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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 μ 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 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 μ 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 μ 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 μ 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.

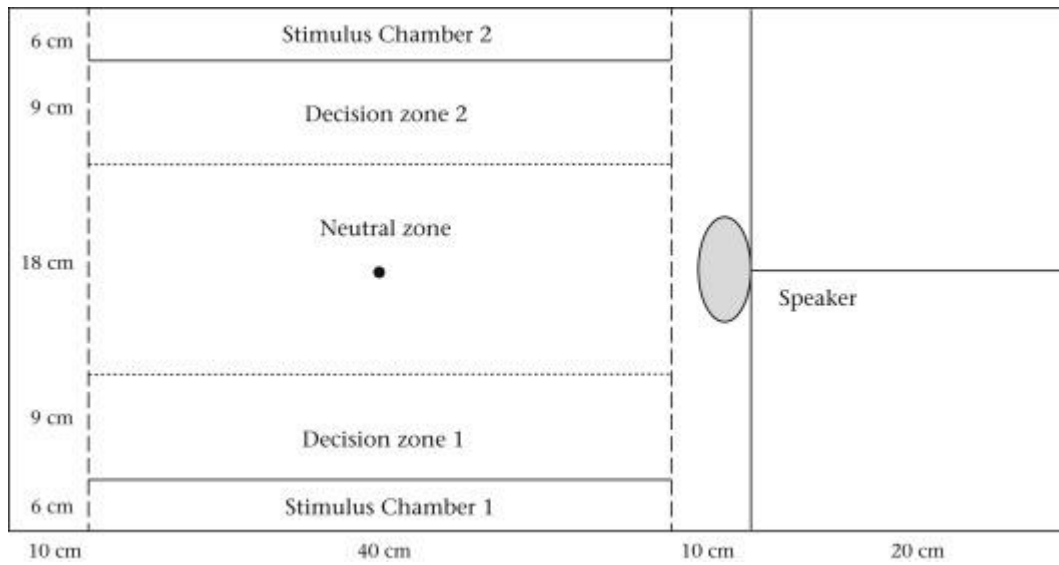
639

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 | χ^2 | P |
|--|------------|--------------|
| Entering the single zone | | |
| 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 |
| Entering the group zone | | |
| 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 |
| Latency to enter the single zone | | |
| Sound treatment * shell size | 5.6 | 0.018 |
| Crab weight | 2.0 | 0.16 |
| Latency to enter the group zone | | |
| 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 |
| Average proportion of time spent in each zone | | |
| Sound treatment * shell size * zones | 7.1 | 0.028 |
| 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.

644

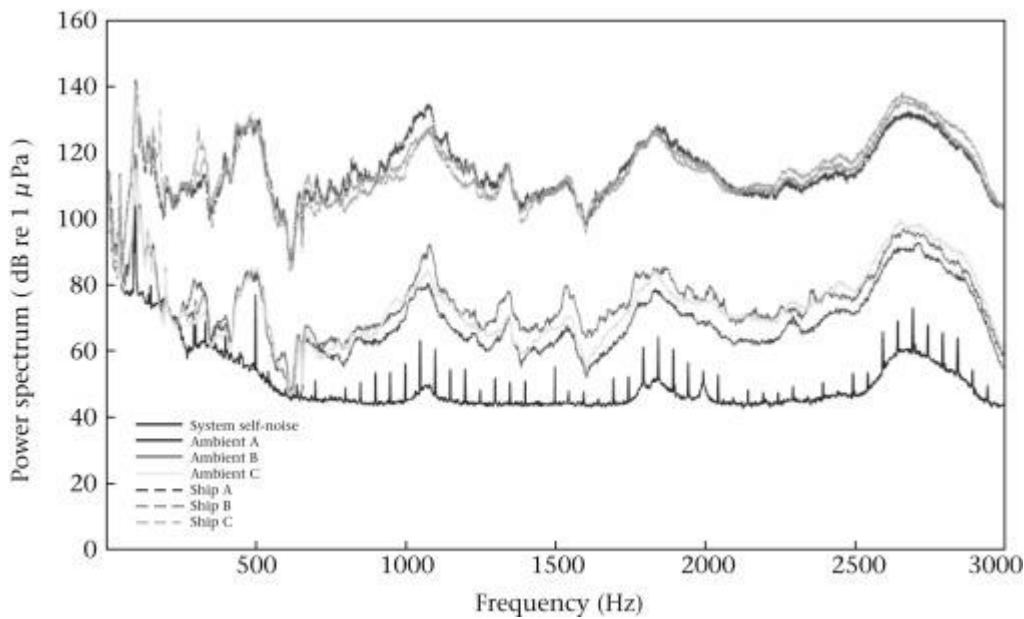


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646

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.

650

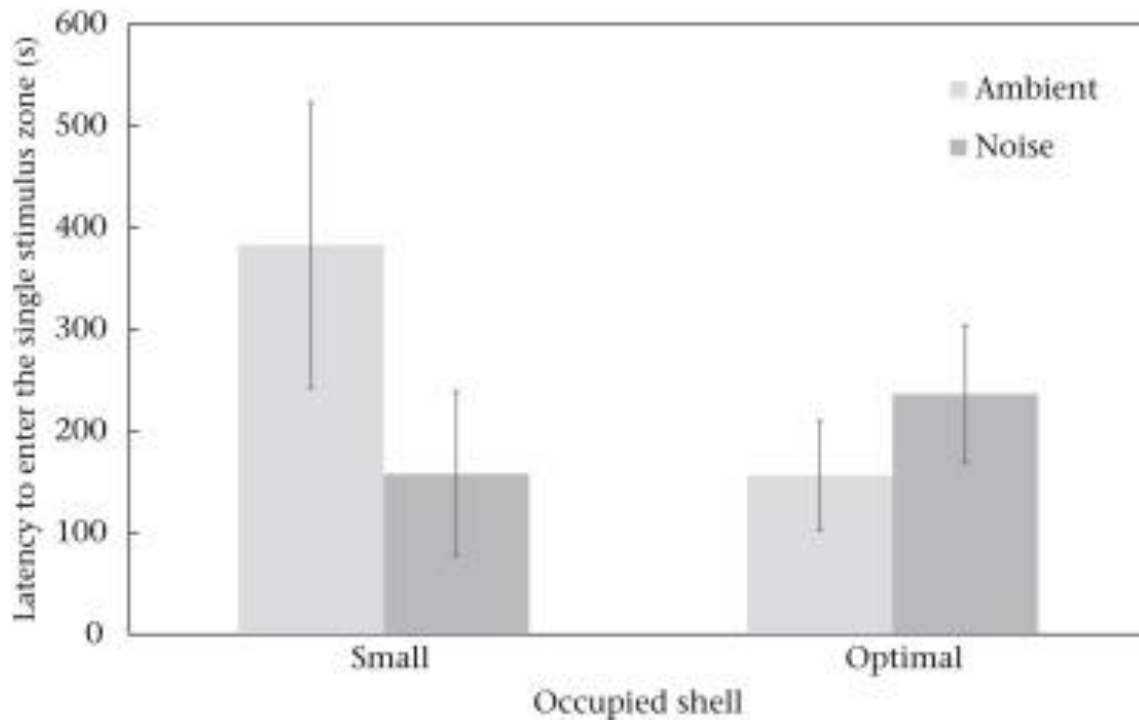


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653 **Figure 2.** Power spectrum analysis for 3 ship noise playbacks and 3 corresponding ambient sound playbacks. The system's
654 self noise characterises the sound output by the equipment without playbacks.

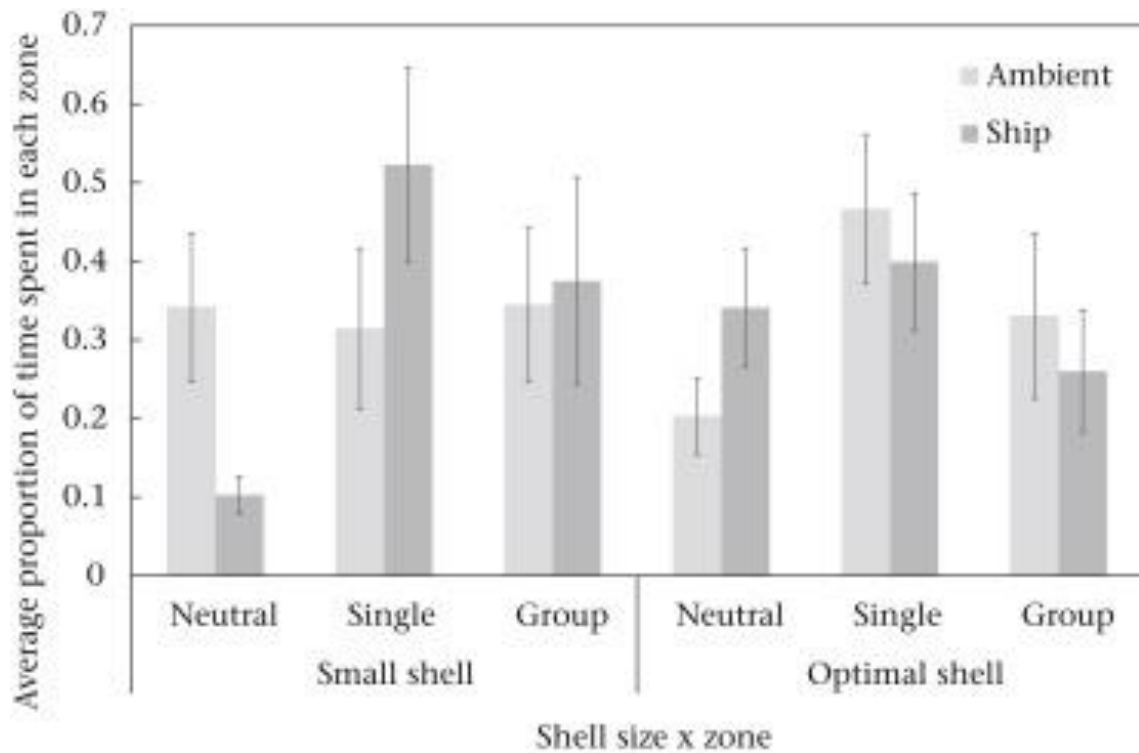
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656

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.