1 **Distracted decision-makers: Ship noise and predation risk**
2 **change shell choice in hermit crabs**

5

6 Svenja Tidau* and Mark Briffa

7

8 * Corresponding author: svenja.tidau@plymouth.ac.uk

9

10 *Address and contact*

11 Svenja Tidau

12 University of Plymouth | Marine Biology & Ecology Research Centre

13 Drake Circus | Plymouth, PL4 8AA | UK

14

15 Mark Briffa

16 University of Plymouth | Marine Biology & Ecology Research Centre

17 Drake Circus | Plymouth, PL4 8AA | UK

Abstract

Human induced rapid environmental change such as noise pollution alters the ability of animals to integrate information cues. Many studies focus on how noise impacts single sensory channels but in reality animals rely on multi-modal sources of information. In this study, we investigated the effect of anthropogenic noise and the visual presence of a predator on tactile information gathering during gastropod shell assessment in the European hermit crab *Pagurus bernhardus*. For hermit crabs, empty gastropod shells are a crucial resource affecting growth, reproduction and survival. We measured shell assessment behavior and manipulated (i) the shell size (50% or 80% of the optimal), (ii) sound condition (ship or ambient) and (iii) visual predator cue (absence/ presence). Overall we found that crabs were less likely to accept an optimal shell in the presence of ship noise, suggesting that exposure to ship noise disrupted the information gathering ability of the crabs. We also found a significant interaction between noise, predator presence and shell size on the mean duration for the final decision to accept or reject the optimal shell. Hermit crabs in 50% shells took less time for their final decision when exposed to both ship noise and predator cue while crabs in 80% shells showed shorter decision time only when the predator cue was absent. Our results indicate that anthropogenic noise can interact with predation threat and resource quality to change resource acquisition, suggesting that noise pollution can disrupt behavior in a non-additive way, by disrupting information use across multiple sensory channels.

Keywords

Introduction

Human induced rapid environmental change (HIREC) (Sih et al. 2011) encompasses global processes such as climate change as well as examples of more localized and transient pollution such as ship noise (Tuomainen and Candolin 2011). HIREC can either affect behavior directly by impacting whole organism performance capacities (via changes to development or physiological state) or indirectly by altering the sensory environment and disrupting the information gathering and decision-making processes that underpin behavior. Both routes have potential implications for survival and fitness. Noise has been shown to affect the detectability (and recognizability) of cues both through masking of sound (Brumm 2004; Foote et al. 2004; Sun and Narins 2005; Clark et al. 2009; Barber et al. 2010; Halfwerk et al. 2012; Lampe et al. 2012; Ladich and Fay 2013; Heiler et al. 2016; Spiga 2016; Simpson et al. 2016) and by distracting an animal's limited attention (Chan et al. 2010a; Chan et al. 2010b; Wale et al. 2013a; Kunc, et al. 2014; Simpson et al. 2015; Radford et al. 2016; Nedelec et al. 2017; Walsh et al. 2017; Tidau and Briffa *In Press*). Since animals perceive and have to process information across various modalities, their limited attention is a cognitive constraint (Dukas 2004). As a consequence, the 'distracted prey hypothesis' (Chan et al. 2010b) suggests that since animals have to divide their attention they may no longer respond appropriately to predator cues in the presence of noise (Chan et al. 2010b). Thus, noise might not only distract attention from acoustic cues but also from non-acoustic cues across visual, chemical and tactile channels and in addition can also disrupt the integration of information across sensory modalities (Halfwerk and Slabbekoorn 2015).

Recent decades have seen mounting evidence for effects of anthropogenic noise pollution across a range of taxa, habitats and behavioral contexts (Barber et al. 2010; Kight and Swaddle 2011; Williams et al. 2015). This includes shifts in the amplitude, duration, timing and patterns of acoustic communication as possible means of

69 compensating for noise, with examples in birds (Brumm 2004; Halfwerk et al. 2012),

70 amphibians (Sun and Narins 2005), insects (Lampe et al. 2012), marine mammals (Foote

71 et al. 2004; Heiler et al. 2016), fish (Ladich and Fay 2013) and snapping shrimp (Spiga

72 2016). However, there is also evidence that behaviors in contexts other than

73 communication can be impacted by noise, and in these cases the scope for animals to

74 compensate may be more limited. Furthermore, due to distraction effects disruption is

75 not limited to behavior that relies on acoustic sources of information only. Examples of

76 the wide range of impacted behavioral contexts include reduced foraging performance

77 in the common shore crab *Carcinus maenas* (Wale et al. 2013a), the greater mouse-

78 eared bat *Myotis myotis* (Siemers and Schaub 2011) and the Black-tailed prairie dog

79 *Cynomys ludovicianus* (Shannon et al. 2014), decreased parental care in the spiny

80 chromis *Acanthochromis polyacanthus* (Nedelec et al. 2017), impaired shoaling in the

81 Bluefin tuna *Thunnus thynnus* (Sara et al. 2007) and reduced predator avoidance in the

82 European eel *Anguilla anguilla* (Simpson et al. 2015).

83   Anthropogenic noise not only disrupts the sensory environment of animals along

84 acoustic, unimodal sensory channels but also across non-acoustic channels for

85 information gathering and processing, such as the visual and tactile sensory systems

86 (Kunc et al. 2014; Tidau and Briffa *In Press*). It has been suggested that such cross-

87 sensory interference can distract organisms, thus explaining behavioral changes in

88 response to anthropogenic pollution in vertebrates and invertebrates alike (reviewed by

89 Halfwerk and Slabbekoorn 2015). However, different sources of information used by

90 animals tend to be studied in isolation. In contrast, few studies have taken a multi-

91 sensory approach to investigating the effects of anthropogenic noise on behaviors that

92 (in nature) are likely to be dependent on information from several channels (Sih et al.

93 2011; Halfwerk and Slabbekoorn 2015). For example, the European hermit crab *Pagurus*

94 *bernhardus* integrates tactile and visual information when assessing the value of an

95   empty gastropod shell. This is a critical resource that provides protection for their weakly

96   calcified abdomen and crabs are known to choose new shells based on information

97   about their mass, species, condition (Elwood and Neil 1992) and color (Briffa et al. 2008).

98   During the process of exchanging an old shell for a new one, hermit crabs are vulnerable

99   to attack and hence they adjust their shell assessment behavior in the presence of

100 predators (Briffa et al. 2008). Hermit crabs rely on a range of tactile, visual and chemical

101 cues in order to compare the quality of a potential new shell with that of the currently

102 occupied shell. Like other coastal species, however, hermit crabs are subject to noise

103 pollution caused by the motors of ships and boats. While *P. bernhardus* is found in

104 coastal intertidal rock pools, as they grow, these hermit crabs prefer to occupy *Buccinum*

105 *undatum* shells and are increasingly found in subtidal areas such as the English Channel.

106 Thus, for *P. bernhardus* noise from ships represents a relevant anthropogenic stimulus.

107 A recent laboratory study has shown that the time taken for *P. bernhardus* to choose a

108 new shell decreases significantly in the presence of white noise (Walsh et al. 2017).

109 While the effects of noise on shell assessment (Walsh et al. 2017) and antipredator

110 behavior (Chan et al. 2010a) have been analyzed in isolation in different species of

111 hermit crabs, the effects of noise on the ability to integrate information about the shell

112 resource and predation threat has yet to be investigated.

113   Here, we investigate the effects of ship noise on the ability of hermit crabs to use

114 tactile and visual information to choose a shell of optimal quality and to adjust their shell

115 assessment behavior in the visual presence of a predator. A common predator of *P.*

116 *bernhardus* is the common shore crab *Carcinus maenas* and previous studies have

117 shown that hermit crabs respond to their chemical cues (Rotjan et al. 2004; Briffa et al.

118 2008). Under normal circumstances the duration of shell investigation and chance of a

119 hermit crab exchanging shells increases with the potential gain in shell quality (Elwood

120 and Stewart 1985; Elwood 1995; Tricario and Gherardi 2007; Turra and Gorman 2014)

121 but decreases with predation risk (Rotjan et al. 2004; Bulinski 2007; Briffa and Austin

122 2009), reflecting a trade-off between the costs and benefits of changing shells. If this

123 trade-off between shell quality and predation risk is altered by the presence of noise, this

124 would indicate that anthropogenic noise reduces the ability of hermit crabs to integrate

125 pertinent information across different sensory channels. We predict that hermit crabs will

126 respond to the visual predator cue by altering their shell assessment and that this is

127 influenced by the quality of shell a hermit crabs occupies, i.e. crabs in small shells (50%

128 of its preferred shell based on the crabs own body mass) will have a large shell gain

129 (50%) but are also more exposed to predators while crabs in larger shells (80% of its

130 preferred shell) have a lower shell gain (20%) but are less exposed to a predator. We

131 predict that crabs in small shells will therefore show greater responses to the predator

132 cue. Moreover, if noise disrupts information gathering across sensory channels, we

133 expect crabs to alter their shell dependent predator response in the presence of noise.

134 Thus, the effect of original shell size on responses to a predator cue should be reduced

135 in the presence of noise. Thereby, we aim to address a current gap in knowledge about

136 how the effects of anthropogenic noise might impact the integration of behavior across

137 the different sensory channels that animals rely on in nature.

Materials and methods

138

Collection and husbandry of hermit crabs

139

140 *P. bernhardus* inhabits subtidal as well as intertidal marine habitats. For practically of

141 sampling, we collected *P. bernhardus* from the rocky intertidal of Hannafore Point,

142 Cornwall, UK (50° 20' 42'' N, 4° 28' 0'' W) adjacent to the English Channel and next to a

143 local fishing harbor between November 2016 and January 2017. We transported the

144 animals directly to a temperature-controlled room at the University of Plymouth. The

145 room was maintained at 15 °C with a 12:12 hour light:dark cycle and hermit crabs kept

146   in a single holding tank containing 125 L of continuously filtered and aerated seawater

147   (Briffa et al. 2013) taken from the laboratory supply obtained from the seaward side of

148   Mount Batten pier (50° 21' 34" N, 4° 8' 8" W) in Plymouth Sound at spring tides. We fed

149   crabs in this stock tank once a week with white fish.

150   At least 16 hours before the observation, we removed crabs with a bench vice

151   from their shell, sexed and weighed each individual. Crab mass ranged from 0.18 g to

152   1.61 g (mean mass ± SE = 0.798 g ± 0.32 g, N = 59). Each crab was assigned a *Littorina*

153   *littorea* shell of either 50% or 80% of its preferred shell mass based on a regression line

154   relating preferred shell mass to body mass (Dowds and Elwood 1983; Briffa and Elwood

155   2007). We housed the crabs in individual white plastic dishes of 15 cm diameter

156   containing continuously aerated seawater to a depth of 5 cm. Since the shell mass

157   preferences of females are subject to change during the breeding season, we used only

158   male crabs without damaged appendages, visible parasites or recent molting in the study

159   (Briffa and Elwood 2007). After the observations we returned the animals unharmed to

160   the sea at the collection point.

161   ***Tank set-up and sound analysis***

162   We carried out the observations in a 80 x 50 x 50 cm sized glass tank filled with ~ 130 L

163   (to a depth of 40 cm) of seawater from the laboratory supply. We placed the tank on a

164   free-standing trolley and cushioned it with at least 1cm Styrofoam plates between tank

165   and trolley as well as the trolley and floor. The speaker was suspended in the tank from

166   a cushioned bamboo stick at 20 cm distance to one end of the tank, such that is was fully

167   submerged in the seawater (Figure 1). In order to ensure that crabs were exposed to

168   similar sound conditions we designed two 20 x 20 cm arenas within the larger tank at

169   equal distances from the speaker. The center of each arena was 30 cm from the center

170   speaker and the other end of the tank. No substrate was provided on the arena floors,

171   as this is known to interfere with the locomotion and general activity of hermit crabs and

172 other non-swimming crustaceans (Wale et al. 2013; Walsh et al. 2017; Tidau and Briffa

173 *In Press*). The arenas were divided by an opaque 15 cm high plastic sheet. In order to

174 disrupt the particle motion resulting from the sound playbacks as little as possible while

175 preventing the crabs from directly escaping from the arena, we constructed the walls of

176 each arena from 1 x 1 cm mesh-size plastic mesh. For the predator cue, we placed a

177 plastic model crab of approximately 10 cm width in an upright position outside of the tank

178 and centered to the arena such that it was visible from inside the arena imitating the

179 natural predator *Carcinus maenas* (Rotjan et al. 2004; Briffa et al. 2008).

180   While some studies use white noise as a substitute sound source to test the effect

181 of anthropogenic noise pollution on animals (Chan et al. 2010a; Stahlman et al. 2011;

182 Walsh et al. 2017), most noise studies utilize playbacks of actual anthropogenic

183 pollutants, for example ships. Ship noise and white noise playbacks not only differ in their

184 spectral properties (frequency, amplitude) but also in their temporal pattern and

185 predictability. Compared to white noise, which is characterized by equal energy intensity

186 across frequencies (Barber et al. 2010), ships produce unique acoustic signals

187 depending on factors such as speed and load (Hildebrand 2009). Consequently, ships

188 produce a more unpredictable signal compared with artificial white noise. It is known that

189 the stress induced by a stimulus is linked to its predictability (Koolhass et al. 2011;

190 Francis and Barber 2013) and that for this reason less predictable stimuli are likely to be

191 more distracting to animals. Relatively few studies have formally compared the effect of

192 artificial white noise and playbacks of anthropogenic noise pollutants (Holles et al. 2013;

193 Bent et al. 2018; Bermúdez-Cuamatzin et al. 2018), but where this has been done noise

194 from anthropogenic pollutants tends to be similarly (Bermúdez-Cuamatzin et al. 2018) if

195 not more distracting than white noise in terms of behavior (Holles et al. 2013; Bent et al.

196 2018). For these reasons we used three ship noise playbacks along with corresponding

197 ambient control sounds from the same sites recorded at three major UK harbors. These

198   recordings were used in previous studies in which the sample location, ship size and

199   speed were detailed (for instance Wale et al. 2013a; Simpson et al. 2015). We used

200   Audacity 2.1.2 (Audacity Team, 2017) to create a total of six sound tracks for playback

201   to the crabs, of either ambient control sound or ship noise. In the case of ship noise

202   tracks, we alternated 2 minutes of ship noise with 2 minutes of ambient sound including

203   15 seconds fading in and out to simulate noise of passing ships. We assigned the crabs

204   randomly to one of the two sound treatments (ambient control or ship noise). Within each

205   of these treatments crabs received one of three alternative sound recordings of ship

206   noise or ambient sound, as appropriate for their treatment group. These recordings were

207   alternated between the successive observations (for details on the noise exposure and

208   behavioral observation see section below).

209   For the playbacks of the sound tracks, we used a Toshiba Portégé R830-13C

210   laptop (Tokyo, Japan) connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou

211   Co., Taiping Town, China) and an underwater speaker (DNH Aqua-30 underwater

212   speaker, effective frequency range 80-20 000 Hz, DNH A/S, Kragerø, Norway). To

213   characterize the acoustic properties of our playbacks within the laboratory aquarium we

214   undertook a spectral analysis as follows. We re-recorded the six sound tracks at the

215   center of the arena at 30cm distance to the speaker and 10cm to the tank wall at 1-2 cm

216   distance to the bottom of the tank with an omnidirectional hydrophone HTI-96-MIN (with

217   inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V µPa-1; frequency

218   range 0.002-30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10

219   recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level

220   calibrated using pure sine wave signals from a function generator with a measured

221   voltage recorded in line on an oscilloscope). At this position, the three ambient sound

222   tracks were played back so that they had an average maximum sound pressure level of

223   119.4 dB RMS re 1 µ Pa (ambient A: 119.7, ambient B: 118.8, ambient C: 119.8) and

224   the ship noise had an average maximum of 143.6 dB RMS re 1 μ Pa (ship A: 143.0, ship

225   B: 143.8, ship C: 143.9). These sound levels were similar to those in previous studies on

226   crustaceans (Wale et al. 2013a, Wale et al. 2013b). We note that hermit crabs are likely

227   to perceive the particle motion component of sound rather than the measured sound

228   pressure levels (Popper et al. 2001; Breithaupt 2002). However, as in in previous studies

229   (see for instance Wale et al. 2013), and due to unresolved challenges of tank acoustics

230   (Rogers et al. 2016) we analyzed the power spectrum of the sound pressure for each

231   playback to make sure that we exposed crabs to two distinctive sound conditions namely

232   ship noise and ambient control, rather than attempting to establish absolute noise

233   sensitivity levels for hermit crabs. We used PAMGuide (Merchant et al. 2015) for

234   MATLAB R2015b (MathWorks, Inc. 2015) to perform a power spectrum analysis of 60

235   seconds recording with Hann evaluation window, overlap 50%, 0.25 second window

236   length, 1 - 48 000 Hz bandwidth normalized to 1 Hz (Figure 2).

237   ***Experimental design and behavioral analysis***

238   We designed a fully orthogonal experiment with the three factors; sound condition

239   (ambient control or ship noise), predator cue (present or absent) and initial shell size (50%

240   adequate or 80% adequate). The combination of these treatments resulted in 8 treatment

241   groups. During each observation session, our set up containing two arenas allowed us

242   to concurrently expose two individuals (that were unable to interact with one another) to

243   the same sound track. At the start of the session we placed a shell of 100% preferred

244   size for the crab allocated to each arena with the aperture facing downwards in the

245   middle of each arena. After starting the sound playback, we placed the crabs in their

246   allocated arenas with the aperture of their gastropod shells facing upwards. To avoid the

247   effect of shell size being confounded by time of day, we always observed concurrently a

248   crab starting in the observation in a 50% adequate shell and a crab starting the

249   observation in an 80% adequate shell, one in each of the two observation arenas. To

250 avoid confounding the data through any directional bias the position (left or right arena)

251 we alternated the two shell size treatments between arenas across consecutive

252 observations. On each day of observation we collected data from a similar number of

253 crabs from each of the four ship noise and predator cue combinations, and the order of

254 treatment combinations was varied from day to day.

255   The shell assessment behavior was recorded with a Canon Legria HF R47

256 (Tokyo, Japan) for a maximum of 25 minutes (up to 5 minutes were allowed for crabs to

257 emerge from their gastropod shell at the start of the observation and 20 minutes of

258 behavior were then quantified). The videos were scored using The Observer version 12

259 (Noldus IT, Wageninngen, The Netherlands) event logger software blind to the sound

260 and predator cue treatments. We scored the frequency, duration and latency for each of

261 the behaviors. The observation started when the crab had emerged from its shell and

262 placed at least one of its appendages on the bottom of the tank. During the 20 minutes

263 of observation the crabs were continuously exposed to either ambient control sound or

264 ship noise playback as described above. We recorded the total decision time defined by

265 the time from the start of the observation when crabs contacted the bottom of the tank

266 with at least one walking leg to the point where the crabs had made a clear decision to

267 reject either the new, optimal shell or the initially occupied shell. We designated the final

268 decision point as that time at which crabs had moved one body length away from either

269 the rejected optimal shell or the previously occupied shell. We also recorded whether

270 crabs contacted the optimal shell with their antennae, whether they entered the optimal

271 shell. For those crabs that did enter the optimal shell we recorded whether or not they

272 finally accepted the optimal shell. Observations were terminated when one of the

273 following conditions was met: The crab swapped into the optimal shell and moved at

274 least as far away from the old shell as the length of its body ("optimal shell accepted"),

275 the crab had contact with the 100% shell but did not swap into it and moved away at

276 least as far as the length of its body ("optimal shell rejected") or after 20 minutes, if the

277 crab had no shell contact ("no decision"). Of the initial 77 observations conducted, 18

278 crabs made no contact with the optimal shell. Since their decision was not affected by

279 any of the predictors (sound: $\chi^2_1 = 0.34$, $P = 0.56$; predator cue: $\chi^2_1 = 1.17$, $P = 0.28$,

280 occupied shell: $\chi^2_1 = 0.02$, $P = 0.89$) or their interaction (see supplemental files for a

281 complete results table), we excluded those 18 crabs from the analysis. This left a sample

282 size of $N = 59$ crabs (see Table 1 for details).

283 ***Statistical analysis***

284 To determine the effects of noise condition, predator cue and shell size on shell

285 assessment behavior we used General and Generalised Linear Mixed Effect Models, as

286 appropriate, implemented in the R-package lme4 (Bates et al. 2015) in R version 3.3.2

287 (R-Core-Team 2017). The fixed effects were sound treatment (ship noise or ambient

288 control), predator cue (present or absent) and initial occupied shell size (50% or 80%),

289 and their interactions. Crab body mass was included as a covariate. In order to account

290 for the potential pseudo-replication that might arise from re-using each of the three ship

291 noise and three ambient control recordings across multiple observations, we included

292 playback identity as a random (intercept) effect. Furthermore, we included a second

293 random intercept to account for the paired observations within each observation session.

294 Where necessary the data (i.e. latency to contact the optimal shell, total decision time to

295 accept or reject the optimal shell) were log transformed to improve normality, so that the

296 assumption of the linear models would be met. For the binary response variables

297 (displaying antennal contact, entering the optimal shell, accepting the optimal shell) we

298 used a binomial distribution and for continuous data (duration and latency) we used a

299 Gaussian distribution. For models with non-Gaussian data we used likelihood ratio tests.

300 To assess model fit we visually inspected the distribution of residuals.

301

302 *Ethical note:* No animals were harmed during the experiments. After the experiment each

303 crab was supplied with an optimal shell, was fed and returned to the sea at the location

304 of collection. No licenses or permits were required for this study.

305

Results

307 There was no effect of the interaction between sound, predator cue and occupied shell

308 size ($\chi^2_1 = 3.08$, $P = 0.08$) or any of the main effects, i.e. sound ($\chi^2_1 = 2.11$, $P = 0.15$),

309 predator cue ($\chi^2_1 = 0.34$, $P = 0.56$) or initially occupied shell size ($\chi^2_1 = 0.99$, $P = 0.32$)

310 on the latency to contact the optimal shell (see supplement for all results tables).

311 Larger hermit crabs approached the optimal shell faster than smaller crabs ($\chi^2_1 = 7.44$,

312 $P = 0.006$). Furthermore, there was a significant three-way interaction between sound,

313 predator cue and shell size on the total decision time to accept or reject the optimal

314 shell ($\chi^2_1 = 5.0$, $P = 0.03$; Figure 3). Crabs in a 50% adequate shell and exposed to a

315 predator took a longer total decision time under ambient control compared to ship

316 noise. In the contrary crabs in 80% shells showed the opposite pattern, taking more

317 time to decide under ambient sound than ship noise when the predator was absent, but

318 being unaffected by the sound treatment when the predator was present. The total

319 decision time decreased with crab mass ($\chi^2_1 = 7.23$, $P = 0.007$).

320   For crabs that contacted the optimal shell, we analyzed the effect of the predictors

321 on the occurrence of antennal contact. Since not every crab decided to contact the

322 optimal shell, we did not have sufficient data on the occurrence of antennal contact to

323 calculate the three-way interaction. For those crabs that did contact the optimal shell,

324 there were no significant two-way interactions: sound and predator cue ($\chi^2_1 = 1.51$, $P = $

325 0.22) or predator cue and occupied shell ($\chi^2_1 = 3.08$, $P = 0.08$). However, under ambient

326   sound conditions, hermit crabs in 50% shells were less likely to contact the optimal shell

327   with their antennae compared to crabs in 80% shells whereas this pattern was absent in

328   the presence of ship noise. (χ^2_1 = 10.0, P = 0.002; Figure 4). In the presence of a predator

329   cue, more crabs displayed antennal contact with the optimal shell (χ^2_1 = 4.07, P = 0.04;

330   Figure 5).

331   Crabs which occupied a 50% shell were more likely to enter the optimal shell than

332   crabs in 80% shells (χ^2_1 = 5.46, P = 0.02; Figure 6). We could not reliably calculate the

333   three-way interaction for this decision since relatively few crabs with an 80% shell that

334   were exposed to ship noise decided to enter the optimal shell (see supplement Table 4).

335   None of the two-way interactions sound and predator (χ^2_1 = 1.57, P = 0.21), sound and

336   occupied shell (χ^2_1 = 3.15, P = 0.08), predator cue and occupied shell (χ^2_1 = 0.67, P =

337   0.41) or the main effects other than occupied shell (sound: χ^2_1 = 2.58, P = 0.11; predator

338   cue: χ^2_1 = 0.17, P = 0.68) had a significant effect on whether crabs entered the optimal

339   shell. None of the factors or their interaction affected the latency to swap into the optimal

340   shell (see supplement Table 5).

341   For the final decision to accept the optimal shell we could not calculate the three-

342   way interaction as relatively few individuals with an 80% adequate shell that were

343   exposed to noise chose to enter the optimal shell (see supplement Table 6). The decision

344   was not affected by the interactions between sound and predator cue (χ^2_1 =0.34, P =

345   0.56), sound and occupied shell (χ^2_1 = 2.19, P = 0.14), predator and occupied shell (χ^2_1

346   = 0.005, P = 0.94) or predator cue (χ^2_1 = 0.38, P = 0.54). However, under ambient sound

347   conditions, crabs accepted the optimal shell more frequently than under noise conditions

348   (χ^2_1 = 8.0, P = 0.005; Figure 7). Crabs in a 50% shell accepted the optimal shell more

349   often than crabs in an 80% shell (χ^2_1 = 11.67, P = 0.0006; Figure 8).

Discussion

Noise exposure significantly influenced the shell assessment behavior of hermit crabs, disrupting both activities during shell assessment and the final decision to accept or reject the optimal. *P. bernhardus* responded to noise in interaction with other (naturally occurring) cues in the case of shell assessment activities but also in isolation in the case of the final decision to accept the optimal shell. For hermit crabs, gastropod shells represent a critical resource, which determines not only survival but also growth and fecundity. Therefore, the assessment process and decision to exchange the current shell for an optimal one will directly influence an individual's fitness. These decisions can be complex because the benefits of swapping into a better shell must be balanced against the temporary predation risk during the assessment process, which might attract the attention of predators. On swapping shells, the weakly calcified abdomen is briefly exposed. Thus, crabs are usually less likely to swap shells when the risk of predation is high (Briffa et al. 2008). The current data show that the way hermit crabs use information on these benefits and risks can be disrupted by changes to the sensory environment caused by anthropogenic noise.

The total decision time taken to find, assess and then finally accept or reject the optimal shell was influenced by a complex three-way interaction between sound treatment, size of the initially occupied shell and the visual predator cue. That crabs in a 50% shell show shorter decision time than crabs in an 80% shell under the control conditions (without predator cue and noise) is in line with previous studies demonstrating that the potential gain in shell quality influences the motivation for changing shells (Elwood 1995). Further, predator cues affected crabs differently depending on the shell quality they hold and generally crabs exposed to predation risk tend to behave more cautiously (Briffa et al. 2008). Here, crabs showed more cautious shell assessment steps such as the antennal contact in the presence of a predator cue. For crabs in a low quality

376   50% adequate shells the visual predator cue led to an increase in decision time under

377   ambient sound but this effect was absent when ship noise was present. Thus, for crabs

378   with the potential for a large increase in shell quality, ship noise appears to negate the

379   normal effect of predator presence. Compared to crabs in a 50% shell, crabs in 80%

380   shells took longer to assess shells in the absence of a predator cue than in its presence

381   and the normal pattern observed under ambient sound was absent in the presence of

382   ship noise (as in the case of crabs in 50% shells). A recent study on the hermit crab

383   *Clibanarius vittatus* showed that the shell quality affects the response time to a predator

384   cue and that crabs in better quality shells show longer startle response without predation

385   risk than crabs exposed to a predator cue (Gorman et al. 2018) as we observed. Here,

386   the decision-making duration of hermit crabs was influenced by two naturally occurring

387   cues, shell quality and predation risk, as well as anthropogenic noise. Therefore, the

388   present data show that anthropogenic noise can lead to changes in behavior through

389   interactions with other sources of information. Previous studies on the response to noise

390   in crustaceans suggest that they adjust the timing or duration of their behavior when

391   noise is the only factor animals were exposed to. The common shore crab *Carcinus*

392   *maenas* retreated more slowly into shelters exposed to ship noise playbacks (Wale et al.

393   2013a) and the hermit crab *P. bernhardus* investigated shells more quickly under white

394   noise (Walsh et al. 2017). Likewise exposed to white noise, the marine rock lobster

395   *Panulirus longipes* took longer to emerge from shelter (Meyer-Rochow et al. 1982) and

396   the Caribbean hermit crab *Coenobita clypeatus* let a predator approach closer before

397   hiding (Chan et al. 2010a). Expanding on those studies, our results indicate that rather

398   than acting in isolation, noise effects are also influenced by at least two other, naturally

399   occurring factors, shell size and predation risk, both of which hermit crabs are likely to

400   experience frequently in nature (as pointed out in the introduction on the natural habitat

401   of *P. bernhardus*). The shell quality has been shown to determine behavior and

402   physiological state in hermit crabs (Briffa and Elwood 2000; Briffa and Elwood 2005).

403   One of the few examples on the effects of ship noise and predation risk in interaction

404   with physiological condition was on the European eel *Anguilla anguilla*. Here, juveniles

405   in poor condition decreased their startle response to ship noise (Purser et al. 2016). Even

406   though the exact mechanisms remain unknown, the differences observed between

407   hermit crabs in 50% (poorer condition) and 80% (better condition) adequate shells seem

408   similar. Future research on examining the mechanisms underpinning interactions

409   between noise and physiology could help to better explain these observed behavioral

410   responses.

411   Further we found evidence that noise effects animals differently depending on

412   the resource quality they hold and the complexity of the task. Under ambient conditions,

413   crabs initially in 80% shells (which had relatively little to gain) employed more antennal

414   contact during shell investigation compared to crabs initially in 50% shells (which could

415   make a relatively large gain). This difference is likely to reflect the fact that those crabs

416   in 80% shell had been presented with a more difficult choice than those in 50% shells

417   and hence made greater efforts to assess the empty shell. In the presence of ship noise,

418   however, this difference between crabs presented with easy and difficult choices (in

419   terms of potential gain in shell quality) was absent, with no difference in the amount of

420   antennal contact shown by crabs supplied with 50% and 80% adequate shells. Although

421   it is difficult to disentangle the effects of motivation from those of task complexity it is

422   likely that animals with more difficult decisions to make are susceptible to distraction by

423   anthropogenic noise. As animals possess a finite amount of attention and hence any

424   attention directed towards a novel cue (e.g. ship noise) is unavailable for other tasks

425   (Dukas 2004). Thus, routine tasks that require attention, such as assessing empty shells,

426   can be disrupted by novel stimuli. Blue jays *Cyanocitta cristata* have been shown to divert

427   their attention from a predator stimulus under more difficult and complex foraging tasks

428   (Dukas and Kamil 2000). That the difficulty of a task has an impact on the ability to detect

429 and respond to a stimulus (such as a predator) is known from other studies on several

430 bird species and the three-spined sticklebacks *Gasterosteus aculeatus* (for an overview

431 see Lawrence 1985). In humans it has been shown that with increasing difficulty of a

432 task less attention was spent on a second stimulus; the perception of the distracting

433 stimulus depends on the cognitive load of the focus task (Rees et al. 1997). Therefore,

434 the fact that crabs with less motivation and a more difficult decision were more

435 susceptible to the effects of noise provides additional support for the distracting effect of

436 noise (such as in the distracted prey hypothesis) which has been shown across humans

437 and non-human vertebrates and invertebrates. Future research on the cognitive

438 processes underlying these observations will allow to better understand the causes and

439 consequences of noise.

440 　　　　Anthropogenic noise exposure can also alter the final outcome of critical decision-

441 making. Under anthropogenic noise fewer crabs accepted the optimal shell; a similar

442 result to that recently obtained in crabs exposed to white noise (Walsh et al. 2017).

443 Rather than being affected by noise in interaction with the additional factors of predator

444 cue and shell size, the final decision to accept or reject the optimal shell was influenced

445 by noise itself. Suboptimal shells can inhibit growth and reproductive success as females

446 carry their eggs within the shell (Bertness 1981). Furthermore, shell fit is important for

447 protection against predators. When shells are too small hermit crabs cannot withdraw

448 fully into the shell and hence are most exposed (Angel 2000). As a consequence,

449 anthropogenic noise could have implications beyond individual crabs at the population

450 level. This effect could also be multiplied as vacated shells serve as a resource for

451 smaller crabs and cascade through the population, a process known as vacancy chain

452 previously described in hermit crabs (Briffa and Austin 2009; Lewis and Rotjan 2009).

453 Thus, noise appears to make it more difficult for hermit crabs to utilize information about

454 predation risk and shell quality. The decisions that are underpinned by such information

455   are also dependent on motivational state and here we also investigated whether noise

456   might interact with the motivation of crabs to change shells.

457   Our findings are broadly in line with the "distracted prey hypothesis" which

458   suggests that animals seem to get distracted by noise when assessing the potential

459   threat of a predator, allocating part of their limited attention away from the threat towards

460   the distracting stimulus (Chan et al. 2010b). For instance, prey showed decreased anti-

461   predator response (Bruintjes and Radford 2013; Bruintjes et al. 2016; Purser et al. 2016),

462   were slower to be startled by a stimulated predator attack (Simpson et al. 2015) and

463   were caught more efficiently and quickly (Nedelec et al. 2015). What we now show is

464   that these patterns of altered responses to information concerning predation threat

465   interact with altered responses to other cues, in this case tactile and visual information

466   gathering concerning resource quality. Moreover, distraction appears to alter the ability

467   of crabs to integrate this information on resource value with information on the risk of

468   predation. Thus, anthropogenic noise pollution alters the multisensory integration of cues

469   during the information gathering, assessment and decision-making process surrounding

470   utilization of a critical resource in the European hermit crab. To the best of our knowledge

471   there are no other studies that have compared the effect of noise (an anthropogenic

472   pollutant) with the effects of variation in the complexity of a cognitive task (driven in this

473   case by the size of the initial occupied shell) and the visual presence of an external threat

474   (visual presence of a predator). As animals live in complex environments with competing

475   information and attention demands (Talsma et al. 2010), it is important to understand the

476   interactive effect of anthropogenic noise with biologically relevant factors such as

477   predator cue and resource value. Under noise, stimulus-selective attention, where less

478   relevant information is ignored (Dukas 2002), seems to be compromised. The result that

479   hermit crabs choose an optimal shell less often under anthropogenic noise is likely a

480   consequence of distraction of their limited attention away from the pertinent natural cues

481 towards the anthropogenic stimuli. The decision to accept or reject an optimal shell has

482 not only implications for the fitness and survival of an individual but potentially cascades

483 up to the population level by reproduction, exposure to predators and freeing resources

484 for conspecifics. Our results provide evidence that pollutants such as noise can act

485 across sensory modalities (Halfwerk and Slabbekoorn 2015) and distract information

486 gathering and decision making of animals, here in using tactile and visual cues for

487 resource assessment. Cross-modal distraction from noise is not limited to the predation

488 context (common cuttlefish *Sepia officinalis* changed its color more frequently during a

489 playback of anthropogenic noise, Kunc et al. 2014) or animals but has been shown in

490 humans as well (Parmentier et al. 2011; Ljungberg and Parmentier 2012). Here, we

491 demonstrate multi-modal effects of human-induced rapid environmental change (HIREC)

492 on the sensory environment of animals and compromises the use of biologically relevant

493 cues, specifically that ship noise disrupts both tactile and visual information gathering

494 under predation risk in the European hermit crab by interacting with these information

495 channels.

506

507   *Data Accessibility*

508   Analyses reported in this article can be reproduced using the data provided by Tidau

509   and Briffa 2019.

References

Angel JE. 2000. Effects of shell fit on the biology of the hermit crab *Pagurus longicarpus* (say). J Exp Mar Biol Ecol. 243:169-184.

Audacity Team. 2017. Audacity(R): Free Audio Editor and Recorder [Computer application]. Version 2.2.1. Avaliable from: https://audacityteam.org/ (Accessed September 2016)

Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol Evol. 25:180-189.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw 67:1-48.

Bent AM, Ings TC, Mowles SL. 2018. Anthropogenic noise disrupts mate searching in *Gryllus bimaculatus*. Behav Ecol. 29:1271-1277.

Bermúdez-Cuamatzin E, López-Hernández M, Campbell J, Zuria I, Slabbekoorn H. 2018. The role of singing style in song adjustments to fluctuating sound conditions: A comparative study on Mexican birds. Behav Process. 157:645-655.

Bertness MD. 1981. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana 40:197-205.

Breithaupt T. 2002. Sound perception in aquatic crustaceans. In: Wiese K, editor. The crustacean nervous system. Berlin, Heidelberg: Springer. p. 548-558.

Briffa M, Austin M. 2009. Effects of predation threat on the structure and benefits from vacancy chains in the hermit crab *Pagurus bernhardus*. Ethology 115:1029-1035.

Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. Anim Behav. 86:47-54.

536   Briffa M, Elwood RW. 2000. Cumulative or sequential assessment during hermit crab

537   shell fights: Effects of oxygen on decision rules. P Roy Soc Lond B Bio.

538   267:2445-2452.

539   Briffa M, Elwood RW. 2005. Rapid change in energy status in fighting animals: Causes

540   and effects of strategic decisions. Anim Behav. 70:119-124.

541   Briffa M, Elwood RW. 2007. Monoamines and decision making during contests in the

542   hermit crab *Pagurus bernhardus*. Anim Behav. 73:605-612.

543   Briffa M, Haskell P, Wilding C. 2008. Behavioural colour change in the hermit crab

544   *Pagurus bernhardus*: Reduced crypticity when the threat of predation is high.

545   Behaviour 145:915-929.

546   Bruintjes R, Purser J, Everley KA, Mangan S, Simpson SD, Radford AN. 2016. Rapid

547   recovery following short-term acoustic disturbance in two fish species. Roy Soc

548   Open Sci 3: 150686.

549   Bruintjes R, Radford AN. 2013. Context-dependent impacts of anthropogenic noise on

550   individual and social behaviour in a cooperatively breeding fish. Anim Behav.

551   85:1343-1349.

552   Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial

553   bird. J Anim Ecol. 73:434-440.

554   Bulinski KV. 2007. Shell-selection behavior of the hermit crab *Pagurus granosimanus*

555   in relation to isolation, competition, and predation. J Shellfish Res. 26:233-239.

556   Chan AAY-H, David Stahlman W, Garlick D, Fast CD, Blumstein DT, Blaisdell AP.

557   2010a. Increased amplitude and duration of acoustic stimuli enhance

558   distraction. Anim Behav. 80:1075-1079.

559   Chan AAY-H, Giraldo-Perez P, Smith S, Blumstein DT. 2010b. Anthropogenic noise

560   affects risk assessment and attention: The distracted prey hypothesis. Biol Lett.

561   6:458-461.

562 Clark CW, Ellison WT, Southall BL, Hatch L, Van Parijs SM, Frankel A, Ponirakis D.
563   2009. Acoustic masking in marine ecosystems: Intuitions, analysis, and
564   implication. Mar Ecol Prog Ser. 395:201-222.

565 Dowds BM, Elwood RW. 1983. Shell wars: Assessment strategies and the timing of
566   decisions in hermit crab shell fights. Behaviour 85:1-24.

567 Dukas R. 2002. Behavioural and ecological consequences of limited attention. Philos T
568   Roy Soc B. 357:1539-1547.

569 Dukas R. 2004. Causes and consequences of limited attention. Brain Behav Evol
570   63:197-210.

571 Dukas R, Kamil AC. 2000. The cost of limited attention in blue jays. Behav Ecol.
572   11:502-506.

573 Elwood RW. 1995. Motivational change during resource assessment by hermit crabs. J
574   Exp Mar Biol Ecol. 193:41-55.

575 Elwood RW, Neil SJ. 1992. Assessments and decisions: A study of information
576   gathering by hermit crabs. London; New York: Chapman & Hall.

577 Elwood RW, Stewart A. 1985. The timing of decisions during shell investigation by the
578   hermit crab, *Pagurus bernhardus*. Anim Behav. 33:620-627.

579 Foote AD, Osborne RW, Hoelzel AR. 2004. Environment: Whale-call response to
580   masking boat noise. Nature 428:910-910.

581 Gorman D, Ragagnin MN, McCarthy ID, Turra A. 2018. Risk-taking and risk-avoiding
582   behaviors by hermit crabs across multiple environmental contexts. J Exp Mar
583   Biol Ecol. 506:25-29.

584 Halfwerk W, Bot S, Slabbekoorn H. 2012. Male great tit song perch selection in
585   response to noise-dependent female feedback. Funct Ecol. 26:1339-1347.

586 Halfwerk W, Slabbekoorn H. 2015. Pollution going multimodal: The complex impact of
587   the human-altered sensory environment on animal perception and performance.
588   Biol Lett. 11:20141051.

589   Heiler J, Elwen SH, Kriesell HJ, Gridley T. 2016. Changes in bottlenose dolphin whistle

590   parameters related to vessel presence, surface behaviour and group

591   composition. Anim Behav. 117:167-177.

592   Hildebrand JA. 2009. Anthropogenic and natural sources of ambient noise in the

593   ocean. Mar Ecol Prog Ser. 395:5-20.

594   Holles S, Simpson SD, Radford AN, Berten L, Lecchini D. 2013. Boat noise disrupts

595   orientation behaviour in a coral reef fish. Mar Ecol Prog Ser. 485: 295-300.

596   Kight CR, Swaddle JP. 2011. How and why environmental noise impacts animals: An

597   integrative, mechanistic review. Ecol Lett. 14:1052-1061.

598   Koolhaas JM, Bartolomucci A, Buwalda B, de Boer SF, Flügge G, Korte SM, Meerlo P,

599   Murison R, Olivier B, Palanza P, et al. 2011. Stress revisited: A critical

600   evaluation of the stress concept. Neurosci Biobehav R. 35:1291-1301.

601   Kunc HP, Lyons GN, Sigwart JD, McLaughlin KE, Houghton JDR. 2014. Anthropogenic

602   noise affects behavior across sensory modalities. Am Nat. 184:E93-E100.

603   Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest package: Tests in

604   linear mixed effects models. J Stat Softw. 1: 1-26.

605   Ladich F, Fay RR. 2013. Auditory evoked potential audiometry in fish. Rev. Fish Biol.

606   Fish. 23:317-364.

607   Lampe U, Schmoll T, Franzke A, Reinhold K. 2012. Staying tuned: Grasshoppers from

608   noisy roadside habitats produce courtship signals with elevated frequency

609   components. Funct Ecol. 26:1348-1354.

610   Lawrence ES. 1985. Vigilance during easy and difficult foraging tasks. Anim. Behav.

611   33:1373-1375.

612   Lewis SM, Rotjan RD. 2009. Vacancy chains provide aggregate benefits to *Coenobita*

613   *clypeatus* hermit crabs. Ethology 115:356-365.

614   Ljungberg JK, Parmentier FBR. 2012. Cross-modal distraction by deviance functional

615   similarities between the auditory and tactile modalities. Exp Psychol 59:355-

616   363.

617   The MathWorks, Inc. 2015. MATLAB and Statistics Toolbox Release 2015b. Natick:

618   USA.

619   Merchant ND, Fristrup KM, Johnson MP, Tyack PL, Witt MJ, Blondel P, Parks SE.

620   2015. Measuring acoustic habitats. Methods Ecol Evol 6:257-265.

621   Meyer-Rochow VB, Penrose JD, Oldfield BP, Bailey WJ. 1982. Phonoresponses in the

622   rock lobster *Panulirus longipes* (Milne Edwards). Behav Neural Biol 34:331-336.

623   Nedelec SL, Radford AN, Pearl L, Nedelec B, McCormick MI, Meekan MG, Simpson

624   SD. 2017. Motorboat noise impacts parental behaviour and offspring survival in

625   a reef fish. P Roy Soc Lond B Bio. 284: 20170143.

626   Nedelec SL, Simpson SD, Morley EL, Nedelec B, Radford AN. 2015. Impacts of regular

627   and random noise on the behaviour, growth and development of larval atlantic

628   cod (*Gadus morhua*). P Roy Soc Lond B Bio. 282: 20151943.

629   Parmentier FBR, Ljungberg JK, Elsley JV, Lindkvist M. 2011. A behavioral study of

630   distraction by vibrotactile novelty. J Exp Psychol Human. 37:1134-1139.

631   Popper AN, Salmon M, Horch WK. 2001. Acoustic detection and communication by

632   decapod crustaceans. J Comp Physiol A 187:83-89.

633   Purser J, Bruintjes R, Simpson SD, Radford AN. 2016. Condition-dependent

634   physiological and behavioural responses to anthropogenic noise. Physiol

635   Behav. 155:157-161.

636   R-Core-Team. 2017. A language and environment for statistical computing. Vienna:

637   Austria: R Foundation for Statistical Computing. Avaliable from: https://www.r-

638   project.org/ (Accessed January 2017)

639   Rees G, Frith CD, Lavie N. 1997. Modulating irrelevant motion perception by varying

640   attentional load in an unrelated task. Science 278:1616-1619.

641   Rogers PH, Hawkins AD, Popper AN, Fay RR, Gray MD. 2016. Parvulescu revisited:

642   Small tank acoustics for bioacousticians. In: Popper AN, Hawkins A, editors.

643   Effects of noise on aquatic life II. p. 933-941.

644   Rotjan RD, Blum J, Lewis SM. 2004. Shell choice in *Pagurus longicarpus* hermit crabs:

645   Does predation threat influence shell selection behavior? Behav Ecol Sociobiol.

646   56:171-176.

647   Sara G, Dean JM, D'Amato D, Buscaino G, Oliveri A, Genovese S, Ferro S, Buffa G,

648   Lo Martire M, Mazzola S. 2007. Effect of boat noise on the behaviour of bluefin

649   tuna *Thunnus thynnus* in the Mediterranean Sea. Mar Ecol Prog Ser. 331:243-

650   253.

651   Shannon G, Angeloni LM, Wittemyer G, Fristrup KM, Crooks KR. 2014. Road traffic

652   noise modifies behaviour of a keystone species. Anim Behav. 94:135-141.

653   Siemers BM, Schaub A. 2011. Hunting at the highway: Traffic noise reduces foraging

654   efficiency in acoustic predators. P Roy Soc Lond B Bio. 278:1646-1652.

655   Sih A, Ferrari MCO, Harris DJ. 2011. Evolution and behavioural responses to human-

656   induced rapid environmental change. Evol Appl 4:367-387.

657   Simpson SD, Purser J, Radford AN. 2015. Anthropogenic noise compromises

658   antipredator behaviour in European eels. Glob Change Biol. 21:586-593.

659   Spiga I. 2016. Acoustic response to playback of pile-driving sounds by snapping

660   shrimp. In: Popper AN, Hawkins A, editors. Effects of noise on aquatic life II.

661   New York: Springer. p. 1081-1088.

662   Stahlman WD, Chan AAY-H, Blumstein DT, Fast CD, Blaisdell AP. 2011. Auditory

663   stimulation dishabituates anti-predator escape behavior in hermit crabs

664   (*Coenobita clypeatus*). Behav Process. 88:7-11.

665   Sun JWC, Narins PM. 2005. Anthropogenic sounds differentially affect amphibian call

666   rate. Biol Conserv. 121:419-427.

667   Talsma D, Senkowski D, Soto-Faraco S, Woldorff MG. 2010. The multifaceted interplay

668   between attention and multisensory integration. Trends Cogn Sci 14:400-410.

669   Tidau S, Briffa M. 2019. Data from: Distracted decision-makers: Ship noise and

670   predation risk change shell choice in hermit crabs. Behav Ecol. DOI:

671   doi:10.5061/dryad.4sm0dq1

672   Tidau S, Briffa M. In Press. Anthropogenic noise pollution reverses grouping behaviour

673   in hermit crabs. Anim. Behav.

674   Tricarico E, Gherardi F. 2007. Resource assessment in hermit crabs: The worth of their

675   own shell. Behav Ecol. 18:615-620.

676   Tuomainen U, Candolin U. 2011. Behavioural responses to human-induced

677   environmental change. Biol Rev. 86:640-657.

678   Turra A, Gorman D. 2014. Subjective resource value and shell abandoning behavior in

679   hermit crabs. J Exp Mar Biol Ecol. 452:137-142.

680   Wale MA, Simpson SD, Radford AN. 2013a. Noise negatively affects foraging and

681   antipredator behaviour in shore crabs. Anim Behav. 86:111-118.

682   Wale MA, Simpson SD, Radford AN. 2013b. Size-dependent physiological responses

683   of shore crabs to single and repeated playback of ship noise. Biol Lett. 9:

684   20121194.

685   Walsh EP, Arnott G, Kunc HP. 2017. Noise affects resource assessment in an

686   invertebrate. Biol Lett. 13: 20170098.

687   Williams R, Wright AJ, Ashe E, Blight LK, Bruintjes R, Canessa R, Clark CW, Cullis-

688   Suzuki S, Dakin DT, Erbe C, et al. . 2015. Impacts of anthropogenic noise on

689   marine life: Publication patterns, new discoveries, and future directions in

690   research and management. Ocean Coast. Manage. 115:17-24.

Figure legends

692

693
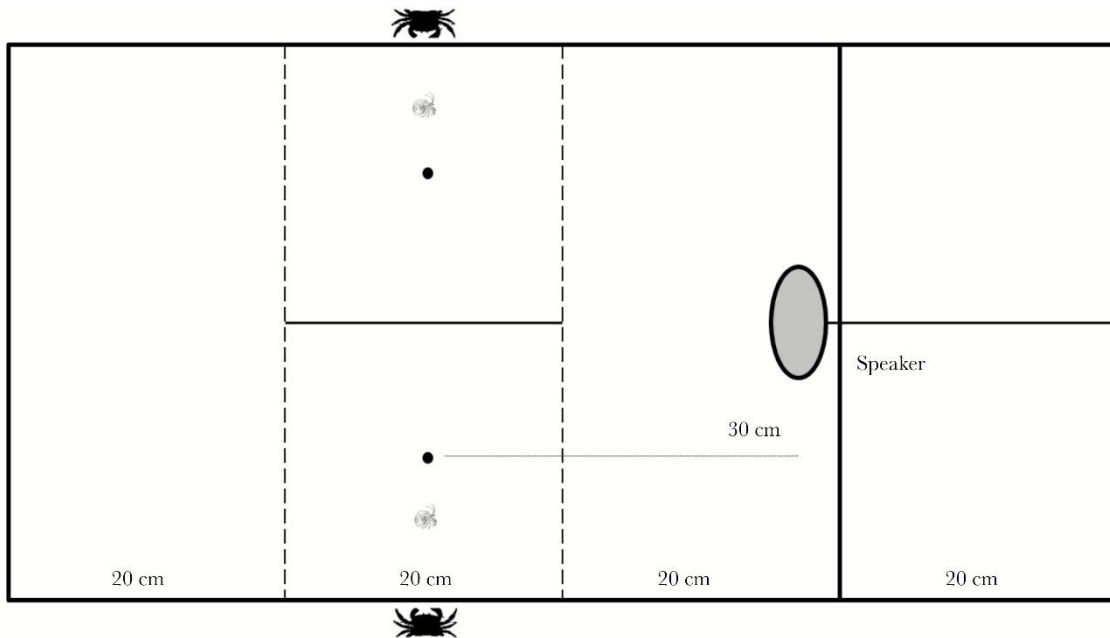
694

695   **Figure 1** Tank set-up and arena (plan view). The dotted lines represent the mesh to

696   separate the arena from the rest of the tank. The blank line represent the opaque

697   plastic sheet to separate the hermit crabs. The empty shells were placed in the center

698   of the arena at 30 cm distance to the speaker. The visual predator cue was placed

699   outside the tank and hermit crabs were placed between the shell and the predator cue.

700
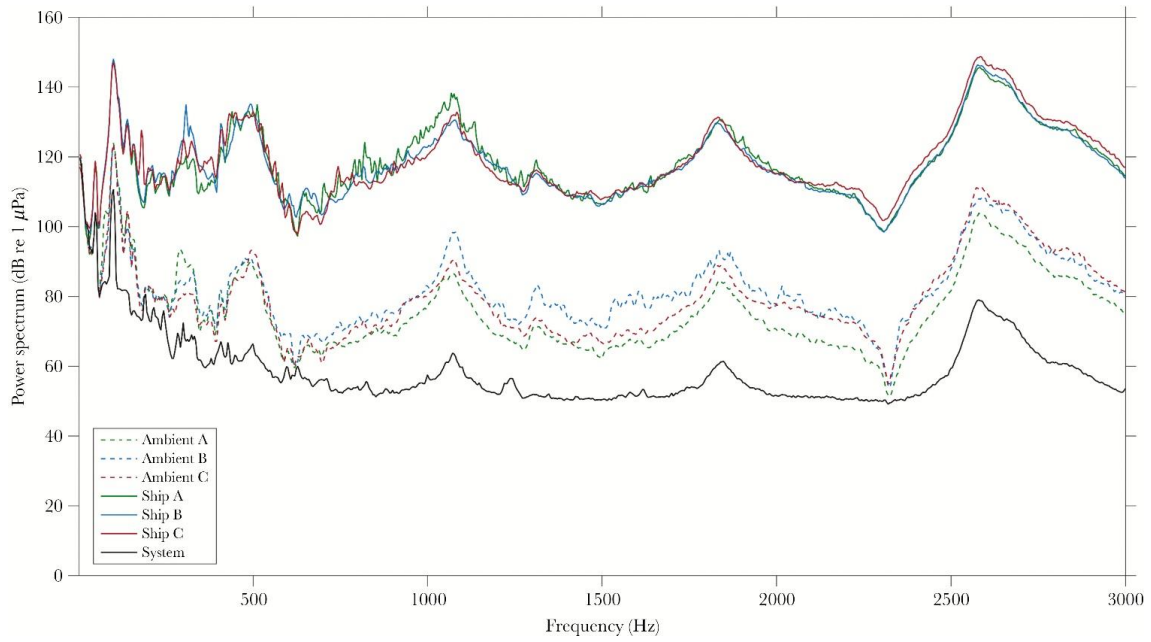
Figure 2 Power spectrum analysis of the playbacks of all six recordings (3 ship noise playbacks, 3 ambient playbacks) in the tank and the system's self-noise (equipment switch on but no playback).


704
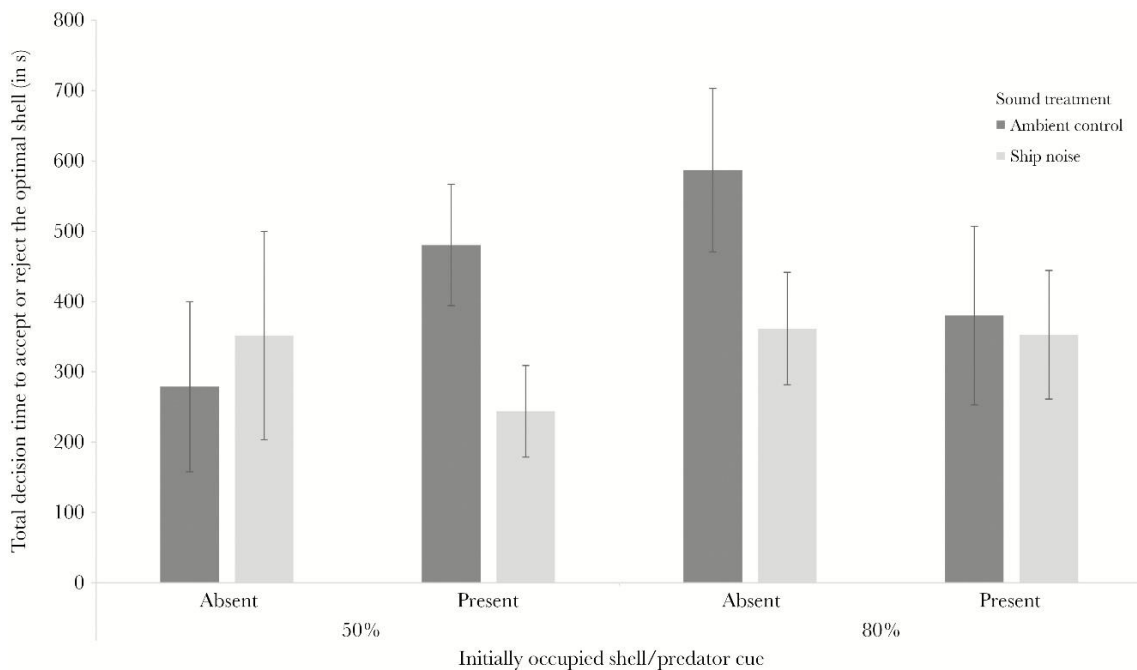
Figure 3 The three-way interaction between sound treatment, predator cue and initially occupied shell size on the total decision time to accept or reject the optimal shell. Error bars show standard errors.
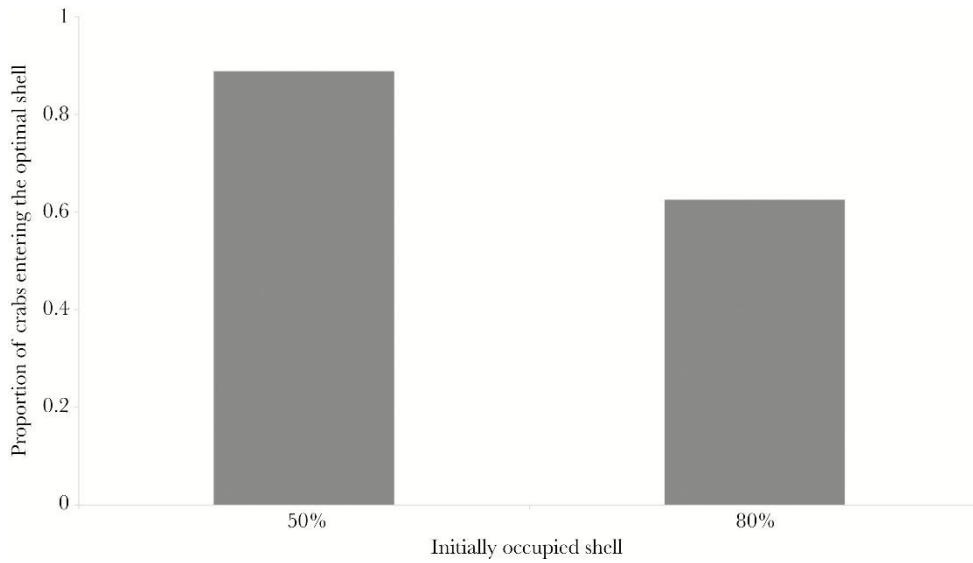
708
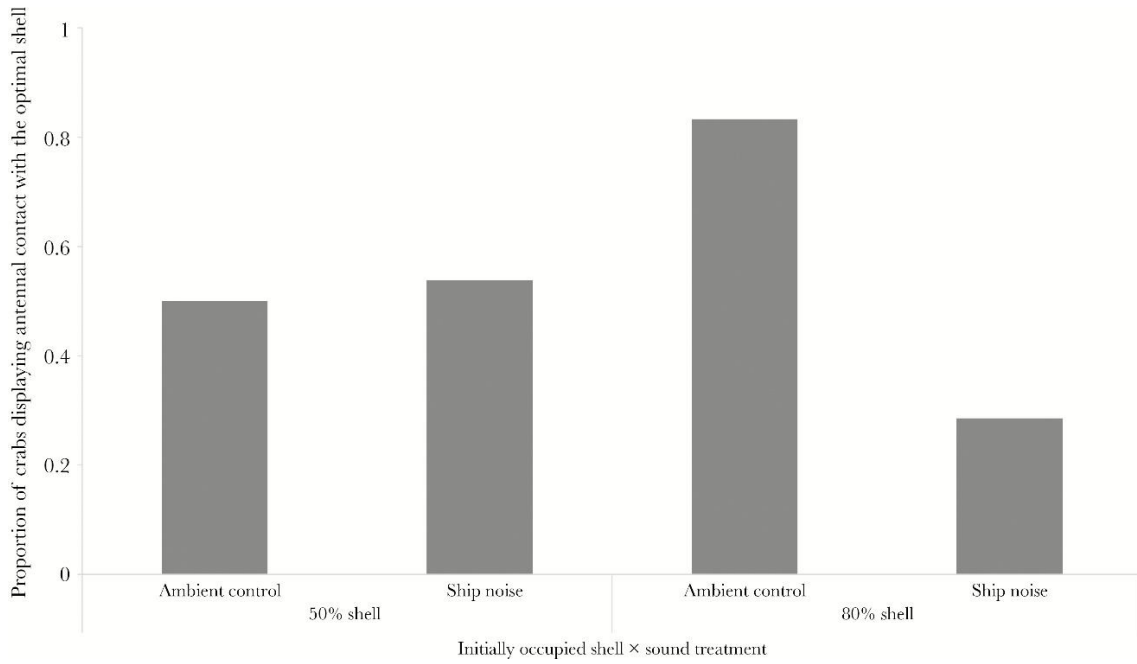
Figure 4 The interaction effect between sound treatment and initially occupied shell
size on the proportion of crabs that contacted the optimal shell with their antennae.

711
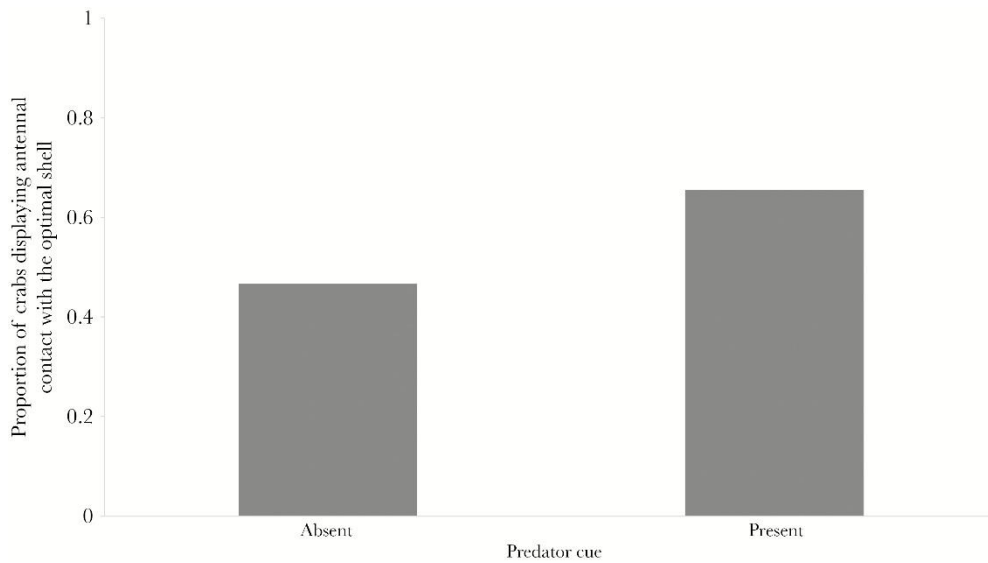
Figure 5 The effect of a visual predator cue on the proportion of crabs that contacted
the optimal shell with their antennae

714

Figure 6 The effect of initially occupied shell size on the proportion of crabs that swap

and did not swap into the optimal shell.

717
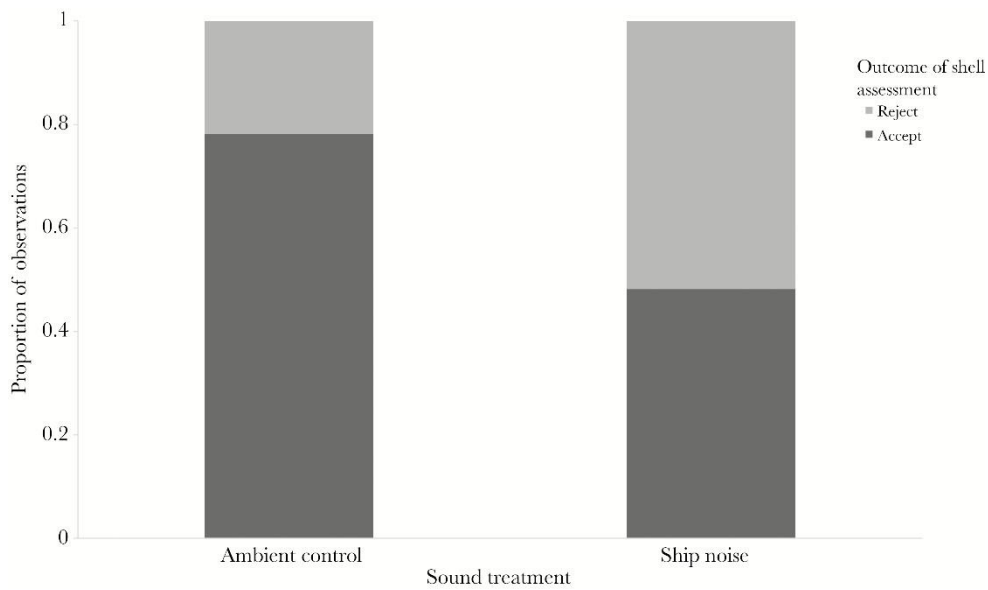
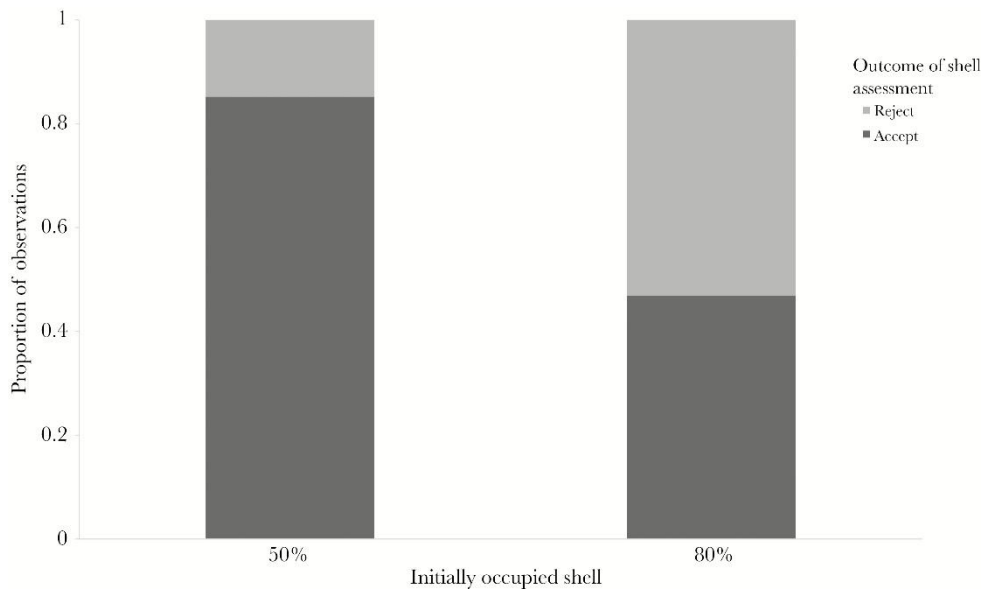**Figure 7** Effect of sound treatment on the decision of hermit crabs to accept or reject

the optimal shell.

720

721   **Figure 8** Effect of initially occupied shell on the decision of hermit crabs to accept or

722   reject the optimal shell.

723 **Tables and table legends**

724

725 **Table 1.** Summary of number of observations in each treatment combination, with the number
726 of crabs that changed shell in each case given in parentheses.

| | Predator absent | | | | | | Predator present | | | | | |
| | 50% shell | | | 80% shell | | | 50% shell | | | 80% shell | | |
	n	entered	accepted	n	entered	accepted	n	entered	accepted	n	entered	accepted
Ambient (n=32)	6	(6)	(6)	10	(8)	(7)	8	(8)	(8)	8	(4)	(4)
Noise (n=27)	7	(5)	(5)	7	(4)	(2)	6	(5)	(4)	7	(4)	(2)

727

728 **SUPPLEMENT**

729

730 **Table 1** Latency to contact the new shell (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	3.08	1	0.08
sound * predator cue	0.02	1	0.88
sound * shell size	0.01	1	0.91
predator cue * shell size	2.11	1	0.15
sound	1.95	1	0.16
predator cue	0.34	1	0.56
shell size	0.99	1	0.32
mass	**7.44**	**1**	**0.006**

731

732 **Table 2** Total decision time (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	**5.0**	**1**	**0.03**
mass	**7.23**	**1**	**0.007**

733 Note that results were obtained using a model simplification approach, and as such reporting is restricted to the highest
734 order effects, where significant interactions are present.

735

736 **Table 3** Occurrence of antennae contact (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	NA	NA	NA
sound * predator cue	1.51	1	0.22
sound * shell size	**10.0**	**1**	**0.002**
predator cue * shell size	3.08	1	0.08
predator cue	**4.07**	**1**	**0.04**
mass	1.91	1	0.17

737 Note that since not every crab decided to contact the optimal shell, we did not have sufficient data on the occurrence of
738 antennal contact to calculate the three-way interaction.

739

740 **Table 4** Enter the optimal shell (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	NA	NA	NA
sound * predator cue	1.57	1	0.21
sound * shell size	3.15	1	0.08
predator cue * shell size	0.67	1	0.41
sound	2.58	1	0.11
predator cue	0.17	1	0.68
shell size	**5.46**	**1**	**0.02**
mass	0.88	1	0.35

741 Note that since relatively few crabs with an 80% shell that were exposed to ship noise decided to enter the optimal shell,
742 there was not sufficient data to calculate the three-way interaction.

743 **Table 5** Latency to enter the optimal shell

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	1.62	1	0.20
sound * predator cue	0.20	1	0.66
sound * shell size	0.41	1	0.52
predator cue * shell size	0.91	1	0.34
sound	0.30	1	0.59
predator cue	1.88	1	0.17
shell size	0.56	1	0.45
mass	0.95	1	0.33

744

745 **Table 6** Final decision to accept new shell (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	NA	NA	NA
sound * predator cue	0.34	1	0.56
sound * shell size	2.19	1	0.14
predator cue * shell size	0.005	1	0.94
sound	**8.0**	**1**	**0.005**
predator cue	0.38	1	0.54
shell size	**11.67**	**1**	**0.0006**
mass	0.48	1	0.49

746
747 Note that sine relatively few individuals with an 80% adequate shell that were exposed to noise chose to enter the optimal shell, there was not sufficient data to calculate the three-way interaction.

748

749 **Table 7** Total decision time (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	**5.0**	**1**	**0.03**
mass	**7.23**	**1**	**0.007**

750

751 **Table 8** Locomotion (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	0.005	1	0.94
sound * predator cue	0.23	1	0.63
sound * shell size	0.58	1	0.45
predator cue * shell size	0.02	1	0.90
sound	0.11	1	0.75
predator cue	1.42	1	0.23
shell size	1.32	1	0.25
mass	**7.35**	**1**	**0.007**

752

753

754