

# Water motion modulates predator nonconsumptive limitation of prey recruitment

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**Abstract.** Predator chemical cues can elicit behavioral changes in prey to minimize predation risk. Recent field studies have shown that such predator nonconsumptive effects (NCEs) can ultimately affect prey demography. The environment is known to modulate predator consumptive effects on prey demography, but the environmental modulation of predator NCEs on prey demography remains unstudied. We investigated this knowledge gap using an intertidal predator–prey system. Dogwhelk (*Nucella lapillus*) chemical cues can limit barnacle (*Semibalanus balanoides*) recruitment by limiting larval settlement. As waves disperse chemicals in coastal environments, we experimentally tested the hypothesis that wave exposure limits dogwhelk NCEs on barnacle recruitment. Shortly before the barnacle recruitment season of 2013 (May–June), we established cages in rocky intertidal habitats in Atlantic Canada under two levels of wave exposure. The cages were used to manipulate the presence and absence of dogwhelks. At the center of each cage, we installed a tile where barnacle pelagic larvae could settle and develop into recruits. Mesh prevented caged dogwhelks from accessing the tiles, but allowed their waterborne cues to reach the tiles. Data collected at the end of the recruitment season indicated that dogwhelk cues limited barnacle recruitment in wave-sheltered habitats but had no effect on recruitment in wave-exposed habitats. These findings suggest that predicting predator NCEs on prey demography may require environmental information related to the ability of prey to locate predators.

**Key words:** barnacle; chemical cue; dogwhelk; intertidal; nonconsumptive effect; predation risk; prey demography; recruitment; wave exposure.

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## INTRODUCTION

Predators regulate prey populations through direct consumption, but they also have a variety of nonconsumptive effects (NCEs) on prey. For instance, when prey species detect chemical cues from nearby predators, immediate responses often include moving away or decreasing feeding activities to reduce predation risk (Trussell et al. 2003, Keppel and Scrosati 2004, Large et al. 2011, Molis et al. 2011, Johnston et al. 2012, Orrock et al. 2013). Such chemically mediated NCEs are common in aquatic and terrestrial predator–prey

systems (Hermann and Thaler 2014, Matassa and Trussell 2015). As predator chemical cues can be detected by many prey individuals simultaneously, the resulting NCEs on prey populations can be extensive (Preisser et al. 2005, Pangle et al. 2007, Matassa and Trussell 2011, Peacor et al. 2013).

Studies on predator NCEs have evaluated behavioral prey responses far more often than demographic responses (Ferrari et al. 2010, Brönmark and Hansson 2012, Weissburg et al. 2014). This disparity may have resulted from the longer duration of experiments needed to study

demographic changes compared with experiments that evaluate behavior, which is a quicker response. This knowledge gap needs to be addressed to better understand prey population dynamics. The few studies on predator NCEs on prey demography have been done mainly with aquatic invertebrates. For example, waterborne predator cues can limit prey larval settlement (Johnson and Strathmann 1989, Welch et al. 1997, Tapia-Lewin and Pardo 2014) and subsequent recruitment (Ellrich et al. 2015a, b), as many larvae move away when predator cues are detected to limit future predation risk (Banks and Dinnel 2000, Metaxas and Burdett-Coutts 2006). Recruitment is an important demographic rate that often influences population persistence (Menge and Menge 2013).

A comprehensive understanding of predator NCEs on prey demography will need to evaluate the environmental context. The environment has long been known to affect the intensity of predator consumptive effects on prey demography (Menge and Sutherland 1987). Recent studies have shown that the environment may also affect the intensity of predator NCEs on prey behavior. For instance, water motion disperses waterborne predator cues, thereby decreasing the ability of prey to detect predators and weakening NCEs on prey behavior (Smee and Weissburg 2006, Smee et al. 2008, Large et al. 2011). Therefore, water motion might ultimately limit predator NCEs on prey demography. This study tested this possibility experimentally for the first time, using intertidal dogwhelks and barnacles as a model predator–prey system.

Barnacles are sessile organisms with pelagic larvae and are common in intertidal habitats worldwide. Dogwhelks are benthic predatory snails that frequently feed on intertidal barnacles. Chemical cues from nearby dogwhelks limit barnacle recruitment (Ellrich et al. 2015a, b) by limiting larval settlement (Ellrich et al. 2016a). In barnacles, settlement refers to the permanent contact with the substrate established by pelagic larvae (Jenkins et al. 2000), while recruitment is the appearance of new benthic individuals that have metamorphosed from the settled larvae (Cole et al. 2011). Water motion caused by waves is a major dispersal agent in intertidal environments (Denny and Wethey 2001, Blanchette et al. 2008) and can disperse waterborne predator cues

in ways that make predator location difficult for mobile organisms (Ferner and Weissburg 2005), such as barnacle larvae. Therefore, we conducted a field experiment to test the hypothesis that wave-generated water motion limits the negative NCEs that dogwhelks have on barnacle recruitment.

## METHODS

We did the experiment in Deming Island (45°12'45" N, 61°10'26" W), located near Whitehead, on the Atlantic coast of Nova Scotia (Canada), during the barnacle recruitment season (May–June) of 2013. We used intertidal habitats composed of stable bedrock. We selected wave-exposed habitats, which face the open ocean directly, and wave-sheltered habitats, which are protected from oceanic swell by natural rocky formations. For both habitat types, we measured water motion using gypsum blocks (Boizard and DeWreede 2006) and maximum water velocity using dynamometers (Bell and Denny 1994). To select both habitat types, we measured maximum water velocity in April. To ensure that exposure differences between both habitat types persisted throughout the experiment, we measured water motion and maximum velocity during the first half (9–27 May) and second half (28 May–25 June) of the barnacle recruitment season. Intertidal temperature measured every 30 min with submersible loggers (HOBO Pendant Logger; Onset Computer, Pocasset, Massachusetts, USA) during the barnacle recruitment season was similar in exposed ( $9.7^{\circ} \pm 0.2^{\circ}\text{C}$ , mean  $\pm$  SE,  $N = 5$  loggers) and sheltered ( $9.9^{\circ} \pm 0.2^{\circ}\text{C}$ ,  $N = 6$  loggers) habitats, with temperatures not exceeding  $20^{\circ}\text{C}$  during low tides.

On the studied coast, *Semibalanus balanoides* is the only intertidal barnacle species (Scrosati and Heaven 2007, Watt and Scrosati 2013). It is a cross-fertilizing hermaphrodite that broods once per year (Bousfield 1954). In Atlantic Canada, *S. balanoides* mates in early autumn, breeds in winter, and releases pelagic larvae in spring (Bousfield 1954, Crisp 1968). Larvae develop over 5–6 weeks in coastal waters (Bousfield 1954). In northern Nova Scotia, barnacle recruits appear in intertidal habitats in May and June (Cole et al. 2011, Beermann et al. 2013). The dogwhelk *Nucella lapillus* is the main predator of *S. balanoides* on this coast.

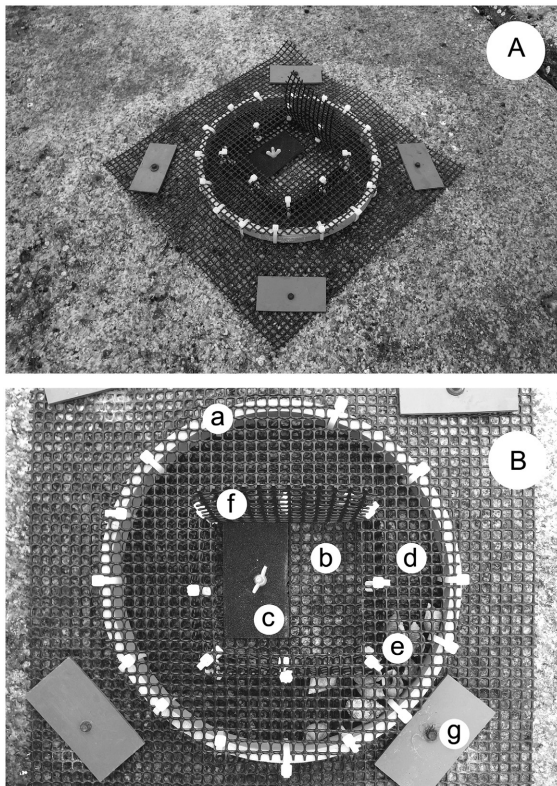


Fig. 1. Experimental unit. (A) Side view of a cage, showing its limited height (2.5 cm). (B) Top view of a cage, showing (a) the PVC ring of 25 cm in diameter, (b) the central compartment with (c) the barnacle recruitment tile, and (d) the peripheral compartment with (e) the dogwhelks. The (f) top mesh of the central compartment is shown open to improve viewing of the recruitment tile, but it remained closed with plastic cable ties during the experiment. The cage was secured with (g) screws to the substrate. Photographs by J. Ellrich.

On the Atlantic coast of Nova Scotia, *N. lapillus* becomes active in April (Hughes 1972, Hunt and Scheibling 1998).

Barnacles and dogwhelks were common organisms under the two studied levels of wave exposure at the elevation where we set up the experiment (two-thirds of the full intertidal range, which is 1.8 m on this coast). Other organisms common under both exposure levels were canopy-forming macroalgae (mainly *Fucus vesiculosus*) and periwinkles (mostly *Littorina littorea*). Mussels (*Mytilus* spp.) were present but in very low abundance. To standardize conditions

for our experiment, fucoid algae, wild barnacles, and free-living dogwhelks were dealt with as explained below, the few existing mussels were removed and relocated elsewhere, and the periwinkles were left in place, as they have no chemical influence on barnacle larval settlement (Holmes 2002).

To test our hypothesis, we used the comparative-experimental method (Menge et al. 1994, Vinuela et al. 2014). We manipulated dogwhelk presence in sheltered and exposed habitats and recorded responses in barnacle recruitment. The experimental unit included a cage (Fig. 1) made of a PVC ring (25 cm in diameter and 2.5 cm tall) and plastic mesh (0.5 cm × 0.5 cm of opening size). Each cage was subdivided by mesh into a central compartment (12 cm × 12 cm) and a peripheral compartment (area = 347 cm<sup>2</sup>). We used the peripheral compartment to manipulate dogwhelk presence by either excluding dogwhelks or by enclosing 10 dogwhelks (2.1–2.3 cm long) collected locally. This density (~3 dogwhelks/dm<sup>2</sup>) represented high natural values, as indicated by 60 random quadrats (40 cm × 40 cm) measured on the studied coast. The central compartment of a cage included a PVC tile (8.9 cm × 4.6 cm) covered with black tape with a sandpaper texture (Permastik self-adhesive anti-skid safety tread; RCR International, Boucherville, Quebec, Canada) to offer a suitable surface for barnacle recruitment. We tightened the tile to the bottom mesh of its cage with a plastic screw, a wing nut, and a washer.

We established 12 cages of each dogwhelk treatment in sheltered habitats and 12 cages of each treatment in exposed habitats (48 cages in total). For each exposure level, we arranged the cages following a randomized complete block design (Quinn and Keough 2002) in which each dogwhelk treatment was replicated twice in each of six blocks (12 blocks in total for the experiment). The blocks for the two exposure levels were interspersed along the coastline. Block size was  $16.5 \pm 2.8$  m<sup>2</sup> (mean ± SE,  $N = 12$  blocks) and cages within blocks were separated by at least 0.5 m. We established the cages on gently sloped substrate using screws, washers, and plastic anchors placed into holes drilled into the substrate. Caged dogwhelks could move freely inside the peripheral compartment and approach the recruitment tile up to 1.5 cm. Thus, settling



cyprids and recruits of barnacles in the central compartment were exposed to dogwhelk cues but not to physical contact with these predators. To exclude cyprid attraction by nearby adult barnacles (Chabot and Bourget 1988, Bertness et al. 1992, Ellrich et al. 2016b), we removed all adult barnacles from 40 cm × 40 cm areas around the center of each cage. To exclude influences of fucoid canopies such as mucus release (Johnson and Strathmann 1989), water flow barriers at high tide (Jenkins et al. 1999), and thermal and humidifying effects at low tide (Beermann et al. 2013), we removed canopies near the cages. We did not feed the caged dogwhelks during the experiment but, to prevent their starvation, we replaced them every two weeks, releasing the removed individuals hundreds of meters away. We also periodically removed any free-living dogwhelks found around the cages. We started the experiment by installing the cages on the shore in late April.

Barnacle recruits started to appear on the tiles on 9 May and ceased to appear on 25 June, indicating the end of the 2013 recruitment season. On 27 May and on 25 June, we took digital pictures of all tiles to enable the accurate counting of recruits on a computer. We tested the effects of dogwhelk presence (fixed factor with two levels: presence vs. absence) and block (random factor with six levels) on barnacle recruit density through analyses of variance (ANOVA) applied to sheltered and exposed habitats and to the May and June data sets. The significance level was set at 0.05 for each ANOVA, following the rationale of Hurlbert and Lombardi (2012) and in agreement with other studies that applied the comparative-experimental method (Menge et al. 1994, Vinuela et al. 2014). Before the ANOVAs, data were log<sub>10</sub>-transformed to meet the homoscedasticity and normality assumptions, which we confirmed through Cochran's C-test and the Kolmogorov-Smirnov test, respectively (Quinn and Keough 2002). We conducted the analyses with STATISTICA 12.5 (Statsoft, Tulsa, Oklahoma, USA).

## RESULTS

Maximum water velocity was significantly higher in wave-exposed habitats than in wave-sheltered habitats shortly before the barnacle recruitment season ( $t_{24} = 2.07$ ,  $P = 0.049$ ,  $N = 13$

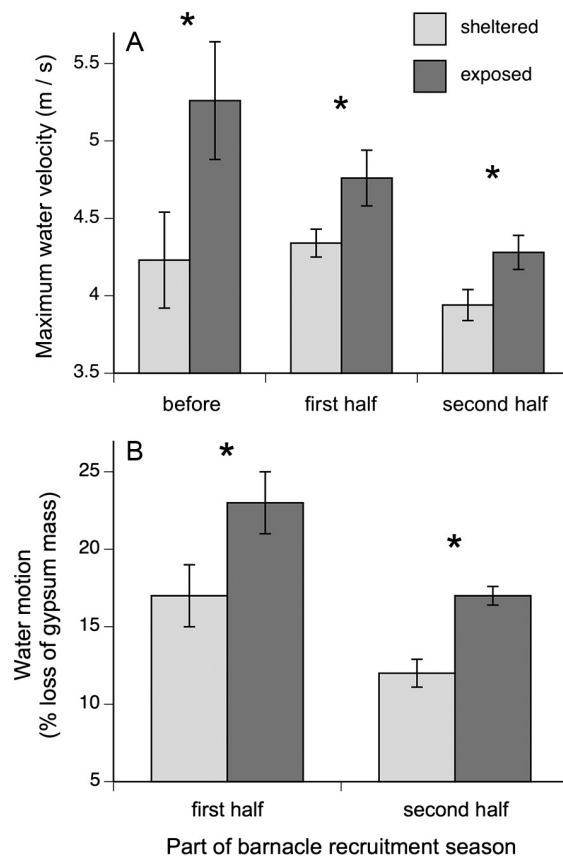


Fig. 2. (A) Maximum water velocity (mean  $\pm$  SE) in sheltered and exposed habitats before and during the 2013 barnacle recruitment season in Nova Scotia, Canada. (B) Water motion (mean  $\pm$  SE) in sheltered and exposed habitats during the same barnacle recruitment season. Asterisks (\*) indicate a significant difference ( $P < 0.05$ ) between both habitat types.

per exposure level), as well as in the first half ( $t_{28} = 2.06$ ,  $P = 0.049$ ,  $N = 15$ ) and second half ( $t_{62} = 2.28$ ,  $P = 0.026$ ,  $N = 32$ ) of the recruitment season (Fig. 2). Water motion, measured as the percent mass loss in gypsum blocks, was significantly higher in exposed habitats than in sheltered habitats both in the first half ( $t_{18} = 2.22$ ,  $P = 0.040$ ,  $N = 10$  per exposure level) and in the second half ( $t_{26} = 4.67$ ,  $P < 0.001$ ,  $N = 14$ ) of the recruitment season (Fig. 2).

In wave-sheltered habitats, the nearby presence of dogwhelks significantly limited barnacle recruit density as measured both at the middle (27 May) and at the end (25 June) of the recruitment season (Table 1, Fig. 3). In exposed habitats,

Table 1. Results of the ANOVAs that tested the effect of dogwhelk nearby presence on barnacle recruitment at the middle (May) and end (June) of the 2013 barnacle recruitment season in wave-sheltered and wave-exposed habitats in Nova Scotia, Canada.

Exposure and month	Source of variation	df	SS	MS	F	P
Sheltered (May)	Dogwhelks	1	3.10	3.10	31.19	<b>0.003</b>
	Block	5	0.77	0.15	1.54	0.323
	Dogwhelks × Block	5	0.50	0.10	0.37	0.859
	Residual	12	3.21	0.27		
Exposed (May)	Dogwhelks	1	0.69	0.69	5.83	0.060
	Block	5	7.47	1.49	12.69	<b>0.007</b>
	Dogwhelks × Block	5	0.59	0.12	0.55	0.734
	Residual	12	2.56	0.21		
Sheltered (June)	Dogwhelks	1	0.95	0.95	13.60	<b>0.014</b>
	Block	5	0.88	0.18	2.51	0.167
	Dogwhelks × Block	5	0.35	0.07	0.44	0.810
	Residual	12	1.89	0.16		
Exposed (June)	Dogwhelks	1	0.01	0.01	0.14	0.724
	Block	5	0.85	0.17	8.72	<b>0.016</b>
	Dogwhelks × Block	5	0.10	0.02	0.58	0.714
	Residual	12	0.40	0.03		

Note: Significant results ( $P < 0.05$ ) are highlighted in boldface.

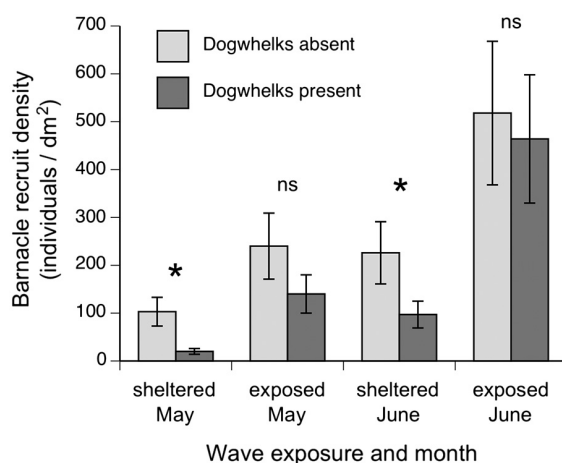


Fig. 3. Barnacle recruit density (mean ± SE) at the middle (May) and end (June) of the 2013 barnacle recruitment season in sheltered and exposed habitats in Nova Scotia, Canada, depending on the nearby presence or absence of dogwhelks. Asterisks (\*) indicate a significant difference ( $P < 0.05$ ) between both dogwhelk treatments, while “ns” indicates a nonsignificant result.

however, barnacle recruit density was unaffected by dogwhelk presence both at the middle and at the end of the recruitment season (Table 1, Fig. 3). The block factor was significant in exposed

habitats at the middle and end of the recruitment season (Table 1). However, those results merely indicate that overall recruit density combining both dogwhelk treatments differed among blocks. The important result is that the dogwhelks × block interaction was never significant for exposed habitats (Table 1), indicating that the lack of dogwhelk NCEs on barnacle recruitment was spatially consistent in such habitats. In sheltered habitats, neither the block factor nor the dogwhelks × block interaction was significant at the middle and end of the recruitment season (Table 1), indicating that the negative dogwhelk NCEs on barnacle recruitment were spatially consistent in such habitats.

## DISCUSSION

Our field experiment has revealed that the nonconsumptive limitation that dogwhelks can exert on barnacle recruitment (Ellrich et al. 2015a) depends on water motion. Thus, this study indicates that water motion can decrease the intensity of predator NCEs not only on prey behavior (Smee and Weissburg 2006, Smee et al. 2008, Large et al. 2011) but also on prey demography as well. This is important because, ultimately, predator NCEs must be understood in terms of prey abundance changes to evaluate

wider impacts on communities (Weissburg et al. 2014, Madin et al. 2016).

The lack of dogwhelk NCEs found in exposed habitats is consistent with a model of cue dispersion under high water velocity and turbulence (Finelli et al. 2000), as such conditions decrease the ability of mobile organisms (such as barnacle larvae) to locate cue sources (Ferner and Weissburg 2005, Robinson et al. 2011). However, high water flow also favors the supply of barnacle larvae to the intertidal zone (Bertness et al. 1992), which was reflected in exposed habitats exhibiting a higher barnacle recruitment than sheltered habitats in our study. Barnacle recruits attract conspecific larvae that are seeking settlement through surface-bound chemical cues, which pelagic larvae detect when exploring the substrate (Knight-Jones 1953, Wetthey 1984, Hills and Thomason 1998, Shanks 2009). Thus, through an abundance of positive cues, high barnacle recruit densities can prevent dogwhelk NCEs on barnacle recruitment (Ellrich et al. 2015a), suggesting that the absence of NCEs observed in exposed habitats at the end of the recruitment season may have occurred also as a result of the flow-driven high recruit density. However, barnacle recruit density in exposed habitats at the middle of the recruitment season was similar to recruit density in sheltered habitats at the end of the recruitment season, but NCEs occurred only in the second case. This comparison reinforces the conclusion that water motion limits dogwhelk NCEs on barnacle recruitment.

Environmental conditions are spatially and temporally variable. Thus, studying the environmental modulation of predator NCEs on prey demography could become a central theme in NCE ecology. The dogwhelk–barnacle system is particularly useful to advance theory on this because the small body sizes and ease of habitat access facilitate field experiments. Conclusions using this system could be applicable, in broad terms, to aquatic predator–prey systems in which benthic prey have pelagic larvae. Specifically regarding water motion, it would be interesting to test if very low water motion (such as in enclosed bays) could decrease dogwhelk NCEs on barnacle recruitment compared with the wave-sheltered habitats that we studied. Calm waters limit the dispersal of chemical cues (Finelli et al. 2000, Pasternak et al. 2004), reducing the ability

of prey to detect cues from predators occurring beyond a small distance (Smee and Weissburg 2006, Large et al. 2011). Thus, for the dogwhelk density and distance to tiles used for our study, very low water motion could limit dogwhelk NCEs on barnacle recruitment, suggesting a possible unimodal relationship between water motion and NCE intensity.

From basic similarities between air and water, this study could have wide-ranging implications for NCE ecology. Animal chemical cues are disseminated through both air and water, and wave-generated water motion has its equivalent in air through winds (Zimmer and Zimmer 2008). As yet, no studies have investigated wind influences on chemically mediated predator NCEs on prey. However, wind has been shown to affect chemically mediated location of mates (Nakamura 1976, Willis et al. 2008) and hosts (Brady et al. 1995) in insects and visually mediated location of potentially threatening moving stimuli in birds (Carr and Lima 2010). Therefore, our findings suggest that, eventually, predator NCEs on prey may be found to depend on air motion in terrestrial environments. Overall, performing experimental research using aquatic and terrestrial predator–prey systems should lead to building a general theory on how the fluid environment influences predator NCEs on prey demography.

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