

# 1 **Anthropogenic noise pollution reverses grouping behaviour** 2 **in hermit crabs**

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8

## 9 **Abstract**

10 Noise is a form of human induced rapid environmental change, and mounting evidence suggests that  
11 it can affect the sensory environment and consequently the decision-making ability of animals.  
12 However, while the effects of anthropogenic noise on individual organisms in the context of  
13 movement patterns, foraging and predator risk have been reported, relatively little is known about  
14 how noise impacts groups and intraspecific interactions. Here we investigated the effects of  
15 anthropogenic noise on grouping preference (i.e. being with conspecifics or alone) in the European  
16 hermit crab, *Pagurus bernhardus*. Hermit crabs live in empty gastropod shells and frequently fight  
17 with each other in order to gain an optimal-fitting shell. Thus crab grouping preference may depend  
18 on the optimality of their own shell and thus on their motivation to gain another. In order to test the  
19 effect of shell size and its interaction with noise exposure on grouping preferences, crabs were  
20 housed in either suboptimal or optimal shells before being exposed to playbacks of either ship noise  
21 or an ambient sound (control) and given the choice to group with either five crabs, one conspecific  
22 or to remain alone in a neutral zone. Crabs occupying suboptimal shells displayed a longer latency to

23 enter the zone with a single crab than crabs in optimal shells. This difference was only seen in the  
24 ambient sound treatment, disappearing completely under ship noise. Under ambient sound, crabs in  
25 optimal shells spent most of their time close to a single crab, while crabs in suboptimal shells  
26 showed no clear preference. However, exposure to ship noise reversed the effect of shell quality on  
27 grouping preference. Our results demonstrate that exposure to anthropogenic noise can not only  
28 alter individual behaviour but also social behaviour.

29

30 **Keywords:** anthropogenic noise, environmental change, grouping preference, hermit crabs,  
31 intraspecific interaction, sensory environment

32

33

## 34 **Introduction**

35 Assessing diverse cues from the environment is an essential component of animals' decision-making.  
36 However, human induced rapid environmental change (HIREC) (*sensu* Sih, Ferrari & Harris, 2011),  
37 caused by noise, chemicals or light, can disrupt information gathering, processing and assessment in  
38 animals both by inducing physiological stress (for review see Kight & Swaddle, 2011) and by changing  
39 animals' sensory environment (for review see Halfwerk & Slabbekoorn, 2015; Tuomainen &  
40 Candolin, 2011). An example of unimodal interference by noise is the masking of acoustic cues and  
41 signals documented in terrestrial and aquatic taxa (Brumm, 2004; Clark et al., 2009; Luo, Siemers &  
42 Koselj, 2015; Simpson et al., 2016a; Sun & Narins, 2005;). This has been demonstrated across  
43 behavioural contexts such as territory defence (Brumm, 2004), mating (Sun & Narins, 2005) and the  
44 detection of habitats (Pine, Jeffs & Radford, 2012), conspecifics (Codarin, Wysocki, Ladich & Picciulin,  
45 2009) and predators (Curé et al., 2013). In addition to these unimodal effects, noise can also have  
46 cross-modal effects where this pollutant disrupts information processing and assessment of non-  
47 acoustic cues (Halfwerk & Slabbekoorn, 2015). For instance, underwater noise has been shown to

48 alter behaviours related to visual and chemical cues used in predator avoidance and detection  
49 (Hasan, Crane, Ferrari & Chivers, 2018; Kunc, Lyons, Sigwart, McLaughlin & Houghton, 2014;  
50 McCormick, Allan, Harding & Simpson, 2018). Such effects have been explained by distraction (Chan,  
51 Giraldo-Perez, Smith & Blumstein, 2010) due to limited attention in animals (Dukas, 2004), which  
52 modulates the multisensory integration (Talsma, Senkowski, Soto-Faraco & Woldorff, 2010). This  
53 effect has also been termed 'info-disruption' (Lürding & Scheffer, 2007) and 'sensory pollution'  
54 (Halfwerk & Slabbekoorn, 2015). In addition to these sensory effects noise has been shown to cause  
55 physiological stress (for review see Kight & Swaddle, 2011), which could also alter animal behaviour.  
56 Cross-modal noise pollution might therefore adversely affect animals even though they do not use  
57 acoustic communication.

58           The behavioural effects of anthropogenic noise have frequently been studied in two  
59 contexts. First, many studies have focussed on individual behaviour, including impacts on  
60 movement, foraging and responses to predators (Chan et al., 2010; Luo et al., 2015; Shafiei Sabet,  
61 Neo & Slabbekoorn, 2015; Shafiei Sabet, Dooren & Slabbekoorn, 2016; Shannon et al., 2016; Siemers  
62 & Schaub, 2011; Simpson, Purser & Radford, 2015; Simpson et al., 2016b; Wale, Simpson & Radford,  
63 2013; Wisniewska et al., 2018). Second, studies on social behaviour have focussed on the potential  
64 masking of acoustic communication in insects, anurans, birds, and mammals (reviewed in Brumm &  
65 Slabbekoorn, 2005; Erbe, Reichmuth, Cunningham, Lucke & Dooling, 2016). In contrast, the effect of  
66 noise on non-vocal social behaviour, such as shoaling, has received relatively little attention. Those  
67 noise exposure experiments which studied intraspecific interactions found altered parental care  
68 (Maxwell et al., 2018; Nedelec et al., 2017) and social interactions (Bas et al., 2017). A basic aspect of  
69 social behaviour is that individuals choose to join groups such as flocks or shoals, which requires  
70 animals to assess cues from their environment. Groups are associated with a range of benefits  
71 (reviewed in Krause & Ruxton, 2002) such as decreased vigilance (Powell, 1974; Ward, Herbert-Read,  
72 Sumpter & Krause, 2011), finding and exploiting resources (Bazazi, Pfennig, Handegard & Couzin,  
73 2012; Childress & Herrnkind, 2001) and conservation of heat (Wilson, 2009). On the other hand,

74 there are also costs associated with group membership such as increased attack rates (for large  
75 groups) (Mooring, Fitzpatrick, Nishihira, Reisig & Hall, 2004), elevated parasite burden (Côté &  
76 Poulinb, 1995; Daviews, Ayres, Dye & Deane, 1991) and foraging competition (Rieucan & Giraldeau,  
77 2009). Noise has been shown to alter grouping (Fewtrell & McCauley, 2012; Herbert-Read, Kremer,  
78 Bruintjes, Radford & Ioannou, 2017) and appears to be highly variable across study systems and  
79 noise regime. Mediterranean spiny lobster, *Palinurus elepha*, (Filiciotto et al., 2014) and bottlenose  
80 dolphin, *Tursiops truncatus*, (Bas et al., 2017) exhibited reduced grouping behaviour when exposed  
81 to boat noise. In contrast noise led to increased grouping in the trevally, *Pseudocaranx dentex*,  
82 (Fewtrell & McCauley, 2012). Divergent social responses to noise can even be seen within the same  
83 species. In the European sea bass, *Dicentrarchus labrax*, the social behaviour differed with the noise  
84 source and regime where fish shoals were less coordinated (cohesion, direction, speed and  
85 directional changes) when exposed to pile-driving (Herbert-Read et al., 2017) but they increased  
86 grouping activities under ship noise (Neo, Hubert, Bolle, Winter & Slabbekoorn, 2018). In the Atlantic  
87 bluefin tuna, *Thunnus thynnus*, noise led to less concentrated and coordinated shoals but individuals  
88 increasingly swam towards one and another and seemed more likely to join a group (Sara et al.,  
89 2007). Although less intensively studied (compared to aquatic examples) anthropogenic noise can  
90 also affect non-vocal social behaviour in terrestrial species. In Carolina chickadees, *Poecilie*  
91 *carolinensis*, and tufted titmice, *Baeolophus bicolor*, flocking density was enhanced in the presence  
92 of traffic noise (Owens, Stec & O’Hatnick, 2012). Thus, as well as changing the propensity to join  
93 groups, noise can influence interactions within groups.

94 In marine environments, grouping is very common among cetaceans and fish (i.e. shoaling)  
95 but has also been demonstrated in crustaceans as a response to predation risk (Evans, Finnie &  
96 Manica, 2007; Ratchford & Eggleston, 1998). Due to their association with gastropod shells hermit  
97 crabs represent an ideal model organism for studying the effects of underwater noise on the drivers  
98 of grouping behaviour. They are globally distributed crustaceans characterised by a weakly calcified  
99 abdomen which they protect from predators (Vance, 1972) and environmental extremes (Taylor,

100 1981; Young, 1978) through occupying empty gastropod shells. They usually obtain these either  
101 when discarded by others or through shell fights with other crabs (snail predation is rare) (Elwood &  
102 Neil, 1992). Hermit crabs need to search for empty shells of increasing size to allow for growth or, in  
103 the case of females, during the reproductive season to accommodate their eggs (Angel, 2000;  
104 Bertness, 1981a). The extent of grouping in hermit crabs differs between species, from those which  
105 are solitary (Hazlett, 1979) to those which form aggregations of hundreds or even thousands of  
106 individuals as in *Clibananus erythropus* (Gherardi, 1991). The drivers for grouping can differ widely  
107 between species. These include attraction to foraging sites (Hazlett, 1979; Hazlett, 2015), shell  
108 exchange (Gherardi & Vannini, 1993; Hazlett, 1978; Hazlett & Herrnkind, 1980) and predator  
109 defence (Bertness, 1981b). The need to obtain new shells could also influence grouping. Shell  
110 exchange markets as observed in the mangal-dwelling hermit, *Clibanarius laevimanus*, and the thin  
111 stripe hermit crab, *Clibanarius vittatus*, (Gherardi & Vannini, 1993; Hazlett & Herrnkind, 1980), and  
112 vacancy chain processes in the European hermit crab, *Pagurus bernhardus*, (Briffa, 2013), predict  
113 that associating with other crabs may increase the chances of finding an optimal shell (Gherardi &  
114 Vannini, 1993). In addition, the larger the group the lower the likelihood at the individual-level of  
115 being preyed upon, an effect known as the dilution effect (Foster & Treherne, 1981; Gherardi &  
116 Benvenuto, 2001). On the other hand, larger groups can be more detectable (Krause & Ruxton,  
117 2002) and for hermit crabs their individual defence mechanisms, primarily withdrawing into their  
118 gastropod shell (Gherardi & Benvenuto, 2001) or fleeing (Mima, Wada & Goshima, 2003; Rosen,  
119 Schwarz & Palmer, 2009; Scarratt & Godin, 1992), might be a better responses to a predator attack  
120 compared with joining a group. Given this array of the potential costs and benefits of grouping, to  
121 make decisions on whether to join a group hermit crabs need to assess information from their  
122 environment across different sensory modalities, including tactile information on the size of the shell  
123 relative to their own size (smaller shells offer less protection).

124 As in other hermit crabs *P. bernhardus* are frequently found in aggregations, and the factors  
125 described above are all likely to contribute to this (Elwood & Neil, 1992). Here we aim to determine

126 whether the decision to join a group in the European hermit crab *P. bernhardus* is influenced by  
127 information on risk level (i.e. shell fit) and information on the number of conspecifics in a group. We  
128 then ask whether the grouping patterns are altered in the presence of anthropogenic noise using  
129 ship noise playbacks and ambient controls. We predict that, due to a combination of shell exchange  
130 markets and the dilution effect, crabs in suboptimal shells are more likely to join a group compared  
131 to crabs in optimal sized shells. Furthermore, if noise distracts hermit crabs and reduces their ability  
132 to use information on shell and group size, we expect these different grouping preferences of crabs  
133 in suboptimal and optimal shells (described above) to be altered by noise.

## 134 **Methods**

### 135 **Collection and husbandry of hermit crabs**

136 We collected *P. bernhardus* from the rocky intertidal of Hannafore Point, Cornwall, UK  
137 (50°20N, 4°27W) in May and July 2017 and transported them directly to the laboratory at the  
138 University of Plymouth, UK. We kept the crabs in a temperature controlled room at 15 °C with a  
139 12:12 hour light:dark cycle in a single holding tank containing 125 l continuously filtered and aerated  
140 seawater (Briffa, Rundle & Fryer, 2008). The laboratory seawater was obtained from the seaward  
141 side of Mount Batten pier (50°36N, 4°13W) in Plymouth Sound, UK, at spring tides. We fed crabs *ad*  
142 *libitum* with white fish. To remove focal crabs from their original gastropod shells (at least 22 hours  
143 prior to observations) we carefully cracked the shell with a bench vice, which allows the crab to be  
144 removed from its shell without injuring the crab. Afterwards the crabs were sexed and weighed  
145 them. The crab mass ranged from 0.36 g to 1.61 g (mean mass  $\pm$  SE = 0.84g  $\pm$  0.045 g,  $N = 45$ ). Based  
146 on a regression line relating preferred shell mass to body mass obtained from a previous shell  
147 selection experiment, where crabs across a range of sizes were provided with free access to a range  
148 of different sized shells (Briffa & Elwood, 2007), we assigned a *Littorina littorea* shell of either 75% or  
149 100% of its preferred shell mass to each crab. Although a range of other shell features might also  
150 influence preferences, the relation between crab mass and shell mass is the primary predictor of  
151 shell preference. To optimise the reliability, the shell selection experiment (Briffa & Elwood, 2007)

152 was conducted using shells collected from the same location as the hermit crabs used in this study to  
153 minimise the effect of factors such as shell internal volume to weight ratio, which can differ between  
154 study sites. Furthermore, following a standard approach, only clean and intact shells, without  
155 encrusting organisms, holes or damage to the aperture were used. Afterwards we housed crabs  
156 individually in a white plastic dish of 15 cm diameter containing continuously aerated seawater to a  
157 depth of 5 cm. Since the breeding season is likely to affect the behaviour of egg-carrying females, we  
158 used only male crabs without obviously damaged appendages, visible parasites or recent moult  
159 (Briffa & Elwood, 2007). After the observations we returned the animals to the sea at the collection  
160 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 (with 1 cm thick  
163 aquarium glass) filled to a depth of 40 cm with seawater from the laboratory supply (~ 160 l). We  
164 placed the tank on a free-standing trolley and cushioned the set-up with 1 cm Styrofoam plates  
165 between tank and trolley as well as between the trolley and floor. We suspended an underwater  
166 speaker from a cushioned bamboo stick at 20 cm distance to one end of the tank, facing towards an  
167 observation arena (Fig. 1). At 10 cm distance to the speaker we divided the observation arena (50 cm  
168 width x 40 cm length) from the rest of the tank with 1x1 cm mesh. Along either side of the glass  
169 walls we separated two 'stimulus chambers (6 cm width) for the two groups of stimulus crabs (see  
170 details below). The chambers were custom-made of 3 mm transparent acrylic sheets. Adjacent to  
171 each of these stimulus chambers, we defined 'decision zones' (9 cm in width) marked by a line on  
172 the base of the arena so that the focal crab could enter freely into either decision zone. We  
173 designated a 'neutral zone' (18 cm width) at the centre of the tank. At the beginning of each  
174 observation, we placed the focal crabs in the centre of the neutral zone at 30 cm distance from the  
175 speaker and equal distance to the walls of the stimulus chambers. At this location (point in Fig. 1) we  
176 analysed the sound pressure levels of the two sound treatments (ship noise and ambient control).

177           While hearing in a narrow definition seems to be absent in nearly all aquatic crustaceans,  
178 sound detection has been widely demonstrated in Decapoda (Budelmann, 1992). Only very few  
179 auditory thresholds have been established for invertebrates but an experiment the common prawn,  
180 *Palaemon serratus*, showed an auditory brain response to acoustics stimuli at a frequency range of  
181 100-3000 Hz with amplitudes varying between 105 and 130 dB RMS re 1  $\mu$  Pa at 1 m (Lovell, Findlay,  
182 Moate & Yan, 2005). There has been no similar study conducted for *P. bernhardus* but behavioural  
183 sensitivity (antennae flicks) to substrate borne vibration in this species has been demonstrated for  
184 frequencies between 5-410 Hz at a particle acceleration of 0.02-0.44  $\text{ms}^{-2}$  RMS (Roberts, Cheesman,  
185 Elliott, & Breithaupt, 2016).

186           For the sound playbacks we used an underwater speaker (DNH Aqua-30 underwater  
187 speaker, effective frequency range 80-20 000 Hz, DNH A/S, Kragerø, Norway) connected to a Lvpin  
188 LP-200 amplifier (Lvpin Technology Suzhou Co., Taiping Town, China). We played back the sound  
189 tracks from a Toshiba Portégé R830-13C laptop (Tokyo, Japan). For the sound treatment we used  
190 three ship noise playbacks and three corresponding ambient control sounds from the same sites  
191 recorded at three major UK harbours (for details on recordings such as ship size and speed see  
192 Simpson et al., 2015; Wale et al., 2013). We used Audacity 2.1.2 (Audacity Team, 2017) to create a  
193 total of six audio tracks. In the case of ship noise tracks we alternated two min of ship noise with two  
194 min of ambient control sound including 15 sec fading in and out to simulate noise of passing by  
195 ships. We assigned the crabs randomly to one of the two sound treatments (ambient, ship) and to  
196 one of the alternative three audio tracks within these sound treatments (ambient A, B, C; ship A, B,  
197 C) and alternated the sound treatment between subsequent observations.

198           To make sure crabs were exposed to two distinct sound treatments we analysed the power  
199 spectrum as a proxy similar as in previous studies on crustaceans (for instance Wale, Simpson &  
200 Radford, 2013). We are aware of the challenges of measuring noise in small tanks (Rogers, Hawkins,  
201 Popper, Fay & Gray, 2016; Simpson et al., 2015) and that hermit crabs are likely to perceive the  
202 particle motion component of sound rather than the measured sound pressure levels (Breithaupt,



203 2002; Popper, Salmon & Horch, 2001). However, as pointed out in previous studies (see for instance  
204 Herbert-Read et al., 2017; Simpson et al., 2015; Wale et al., 2013), we do not aim to establish  
205 absolute noise sensitivity levels for hermit crabs but analysed the power spectrum to confirm that  
206 we exposed crabs to two different sound treatments, namely ship noise and ambient control. To do  
207 that, we re-recorded the six audio tracks at the centre of the arena at 30 cm distance to the speaker  
208 and 25 cm to the glass walls (where the crabs were placed at the beginning of the experiment) at  
209 1-2 cm distance to the bottom of the tank with an omnidirectional hydrophone HTI-96-MIN (with  
210 inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V  $\mu$ Pa-1; frequency range  
211 0.002-30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10 recorder (48 kHz  
212 sampling rate, Sony Corporation, Tokyo, Japan; recording level calibrated using pure sine wave  
213 signals from a function generator with a measured voltage recorded in line on an oscilloscope). At  
214 this position, the three ambient control sounds had an average maximum sound pressure level of  
215 74.5 dB RMS re 1  $\mu$  Pa (ambient A: 70.8, ambient B: 76.2, ambient C: 76.6) and the ship noise an  
216 average maximum of 119.4 dB RMS re 1  $\mu$  Pa (ship A: 124.4, ship B: 118.7, ship C: 115.2) at 1000Hz.  
217 We used PAMGuide (Merchant et al., 2015) for MATLAB R2015b (MathWorks Inc., 2015) to perform  
218 a power spectrum analysis of 60 sec recording with Hann evaluation window, overlap 50%, 0.25 sec  
219 window length, 1 - 48 000 Hz bandwidth normalised to 1 Hz (Fig. 2).

## 220 **Experimental design and behavioural analysis**

221 We designed a classical choice experiment with three zones (Krause & Ruxton, 2002) (see  
222 Fig. 1), which has previously been applied on shoaling in crustaceans (Evans, Finnie & Manica, 2007).  
223 Consequently, the observation arena had a neutral zone in the centre (1/2 of the arena) and two  
224 decision zones (each 1/4 of the arena) between the neutral zone and two stimuli chambers for the  
225 stimuli crabs. One chamber was the single crab stimulus chamber (SSC) containing one crab and the  
226 second chamber was the group stimulus chamber (GSC) containing five stimuli crabs as in a previous  
227 study (Evans, Finnie & Manica, 2007). That led to a neutral zone of 18 cm width in the centre,  
228 surrounded by two decision zones each of 9 cm width and two stimulus chambers of 6 cm width

229 (plus 1 cm thick glass tank on either side). In order to remove the possibility of directional bias we  
230 alternated the sides of the SSC and GSC between each day of observations. After being placed in a  
231 stimulus chambers, we gave the stimulus crabs 20 min to acclimatise to the tank before any of the  
232 six sound tracks was played. We ran the experiment in blocks of observations where the same  
233 stimuli crabs (one and five individuals in each observation) were used repeatedly for eight  
234 observations of focal individuals (thus an experimental block = eight observations of unique focal  
235 crabs per day, reusing the same stimuli crabs across these eight observations). Furthermore,  
236 observations within each block consisted of four observations in the presence of ship noise and four  
237 observations under ambient control conditions). We matched focal and stimulus crabs for size based  
238 on sight as closely as possible. After observations were completed, we removed the stimulus crabs  
239 from their shells, sexed and weighed each crab to test the effectiveness of matching focal and  
240 stimulus crabs by calculating the relative weight differences between focal and stimulus crabs. The  
241 weight of the focal crabs was positively correlated with the weight of SSC crabs (Spearman's rank  
242 correlation:  $r_s = 0.67$ ,  $N = 45$ ,  $P < 0.0001$ ) and the average weight of crabs in the GSC group weight ( $r_s$   
243 =  $0.63$ ,  $N = 45$ ,  $P < 0.0001$ ). Immediately following the start of the playback, of either ship noise or  
244 ambient control, we placed the focal crab in the centre of the neutral zone (equidistant from the  
245 boundary of each association zone) and in an inverted position with the aperture of the shell facing  
246 upwards. Once the focal crab recovered from the startle response (it emerged from its shell and  
247 contacted the bottom of the tank with a walking leg), we recorded its behaviour for 20 min (Canon  
248 Legria HF R47 digital video camera; Tokyo, Japan). We assigned focal crabs to be in association with  
249 either the single conspecific or the group of five conspecifics when the whole of their occupied shell  
250 had crossed the outer boundary of the appropriate decision zone. We excluded crabs that climbed  
251 up the mesh and escaped the arena or did not emerge from their shell after five min from the  
252 analysis. We coded the behaviour with The Observer version 12 (Noldus IT, Wageningen, the  
253 Netherlands) event logger software blind to the sound treatment and the occupied shell size. We  
254 recorded whether each decision zone was entered, the latency to enter each decision zone and the

255 average proportion of the total observation time spent in each of the three zones. Thus, the  
256 experiment contained two factors, sound treatment and shell size, and four treatment combinations  
257 (Table 1).

## 258 **Statistical analysis**

259 In order to determine whether ship noise and shell size influenced the chance of crabs  
260 entering the single and group stimulus zone we used Generalised Linear Mixed Effect Models  
261 implemented in the R-package lme4 (Bates, Mächler, Bolker & Walker, 2015) in R version 3.3.2 (R  
262 Core Team, 2017) with a binary response variable. For the response variable of whether or not crabs  
263 entered a zone (yes or no), sound (ambient and noise) and occupied shell (suboptimal = 75% and  
264 optimal = 100%) were the fixed factors and body mass was also included as a covariate. In order to  
265 account for the repeated use of three different sound playbacks for both sound treatments (noise  
266 and ambient) we included playback as a random factor. To account for the fact that each set of  
267 stimuli crabs was used for eight observations of focal crabs per day, block was also treated as a  
268 random factor. In order to determine the effects of sound treatment and shell size on the latency  
269 and average proportion of time spent in each zone, we used linear mixed effect models, again  
270 implemented using the lme4 package. As above, we included playback ID and block of the  
271 experiment as random factors. Finally, to determine whether shell size and noise treatment  
272 influenced the average proportion of time spent in all three zones, we used a single linear mixed  
273 effects model and to account for the fact that we took three measurements from each focal crabs to  
274 analyse the average proportion of time spent in each zone (single/neutral/group), we added zone as  
275 a fixed factor and the focal crab ID as a third random factor. We used post-hoc residual plots to  
276 assess the fit of each model. Where necessary we natural log transformed the data to improve  
277 normality, such that the assumption of the linear models would be met.

278

279 *Ethical note:* No animals were harmed during the experiment. After the experiment each crab was  
280 supplied with an optimal shell, fed and returned to the sea at the location of collection. No licences  
281 or permits were required for this study.

282

## 283 **Results**

284           There was no interaction between sound treatment and shell size and no main effects of  
285 sound treatment, shell size or crab weight on whether crabs entered the single zone (Table 2).

286 Similarly, there was no interaction between sound treatment and shell size and no main effect sound  
287 treatment, shell size or crab weight on whether crabs entered the group zone (Table 2).

288           There was, however, a significant interaction between sound treatment and shell size on the  
289 latency to enter the single zone (Table 2, Fig. 3). Under the ambient control treatment, crabs in  
290 suboptimal shells showed a longer latency to enter the single crab decision zone compared with  
291 crabs in optimal shells, but in the presence of noise this pattern was absent. The weight of the focal  
292 crab had no effect on the latency to enter the single zone (Table 2). There was no interaction  
293 between sound treatment and shell size and no main effect of sound treatment, shell size or the  
294 weight of the focal crab on the latency to enter the group zone (Table 2).

295           There was a significant three way interaction between sound treatment, shell size and zone  
296 on the average proportion of time spent in each zone (Table 2, Fig. 4). Under ambient sound, crabs  
297 in suboptimal shells showed no discernible preference for any of the three zones while crabs in  
298 optimal shells spent more time with conspecifics; mostly with a single crab. Under ship noise this  
299 pattern was reversed. Crabs in a suboptimal shell strongly preferred the zone adjacent to a single  
300 crab and spent very little time in the neutral zone whereas for crabs in optimal shells the preference  
301 for the zone adjacent to a single crab was reduced under noise and spent their time more evenly in  
302 all three zones compared to ambient sound. Crabs in suboptimal shells spent significantly less time

303 in the neutral zone than crabs in optimal shells. The weight of the focal crab had no effect on the  
304 average proportion of time spent in each zone (Table 2).

## 305 **Discussion**

306 We predicted, based on the ideas of shell exchange markets and predator dilution, that  
307 hermit crabs in suboptimal shells would show a stronger preference for joining groups compared  
308 with crabs in optimal shells. Furthermore, we predicted that noise would disrupt this behaviour.  
309 Surprisingly, we found the opposite pattern under ambient control, where crabs in suboptimal shells  
310 did not show a preference for either zone but crabs in optimal shells preferred to group with a single  
311 conspecific. Noise, however, reverses the grouping pattern. While crabs in suboptimal shells now  
312 preferred to group with conspecifics and particularly with a single crab, crabs in optimal shells  
313 showed no clear preference and spent their time more evenly across all three zones. Thus, although  
314 our overarching prediction that noise pollution would disrupt the grouping behaviour of hermit  
315 crabs (expressed under ambient conditions) was upheld, the direction of that effect differed from  
316 what we expected.

317 The unexpected pattern under ambient sound that crabs in small shells showed longer  
318 latency than crabs in optimal shells might be explained by considering some wider behavioural  
319 consequences of shell size. In hermit crabs the latency to emerge from the shell after a short  
320 disturbance, also called startle response, is a common measure for boldness (Briffa et al., 2008;  
321 Gherardi, Aquiloni, & Tricarico, 2012). Previous experiments have shown that hermit crabs in a  
322 100% optimal shell showed shorter startle response than individuals in 75% shells (Briffa & Bibost,  
323 2009). Furthermore, bolder crabs are also more inquisitive and more likely to investigate empty  
324 shells compared with shy crabs (Mowles, Cotton & Briffa, 2012). Thus, the relative lagging of crabs in  
325 suboptimal shells to join another individual might be driven by the effect of shell size on  
326 inquisitiveness, rather than by the relative costs and benefits of joining a group as we initially  
327 hypothesised. Indeed, grouping behaviour has been shown to be influenced by personality (such as

328 shy-bold) in a wide range of species (for review see Webster & Ward, 2011) and gregarious species  
329 showed stronger personality differences (von Merten, Zwolak & Rychlik, 2017).

330           The grouping pattern we found under ambient sound suggests that shell exchange markets  
331 or the dilution effect do not lead to the clusters we observed in *P. bernhardus* in the wild (S. Tidau,  
332 Pers. obs.) and which have been reported in other species (Hazlett, 1966; Hazlett, 1979; Tricarico &  
333 Gherardi, 2006). One factor could be that under ambient sound crabs in suboptimal shells perceived  
334 a greater costs from grouping than being solitary. As shown by Briffa and Bibost (2009), crabs in  
335 suboptimal shells stay hidden for longer than crabs in optimal shells indicating that they perceive a  
336 greater level of risk from conspecifics. Such risk could steam from cannibalism which has  
337 occasionally been observed in *P. bernhardus* (S. Tidau, Pers. obs.) and is also known for other hermit  
338 crab species (Tran, O'Grady, Colborn, Van Ness & Hill, 2014). While some species cluster up to  
339 hundreds or thousands (Gherardi, 1991) solitary behaviour has been reported in some species  
340 (Hazlett, 1966; Hazlett, 1979) and demonstrated in the field in the long-clawed hermit crab, *Pagurus*  
341 *longicarpus*, (Tricarico & Gherardi, 2006). As a consequence of the variety of grouping behaviour  
342 across hermit crab species, the clustering and grouping preferences observed in *P. bernhardus* might  
343 be species specific. Alternatively, for the baseline behaviour under ambient sound conditions we  
344 cannot rule out that our groups (here of two or six crabs) could have been too small to provide  
345 predator protection in hermit crabs as predicted due to the 'dilution effect' (Foster & Treherne,  
346 1981). Indeed, being in small groups might make crabs more apparent to predators than being  
347 single. If a predator would detect the group, the crab in a suboptimal shell would be particularly  
348 vulnerable to that predator, and if that crab had a smaller apparent body size than other group  
349 members, it may be easier to detect due to 'standing out' (Krause & Godin, 1994). To withdraw into  
350 the shell (Gherardi & Benvenuto, 2001) or flee (Mima, Wada & Goshima, 2003; Rosen, Schwarz &  
351 Palmer, 2009; Scarratt & Godin, 1992) thus might be the better strategy to avoid predation by *P.*  
352 *bernhardus*. Finally, we cannot eliminate the possibility that crabs might be attracted by something

353 else in the field or driven by abiotic factors such as water currents (Pallas, Garcia-Calvo, Corgos,  
354 Bernardes & Freire, 2006) which opens up questions for further research.

355           Although the grouping pattern of under ambient sound differed from our initial  
356 expectations, it is clear that grouping behaviour is altered by exposure to noise. Indeed, the usual  
357 (i.e. under ambient sound) pattern was reversed in the presence of noise. One explanation for why  
358 noise reverses decisions about joining a group is that crabs were distracted by the noise so that their  
359 ability to make appropriate decisions was impaired leading to the opposite decision made under  
360 ambient sound. Thus, crabs in suboptimal shells that would normally behave cautiously fail to adjust  
361 their behaviour to match the size of their shell in the presence of noise i.e. crabs in suboptimal shells  
362 showed more cautious behaviour by having longer latency to encounter a single conspecific. This  
363 distraction effect of noise on crustaceans has been observed under predation risk (Chan et al., 2010)  
364 and suggested as a mechanism to explain behavioural changes in other taxa under noise (Simpson et  
365 al., 2015). An alternative explanation is that crabs exposed to noise might have perceived the noise  
366 itself as a threat. Besides functioning as a novel and unpredictable stimulus for animals, some sound  
367 properties of noise could also be biologically similar to relevant stimuli i.e. elicit similar responses  
368 (Francis & Barber, 2013; Shannon et al., 2016). For instance, the Blainville's beaked whales,  
369 *Mesoplodon densirostris*, responded in similar ways to simulated military sonar and to playbacks of  
370 predatory killer whale, *Orcinus orca*, calls (Tyack et al., 2011). In this case, crabs in suboptimal shells  
371 may have weighed the potential benefits of associating with another crab (e.g. the dilution effects)  
372 higher than the costs (e.g. attacks by other hermit crabs). Under acute predation threat, animals are  
373 expected to join larger shoals (e.g. Hager & Helfman, 1991). Here crabs that were both exposed to  
374 noise and supplied with suboptimal shells (and were therefore at a high risk of predation) chose to  
375 avoid the neutral zone. The current data do not allow us to distinguish between these two  
376 possibilities (distraction and perception of threat) directly. However, we note that crabs in optimal  
377 shells also changed their preference i.e. associating with another individual was reduced under ship  
378 noise compared with ambient noise. That implies that noise disrupted the usual decision-making

379 process in both groups, crabs in suboptimal and optimal shells alike. Furthermore, the size of the  
380 shell does not seem to protect from the impacts of noise.

381 Our data add to the growing body of evidence that anthropogenic noise can clearly influence  
382 group dynamics from mammals to crustaceans. As noted above, the direction, intensity and  
383 consequences for survival and fitness are far less obvious. Groups of Mediterranean spiny lobsters,  
384 *P. elepha*, (Filiciotto et al., 2014), European sea bass, *D. labrax*, (when exposed to pile-driving,  
385 Herbert-Read et al., 2017), bottlenose dolphins, *T. truncatus*, (Bas et al., 2017) and red swamp  
386 crayfish, *P. clarkii*, (Celi et al., 2013) were less cohesive, decreases cooperative interactions among  
387 conspecifics and cichlid fish, *Neolamprologus pulcher*, even more aggressive (Bruitjes & Radford,  
388 2013). On the other hand, in the trevally *P. dentex* (Fewtrell & McCauley, 2012), the European sea  
389 bass *D. labrax* (when exposed to ship noise, Neo et al., 2018), the Carolina chickadees, *P.*  
390 *carolinensis*, and tufted titmice, *B. bicolor*, (Owens et al., 2012) shoals respectively flocks formed  
391 tighter groups under anthropogenic noise. These effects could be due to stress and distraction of  
392 attention, stimulus perception and filtering or combination of these mechanisms. Since an animal's  
393 attention to perceive and process stimuli is limited (Dukas, 2004) and since noise and other  
394 pollutants have been shown to affect animals across sensory channels (Halfwerk & Slabbekoorn,  
395 2015), it has been suggested that anthropogenic noise acts as a distracting stimulus (Chan et al.,  
396 2010; Simpson et al., 2015).

397 Our study is one of few which looked at cross-modal effects of anthropogenic noise on  
398 grouping behaviour and shows that this occurs in hermit crabs. Specifically, in *P. bernhardus*,  
399 exposure to ship noise causes crabs that occupy suboptimal resource units (a shell that is too small)  
400 to behave as if they possessed an optimal resource unit in terms of their interactions with other  
401 individuals. Further work will be warranted to investigate the underlying causes of the behavioural  
402 changes (for example lack of caution or risk avoidance). Nevertheless, given that survival in hermit  
403 crabs is strongly tied to the quality of their gastropod shell, any changes to shell-mediated behaviour  
404 could impact individual survival and hence population structure. Grouping behaviour is a common



405 phenomenon in nature with consequences for survival and fitness and potential noise effects should  
406 be further investigated.

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635 **Tables**

636 **Table 1** The orthogonal design of the interaction between sound treatment and occupied shell.

<i>n</i> = 45		Sound treatment	
		Ambient control	Ship noise
Initially occupied shell	75% (suboptimal)	<i>n</i> = 9	<i>n</i> = 10
	100% (optimal)	<i>n</i> = 11	<i>n</i> = 15

637 The values in each cell of the table indicate the proportion of preferred shell weight of shells  
 638 supplied to crabs in each group prior to observations.

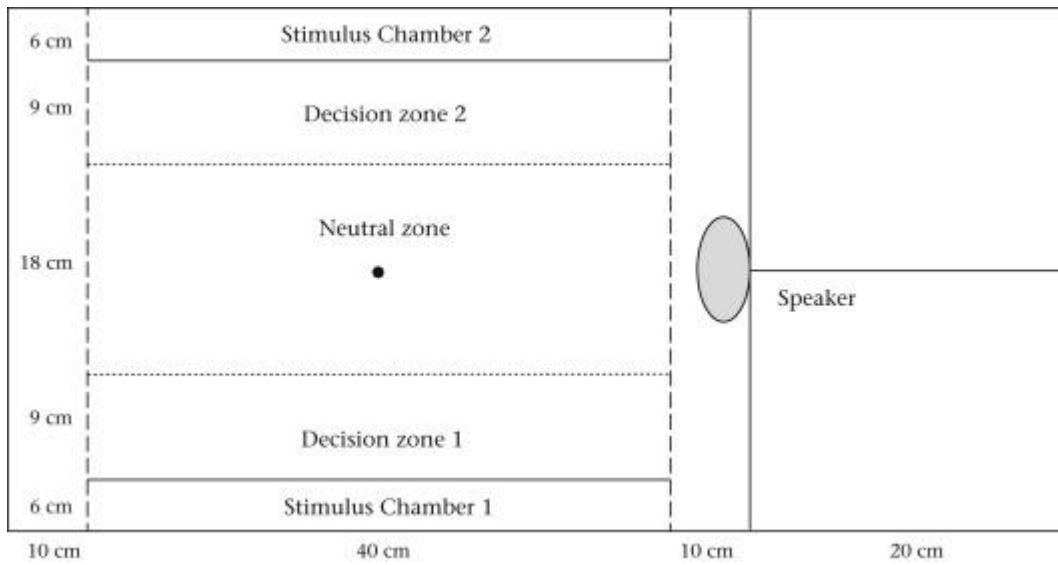
639

640 **Table 2** Summary of results mixed effects models (GLMM and LMM) used to determine the effects of  
 641 predictors on measures grouping behaviour.

Variable	$\chi^2$	P
<b>Entering the single zone</b>		
Sound treatment * shell size	1.27	0.26
Sound treatment	0.003	0.96
Shell size	1.25	0.26
Crab weight	2.5	0.11
<b>Entering the group zone</b>		
Sound treatment * shell size	0.06	0.81
Sound treatment	0.03	0.87
Shell size	1.04	0.31
Crab weight	0.13	0.72
<b>Latency to enter the single zone</b>		
Sound treatment * shell size	<b>5.6</b>	<b>0.018</b>
Crab weight	2.0	0.16
<b>Latency to enter the group zone</b>		
Sound treatment * shell size	0.4	0.55
Sound treatment	0.06	0.81
Shell size	2.45	0.11
Crab weight	0.8	0.38
<b>Average proportion of time spent in each zone</b>		
Sound treatment * shell size * zones	<b>7.1</b>	<b>0.028</b>
Crab weight	0.4	0.51

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

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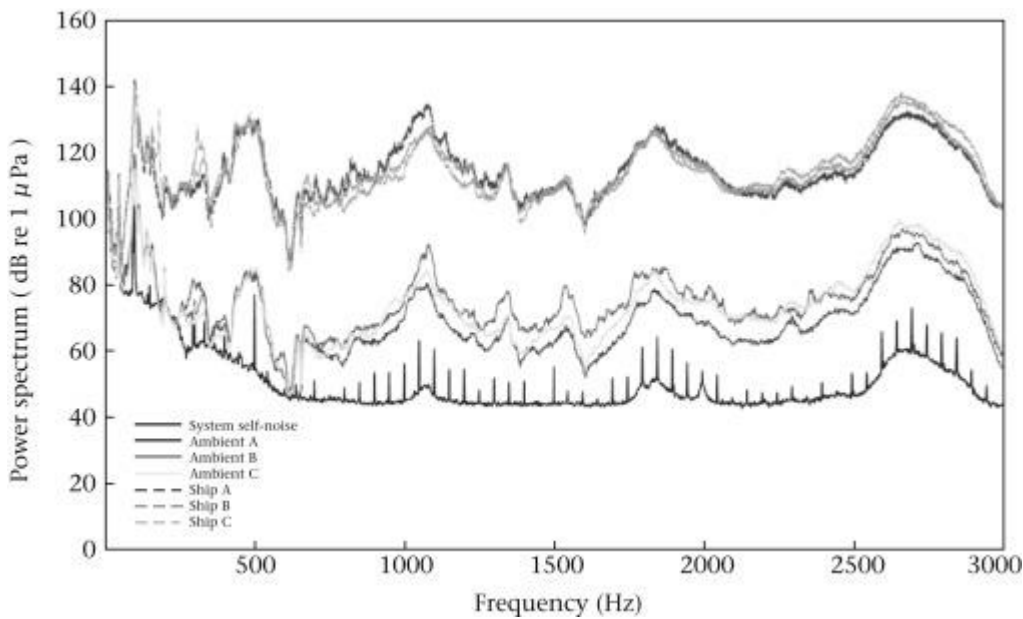


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647 **Figure 1.** Tank set-up and observation arena. Thick solid lines represent the tank walls and speaker supports, the dashed  
648 lines represent the mesh separating the arena from the rest of the tank, the tin solid lines show the walls of the stimulus  
649 chambers and the dotted lines show the decision zones marked at the bottom of the tank.

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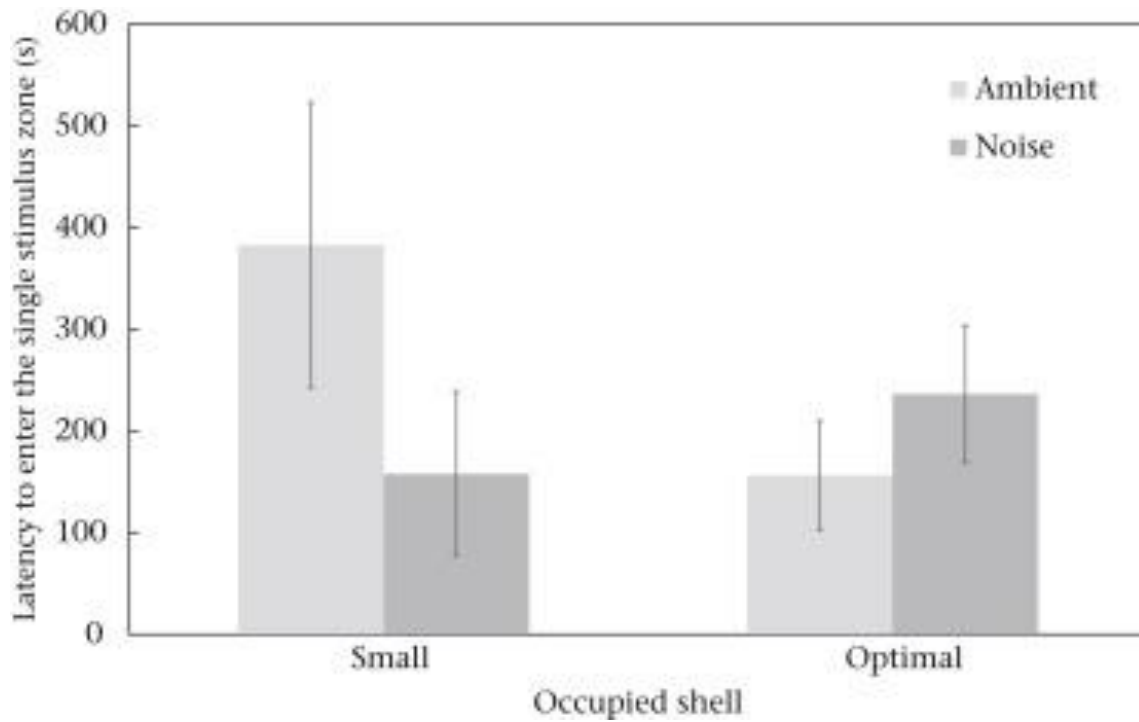


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653 **Figure 2.** Power spectrum analysis for 3 ship noise playbacks and 3 corresponding ambient sound playbacks. The system's  
654 self noise characterises the sound output by the equipment without playbacks.

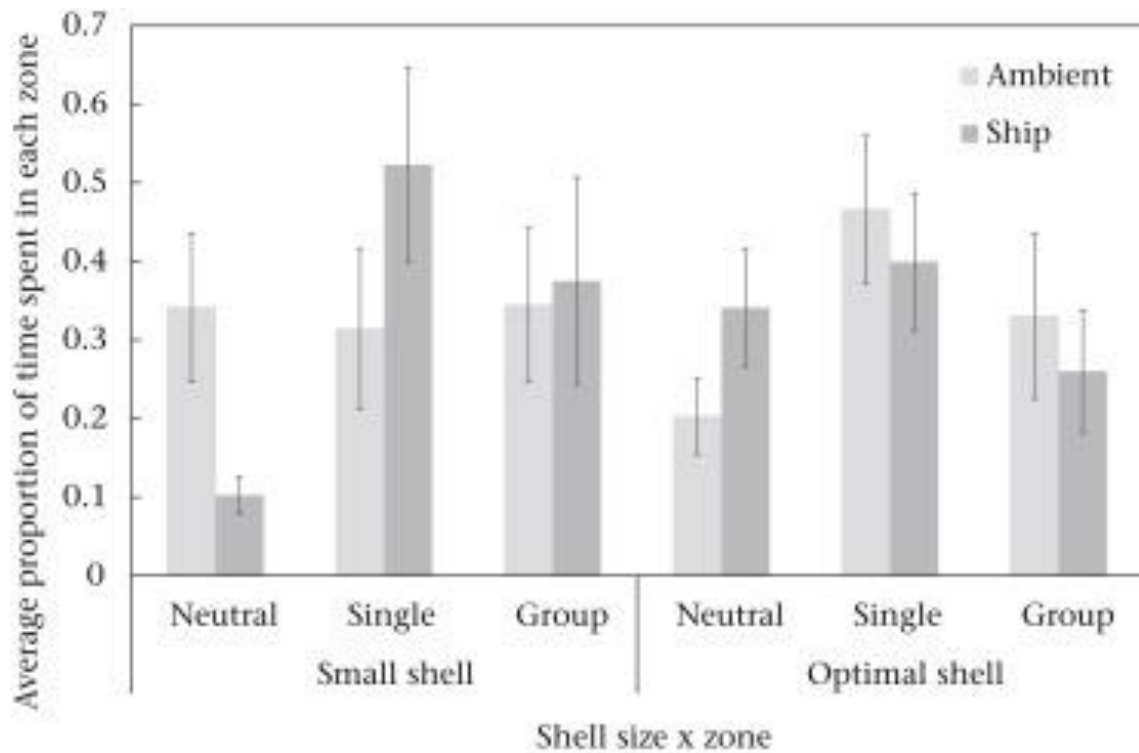
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657 **Figure 3.** The interaction effect between sound treatment and shell size on the latency to enter the single stimulus zone.  
 658 Error bars show standard error.

659



660

661

662 **Figure 4.** Proportion of time (out of a maximum of 20 min) spent in each of the three zones under ambient sound and ship  
 663 noise. Error bars show standard errors.