

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14

**Experimental evidence of invasion facilitation in the  
zebra mussel-killer shrimp system**

Matteo Rolla<sup>1</sup>, Sofia Consuegra<sup>1</sup>, Ellie Carrington<sup>1</sup>, David Hall<sup>2</sup>,  
Carlos Garcia de Leaniz\*<sup>1</sup>

<sup>1</sup>Department of BioSciences, Centre for Sustainable Aquatic Research, Swansea University,  
Singleton Park, Swansea SA2 8PP, UK

<sup>2</sup>Cardiff Harbour Authority, Queen Alexandra House, Cargo Road, Cardiff CF10 4LY

\*corresponding author: [c.garciadeleaniz@swansea.ac.uk](mailto:c.garciadeleaniz@swansea.ac.uk)

15 **Abstract**

16 Invasion facilitation, whereby one species has a positive effect on the establishment of another  
17 species, could help explain the rapid colonisation shown by some freshwater invasive species,  
18 but the underlying mechanisms remain unclear. We employed two-choice test arenas to test  
19 whether the presence of zebra mussel (*Dreissena polymorpha*) could facilitate the establishment  
20 of the killer shrimp (*Dikerogammarus villosus*). Killer shrimp preferred to settle on mats of zebra  
21 mussel, but this was unrelated to mat size, and was not different from attraction shown to  
22 artificial grass, suggesting that zebra mussel primarily provides substrate and refuge to the killer  
23 shrimp. Killer shrimp were strongly attracted to water scented by zebra mussel, but not to water  
24 scented by fish. Chemical attraction to the zebra mussel's scent did not differ between sympatric  
25 and allopatric populations of killer shrimp, suggesting that chemical facilitation is not an  
26 acquired or learned trait. Our results have implications for managing the spread of killer shrimp,  
27 and perhaps other freshwater invasive species, because invasion facilitation could significantly  
28 increase establishment success. Failure to consider invasion facilitation may underestimate the  
29 risk of establishment and likely impact of some aquatic invaders.

30

31 **Keywords**

32 Invasive species, Synergy, Chemical recognition, Zebra mussel, Killer shrimp

33

## 34 **Introduction**

35 The impact of biological invasions has often been examined in isolation, under the implicit  
36 assumption that invaders do not interact with each other (Consuegra et al. 2011; Vanhaecke et al.  
37 2015; Young et al. 2010; Young et al. 2009). However, invasion facilitation, whereby one  
38 species has a positive effect on the introduction, establishment or dispersal of other invasive  
39 species, is well documented, particularly in terrestrial plants and animals (Adams et al. 2003;  
40 Altieri et al. 2010). For example, the presence of the European honey bee (*Apis mellifera*) has  
41 increased the reproduction success of the invasive shrub *Lantana camara* in Australia (Goulson  
42 & Derwent 2004), and similar positive synergies among invasive species have also been reported  
43 across many taxa (Woodward et al. 1990). This led Simberloff & Von Holle (1999) to coin the  
44 term ‘invasional meltdown’ to describe the process by which the negative impacts triggered by  
45 one invasive species could be exacerbated by the interactions with other exotic species  
46 (Simberloff 2006).

47 However, invasion facilitation has not received as much attention in freshwater habitats  
48 as it has in terrestrial ecosystems, possibly because it is more difficult to detect (Ricciardi 2005),  
49 and because it typically only benefits one species (i.e. commensalism, (Laihonen & Furman  
50 1986; Ricciardi 2005). This lack of information is unfortunate because freshwater habitats,  
51 particularly lakes and ponds, rank among the most threatened ecosystems in the world, and this  
52 makes them particularly vulnerable to the threat of aquatic invasive species (AIS; (Dudgeon et  
53 al. 2006). Habitat suitability models for invasive species, as well as risk maps (Crall et al. 2013;  
54 Jiménez-Valverde et al. 2011), rarely take into account the fact that some invaders can  
55 bioengineer their new habitat to suit their needs, or that the presence of one invasive species may  
56 make the habitat more attractive to other invaders (Strayer 2012). Thus, the synergistic effects of

57 invasive species and their cumulative impacts on native fauna may be underestimated in aquatic  
58 habitats if invasion facilitation exists and is not taken into account.

59 Two aquatic invaders that often occur together and may benefit from invasion facilitation  
60 are the zebra mussel (*Dreissena polymorpha*) and the killer shrimp (*Dikerogammarus villosus*).  
61 The two species are included in the 100 worst invasive species in Europe ([www.europe-](http://www.europe-aliens.org)  
62 [aliens.org](http://www.europe-aliens.org)), and in the case of zebra mussel, in the world (Lowe et al. 2000). Zebra mussels form  
63 dense mats on natural and artificial substrates which require expensive eradication programmes  
64 (Lovell et al. 2006), and compete directly for food and space with native bivalves (Fahnenstiel et  
65 al. 1995a; Fahnenstiel et al. 1995b; Johengen et al. 1995), sometimes driving them to extinction  
66 (Baker & Hornbach 1997). The killer shrimp, on the other hand, has the typical profile of an  
67 efficient and plastic invader (Rewicz et al. 2014), being able to adapt to a wide range of waters  
68 and conditions (Piscart et al. 2003). Its wide diet includes many macroinvertebrates, including  
69 native gammarids, which may be displaced and driven to local extinction (Dick & Platvoet 2000;  
70 Piscart et al. 2003).

71 Both species share a broad, common Ponto-Caspian geographical origin, but the extent of  
72 sympatry in their native, as well as in the invaded areas, is unclear. The zebra mussel was first  
73 reported in Europe during the nineteenth century, becoming highly invasive and forming large  
74 populations (Son 2007). In contrast, the killer shrimp is a much more recent invader, it has only  
75 been detected in Europe during the last 20 years, but has spread rapidly ever since (MacNeil et  
76 al. 2010; Rewicz et al. 2014; Rewicz et al. 2017; Tricarico et al. 2010).

77 While many of the sites colonised by the killer shrimp in Europe had already established  
78 populations of zebra mussel, that might be indicative of invasion facilitation (Gallardo &  
79 Aldridge 2015), the killer shrimp has also invaded many areas devoid of zebra mussel ((Rewicz

80 et al. 2015; van der Velde et al. 2010). Thus, whether there have been synergies in the  
81 establishment of these two species is not clear (Devin et al. 2003). The zebra mussel has shown  
82 mutualistic interactions with one gastropod (Ricciardi 2005; Ricciardi et al. 1997), and two  
83 macrophytes (MacIsaac 1996; Skubinna et al. 1995), and can benefit the killer shrimp in various  
84 ways. For example, the dense interstitial matrix formed by the shells of zebra mussels provides  
85 refuge for the killer shrimp (Ricciardi et al. 1997), allowing it to survive outside the water, while  
86 the production of faeces and pseudo faeces provides food (Gergs & Rothhaupt 2008a; Gergs &  
87 Rothhaupt 2008b; Ricciardi et al. 1997; Stewart et al. 1998b). Similarly, zebra mussel larvae can  
88 attach to the hard chitin cover of the killer shrimp which could facilitate their dispersal  
89 (Kenderov 2017; Yohannes et al. 2017).

90         Given their common geographical origin, and recent evidence suggesting that the two  
91 species often occur together and might benefit each other, we hypothesized that killer shrimp  
92 might be chemically attracted to the presence of zebra mussel. We further hypothesized that  
93 attraction might differ depending on whether killer shrimp were found in habitats already  
94 colonised by the zebra mussel, i.e. whether attraction differed between sympatric and allopatric  
95 conditions. Ultimately, our aim was to address some of the underlying mechanisms of invasion  
96 facilitation as this might help design better predictive models and more effective control  
97 measures of these two aquatic invaders.

98

## 99 **Materials and Methods**

### 100 *Collection and origin of samples*

101 Sympatric zebra mussel and killer shrimp were collected from Cardiff Bay (Cardiff, UK – Grid  
102 reference: ST 19210 73510) in April 2016, whereas allopatric killer shrimp were collected from  
103 the Upper Mother Ditch (Margam, UK, Grid reference: SS 79029 85506) in September 2016,  
104 where the zebra mussel is not yet present (Figure 1). These were brought to the CSAR facilities  
105 at Swansea University and maintained in 6 x 20 L tanks fed by separated recirculation  
106 aquaculture systems, with a weekly replacement of c. 20% volume. Zebra mussels (~2.4 kg)  
107 were fed three times per week with a 2L mixture of *Scenedesmus* sp. and *Chlorella* sp., while  
108 killer shrimps (~100g) were fed three times per week with 6g of frozen bloodworms. Water  
109 temperature was maintained at 15-16.5°C.

110

### 111 *Experimental design*

112 We set up three experiments to test possible synergies between the two species. In the first  
113 experiment we tested if killer shrimp had a preference for particular densities of zebra mussel; in  
114 the second experiment we tested if killer shrimp had a preference for zebra mussel cover  
115 compared to an artificial substrate; in the third experiment we tested if killer shrimp could detect  
116 the presence of zebra mussel through chemical cues in the water. The killer shrimp used in the  
117 tests had an average size of 16.8±0.9 mm and the water temperature during tests ranged between  
118 15.4 °C and 16.2 °C.

119

120

121

122 Experiment 1. Choice of zebra mussel density

123 To test if killer shrimp had a preferred density of zebra mussel to settle on, we employed a 3L  
124 tank (L25 x H 10 x W12 cm; Figure 2a) divided into two equal sections, each with a different  
125 density of zebra mussel (0, 33, 67, or 100% cover), and an acclimatisation plastic cylinder in the  
126 middle. Individual killer shrimp (n = 96) were allowed to acclimatise for five minutes in the  
127 cylinder, then the cylinder was lifted and the position and behaviour (swimming or hiding) of the  
128 shrimp after 20 minutes was recorded. We assumed that if the shrimp was hiding it meant it had  
129 found a suitable substrate, whereas if it was still swimming it meant it was still looking for a  
130 refuge. We tested the killer shrimp's binary choice over six matched densities (n = 16) of zebra  
131 mussel: 0-33%, 0-66%, 0-100%, 33-66%, 33-100%, and 66-100% employing a total of 96  
132 specimens, and allocating the densities to the left or right sides of the test arena at random.

133

134 Experiment 2. Preference for zebra mussel over an artificial substrate

135 To test if the attraction of killer shrimp for zebra mussel-beds was simply related to the presence  
136 of cover or to other factors (such as bio-deposited material) we compared preference for living  
137 shells against either empty shells of zebra mussel or artificial grass (PE thickness 15mm) of  
138 similar texture and extent of refuge . We used one killer shrimp per trial (n= 30), and then twenty  
139 killer shrimp per trial (n = 80) to understand if substrate choice was affected by group dynamics.  
140 The experimental protocol was the same as in Experiment 1, but in this case each side of the test  
141 arena afforded 50% cover and we used a 20 L test tank (L40 x H15 x W35 cm).

142

143

144

145 Experiment 3. Chemical attraction to zebra mussel

146 To test if killer shrimp could chemically recognise the scent of zebra mussel we employed a  
147 simplified version of the two-choice Perspex fluvium used by Kroon (2005) in the preference  
148 of another crustacean (Figure 2b). The fluvium consisted of an acclimatization chamber (L5 x  
149 H6.5 x W5 cm) and two 0.3L choice chambers (L20 x H6.5 x W10 cm) with a total volume of  
150 approximately 0.7L. We tested preferences against dechlorinated tap water (blank), water  
151 scented with zebra mussel and Nile tilapia (*Oreochromis niloticus*) to control for possible  
152 attraction to organic matter, as well as blank water vs blank water to control for chamber bias.  
153 Killer shrimp were allowed to acclimatize for five minutes, the valves connected to the two water  
154 inlets were opened, the gate was lifted, and the time spent in each chamber was recorded for 15  
155 minutes with a GoPro Hero camera. We compared the time spent in each arm as well as the  
156 number of transitions between arms as a measure of activity. Scent drip dosage was adjusted at  
157 200 ml/min.

158 To prepare the scented water we placed either zebra mussels or fish (tilapia) in a tank  
159 filled with dechlorinated water for 24 hours at a biomass of 50g/L. The fluvium was drained,  
160 cleaned with 90% ethanol and rinsed with fresh water between trials to remove potential  
161 chemical cues that could affect the next experiment. We repeated the experiment with killer  
162 shrimp originating from a population living in sympatry (Cardiff Bay, n = 60) or allopatry  
163 (Margam, n = 60) with zebra mussels. All the zebra mussel came from Cardiff Bay.

164

165 *Statistical analysis*

166 We used R 3.3 (R Core Team, 2017) for all analysis. In experiments 1 and 2, we used a  
167 generalized linear model (GLM) with a binomial log-link to test if the number of killer shrimp in



168 the scented arm differed with treatment, and we then used a two-sided binomial test to assess if  
169 there was a statistically significant preference for the high or low density (Exp 1) or different  
170 substrate combinations (Exp 2) at each binary choice comparison. For experiment 3 (two-way  
171 choice fluvium), we used a linear model with time spent in the scented arm as the dependent  
172 variable and origin (allopatry vs sympatry) and type of scent (blank, zebra mussel, tilapia) as the  
173 predictors; we then used paired t-tests to assess which type of matched scent comparisons was  
174 statistically significant.

175

#### 176 *Ethics Statement*

177 All experiments were carried out in accordance with Swansea University Ethical guidelines and  
178 were approved by the Ethics Committee (300419/1557). Water removed from the system was  
179 treated with bleach before disposing, to avoid accidental dispersion of zebra mussel larvae.

180

181 **Results**

182 *Experiment 1. Zebra mussel density preference*

183 Preference for zebra mussel varied depending on the densities being compared ( $\chi^2 = 29.09$ ,  $df =$   
184  $1$ ,  $P < 0.001$ ; Figure 3). Killer shrimp showed a clear preference for the side of the tank with  
185 zebra mussel when the alternative was a bare tank bottom (binomial proportion test: 0-33%  $P =$   
186  $0.004$ ; 0-66%  $P < 0.001$ ; 0-100%  $P < 0.001$ ). However, when both sides of the test arena had  
187 different densities of zebra mussel there was no preference (binomial proportion test 33-66%,  $P$   
188  $= 0.454$ ; 66-100%,  $P = 1.00$ ) or preferred the lower density (33-100%,  $P = 0.004$ ). After 20  
189 minutes, the majority of killer shrimp (85/96 or 88.5%) were found to be hiding, rather than  
190 swimming (binomial proportion test  $P < 0.001$ ) regardless of treatment ( $\chi^2 = 1.745$ ,  $df = 1$ ,  $P =$   
191  $0.883$ ).

192

193 *Experiment 2. Substrate preference*

194 When tested individually, killer shrimp did not prefer live zebra mussels over artificial grass  
195 (binomial proportion test,  $P = 0.584$ ), or over empty zebra mussel shells (binomial proportion  
196 test,  $P = 0.200$ , Figure 4a). The majority of individuals were found hiding (rather than  
197 swimming), both when the comparison was against artificial grass (binomial proportion test,  
198  $83.3\%$   $P < 0.001$ ) and also when there were empty shells (binomial proportion test,  $76.6\%$   $P =$   
199  $0.005$ ).

200 When the experiments were repeated with 20 shrimps per trial (4 trials or 80 shrimp),  
201 killer shrimp strongly preferred the zebra mussel substrate over artificial grass (binomial  
202 proportion test,  $P = 0.006$ ) and also over empty shells (binomial proportion test,  $P = 0.006$ ;  
203 Figure 4b). As before, at the end the trials the majority of individuals were hiding, both when the

204 comparison was against artificial grass (binomial proportion test, 77.5%  $P < 0.001$ ) and also  
205 against empty shells (binomial proportion test, 72.5%  $P = 0.006$ ).

206

### 207 *Experiment 3. Chemical attraction to zebra mussel*

208 No side preference was detected when killer shrimp were tested against blank water in both arms  
209 of the 2-choice fluvium, either in the sympatric ( $t_9 = 1.343$ ,  $P = 0.212$ ; Figure 5a) or allopatric  
210 killer shrimp populations ( $t_{19} = -1.280$ ,  $P = 0.216$ ; Figure 5b), indicating that there was no side  
211 bias. When killer shrimp were tested against water conditioned with tilapia scent, no preference  
212 was observed over blank water, either in sympatry ( $t_{19} = 0.819$ ,  $P = 0.423$ ; Figure 5c) or allopatry  
213 ( $t_{19} = -0.687$ ,  $P = 0.500$ ; Figure 5d). However, when killer shrimp were tested against water  
214 conditioned with zebra mussel scent, there was a strong chemical attraction to the zebra mussel  
215 scent, both in the sympatric ( $t_{27} = -2.176$ ,  $P = 0.038$ ; Figure 5e) and allopatric population ( $t_{19} = -$   
216  $2.614$ ,  $P = 0.017$ ; Figure 5f). Chemical attraction for zebra mussel scent was equally strong in  
217 the sympatric and allopatric populations ( $F_{1,118} = 1.036$ ,  $P = 0.311$ ).

218 The analysis of activity (measured as the number of transitions between arms) indicates that  
219 activity was influenced by the type of test scent (Figure 6), as killer shrimp made more changes  
220 when both arms were dosed with blank water than when one arm was dosed with zebra mussel  
221 scent (test,  $P = 0.002$ ) or tilapia scent ( $P < 0.001$ ). No difference in activity was observed  
222 between the zebra mussel scent and the tilapia scent ( $P = 0.759$ ). Overall, the sympatric  
223 population made more choices and was more active than the allopatric population ( $P = 0.005$ ).

224

225

226 **Discussion**

227 Our study provides experimental insights into the underlying reasons for the joint occurrence of  
228 zebra mussel and the killer shrimp, two of the world's worst aquatic invaders (Lowe et al. 2000).  
229 We found that killer shrimp showed a strong tendency for hiding in zebra mussel beds, and were  
230 also chemically attracted to the scent of zebra mussels, which may facilitate their invasion.

231 In our experiments, killer shrimp consistently avoided the empty side of the tank  
232 (substrate coverage 0%) that did not afford any refuge, and generally preferred to settle on zebra  
233 mussel beds, even when tested with blank water and without any threat of predation. The strong  
234 preference for a substrate that offers refuge is in agreement with observations under natural  
235 conditions, where the species is typically found living among gravel, cobbles and boulders, and  
236 absent in places where there is silt or substrates that do not afford refuge (Boets et al. 2010;  
237 MacNeil et al. 2010). While juvenile killer shrimp may also be found living among macrophytes  
238 (Devin et al. 2003), as happens for juveniles of several other predatory amphipods (Berezina  
239 2007), adults tend to prefer hard substrates of large grain size, including cobble and roots (Devin  
240 et al. 2003), pebbles (Van Riel et al. 2009), fissured stones (Kley et al. 2009), and coarse gravel  
241 (Boets et al. 2010). Kobak et al. (2015) have suggested that the substrate preference of the killer  
242 shrimp is size dependent and determined by the interstitial spaces of the substrate, as this  
243 influences ease of movement and the ability to find refuge. The species appears to choose  
244 fissures that closely match its body size (Platvoet et al. 2009), which might explain why they  
245 prefer larger substrates as they become older. In this sense, zebra mussel beds provide an ideal  
246 refuge for juveniles and adults alike, because as the mussels grow the interstitial spaces also  
247 become larger.

248 The findings of Experiment 2, where we tested the preference of killer shrimp for zebra mussel  
249 over other textured substrates, are more difficult to interpret as different results were obtained  
250 depending on group size. When killer shrimp were tested singly, no preference was detected for  
251 live zebra mussels over empty shells or artificial grass of similar texture, suggesting that  
252 substrate preference was mainly governed by the availability of refuge, which previous  
253 experiments have shown confers protection from fish predators (Kinzler & Maier 2006).  
254 However, when groups of twenty shrimp were tested, a strong preference for live zebra mussel  
255 over other substrates was found, suggesting the existence of group behaviour (sociability) that  
256 cannot solely be explained by refuge availability and deserves further investigation. Killer  
257 shrimp tend to form aggregations, and these are thought to be advantageous and increase the  
258 chances of successfully colonising new areas (Truhlar & Aldridge 2015). However, while  
259 sociability within a group can increase fitness and reproductive success (Réale et al. 2007), it can  
260 also facilitate intraspecific predation (cannibalism), which is frequently observed in amphipods  
261 (Dick et al. 1993; Hunte & Myers 1984; Ward 1985), including the killer shrimp (Dick &  
262 Platvoet 2000; Dick et al. 2002; MacNeil et al. 1997). An inverse association may exist between  
263 sociability and cannibalism in amphipods (Kinzler et al. 2009; Truhlar & Aldridge 2015),  
264 although this may also be influenced by predation pressure (Dick et al. 1993). Cannibalism in  
265 killer shrimp does not appear to be so strong as to reduce the species' sociability, possibly  
266 because cannibalism mainly targets small juveniles (Kinzler & Maier 2003) which tend to be  
267 spatially segregated from larger adults that could prey on them (Devin et al. 2003).

268 One novel finding of our study was the strong chemical attraction shown by killer shrimp  
269 to the scent of live zebra mussels (or something associated with them), a response not seen to  
270 blank water or the scent of non-predatory fish. Amphipods use chemical cues as their main form

271 of communicating between conspecifics (Thiel 2011), and also to recognize and avoid predators  
272 (Wooster 1998), but chemical attraction to other species has, to our knowledge, not been  
273 reported before. Chemical detection in amphipods is mediated mainly via specific sensillae  
274 located on the antennae (Hallberg & Skog 2011) and is used in mate choice and species  
275 discrimination, reducing the chances of interspecific mating between similar species (Dick and  
276 Elwood 1990 (Cothran et al. 2013; Dick & Elwood 1990). Chemical cues are also used by  
277 females to recognize and defend their offspring against conspecifics (Mattson & Cedhagen  
278 1989), and some amphipods can also recognize alarm cues from damaged conspecifics and  
279 mount a strong freezing response as an anti-predatory strategy (Sehr & Gall 2016). Killer shrimp  
280 have been reported to use chemical cues to recognize and avoid potential predators such as the  
281 spiny-cheek crayfish *Orconectes limosus* (Hesselschwerdt et al. 2009), the European  
282 bullhead *Cottus gobio* (Sornom et al. 2012) and the racer goby *Babka gymnotrachelus* (Jermacz  
283 et al. 2017), and our study shows they can also use chemical cues to find zebra mussels that  
284 provide not only cover and refuge, as seen in our study and other studies (Ricciardi et al. 1997),  
285 but also food through the production of faeces and pseudo faeces (Gergs & Rothhaupt 2008a;  
286 Gergs & Rothhaupt 2008b; Ricciardi et al. 1997; Stewart et al. 1998a).

287 The preference for zebra mussel beds shown by the killer shrimp (at least when they are  
288 tested in groups), and the fact that they are strongly attracted to the zebra mussel scent, suggests  
289 this could be an example of invasion facilitation, as seen in other studies. For example, positive  
290 synergies resulting in invasion facilitation have been reported for an invasive algae and an  
291 invasive bryozoan (Levin et al. 2002), as well as among invasive fish parasites (Hohenadler et al.  
292 2018). Other well known examples of invasion facilitation, include the bullfrog-sunfish system,  
293 where the survival of the invasive bullfrog (*Rana catesbeiana*) was enhanced by the presence of

294 the non-native bluegill sunfish (*Lepomis macrochirus*) because the latter preyed on native  
295 dragonfly which in turn preyed on bullfrog tadpoles (Adams et al. 2003). Similarly, predation  
296 by an invasive crab on a large native clam resulted in the spread of a smaller invasive clam due  
297 to competitive release (Grosholz 2005). Our study indicates that chemical attraction by the killer  
298 shrimp to the zebra mussel scent was as strong under sympatric as it was under allopatric  
299 conditions, suggesting this is not a recently acquired or learned trait, but rather an older  
300 behavioural adaptation. However, the absence of population replication (it is very difficult to  
301 find populations of killer shrimp that do not coexist with zebra mussel) makes it difficult to draw  
302 firm conclusions and would warrant further studies.

303 In general, mutualist interactions are less well studied than competitive ones (Simberloff  
304 & Von Holle 1999), and interactions between invasive species are less well known than those  
305 between invasive and native species (Gallardo & Aldridge 2018). There is still limited  
306 knowledge on positive interactions among invasive species, despite the fact that this may hold  
307 the key for more effective control of new invasions. Given the strong preference for settling on  
308 zebra mussel mats, and the benefits that this entails (Gergs & Rothhaupt 2008b; MacNeil et al.  
309 2008) – including not just refuge, but also benthic organic matter that can be a source of food  
310 (Ricciardi et al. 1997; Stewart et al. 1998b), chemical attraction may help understand synergies  
311 between these two invasive species. Chemical attraction may need to be taken into account in the  
312 study of patterns of distribution of these two invasive species, since the presence of zebra mussel  
313 could make the killer shrimp more likely to become established, and hence a more successful  
314 invader. The zebra mussel's ability to settle on a wide range of substrate (Marsden & Lansky  
315 2000) and bioengineer its own environment (Mayer et al. 2001) can turn formerly unsuitable  
316 habitats into favourable locations for killer shrimp settlement, expanding the potential range of

317 suitable environments. For example, the NBN Atlas (<https://nbnatlas.org/>), the UK's largest  
318 biodiversity database, holds 3,182 records of zebra mussel but only 317 observations of killer  
319 shrimp and information on the presence of zebra mussel could help make more accurate  
320 predictions of the likely spread of killer shrimp. This is of particular concern when the species is  
321 a recent invader since there is typically insufficient information to predict areas at risk or to  
322 guide management (Morales et al. 2017). In Great Britain, the killer shrimp was first detected in  
323 2010 (Rewicz et al. 2014) and is only present in 8 locations, making it difficult to predict its  
324 future dispersal (Rodriguez-Rey et al., under review). The zebra mussel, in contrast, was first  
325 detected in 1824 and is now established in 376 locations in England and Wales (Aldridge et al.  
326 2004), Rodriguez-Rey et al., under review), potentially increasing the number of favourable  
327 locations for killer shrimp many fold. Yet, current invasive species prioritisation lists (Boets et  
328 al. 2014; Carboneras et al. 2018) and risk assessment guidelines (Roy et al. 2018) tend to view  
329 invasive species in isolation, making no allowance for invasion facilitation. Our study suggests  
330 that information on the presence of zebra mussel should be incorporated into risk maps and  
331 models of killer shrimp dispersal, because ignoring chemical attraction will likely underestimate  
332 the extent and consequences of invasion facilitation.

333

### 334 **Acknowledgments**

335 We are grateful to Teja Muha (Swansea University), Emma Keenan and Graham Rutt (Natural  
336 Resources Wales) for help with the sampling. Funding was provided by the EC Horizon 2020  
337 Aquainvad-ED project (Marie Skłodowska-Curie ITN-2014-ETN-642197) to SC.

338

339



## 340 **Author Contributions & Competing Interests**

341 CGL and SC designed the study and secured the funding. MR and EC collected the data and  
342 carried out the analyses with advice from CGL. MR and CGL wrote the MS with contributions  
343 from SC and DH. The authors declare no competing interests.

344

## 345 **References**

- 346 Adams MJ, Pearl CA, and Bruce Bury R. 2003. Indirect facilitation of an anuran invasion by  
347 non-native fishes. *Ecology Letters* 6:343-351.
- 348 Aldridge DC, Elliott P, and Moggridge GD. 2004. The recent and rapid spread of the zebra  
349 mussel (*Dreissena polymorpha*) in Great Britain. *Biological Conservation* 119:253-261.
- 350 Altieri AH, van Wesenbeeck BK, Bertness MD, and Silliman BR. 2010. Facilitation cascade  
351 drives positive relationship between native biodiversity and invasion success. *Ecology*  
352 91:1269-1275.
- 353 Baker S, and Hornbach D. 1997. Acute physiological effects of zebra mussel (*Dreissena*  
354 *polymorpha*) infestation on two unionid mussels, *Actiononaias ligamentina* and *Amblema*  
355 *plicata*. *Canadian Journal of Fisheries and Aquatic Sciences* 54:512-519.
- 356 Berezina NA. 2007. Invasions of alien amphipods (Amphipoda: Gammaridea) in aquatic  
357 ecosystems of North-Western Russia: pathways and consequences. *Hydrobiologia*  
358 590:15-29.
- 359 Boets P, Lock K, Messiaen M, and Goethals PL. 2010. Combining data-driven methods and lab  
360 studies to analyse the ecology of *Dikerogammarus villosus*. *Ecological Informatics*  
361 5:133-139.
- 362 Boets P, Pauwels IS, Lock K, and Goethals PLM. 2014. Using an integrated modelling approach  
363 for risk assessment of the killer shrimp '*Dikerogammarus villosus*'. *River Research and*  
364 *Applications* 30:403-412. 10.1002/rra.2658
- 365 Carboneras C, Genovesi P, Vilà M, Blackburn TM, Carrete M, Clavero M, D'hondt B, Orueta JF,  
366 Gallardo B, and Gerales P. 2018. A prioritised list of invasive alien species to assist the  
367 effective implementation of EU legislation. *Journal of Applied Ecology* 55:539-547.
- 368 Consuegra S, Phillips N, Gajardo G, and Garcia de Leaniz C. 2011. Winning the invasion  
369 roulette: Escapes from fish farms increase admixture and facilitate establishment of  
370 non-native rainbow trout. *Evolutionary Applications* 4:660-671.
- 371 Cothran RD, Henderson KA, Schmidenberg D, and Relyea RA. 2013. Phenotypically similar but  
372 ecologically distinct: differences in competitive ability and predation risk among  
373 amphipods. *Oikos* 122:1429-1440.
- 374 Crall AW, Jarnevich CS, Panke B, Young N, Renz M, and Morisette J. 2013. Using habitat  
375 suitability models to target invasive plant species surveys. *Ecological Applications* 23:60-  
376 72.
- 377 Devin S, Piscart C, Beisel J-N, and Moreteau J. 2003. Ecological traits of the amphipod invader  
378 *Dikerogammarus villosus* on a mesohabitat scale. *Archiv für Hydrobiologie* 158:43-56.

- 379 Dick JT, and Elwood RW. 1990. Symmetrical assessment of female quality by male *Gammarus*  
380 *pulex* (Amphipoda) during struggles over precopula females. *Animal Behaviour* 40:877-  
381 883.
- 382 Dick JT, Montgomery I, and Elwood RW. 1993. Replacement of the indigenous amphipod  
383 *Gammarus duebeni celticus* by the introduced *G. pulex*: differential cannibalism and  
384 mutual predation. *Journal of Animal Ecology*:79-88.
- 385 Dick JT, and Platvoet D. 2000. Invading predatory crustacean *Dikerogammarus villosus*  
386 eliminates both native and exotic species. *Proceedings of the Royal Society of London*  
387 *Series B: Biological Sciences* 267:977-983.
- 388 Dick JT, Platvoet D, and Kelly DW. 2002. Predatory impact of the freshwater invader  
389 *Dikerogammarus villosus* (Crustacea: Amphipoda). *Canadian Journal of Fisheries and*  
390 *Aquatic Sciences* 59:1078-1084.
- 391 Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ,  
392 Prieur-Richard A-H, Soto D, and Stiassny ML. 2006. Freshwater biodiversity:  
393 importance, threats, status and conservation challenges. *Biological Reviews* 81:163-182.
- 394 Fahnenstiel GL, Bridgeman TB, Lang GA, McCormick MJ, and Nalepa TF. 1995a.  
395 Phytoplankton productivity in Saginaw Bay, Lake Huron: effects of zebra mussel  
396 (*Dreissena polymorpha*) colonization. *Journal of Great Lakes Research* 21:464-475.
- 397 Fahnenstiel GL, Lang GA, Nalepa TF, and Johengen TH. 1995b. Effects of zebra mussel  
398 (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake  
399 Huron. *Journal of Great Lakes Research* 21:435-448.
- 400 Gallardo B, and Aldridge DC. 2015. Is Great Britain heading for a Ponto–Caspian invasional  
401 meltdown? *Journal of Applied Ecology* 52:41-49.
- 402 Gallardo B, and Aldridge DC. 2018. Inter-basin water transfers and the expansion of aquatic  
403 invasive species. *Water Research* 143:282-291.
- 404 Gergs R, and Rothhaupt K-O. 2008a. Effects of zebra mussels on a native amphipod and the  
405 invasive *Dikerogammarus villosus*: the influence of biodeposition and structural  
406 complexity. *Journal of the North American Benthological Society* 27:541-548.
- 407 Gergs R, and Rothhaupt KO. 2008b. Feeding rates, assimilation efficiencies and growth of two  
408 amphipod species on biodeposited material from zebra mussels. *Freshwater Biology*  
409 53:2494-2503. 10.1111/j.1365-2427.2008.02077.x
- 410 Goulson D, and Derwent LC. 2004. Synergistic interactions between an exotic honeybee and an  
411 exotic weed: pollination of *Lantana camara* in Australia. *Weed Research* 44:195-202.
- 412 Grosholz ED. 2005. Recent biological invasion may hasten invasional meltdown by accelerating  
413 historical introductions. *Proceedings of the National Academy of Sciences* 102:1088-  
414 1091.
- 415 Hallberg E, and Skog M. 2011. Chemosensory sensilla in crustaceans. In: Breithaupt T, and  
416 Thiel M, eds. *Chemical Communication in Crustaceans*. New York, NY: Springer, 103 –  
417 121.
- 418 Hesselschwerdt J, Tscherner S, Necker J, and Wantzen KM. 2009. A local gammarid uses  
419 kairomones to avoid predation by the invasive crustaceans *Dikerogammarus villosus* and  
420 *Orconectes limosus*. *Biological Invasions* 11:2133.
- 421 Hohenadler M, Honka K, Emde S, Klimpel S, and Sures B. 2018. First evidence for a possible  
422 invasional meltdown among invasive fish parasites. *Scientific Reports* 8:15085.
- 423 Hunte W, and Myers R. 1984. Phototaxis and cannibalism in gammaridean amphipods. *Marine*  
424 *Biology* 81:75-79.

- 425 Jermacz Ł, Andrzejczak J, Arczyńska E, Zielska J, and Kobak J. 2017. An enemy of your enemy  
426 is your friend: Impact of predators on aggregation behavior of gammarids. *Ethology*  
427 123:627-639.
- 428 Jiménez-Valverde A, Peterson AT, Soberón J, Overton J, Aragón P, and Lobo JM. 2011. Use of  
429 niche models in invasive species risk assessments. *Biological Invasions* 13:2785-2797.
- 430 Johengen TH, Nalepa TF, Fahnenstiel GL, and Goudy G. 1995. Nutrient changes in Saginaw  
431 Bay, Lake Huron, after the establishment of the zebra mussel (*Dreissena polymorpha*).  
432 *Journal of Great Lakes Research* 21:449-464.
- 433 Kenderov LA. 2017. An invader along with an invader: an unusual record of a zebra mussel  
434 *Dreissena polymorpha* (Pallas, 1771) (Bivalvia) living phoretically on a killer shrimp  
435 *Dikerogammarus villosus* (Sowinsky, 1894) (Amphipoda). *Acta Zoologica Bulgarica*  
436 Suppl. 9:287-291.
- 437 Kinzler W, Kley A, Mayer G, Waloszek D, and Maier G. 2009. Mutual predation between and  
438 cannibalism within several freshwater gammarids: *Dikerogammarus villosus* versus one  
439 native and three invasives. *Aquatic Ecology* 43:457.
- 440 Kinzler W, and Maier G. 2003. Asymmetry in mutual predation: possible reason for the  
441 replacement of native gammarids by invasives. *Archiv für Hydrobiologie* 157:473-481.
- 442 Kinzler W, and Maier G. 2006. Selective predation by fish: a further reason for the decline of  
443 native gammarids in the presence of invasives? *Journal of Limnology* 65:27-34.
- 444 Kley A, Kinzler W, Schank Y, Mayer G, Waloszek D, and Maier G. 2009. Influence of substrate  
445 preference and complexity on co-existence of two non-native gammarideans (Crustacea:  
446 Amphipoda). *Aquatic Ecology* 43:1047-1059.
- 447 Kobak J, Jermacz Ł, and Dzierżyńska-Białończyk A. 2015. Substratum preferences of the  
448 invasive killer shrimp *Dikerogammarus villosus*. *Journal of Zoology* 297:66-76.  
449 10.1111/jzo.12252
- 450 Kroon FJ. 2005. Behavioural avoidance of acidified water by juveniles of four commercial fish  
451 and prawn species with migratory life stages. *Marine Ecology Progress Series* 285:193-  
452 204.
- 453 Laihonon P, and Furman E. 1986. The site of settlement indicates commensalism between  
454 bluemussel and its epibiont. *Oecologia* 71:38-40.
- 455 Levin PS, Coyer JA, Petrik R, and Good TP. 2002. Community-wide effects of nonindigenous  
456 species on temperate rocky reefs. *Ecology* 83:3182-3193.
- 457 Lovell SJ, Stone SF, and Fernandez L. 2006. The economic impacts of aquatic invasive species:  
458 a review of the literature. *Agricultural and Resource Economics Review* 35:195-208.
- 459 Lowe S, Browne M, Boudjelas S, and De Poorter M. 2000. *100 of the world's worst invasive*  
460 *alien species: a selection from the global invasive species database*: Invasive Species  
461 Specialist Group Auckland.
- 462 MacIsaac HJ. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of  
463 North America. *American Zoologist* 36:287-299.
- 464 MacNeil C, Dick JT, and Elwood RW. 1997. The trophic ecology of freshwater *Gammarus*  
465 spp.(Crustacea: Amphipoda): problems and perspectives concerning the functional  
466 feeding group concept. *Biological Reviews* 72:349-364.
- 467 MacNeil C, Platvoet D, Dick J, Fielding N, Constable A, Hall N, Aldridge D, Renals T, and  
468 Diamond M. 2010. The Ponto-Caspian 'killer shrimp', *Dikerogammarus villosus*  
469 (Sowinsky, 1894), invades the British Isles. *Aquatic Invasions* 5:441-445.  
470 10.3391/ai.2010.5.4.15

- 471 MacNeil C, Platvoet D, and Dick JT. 2008. Potential roles for differential body size and  
472 microhabitat complexity in mediating biotic interactions within invasive freshwater  
473 amphipod assemblages. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*  
474 172:175-182.
- 475 Marsden JE, and Lansky DM. 2000. Substrate selection by settling zebra mussels, *Dreissena*  
476 *polymorpha*, relative to material, texture, orientation, and sunlight. *Canadian Journal of*  
477 *Zoology* 78:787-793.
- 478 Mattson S, and Cedhagen T. 1989. Aspects of the behaviour and ecology of *Dyopedos*  
479 *monacanthus* (Metzger) and *D. porrectus* Bate, with comparative notes on *Dulichia*  
480 *tuberculata* Boeck (Crustacea: Amphipoda: Podoceridae). *Journal of Experimental*  
481 *Marine Biology and Ecology* 127:253-272.
- 482 Mayer C, Rudstam L, Mills E, Cardiff S, and Bloom C. 2001. Zebra mussels (*Dreissena*  
483 *polymorpha*), habitat alteration, and yellow perch (*Perca flavescens*) foraging: system-  
484 wide effects and behavioural mechanisms. *Canadian Journal of Fisheries and Aquatic*  
485 *Sciences* 58:2459-2467.
- 486 Morales NS, Fernández IC, and Baca-González V. 2017. MaxEnt's parameter configuration and  
487 small samples: are we paying attention to recommendations? A systematic review. *PeerJ*  
488 5:e3093. 10.7717/peerj.3093
- 489 Piscart C, Devin S, Beisel J-N, and Moreteau J-C. 2003. Growth-related life-history traits of an  
490 invasive gammarid species: evaluation with a Laird–Gompertz model. *Canadian Journal*  
491 *of Zoology* 81:2006-2014.
- 492 Platvoet D, Dick JTA, MacNeil C, van Riel MC, and van der Velde G. 2009. Invader–invader  
493 interactions in relation to environmental heterogeneity leads to zonation of two invasive  
494 amphipods, *Dikerogammarus villosus* (Sowinsky) and *Gammarus tigrinus* Sexton:  
495 amphipod pilot species project (AMPIS) report 6. *Biological Invasions* 11:2085-2093.
- 496 Réale D, Reader SM, Sol D, McDougall PT, and Dingemanse NJ. 2007. Integrating animal  
497 temperament within ecology and evolution. *Biological Reviews* 82:291-318.
- 498 Rewicz T, Grabowski M, MacNeil C, and Bacela-Spychalska K. 2014. The profile of a 'perfect'  
499 invader--the case of killer shrimp, *Dikerogammarus villosus*. *Aquatic Invasions* 9.
- 500 Rewicz T, Wattier R, Grabowski M, Rigaud T, and Bacela-Spychalska K. 2015. Out of the Black  
501 Sea: phylogeography of the invasive killer shrimp *Dikerogammarus villosus* across  
502 Europe. *PloS one* 10:e0118121. 10.1371/journal.pone.0118121
- 503 Rewicz T, Wattier R, Rigaud T, Grabowski M, Mamos T, and Bacela-Spychalska K. 2017. The  
504 killer shrimp, *Dikerogammarus villosus*, invading European Alpine Lakes: A single main  
505 source but independent founder events with an overall loss of genetic diversity.  
506 *Freshwater Biology* 62:1036-1051. 10.1111/fwb.12923
- 507 Ricciardi A. 2005. Facilitation and synergistic interactions between introduced aquatic species.  
508 In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, and Waage J, eds.  
509 *Invasive Alien Species: A New Synthesis*: Island Press, 162-178.
- 510 Ricciardi A, Whoriskey FG, and Rasmussen JB. 1997. The role of the zebra mussel (*Dreissena*  
511 *polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian*  
512 *Journal of Fisheries and Aquatic Sciences* 54:2596-2608.
- 513 Roy HE, Rabitsch W, Scalera R, Stewart A, Gallardo B, Genovesi P, Essl F, Adriaens T, Bacher  
514 S, and Booy O. 2018. Developing a framework of minimum standards for the risk  
515 assessment of alien species. *Journal of Applied Ecology* 55:526-538.

- 516 Sehr EK, and Gall BG. 2016. Responses of an aquatic isopod and amphipod to chemical alarm  
517 cues from damaged conspecifics. *Journal of Freshwater Ecology* 31:231-237.
- 518 Simberloff D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate  
519 metaphor, or both? *Ecol Lett* 9:912-919. 10.1111/j.1461-0248.2006.00939.x
- 520 Simberloff D, and Von Holle B. 1999. Positive interactions of nonindigenous species: invasional  
521 meltdown? *Biological Invasions* 1:21-32.
- 522 Skubinna JP, Coon TG, and Batterson TR. 1995. Increased abundance and depth of submersed  
523 macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. *Journal of*  
524 *Great Lakes Research* 21:476-488.
- 525 Son MO. 2007. Native range of the zebra mussel and quagga mussel and new data on their  
526 invasions within the Ponto-Caspian Region. *Aquatic Invasions* 2:174-184.
- 527 Sornom P, Gismondi E, Vellinger C, Devin S, Féraud J-F, and Beisel J-N. 2012. Effects of  
528 sublethal cadmium exposure on antipredator behavioural and antitoxic responses in the  
529 invasive amphipod *Dikerogammarus villosus*. *PloS one* 7:e42435.
- 530 Stewart TW, Miner JG, and Lowe RL. 1998a. Macroinvertebrate communities on hard substrates  
531 in western Lake Erie: structuring effects of *Dreissena*. *Journal of Great Lakes Research*  
532 24:868-879.
- 533 Stewart TW, Miner JG, and Lowe RL. 1998b. Quantifying mechanisms for zebra mussel effects  
534 on benthic macroinvertebrates: organic matter production and shell-generated habitat.  
535 *Journal of the North American Benthological Society* 17:81-94.
- 536 Strayer DL. 2012. Eight questions about invasions and ecosystem functioning. *Ecology Letters*  
537 15:1199-1210.
- 538 Thiel M. 2011. The evolution of sociality: peracarid crustaceans as model organisms. *New*  
539 *frontiers in crustacean biology*: Brill, 285-297.
- 540 Tricarico E, Mazza G, Orioli G, Rossano C, Scapini F, and Gherardi F. 2010. The killer shrimp,  
541 *Dikerogammarus villosus* (Sowinsky, 1894), is spreading in Italy. *Aquatic Invasions*  
542 5:211-214. 10.3391/ai.2010.5.2.14
- 543 Truhlar AM, and Aldridge DC. 2015. Differences in behavioural traits between two potentially  
544 invasive amphipods, *Dikerogammarus villosus* and *Gammarus pulex*. *Biological*  
545 *Invasions* 17:1569-1579.
- 546 van der Velde G, Rajagopal S, and bij de Vaate A. 2010. *The zebra mussel in Europe*: Backhuys  
547 Leiden/Margraf, Weikersheim.
- 548 Van Riel M, Van der Velde G, and Bij de Vaate A. 2009. Interference competition between alien  
549 invasive gammaridean species. *Biological Invasions* 11:2119.
- 550 Vanhaecke D, Garcia de Leaniz C, Gajardo G, Dunham J, Giannico G, and Consuegra S. 2015.  
551 Genetic signatures of historical dispersal of fish threatened by biological invasions: the  
552 case of galaxiids in South America. *Journal of Biogeography* 42:1942-1952.
- 553 Ward PI. 1985. The breeding behaviour of *Gammarus duebeni*. *Hydrobiologia* 121:45-50.
- 554 Woodward SA, Vitousek PM, Matson K, Hughes F, Benvenuto K, and Matson PA. 1990. Use of  
555 the exotic tree *Myrica faya* by native and exotic birds in Hawai'i Volcanoes National  
556 Park.
- 557 Wooster DE. 1998. Amphipod (*Gammarus minus*) responses to predators and predator impact on  
558 amphipod density. *Oecologia* 115:253-259.
- 559 Yohannes E, Ragg RB, Armbruster JP, and Rothhaupt K-O. 2017. Physical attachment of the  
560 invasive zebra mussel *Dreissena polymorpha* to the invasive gammarid *Dikerogammarus*

561 villosus: supplementary path for invasion and expansion? *Fundamental and Applied*  
562 *Limnology/Archiv für Hydrobiologie* 191:79-85.  
563 Young KA, Dunham JB, Stephenson JF, Terreau A, Thailly AF, Gajardo G, and Garcia de  
564 Leaniz C. 2010. A trial of two trouts: comparing the impacts of rainbow and brown trout  
565 on a native galaxiid. *Animal Conservation* 13:399-410.  
566 Young KA, Stephenson J, Terreau A, Thailly A-F, Gajardo G, and Garcia de Leaniz C. 2009.  
567 The diversity of juvenile salmonids does not affect their competitive impact on a native  
568 galaxiid. *Biological Invasions* 11:1955-1961.

569

570

571 **Figure legends**

572 Figure 1. Map showing the sampling point of (A) sympatric (Cardiff Bay) and (B) allopatric  
573 (Upper Mother Ditch) populations of zebra mussel and killer shrimp.

574

575 Figure 2. Experimental set up used to test (A) substrate preferences of killer shrimp, and (B)  
576 chemical attraction to water scented by zebra mussel

577

578 Figure 3. Proportion of killer shrimp (binomial 95 CI) settling in zebra mussel beds of different  
579 sizes in binary choice tests involving different amount of zebra mussel cover (0, 33, 66, and  
580 100% tank cover).

581

582 Figure 4. Proportion of killer shrimp (binomial 95 CI) settling in binary choice tests involving  
583 different substrates (live zebra mussel, empty shells of zebra mussel, artificial grass)

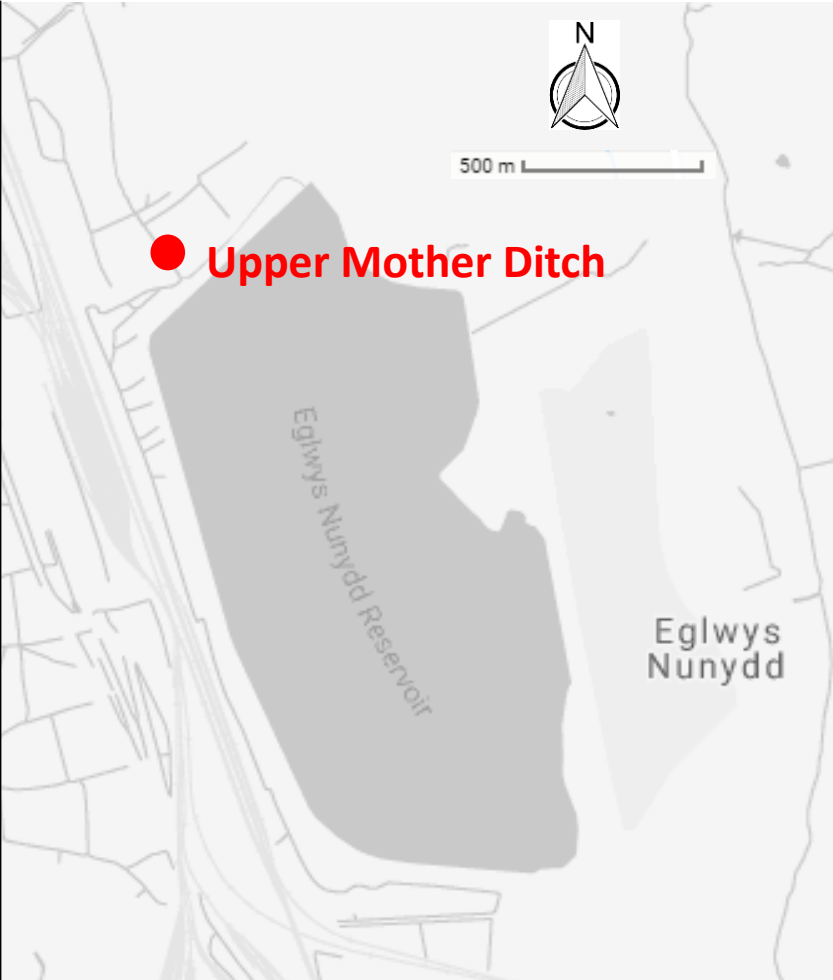
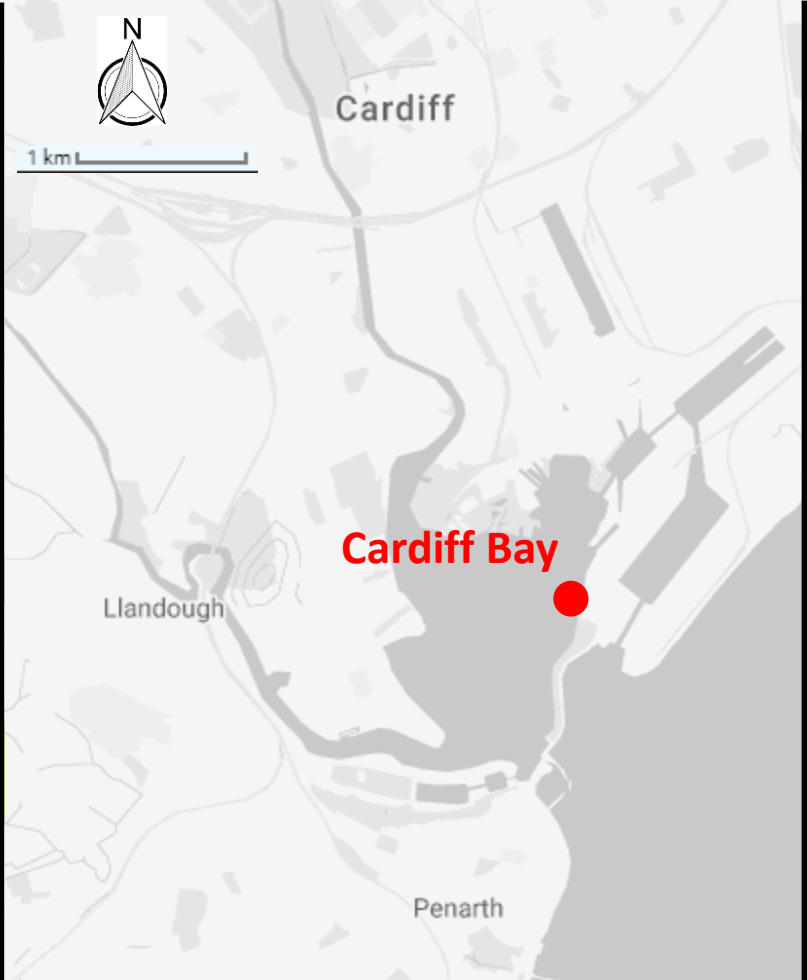
584

585 Figure 5. Preference by killer shrimp (mean time spent,  $s \pm 95$  CI) in water conditioned with  
586 different scents (blank water, tilapia scent, zebra mussel scent).

587

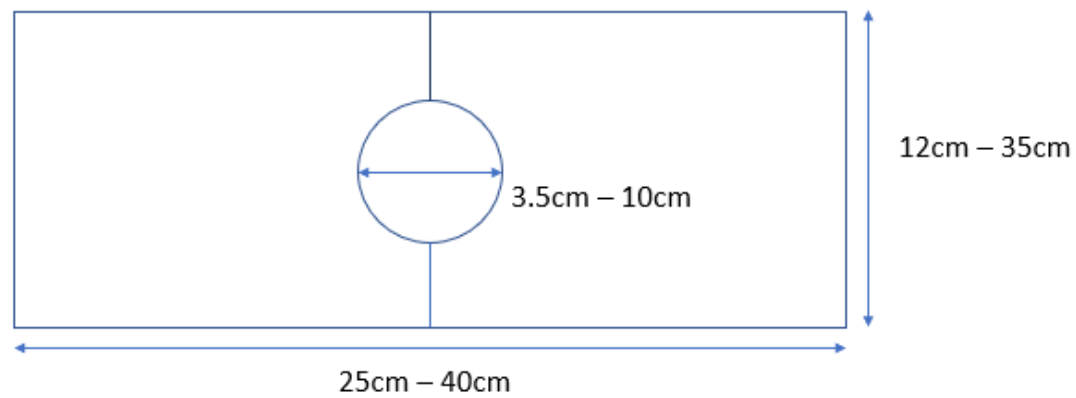
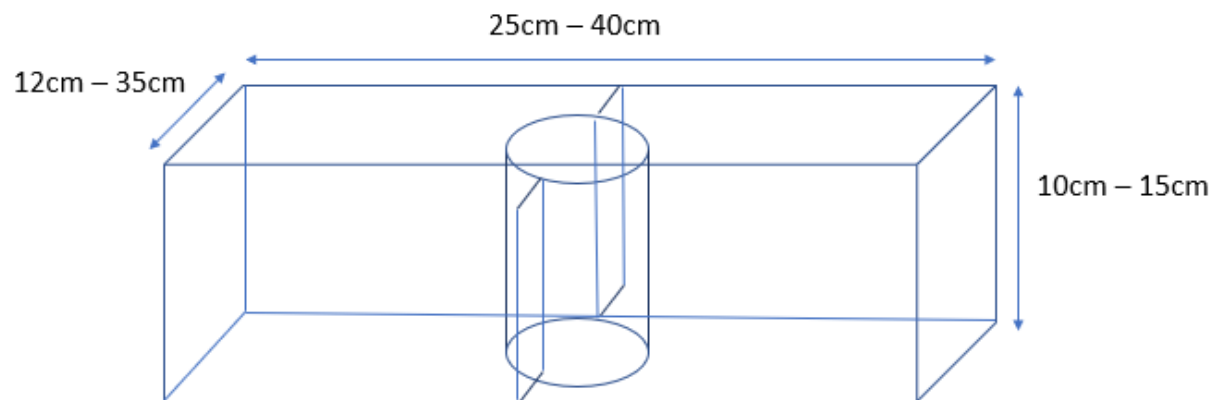
588 Figure 6. Activity (mean number of transitions  $\pm 95$  CI) of killer shrimp tested in water  
589 conditioned with different scents (blank water, tilapia scent, zebra mussel scent).

590

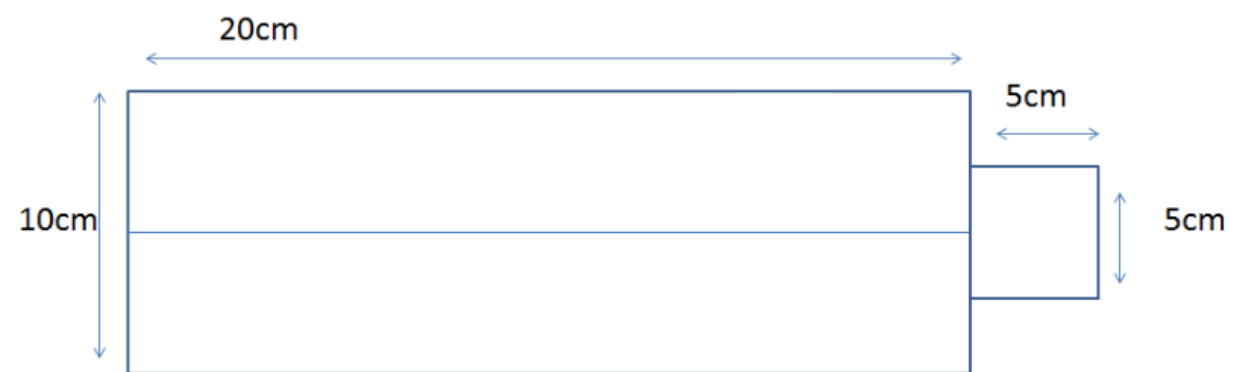
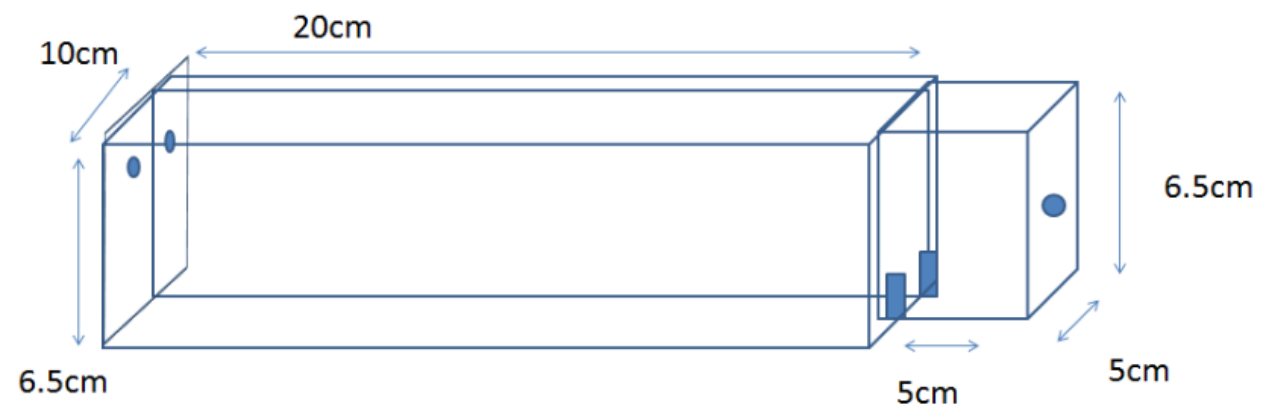




# 2A



# 2B

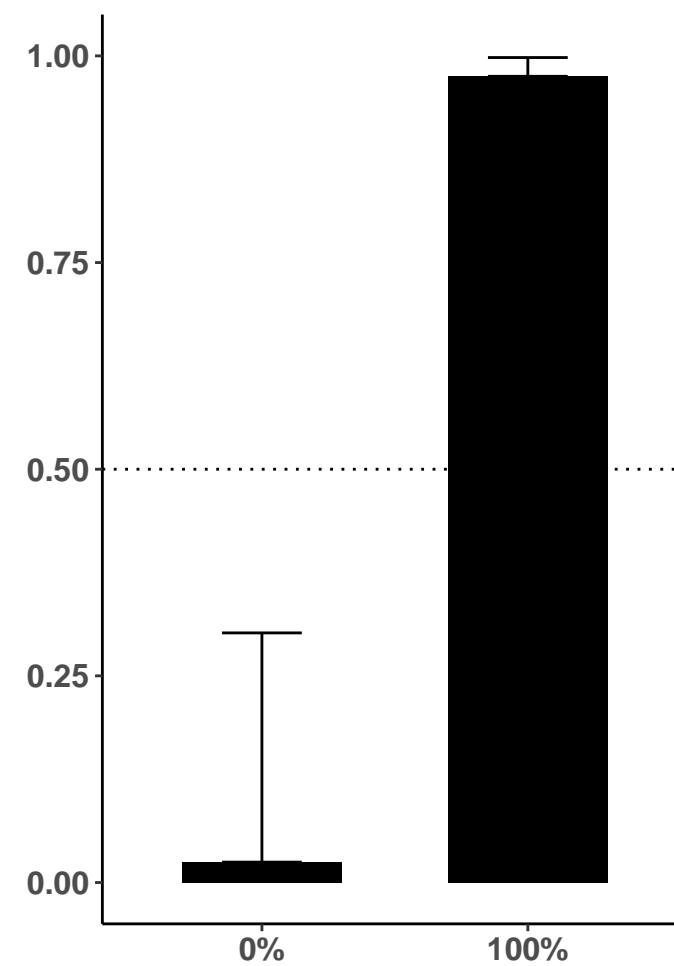
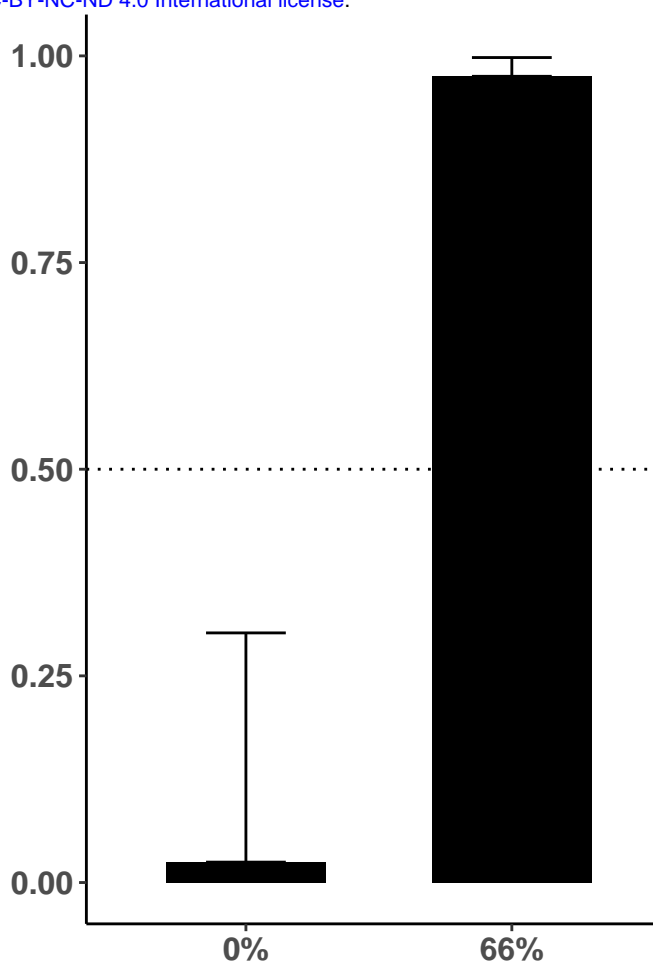
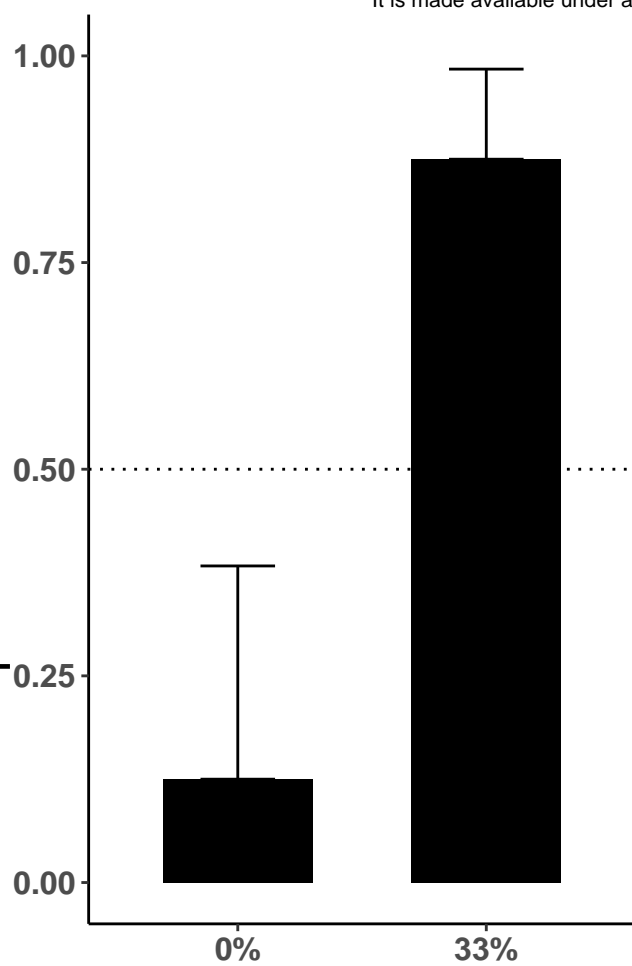


**A**

**B**

**C**

Proportion of individuals

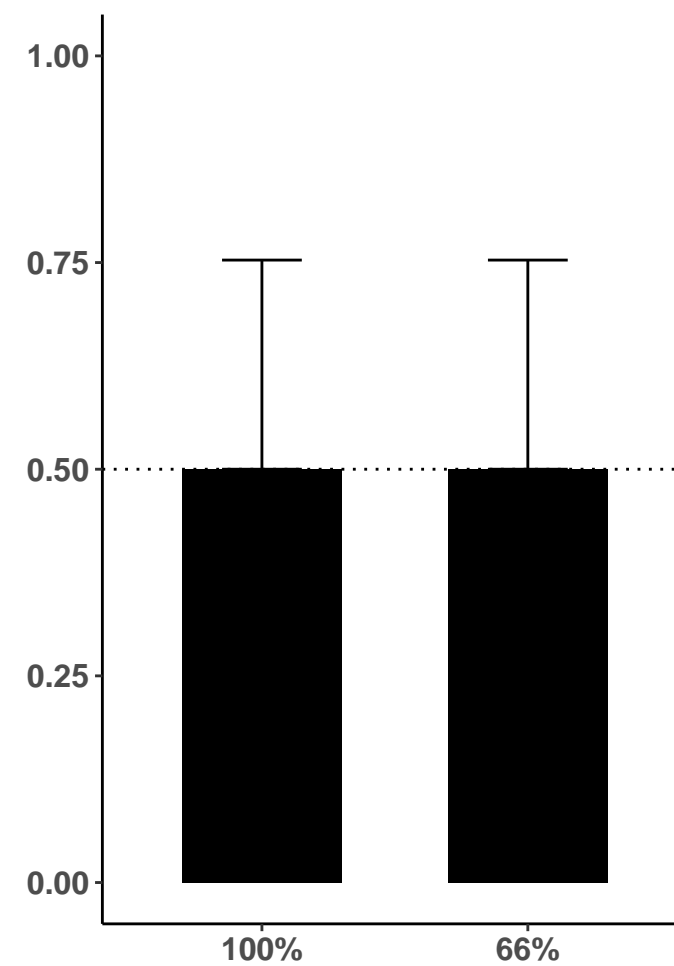
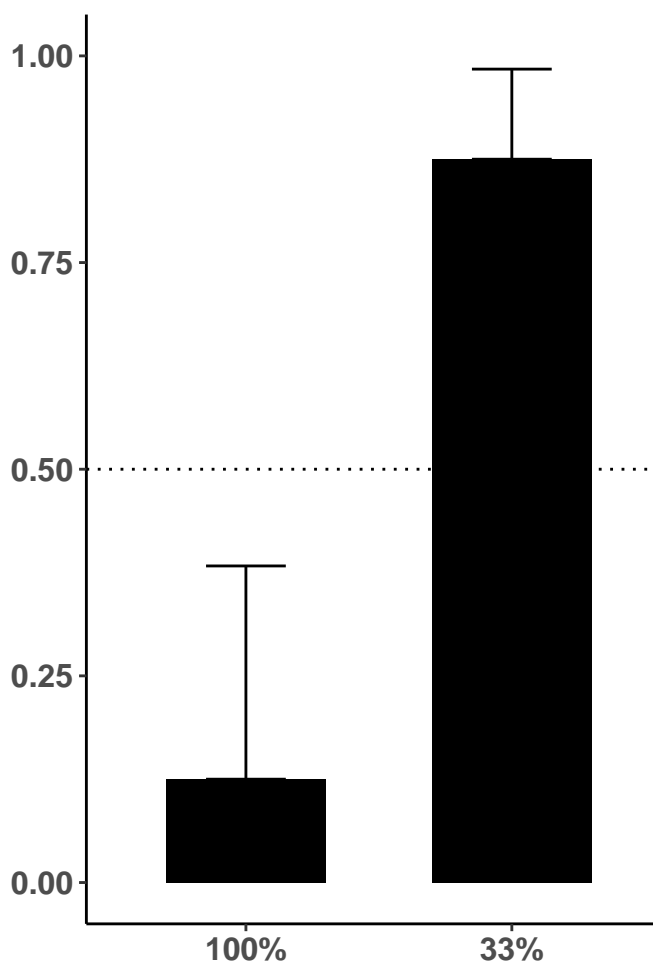
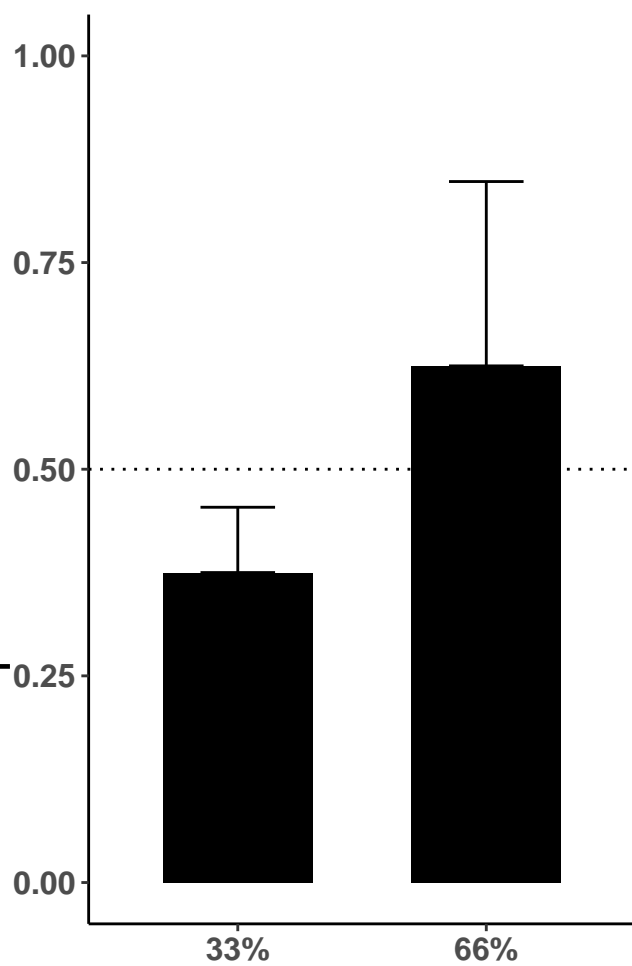


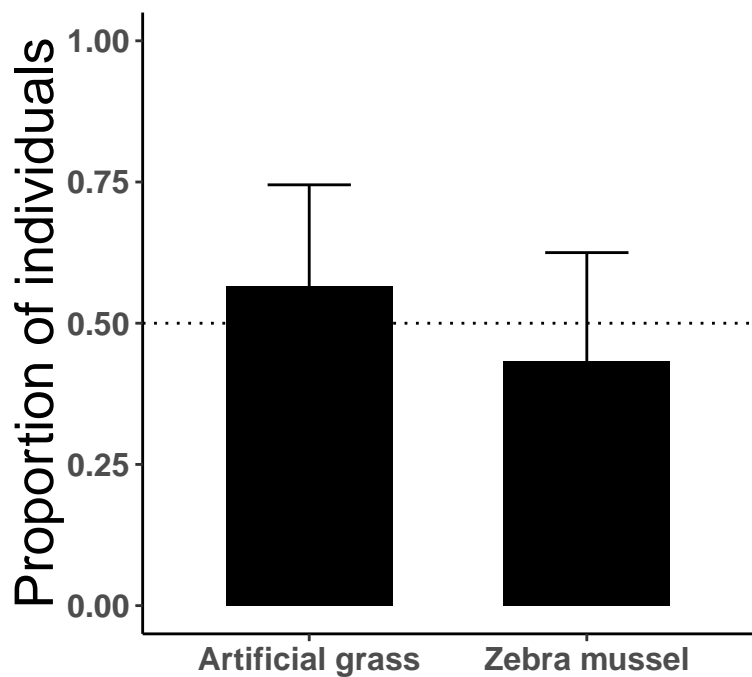
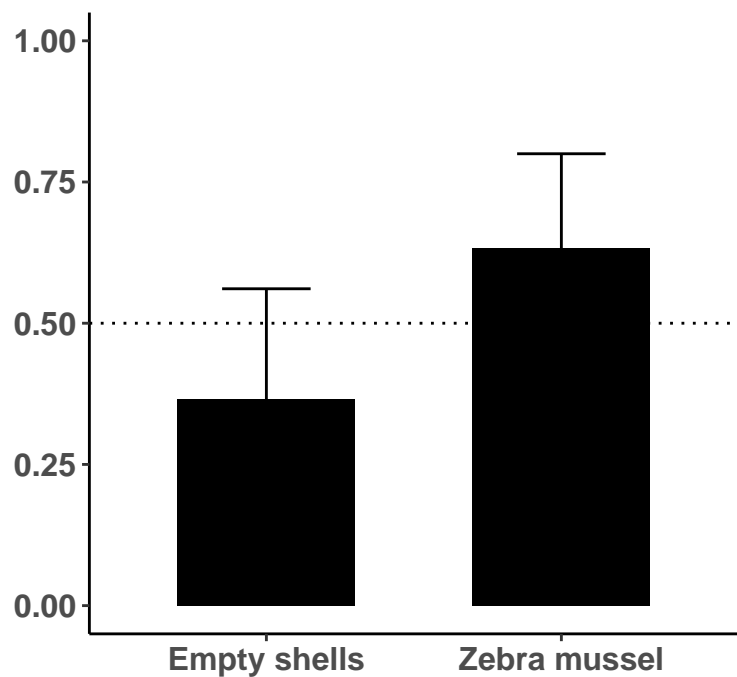
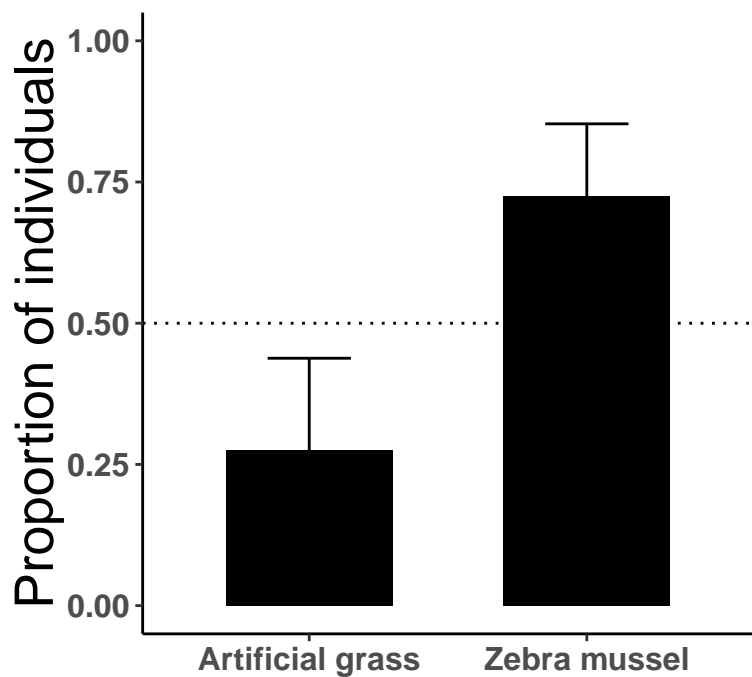
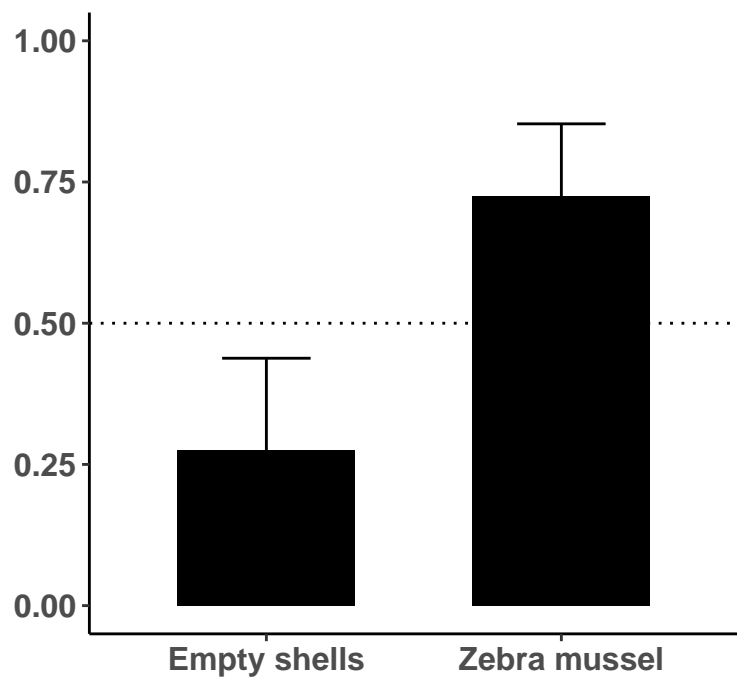
**D**

**E**

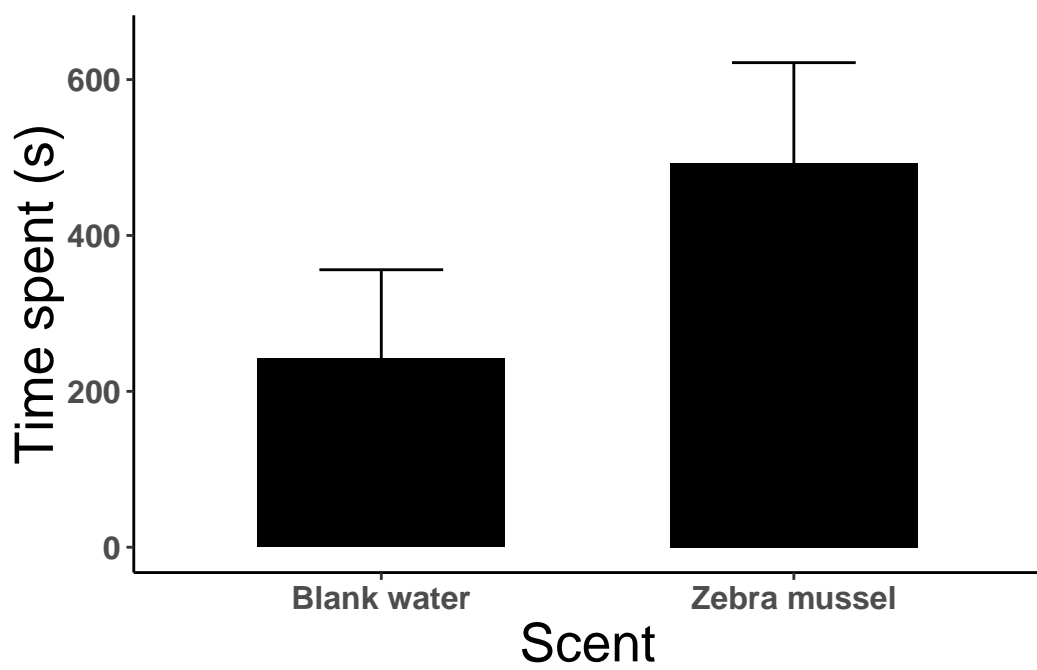
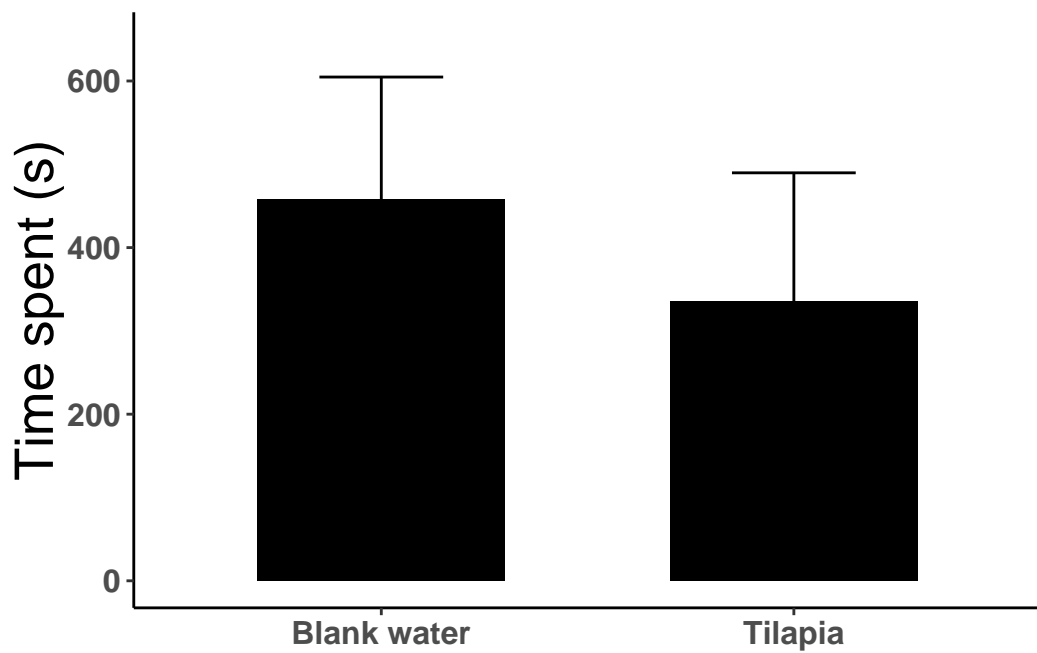
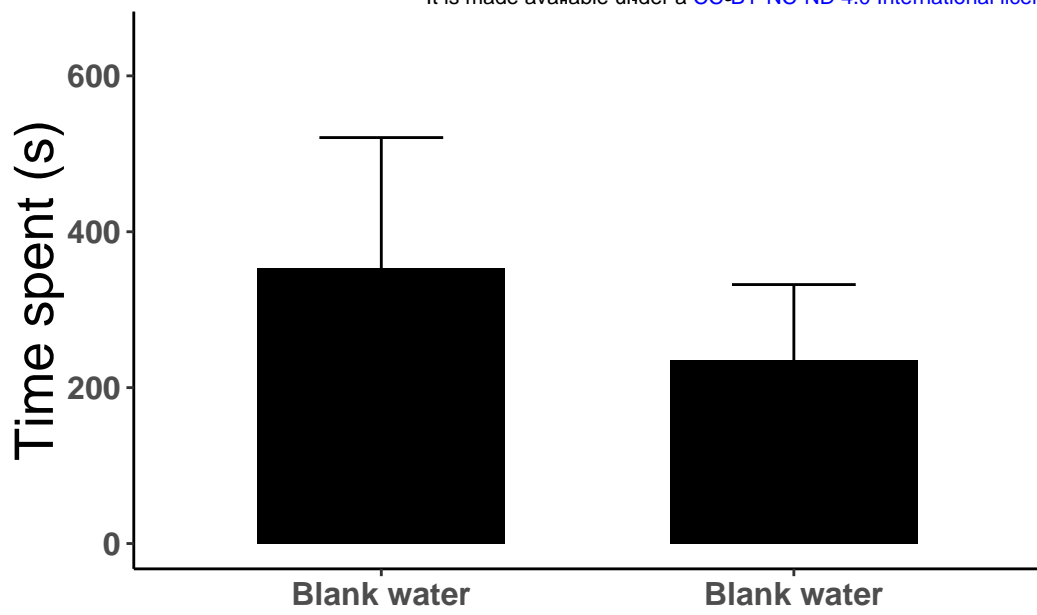
**F**

Proportion of individuals

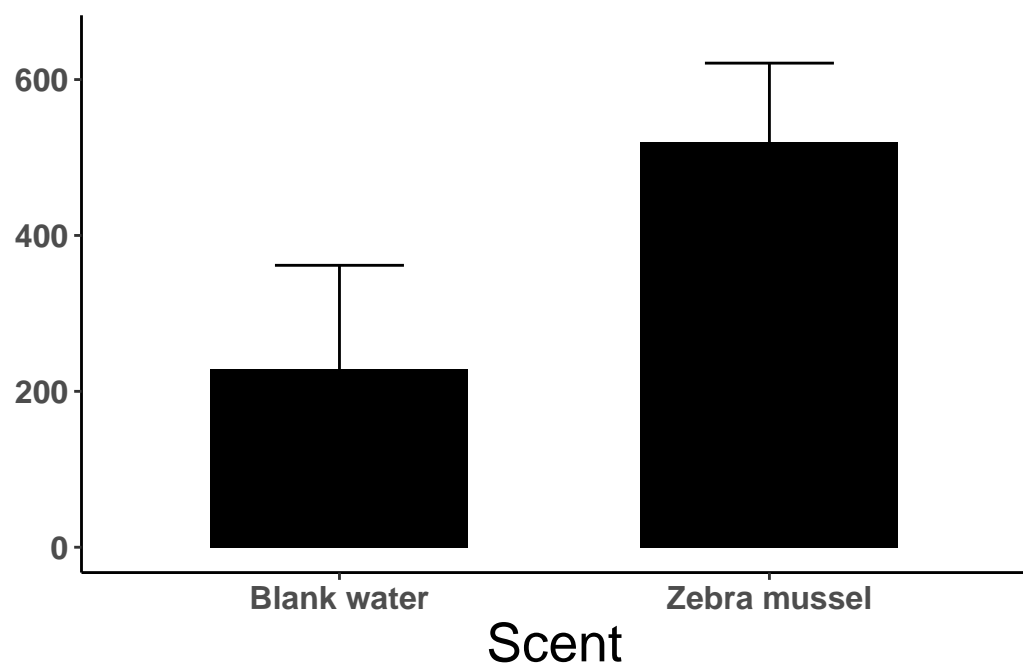
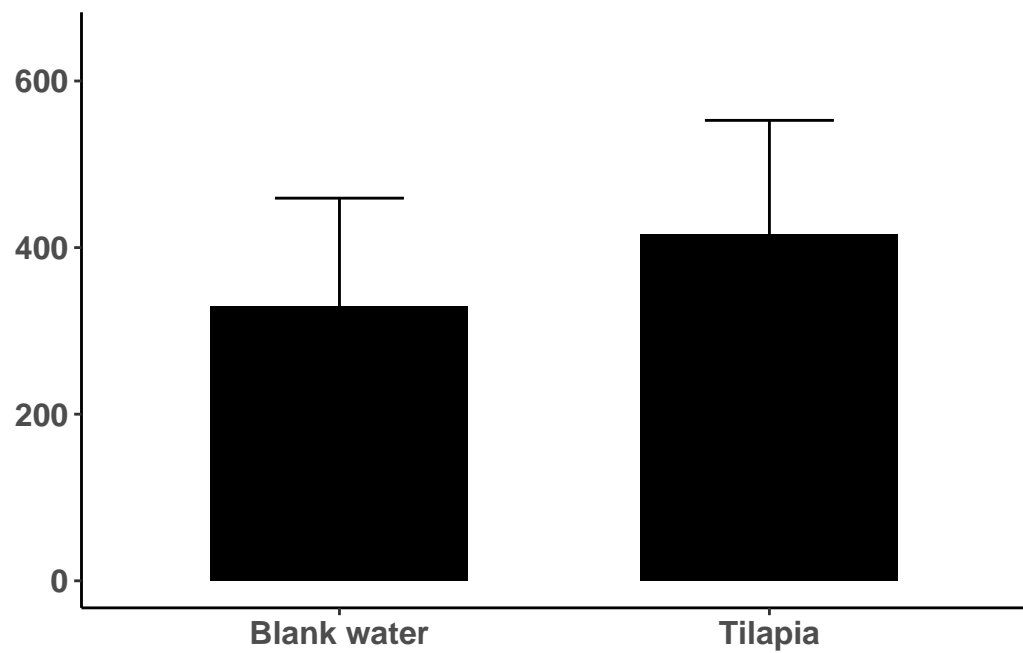
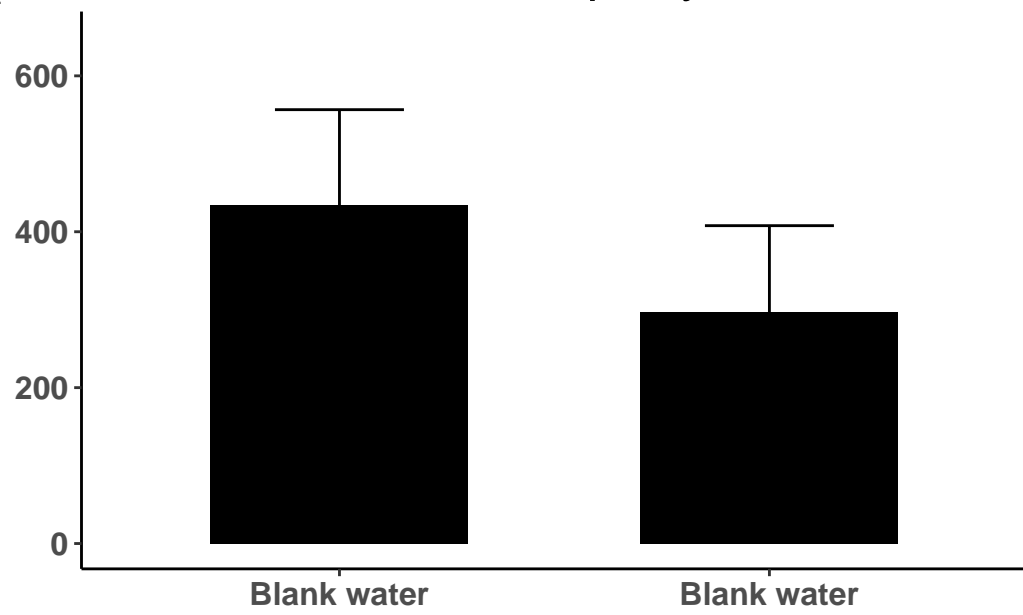


**A****B****C****D**

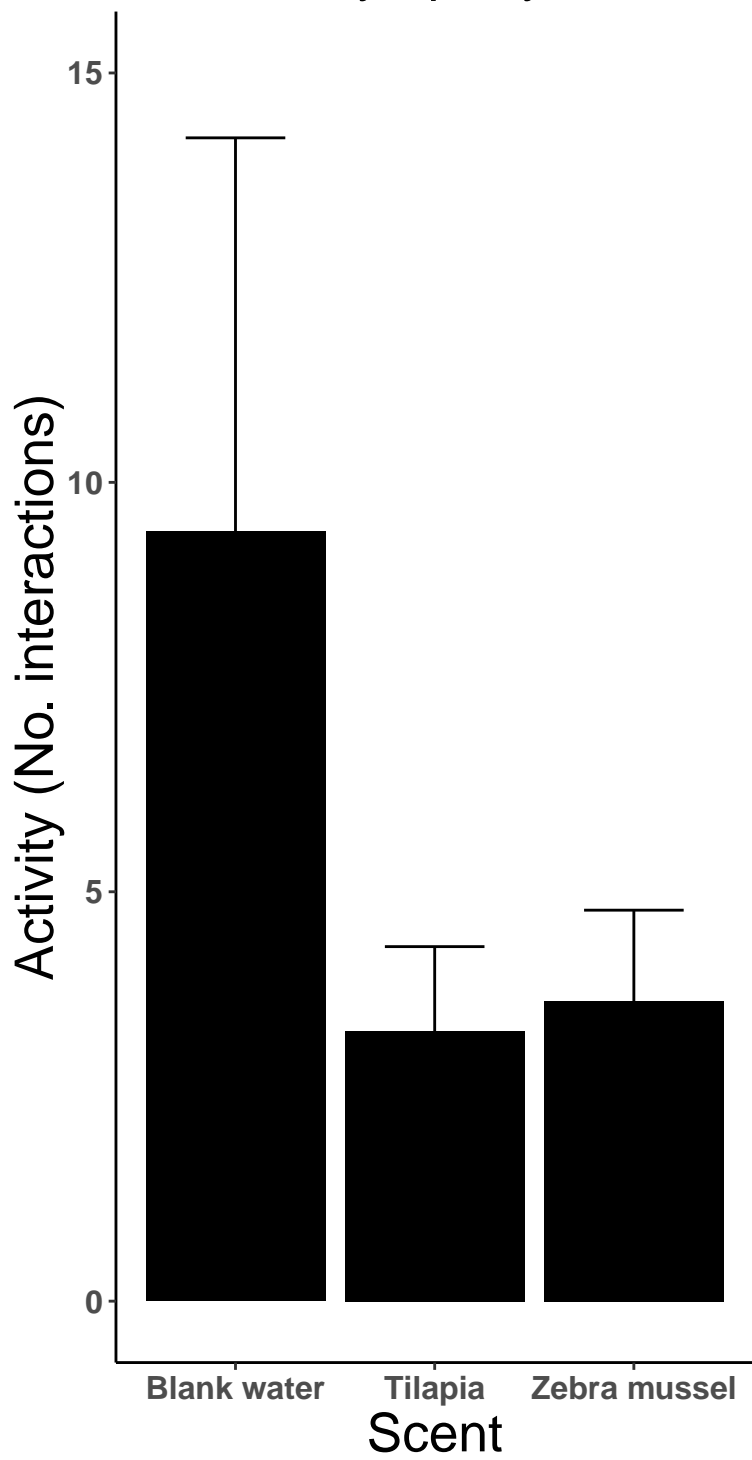
## A – Sympatry



## B – Allopatry



## Sympatry



## Allopatry

