

1     **Limitation of dogwhelk consumption of mussels by crab cues depends**  
2                     **on dogwhelk density and cue type**

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9

9 **Abstract**

10 Predator nonconsumptive effects (NCEs) on prey activity are common in nature. Upon sensing  
11 predator cues, a common prey response is to reduce feeding to avoid being detected by predators.  
12 Using an aquatic system, this study investigated how prey density and predator cue type affect  
13 predator NCEs on prey feeding. Prey density was investigated because, as it increases, the  
14 individual risk of being preyed upon decreases, which may reduce NCEs if prey can detect  
15 conspecifics. Predator cue type was investigated because waterborne cues would trigger weaker  
16 NCEs than waterborne and tactile cues combined, as predation risk may be perceived by prey to  
17 be stronger in the second case. Specifically, a factorial experiment tested the hypotheses that (i)  
18 increasing dogwhelk (prey) density reduces the limitation that crab (predator) chemical cues can  
19 have on dogwhelk consumption of mussels and that (ii) chemical and tactile crab cues combined  
20 limit dogwhelk feeding more strongly than chemical crab cues alone. The results broadly  
21 supported these hypotheses. On the one hand, crab chemical cues limited the per-capita  
22 consumption of mussels by dogwhelks at a low dogwhelk density, but such NCEs disappeared at  
23 intermediate and high dogwhelk densities. On the other hand, the combination of chemical and  
24 tactile cues from crabs caused stronger NCEs, as dogwhelk consumption of mussels was  
25 negatively affected at all three dogwhelk densities. The structurally complex mussel beds may  
26 provide not only food for dogwhelks but a refuge from crab predation that allows dogwhelk  
27 density to limit crab NCEs when mediated by waterborne cues. Overall, this study suggests that  
28 prey evaluate conspecific density when assessing predation risk and that the type of cues prey are  
29 exposed to can affect their interpretation of risk.

30 Keywords: *Carcinus maenas*, *Mytilus edulis*, Nonconsumptive effects, *Nucella lapillus*,  
31 Predation risk, Predator cues

32

32        **Introduction**

33        Predators regulate prey populations through direct consumption, but they also often have  
34 nonconsumptive effects (NCEs). Upon detection of predator cues, prey commonly react by  
35 moving away or reducing feeding activities to reduce predation risk (Keppel and Scrosati, 2004;  
36 Molis et al., 2011; Hossie et al., 2017). Such responses may, in turn, favor species at a lower  
37 trophic level as consumption by the intermediate level decreases due to the NCEs from the top  
38 predator. As predator NCEs can influence many prey organisms simultaneously, the cascading  
39 effects on communities can be extensive (Preisser et al., 2005; Madin et al., 2016). Thus,  
40 understanding the factors that affect the occurrence of NCEs is a central theme in NCE research  
41 (Weissburg et al., 2014).

42        A number of studies have found that conspecific prey density may influence the occurrence  
43 of predator NCEs on prey (Ferrari et al., 2010; Guariento et al., 2015). For example, on marine  
44 shores, the presence of adult barnacles or a high density of barnacle recruits neutralize the  
45 limitation that cues from predatory dogwhelks would otherwise exert on barnacle recruitment  
46 (Ellrich et al., 2015, 2016). The absence of such NCEs in the presence of barnacle conspecifics  
47 likely occurs because pelagic barnacle larvae seeking settlement are attracted by chemical cues  
48 from conspecific recruits and adults (Crisp and Meadows, 1962; Matsumura et al., 2000).  
49 Benthic conspecifics would indicate to settling larvae that local conditions are adequate for  
50 survival and development (Clare, 2011). Prey larvae thus seem to assess conspecific density as  
51 part of their evaluation of future predation risk as settled larvae develop into adults. Microcosm  
52 experiments with other aquatic species have found that predator NCEs on prey activity and  
53 growth also weaken with prey density (Turner, 2004; Van Buskirk et al., 2011). The importance  
54 of prey density for the occurrence of predator NCEs has also been recognized from a theoretical  
55 viewpoint (Peacor, 2003).

56        In contrast to those studies, however, other studies have found that increasing prey density  
57 does not eliminate predator NCEs, raising the question of under what circumstances does prey  
58 density matter. These other studies used green crabs (*Carcinus maenas*), dogwhelks (*Nucella*  
59 *lapillus*), and barnacles (*Semibalanus balanoides*). Green crabs consume mussels (*Mytilus*  
60 *edulis*) and also dogwhelks (Ropes, 1968; Elner, 1978; Hughes and Elner, 1979), while  
61 dogwhelks consume barnacles and mussels (Dunkin and Hughes, 1984; Hughes and Dunkin,

62 1984; Crothers, 1985). Dogwhelks can detect chemical cues released by crabs fed either mussels  
63 or dogwhelks (Large and Smee, 2010) and also metabolites released by conspecific dogwhelks  
64 while they consume mussels (Hughes and Dunkin, 1984; Large and Smee, 2010). Experimental  
65 work has shown that chemical cues from green crabs reduce the per-capita consumption of  
66 barnacles by dogwhelks, but doubling or even tripling dogwhelk density does not neutralize such  
67 NCEs (Trussell et al., 2003, 2006). Later work showed that the limitation of dogwhelk  
68 consumption caused by crab cues is stronger when dogwhelks feed on barnacles than when they  
69 feed on mussels (Trussell et al., 2008). It was suggested that, because mussel beds are  
70 structurally more complex than the relatively flat barnacle stands, dogwhelks would find better  
71 refuge opportunities in mussel beds, prompting dogwhelks to react less strongly to waterborne  
72 crab cues. Therefore, an increasing dogwhelk density might reduce crab NCEs on dogwhelk  
73 feeding when the dogwhelks consume mussels from extensive beds. This paper tests this  
74 hypothesis experimentally using the species mentioned above. Although a recent study suggested  
75 that refuge availability may intensify predator NCEs because prey in refuges often have lower  
76 access to food (Orrock et al., 2013), mussel beds provide both a refuge as well as food (in  
77 contrast to inert refuges; see also Donelan et al., 2017), which supports testing the above  
78 hypothesis.

79 In addition to prey density, cue type may also affect the occurrence of NCEs (Stauffer and  
80 Semlitsch, 1993; Chivers et al., 2001; Luttbeg and Trussell, 2013). For example, predator  
81 chemical cues alone may indicate to prey a less immediate risk of predation than the combination  
82 of chemical and tactile (predators touching the prey) cues from the predators. Therefore, this  
83 paper also evaluates whether crab cue type interacts with dogwhelk density to influence crab  
84 NCEs. Thus, the second hypothesis of this study is that dogwhelk density weakens crab NCEs on  
85 dogwhelk feeding more strongly under chemical crab cues alone than under chemical and tactile  
86 crab cues combined.

## 87 **Materials and methods**

88 The hypotheses were tested through a laboratory experiment conducted between late  
89 summer and early fall. The experimental units that contained the crabs, dogwhelks, and mussels  
90 were glass aquaria of 54 L (60 cm x 30 cm x 30 cm) with flow-through seawater running at a rate  
91 of 2 L min<sup>-1</sup>. The photoperiod was 12:12 and seawater temperature averaged 12.5 °C. All

92 organisms were collected on the Atlantic coast of Nova Scotia, Canada. The mussels (15–20 mm  
93 long) were collected at the rocky intertidal zone of Chebucto Head (N44 40.967, W63 36.790),  
94 the dogwhelks (18–23 mm long) at Blandford (N44 28.666, W64 5.897), and the green crabs  
95 (50–60 mm of carapace width) at Little Port Joli Lagoon (N43 52.315, W64 49.381). These  
96 species coexist along this shore, but doing the collections at these locations facilitated obtaining  
97 enough organisms for the study. The size ranges were selected based on preliminary trials that  
98 identified appropriate mussel sizes to maximize dogwhelk feeding and to ensure crab predation  
99 on mussels in the treatment with chemical and tactile crab cues (described below). For  
100 consistency, only male crabs without missing limbs and dogwhelks and mussels with intact  
101 shells were used. Once collected in the field, the organisms were kept in laboratory tanks with  
102 flow-through seawater for 12 days before the start of each of the three experimental blocks  
103 described below. During that acclimation periods in the tanks, the crabs were fed a combination  
104 of mussels and whitefish, while the dogwhelks were fed mussels. Crabs and dogwhelks were  
105 subjected to a starvation period of five days before the start of each experimental block to  
106 standardize their hunger level.

107 The experiment evaluated the effects of dogwhelk density and crab cue type following a  
108 randomized complete block design with replicated treatments within blocks (Quinn and Keough,  
109 2002). Dogwhelk density included three treatments: low (6 dogwhelks per aquarium),  
110 intermediate (11 dogwhelks), and high density (17 dogwhelks), corresponding to 33, 61, and 94  
111 dogwhelks m<sup>-2</sup>. These densities are within the natural range found on the coast where the  
112 organisms were collected. Crab cue type included three treatments: no cues (NC), chemical cues  
113 (CC), and tactile and chemical cues (TCC). The NC treatment represented a crab absence in an  
114 aquarium. The CC treatment represented the occurrence of a crab in a perforated circular  
115 container (15.7 cm in diameter and 7.6 cm tall) in an aquarium, enabling the crab's chemical cues  
116 to reach the dogwhelks without allowing the crab to touch the dogwhelks. The TCC treatment  
117 represented a free-living crab in an aquarium, the crab being able to touch the dogwhelks. Each  
118 replicate aquarium contained 400 mussels, simulating the extensive mussel patches that are  
119 common in the habitats where the organisms were collected (Arribas et al., 2014). This number  
120 of mussels also ensured that they did not become limiting (less than 200 mussels per aquarium)  
121 during the experiment, as found by preliminary trials. Each crab in the CC treatment was fed six  
122 dogwhelks (placed in the circular container at the beginning of the experiment), while the crabs

123 in the TCC treatment were able to feed on the mussels that were also available for the dogwhelks  
124 (the crabs in this treatment did not eat dogwhelks). The experiment used three blocks, each one  
125 lasting for seven days and consisting of three independent replicates of each of the nine  
126 treatments described above (three levels of dogwhelk density crossed with three levels of crab  
127 cue type), yielding a total of nine replicates for each treatment for the experiment. Separate  
128 aquaria not used for the experiment included 400 mussels and a free-living crab but no  
129 dogwhelks, which confirmed that the presence of dogwhelks did not affect the consumption rate  
130 of mussels by crabs. Three other aquaria contained each 400 mussels in the absence of  
131 dogwhelks and crabs to quantify the appearance of empty shells unrelated to predation.

132 At the end of each weekly block, the per-capita rate of consumption of mussels by  
133 dogwhelks was calculated for each aquarium by observing the condition of all mussels. A  
134 dogwhelk commonly drills a borehole through the shell of a mussel to consume its internal  
135 tissues (Carriker and Williams, 1978). Less often, a dogwhelk can consume a mussel by forcing  
136 its proboscis between the mussel valves, without leaving a borehole (M. L. Boudreau, pers. obs.;  
137 Rovero et al., 1999). At the end of each weekly block, the mussels from every aquarium were  
138 sorted into nine categories: (1) alive, (2) empty shell with no borehole (indicating either natural  
139 mortality or full dogwhelk consumption between the mussel valves), (3) empty shell with one  
140 borehole, (4) empty shell with two boreholes, (5) partial internal remains with no borehole, (6)  
141 partial internal remains with one borehole, (7) partial internal remains with two boreholes, (8)  
142 fragmented shell with boreholes (indicating a combined crab and dogwhelk consumption in the  
143 TCC treatment), and (9) gaping mussel with all internal biomass and no borehole (indicating  
144 natural mortality). Fragmented shells with no boreholes were found only in the TCC treatment  
145 and suggested consumption of mussels only by crabs, so the number of such shells was not used  
146 to calculate dogwhelk consumption rates.

147 The per-capita rate of consumption of mussels by dogwhelks (mussels dogwhelk<sup>-1</sup> week<sup>-1</sup>)  
148 was calculated for each aquarium using this formula:  $\{[(N_2 - N_d) + N_3 + N_4 + (N_5 / 2) + (N_6 / 2) +$   
149  $(N_7 / 2) + (N_8 \times 0.25)] / D\}$ . The expressions  $N_2$  to  $N_8$  refer to the number of mussels found  
150 respectively for categories 2 to 8 described above,  $N_d$  refers to the average number of mussels  
151 that died naturally leaving empty shells in the three aquaria without dogwhelks or crabs, and  $D$   
152 refers to the number of dogwhelks. The formula subtracts  $N_d$  from  $N_2$  to determine as realistically  
153 as possible the number of category-2 mussels that were consumed by dogwhelks. Even though

154 category-4 mussels had two boreholes, their number ( $N_4$ ) was not divided by 2 because the  
155 dogwhelk per-capita consumption rate must necessarily be calculated, when using data for fully  
156 consumed mussels, by dividing the number of such mussels by the number of dogwhelks in the  
157 aquarium. As mussels from categories 5, 6, and 7 were partially consumed, an average of 50 %  
158 of their internal biomass was estimated to remain, so their respective numbers ( $N_5$ ,  $N_6$ , and  $N_7$ )  
159 were divided by 2. Even though category-7 mussels had two boreholes, their number ( $N_7$ ) was  
160 not further divided by 2 for the reason given above for  $N_4$ . The number of category-8 mussels  
161 ( $N_8$ ) was multiplied by 0.25 because the mussels consumed by both a crab and a dogwhelk (in  
162 the TCC treatment) were mostly eaten (ca. 3/4) by the crab, which often interrupted dogwhelk  
163 feeding at an early stage.

164 Once the per-capita dogwhelk consumption rate of mussels was determined for each  
165 aquarium, the effects of dogwhelk density and crab cue type were analyzed through a factorial  
166 analysis of variance (ANOVA; Quinn and Keough, 2002). Dogwhelk density was considered as  
167 a fixed factor with three levels (low, medium, and high), crab cue type as a fixed factor with  
168 three levels (NC, CC, and TCC), and block as a random factor with three levels (the three weekly  
169 periods). The assumptions of normality and homoscedasticity were verified with the  
170 Kolmogorov-Smirnov test and Cochran's *C*-test, respectively (Quinn and Keough, 2002).  
171 Because blocks and the interaction terms including blocks yielded *P* values higher than 0.2  
172 (Table 1), those sources of variation were removed from the model and a final ANOVA was  
173 done without them (Winer et al., 1991). Although the interaction term was not significant in the  
174 final ANOVA, the observed trends in the data suggested an apparent dependence of crab cue  
175 effects on dogwhelk density. To examine that possibility in more detail, a post-hoc power  
176 analysis was conducted for the interaction term (Zar, 1999). Because power was low for the  
177 interaction (see Results), tests of simple effects were done to evaluate crab cue effects separately  
178 for each dogwhelk density. Each of such tests was done as a one-way ANOVA using the error  
179 term from the final factorial ANOVA, followed by Tukey HSD tests to compare crab cue  
180 treatments (Quinn and Keough, 2002). The data analyses were conducted with SYSTAT 12.

## 181 **Results**

182 The final factorial ANOVA (Table 1) indicated that the type of crab cue significantly  
183 affected the per-capita rate of consumption of mussels by dogwhelks. Although the interaction

184 between crab cue type and dogwhelk density was not significant, a post-hoc power analysis  
185 revealed that the statistical power associated to testing that interaction was lower than 0.25. The  
186 tests of simple effects that evaluated that interaction in more detail revealed that the influence of  
187 crab cue type depended on dogwhelk density. Crab chemical cues (CC) limited dogwhelk  
188 consumption rate at low dogwhelk density, but such an effect disappeared at intermediate and  
189 high dogwhelk densities (Table 1, Fig. 1). On the contrary, the combination of tactile and  
190 chemical cues from crabs (TCC) limited dogwhelk consumption rate at the three studied levels of  
191 dogwhelk density (Table 1, Fig. 1).

## 192 **Discussion**

193 This study shows that increasing dogwhelk density eliminates the limitation that a green  
194 crab can exert on dogwhelk feeding through waterborne cues released by the crab. In general, the  
195 reduction of prey feeding upon detection of predator chemical cues is thought to limit the release  
196 of waterborne metabolites by prey to reduce the attraction of predators (Barnes, 1999; Johnston  
197 et al., 2012). However, under a constant density and energetic requirements of predators,  
198 increasing prey density reduces the per-capita predation risk of prey (Ferrari et al., 2010;  
199 Guariento et al., 2015). Thus, if prey can detect conspecific density, the need for prey to reduce  
200 feeding should decrease with prey density. As dogwhelks can sense the presence of feeding  
201 conspecifics (Hughes and Dunkin, 1984; Large and Smee, 2010), the absence of crab NCEs on  
202 dogwhelk feeding at intermediate and high dogwhelk densities may therefore have resulted from  
203 dogwhelks perceiving a lower predation risk.

204 A separate study (Trussell et al., 2008) found that waterborne crab cues limited dogwhelk  
205 consumption of mussels despite using a higher dogwhelk density (833 dogwhelks m<sup>-2</sup>) than the  
206 highest density used for this study. Both that study and this one used one green crab per  
207 aquarium and fed dogwhelks to the crabs. However, the aquaria used in this study were 45 times  
208 larger than those used in the study by Trussell et al. (2008). This difference suggests that  
209 waterborne crab cues may have been more diluted in this study, in that way allowing for  
210 dogwhelk density to play a larger role and effectively limit crab NCEs. This notion is in line with  
211 studies that found that increasing predator cue concentrations often trigger stronger NCEs on  
212 prey (Loose and Dawidowicz, 1994; von Elert and Ponert, 2000; Kesavaraju et al., 2007;  
213 Ferland-Raymond et al., 2010).



214 The present study also clarifies the modulation of predator NCEs by prey density for the  
215 studied species assemblage. Dogwhelks feeding on barnacles slow down consumption when they  
216 detect chemical cues from green crabs, but increasing dogwhelk density does not eliminate such  
217 NCEs (Trussell et al., 2003, 2006). The results of this study support the suggestion (Trussell et  
218 al., 2008) that the higher structural complexity of mussel stands (compared with barnacle stands)  
219 may provide more refuge opportunities for dogwhelks (in addition to abundant food), facilitating  
220 the limitation of crab NCEs by dogwhelk density.

221 Also as predicted, crab NCEs were more influenced by dogwhelk density under crab  
222 chemical cues alone than under chemical and tactile cues combined. In fact, under chemical and  
223 tactile cues, crab NCEs always occurred regardless of dogwhelk density. This result supports the  
224 notion that prey perceive a higher predation risk when predators can physically contact the prey  
225 (albeit without consuming it) in addition to releasing waterborne cues (Luttbegg and Trussell,  
226 2013). In such a scenario, the perceived imminence of predation risk would render prey density  
227 less relevant (or irrelevant, as found in this study) in triggering a predator avoidance response.  
228 The persistence of crab NCEs despite changes in dogwhelk density under chemical and tactile  
229 crab cues could in theory also have been influenced by the amount of chemical cues released by  
230 the mussels that were being consumed. Crabs alone consumed more mussels in the TCC  
231 environment than the dogwhelks did in the CC environment. However, dogwhelks have been  
232 found not to respond to cues from damaged mussels (Large and Smee, 2010), so the difference in  
233 such cues between the CC and TCC treatments likely had no influence.

234 Overall, this study reinforces the notions that prey evaluate conspecific density when  
235 assessing predation risk and that the type of cues that prey are exposed to affect their  
236 interpretation of risk. These results provide further evidence of the complexities of  
237 nonconsumptive interspecific interactions that shape aquatic communities.

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243           **References**

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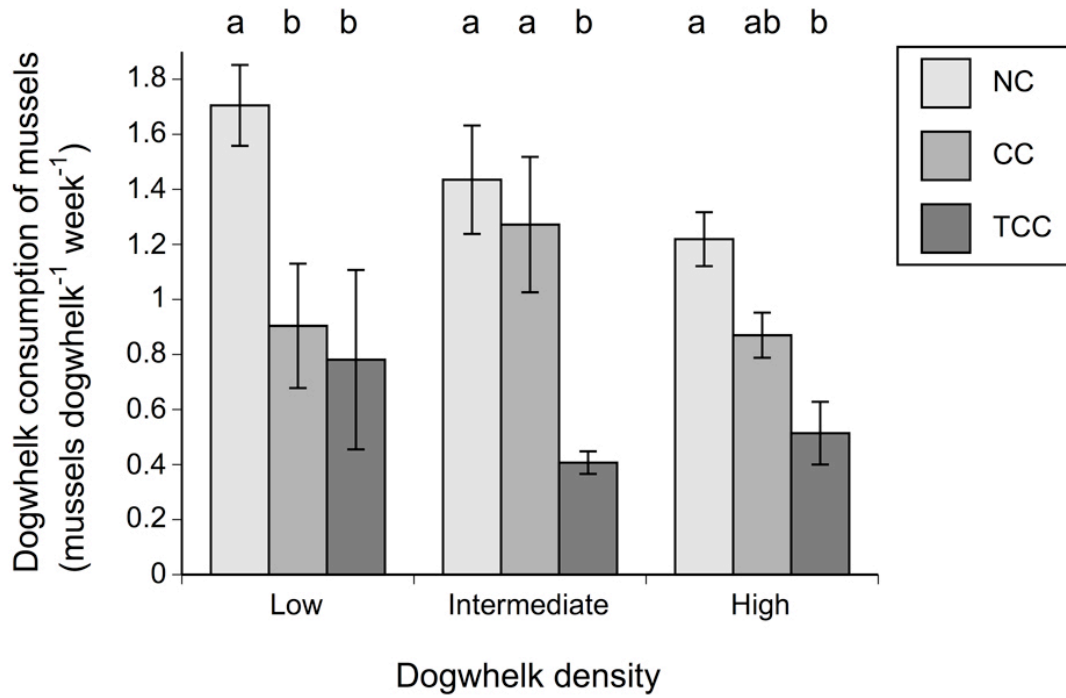
335 **Table 1.** Summary results of (A) the initial ANOVA that tested the effects of dogwhelk density,  
 336 crab cue type, and blocks on the per-capita consumption rate of mussels by dogwhelks, (B) the  
 337 final ANOVA after the sum of squares for the sources of variation that included blocks was  
 338 pooled with the residual variation (because their  $P > 0.2$ ), and (C) the tests of simple effects done  
 339 at the three evaluated levels of dogwhelk density. See the Results section for the rationale that  
 340 supported performing the tests of simple effects.  
 341

Source of variation	df	SS	MS	<i>F</i>	<i>P</i>
<b>(A) Initial ANOVA</b>					
Dogwhelk density	2	0.102	0.051	1.134	0.407
Crab cue type	2	3.212	1.606	66.463	0.001
Dogwhelk density x Crab cue type	4	0.349	0.087	2.330	0.143
Blocks	2	0.097	0.049	0.645	0.529
Blocks x Dogwhelk density	4	0.180	0.045	0.592	0.670
Blocks x Crab cue type	4	0.097	0.024	0.316	0.866
Blocks x Dogwhelk density x Crab cue type	8	0.299	0.037	0.495	0.854
Residual	53	4.005	0.076		
<b>(B) Final ANOVA</b>					
Dogwhelk density	2	0.101	0.051	0.764	0.470
Crab cue type	2	3.246	1.623	24.538	< 0.001
Dogwhelk density x Crab cue type	4	0.348	0.087	1.315	0.273
Pooled	71	4.686	0.066		
<b>(C) Tests of simple effects</b>					
Low dogwhelk density	2	1.326	0.663	10.045	< 0.001
Intermediate dogwhelk density	2	1.534	0.767	11.621	< 0.001
High dogwhelk density	2	0.758	0.379	5.742	0.005

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346 **Fig. 1.** Per-capita rate of consumption of mussels by dogwhelks (mean  $\pm$  SE) at the three levels  
347 of dogwhelk density and crab cue type considered in this study. For each level of dogwhelk  
348 density, significant differences between crab cue treatments are indicated if the two  
349 corresponding bars do not share the same letter. NC = no cues, CC = chemical cues, TCC =  
350 tactile plus chemical cues.

351