

1 **Nonconsumptive predator effects on prey demography: Dogwhelk**
2 **cues decrease benthic mussel recruitment**

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7

7 **Abstract**

8 Predators have often been shown to have nonconsumptive effects (NCEs) on prey behaviour, but
9 the demographic consequences for prey remain poorly known. This is important to understand
10 because demography influences the impact of a species in its community. We used an intertidal
11 predator–prey system to investigate predator NCEs on prey recruitment, a key demographic
12 process for population persistence. Pelagic mussel larvae are known to avoid waterborne cues
13 from dogwhelks, which prey on intertidal mussels. Through a field experiment done in Atlantic
14 Canada, we manipulated the presence of dogwhelks in intertidal habitats during the mussel
15 recruitment season. We measured mussel recruitment in collectors that could be reached by
16 waterborne dogwhelk cues but not by dogwhelks themselves. We found that the nearby presence
17 of dogwhelks significantly decreased mussel recruit density. A previous study done in the same
18 habitats under the same experimental conditions showed that dogwhelk cues also limit the
19 recruitment of barnacles, another prey item for dogwhelks. However, such NCEs were four times
20 stronger than those observed for mussel recruitment. This difference relates well to the higher
21 ability of mussels to escape predation, as mussels can relocate while barnacles cannot. Therefore,
22 basic features of natural history may be useful to predict predator NCEs on prey recruitment.

23 Keywords: nonconsumptive effect; mussel; predator; prey; recruitment; snail.

24

24 **Introduction**

25 Nonconsumptive effects (NCEs) of predators on prey are ubiquitous in nature. When
26 organisms of a prey species detect cues from nearby predators, a variety of responses are often
27 triggered to limit predation risk (Ferrari *et al.*, 2010; Brönmark & Hansson, 2012). As cues from
28 a predator can reach many prey organisms at the same time, NCEs can be extensive in prey
29 populations (Preisser *et al.*, 2005; Peacor *et al.*, 2013). Thus, understanding what prey traits are
30 affected and how has become an important research line in ecology (Weissburg *et al.*, 2014).

31 Immediate prey responses are typically behavioural. They include moving away to minimize
32 the chance of being reached by predators or limiting movements to avoid being detected by
33 predators (Keppel & Scrosati, 2004; Molis *et al.*, 2011; Johnston *et al.*, 2012; Matassa *et al.*,
34 2016, Johnson *et al.*, 2017). The consequences of such behavioural responses for prey
35 demography have received, however, little attention (Creel *et al.*, 2007; Schoener & Spiller,
36 2012; Ellrich *et al.*, 2016a). This is important to understand because demography ultimately
37 determines to a large extent the function of a species in its community. This paper focuses on
38 predator NCEs on prey recruitment, which is a key demographic process for population
39 persistence (Caley *et al.*, 1996; Palumbi & Pinsky, 2014).

40 Benthic invertebrates with pelagic larvae are useful model organisms for this kind of
41 research. For instance, a laboratory experiment has shown that larvae of blue mussels (*Mytilus*
42 *edulis*) avoid waterborne chemical cues from predatory dogwhelks (*Nucella lapillus*; Morello &
43 Yund, 2016). Dogwhelks feed on benthic mussel stages, not on their pelagic larvae (Hunt &
44 Scheibling, 1998). However, larval avoidance of dogwhelk cues may have evolved to aid
45 settlement-seeking larvae to find habitats with a reduced predation pressure for juveniles and
46 adults. Such an avoidance behaviour might ultimately decrease benthic recruitment (the addition

47 of new organisms to a benthic population after larval settlement and metamorphosis). In fact,
48 field experiments in intertidal habitats have shown that cues from *N. lapillus* limit barnacle
49 (*Semibalanus balanoides*) recruitment (Ellrich *et al.*, 2015a,b). This barnacle is another
50 important prey for *N. lapillus* and it also has pelagic larvae, which settle elsewhere when
51 dogwhelk cues are detected (Ellrich *et al.*, 2016a). Thus, the mussel–dogwhelk system offers the
52 opportunity to start evaluating how broadly predator NCEs can limit the recruitment of benthic
53 invertebrate prey. Through a field experiment, the present study tests the hypothesis that
54 dogwhelk cues limit intertidal mussel recruitment.

55 Basic differences in natural history between mussels and barnacles may influence the
56 intensity of such NCEs, however. The location of a barnacle is fixed for life after a larva settles
57 and metamorphoses into a recruit (Jenkins *et al.*, 2000). However, mussel recruits can detach
58 themselves from the substrate and relocate (Bayne, 1964; Le Corre *et al.*, 2013). Additionally,
59 older mussels can immobilize dogwhelks through the production of byssus threads (Farrell &
60 Crowe, 2007). These processes provide mussels with opportunities to escape predation that
61 barnacles lack. Thus, we also predict that the expected dogwhelk NCEs on mussel recruitment
62 are weaker than the NCEs recently reported for barnacles.

63 **Materials and Methods**

64 We did the experiment in rocky intertidal habitats from Deming Island (45° 12' 45" N, 61°
65 10' 26" W), on the Atlantic coast of Nova Scotia (Canada), between May–July 2016. These
66 habitats are constituted by stable bedrock and are protected from direct oceanic swell by rocky
67 formations. Maximum water velocity measured with dynamometers (see design in Bell &
68 Denny, 1994) during the study period was $6.0 \pm 0.3 \text{ m s}^{-1}$ (mean \pm SE, $n = 48$). These wave-
69 sheltered habitats were used in previous years to demonstrate that dogwhelk cues limit barnacle

70 recruitment (Ellrich & Scrosati, 2016; Ellrich *et al.*, 2015b, 2016b). In-situ temperature measured
71 every 30 minutes during the study period using submersible loggers (HOBO Pendant Logger,
72 Onset Computer Corp., Pocasset, MA, USA) was 12.8 ± 0.1 °C (mean \pm SE, $n = 7$ loggers).
73 Coastal seawater salinity measured on 21 May 2016 with a refractometer was 35 ‰.

74 The dogwhelk used for this study was *Nucella lapillus*, which is the only dogwhelk species
75 on the studied coast (Scrosati & Heaven, 2007). On the Atlantic coast of Nova Scotia, two blue
76 mussel congeners, *Mytilus edulis* and *M. trossulus*, co-occur (Tam & Scrosati, 2011, 2014) and
77 are preyed upon by *N. lapillus* (Hunt & Scheibling, 1998). These mussel species show only
78 subtle morphological differences (Innes & Bates, 1999) and can form hybrids (Riginos &
79 Cunningham, 2005). Thus, their visual identification is very difficult, especially at the recruit
80 stage. Therefore, recruit counts in this study were done as *Mytilus* spp., as commonly done in
81 ecological field studies involving these species (Cusson & Bourget, 2005; Le Corre *et al.*, 2013).

82 We evaluated dogwhelk cue effects on mussel recruitment by manipulating dogwhelk
83 presence in cages attached to the intertidal substrate. Each cage (Fig. 1) was made using a PVC
84 ring (25 cm in diameter and 2.5 cm tall) and plastic mesh (0.5 cm x 0.5 cm of opening size).
85 Each cage was divided by mesh into a central compartment (area = 144 cm²) and a peripheral
86 compartment (area = 347 cm²). The peripheral compartment was used to create two dogwhelk
87 treatments (presence vs. absence) by enclosing either 10 dogwhelks (2.23 ± 0.02 cm in shell
88 length, mean \pm SE, $n = 104$) or none. The used dogwhelk density (ca. 3 individuals dm⁻²) was
89 representative of the studied coast (Ellrich & Scrosati, 2016). The central compartment held a
90 plastic mesh scourer (Our Compliments Poly Pot Scrubbers, Mississauga, ON, Canada) attached
91 with cable ties (Fig. 1). Mesh scourers have often been used to measure intertidal mussel
92 recruitment (Menge & Menge, 2013; South, 2016), as scourers resemble habitats where mussel

93 larvae preferentially settle (filamentous algae or byssal threads of established mussels; Menge,
94 1992; Le Corre *et al.*, 2013). For *Mytilus edulis* and *M. trossulus*, pelagic pediveliger larvae of at
95 least approximately 0.25 mm in shell length settle in those habitats and, then, undergo
96 metamorphosis, becoming recruits (Bayne, 1965; Menge *et al.*, 2009; Martel *et al.*, 2014). After
97 growing to a shell length of about 0.5 mm (Hunt & Scheibling, 1996; Le Corre *et al.*, 2013), such
98 recruits may enter a second pelagic dispersal phase (Bayne, 1964). For instance, recruits of *M.*
99 *edulis* up to 2.5 mm long can passively drift in the water aided by a byssus thread (Sigurdsson *et*
100 *al.*, 1976). In our study, observations under a stereomicroscope indicated that 70-80 % of the
101 recruits found in the scourers belonged to the first phase, the remaining organisms belonging to
102 the second phase. Precise counts are unavailable because the threshold size between both phases
103 is not accurately known (Le Corre *et al.*, 2013). As all of those organisms ultimately contribute
104 to mussel recruitment (Le Corre *et al.*, 2013), at the end of the experiment we counted the
105 recruits of both phases together to determine recruit density for each scourer, as often done in
106 field studies of this kind (Menge & Menge, 2013).

107 We set up the experiment on 21 May 2016 following a randomized complete block design
108 with replicated treatments within blocks (Quinn & Keough, 2002). We established 12 blocks,
109 each one including two replicate cages of each of the two dogwhelk treatments, thus yielding 24
110 replicates for each dogwhelk treatment. Block size was $7.7 \pm 0.4 \text{ m}^2$ (mean \pm SE, $n = 12$ blocks)
111 and the distance between cages within blocks was at least 0.5 m. We established the blocks at an
112 intertidal elevation of $0.9 \pm 0.1 \text{ m}$ (mean \pm SE, $n = 12$ blocks) above chart datum (the full vertical
113 intertidal range is 1.8 m). We attached the cages to the substrate using PVC plates and screws
114 (Fig. 1). Before installing the cages, we removed all seaweeds (mainly *Ascophyllum nodosum*
115 and *Fucus vesiculosus*) and benthic invertebrates from the substrate to avoid chemical and

116 physical influences from those organisms (Johnson & Strathmann, 1989; Jenkins *et al.*, 1999;
117 Beermann *et al.*, 2013). During the experiment, we kept these areas devoid of free-living
118 dogwhelks. We did not feed the caged dogwhelks during the experiment but, to prevent their
119 starvation, we replaced them every 10-14 days with mussel-fed dogwhelks that were kept in
120 separate cages tens of meters away from the blocks. We used mussel-fed dogwhelks because
121 prey reacts strongly to chemical cues from predators fed conspecific prey (Cheung *et al.*, 2006;
122 Weissburg & Beauvais, 2015; Scherer & Smee, 2016). We ended the experiment on 29 July
123 2016, when we took all of the scourers to the laboratory to measure mussel recruit density.

124 In the laboratory, we stored the scourers in a freezer to preserve the integrity of the recruits
125 until each scourer was analyzed. To count the recruits in a scourer, we unrolled the scourer and
126 manually rinsed it in tap water to separate the recruits from the mesh. The recruits were retained
127 in a sieve (0.212 mm x 0.212 mm of opening size) and then transferred to a Petri dish. We
128 subsequently counted the recruits under a stereomicroscope. For each scourer, we calculated
129 mussel recruit density by dividing the encountered number of recruits by the total area of the
130 scourer. This standardization was necessary because small area differences could exist among
131 the replicate scourers provided by the vendor. To calculate the total area of a scourer, we first
132 unrolled the scourer. Then, we used scissors to cut alongside the resulting cylindrical mesh to
133 produce a two-dimensional mesh, which we extended flat on a table. As mussel recruits occurred
134 on both sides of this surface, we calculated the total area of the scourer as the area of that two-
135 dimensional mesh viewed from the top multiplied by two. We evaluated the effect of dogwhelk
136 cues (fixed factor with two levels: dogwhelk presence and absence) on mussel recruit density
137 through an analysis of variance (ANOVA) that was appropriate for a randomized complete block
138 design with replicated treatments within blocks (random factor with 12 levels). We confirmed

139 the homoscedasticity and normality assumptions using Cochran's *C*-test and the Kolmogorov-
140 Smirnov test, respectively.

141 We also conducted a side experiment to verify that the presence of dogwhelks in a cage did
142 not alter water motion at the place of attachment of the mesh scourer. For this purpose, we
143 established 24 different cages on the shore on 1 June 2016. Each of those cages held a gypsum
144 piece (Jonsson *et al.*, 2006; Beermann *et al.*, 2013) in the same place in which the cages used for
145 the main experiment held a mesh scourer. We prepared the gypsum pieces following Howerton
146 & Boyd (1992). We determined the initial dry mass of each gypsum piece to the nearest 0.1 mg.
147 Twelve randomly selected cages each contained 10 dogwhelks in the peripheral compartment,
148 whereas the other 12 cages lacked dogwhelks. On 2 June 2016, we collected the gypsum pieces,
149 dried them at 60 °C for 24 h, and then measured the percent loss of mass for each piece. We
150 compared percent loss of gypsum mass between both treatments with a *t*-test. We conducted all
151 of the data analyses with STATISTICA 13.5 (Statsoft, Tulsa, OK, USA).

152 **Results**

153 The ANOVA for the field experiment revealed that the presence of dogwhelks decreased
154 intertidal mussel recruitment (Table 1). On average, mussel recruit density was 13 % lower with
155 nearby dogwhelks than in their absence (Fig. 2). Blocks had a significant effect on mussel recruit
156 density (Table 1), but that result merely indicates that mussel recruitment differed among blocks.
157 The important result is that the interaction between the dogwhelks factor and the blocking factor
158 was not significant (Table 1), indicating that the negative dogwhelk NCEs on mussel recruitment
159 were spatially consistent on the shore. The side field experiment revealed that the presence of
160 dogwhelks in the cages did not affect water motion ($t_{22} = 1.14$, $P = 0.267$) in the place in which
161 the cages used for the main experiment held a mesh scourer.

162 **Discussion**

163 This study has experimentally demonstrated that cues from predatory dogwhelks decrease
164 mussel recruitment in intertidal habitats. This is a valuable contribution because it adds to the
165 growing literature that is revealing predator NCEs on prey demography. Other studies have
166 shown negative NCEs on prey reproduction (Selden *et al.*, 2009; Zanette *et al.*, 2011; Ellrich *et*
167 *al.*, 2016a) and also recruitment (Creel *et al.*, 2011; Ellrich *et al.*, 2015a; Benkwitt, 2017). These
168 studies are important because most NCE research to date has focused on behavioural responses
169 in prey (Ferrari *et al.*, 2010; Brönmark & Hansson, 2012; Schoener & Spiller, 2012), likely
170 because of the short times required to document such responses. Evaluating the demographic
171 consequences requires more time, but this knowledge is necessary to better understand predator
172 NCEs on prey population dynamics (Weissburg *et al.*, 2014).

173 *Nucella lapillus* preys on blue mussels (Crothers, 1985). Young *N. lapillus* consume
174 juvenile mussels and even recently hatched *N. lapillus* prey on young mussels by drilling a hole
175 through their shells (Largen, 1967). Hence, dogwhelks are a threat to various age classes of
176 mussels. Such an extended predation pressure is, therefore, what may have selected for the larval
177 avoidance behaviour (Morello & Yund, 2016) that can ultimately decrease recruitment. In
178 intertidal habitats, dogwhelks are patchily distributed (Johnson *et al.*, 1998) and have a restricted
179 activity range (Crothers, 1985; Fretter & Graham, 1994; Carro *et al.*, 2012). Thus, by avoiding
180 dogwhelk cues, young mussels likely contribute to limiting future predation risk.

181 This study has also revealed that the recruitment limitation caused by dogwhelk cues is
182 weaker for mussels than for barnacles. Barnacles cannot change their location once recruited
183 (Anderson, 1994) and cues from *Nucella lapillus* were found to limit barnacle (*Semibalanus*
184 *balanoides*) recruitment by 50 % in the same habitats where we conducted the present study and

185 under the same dogwhelk density (Ellrich *et al.*, 2016b). Mussels are also sessile, but to some
186 extent they can relocate across the substrate throughout their benthic existence (Bayne, 1964;
187 Hunt & Scheibling, 2002; de Vooy, 2003; van de Koppel *et al.*, 2008). Older mussels can also
188 immobilize dogwhelks using byssus threads (Farrell & Crowe, 2007). Therefore, mussels have
189 more opportunities to escape predation than barnacles, which might explain why mussel
190 recruitment is less responsive to dogwhelk cues than barnacle recruitment.

191 Pre-recruitment avoidance of predator cues has been found not only for mussels and
192 barnacles, but also for lobsters (Boudreau *et al.*, 1993), crabs (Welch *et al.*, 1997; Banks &
193 Dinnel, 2000; Tapia-Lewin & Pardo, 2014), and sea urchins (Metaxas & Burdett-Coutts, 2006).
194 Thus, negative predator NCEs on prey recruitment might be common in benthic invertebrates
195 with pelagic dispersal stages. The intensity of such NCEs may depend, as discussed above and
196 among other factors, on the capacity of benthic prey stages to relocate across the substrate.

197 Indirect NCEs of predators on third species mediated by the direct NCEs on the predator's
198 prey have often been reported (Molis *et al.*, 2011; Schoener & Spiller, 2012; Matassa *et al.*,
199 2016). Those studies have generally evaluated effects on only one or a few of such third species
200 (although exceptions evaluating responses on entire assemblages exist; Hammill *et al.*, 2015).
201 Intertidal mussels are foundation species (Altieri & van de Koppel, 2014), because they often
202 occur in extensive patches that host several small species among the mussels (Valdivia & Thiel,
203 2006; O'Connor & Crowe, 2007; Arribas *et al.*, 2014). Therefore, by nonconsumptively limiting
204 mussel recruitment, dogwhelks have the potential to alter intertidal species composition.
205 Evaluating this possibility would enrich models of community organization that currently
206 consider only the consumptive effects of predators on foundation species and its associated
207 biodiversity (Bruno *et al.*, 2003; Scrosati *et al.*, 2011).

208 Overall, the present study shows that predator NCEs limit intertidal mussel recruitment,
209 potentially affecting mussel population dynamics. Moreover, the study has linked behavioural
210 observations obtained in the laboratory (Morello & Yund, 2016) to population processes
211 occurring under natural conditions. The field nature of our experiment is important because the
212 complexity of intertidal environments cannot be replicated in laboratory settings. Thus, our
213 approach agrees with recent calls to study predator NCEs under realistic conditions in order to
214 advance NCE theory further (Weissburg *et al.*, 2014; Babarro *et al.*, 2016).

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Table 1. Results of the ANOVA conducted to evaluate dogwhelk NCEs on mussel recruitment.

Source of variation	df	SS	MS	<i>F</i>	<i>P</i>
Dogwhelks	1	43.86	43.86	7.37	0.020
Blocks	11	401.36	36.49	2.29	0.044
Dogwhelks x Blocks	11	65.50	5.96	0.37	0.954
Residual	24	382.70	15.95		

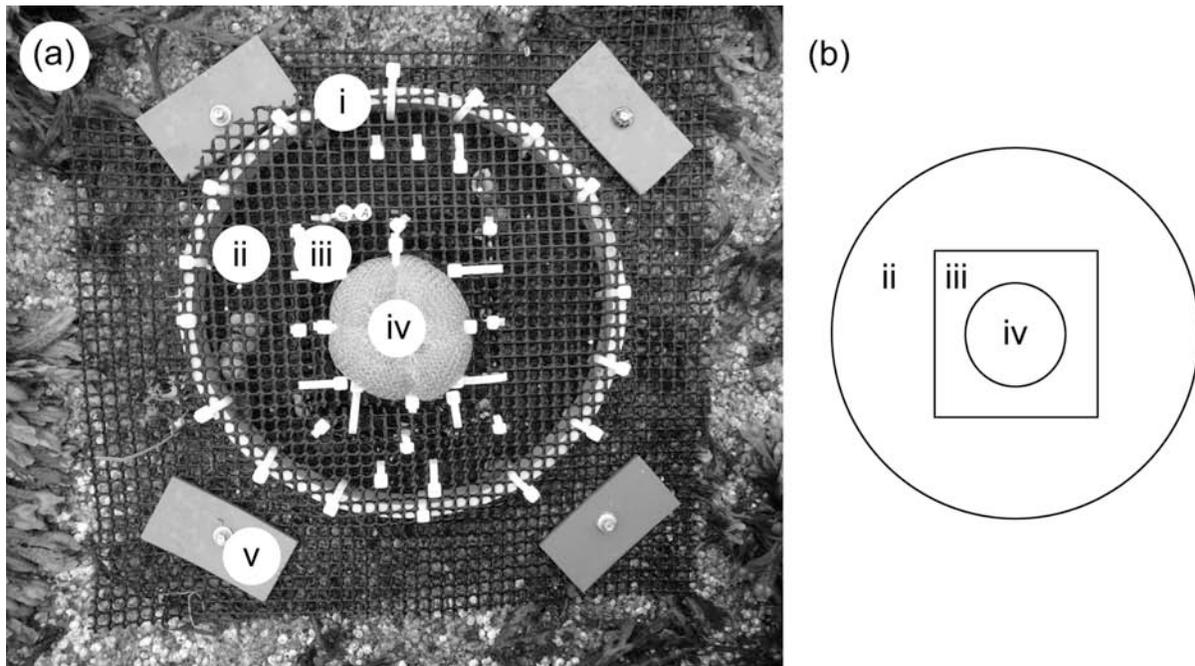


Figure 1. (a) Top view of a cage, showing: (i) the PVC ring determining the cage's shape (25 cm in diameter and 2.5 cm tall), (ii) the peripheral compartment (which had 10 dogwhelks or none, depending on the treatment), (iii) the central compartment with (iv) the mesh scourer to collect mussel recruits, and (v) the four plates used to secure the cage to the intertidal substrate.

(b) Simplified diagram of a cage, showing: (ii) its peripheral compartment, (iii) its central compartment, and (iv) the mesh scourer.

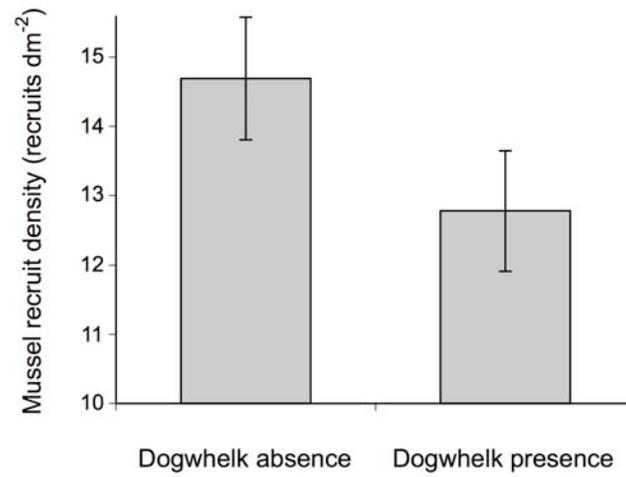


Figure 2. Mussel recruit density (recruits dm⁻², mean \pm SE, $n = 24$) depending on the presence or absence of dogwhelks during the field experiment.