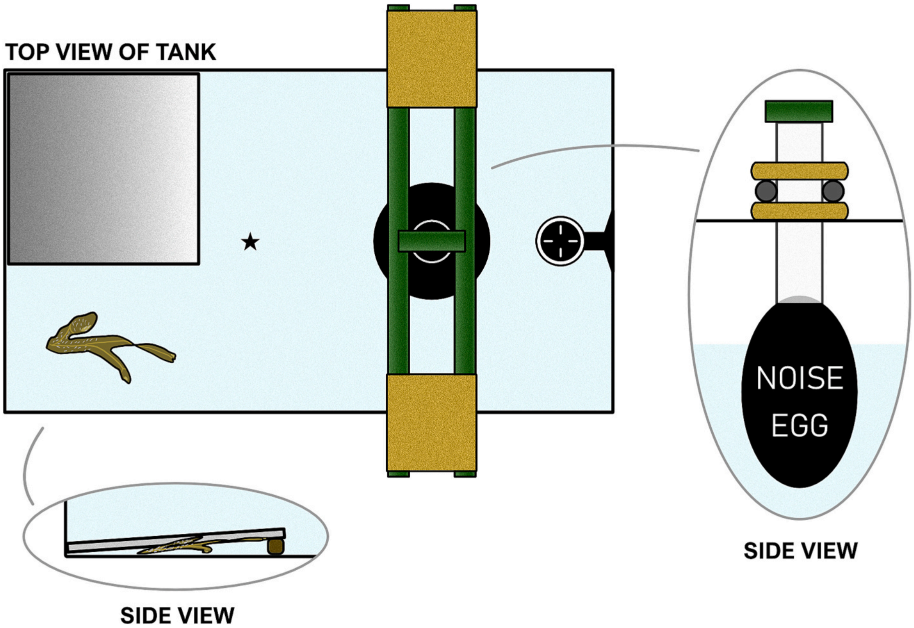

Fig. 1. Top-down illustration of an experimental tank setup with side view callouts. The surveyed microhabitats are as follows: (1) attached to the noise egg, (2) on the algal thallus (bottom left), (3) under the tile (top left), (4) attached to the tank wall at or above the waterline, and (5) elsewhere in the aquarium. The black star indicates the hydrophone position when monitoring sound. The noise egg apparatus is described in section 2.3.

motor and battery pack, were employed to produce an added continuous low-frequency noise (LFN) treatment (see de Jong et al. (2017), Wang et al. (2022)). Two 2600 mAh rechargeable batteries were used in parallel to extend uptime compared to the original design. The batteries were made of nickel-metal hydride (NiMH) which provided a relatively flat discharge curve; this is important as the motor frequency was modulated by the voltage provided (in this case, 1.2 V for most of the uptime). Further, coin motors were used instead of the pager motors from the original design to produce slightly lower dominant frequencies (~100 Hz). A peak at approximately 70 Hz was present in all recordings regardless of treatment, most likely due to ambient machinery and air conditioning noise. As the control was not completely free from ambient low-frequency sounds, the term “control” will henceforth signify “no added noise” for the current study.

Similar to Wang et al. (2022), each noise egg was attached to a short PVC pipe section with two sticks on either side that were perpendicular to the pipe but parallel to each other. The noise egg was approximately two-thirds submerged in the middle of the water column, but closer to the side of the tank with the air stone (Fig. 1). Small sandbags rested on the rim of the tank, where they helped reduce the conduction of vibration between the egg and the tank walls.

The sound in each tank was monitored using a hydrophone (Aquarian Scientific AS-1) coupled with a preamplifier (Aquarian Scientific PA-6) and plugged into an audio interface (ZOOM UAC-2). The interface itself was powered by a laptop via USB. The software Audacity (3.2.5) was used to make 30 s recordings of each tank on days 1 and 4 with the hydrophone positioned halfway between the noise egg and the tile/algae (Fig. 1) in the middle of the water column. The recordings were then analyzed in R (3.5.1) (R Core Team, 2022) using PAMGuide code (Merchant et al., 2015) to generate aggregate power spectral density (PSD) graphs (Fig. 2). The settings were as follows: Fs(Hz) = 44,100, Window = Han 50 % for SPL; Fs(Hz) = 44,100, Window = Hann 50 %, and Average = 1 s for PSD. The manufacturer technical specifications for the hydrophone (receiving sensitivity: −208 dBV re 1μPa), the preamplifier (gain: +26 dB), and the audio interface were included during the analysis for calibration correction. Particle motion was not measured due to lack of technical opportunity.

2.4. Experimental protocol

For each replicate, 15 individuals of *M. marinus* (17 ± 2 mm body length) were randomly selected from the pooled population in the

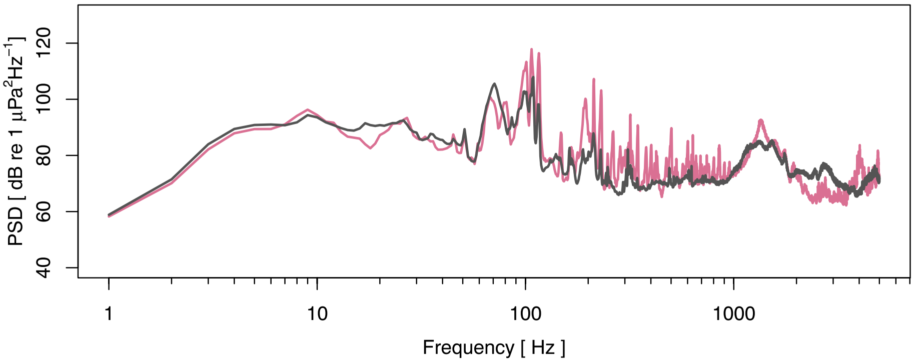

Fig. 2. Power spectral density (PSD) graph of the control (gray) and added noise (pink) treatment conditions. The lines depict the root mean square levels (RMS). Higher decibels (dB) indicate greater sound intensity and as the dB scale is logarithmic, an increase of 10 dB corresponds to a 10-fold increase in PSD at that frequency. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

acclimation tank and placed in an experimental tank without replacement for the experiment duration. The amphipods were randomly allocated to ensure that any observed effects would not be specific to a certain sex or life phase, but rather representative of an average reaction of the natural population at the time of investigation. Ten replicate tanks were implemented for each treatment (added noise, no added noise) and 300 individuals were employed in total (2 treatments × 10 replicates × 15 amphipods per replicate). After an initial 24 h acclimation and starvation period, the experiment was started with the addition of the noise treatment and small thalli of *F. spiralis* (0.80 ± 0.02 g wet weight). The experiment lasted 5 days (120*h*) total. Every 24 h, the position of all amphipods within each tank was assessed without manipulating the experimental environment. Five distinct locations were selected for the evaluations: (1) attached to the noise egg, (2) on the algal thallus, (3) under the tile, (4) attached to the tank wall at or above the waterline, and (5) elsewhere in the aquarium (Fig. 1). Dead individuals were noted and removed from the tank together with the algae.

Every 24 h, all algae were carefully removed after each habitat choice assessment, blotted dry with paper towels, and weighed for their wet weights. Fresh thalli were then immediately supplied. A separate control run without animals was conducted using ten tanks (5 with noise, 5 without noise; 24 h runtime) to control for autogenic algae weight changes. Feeding rates per tank were then calculated as follows according to Cronin and Hay (1996):

$$Feeding\ rate = \frac{\left(W_i \times \frac{C_f}{C_i}\right) - W_f}{Day}$$

where W_i = initial weight, W_f = final weight, C_i = initial control weight, C_f = final control weight. The obtained rates were divided by the number of live individuals per tank to calculate the average per-individual feeding rate for comparison. The average overall consumption per individual was calculated for each tank by adding up the average daily per-individual feeding rates (which also serve as consumption per day) from days 2 to 5 (explained in section 2.5.2). After the final habitat assessment and algae sampling at the end of day 5, one male and one female were collected as a pre-copulatory couple from each tank and flash frozen using liquid nitrogen before being stored at −80 °C for metabolic enzymology. In the pre-copulatory phase, male amphipods mate-guard receptive females until they molt. Collecting amphipods in this phase thus ensured that all individuals were correctly sexed and at similar points in their reproductive- and molt cycles.

In order to analyze mitochondrial enzymatic activity, a homogenization buffer (20 mM Tris(hydroxymethyl)aminomethane, 1 mM EDTA, 0.1 % Tween 20, pH 7.4) was added to the flash-frozen samples in a ratio of 1:4 (weight/volume, or *w/v*) for males and 1:6 for females (Hardewig et al., 1999). Ratios differed between sexes as the collected females (65 mg ± 13 mg) were lighter than the males (90 mg ± 7 mg) and thus required more buffer to have enough sample extract for all enzymatic measurements. The samples were homogenized using a Mixer Mill 301 (Retsch GmbH & Co. KG, Germany) at its maximum power of 1800 rpm for 2 min and centrifuged at 500 ×*g* at 4 °C for 5 min (HERMLE Z383K, Germany) (Chatelain et al., 2008). All enzyme activities were measured in supernatant. The remaining supernatant was frozen at −20 °C for soluble protein measurements (Bradford, 1976) to standardize enzyme activities per mg protein ($\text{U}\cdot\text{mg}^{-1}_{\text{protein}}$; U = μmol substrate$\cdot$min^{-1}). The activities of four enzymes were measured in triplicates at room temperature using a microplate photometer (Multiskan Spectrum 1500, Thermo Scientific, USA) following their respective methods in the order listed: 1) cytochrome *c* oxidase (COX), representing complex IV of the mitochondrial electron transport system in aerobic respiration, by following the decrease of the extinction of cytochrome *c* at 550 nm (Moyes et al., 1997). Sodium dithionite in excess (removed after with G-25 gel filtration) was used to reduce cytochrome *c*; 2) electron transport system (ETS), representing complexes I and III, by monitoring the reduction of Iodonitrotetrazolium chloride (INT) (Lannig et al., 2003) which shows an increase in absorbance at 485 nm; 3) citrate synthase (CS), representing the Krebs cycle, by detecting the transfer of sulphydryl groups to 5,5’dithiobis-2-nitrobenzoic acid (DTNB) at 420 nm (Srere et al., 1963); 4) lactate dehydrogenase (LDH), a marker of the anaerobic pathway, by following NADH absorbance when the enzyme converts pyruvate to lactate at 340 nm (Greenway and Storey, 1999; Thibault et al., 1997).

2.5. Statistical analyses

All analyses were performed in RStudio (2023.12.1) with R (4.3.2). Model assumption validations were checked and descriptive statistics and graphical figures were produced using GraphPad Prism (8.0.2).

2.5.1. Habitat choice

For the comparison of habitat choice, a multinomial regression was performed for each day of the experiment at a 95 % confidence level using the package *nnet* (Venables and Ripley, 2002). “Added noise” (present and absent) was designated as the predictor while “Habitat choice” was designated as the response variable and comprised of six categories: (1) noise egg, (2) algae thallus, (3) tile, (4) waterline, (5) elsewhere, and (6) dead. All categories were mutually exclusive as well as exhaustive, i.e. one individual could only belong to one of the categories, and all individuals had to belong to a category. The habitat “Elsewhere” was designated as the reference category.

The habitat choice of *M. marinus* under noise exposure through time was analyzed using an additive and an interactive repeated measures multinomial regression at a 95 % confidence level using the package *nnet* (Venables and Ripley, 2002). The variable specification was the same, except that “Day” was added as a second predictor and “Tank” nested within “Day” was added as a random within-subjects factor. The significances of individual predictors were ascertained by performing likelihood ratio tests (χ^2-test, type III), also at a 95 % confidence level, between the full and null models for each predictor and their interaction using the package *car* (Fox and Weisberg, 2019). Using the coefficients from the full interactive model, the predicted probabilities (in %) of amphipods appearing in each habitat under both control and noise conditions was also calculated for each day using the function predict() in the package *stats* (R Core Team, 2022).

The noise treatments of four of the ten replicates broke down over the course of the experiment due to noise egg motor malfunctions. They were thus excluded from the repeated measures analyses across all days for habitat choice and feeding rate as well as from the enzymatic activity analyses. Analyses of individual days for both habitat choice and feeding rate, however, included all active replicates from that day, i.e. replicates where the noise egg did not stop.

2.5.2. Feeding rates

For each individual day, a linear model of the calculated feeding rates was performed at a 95 % confidence level using the package *stats* (R Core Team, 2022). “Feeding rate” was designated as the response variable while “Added noise” (present and absent) was designated as the predictor. The same model was performed to describe the influence of noise on overall algae consumption from day 2 to 5. To describe how noise affects the feeding rate of *M. marinus* through time, an additive and an interactive repeated measures linear model were performed at a 95 % confidence level using the package *lme4* (Bates et al., 2015). As with habitat choice, “Day” was added as a second predictor and “Tank” nested within “Day” was added as a random within-subjects factor. The significances of individual predictors were ascertained by performing likelihood ratio tests (F-test, type III), also at a 95 % confidence level, between the full and null models for each predictor and their interaction using the package *car* (Fox and Weisberg, 2019).

Day 1 (24 h) was excluded from the repeated measures analyses as the starvation period meant that the initial condition of the amphipods differed from that of days 2 to 5. The normality of residuals and homogeneity of variances were visually inspected through QQ- and residual vs. predicted plots and verified using Shapiro-Wilk tests. Based on these assessments, one outlier from day 5 was removed from the datasets used for the statistical analyses.

2.5.3. Enzymatic activity

As the enzymatic activity data did not meet normality and homoscedasticity assumptions despite data transformations, the non-parametric PERMANOVA (Permutational Multivariate Analysis of Variance) was chosen to allow for the comparison of between-group and within-group variation using permutations instead of a specific distribution (as ANOVA does). The effect of the factors “Sex” and “Added noise” for all enzymes was tested using two-way PERMANOVAS in a fully crossed design with 999,999 permutations and at a 95 % confidence level for each enzyme. The tests were performed using the package *RVAideMemoire* (Hervé and Hervé, 2020).

3. Results

3.1. Habitat choice

Added noise did not affect the habitat choice of *M. marinus* over time ($\mathrm{LRT}_{\mathrm{noise:day}}$: $\chi^2(5) = 1.329$; $p = 0.932$; Fig. 3). Correspondingly, noise and time as main effects also had no significant effect on habitat choice ($\mathrm{LRT}_{\mathrm{noise}}$: $\chi^2(5) = 8.673$; $p = 0.123$, $\mathrm{LRT}_{\mathrm{day}}$: $\chi^2(5) = 4.871$; $p = 0.432$). There was also no significant effect of added noise on habitat choice in the direct comparisons of individual days (Table S2).

3.2. Feeding rates

Added noise did not affect the feeding rate of *Marinogammarus marinus* over time ($\mathrm{LRT}_{\mathrm{noise:day}}$: $F_{(1,13)} = 0.379$; $p = 0.549$; Fig. 4). Correspondingly, time as a main effect also did not seem to affect amphipod feeding ($\mathrm{LRT}_{\mathrm{day}}$: $F_{(1,14)} = 1.787$; $p = 0.203$). Noise in general had a marginally significant effect on amphipod feeding ($\mathrm{LRT}_{\mathrm{noise}}$: $F_{(1,13)} = 4.243$; $p = 0.060$). When individual days were analyzed, animals under added noise conditions fed significantly less algal material than those under control conditions on day 3 ($\mathrm{LRT}_{\mathrm{noise}}$: $F_{(1)} = 7.831$; $p = 0.014$). Though non-significant, this trend could also be observed on days 2, 4, and 5 (Fig. 4; Table S1). In both treatments, the amphipods consumed on average more in the first day than they did on all subsequent days (Fig. 4).

That animals under noise conditions fed generally less than those under control conditions after day 1 was confirmed by a clear effect of noise on the total amount of consumed algal material by *M. marinus* ($\mathrm{LRT}_{\mathrm{noise}}$: $F_{(1)} = 10.561$; $p = 0.006$; Fig. 5) from day 2 to 5. Individuals under added noise conditions fed significantly less overall than those under control conditions. Over a period of 96 h, *M. marinus* under noisy conditions consumed an average of 0.023 ± 0.004 (SD) mg per individual while those under control conditions consumed an average of 0.031 ± 0.006 mg per individual.

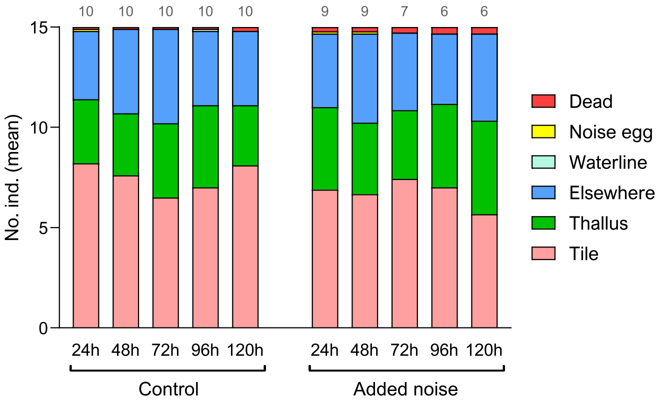

Fig. 3. Spatial distribution of *Marinogammarus marinus* individuals over time under control and added noise conditions. The count on top of each bar indicates the number of active replicates from that day. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

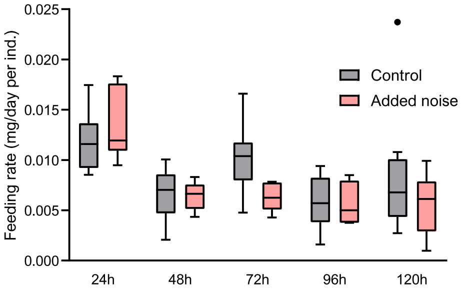

Fig. 4. Feeding rates (mg/day per ind.) of *Marinogammarus marinus* under control (gray) and added noise (pink) conditions over a 5-day period (120 h). The median, first and third quartile, and 1.5 interquartile range Tukey fences are depicted. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Enzymatic activity

The response of ETS activity to added noise was not sex-specific (PERMANOVA; $F_{(1,28)} = 0.787$, $p = 0.404$, Fig. 6B). However, the added noise treatment significantly increased ETS activity in both sexes (PERMANOVA; $F_{(1,28)} = 4.468$, $p = 0.037$; Fig. 6B). Male *M. marinus* exhibited ETS activities of 2.97 ± 0.862 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ and 3.47 ± 1.06 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ in control and noise treatments, respectively, while females were characterized by ETS activities of 2.71 ± 0.728 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ and 3.93 ± 1.87 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ in control and noise treatments, respectively (Fig. 6B). The ETS activity did not differ significantly between sexes (PERMANOVA; $F_{(1,28)} = 0.001$, $p = 0.976$, Fig. 6B).

The CS activity of males and females were differently affected by the added noise (PERMANOVA; $F_{(1,28)} = 4.741$, $p = 0.036$, Fig. 6C). The added noise treatment significantly elevated CS activity (PERMANOVA; $F_{(1,28)} = 4.680$, $p = 0.036$; Fig. 6C). Males exhibited similar CS activities of 5.08 ± 3.50 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ and 5.07 ± 1.21 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ under control and added noise conditions, respectively, while females exhibited CS activities of 4.15 ± 1.10 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ under control conditions and 8.36 ± 3.73 $\mathrm{mU{\bullet}mg_{protein}^{-1}}$ (nearly two-fold) under added noise conditions (Fig. 6C).

The activities of COX and LDH were not affected by the added noise

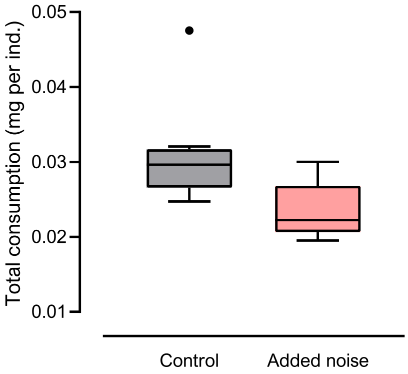

Fig. 5. Total amount of algal material consumed per individual of *Marinogammarus marinus* (mg) under control and noise conditions from day 2 to 5 (96 h). The median, first and third quartile, and 1.5 interquartile range Tukey fences are depicted.

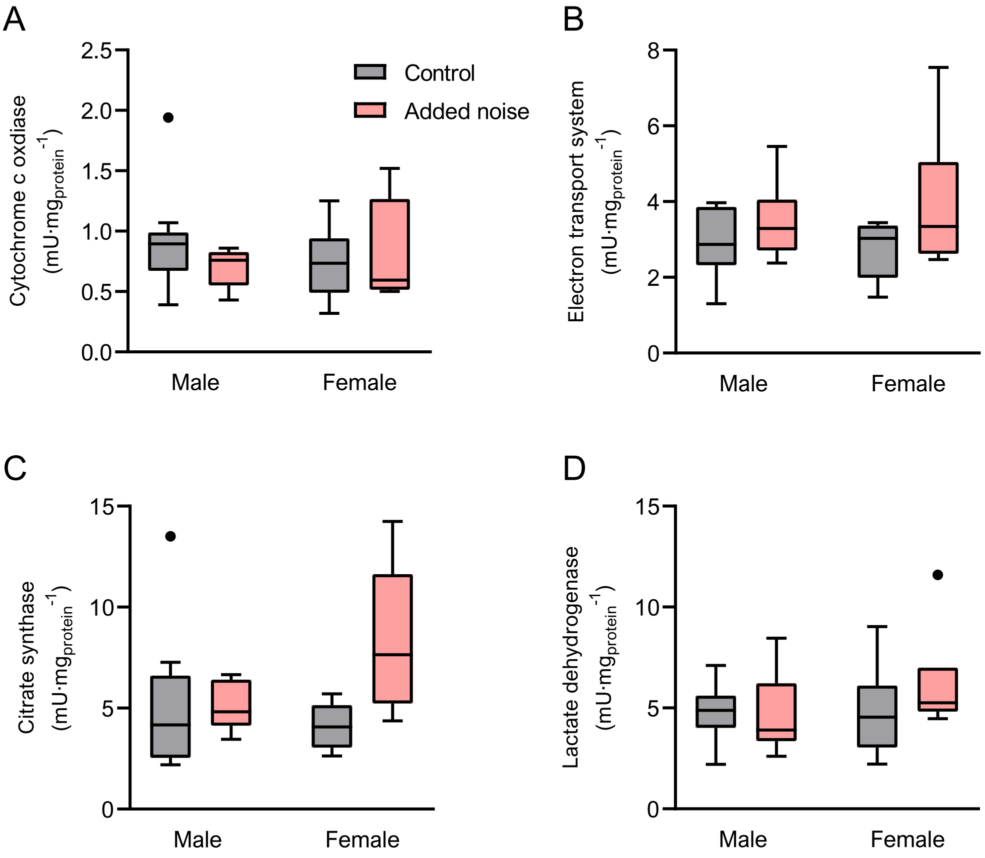

Fig. 6. Enzymatic activities (mU•$\text{mg}_{\text{protein}}^{-1}$) of cytochrome *c* oxidase (A), electron transport system (B), citrate synthase (C), and lactate dehydrogenase (D) measured in *Marinogammarus marinus* individuals after 5 days under control (gray; $n = 10$ for each sex) and added noise (pink; $n = 6$ for each sex) conditions. The median, first and third quartile, and 1.5 interquartile range Tukey fences are depicted. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

treatment and were not different between sexes (Fig. 6A, D; Table S3).

4. Discussion

4.1. Habitat choice

The habitat choice of *M. marinus* seemed unaffected by the presence of added continuous noise. Amphipods have been shown to shift their habitat usage or emigrate altogether in response to different environmental drivers, of which predator presence has been particularly studied (Beermann et al., 2018; de Oliveira Fernandes et al., 2022; Thiel and Reise, 1993). Habitat choice has also been observed to be both directly and indirectly influenced by factors such as competitor presence and intraspecific dynamics (Drolet et al., 2013; Piscart et al., 2011) as well as anthropogenic pollutants such as toxic substances and light (De Lange et al., 2006; Eriksson Wiklund et al., 2009; Lynn et al., 2021). Here, *M. marinus* could have simply been unaffected by added noise. However, probable differences in noise levels across the different habitats could have affected the results of this parameter. This is particularly true of smaller tank setups where dimensions constrain sound propagation and result in acoustic distortions and boundary effects (Filiciotto et al., 2016; Parvulescu, 1967). Still, comparison of the control and added noise treatments show that the low frequencies remain the dominant difference (Fig. 2). It also cannot be excluded that the effects could not be detected in the current setup as habitat choice was only assessed during the daytime. Results may be different during the nighttime when mesograzing amphipods are probably more active (e.g., less association with shelter, more association with algae thallus) (Buschmann, 1990; Navarro-Barranco et al., 2020). This would corroborate the discrepancy between the observed habitat choices and the measured feeding rates as the latter implies that the amphipods had a stronger association with the algal habitat under control conditions.

4.2. Response of feeding to noise exposure

In the presence of added noise, the amphipod mesograzer *M. marinus* generally showed lower feeding rates, particularly pronounced in the comparison of average algal material consumed over the course of the entire experiment. Higher feeding rates in both treatments in the first day of the experiment were likely due to the initial starvation period. Other crustaceans also exhibited impaired foraging behavior in response to “white” noise or ship noise playback exposure, detecting food less often and/or getting distracted from feeding more often (Azarm-Karnagh et al., 2023; Wale et al., 2013). Accordingly, *M. marinus* may have been more distracted from feeding, resulting in lower feeding rates although this could not be supported by the habitat choice outcomes observed in the daytime.

Although it is largely unknown how amphipod crustaceans perceive sounds, a structure found in gammarids has been interpreted as a kind of lateral line organ which could allow for the sensing of vibrations within some frequency range (Beermann et al., 2015; Platvoet et al., 2007) and thus the detection of potential threats. Amphipods have been shown to display predator-specific avoidance behaviors seemingly based on factors such as predator type and predation risk (Åbjörnsson et al., 2000; Reynolds and Bruno, 2013; Van Son and Thiel, 2006). Most behavioral responses of amphipods to predator presence had been attributed to chemical cues (e.g., Beermann et al., 2018; Reynolds and Sotka, 2011), but responses to acoustic cues of natural predators have been reported for other malacostracan crustaceans such as crabs (Hughes et al., 2014). The added noise employed in the current study only had a mechanical component, thus the gammarids in the current experiment may have perceived a potential threat through vibrations in the water and/or substrate but without the chemical confirmation. A reduction in foraging activities in response to acoustic cues has been reported for decapod crustaceans (e.g., Hughes et al., 2014; Wale et al., 2013). Juveniles of the brachyuran crabs *Cyrtograpsus altimanus* and *Neohelice granulata* actively oriented away from predator-associated sounds (Moyano et al., 2021). Therefore, a similar reaction by the amphipods used in the current experiment (i.e. reduced feeding due to a stress response to a potential threat) may be likely.

Reduced feeding from noise-induced stress may negatively impact amphipods in several ways. The most direct potential effects would be lower growth rates and, if juveniles would be similarly affected, timelines for reaching sexual maturity that deviate from the norm (Maszczyk and Brzezinski, 2018; Moore and Farrar, 1996). Reproductive success may also be affected if there is insufficient energy available for processes such as egg production and brooding (Moore and Farrar, 1996; Sutcliffe, 1993; Wiklund et al., 2008). Behavioral changes (e.g., reduced activity, different feeding strategies) as well as metabolic adjustments are also possible to cope with limited availability or intake of resources (Hervant et al., 1997; Lehtonen, 1994; Sutcliffe, 1993). Starvation has been shown to influence the sensitivity of amphipods to other factors such as temperature and chemical pollutants (Alonso et al., 2010; Semsar-kazerouni et al., 2020). Consequently, the survival of affected individuals may be jeopardized, or at least impaired, if their reduced consumption is sustained. At the same time, as mesograzers exert top-down effects on the algae, the reduced grazing pressure could benefit algae growth. While LFN has been shown to be detrimental to some macrophytes (Solé et al., 2021), added continuous LFN may, at least in the current system, have indirect positive effects on the macroalgae.

4.3. Mitochondrial enzyme activity

Added noise increased the activities of two key enzymes linked to the aerobic metabolic pathway in *M. marinus*: the electron transport system (ETS) and citrate synthase (CS). Electron transport system activity is often used as an estimator for the respiratory rate of an organism (e.g., Båmstedt, 1980; Verslycke et al., 2004). Accordingly, though not a one-to-one equivalence, added noise probably led to an increase in respiration (and transitively, oxygen consumption) rates of *M. marinus* which could be an indication for a stress response. This is in line with the observed lactate dehydrogenase (LDH) activity, which remained stable. As LDH is a core part of the anaerobic metabolic pathway (Farhana and Lappin, 2020), the absence of significant fluctuations in its activity signifies that the animals and their tissues did not incur oxygen debts in the current experiment and that *M. marinus* did not resort to anaerobic respiration under stress from added noise alone. Nonetheless, the simultaneous reduction in feeding rates indicates that *M. marina* experienced stress under added LFN. Chronic exposure to a stressor, or a combination of stressors, that exceeds the resilience of an organism may cause the concurrent symptoms of increased ETS and decreased feeding rates in amphipods (Wüthrich et al., 2025). In this state, survival is prioritized and resources are allocated away from digestion while maintaining high respiratory activity levels.

In contrast, the gammarid amphipod *Gammarus locusta* displayed significantly lower oxygen consumption rates with no changes in the same enzymatic activities measured in the current study when exposed to the same sounds emitted by a noise egg (Terschek et al., 2025). The exposure time was, however, shorter at three days and thus may have been insufficient for stress effects to reflect in enzyme activities. The effects of multiple stressors on both feeding and ETS in *Gammarus fossarum*, for example, only became apparent after chronic (and not an acute) exposure (Wüthrich et al., 2025). The contrasting results could also potentially indicate species-specific behavioral differences in response to anthropogenic noise, even among species that are taxonomically closely related and ecologically very similar. *Gammarus locusta* and *M. marinus* are known, however, to have similar anti-predator responses, which is to reduce activity in the presence of fish predators (Alexander et al., 2013; Beermann et al., 2018; Kaiser et al., 1992). Further research is therefore needed to confirm the differing responses to LFN and to elucidate the mechanisms underlying the seemingly greater sensitivity of *M. marinus* to added LFN.

That ETS (representing complexes I and III in the current study) activity increased while cytochrome *c* oxidase (COX; complex IV) activity stayed the same may signify a functional imbalance or dysfunction in the mitochondria. Complexes I and III are the main sites of electron leakage (and thus mitochondrial reactive oxygen species (ROS) production), while COX catalyzes the transfer of electrons to oxygen to form water, a stable end-product. Thus, an increase in the activities of complexes I and III without a concomitant increase in that of COX may result in an increase in ROS generation (Hernansanz-Agustín and Enríquez, 2021; Sabharwal and Schumacker, 2014; Srinivasan and Avadhani, 2012).

Citrate synthase is a key enzyme of the aerobic metabolic pathway that catalyzes the Krebs cycle, a series of reactions through which the molecule acetyl coenzyme A (derived mostly from pyruvate from sugars) is oxidized to produce energy as well as intermediates that feed into further energy-generating processes (Berg et al., 2019). As this cycle takes place in the mitochondria, CS activity can be used as a biomarker for mitochondrial density and tissue oxidative capacity (e.g., Larsen et al., 2012; Lemos et al., 2003; Vigelsø et al., 2014). Interestingly, while ETS displayed elevated activity in both sexes when exposed to added noise, CS activity increased only in females. All females sampled for the enzymatic activity analysis were in the pre-copulatory phase, an energetically-intensive phase as the body prepares for molting and ovulation (Hyne, 2011; Vlasblom, 1969). Females stressed during this demanding, critical phase may thus require even more energy on top of what is already required for survival and reproduction. Therefore, the increase in CS activity suggests that female *M. marinus* possibly increased their mitochondrial density to hike the rate of energy production in order to meet increased energy demands under stressful conditions.

Increased energy demands in females combined with the decreased feeding (nutrient intake) in all noise-exposed *M. marinus* hints toward a plausible and unsustainable increase in reliance on the breakdown of energy storages (e.g., glycogen, triglycerides) for energy production and maintenance of homeostasis. In general, starvation experiments with *Gammarus fossarum* suggested that gammarid sexes seem to display different metabolic needs (Charron et al., 2014). Female amphipods may therefore be even more sensitive than males to the effects of anthropogenic noise pollution despite all amphipods feeding generally less in noisy conditions.

In amphipods, the measurement of mitochondrial enzyme activities and expression has been used to evaluate metabolic responses and/or plasticity to factors such as temperature (Jakob et al., 2021; Vereshchagina et al., 2021), chemical pollutants (Wu et al., 2014), and multiple stressor scenarios (Collins et al., 2021; Elder and Seibel, 2015). This current study indicates that these mitochondrial biomarkers hold potential for assessing the effects of anthropogenic noise on amphipods.

4.4. Conclusion

Anthropogenic noise pollution can affect marine invertebrates in ways that impact the functions they serve in their respective ecosystems (e.g., Solan et al., 2016; Wang et al., 2023; Wang et al., 2022). Here, a mesograzing amphipod exhibited reduced feeding performance and elevated activity levels in some enzymes associated with aerobic respiration when exposed to anthropogenic low-frequency sounds. The reduction in feeding combined with an increased metabolism and possibly increased ROS production would likely affect the overall homeostasis of some mesograzers if sustained over longer periods of time. The ever-rising sound levels in the oceans may thus have consequences for algae-dominated animal communities in coastal areas.

CRediT authorship contribution statement

Sheng V. Wang: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Anna Terschek:** Writing – review & editing, Resources, Methodology, Investigation. **Nelly Tremblay:** Writing – review & editing, Methodology, Formal analysis. **Maarten Boersma:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Alexa Wrede:** Supervision, Writing – review & editing. **Jan Beermann:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

Funding

This study was conducted within the framework of the project CoastalFutures (grant no. 03F0911J) with funding from the German Federal Ministry of Education and Research (BMBF). SVW is financially supported by and MB acknowledges funding from the BMBF under the same grant and project (CoastalFutures). JB was financially supported by the German Federal Agency for Nature Conservation (BfN) under grant no. 3519532201 and 3522521401 (LABEL project). AW is financially supported by funding from the BMBF to JB and MB under grant no. 03F0932A (JPI-Oceans project ORCHESTRA). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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.

Acknowledgements

The authors would like to thank Dr. Karin Boos for her assistance with the habitat choice statistical analysis. Further, we thank the two anonymous reviewers for their constructive feedback on an earlier version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.118764.

Data availability

Data will be made available on request.

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