1 **Effects of broadband sound exposure on the interaction between foraging**

2 **crab and shrimp – a field study**

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13 Capsule:

14 Man-made sound may reduce food aggregation in crabs and thereby release competition for
15 shrimps

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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

73 shrimps do not only snap to stun prey items, but also snap during agonistic interactions; both

74 the jet stream of water and the emitted sound possibly play a role in this potential case of multi-

75 modal communication in an invertebrate (Au and Banks, 1998; Schein, 1975).

76   There are also some studies that indicate that elevated sound conditions may have

77 physiological effects on decapod crustaceans. Studies in both common shrimps (*Crangon*

78 *crangon*) and shore crabs (*Carcinus maenas*) show an increased oxygen consumption in

79 elevated sound conditions (Regnault and Lagardère, 1983; Wale et al., 2013a). Lobsters

80 (*Palinurus elephas*) and common prawn (*Palaemon serratus*) that were exposed to boat noise

81 exhibited significant changes in stress-related biochemistry (Filiciotto et al., 2014; Filiciotto et

82 al., 2016). Furthermore, an early, long-term experiment with common shrimps under elevated

83 sound conditions showed a reduced growth and delayed reproduction in comparison to the

84 control (Lagardère, 1982).

85   The available studies investigating effects of elevated sound conditions on behaviour

86 of decapod crustaceans are typically conducted in captivity. Terrestrial hermit crabs (*Coenobita*

87 *clypeatus*), exposed to white noise in captivity, increased latency time to withdraw in their shell

88 upon visual display of a predator (Chan et al., 2010) and marine hermit crabs (*Pagurus*

89 *bernhardus*) took less time to approach, investigate, and enter a shell (Walsh et al., 2017).

90 Filiciotto and colleagues (2016) found several noise-induced behavioural effects in captive

91 common prawn: reduced locomotor activity, less encounters with conspecifics and differences

92 in use of shelter. In contrast, lobsters increased locomotor behaviour during boat noise exposure

93 (Filiciotto et al., 2014). Most relevant to the current study, Wale and colleagues (2013b) found

94 no difference in food finding in captive crabs exposed to ambient noise or ship noise. But when

95 they started the boat sound after the crabs began eating, the crabs were (temporary) disrupted

96 in the first minute after the onset. It remains to be tested whether similar effects of noise on

97 behaviour occur under natural conditions in the wild.

98   In the current study, we explored the effect of experimental playback of broadband

99   noise on the foraging behaviour of shore crabs and common shrimps. We conducted this

100   experiment in situ, in a cove without boat traffic, to ensure natural conditions in terms of sound

101   field, animal behaviour, and species interactions. We aimed at answering three questions: (1)

102   Do elevated sound levels affect the aggregation of crabs and shrimps at a food source? (2) Do

103   elevated sound levels affect feeding rates in crabs and shrimps once they have arrived at a food

104   source? (3) Are there any noise-dependent interactions among the two species?

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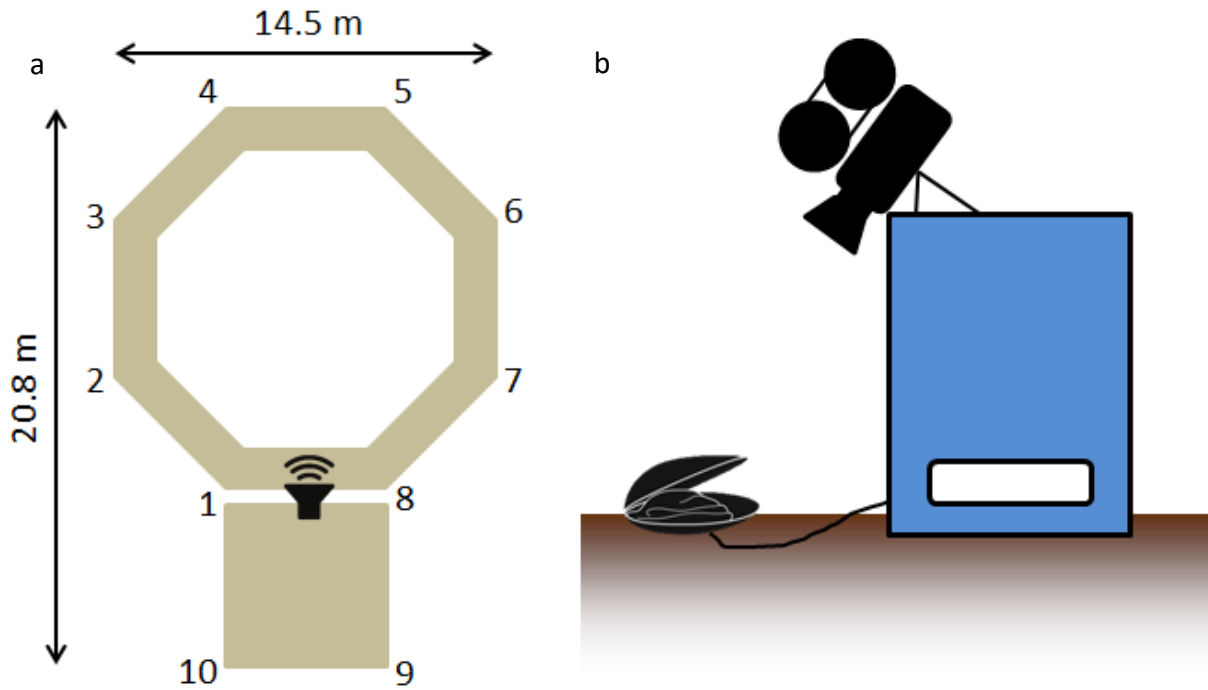
Materials and methods

107   Study animals and location

108   The experiment was performed in the Jacobahaven, an artificial cove in the Oosterschelde

109   estuary in The Netherlands. The cove is about 200 m by 300 m in size and depending on the

110   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

111   food chain and typical of the region. Prominent plants are sea lettuce (*Ulva lactuca*) and sugar

112   kelp (*Saccharina sp.*), prominent molluscs are blue mussels (*Mytilus edulis*) and Japanese

113   oysters (*Magallana gigas*), and there is a variety of jellyfish and sea stars. Fish species include

114   gobies (*Pomatoschistus* spp.) and European seabass (*Dicentrarchus labrax*). Our study species,

115   shore crab and common shrimp are very abundant. In the middle of the cove, we constructed a

116   floating research platform from a plastic modular floating dock system (Candock, Canada).

117   The platform consisted of a square platform with a tent for equipment connected to an

118   octagonal walkway and has been used in previous experiments (*cf*. Neo et al., 2018). We used

119   the 10 corners of the platforms as the locations for the trials and all locations were at least 5.5

120   m apart (figure 1a). The position of the speaker was fixed and the distance from the trial-

121   location to the speaker varied between 3 and 14 m. Trials were performed around low tide on

122   May 9th-11th 2017.

123

124   Figure 1

125

126   Fig. 1a-b. (a) Top view schematic of the research platform; the numbers indicate the 10
127   different locations for the trials and the speaker symbol indicates the fixed location of the
128   omnidirectional underwater speaker. (b) Side view schematic of a crate with camera and food
129   item (mussel) to video and attract crabs and shrimps.
130

131   Experimental procedure

132   We used two weighted crates as mooring device for an underwater camera (GoPro HERO4

133   Black and JVC Everio R GZ-R415) so we could perform paired trials at different locations.

134   The cameras were positioned to film the sea floor around a cooked mussel (*Mytilus edulis*) that

135   was connected to the crate using iron wire (figure 1b). For each trial, we lowered both crates

136   to the sea bottom from two of the 10 corners of the research platform. After 2 min of baseline

137   data collection, we started a playback of either 5 min of silence (control) or 5 min of white

138 noise (see Sound characteristics). The locations were allocated using an incomplete

139 counterbalanced design, in which neighbouring locations during a single sound exposure and

140 same locations in consecutive exposures were avoided. The time between sound exposures was

141 at least 10 min.

142

143 Behavioural measurements

144 We analysed 49 video recordings, 27 control trials and 22 white noise treatment trials. Due to

145 variable visibility, not all videos could be analysed, typically caused by sea weed obstructing

146 the camera view. We analysed the first 4 min of every video: 2 min immediately before the

147 start of the treatment and 2 min immediately after. Every 10 s we scored the number of crabs

148 and shrimps in view of the camera and the number of crabs and shrimps that were eating the

149 mussel. We did not analyse video after 4 min as the crabs regularly finished the mussel soon

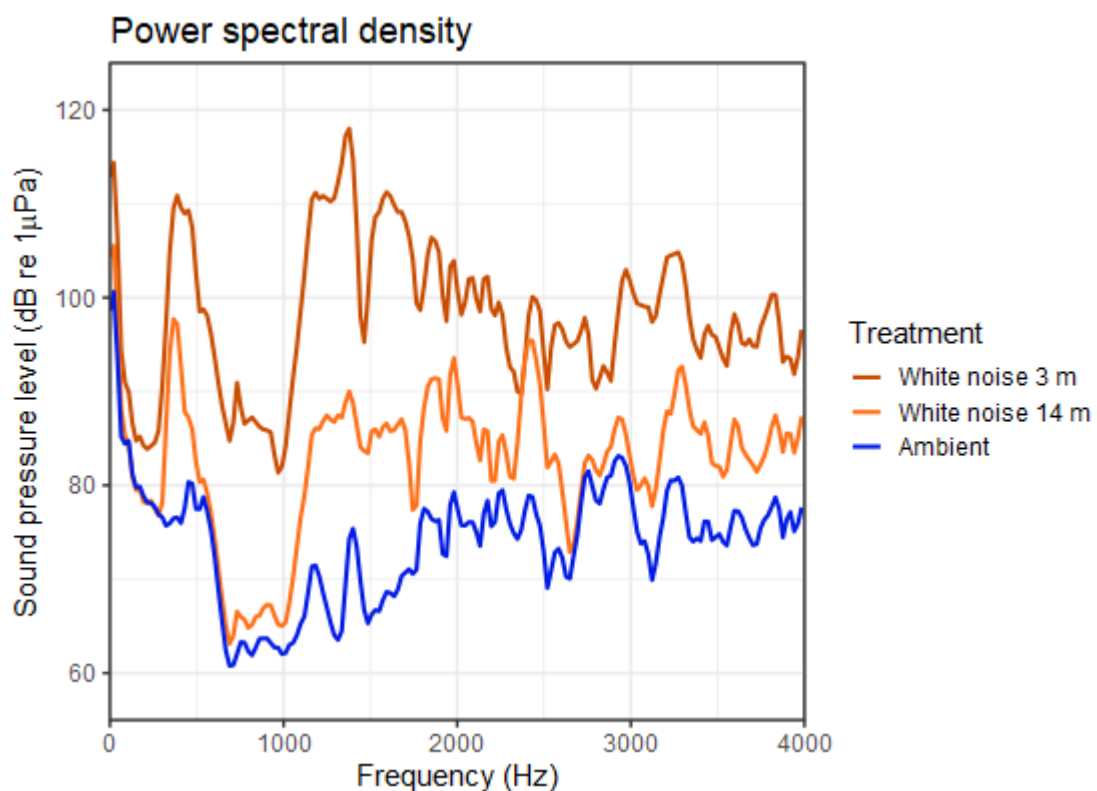150 after this mark or removed the food from view.

151

152 Sound characteristics

153 The Gaussian white noise sound treatment was created using Audacity v2.1.0 and played back

154 using an underwater speaker (SynchroSound Aqua IIB). Standard spectra of white noise will

155 have changed upon arrival at the animal depending on speaker characteristics and underwater

156 propagation. We calibrated the microphone of the JVC Everio R GZ-R415 using a calibrated

157 hydrophone to be able to use the audio track from the videos to determine the sound levels and

158 spectra of the sound conditions. We analysed the audio tracks in Rstudio (R Core Team, 2016)

159 using custom R scripts. The sound pressure levels (SPL) were calculated by summing the

160 power spectral density (PSD) values within the $0 - 3000$ Hz frequency range, which was

161   assumed to be most representative of shrimps' hearing range (based on a single study: Lovell

162   et al., 2005). The SPL of the ambient recordings was 119.5 dB re 1 µPa and during the playback

163   of white noise this ranged from 129.5 to 142.0 dB re 1 µPa depending on the location (figure

164   2).

165

166   Figure 2

167

168   Fig. 2. Power spectral density (window length: 2048, window type: Hann) of the ambient
169   (control) and white noise condition (spectrum altered by speaker and propagation) at the closest
170   and furthest position from the speaker (resp. 3 & 14 m).
171

172   Statistics

173   We calculated the cumulative counts of 'crabs present', 'shrimps present', 'crabs eating' and

174   'shrimps eating' within the 2 min period before sound exposure (t = 0-2 min) and after the start

175   of the sound exposure (t = 2-4 min). All cumulative counts at t = 2-4 min were used as response

176   variables in Poisson Generalized Linear Mixed-effect Models. All models included the

177   treatment and cumulative count of the response variable at t = 0-2 min and the pair-ID of the

178   trial as a fixed effect. For the response variables 'crabs present' and 'shrimps present', we also

179   used the presence of the other species (shrimps or crabs) at t = 2-4 min as a fixed effect in the

180   full model to gain insight into a possible interaction between species. For the response variables

181   'crabs eating' and 'shrimps eating', we also used the presence of the eating species (crabs or

182   shrimps) at t = 2-4 min as a fixed effect in the full model. The location of the trial (1 thru 10)

183   was included as a random effect.

184   The best model was chosen by AICc using dredge model selection (package MuMIn).

185   Models differing in ΔAICc $\geq$ 2 are considered to have a significantly different fit. We

186   calculated the marginal (R^2m) and conditional (R^2c) R^2 values of the models to show the

187   proportion of variance of the response variable explained by the fixed effects (R^2m) and the

188   entire model (R^2c) (Nakagawa and Schielzeth, 2013). To further examine the potential

189   interaction between crab and shrimp numbers, we applied a cross-correlation analysis to the

190   time series of count data. As our dataset consisted of multiple small time series (25 time points

191   per trial), we opted to analyse all our trials as a single time series to reduce the variation in the

192   cross-correlation results and give a broad overview of the correlation between shrimp and crab

193   presence over all trials. To apply the cross correlation analysis, we did the following: 1) Align

194   the paired crab and shrimp counts and offset the shrimp with respect to a given lag value for

195   all trials; 2) remove crab or shrimp time points at the beginning and end of each trial which do

196   not have a paired sample; 3) append the paired time series across all trials, resulting in a single

197   paired time series of crab and offset shrimp counts for the entire experiment; 4) calculate the

198   Pearson's correlation coefficient between the paired series. This process was repeated for

199   multiple lag values. All analyses were conducted in Rstudio (R Core Team, 2016) using the

200   packages lme4 (Bates et al., 2015), MuMIn (Barton, 2016) and piecewiseSEM (Lefcheck,

201   2016).

202

203   **Results**

204   We consistently observed an increasing number of crabs and shrimps approaching the crates

205   and accumulating at the cooked mussel during the 4-min trials (figure 3a-b). After the playback

206   started in the white noise trials, the accumulation of crabs slowed down relative to the ambient

207   control trials, while shrimp accumulation showed the opposite pattern. The relatively high and

208   variable baseline counts of shrimps in the white noise trials can be attributed to a single trial

209   that started off with the exceptionally numerous presence of seven shrimps (figure 3b).

210   Model selection showed that the cumulative crab count of the second half of the trial

211   was best explained by the treatment, crab presence during the first half (baseline) of the trial

212   and shrimp presence during the second half of the trial (df = 5, R^2m = 0.55, R^2c = 0.76, table

213   1). Running this model showed that significantly fewer crabs were counted during the white

214   noise exposures than during the control trials (Intercept: 2.27, Treatment WN: -0.62; figure 4a)

215   and fewer crabs were associated with more shrimps (Slope shrimp present: -0.01). The variance

216   in cumulative shrimp count was best explained by the shrimp presence during the baseline and

217   crab presence during the second half of the trial (df = 4, R^2m = 0.41, R^2c = 0.89, table 1). There

218   was no significant effect of treatment for the shrimps (figure 4b), but running the model

219   confirmed a negative correlation between shrimp and crab numbers (Intercept: 1.54, Slope crab
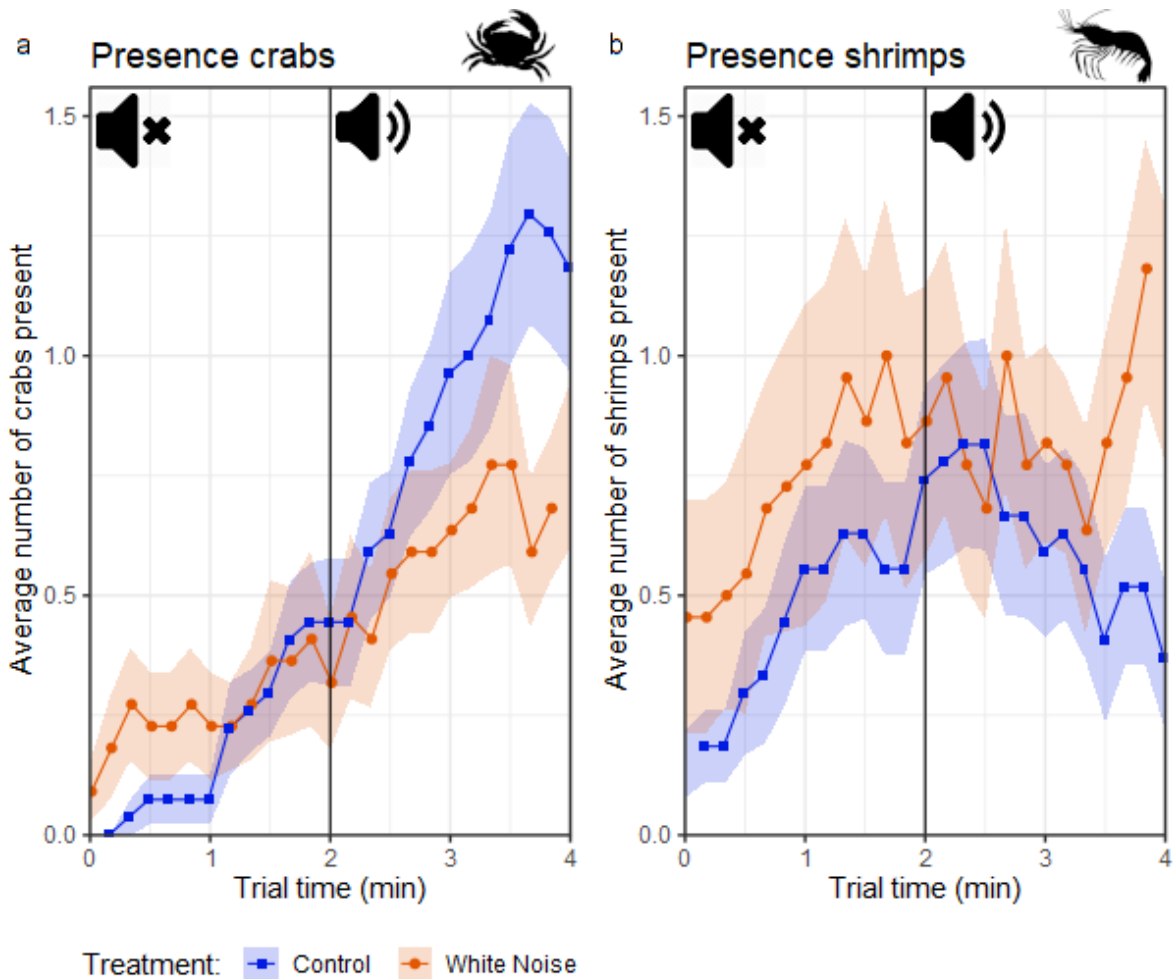
220   present: -0.02).

221   The cumulative count of eating crabs was best explained by just crab presence (df = 3,

222   R^2m = 0.58, R^2c = 0.76, table 1), so there was no significant effect of treatment (figure 4c).

223   When more crabs were present, more were actively eating (Intercept: 0.63, Slope crab present:

224   0.07). Similarly, the cumulative count of eating shrimps was best explained by shrimp presence

225   (df = 3, R^2m = 0.23, R^2c = 0.70, table 1), so there was also no significant effect of treatment

226   (figure 4d). Also, when more shrimps were present, more were actively eating (Intercept: -2.60,

227   Slope shrimp present: 0.09).

228   The first two models showed a negative correlation between crab and shrimp presence.

229   To explore whether crab numbers followed shrimp numbers or vice versa, we applied a cross-

230   correlation on the time series count data. The plot of the cross-correlation (figure 5) confirms

231   that shrimp and crab numbers are negatively correlated. The strongest correlations are found

232   in the lag range +10 to +50, suggesting that crab presence correlates best with shrimp presence

233   10-50 s later (i.e. crab changes precede shrimp changes).

234

235   Figure 3

Fig. 3a-b. 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.

Table 1

Table 1: Best $\geq$ 3 results of model selection (ranked by AICc) and null models for all four response variables (in bold). The marginal R^2 (R^2m) shows the proportion of variance explained by the fixed effects, the conditional R^2 (R^2c) shows the proportion of variance explained by the entire model. ΔAICc $\geq$ 2 indicates a significant difference between the models. * indicates best model.
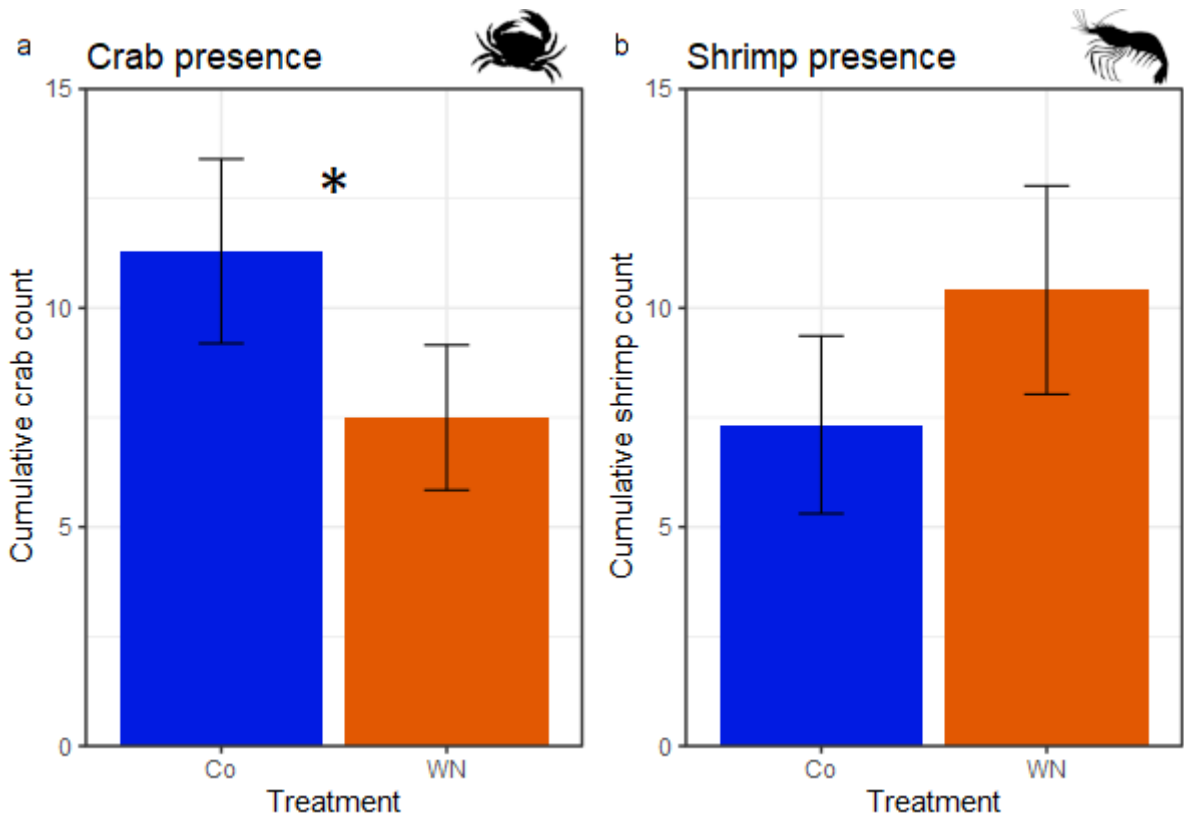
#	Model	df	R^2m	R^2c	AICc	ΔAICc
Cum crabs presence t = 2-4 min ~ …						
1*	Cum crabs presence t = 0-2 min + Cum shrimps presence t = 2-4 min + Treatment + (1 | Position)	5	0.55	0.76	484.7	-

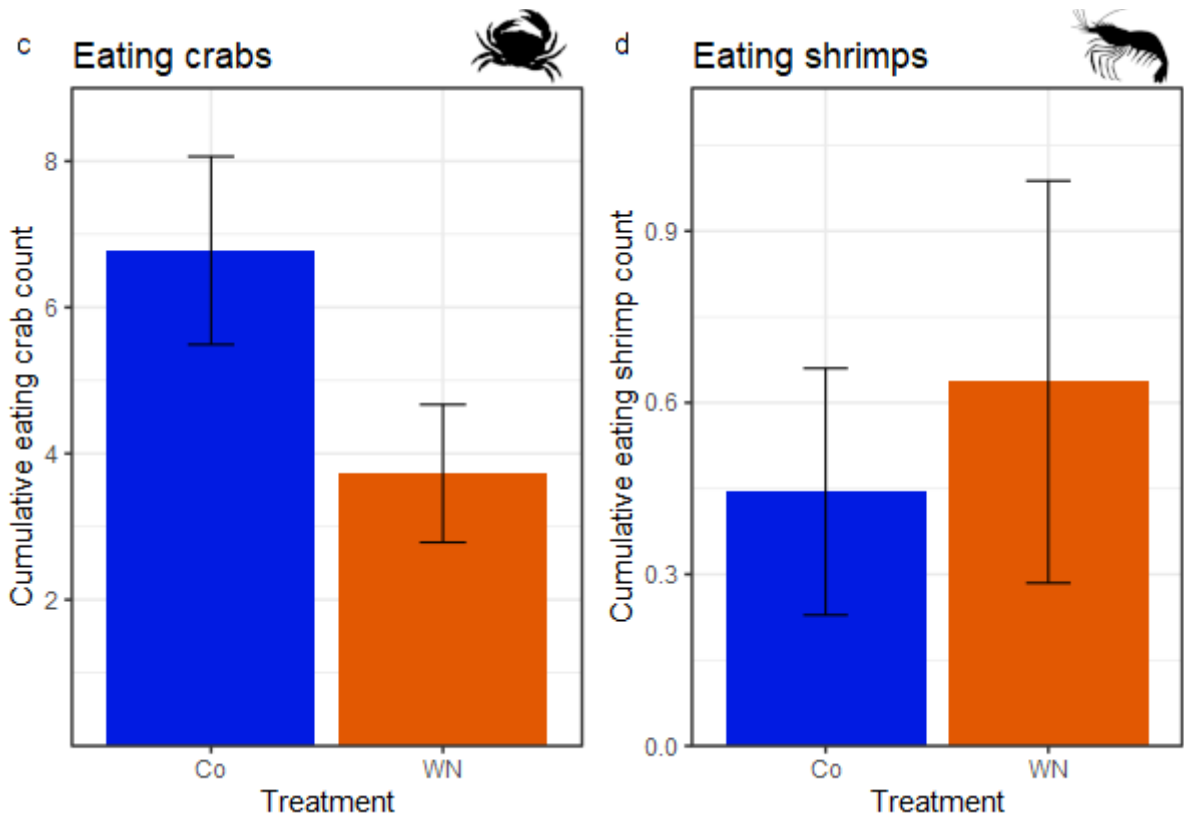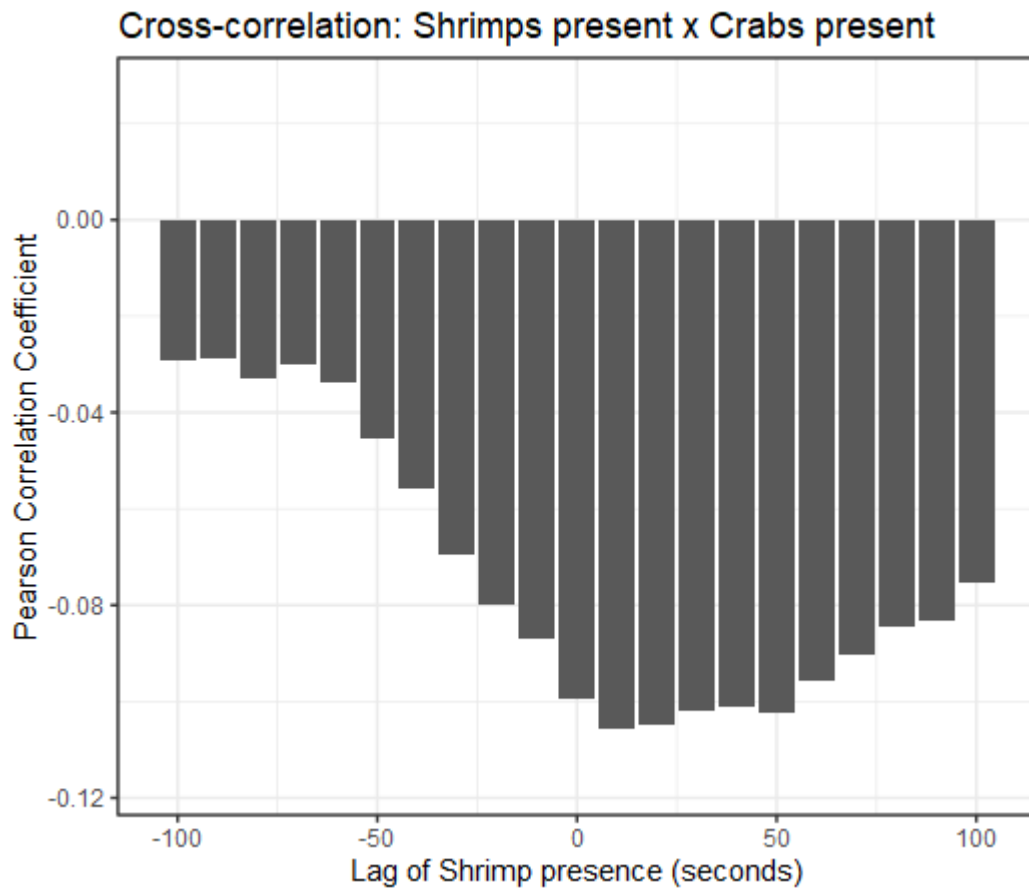|						
2	Cum crabs presence t = 0-2 min + Treatment + (1 | Position)	4	0.54	0.74	489.5	4.81
3	Cum crabs presence t = 0-2 min + Cum shrimps presence t = 2-4 min + (1 | Position)	4	0.34	0.72	510.0	25.30
null	(1 | Position)	2		0.74	573.7	88.97
Cum shrimps presence t = 2-4 min ~ …						
1	Cum shrimps presence 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
4	Cum crabs presence t = 2-4 min + Cum crabs eating t = 0-2 + Treatment + (1 | Position)	5	0.57	0.76	277.0	3.65
5	Cum crabs eating t = 0-2 + Treatment + (1 | Position)	4	0.45	0.67	349.2	75.81
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
4	Cum shrimps presence t = 2-4 min + Cum shrimps eating t = 0-2 + Treatment + (1 | Position)	5	0.23	0.71	106.9	4.21
null	(1 | Position)	2	-	0.44	121.9	19.15

249

250   Figure 4

251

252

Fig. 4a-d. 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

255 *. 'Co' refers to the control (silence) treatment, 'WN' to the white noise treatment. The error
256 bars represent the error of the mean.

257

258   Figure 5

Cross-correlation: Shrimps present x Crabs present

259

260 Fig. 5. Cross-correlation of 'shrimp present' and 'crab present' using the time series count data
261 (25 time points per trial, 49 trials). The strongest correlation is found where the shrimp time
262 series were delayed by 10 s relative to the crab time series (lag 10). Strongest correlations were
263 found across positive lag values, suggesting that changes in shrimp presence follow changes in
264 crab presence.
265

266 **Discussion**

267 In the current study, we experimentally exposed shore crabs and common shrimps to elevated

268 sound levels after offering a food item. This experiment was performed in situ, ensuring high

269 acoustic and behavioural validity. Our results demonstrate that: (1) The current sound exposure

270 reduced aggregation at a food item in shore crabs, but not in common shrimps. (2) The feeding

271 rate, in both crabs and shrimps, was not directly affected by the sound exposures. (3) There

272 was a negative correlation between crab and shrimp numbers that was likely driven by crabs.

273 Even though the sound exposure did not affect shrimp aggregation directly, shrimps may have

274 indirectly benefitted as lower numbers of crabs due to sound exposures released competition

275 for shrimps.

276

277 Crab foraging behaviour

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

279 study on shore crabs. Wale and colleagues (2013b) did not find an effect of ship noise on a

280 food item being found by crabs and the time taken to find the food source. However, this

281 experiment was conducted in a relatively small tank (0.12 m^2) with a single crab whereas the

282 current experiment was conducted in the wild where it is possibly much more challenging to

283 find a food item. Also, the crabs in the indoor experiment were food deprived for 96 h before

284 the foraging experiment, this might have led to a different trade-off in exploration and risk-

285 taking behaviour than in the current experiment. The researchers did find increased disruption

286 of feeding in the first minute after onset of the ship noise. This was defined as a ≥ 5 s

287 interruption of feeding, freezing, or the animal moving away from the food. We did not find a

288 drop in feeding rate. This might be because the sound that was played back in the current study

289 was much softer (~ 12-32 dB re 1 µPa quieter than in Wale et al. 2013b). This might mean that

290 crabs are only disturbed in their feeding activity above a certain sound level, from a louder or

291 closer source.

292   There are several possible explanations for the reduced aggregation at a food item by

293 crabs. It may be the case that crabs eating or interacting at a food item produce sound that

294 attracts others (e.g. Coquereau et al., 2016). Such sounds could have been masked in our

295   experiment during the playback of white noise. An alternative explanation of our results is that

296   the playback sound disturbed them (*cf.* Chan et al., 2010; Walsh et al., 2017). This might have

297   resulted in reduced exploration and risk-taking behaviour in crabs due to potential masking of

298   sounds from predators (Lima and Dill, 1990). In line with this, it might also be that crabs

299   reduced their overall activity to increase readiness for escape responses (Edmonds et al., 2016).

300   Confirmation of the latter hypothesis would require individual tracking instead of bait-targeted

301   observations.

302   We did not find evidence that aggregation at a food item and feeding in shrimps were

303   affected by the sound exposure. Shrimp presence (aggregation at a food item) could best be

304   explained by crab presence. In contrast, Filiciotto and colleagues (2016) showed that captive

305   common prawns in a controlled experiment reduced locomotor activity during the playback of

306   boat recordings. Such direct effects might have been overshadowed by the interaction with

307   crabs in the current study, thus highlighting the importance of looking beyond single species

308   effects in sound impact studies (Francis et al., 2009; Shafiei Sabet et al., 2016).

309

310 Interaction between crabs and shrimps

311   We found a negative correlation between crab and shrimp presence. The cross-

312   correlation showed that crab presence correlates best with later shrimp presence, this supported

313   our expectation that crabs were deterring shrimps. Competition and interaction between species

314   can be found throughout the animal kingdom. For example, Stahl and colleagues (2006) found

315   that European brown hares (*Lepus europaeus*) naturally selected high biomass swards to forage

316   on. However, after experimentally excluding geese from swards, hares foraged more on swards

317   with both high plant quality and high biomass. Another prominent example by Estes and

318   colleagues (1998) concerned killer whales (*Orcinus orca*) shifting prey choice towards sea otter

319 (*Enhydra lutris*), which undermined the sea otters' control of the dominant herbivores, sea

320 urchins (Echinoidea). As a consequence, the flourishing sea urchins overgrazed the kelp forest

321 which dramatically changed the local ecosystem (Estes and Palmisano, 1974; Estes et al.,

322 1998).

323   When interacting species respond differently to human influences, competitive

324 balances between species may also shift (Tylianakis et al., 2008; Worm and Paine, 2016).

325 Previous research has shown that anthropogenic sound can reduce species richness in avian

326 communities, but may also indirectly facilitate breeding success of particular species because

327 of lower abundance of a nest predator species (Francis et al., 2009; Slabbekoorn and Halfwerk,

328 2009). This avian example concerned a case of predator-release, while the current crustacean

329 example concerns competitive release between two species competing over the same resources.

330 The sound exposures released competition by the dominant species allowing the subordinate

331 species to make use of the resource. Competitive release is often shown in long term-studies

332 by contrasting shifts in distribution (e.g. Anderson et al., 2002). We here provide evidence for

333 a more short-term release in competition mediated by a species-specific behavioural response

334 to sound exposures.

335   Revealing such interactions between species shows that single-species studies alone are

336 not sufficient for determining impact of sound as there may be (local) community effects

337 (Francis et al., 2009; Slabbekoorn and Halfwerk, 2009; Shafiei Sabet et al., 2016). Besides the

338 importance of in situ studies, we also think that conducting controlled studies on captive

339 animals can help in understanding processes that are important to free-ranging animals in the

340 real world (Slabbekoorn, 2014). For example, it would be interesting to conduct a number of

341 parallel exposure trials to study the effects of sound solely on crab food aggregation and eating,

342 solely on shrimp food aggregation and eating, and on both species at the same time. In such a

343 controlled study, it is likely possible to follow individual animals throughout entire trials, which

344 should increase insights into the underlying mechanisms of our current results. In this way,

345 synergy through studies in the lab and the wild will help in gaining understanding of biological

346 processes and thereby increase the validity of sound impact assessments.

347

348 Conclusion

349   Our study provides evidence for the fact that artificial sound exposures can decrease

350 the number of crabs aggregating at a food item and provide indirect benefits for shrimps via

351 competitive release. This highlights the importance to study the potential impact of

352 anthropogenic sound in situ and consider cross-species interactions. We believe it is especially

353 important to study effects at and among lower trophic levels (e.g. invertebrates) as subtle

354 effects here may accumulate at higher trophic levels (e.g. fish or marine mammals). We like to

355 stress that our study provides a proof of concept and that our in situ approach strengthens

356 behavioural and acoustic validity. However, our set-up does not provide insight into ecological

357 relevance in absolute sense and more sound studies are needed for a better understanding of

358 individual and population consequences of changes in multi-trophic interactions due to changes

359 in underwater soundscapes.

360

361 **Ethical statement**

362 There are no legal requirements for studies involving decapod crustaceans and molluscs in The

363 Netherlands. Our experiment likely only caused short periods of mild discomfort in crabs and

364 shrimps, as we observed free-ranging animals and only exposed them to short-lasting exposures

365 with moderate sound levels. The sound exposure and food provisioning in our study are

366 therefore unlikely to have caused any welfare problems to either species.

367

Acknowledgements

376

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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