Sound investigation: effects of noise on marine animals across trophic levels

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Effects of broadband sound exposure on the interaction between foraging crab and shrimp – A field study

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Abstract

Aquatic animals live in an acoustic world in which they often rely on sound detection and recognition for various aspects of life that may affect survival and reproduction. Human exploitation of marine resources leads to increasing amounts of anthropogenic sound underwater, which may affect marine life negatively. Marine mammals and fishes are known to use sounds and to be affected by anthropogenic noise, but relatively little is known about invertebrates such as decapod crustaceans. We conducted experimental trials in the natural conditions of a quiet cove. We attracted shore crabs (*Carcinus maenas*) and common shrimps (*Crangon crangon*) with an experimentally fixed food item and compared trials in which we started playback of a broadband artificial sound to trials without exposure. During trials with sound exposure, the cumulative count of crabs that aggregated at the food item was lower, while variation in cumulative shrimp count could be explained by a negative correlation with crabs. These results suggest that crabs may be negatively affected by artificially elevated noise levels, but that shrimps may indirectly benefit by competitive release. Eating activity for the animals present was not affected by the sound treatment in either species. Our results show that moderate changes in acoustic conditions due to human activities can affect foraging interactions at the base of the marine food chain.

Introduction

Over the last century, anthropogenic sources have increasingly interfered with the natural cacophony of sounds in the aquatic environment (Andrew et al., 2002; Hildebrand, 2009). Many animals use sound for activities such as orientation, predator and prey detection, and communication, of which the latter can play a critical role in aggregation and reproduction (Slabbekoorn et al., 2010). Most energy of anthropogenic sounds is concentrated in the same frequency range as biologically relevant sounds and thereby has the potential to impact aquatic life (Kunc et al., 2016). This has led to an increased interest in the effects of anthropogenic sound sources on marine mammals and fish, but relatively little work has been done on invertebrates, including decapod crustaceans (Hawkins and Popper, 2016; Morley et al., 2013; Williams et al., 2015). Yet, invertebrates form the majority of the marine biomass and their abundance is critical for species in higher trophic levels (cf. Morley et al., 2013; Solan et al., 2016).

For decapod crustaceans, both the sensory mechanisms involved in hearing and their utilization of sound are not yet well understood. They are thought to be most sensitive to low-frequency particle motion as they lack gas-filled organs such as swim bladders (Edmonds et al., 2016). Hearing sensitivity curves of mud crabs (*Panopeus* spp.) and common prawn (*Palaemon serratus*) show highest sensitivity for the lowest tested frequencies (resp. 75 and 100 Hz) with decreasing sensitivity up to at least 1600 and 3000 Hz (Hughes et al., 2014; Lovell et al., 2005). There is also some evidence that decapod crustaceans use sound for orientation, experiments using light traps and binary choice chambers suggested that shrimps and coastal crabs species in their pelagic stages use coastal reef sound to orient on the coast (Jeffs et al., 2003; Radford et al., 2007; Simpson et al., 2011). Crabs in later life stages may also use acoustic cues to avoid predators. Mud crabs changed foraging behaviour during the playback of vocalisations of three predator fish species (Hughes et al., 2014). Furthermore, snapping shrimps do not only snap to stun prey items, but also snap during agonistic interactions; both the jet stream of water and the emitted sound possibly play a role in this potential case of multi-modal communication in an invertebrate (Au and Banks, 1998; Schein, 1975).

There are also some studies that indicate that elevated sound conditions may have physiological effects on decapod crustaceans. Studies in both common shrimps (*Crangon crangon*) and shore crabs (*Carcinus maenas*) show an increased oxygen consumption in elevated sound conditions (Regnault and Lagardère, 1983; Wale et al., 2013a). Lobsters (*Palinurus elephas*) and common prawn (*Palaemon serratus*) that were exposed to boat noise exhibited significant changes in stress-

related biochemistry (Filiciotto et al., 2014; Filiciotto et al., 2016). Furthermore, an early, long-term experiment with common shrimps under elevated sound conditions showed a reduced growth and delayed reproduction in comparison to the control (Lagardère, 1982).

The available studies investigating effects of elevated sound conditions on behaviour of decapod crustaceans are typically conducted in captivity. Terrestrial hermit crabs (*Coenobita clypeatus*), exposed to white noise in captivity, increased latency time to withdraw in their shell upon visual display of a predator (Chan et al., 2010) and marine hermit crabs (*Pagurus bernhardus*) took less time to approach, investigate, and enter a shell (Walsh et al., 2017). Filiciotto and colleagues (2016) found several noise-induced behavioural effects in captive common prawn: reduced locomotor activity, less encounters with conspecifics and differences in use of shelter. In contrast, lobsters increased locomotor behaviour during boat noise exposure (Filiciotto et al., 2014). Most relevant to the current study, Wale and colleagues (2013b) found no difference in food finding in captive crabs exposed to ambient noise or ship noise. But when they started the boat sound after the crabs began eating, the crabs were (temporary) disrupted in the first minute after the onset. It remains to be tested whether similar effects of noise on behaviour occur under natural conditions in the wild.

In the current study, we explored the effect of experimental playback of broadband noise on the foraging behaviour of shore crabs and common shrimps. We conducted this experiment in situ, in a cove without boat traffic, to ensure natural conditions in terms of sound field, animal behaviour, and species interactions. We aimed at answering three questions: (1) Do elevated sound levels affect the aggregation of crabs and shrimps at a food source? (2) Do elevated sound levels affect feeding rates in crabs and shrimps once they have arrived at a food source? (3) Are there any noise-dependent interactions among the two species?

Materials and methods

Study subjects and location

The experiment was performed in the Jacobahaven, an artificial cove in the Oosterschelde estuary in The Netherlands. The cove is about 200 m by 300 m in size and depending on the tide, 1.5 to 4.8 m deep. The cove is home to a large variety of marine life that is part of a natural food chain and typical of the region. Prominent plants are sea lettuce (*Ulva lactuca*) and sugar kelp (*Saccharina* sp.), prominent molluscs are blue mussels (*Mytilus edulis*) and Japanese oysters (*Magallana gigas*), and there is a variety of jellyfish and sea stars. Fish species include gobies (*Pomatoschistus* spp.) and European seabass (*Dicentrarchus*

labrax). Our study species, shore crab and common shrimp are very abundant. In the middle of the cove, we constructed a floating research platform from a plastic modular floating dock system (Candock, Canada). The platform consisted of a square platform with a tent for equipment connected to an octagonal walkway and has been used in previous experiments (cf. Neo et al., 2018). We used the 10 corners of the platforms as the locations for the trials and all locations were at least 5.5 m apart (fig. 1a). The position of the speaker was fixed and the distance from the trial-location to the speaker varied between 3 and 14 m. Trials were performed around low tide on May 9th-11th 2017.

Experimental procedure

We used two weighted crates as mooring device for an underwater camera (GoPro HERO4 Black and JVC Everio R GZ-R415) so we could perform paired trials at different locations. The cameras were positioned to film the sea floor around a cooked mussel (*Mytilus edulis*) that was connected to the crate using iron wire (fig. 1b). For each trial, we lowered both crates to the sea bottom from two of the 10 corners of the research platform. After 2 min of baseline data collection, we started a playback of either 5 min of silence (control) or 5 min of white noise (see Sound characteristics). The locations were allocated using an incomplete counterbalanced design, in which neighbouring locations during a single sound exposure and same locations in consecutive exposures were avoided. The time between sound exposures was at least 10 min.

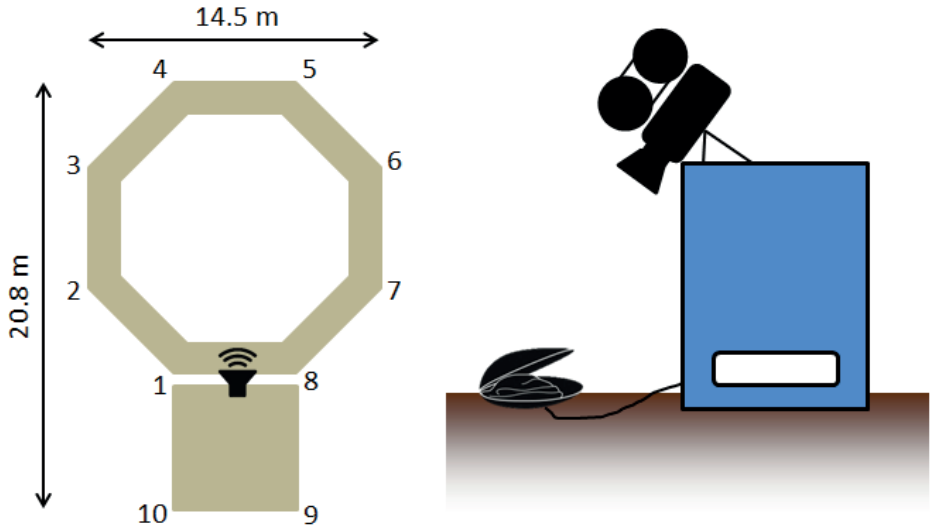

Fig. 1: (a) Top view schematic of the research platform; the numbers indicate the 10 different locations for the trials and the speaker symbol indicates the fixed location of the omnidirectional underwater speaker. (b) Side view schematic of a crate with camera and food item (mussel) to video and attract crabs and shrimps.

Behavioural measurements

We analysed 49 video recordings, 27 control trials and 22 white noise treatment trials. Due to variable visibility, not all videos could be analysed, typically caused by sea weed obstructing the camera view. We analysed the first 4 min of every video: 2 min immediately before the start of the treatment and 2 min immediately after. Every 10 s we scored the number of crabs and shrimps in view of the camera and the number of crabs and shrimps that were eating the mussel. We did not analyse video after 4 min as the crabs regularly finished the mussel soon after this mark or removed the food from view.

Sound characteristics

The Gaussian white noise sound treatment was created using Audacity v2.1.0 and played back using an underwater speaker (SynchroSound Aqua IIB). Standard spectra of white noise will have changed upon arrival at the animal depending on speaker characteristics and underwater propagation. We calibrated the microphone of the JVC Everio R GZ-R415 using a calibrated hydrophone to be able to use the audio track from the videos to determine the sound levels and spectra of the sound conditions. We analysed the audio tracks in Rstudio (R Core Team, 2016) using custom R scripts. The sound pressure levels (SPL) were calculated by summing the power spectral density (PSD) values within the 0 – 3000 Hz frequency range, which was assumed to be most representative of shrimps' hearing range (based on a single study: Lovell et al., 2005). The SPL of

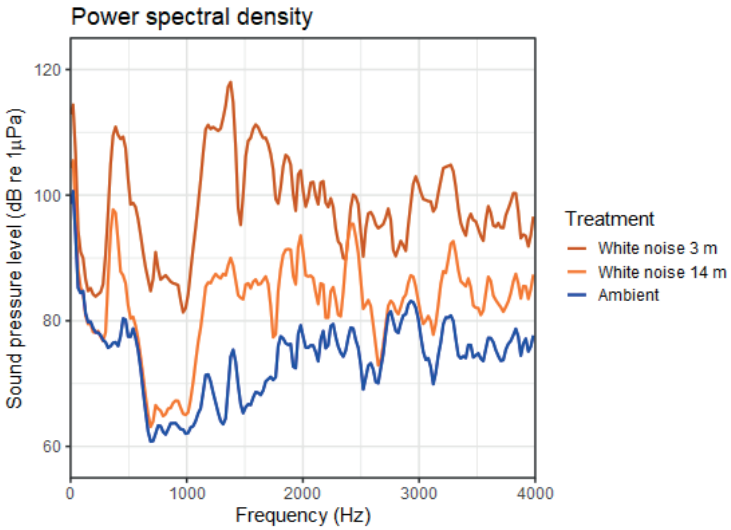

Fig. 2: Power spectral density (window length: 2048, window type: Hann) of the ambient (control) and white noise condition (spectrum altered by speaker and propagation) at the closest and furthest position from the speaker (resp. 3 & 14 m).

the ambient recordings was 119.5 dB re 1 µPa and during the playback of white noise this ranged from 129.5 to 142.0 dB re 1 µPa depending on the location (fig. 2).

Statistics

We calculated the cumulative counts of 'crabs present', 'shrimps present', 'crabs eating' and 'shrimps eating' within the 2 min period before sound exposure (t = 0-2 min) and after the start of the sound exposure (t = 2-4 min). All cumulative counts at t = 2-4 min were used as response variables in Poisson Generalized Linear Mixed-effect Models. All models included the treatment and cumulative count of the response variable at t = 0-2 min and the pair-ID of the trial as a fixed effect. For the response variables 'crabs present' and 'shrimps present', we also used the presence of the other species (shrimps or crabs) at t = 2-4 min as a fixed effect in the full model to gain insight into a possible interaction between species. For the response variables 'crabs eating' and 'shrimps eating', we also used the presence of the eating species (crabs or shrimps) at t = 2-4 min as a fixed effect in the full model. The location of the trial (1 thru 10) was included as a random effect.

The best model was chosen by AICc using dredge model selection (package MuMIn). Models differing in $\Delta AICc \geq 2$ are considered to have a significantly different fit. We calculated the marginal (R2m) and conditional (R2c) R2 values of the models to show the proportion of variance of the response variable explained by the fixed effects (R2m) and the entire model (R2c) (Nakagawa and Schielzeth, 2013). To further examine the potential interaction between crab and shrimp numbers, we applied a cross-correlation analysis to the time series of count data. As our dataset consisted of multiple small time series (25 time points per trial), we opted to analyse all our trials as a single time series to reduce the variation in the cross-correlation results and give a broad overview of the correlation between shrimp and crab presence over all trials. To apply the cross correlation analysis, we did the following: 1) Align the paired crab and shrimp counts and offset the shrimp with respect to a given lag value for all trials; 2) remove crab or shrimp time points at the beginning and end of each trial which do not have a paired sample; 3) append the paired time series across all trials, resulting in a single paired time series of crab and offset shrimp counts for the entire experiment; 4) calculate the Pearson's correlation coefficient between the paired series. This process was repeated for multiple lag values. All analyses were conducted in Rstudio (R Core Team, 2016) using the packages lme4 (Bates et al., 2015), MuMIn (Barton, 2016) and piecewiseSEM (Lefcheck, 2016).

Results

We consistently observed an increasing number of crabs and shrimps approaching the crates and accumulating at the cooked mussel during the 4-min trials (figure 3a-b). After the playback started in the white noise trials, the accumulation of crabs slowed down relative to the ambient control trials, while shrimp accumulation showed the opposite pattern. The relatively high and variable baseline counts of shrimps in the white noise trials can be attributed to a single trial that started off with the exceptionally numerous presence of seven shrimps (figure 3b).

Model selection showed that the cumulative crab count of the second half of the trial was best explained by the treatment, crab presence during the first half (baseline) of the trial and shrimp presence during the second half of the trial (df = 5, R2m = 0.55, R2c = 0.76, table 1). Running this model showed that significantly fewer crabs were counted during the white noise exposures than during the control trials (Intercept: 2.27, Treatment WN: -0.62; figure 4a) and fewer crabs were associated with more shrimps (Slope shrimp present: -0.01). The variance in cumulative shrimp count was best explained by the shrimp presence during the baseline and crab presence during the second half of the trial (df = 4, R2m = 0.41, R2c = 0.89, table 1). There was no significant effect of treatment for the shrimps (figure 4b), but running the model confirmed a negative correlation between shrimp and crab numbers (Intercept: 1.54, Slope crab present: -0.02).

The cumulative count of eating crabs was best explained by just crab presence (df = 3, R2m = 0.58, R2c = 0.76, table 1), so there was no significant effect of treatment (figure 4c). When more crabs were present, more were actively eating (Intercept: 0.63, Slope crab present: 0.07). Similarly, the cumulative count of eating shrimps was best explained by shrimp presence (df = 3, R2m = 0.23, R2c = 0.70, table 1), so there was also no significant effect of treatment (figure 4d). Also, when more shrimps were present, more were actively eating (Intercept: -2.60, Slope shrimp present: 0.09).

The first two models showed a negative correlation between crab and shrimp presence. To explore whether crab numbers followed shrimp numbers or vice versa, we applied a cross-correlation on the time series count data. The plot of the cross-correlation (figure 5) confirms that shrimp and crab numbers are negatively correlated. The strongest correlations are found in the lag range +10 to +50, suggesting that crab presence correlates best with shrimp presence 10-50 s later (i.e. crab changes precede shrimp changes).

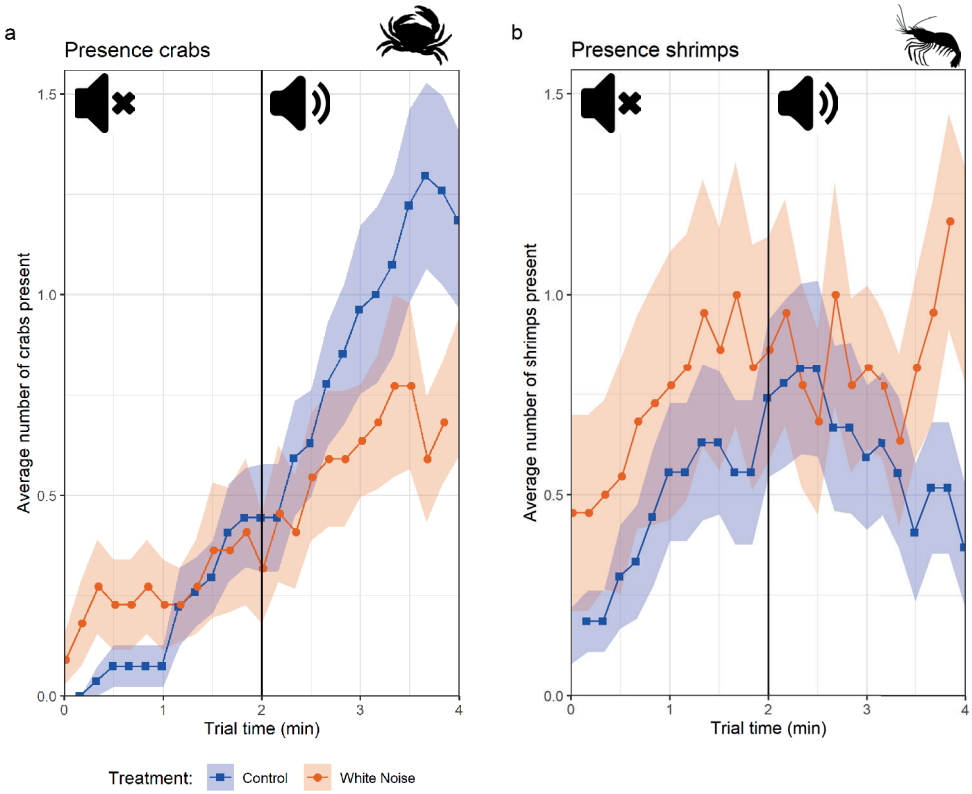

Fig. 3: The average number of crabs (left) and shrimps (right) counted from the videos of both treatments (Control (Co) n = 27 trials; White noise (WN) n = 22 trials). The shaded area indicates the standard error of the mean. The playback in the white noise trials started after 2 min, indicated with the vertical line and the speaker symbols.

Discussion

In the current study, we experimentally exposed shore crabs and common shrimps to elevated sound levels after offering a food item. This experiment was performed in situ, ensuring high acoustic and behavioural validity. Our results demonstrate that: (1) The current sound exposure reduced aggregation at a food item in shore crabs, but not in common shrimps. (2) The feeding rate, in both crabs and shrimps, was not directly affected by the sound exposures. (3) There was a negative correlation between crab and shrimp numbers that was likely driven by crabs. Even though the sound exposure did not affect shrimp aggregation directly, shrimps may have indirectly benefitted as lower numbers of crabs due to sound exposures released competition for shrimps.

Crab foraging behaviour

Our finding that sound exposure reduced food aggregation is in contrast with an

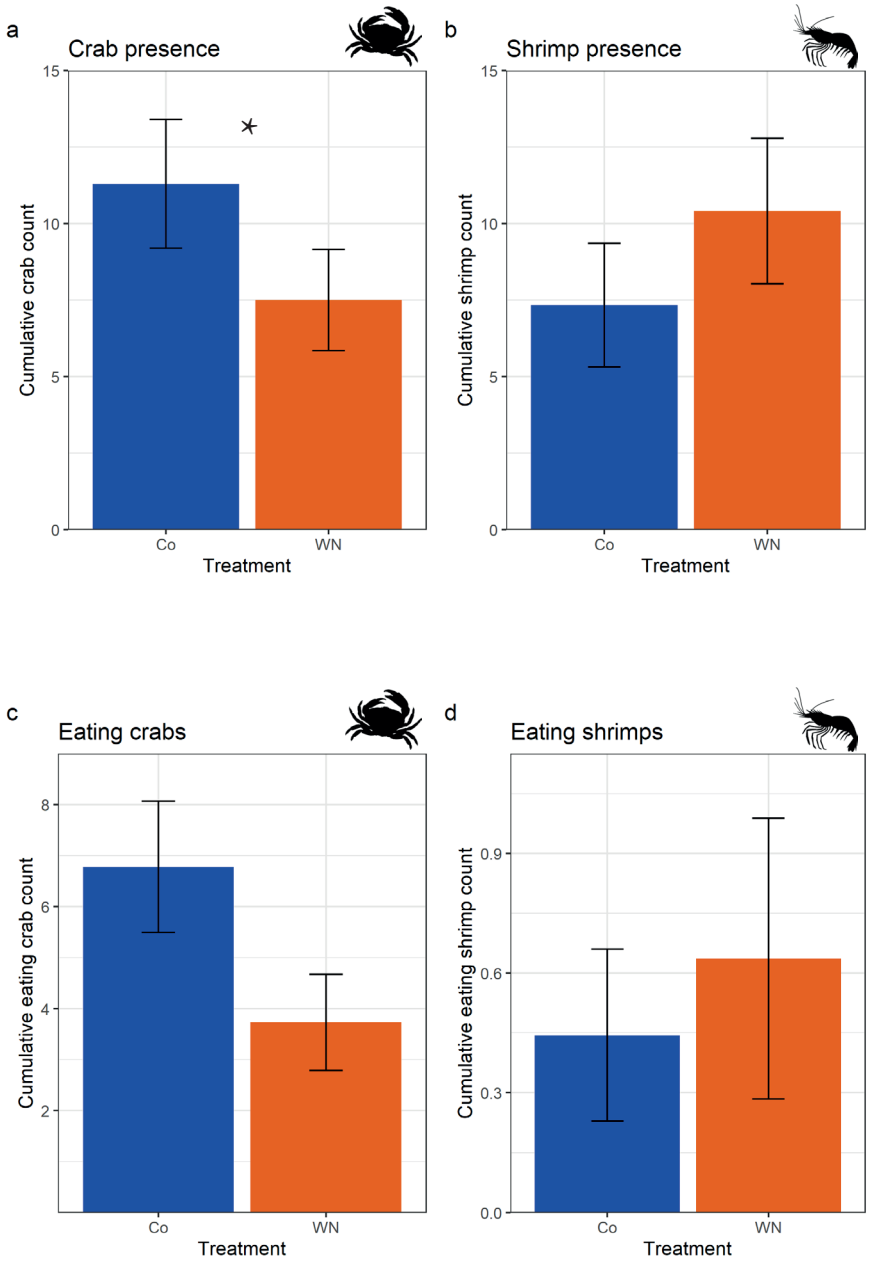

Fig. 4: Mean cumulative counts of the response variables during the second half of each trial. For the cumulative crab count, there was a significant effect of treatment, indicated by the *. 'Co' refers to the control (silence) treatment, 'WN' to the white noise treatment. The error bars represent the error of the mean.

Table 1: Best 3 results of model selection (ranked by AICc) and null models for all four response variables (in front of ~). The marginal R^2 (R^2m) shows the proportion of variance explained by the fixed effects, the conditional R2 (R^2c) shows the proportion of variance explained by the entire model. ΔAICc ≥ 2 indicates a significant difference between the models. * indicates best model.

#	Model	df	R^2m	R^2c	AICc	ΔAICc
Cum crabs presence t = 2-4 min ~ …						
1*	Cum crabs presence t = 0-2 min + Cum shrimps presence t = 2-4 min + Treatment + (1 | Position)	5	0.55	0.76	484.7	-
2	Cum crabs presence t = 0-2 min + Treatment + (1 | Position)	4	0.54	0.74	489.5	4.81
3	Cum crabs presence t = 0-2 min + Cum shrimps presence t = 2-4 min + (1 | Position)	4	0.34	0.72	510.0	25.30
null	(1 | Position)	2		0.74	573.7	88.97
Cum shrimps presence t = 2-4 min ~ …						
1	Cum shrimps presence t = 0-2 min + Cum crabs presence t = 2-4 min + Treatment + (1 | Position)	5	0.40	0.90	472.1	-
2*	Cum shrimps presence t = 0-2 min + Cum crabs presence t = 2-4 min + (1 | Position)	4	0.41	0.89	473.9	1.79
3	Cum shrimps presence t = 0-2 min + Treatment + (1 | Position)	4	0.37	0.90	478.4	6.36
null	(1 | Position)	2		0.75	693.1	220.99
Cum crabs eating t = 2-4 min ~ …						
1*	Cum crabs presence t = 2-4 min + (1 | Position)	3	0.58	0.76	273.4	-
2	Cum crabs presence t = 2-4 min + Cum crabs eating t = 0-2 + (1 | Position)	4	0.57	0.76	274.6	1.16
3	Cum crabs presence t = 2-4 min + Treatment + (1 | Position)	4	0.58	0.76	275.8	2.35
null	(1 | Position)	2		0.59	416.1	142.73
Cum shrimps eating t = 2-4 min ~ …						
1*	Cum shrimps presence t = 2-4 min + (1 | Position)	3	0.23	0.70	102.7	-
2	Cum shrimps presence t = 2-4 min + Treatment + (1 | Position)	4	0.23	0.73	104.7	1.98
3	Cum shrimps presence t = 2-4 min + Cum shrimps eating t = 0-2 + (1 | Position)	4	0.23	0.69	104.8	2.10
null	(1 | Position)	2	-	0.44	121.9	19.15

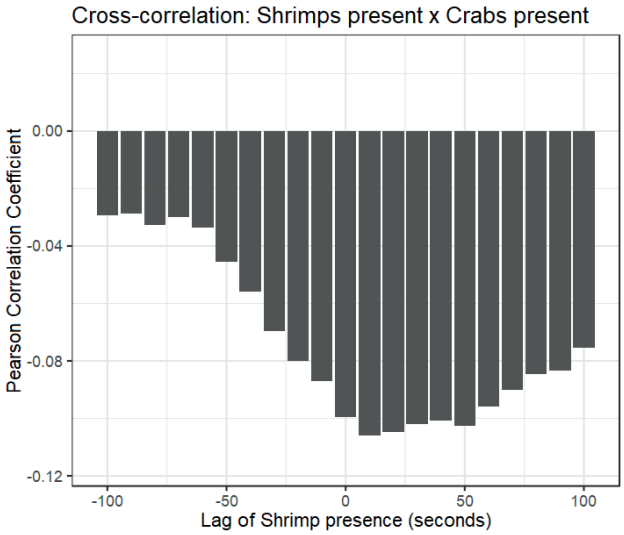

Fig. 5: Cross-correlation of 'shrimp present' and 'crab present' using the time series count data (25 time points per trial, 49 trials). The strongest correlation is found where the shrimp time series were delayed by 10 s relative to the crab time series (lag 10). Strongest correlations were found across positive lag values, suggesting that changes in shrimp presence follow changes in crab presence.

earlier study on shore crabs. Wale and colleagues (2013b) did not find an effect of ship noise on a food item being found by crabs and the time taken to find the food source. However, this experiment was conducted in a relatively small tank (0.12 m2) with a single crab whereas the current experiment was conducted in the wild where it is possibly much more challenging to find a food item. Also, the crabs in the indoor experiment were food deprived for 96 h before the foraging experiment, this might have led to a different trade-off in exploration and risk-taking behaviour than in the current experiment. The researchers did find increased disruption of feeding in the first minute after onset of the ship noise. This was defined as a ≥ 5 s interruption of feeding, freezing, or the animal moving away from the food. We did not find a drop in feeding rate. This might be because the sound that was played back in the current study was much softer (~ 12-32 dB re 1 µPa quieter than in Wale et al. 2013b). This might mean that crabs are only disturbed in their feeding activity above a certain sound level, from a louder or closer source.

There are several possible explanations for the reduced aggregation at a food item by crabs. It may be the case that crabs eating or interacting at a food item produce sound that attracts others (e.g. Coquereau et al., 2016). Such sounds could have been masked in our experiment during the playback of white noise. An alternative explanation of our results is that the playback sound disturbed

them (cf. Chan et al., 2010; Walsh et al., 2017). This might have resulted in reduced exploration and risk-taking behaviour in crabs due to potential masking of sounds from predators (Lima and Dill, 1990). In line with this, it might also be that crabs reduced their overall activity to increase readiness for escape responses (Edmonds et al., 2016). Confirmation of the latter hypothesis would require individual tracking instead of bait-targeted observations.

We did not find evidence that aggregation at a food item and feeding in shrimps were affected by the sound exposure. Shrimp presence (aggregation at a food item) could best be explained by crab presence. In contrast, Filiciotto and colleagues (2016) showed that captive common prawns in a controlled experiment reduced locomotor activity during the playback of boat recordings. Such direct effects might have been overshadowed by the interaction with crabs in the current study, thus highlighting the importance of looking beyond single species effects in sound impact studies (Francis et al., 2009; Shafiei Sabet et al., 2016).

Interaction between crabs and shrimps

We found a negative correlation between crab and shrimp presence. The cross-correlation showed that crab presence correlates best with later shrimp presence, this supported our expectation that crabs were deterring shrimps. Competition and interaction between species can be found throughout the animal kingdom. For example, Stahl and colleagues (2006) found that European brown hares (*Lepus europaeus*) naturally selected high biomass swards to forage on. However, after experimentally excluding geese from swards, hares foraged more on swards with both high plant quality and high biomass. Another prominent example by Estes and colleagues (1998) concerned killer whales (*Orcinus orca*) shifting prey choice towards sea otter (*Enhydra lutris*), which undermined the sea otters' control of the dominant herbivores, sea urchins (Echinoidea). As a consequence, the flourishing sea urchins overgrazed the kelp forest which dramatically changed the local ecosystem (Estes and Palmisano, 1974; Estes et al., 1998).

When interacting species respond differently to human influences, competitive balances between species may also shift (Tylianakis et al., 2008; Worm and Paine, 2016). Previous research has shown that anthropogenic sound can reduce species richness in avian communities, but may also indirectly facilitate breeding success of particular species because of lower abundance of a nest predator species (Francis et al., 2009; Slabbekoorn and Halfwerk, 2009). This avian example concerned a case of predator-release, while the current crustacean example concerns competitive release between two species competing over the same resources. The sound exposures released competition by the dominant species allowing the subordinate species to make use of the resource. Competitive

release is often shown in long term-studies by contrasting shifts in distribution (e.g. Anderson et al., 2002). We here provide evidence for a more short-term release in competition mediated by a species-specific behavioural response to sound exposures.

Revealing such interactions between species shows that single-species studies alone are not sufficient for determining impact of sound as there may be (local) community effects (Francis et al., 2009; Slabbekoorn and Halfwerk, 2009; Shafiei Sabet et al., 2016). Besides the importance of in situ studies, we also think that conducting controlled studies on captive animals can help in understanding processes that are important to free-ranging animals in the real world (Slabbekoorn, 2014). For example, it would be interesting to conduct a number of parallel exposure trials to study the effects of sound solely on crab food aggregation and eating, solely on shrimp food aggregation and eating, and on both species at the same time. In such a controlled study, it is likely possible to follow individual animals throughout entire trials, which should increase insights into the underlying mechanisms of our current results. In this way, synergy through studies in the lab and the wild will help in gaining understanding of biological processes and thereby increase the validity of sound impact assessments.

Conclusions

Our study provides evidence for the fact that artificial sound exposures can decrease the number of crabs aggregating at a food item and provide indirect benefits for shrimps via competitive release. This highlights the importance to study the potential impact of anthropogenic sound in situ and consider cross-species interactions. We believe it is especially important to study effects at and among lower trophic levels (e.g. invertebrates) as subtle effects here may accumulate at higher trophic levels (e.g. fish or marine mammals). We like to stress that our study provides a proof of concept and that our in situ approach strengthens behavioural and acoustic validity. However, our set-up does not provide insight into ecological relevance in absolute sense and more sound studies are needed for a better understanding of individual and population consequences of changes in multi-trophic interactions due to changes in underwater soundscapes.

Ethical statement

There are no legal requirements for studies involving decapod crustaceans and molluscs in The Netherlands. Our experiment likely only caused short periods

of mild discomfort in crabs and shrimps, as we observed free-ranging animals and only exposed them to short-lasting exposures with moderate sound levels. The sound exposure and food provisioning in our study are therefore unlikely to have caused any welfare problems to either species.

Data Accessibility

All data used for the analyses reported in this article is available from the Zenodo Repository, DOI:10.5281/zenodo.1403042.

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