

8 ABSTRACT: Sessile invertebrate prey that detect waterborne predator cues often respond by
9 strengthening their structural defenses. Experimental evidence of the functional significance of
10 such modifications using field-raised organisms is lacking. This study addresses that gap using
11 intertidal mussels and predatory dogwhelks from Atlantic Canada. During the spring and
12 summer of 2016, we ran a field experiment that manipulated dogwhelk presence to test their
13 nonconsumptive effects on mussel traits. Dogwhelk cues elicited thickening at the lip, centre,
14 and base of mussel shells, although simultaneously limiting shell growth in length. As shell mass
15 was unaffected by dogwhelk presence, a trade-off between shell thickening and elongation was
16 revealed. Thickening was strongest at the thinnest parts of the shell. Using the field-raised
17 organisms, a lab experiment found that dogwhelks took, on average, 55 % longer to drill and
18 consume mussels previously exposed to dogwhelk cues than mussels grown without such a cue
19 exposure. Dogwhelks drilled at the thinnest parts of the shell but, nonetheless, the consumed
20 cue-exposed mussels had thicker shells at the borehole than the consumed mussels not exposed
21 to cues, which likely explains the observed difference in handling time. As handling time
22 normally decreases predation success, this study indicates that the plastic structural modifications
23 in mussels triggered by dogwhelk cues in the field hinder predation by these drilling predators.

24 KEY WORDS: Dogwhelk · Intertidal · Mussel · *Mytilus* · Nonconsumptive predator effect ·
25 *Nucella* · Phenotypic plasticity

26

26 **INTRODUCTION**

27 Nonconsumptive effects (NCEs) of predators on prey mediated by chemical cues are
28 ubiquitous in aquatic systems (Ferrari et al. 2010, Brönmark & Hansson 2012). For example,
29 when aquatic prey detect waterborne predator cues, short-term responses often include
30 behavioural changes such as moving away or reducing feeding activities to decrease predation
31 risk (Keppel & Scrosati 2004, Molis et al. 2011). Longer-term responses include the
32 phenotypically plastic strengthening of morphological defenses, especially in prey with little or
33 no escape capabilities, such as slow-moving and sessile species (Leonard et al. 1999, Nakaoka
34 2000, Freeman & Byers 2006). Predator NCEs may ultimately influence prey demography
35 (Ellrich et al. 2015) and, indirectly, the abundance of other species in the community (Weissburg
36 et al. 2014, Matassa et al. 2016). Thus, NCE research has become an important part of ecology.
37 The present contribution investigates the functional significance of structural changes in sessile
38 prey that are triggered by waterborne predator cues.

39 Morphological changes in shell-bearing invertebrate prey can be induced by waterborne
40 cues from predatory snails, crabs, and sea stars (Reimer & Tedengren 1996, Smith & Jennings
41 2000, Cheung et al. 2004, Freeman 2007, Newell et al. 2007, Lord & Whitlatch 2012, Lowen et
42 al. 2013, Robinson et al. 2014, Babarro et al. 2016). For some cases, experimental evidence
43 indicates that such modifications increase the resistance to predation (Boulding 1984, Norberg &
44 Tedengren 1995, Reimer & Tedengren 1996, Freeman 2007, Newell et al. 2007, Robinson et al.
45 2014). Mussels have been useful model systems in this regard. For example, when exposed to
46 cues from sea stars, mussels develop thicker and more rounded shells, stronger adductor muscles,
47 and more byssal threads (Côté 1995, Reimer & Tedengren 1997, Leonard et al. 1999, Reimer &
48 Harms-Ringdahl 2001, Freeman & Byers 2006, Freeman 2007, Shin et al. 2009, Lowen et al.

49 2013). Live-feeding experiments have shown that those responses improve mussel survival and
50 increase the time and energy required for sea stars to pry open mussels (Norberg & Tedengren
51 1995, Reimer & Tedengren 1996, 1997, Freeman 2007, Lowen et al. 2013). When exposed to
52 crab cues, mussels increase shell thickness –sometimes at the expense of shell elongation–
53 (Leonard et al. 1999, Caro & Castilla 2004, Cheung et al. 2004, Freeman & Byers 2006,
54 Freeman 2007, Shin et al. 2009, Lowen et al. 2013, Naddafi & Rudstam 2014) and reinforce
55 attachment to the substrate (Wang et al. 2010, Lowen et al. 2013). Shell thickening increases the
56 handling time and force required for crabs to crush and consume a mussel (Boulding 1984,
57 Leonard et al. 1999, Freeman 2007).

58 Drilling predators, such as many snail species, are also common predators of mussels
59 worldwide. When exposed to cues from such predators, mussels also respond by thickening their
60 shells (Smith & Jennings 2000, Cheung et al. 2004, Freeman 2007, Babarro et al. 2016).
61 However, whether such modifications improve the ability of mussels to cope with drilling
62 predators has not been experimentally evaluated as yet. Moreover, the studies that have shown
63 that predator-induced morphological plasticity in bivalves hampers predation were done using
64 lab-reared organisms, which is a less realistic approach than using organisms raised under natural
65 conditions (Weissburg et al. 2014). To address these knowledge gaps, we conducted experiments
66 using intertidal mussels and dogwhelks from Atlantic Canada. First, we tested the hypothesis
67 that, in the presence of waterborne dogwhelk cues in the field, mussels would thicken their shells
68 but grow less in length. Then, assuming the predicted shell thickening, we tested the hypothesis
69 that the handling time required by dogwhelks to prey upon mussels would be higher when
70 consuming mussels that were previously exposed to dogwhelk cues in the field.

71

71 **MATERIALS AND METHODS**

72 **Effects of dogwhelk cues on mussel traits**

73 To evaluate the effects of dogwhelk cues on mussel traits, we did a field experiment in
74 rocky intertidal habitats from Deming Island (between 45° 12' 41" N, 61° 10' 50" W and 45° 12'
75 45" N, 61° 10' 26" W), Nova Scotia, Canada, during the spring and summer of 2016. The
76 substrate of the studied habitats is stable bedrock. Maximum water velocity measured with
77 dynamometers (Bell & Denny 1994) in these habitats was $6.0 \pm 0.4 \text{ m s}^{-1}$ (mean \pm SE, $n = 24$),
78 indicating that wave exposure was moderate, as values can reach 12 m s^{-1} at exposed sites in
79 Nova Scotia (Hunt & Scheibling 2001). Intertidal temperature measured every 30 min during the
80 study period with Hobo Pendant loggers (Onset Computer Corp., Pocasset, MA, USA) attached
81 to the substrate was $14.2 \pm 0.1 \text{ }^\circ\text{C}$ ($n = 9$ loggers). Seawater salinity measured with a handheld
82 RF20 refractometer (Extech Instruments, Boston, MA, USA) was 35 ‰. We used *Nucella*
83 *lapillus*, which is the only local intertidal dogwhelk (Scrosati & Heaven 2007), and *Mytilus*
84 *edulis* and *M. trossulus*, which are the two local intertidal mussels and an important prey item for
85 dogwhelks (Largen 1967). It is highly difficult to visually identify both mussels because of
86 morphological similarities. However, recent genetic studies have revealed that *M. trossulus*
87 predominates over *M. edulis* in moderately exposed habitats on this coast (Tam & Scrosati
88 2014). Thus, given that we collected mussels at random for this study, our samples likely
89 exhibited a predominance of *M. trossulus* over *M. edulis*.

90 We evaluated dogwhelk cue effects on mussel traits by manipulating dogwhelk presence in
91 cages attached to the intertidal substrate. Each cage (Fig. 1) was made of a PVC ring (25 cm in
92 diameter and 2.5 cm tall) and plastic mesh (0.5 cm x 0.5 cm of opening size). Each cage was
93 divided by mesh into a central compartment (12 cm x 12 cm) and a peripheral compartment (area

94 = 347 cm²). We used the peripheral compartment to create two dogwhelk treatments: either 10
95 enclosed dogwhelks (2.23 ± 0.02 cm long, $n = 104$) or none. The used dogwhelk density (ca. 3
96 individuals dm⁻²) was representative of the studied coast (Ellrich & Scrosati 2016). The central
97 compartment of each cage contained a conical mesh compartment (6 cm in base diameter and 2.5
98 cm tall) that enclosed two mussels (1.86 ± 0.01 cm, $n = 120$) and, left to attach freely around the
99 conical compartment, 18 mussels (3.5 ± 0.1 cm long, $n = 30$) to simulate a natural mussel patch.
100 One of the two mussels in the conical compartment was eventually used to take the growth
101 measurements, while the other mussel was used for the lab experiment on handling time
102 described below. The size of the enclosed mussels is favourable for dogwhelk predation (Hughes
103 & Dunkin 1984), which suggested that it was also suitable to detect NCEs. The cages were
104 attached to the substrate with screws and PVC tiles, previously removing seaweeds and
105 invertebrates to prevent potential influences (Beermann et al. 2013). Any dogwhelks found near
106 the cages during the experiment were also periodically removed.

107 The experiment was arranged as a randomized complete block design with replicated
108 treatments within blocks (Quinn & Keough 2002). We established 15 blocks at an intertidal
109 elevation of 0.99 ± 0.04 m above chart datum, or lowest normal tide (the tidal range is 1.8 m).
110 Each block included two replicates of each of the two dogwhelk treatments, thus yielding a total
111 of 60 cages (30 cages per dogwhelk treatment). We started the experiment on 6 June 2016.
112 During the experiment, we did not feed the caged dogwhelks but, to prevent their starvation, we
113 replaced them every 10 days with mussel-fed dogwhelks kept in separate cages nearby. We used
114 mussel-fed dogwhelks to elicit strong responses in the experimental mussels, as prey often reacts
115 most strongly to cues from predators fed conspecific prey (Hagen et al. 2002, Schoeppner &

116 Relyea 2005, Weissburg & Beauvais 2015). We ended the experiment on 16 August 2016, time
117 at which we transported the mussels from the conical mesh compartments to the laboratory.

118 In the laboratory, we randomly selected one of the two mussels from each conical
119 compartment for measurements. For each selected mussel, we measured shell length to the
120 nearest 0.01 mm using a digital vernier caliper. Since we had also measured shell length at the
121 beginning of the experiment (marking one of the two mussels in each conical compartment with
122 nail polish for later identification), we measured relative length increment as $[(L_f - L_i)/L_i]$, where
123 L_f was final length and L_i was initial length. Using a vernier caliper modified with metal
124 extensions attached to the tip of each caliper jaw, we also measured shell thickness at the lip
125 (1 mm from the apex), centre, and base (1 mm from the base) of the right valve (looking from a
126 dorsal view) of each mussel. Then, we dried the mussels at 50 °C for 72 hours. After that, we
127 separated the soft tissues from the shells and measured shell mass and soft tissue dry mass to the
128 nearest 0.1 mg.

129 **Effects of mussel shell thickness on dogwhelk handling time**

130 To evaluate the effects of mussel shell thickness on dogwhelk handling time, we did a lab
131 experiment based on the finding (see Results) that shells thickened in the presence of dogwhelk
132 cues in the field. For the lab experiment, we used from each conical compartment the mussel that
133 was not used for the measurements described above. Because some mussels died during the field
134 experiment, we used 26 mussels from the dogwhelk-presence treatment and 22 mussels from the
135 no-dogwhelk treatment. We started the lab experiment on 17 August 2016, having kept the
136 mussels overnight since collected from the field in a culture room at 17 °C (water temperature on
137 the studied coast in August). We placed each of the 48 mussels in a separate container with 250
138 ml of seawater. We then secured with epoxy glue the left valve of each mussel to a PVC tile at

139 the bottom of each container, leaving the right valve facing upwards, exposed to predation. We
140 selected the right valve because whelks bore the right valve more often than the left (Alexander
141 et al. 2015). We allowed the glue to harden overnight and, then, we placed one dogwhelk ($2.22 \pm$
142 0.01 cm long, $n = 48$) in each container. The dogwhelks had been previously starved for 10 days
143 to standardize starvation level, which could have otherwise affected their feeding rate (Hughes &
144 Drewett 1985, Bayne & Scullard 1978). We attached a GoPro Hero4 Black camera (GoPro, San
145 Mateo, CA, USA) to the ceiling of the culture room to take pictures of the entire set of containers
146 every 30 sec. We checked the containers every two hours and changed their seawater (collected
147 on the studied coast) daily using a pipette to minimize disturbance. We ran the experiment for 18
148 days until 3 September 2016, although no dogwhelks fed after the thirteenth day. We measured
149 handling time from the moment when a dogwhelk mounted its prey to the moment when the
150 dogwhelk moved away from the formed borehole (or, in one case, when the mussel shell was
151 empty – see Results). To confirm that shell thickening was higher in the consumed cue-exposed
152 mussels than in the consumed mussels not exposed to cues, we measured shell thickness around
153 the borehole of each consumed mussel. Finally, to evaluate if dogwhelks bore into a shell at
154 points of reduced thickness, for each consumed mussel we also measured shell thickness at five
155 intact random points on the shell.

156 **Data analyses**

157 We tested the effects of dogwhelk cues (fixed factor with two levels: dogwhelk presence
158 and absence) on shell thickness at the lip, centre, and base of mussel shells, on mussel relative
159 length increment, on mussel shell mass, and on mussel soft tissue dry mass through separate
160 analyses of variance (ANOVAs) appropriate for a randomized complete block design with
161 replicated treatments within blocks (random factor with 15 levels). The assumptions of normality

162 and homoscedasticity were tested for each variable with the Kolmogorov-Smirnov test and
163 Cochran's *C*-test, respectively (Quinn & Keough 2002). Such assumptions were met using the
164 raw data for relative length increment, shell mass, and thickness at the centre of the shell, and
165 using square-root-transformed data for thickness at the lip and base of the shell and soft tissue
166 dry mass. We compared dogwhelk handling time and mussel shell thickness at the borehole
167 between cue-exposed mussels and mussels without a previous cue exposure through
168 independent-samples *t*-tests. Separately for each cue treatment, we compared shell thickness
169 between the borehole area and intact shell areas (mean of the five measurements per mussel)
170 through a paired-samples *t*-test. We did these analyses with STATISTICA 12.5 (Statsoft, Tulsa,
171 OK, USA).

172 **RESULTS**

173 At the intertidal zone, waterborne dogwhelk cues elicited an increase in the thickness of the
174 lip, centre, and base of mussel shells but a slower growth in terms of length (Table 1, Fig. 2).
175 Relative to the no-cue treatment, mean thickness in the presence of cues increased more (87 %)
176 in thinner areas of the shell (lip) than in thicker areas (32 % increase at the shell centre and 47 %
177 at the shell base; Fig. 2). Neither the mass of mussel shells nor the dry mass of mussel soft
178 tissues was affected by dogwhelk cues (Table 1, Fig. 2). The blocks factor was only significant
179 in one case (relative length increment, Table 1), but that result merely indicates that relative
180 length increment varied among blocks. The important result is that the interaction between the
181 dogwhelks factor and the blocks factor was not significant for any case, indicating that the
182 presence or absence of NCEs, depending on the case as described above, was spatially
183 consistent.

184 In the lab experiment, 16 dogwhelks consumed their provided mussel by drilling a hole in
185 the mussel's shell. One dogwhelk waited for its mussel to gape to then insert its proboscis
186 through the opening, while the remaining tested dogwhelks made no apparent attempt to feed.
187 The drilling dogwhelks needed a longer handling time to consume mussels previously exposed to
188 dogwhelk cues compared with mussels without a cue exposure ($t_{12} = 1.91$, $p = 0.040$; Fig. 3).
189 Data for two drilling dogwhelks could not be used for that t -test because such dogwhelks started
190 to handle their respective mussel during a short initial period when the camera did not record
191 images. Handling time was accurately calculated for all of the other dogwhelks. Shell thickness
192 at the borehole was higher in mussels previously exposed to dogwhelk cues than in mussels
193 without a previous cue exposure ($t_{14} = 5.02$, $p < 0.001$; Fig. 3). Shell thickness at the borehole
194 was lower than at intact parts of the shell regardless of previous cue exposure ($t_8 = 5.50$, $p <$
195 0.001 for cue-exposed mussels and $t_6 = 4.89$, $p = 0.003$ for mussels not previously exposed to
196 cues; Fig. 3). Six mussels released gametes to the water soon after a dogwhelk was introduced in
197 the container.

198 DISCUSSION

199 The present study has revealed that mussels in natural environments respond to dogwhelk
200 cues by thickening their shells, although simultaneously limiting linear shell growth. Since the
201 mass of mussel shells was not affected by dogwhelk presence, a trade-off between shell
202 thickening and elongation was identified. Such a plastic trade-off has been observed for mussels
203 in general in response to crab cues (Reimer & Tedengren 1997, Leonard et al. 1999, Freeman
204 2007, Shin et al. 2009, Lowen et al. 2013, Naddafi & Rudstrom 2014) and cues from other
205 whelks (Smith & Jennings 2000, Freeman 2007). For other bivalves (i.e., oysters), changes in
206 shell thickness come at a cost to soft tissue growth (Robinson et al. 2014). However, there has

207 been no indication of such a trade-off for mussels (Reimer & Tedengren 1997, Cheung et al.
208 2004, Babarro et al. 2016) and the lack of dogwhelk effects on mussel soft tissue mass in our
209 study supports that notion. Besides their NCEs on mussel shells, dogwhelks also triggered short-
210 term responses, as some mussels exhibited a broadcast reproductive response to direct predatory
211 threat in the lab experiment. Such a response may have been a last attempt by mussels to spawn,
212 which aligns with findings that *Mytilus edulis* reacts to predator cues by escalating short-term
213 investments in reproductive output (Reimer 1999).

214 This study also confirms that induced shell thickening in mussels occurs throughout the
215 entire shell (Leonard et al. 1999) and it shows for the first time that thickening varies across the
216 shell. Thickening resulting from exposure to dogwhelk cues was most pronounced in thinner
217 areas of the shell, which are potentially most vulnerable to drilling by predators. Despite the
218 overall thickening of mussel shells, however, dogwhelks were still able to find the thinnest part
219 to drill, as shell thickness at the borehole was lower than at intact parts of the shell.

220 The functional significance of the plastic response in mussels observed in the field was
221 revealed by the lab experiment as, on average, dogwhelks took 55 % longer to handle to full
222 consumption mussels that had been exposed to dogwhelk cues and, hence, had thicker shells.
223 These results show for the first time that predator-induced shell thickening in mussels hinders the
224 feeding of drilling predators. Induced morphological defenses in mussels also increase handling
225 time for predatory crabs (Boulding 1984, Reimer & Tedengren 1997, Freeman 2007) and sea
226 stars (Norberg & Tedengren 1995, Freeman 2007). However, comparable proportional increases
227 in handling time may be more detrimental for dogwhelks. The regular handling time required for
228 dogwhelks to drill into mussels is considerably longer than for crabs and sea stars to crush or pry
229 open a mussel (Freeman 2007, Miller 2013). Thus, a similar proportional increase in handling

230 time would expose dogwhelks considerably longer than those predators to desiccation stress
231 (Hughes & Dunkin 1984, Davenport & MacAlister 1996), to competitors that can displace a
232 feeding dogwhelk (Hughes & Dunkin 1984, Quinn et al. 2012, Chattopadhyay & Baumiller
233 2007, Hutchings & Herbert 2013), to predators (Vadas et al. 1994), to entrapment by neighboring
234 mussels (Davenport et al. 1996, Farrell & Crowe 2007), and to dislodgement by waves (Denny
235 1988). Thus, the morphological alterations that increase the time a mussel is handled by a
236 dogwhelk should increase the likelihood that the mussel survives a predation attempt.

237 Future research could investigate if the dogwhelk-induced responses differ to some extent
238 between *Mytilus edulis* and *M. trossulus*. Recent research has found that *M. edulis* exhibits
239 stronger morphological responses to crab and sea star cues than *M. trossulus* (Lowen et al. 2013),
240 but this may not be the case when presented with more reliable cues from slower-moving
241 predators such as dogwhelks (Burrows & Hughes 1991). Since cue release by dogwhelks
242 increases their vulnerability to byssal entrapment by mussels (Farrell & Crowe 2007) and elicits
243 prey structural changes that reduce feeding success, future studies could also investigate
244 behavioural adaptations of dogwhelks to begin feeding during low tides to delay cue
245 dissemination in the water.

246 Overall, this is the first study that has used organisms raised in the field, rather than in the
247 lab, to demonstrate that predator-induced morphological responses in bivalve prey hinder
248 predation. The complex abiotic and biotic conditions of intertidal environments, almost
249 impossible to replicate in a lab, conferred a high degree of realism to the results from the field
250 experiment and the organisms used for the feeding assay. This approach is thus in line with
251 recent studies that have highlighted the need to understand NCEs under realistic conditions in
252 order to improve theory development (Weissburg et al. 2014, Babarro et al. 2016).

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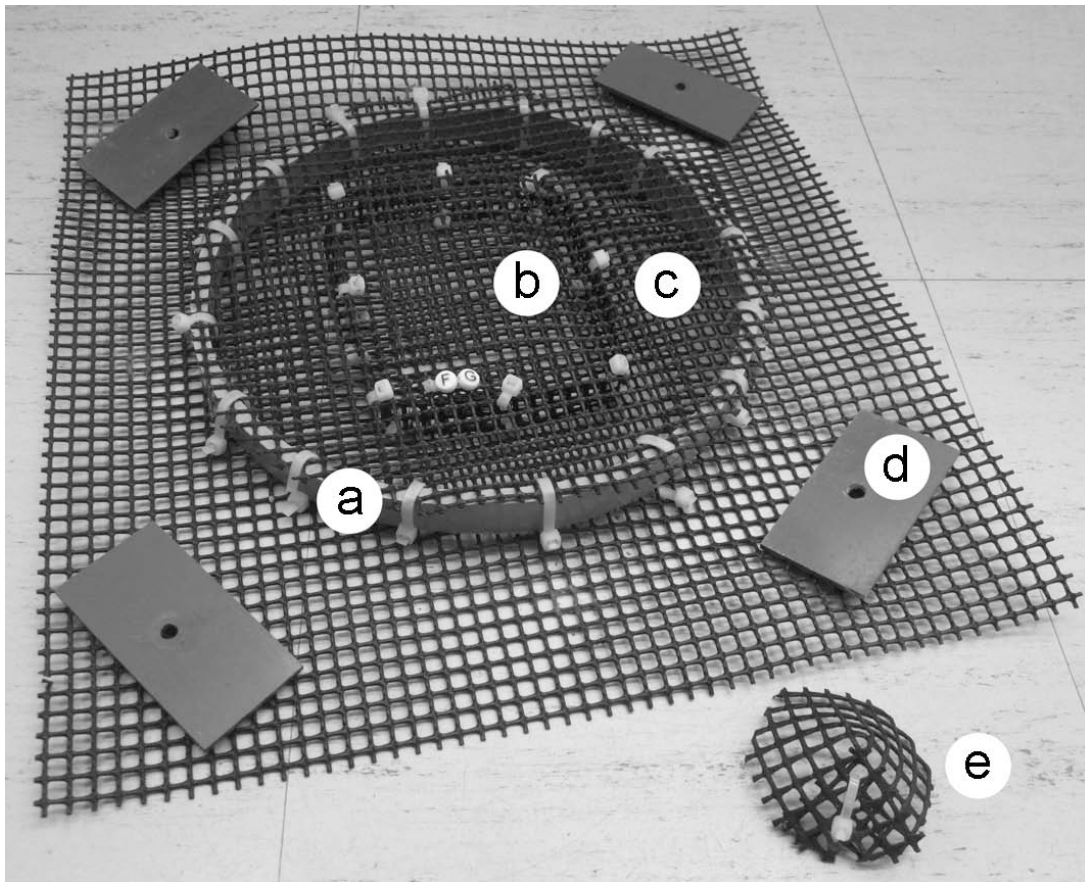
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389 **Table 1.** Summary results of the analyses of variance conducted to evaluate the effects of
 390 dogwhelk cues on various mussel traits through a field experiment.

	SS	df	MS	<i>F</i>	<i>p</i>
Shell thickness (lip)					
Dogwhelks	0.696	1	0.696	61.56	< 0.001
Blocks	0.173	14	0.012	1.09	0.437
Dogwhelks x Blocks	0.158	14	0.011	1.34	0.240
Residual	0.252	30	0.008		
Shell thickness (centre)					
Dogwhelks	0.267	1	0.267	10.11	0.007
Blocks	0.334	14	0.024	0.90	0.574
Dogwhelks x Blocks	0.370	14	0.026	1.45	0.190
Residual	0.545	30	0.018		
Shell thickness (base)					
Dogwhelks	0.300	1	0.300	21.00	< 0.001
Blocks	0.094	14	0.007	0.47	0.915
Dogwhelks x Blocks	0.200	14	0.014	1.25	0.292
Residual	0.342	30	0.011		
Relative length increment					
Dogwhelks	0.019	1	0.019	18.53	< 0.001
Blocks	0.142	14	0.010	9.65	< 0.001
Dogwhelks x Blocks	0.015	14	0.001	0.25	0.996
Residual	0.128	30	0.004		
Shell mass					
Dogwhelks	0.020	1	0.021	1.02	0.329
Blocks	0.284	14	0.020	1.00	0.504
Dogwhelks x Blocks	0.285	14	0.020	1.00	0.479
Residual	0.612	30	0.020		
Soft tissue dry mass					
Dogwhelks	0.001	1	0.001	0.87	0.368
Blocks	0.014	14	0.001	0.91	0.567
Dogwhelks x Blocks	0.015	14	0.001	0.95	0.526
Residual	0.034	30	0.001		

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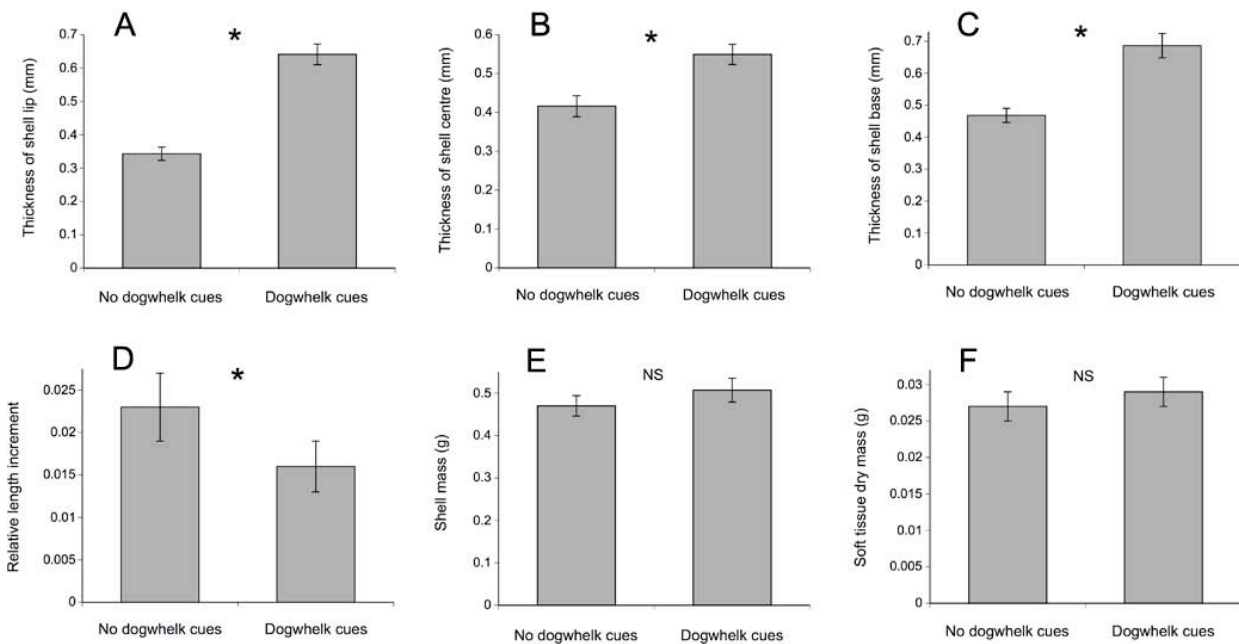
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394 **Fig. 1.** Experimental cage, showing (a) the outer PVC ring, (b) the central compartment, (c) the
395 peripheral compartment, (d) one of the four PVC tiles used to keep the cage attached to the
396 intertidal substrate, and (e) the conical compartment that was kept inside the central
397 compartment holding two experimental mussels during the experiment. The PVC ring is 25 cm
398 in diameter and 2.5 cm tall.

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402 **Fig. 2.** Mussel traits (mean ± SE) depending on the presence or absence of dogwhelk cues:

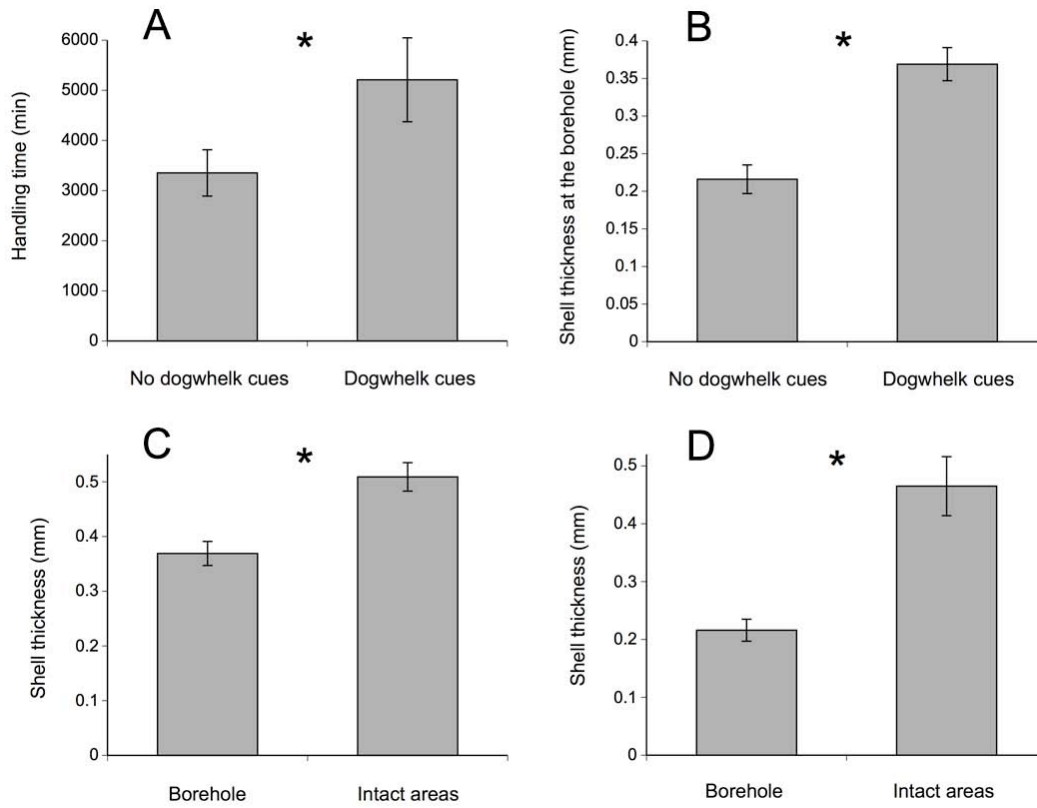
403 (A) thickness at the lip, (B) centre, and (C) base of mussel shells, (D) relative length increment

404 of shells, (E) shell mass, and (F) soft tissue dry mass. Asterisks indicate a significant difference

405 between both treatments, whereas "NS" indicates a nonsignificant result.

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409 **Fig. 3.** (A) Handling time by dogwhelks (mean \pm SE) and (B) shell thickness at the borehole of
410 mussels previously exposed to dogwhelk cues and mussels not exposed to such cues. Shell
411 thickness at the borehole and at intact shell areas of mussels (C) previously exposed to
412 dogwhelk cues and (D) mussels not exposed to such cues. Asterisks indicate a significant
413 difference between both treatments.