Noisy waters can influence young-of-year lobsters' substrate choice and their antipredatory responses[☆]

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ABSTRACT

Offshore human activities lead to increasing amounts of underwater noise in coastal and shelf environments, which may affect commercially-important benthic invertebrate groups like the re-stocked Helgoland European lobster (*Homarus gammarus*) in the German Bight (North Sea). It is crucial to understand the impact tonal low-frequency noises, like maritime transport and offshore energy operations, may have on substrate choice and lobsters' behavior to assess potential benefits or bottlenecks of new hard-substrate artificial offshore environments that become available. In this study, we investigated the full factorial effect of a tonal low-frequency noise and predator presence on young-of-year (YOY) European lobsters' in a diurnal and nocturnal experiment. Rocks and European oyster shells (*Ostrea edulis*) were offered as substrate to YOY lobsters for 3 h. Video recordings (n = 134) allowed the identification of lobsters' initial substrate choice, diel activity and key behaviors (peeking, shelter construction, exploration and hiding). To ensure independence, YOY lobsters in the intermolt stage were randomly selected and assigned to the experimental tanks and used only once. We provide the first evidence that stressors alone, and in combination, constrain YOY lobsters' initial substrate choice towards rocks. During nighttime, the joint effect of exposure to a constant low-frequency noise and predator presence decreased antipredator behavior (i.e., hiding) and increased exploration behavior. Noise may thus interfere with YOY lobsters' attention and decision-making processes. This outcome pinpoints that added tonal low-frequency noise in the environment have the potential to influence the behavior of early-life stages of European lobsters under predator pressure and highlights the importance of including key benthic invertebrates' community relationships in anthropogenic noise risk assessments. Among others, effects of noise must be taken into consideration in plans involving the multi-use of any offshore area for decapods' stock enhancement, aquaculture, and temporary no-take zones.

1. Introduction

Sounds generated by human activities can be divided into high-intensity impulsive noise (e.g. pile-driving, underwater blasting) and low-frequency stationary noise (e.g. tidal and wind turbines) (Peng et al., 2015; Tidau and Briffa, 2016; Duarte et al., 2021). High-intensity impulsive noise has been linked to numerous negative responses amongst marine mammals (Lucke et al., 2009), fish (Casper et al., 2013; Fewtrell and McCauley, 2012) and invertebrates (Day et al., 2019). In

turn, constant exposure to low-frequency stationary noise has received less attention, but hearing sensitivity curves for decapod crustaceans such as common prawns (*Palaemon serratus*), mud crabs (*Paneopus* spp) and Norway lobsters (*Nephrops norvegicus)* show the highest sensitivity for the lowest tested frequencies (100 Hz, 75 Hz and 20–200 Hz respectively) (Goodall et al., 1990; Hughes et al., 2014; Lovell et al., 2005). Crustaceans are more perceptive to low-frequency particle motion instead of sound pressure variations due to their lack of gas filled organs (e.g. swim bladders) (Breithaupt, 2002). Particle motion

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detection is used by invertebrates to locate sound sources in their environment (Popper et al., 2014; Hawkins et al., 2015; Nedelec et al., 2016). Locating the position of a sound source can allow animals to determine the direction and distance of predators or prey and consequently respond appropriately to the stimuli (Popper and Hawkins, 2018). Experimental results suggest that low-frequency (generally defined as <500 Hz) (Carey and Evans, 2011) anthropogenic noise can alter several key behaviors in crustaceans such as: foraging, antipredator responses, shell searching behavior and grouping behavior (Wale et al., 2013a; Roberts and Laidre, 2019; Tidau and Briffa, 2019a). Furthermore, Filiciotto et al. (2014) observed that boat noise induced biochemical stress responses in Mediterranean spiny lobsters (*Palinurus elephas)* and increased locomotor behavior. The latter may be ecologically detrimental as animals may expose themselves more to predators under noisy conditions.

The European lobster (*Homarus gammarus*) habitat extends along the west coast of Europe, from northern Norway to the Iberian Peninsula and further south to the Azores and Morocco. They are also present in most of the Mediterranean Sea (Holthuis, 1991). Young-of-year (YOY) lobsters' density is usually used as recruitment index in lobster populations (Howell, 2012) and to identify nursing grounds, as YOY lobsters have molted to juvenile stages within the past 12 months (Cowan et al., 2001). In the German Bight, the Helgoland European lobster population was an important source of income for the island until the 1950s, with landings reaching 50 T yr^{-1} (Klimpel, 1965). A combination of overfishing, pollution and extensive habitat destruction by the bombing of the island during and after the Second World War, are used to explain the 1960s' collapse in fisheries yields and population densities (Franke and Gutow, 2004). To counter this, the Alfred-Wegener-Institut (AWI) Helmholtz-Zentrum für Polar-und Meeresforschung-Biologische Anstalt Helgoland initiated a program between 1999 and 2009 to investigate whether lobster restocking was possible (Schmalenbach et al., 2011). Through this initiative, a total of over 14,000 YOY lobsters were released between 2000 and 2017 around Helgoland. Presently, restocking has taken off in earnest through the lobster conservation company Reefauna, with up to 6000 YOY lobsters released annually. As the construction of an offshore wind farm cluster in the German Bight (North Sea) led to an examination on the potential of turbine foundations as an artificial hard substrate habitat for decapods (Krone et al., 2017), YOY lobsters were released in these sites in a pilot project. Moreover, this study (Krone et al., 2017) is often cited in Germany and elsewhere in offshore wind farm multi-use project proposals to support the concept of founding structures as suitable rocky habitats for key exploitable species (Tonk and Rozemeijer, 2019). In the North Sea, offshore wind farms, as well as approximately 1500 shipwrecks (Krone and Schröder, 2011), few glacial bolder fields (BSH, 2016) and the natural subtidal cliffs of Helgoland offer substrata for the development of the local population of several species requiring hard substrates, including the European lobster (Schütt et al., 2001).

To tackle the lack of knowledge about the responses of *H. gammarus* to anthropogenic low-frequency sources, which are increasing in its natural environment, we investigated the full factorial effect of low-frequency tonal noise in addition to crab predator presence on hatchery born YOY European lobsters. We used YOY lobsters because this life stage is vulnerable as its survival depends on finding suitable shelter for protection. YOY lobsters are cryptic in the wild as they spend most of their time hiding in complex shelters such as rocks, seaweed, reefs (Able et al., 1988; Lawton and Lavalli, 1995), and other interstitial spaces like cobble and mussel shells (Linnane et al., 2000). As substrates, we used rocks and shells of European oyster (*Ostrea edulis*) because past studies on substrate selection on the congeneric American lobster (*Homarus americanus)* revealed that substrates with preformed crevices were the preferred settlement habitats (Botero and Atema, 1982). The use of oyster shells in particular is motivated by the fact that historically large sections of the German Bight were covered by reefs of *O. edulis*, which may have played an important role in providing refuge to young

lobsters. The "RESTORE- Restoration of the stocks of the European oyster in the German North Sea" program, financed by the German Federal Agency for Nature Conservation (BfN) and conducted by AWI, aims to reestablish the extensive sublittoral European oyster reefs that were extirpated by overfishing and demersal trawlers in the 1950s (Gercken and Schmidt, 2014; Pogoda, 2019). As O. edulis can form a reef-type habitat, which offers small crevices for small benthic fauna to seek shelter, assessing the suitability of oyster reefs for released YOY lobsters is a pertinent topic.

We included predator presence as a potential driver of behavior because predatory crabs, like the green crab *Carcinus maenas* (Rayner and McGaw, 2019; Mercer et al., 2001) and the edible crab *Cancer pagurus* (van der Meeren, 2000) are common in the subtidal habitats of the German Bight. Natural and artificial hard-substrate habitats available in the North Sea should provide shelter and resources to juvenile lobsters and potential predators, such as *C. maenas* which can influence foraging and shelter behavior (time spent hiding) of juvenile lobsters (Rossong et al., 2011). Few studies have investigated whether noise is an additional stressor that alone or in combination with predator presence has an influence on substrate choice and behaviors associated with survival. The assessment of prey-predator and substrate choice relationships in a constant low-frequency noise context can provide insights into natural and artificial hard-substrate community dynamic exposed to low-frequency anthropogenic noise.

We aimed at answering three questions: (1) Does tonal low-frequency noise and/or predator presence affect the behavior of YOY lobsters? (2) In the view of European oyster reestablishment, do YOY lobsters prefer to seek shelter amongst oyster shell or rock substrates? (3) Does noise exposure and/or predator presence influence this choice?

2. Material and methods

2.1. Origin of animals and maintenance

The study was carried out at AWI Helmholtz-Zentrum für Polar-und Meeresforschung (Helgoland, Germany). Young-of-year (YOY) European lobsters (*H. gammarus)* were born from ovigerous females captured by local fishermen in the rocky subtidal zone around the island of Helgoland (German Bight, North Sea, 54°11:3′N, 7°54.0′E). After hatching, lobsters were reared in batch cultures until post-larval stage and kept in individual basins connected to a flow-through seawater system (pH: 7.98 ± 0.08, salinity: 33.63 ± 0.22, temperature: 14.78 ± 0.20) under natural photoperiods. Lobsters were fed daily *ad libitum* with *Artemia salina* nauplii. YOY lobsters with carapace length of 13.0 ± 1.5 mm (mean ± SD) were used for the experiments. To act as predator, green crabs (*C. maenas*) with carapace width of 62.0 ± 1.0 mm were captured two weeks prior to the experiments by research vessel *Aade* using baited traps. Crabs were kept in holding tanks in a temperature (14 °C) and light (12:12 h light/dark) controlled room with circulating ultraviolet and biofiltered seawater. Crabs were daily fed with frozen shrimps prior to their transfer to the experimental tanks.

2.2. Experimental design

Experiments were carried out under the following setup in a separated temperature (14 °C) and light (12:12 h light/dark) controlled room. The bottom part of 16 identical plastic rectangular tanks (56.6 × 36.0 × 42.0 cm) filled with 60 L of seawater (pH: 7.97 ± 0.04, salinity: 32.72 ± 0.77, temperature: 14.27 ± 1.00) was uniformly covered with a 3.0 cm layer of coarse sand. The tanks were divided into four equally sized substrate areas providing shelters (each corner; 19.0 × 17.0 cm) containing (1) rocks (6.0–14.5 cm long) placed close together and on top of each other, creating spaces and crevices and (2) *O. edulis* shells (9–12 cm long) likewise placed close together and on top of each other (Fig. S1). Each tank had rocks and oyster shells substrates placed diagonally across each other and their position was alternated for each run.

At the center of the tank, a concrete tetrapod (height: 7.5 cm, width: 9 cm) was attached to a plastic mesh cage to hold the crabs (12 × 6.5 × 5 cm; 5 mm mesh size) and a "noise egg" (see explanations section 2.3; de Jong et al., 2017) was positioned on top. This setup was the same for all tanks independent of treatment in order to maintain an identical land-scape. Each run, the tanks were physically placed randomly around the experimental room and then were randomly assigned to one of the four conditions: control (C), predator presence (P), added noise (N) and added noise + predator presence (NP). In the C and P treatments, the vibration-motor inside the noise egg was without batteries, and the crab cage was empty for N and C treatments. Above the tanks, a scaffold with a video camera (MQ8 Mini Camera, Shenzhen Qilesi Electronic Commerce Co, China) was placed to video-record lobster behaviors. This low-cost video camera allows multiple video recording at the same time with high-resolution imaging. The only downside is the limited recording time, which was about 1h30 in most cases. YOY lobsters in the intermolt stage were randomly selected and assigned to the experimental tanks and used only once to ensure experimental independence. All YOY lobsters were fed 3 h before the start of each experimental run. Each run, YOY lobsters were individually removed from the rearing compartment and released into the upper or lower side of the experimental tank equidistant from rocks and oyster shells (Fig. 1). At the moment of release into the experimental tank the corresponding condition (C, N, P, NP) was already in effect. All experimental tanks and substrates were rearranged, rinsed and refilled with new seawater in between trials. The daytime experiments were done in two daily runs from 9:00–12:00 h and 13:00–16:00 h, when YOY lobsters (n = 48; distributed into C = 11, N = 12, P = 11, NP = 14) were video-recorded and assigned to the experimental conditions. The nighttime experiments were done during natural darkness hours to respect the biological clock (18:00–21:00 h). For this setting, the tanks were fitted above with

Fig. 1. Diagram of experimental setup. At the center of the tank, a concrete tetrapod was attached to a plastic mesh cage to hold the crabs and a "noise egg" was positioned on top. Top view of experimental tank shows noise egg position (red asterisk), substrates (rocks and oyster shells), two release sites of lobsters (black X), and hydrophone position (gray oval). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

redlights (Mitras GHL, Prolifux) to record the lobsters' behavior without any disturbance. For the nighttime experiment, an increased number of YOY lobsters (n = 86; distributed into C = 23, N = 19, P = 22, NP = 22) were filmed and assigned to the experimental conditions. Daytime and nighttime YOY lobsters were a distinct set of individuals, and each lobster was used only once. As the experiment caused a minimum period of discomforts for YOY lobsters (3 h exposure), all specimens used were later returned to the Reefauna facilities. No post-experimental stress was observed. All procedures presented in this paper comply with the guidelines from the directives 2010/63/EU of the European parliament and of the Council of 22nd September 2010 on the protection of animals used for scientific purposes.

2.3. Sound characteristics

We used the "noise egg", a standardized device to produce low-frequency underwater noise for laboratory and field experiments. The sound produced is characterized as a constant low-frequency multi-tone with source frequency around 100 Hz (de Jong et al., 2017). The device has been previously used in aquarium experiments on the effect of noise on fish communication and courtship behavior (de Jong et al., 2018a; de Jong et al., 2018b). To confirm lobsters were exposed to distinct sound treatments (ambient and added noise), two calibrated SM3 hydrophones (sensitivity of −165 dB re: 1 V/μPa, Wildlife Acoustics Song Meter Automated Audio Recorder SongMeter, Wildlife Acoustics Inc., USA) were positioned on the sand beside the tetrapod (10.0 cm distance) to record the noise levels in all treatments (Fig. 1) in runs without lobsters during 4 h. The hydrophones were programmed at a sampling rate of 44, 100 (44•1 kHz) samples per second. The sound pressure level (SPL) and the Power Spectral Density (PSD) were computed, calibrated and visualized on 10 s records (see Table S1 for the noise conditions in each experimental treatment) using the R PAMGuide code (Merchant et al., 2015) (SPL: Fast Fourier Transforms 44,100, Hann window, 50% overlap, average for each file; PSD: Fast Fourier Transforms 44,100, Hann window, 50% overlap, 1 s average). For each treatment, recorded sounds were concatenated to form a single contiguous spectrogram. The correction factor for calibration was calculated using manufacturer's technical specifications, the sensitivity of the transducer, the user-defined gain settings for the deployment in decibels, and the zero-to-peak voltage of the analogue-to-digital converter.

We made sure YOY lobsters were exposed to distinct sound treatments by measuring the power spectrum, as in previous studies (Tidau and Briffa, 2019a, 2019b; Hubert et al., 2018). However, a limitation of our study was that we could not model particle motion due to the challenges of working in small tanks and the limitation of not having specialized equipment and sensors to do so (Martin et al., 2016; Roberts et al., 2016; Hawkins and Popper, 2016).

2.4. Video-recording analysis and substrate choice

For the analyses of lobster behavior, we watched 60 min of footage in the daytime experiment due to lower levels of lobster activity compared to nighttime (Fig. S2). The first 5 min were excluded after the lobsters were placed in the tanks to account for tank acclimation. Lobster behaviors that lasted a minimum of 1 s were identified and quantified by a visual continuous sampling procedure (each observed event duration was annotated in a sampling table). The following four behavioral units were defined and observed (Table S1):

Peeking: the lobster rostrum faces toward the outside of the shelter or is visible within the shelter crevices and then withdraws into the shelter in a backward movement or by changing direction; similar to retreat as defined in a previous study (Wickins et al., 1996);

Shelter construction: includes substrate manipulation observed as backward digging (using the first two or three pairs of walking legs and fanning the pleopods) and bulldozing, *i.e.* pushing sand using the chelipeds and first two or three pairs of walking legs (Cobb and Stanley
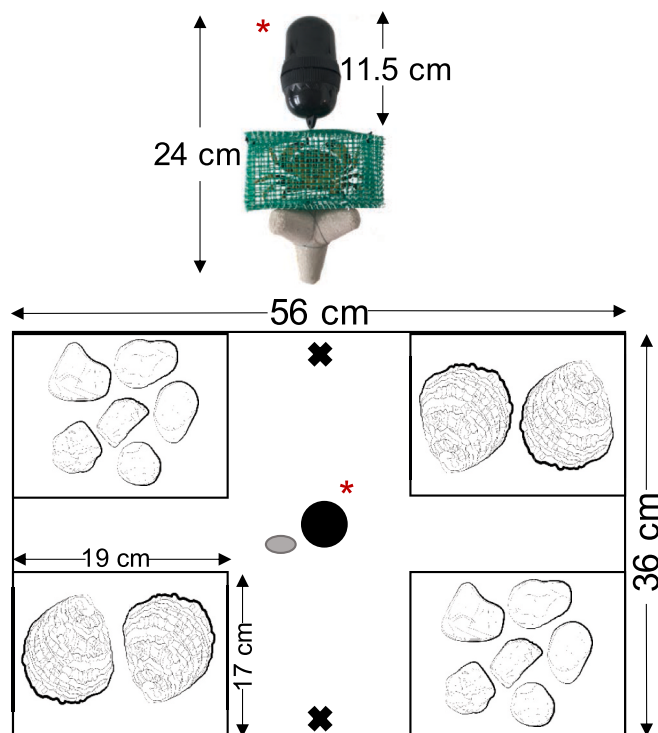
Cobb, 1971; Berrill, 1974; Wickins et al., 1996);

Exploration: the lobster leaves the substrate completely exposing its whole body (Mehrtens et al., 2005);

Hiding: lobster remains within the substrate and is not visible at all; Substrate choice was assessed manually twice, at the beginning using the video recorded (after 5 min acclimation) and at the end of each trial (after 3 h) when removing the lobsters from the experimental tanks. These were classified as initial and final choice, respectively.

2.5. Data analysis

All statistical data analyses were performed in RStudio (RStudio Team, 2021). For lobster activity analyses, the time spent by each individual engaging in a particular behavior was expressed as a proportion of the total observation time and analysis was carried out in arcsine transformed data. Arcsine transformation was used because data were better fitted when visualized through a quantile-quantile normal plot. Data were analyzed through linear mixed model effects with package *nlme* (Pinheiro et al., 2021). The full model included date of experimental repetition as a random factor, while added noise and predator presence and their interaction were considered fixed factors (full factorial design). Backward model selection for GLM and linear mixed models for both substrate choice and behavior analyses respectively (Table S2 and S3), were carried through the Akaike information criterion (AIC) score. Several models were created starting from the most complex, the full model (interaction between added noise and predator

presence), then the additive model (no interaction of factors), then the simplest with added noise and predator presence. Models were then ranked according to their AIC score, when the simplest model had the lowest AIC, that model was chosen. If the difference between the lowest AIC score and the second lowest score (ΔAIC) was greater than 3, the model with lower AIC was selected regardless of differences in complexity. Likelihood ratio test or chi-square test (depending on data set, see Table S2 and S3) was applied as hypothesis testing only when ΔAIC was less than 3, and the most complex test had a lower AIC score. When models differed significantly ($p < 0.05$), the one with lower AIC score was selected. If models did not differ, the simplest model was chosen. Additionally, a multivariate analysis using a principal component analysis (PCoA) to visualize results and permutational multivariate analysis of variance (PERMANOVA) to test significance was performed on all behaviors to complement the univariate analyses (see Fig. S6). For the substrate choice, Holm-Bonferroni was used to test significant difference amongst treatments (pairwise comparison based on p-values from the "summary" function); for time allocation to specific behaviors, Tukey's (HSD) post-hoc comparisons were performed through the package *emmeans* (Lenth, 2021). Substrate choice (*i.e.* the proportion of lobsters choosing a given substrate) was analyzed through generalized linear models (GLM). The full model included time of the day (day or night) and treatment interactions (control, predator presence, added noise and added noise + predator presence).
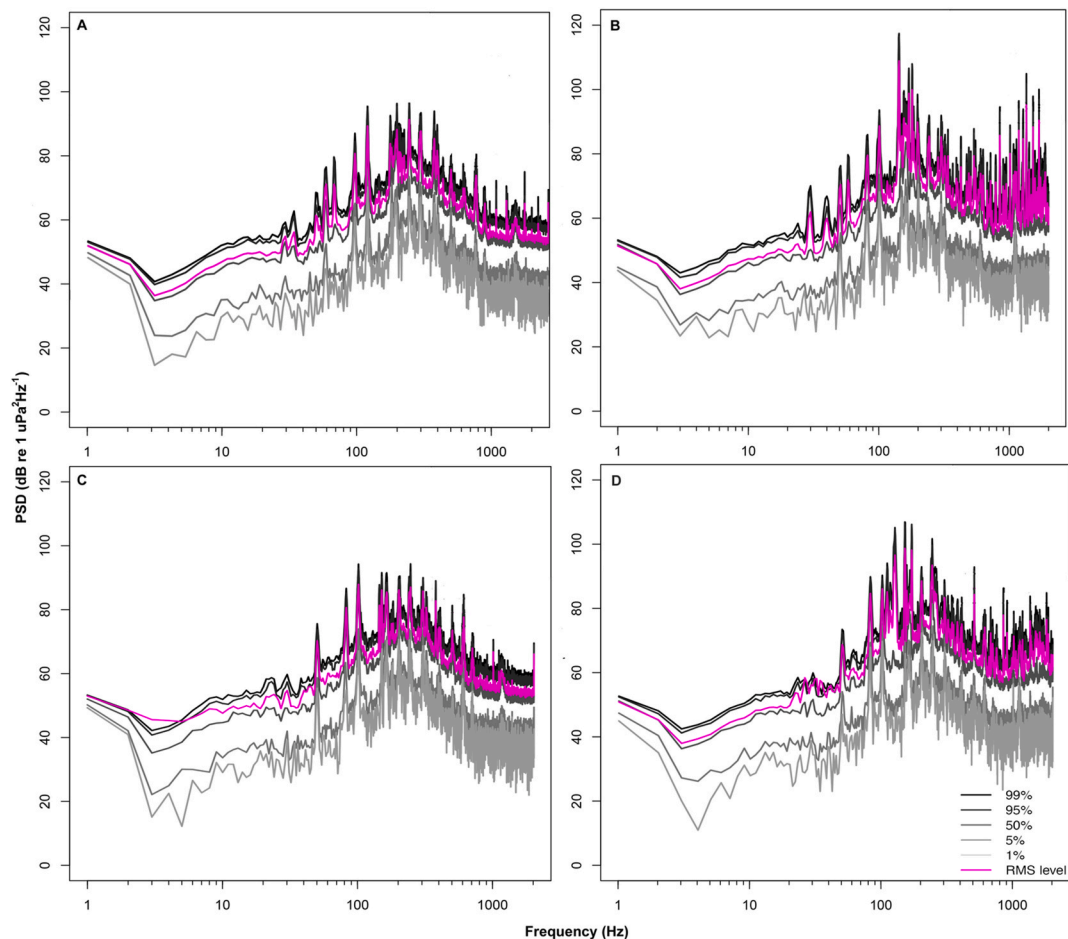

Fig. 2. Diagram of treatments' noise condition. Power Spectral Density (PSD) for each treatment, A = control, B = added noise, C = predator presence, D = added noise + predator presence. Recorded sounds (C = 8, N = 6, P = 4, NP = 6) were concatenated to form a single contiguous spectrogram. The plots depict the different percentiles (1%, 5%, median, 95%, 99%) and the Root Mean Square level (RMS). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

3. Results

YOY lobsters (total = 134) were randomly assigned to four conditions in a daytime or nighttime experiment: control (C = no predator nor noise), added noise (N), predator presence (P), and added noise + predator presence (NP). Recorded sounds (C = 8, N = 6, P = 4, NP = 6) were concatenated to form a single contiguous spectrogram for each treatment. The noise levels were measured with control and treatment tanks running concurrently, in order to ensure there was no cross-contamination of noise between tanks. The added noise treatment consisted of a low-frequency multi-tone sound with sound pressure level approximately 20 dB above non added noise (control and predator) conditions between frequencies 100–200 Hz (Fig. 2).

3.1. Lobster behavior

The primary focus of the study was the different behavioral patterns (see methods section) and the relative percent time engaging in a specific behavior. As expected for YOY lobster life stage, the most common behavior was hiding (daytime: 81.93 [15.41]% of total time, median [IQR]; nighttime: 80.50 [22.13]% of total time) in the substrates (Fig. 3; *i.e.*, lobsters were not visible on video recording). Lobsters' hiding behavior decreased significantly by 13% during the nighttime under the combination of added noise and predator presence than under any other tested conditions. During daytime there was no evidence of any treatment affecting lobster hiding behavior.

When lobsters were not hiding (nighttime), they were engaged in shelter construction (3.5 [8.6] %), peeking (7.8 [9.2] %) and exploration (3.3 [8.8]%) (Fig. 4). We found no evidence that added noise (N) and predator presence (P) alone influenced lobster behavior during night-time or daytime. However, under the combination of predator and noise during nighttime, YOY lobsters were significantly more active, exploring approximately 2-fold more than in other control and noise conditions (Fig. 4).

3.2. Substrate choice

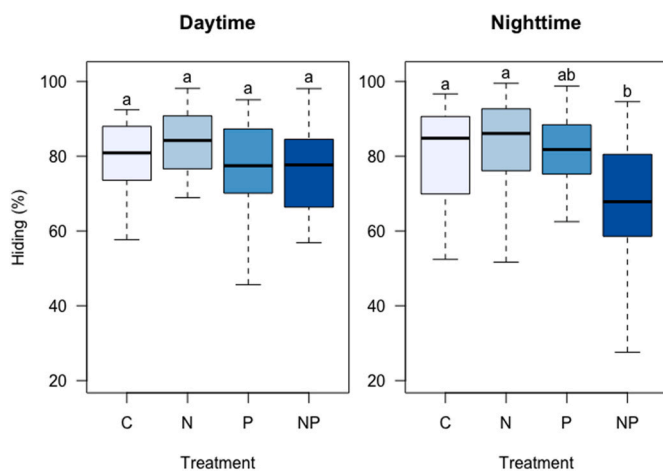Substrate choice was assessed twice, at the beginning (substrate

Fig. 3. Diel boxplots of hiding behavior. Comparative results of time (in %) young-of-year lobsters spent hiding during daytime and nighttime under (C) control, (N) added noise, (P) predator presence and (NP) added noise + predator presence treatments. Horizontal bars in the boxplots indicate the median; upper and lower edges of the rectangles show the first and third quartiles, respectively; vertical error bars extend to the lowest and highest values in a 1.5-fold inter-quartile range (R Core Team, 2021). Different letters (a,b) indicate significant differences. A notation with more than one letter (a,b) means that there is no significant difference with either (a) or (b) (Tukey's post-hoc test, *p* < 0.03).
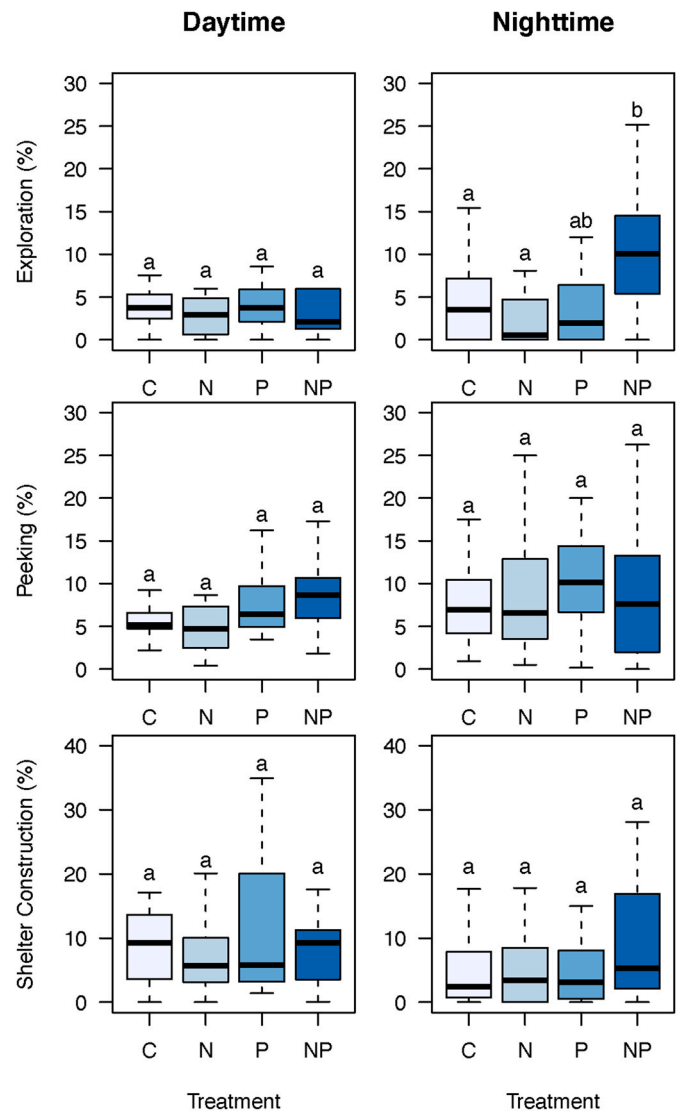

Fig. 4. Diel boxplots of active behaviors. Comparative results of time (in %) young-of-year lobsters spent in active behaviors (exploration, peeking, shelter construction) during daytime and nighttime under (C) control, (N) added noise, (P) predator presence and (NP) added noise + predator presence treatments. Horizontal bars in the boxplots indicate the median; upper and lower edges of the rectangles show the first and third quartiles, respectively; vertical error bars extend to the lowest and highest values in a 1.5-fold inter-quartile range (R Core Team, 2021). Different letters (a,b) indicate significant differences. A notation with more than one letter (a,b) means that there is no significant difference with either (a) or (b) (Tukey's post-hoc test, *p* < 0.03).

chosen when released into the experimental tank, after 5 min acclimation) and at the end of each trial (substrate where lobsters were found after 3 h). YOY lobsters in absence of noise and predator did not have any particular preference for rock or oyster shells, contrary to those exposed to either noise or predator, or both in combination where there was a preference for rocks (Fig. 5). In control conditions, no initial preference between rocks or oysters was observed, irrespective of time of day. Rocks was the preferred final choice under all conditions in both diurnal and nocturnal trials. All lobsters chose to hide among rocks or oyster shells within the first 5 min, time lobsters spent within each substrate did not significantly differ among treatments (Fig. S3), or the number of times lobsters switched between substrates (Fig. S4). No lobsters were observed settling on the bare sand in the video-recordings and after 3 h.
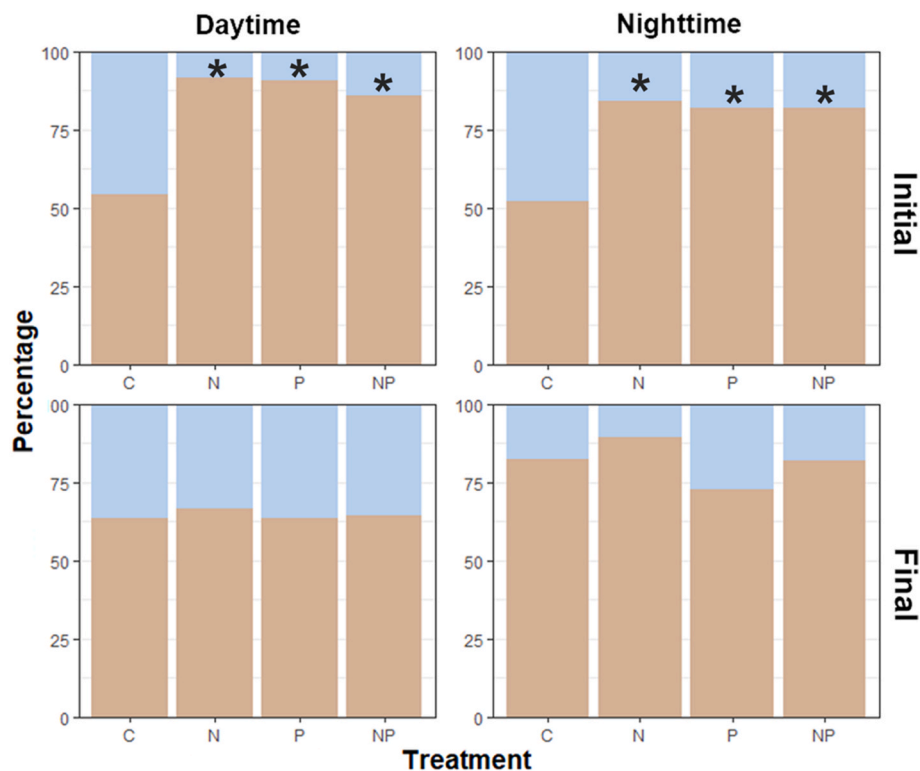
Fig. 5. Substrate choice of young-of-year lobsters. Initial and final choice were assessed after 5 min acclimation and 3 h of exposure, respectively. Treatments are (C) control, (N) added noise, (P) predator presence and (NP) added noise + predator presence. Colors represent the substrates, brown = rocks and blue = oyster shells. Stacked bars with asterisks are significantly different from the control condition (Holm-Bonferonni correction see Table S4). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

We have demonstrated how the joint effect of added low-frequency noise and predator presence modified YOY lobsters' behavior. With potential ecological consequences, YOY lobsters under the added noise and predator presence treatment spent more time outside their substrate (shelter), exploring, and less time hiding. Increase in time spent outside may be correlated with higher mortality in small juvenile lobsters as shown in previous studies with juvenile American lobsters and predatory green crabs (*C. maenas*) (Rossong et al., 2011). An explanation for this exploration under noise and predator presence treatment could be described by the "distracted prey hypothesis" (Chan et al., 2010). This hypothesis implies anthropogenic noise may reallocate the organism's finite attention, distracting them, and therefore preventing them to respond to predatory threats. A similar reaction was observed in other taxa in both aquatic (Voellmy et al., 2014) and terrestrial habitats (Dukas, 2004). For example, an experiment done on European seabass (*Dicentrarchus labrax*) tested the fish's response to a rapidly increasing piling noise (Spiga et al., 2017). The seabass reacted with startle responses to piling noise, which led to an increased turning behavior and less time spent in the safe zone (zone of the tank furthest from the predator). While the fish appeared to exhibit increased vigilance, they also reduced their predator inspection behavior. Studies focused on the behavioral impact effect of anthropogenic noise on decapods are limited. However, research on *C. maenas* has led to the distinction of stage-specific responses to noise (Carter et al., 2020, Wale et al., 2013b). Ship noise exposure in juvenile crabs increased the time for them to seek shelter after a simulated attack, like the adult crabs (Wale et al., 2013a), but it made juveniles less likely to respond to predator threats (Carter et al., 2020). To our knowledge, the current study is the first focused on European lobster juvenile behavioral response to the joint effect of predator presence and added noise. Interestingly our findings are similar to *C. maenas* juvenile's lack of response to predator threats, YOY lobsters demonstrated a decreased antipredator behavior (i.e., hiding) and increased exploration behavior. The increase in exploration behavior seen in YOY lobsters under the joint effect of noise and predator could be

attributed as an indicator of stress, as lobster might have attempted to avoid the noise and perceived it as a threat (Aimon et al., 2021; Stoner, 2012). Aimon et al. (2021) recent experiment revealed that *C. maenas* increased its activity and antennae beats when exposed to seabed vibrations of 20 Hz frequency, indicating that anthropogenic underwater vibration could induce a behavioral response and cause higher stress levels. Nevertheless, YOY lobster under noise and predator presence treatments alone did not increase their exploration behavior. Our interpretation is that the stressors separately did not have the magnitude to elucidate a significant behavioral response, while joint exposure (noise and predator presence) led to an additive stress level effect expressed in increased activity.

An alternative explanation for the lobsters' higher exploration activity under the noise and predator presence treatment, could be that noise masked the auditory cues that lobsters perceived from the predator. Our added noise may be modest in comparison with other anthropogenic noise sources, but it produces a tonal sound that overlaps with lobster's natural environmental signals for predator detection and 'buzzing' sounds (low-frequencies ~100 Hz) produced by adult *H. gammarus* (Jézéquel et al., 2018). As animals rely on multiple senses, it is difficult to fully understand the multimodal impact of sensory pollutants on animal behavior and perception. It is known that lobsters principally use olfactory and visual cues to detect predators (Wahle, 1992) and food (Mackie, 1973), but as noise exposure has been demonstrated to reduce foraging behavior in decapods (Wale et al., 2013a), the higher exploration activity might not be related to masked auditory cues or an urgent food craving.

Our results also demonstrated that the single and joint effect of noise and predator presence influenced initial substrate choice (rocks or oyster shells) of young-of-year (YOY) *H. gammarus* lobster. Overall, rocks were the preferred substrate, but oyster shells also appeared to be a favorable substrate providing habitat where YOY lobsters can hide. In the control conditions, lobsters did not have a significant preference for rocks over oyster shells in their initial choice (first substrate chosen after 5 min acclimation). It was exclusively after exposure to predator presence and/or added noise that the majority of lobster preferred to hide in

the rocks as their initial choice. To date, there are no studies linking substrate choice with stress responses in European lobsters. Nevertheless, an experiment on captive juvenile European spiny lobsters (*P. elephas)* explored how the physical properties (e.g. shape, size) of shelters influenced the animals' choice (Gristina et al., 2009). Contrary to our results, *P. elephas* preferred shelters with holes closer to body size under control conditions and had no shelter preference in predator presence. In our results, YOY lobsters' initial substrate selectivity under added stressors might be a response to a potential threat. Preference for rocks may be based on their geometry (size, shape and weight) which provided wider and more stable spaces where lobsters could change direction easier within the substrate. The substrate providing shelters offered in our experiment did not simulate the complexity of a rocky benthic community or a European oyster reef. However, they complied with their refuge function similar to natural hard substrate and interstitial spaces where juvenile lobster sought shelter. If repopulation of *O. edulis's* reefs in the German Bight were to be successful, these habitats are worth assessing since every possible addition of hard substrates in the area could potentially lead to an increase in lobster's survival.

Marine noise pollution research frequently focuses on the effect of short-lived intense noise (seismic surveys, offshore wind farm construction, pile drilling) on marine taxa. Here, we were interested in demonstrating that a subtle constant noise also poses a significant risk. It is ecologically important to set a baseline to sound levels that can elucidate a response in animals, this can help in noise pollution mitigation efforts as well as improving aquaculture methods. The added noise in our experiments is comparable to ocean traffic noise, as reported in generalized "ambient" underwater noise spectra in the sea (Wenz, 1962). The results from in-tank laboratory experiments are always hard to extrapolate to the field, and this is especially true for experiments using sound. One of the many constraints might be the presence of pressure release boundaries that would transfer part of the sound energy across the boundary (mainly at water surface) and reflect the other part into the original medium (effect accentuated here by the tank walls). However, one strength of our study is the use of a cheap and easy to replicate sound source that can increase the amount of data currently available on the effects of noise pollution (de Jong et al., 2017). Our lobsters were not reared in pristine soundscape conditions (see Fig. S5), as they were subject to aquaculture settings (Slater et al., 2020). However, they were naive to predator presence, which combined with noise, uncovered the negative impact noise has on them. We could not include historical noise and direct predator exposure, as lobsters were borrowed and were aimed for conservation purposes. We note further work is needed to understand European juvenile lobster's sensitivity to substrate vibration and particle motion. There are several studies (see Table S5) and key review articles specialized in particle motion components (Nedelec et al., 2016; Roberts and Elliott, 2017; Popper and Hawkins, 2018; Hawkins et al., 2021) which can provide guidance for future studies tackling these components.

5. Conclusion

This paper is the first to test the joint and separate effect of added noise and predator presence on substrate preference and antipredatory responses of YOY European lobsters. As current understanding of how underwater noise may synergize with other stressors is limited, our research is fundamental. While the results show that noise influences the antipredator behavior of YOY *H. gammarus*, it is not yet clear if this will indeed have an adverse effect on the lobster's survival. Care is needed when interpreting our predator-prey interaction, as our predator was restrained. Furthermore, the effects of long-term noise exposure and the potential of sensitization, habituation and/or possible long-term damage that could persist even after exposure ended are still unknown. However, if low-frequency noise disrupts antipredatory behavior in YOY lobsters increasing their vulnerability, its effects could resonate in the overall lobster stocks. This outcome pinpoints the importance of

including key benthic community relationships in anthropogenic noise risk assessments. Among others, effects of noise must be taken into consideration in plans involving the multi-use of any offshore area for decapods' stock enhancement, aquaculture, and temporary no-take zones.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2021.118108.

Author contributions

Laura Leiva: Conceptualization, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Sören Scholz**: Investigation, Data curation, Writing – review & editing. **Luis Giménez**: Conceptualization, Data curation, Writing – review & editing. **Maarten Boersma**: Conceptualization, Resources, Writing – review & editing. **Gabriela Torres**: Conceptualization, Investigation, Writing – review & editing. **Roland Krone**: Conceptualization, Resources, Writing – review & editing. **Nelly Tremblay**: Conceptualization, Investigation, Data curation, Writing – original draft, Writing – review & editing.

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