

Predator density affects nonconsumptive predator limitation of prey recruitment: Field experimental evidence



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ABSTRACT

The influence of predator density on the chemically mediated nonconsumptive effects (NCEs) that predators have on prey recruitment was investigated through a field experiment. In rocky intertidal habitats from Nova Scotia, Canada, cages were established to manipulate the density of predatory dogwhelks (zero, one, five, or ten individuals per cage) surrounding tiles where barnacles were recruited during the 2013 recruitment season (May–June). The used range of dogwhelk density spanned the range found naturally in habitats. The tiles were exposed to chemical cues from the dogwhelks, but not to physical contact with these predators. Barnacle recruit density was measured at the end of the recruitment season (late June), when the highest recruit densities occurred. Compared with the control treatment (no dogwhelks), the one- and five-dogwhelk treatments did not affect barnacle recruit density. However, the occurrence of ten dogwhelks in the cages reduced barnacle recruit density by 54%, on average. A previous study indicated that higher recruit densities than values found in this study can neutralize the negative NCEs of ten dogwhelks, as established recruits chemically attract larvae that are seeking settlement. Therefore, the accumulating evidence indicates that the relative density of predators and prey recruits influences the occurrence of predator NCEs on prey recruitment.

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1. Introduction

Predators control prey populations through the consumption of prey, but they also have nonconsumptive effects (NCEs) that are often mediated by chemical cues, especially in aquatic habitats (Ferrari et al., 2010; Brönmark and Hansson, 2012). For example, as prey organisms detect waterborne chemical cues from nearby predators, prey may decrease feeding or move away to decrease predation risk (Trussell et al., 2003; Keppel and Scrosati, 2004; Molis et al., 2011; Johnston et al., 2012; Orrock et al., 2013). As predator NCEs can influence many prey organisms simultaneously, NCEs may have larger consequences for prey populations than consumptive effects (Turner and Montgomery, 2003; Preisser et al., 2005; Trussell et al., 2006; Matassa and Trussell, 2011). Therefore, identifying the factors that affect the intensity of predator NCEs is relevant to predict their impact on prey populations under different scenarios (Weissburg et al., 2014).

Studies with freshwater (Van Buskirk and Arioli, 2002; Schoeppner and Relyea, 2008; Silberbush and Blaustein, 2011) and estuarine (Hill and Weissburg, 2013) predator–prey systems have shown that negative NCEs on prey intensify as predators become more numerous, although the response function differs among cases. That is consistent with the notion of increasing predator chemical cues in the water as predator

density rises. In fact, the experimental increase of the concentration of predator chemical cues leads to stronger predator NCEs on prey (Loose and Dawidowicz, 1994; von Elert and Ponert, 2000; Ferland-Raymond et al., 2010).

Those studies investigated behavioral and morphological responses of prey. However, as prey population dynamics are ultimately determined by demographic rates, it is necessary to evaluate whether predator density can also influence predator NCEs on prey demography. No studies have addressed this question as yet, and just a few studies have examined predator NCEs on prey demographic rates. Examples include predator NCEs that have been found to limit the rates of settlement (Johnson and Strathmann, 1989; Welch et al., 1997; Tapia-Lewin and Pardo, 2014) and recruitment (Ellrich et al., 2015) of benthic invertebrate prey. To start covering this knowledge gap, this study did a field experiment using an intertidal predator–prey system to test the hypothesis that predator (dogwhelk) density affects the intensity of negative NCEs on prey (barnacle) recruitment. Barnacle settlement is positively related to the concentration of conspecific chemical cues (Crisp, 1990; Dreanno et al., 2007), which suggests that barnacle larvae seeking settlement may also react to dogwhelk cue gradients resulting from dogwhelk density changes, higher densities indicating higher predation risk and presumably stronger NCEs. The particular shape of the NCE functional response to dogwhelk density was difficult to predict, however, as the response function has been found to take different forms in studies that focused on prey behavior and morphology (Van Buskirk and Arioli, 2002; Schoeppner and Relyea, 2008).

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2. Materials and methods

For barnacles, settlement refers to the permanent contact with the substrate established by pelagic cyprid larvae (Jenkins et al., 2000), while recruitment refers to the appearance of new individuals in the population that have metamorphosed after settlement and have reached an arbitrary size that allows them to be counted (Cole et al., 2011). The experiment was done in rocky intertidal habitats in Deming Island (45° 12' 45" N, 61° 10' 26" W), near Whitehead, Nova Scotia, Canada, during the 2013 barnacle recruitment season (May–June). Maximum water velocity measured on site with dynamometers (see design in Bell and Denny, 1994) was $4.2 \pm 0.1 \text{ m s}^{-1}$ (mean \pm SE, range = 3.0–6.9 m s^{-1} ; $n = 94$) during the study period. Thus, the studied habitats were subjected to a moderate wave action, since habitats directly facing the open ocean in Nova Scotia experience water velocities up to 12 m s^{-1} (Hunt and Scheibling, 2001). Intertidal temperature measured every 30 min with submersible loggers (HOBO Pendant Logger, Onset Computer Corp., Pocasset, MA, USA) during the recruitment season was $9.2 \pm 0.2 \text{ }^\circ\text{C}$ (mean \pm SE, $n = 6$ loggers), values not exceeding $20 \text{ }^\circ\text{C}$ during low tides. Coastal seawater salinity was 30 ppt (DFO, 2015). Abundance of coastal phytoplankton (food for barnacle nauplius larvae and recruits; Anderson, 1994; Vargas et al., 2006), measured as chlorophyll-*a* concentration, was $3.22 \pm 0.02 \text{ mg m}^{-3}$ (mean \pm SE, $n = 2$) during the recruitment season, according to MODIS-Aqua satellite data (NASA, 2015).

Semibalanus balanoides (Linnaeus, 1767) is the only intertidal barnacle species on the studied coast (Scrosati and Heaven, 2007). It is a cross-fertilizing hermaphrodite (Anderson, 1994) that broods once per year (Bousfield, 1954; Pineda et al., 2002). In Atlantic Canada, *S. balanoides* mating occurs in early autumn, breeding in winter, and larval release in spring (Bousfield, 1954; Bouchard and Aiken, 2012). Larvae develop over 5–6 weeks in the water column, after which they settle in intertidal habitats (Bousfield, 1954). In northern Nova Scotia, recruits appear in May and June (MacPherson et al., 2008; Beermann et al., 2013). The dogwhelk *Nucella lapillus* (Linnaeus, 1758) is the main predator of *S. balanoides*. Its feeding activity starts at 3–5 °C of water temperature (Largen, 1967a). On the Atlantic coast of Nova Scotia, *N. lapillus* becomes active in April (Hughes, 1972; Hunt and Scheibling, 1998), when it can be found preying on adult barnacles.

Each experimental unit (Fig. 1) consisted in a cage made of a PVC ring (25 cm in diameter and 2.5 cm tall) encased in plastic mesh (openings of 0.5 cm \times 0.5 cm). The cage was subdivided with mesh into a central compartment (12 cm \times 12 cm) and a peripheral compartment (area = 347 cm²). The peripheral compartment was used to manipulate dogwhelk density. The caged dogwhelks could move freely inside the peripheral compartment, but could not access the central compartment. In the central compartment, a PVC tile (8.9 cm \times 4.6 cm \times 0.35 cm) covered with black tape with a sandpaper texture (Permastik self-adhesive anti-skid safety tread, RCR International, Boucherville, Quebec, Canada) was included as a suitable surface for barnacle recruitment. The tile was attached to the bottom mesh of the cage with a plastic screw, a wingnut, and a washer. The caged dogwhelks could approach the tiles only up to 1.5 cm, so settling barnacle larvae and recruits were exposed to dogwhelk cues but not to physical contact with these predators. The cages were held in place with PVC plates and metallic screws inserted in plastic wall anchors in holes drilled in the substrate. To avoid cyprid attraction by adult barnacles (Chabot and Bourget, 1988; Bertness et al., 1992), all barnacle adults found on 40 cm \times 40 cm areas around the center of each cage were removed. Seaweeds (mainly *Fucus vesiculosus* Linnaeus and secondarily *Ascophyllum nodosum* (Linnaeus) Le Jolis) found around the cages were removed to exclude potential effects of seaweed mucus (Johnson and Strathmann, 1989), canopy flow barriers (Jenkins et al., 1999), or canopy thermal and humidifying effects (Beermann et al., 2013) on barnacle recruitment. To exclude NCEs from free-living dogwhelks, any dogwhelks found in a radius of 2 m around each cage were removed at the beginning of the experiment

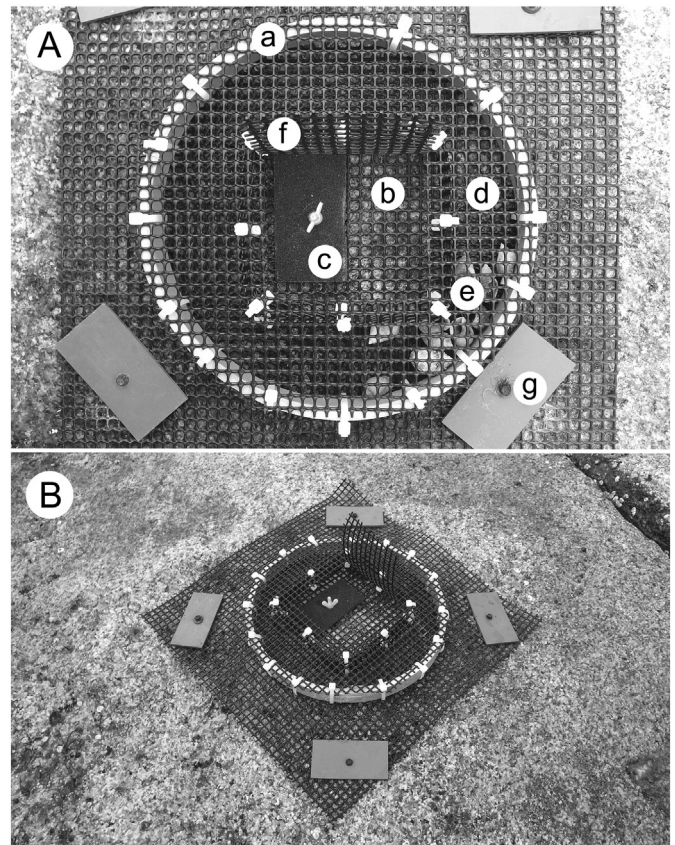


Fig. 1. A: Top view of a cage, showing (a) the PVC ring of 25 cm in diameter, (b) the central compartment with (c) the barnacle recruitment tile, and (d) the peripheral compartment with (e) the dogwhelks. The (f) top mesh of the central compartment is shown open in this picture to improve viewing of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

and every two weeks afterwards; this procedure effectively kept free-living dogwhelks away.

To evaluate the study's hypothesis, four treatments of dogwhelk density were created by placing either zero, one, five, or ten dogwhelks (2.1–2.3 cm long) in the peripheral compartment of a cage. These treatments covered the natural range of dogwhelk density measured in 60 quadrats (40 cm \times 40 cm) on the study area in the 2012 barnacle recruitment season: 0–2.9 dogwhelks dm^{-2} . The caged dogwhelks were collected at the study site. They were not fed during the experiment but, to prevent their starvation, they were replaced every two weeks, releasing the removed dogwhelks hundreds of meters away. The experiment was set up as a randomized complete block design, with each treatment replicated twice in each block (Quinn and Keough, 2002). Six blocks were established at random on the shore at an elevation of 2/3 of the full intertidal range, which is 1.8 m on the studied coast. The experiment thus had 12 replicate cages for each treatment and 48 cages in total. The treatments were set up in late April 2013.

Settled cyprids and recruits appeared for the first time on the shore on 9 May 2013. Settled cyprids (0.8–1 mm long) ceased to appear on the substrate in mid-June. The density of barnacle recruits (1–2 mm in basal diameter) on the tiles was measured on 26 June 2013 using digital pictures of the tiles. No new recruits appeared after our sampling, as indicated by subsequent site inspections. Thus, recruit density was measured at the end of the 2013 recruitment season, when maximum recruit densities were reached.

To test the effects of dogwhelk density (fixed factor with four levels) on barnacle recruit density, an analysis of variance (ANOVA)

appropriate for a randomized complete block design with replicated treatments within blocks (random factor with six levels) was done. The homoscedasticity and normality assumptions were confirmed using Cochran's C-test and Shapiro–Wilk test, respectively, after square-root transformation of the data. After the ANOVA, treatment means were compared through Fisher's Least Significant Difference (LSD) tests (Winer et al., 1991; Zar, 1999), following the recommendations on the error rate of tests made by Carmer and Walker (1982), Moran (2003), and Hurlbert and Lombardi (2012). The data analyses were done with Statistica 12.

3. Results

The ANOVA revealed that dogwhelk density significantly affected barnacle recruit density at the end of the 2013 recruitment season (Table 1). Blocks also significantly affected recruit density (Table 1), but such a result merely indicates that the density of barnacle recruits differed among some blocks. The important result is that the lack of a significant interaction between dogwhelk density and blocks (Table 1) indicates that the effects of dogwhelk density were spatially consistent on the shore.

Fisher's LSD tests indicated that neither one nor five dogwhelks per cage affected barnacle recruit density, as those two treatments did not differ significantly in recruit density from the treatment without dogwhelks ($P = 0.976$ for one dogwhelk and $P = 0.323$ for five dogwhelks; Fig. 2). However, ten dogwhelks per cage significantly limited barnacle recruit density (by 54%, on average), as the comparison with the treatment without dogwhelks indicated ($P = 0.023$; Fig. 2). Barnacle recruit density with ten dogwhelks per cage was also significantly higher than with one dogwhelk (by 52%, on average; $P = 0.021$) but statistically similar as with five dogwhelks ($P = 0.169$; Fig. 2). Recruit density was statistically similar between the treatments with one and five dogwhelks ($P = 0.309$; Fig. 2).

4. Discussion

This study has revealed that predator density affects the occurrence of negative predator NCEs on prey recruitment. The lowest dogwhelk density tested (0.3 individuals dm^{-2}) caused no effects on barnacle recruitment, but the highest density tested (2.9 individuals dm^{-2}) limited recruitment. Peacor (2003) has argued that the occurrence of predator NCEs on prey depends on the balance between predator and prey cues in the environment. Predator cues indicate risk of predation, but prey cues indicate to prey the existence of potentially benign conditions, including a reduced predation risk. Barnacle larvae that are seeking settlement are attracted by chemical cues from recently settled larvae and recruits (Knight-Jones, 1953; Wethey, 1984; Chabot and Bourget, 1988; Hills and Thomason, 1998), which is thought to enhance future survival and reproduction (Clare, 2011). Thus, the lack of predator NCEs at the lowest dogwhelk density tested may have resulted from the relative scarcity of predator cues and abundance of conspecific cues, especially as recruit density increased during the recruitment season. The occurrence of ten times more dogwhelks seems to have reached a necessary level in predator cues for negative NCEs to occur. A separate study has shown that higher recruit densities than those reported here can neutralize the NCEs of ten dogwhelks on

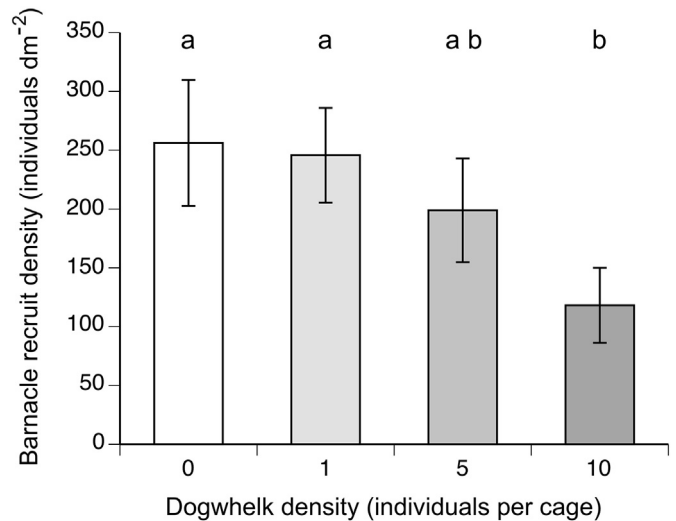


Fig. 2. Density of barnacle recruits (mean \pm SE) at the end of the 2013 recruitment season in Nova Scotia, Canada, depending on the density of nearby dogwhelks. Significant differences ($P < 0.05$) between treatments are indicated when the two corresponding bars do not share the same letter.

barnacle recruitment (Ellrich et al., 2015). Therefore, in combination, these two studies indicate that the occurrence of dogwhelk NCEs on barnacle recruitment indeed depends on the balance between predator and prey cues.

The accumulating knowledge about dogwhelk NCEs on barnacle recruitment suggests that the dogwhelk–barnacle system could be useful to investigate the context dependency of predator NCEs in natural, unmanipulated habitats. For example, coastal phytoplankton abundance enhances intertidal barnacle recruitment (Cole et al., 2011; Menge and Menge, 2013; Ellrich et al., 2015) and habitat-wide dogwhelk density often increases with intertidal crevices, as dogwhelks find refuge from environmental stresses in such places (Menge, 1978; Gosselin and Bourget, 1989; Johnson et al., 1998). Thus, field surveys could test whether nearshore phytoplankton abundance and intertidal substrate heterogeneity act as antagonistic factors regulating dogwhelk NCEs on habitat-wide barnacle recruitment. Another implication of our study is that, at smaller spatial scales within habitats, dogwhelk NCEs on barnacle recruitment could be patchy, as dogwhelk density is spatially heterogeneous, likely as a result of the patchiness of environmental refuges such as crevices and algal canopies (Watt and Scrosati, 2013).

Other studies have found that predator diet and water movement can also affect NCEs from aquatic predators, so a few considerations on the design used for this study are worth making. Predator NCEs on a given prey species may be strongest when the predator feeds on that prey species, as chemicals released by injured conspecifics and by predators as digestive byproducts may indicate to prey a high predation risk (Keppel and Scrosati, 2004; Turner, 2008; Large and Smees, 2010). At the site used for this experiment, barnacles were virtually the only food source for dogwhelks, as mussels (another potential food source; Largen, 1967b) were almost absent. Therefore, the chemical cues released by the caged dogwhelks were related to previous barnacle predation, suggesting that the used dogwhelk diet had the highest possible capacity to elicit NCEs on barnacles. On the other hand, the caged dogwhelks were replaced with free-living dogwhelks every two weeks to avoid starvation, but the caged organisms were not fed during the two-week periods. Thus, allowing caged dogwhelks to continuously feed on barnacles might have strengthened the observed NCEs because of a higher alarm cue concentration in seawater around the recruitment tiles (Smees and Weissburg, 2006a; Large and Smees, 2010). Regarding water movement, the concentration and dispersal of predator chemical cues are influenced by water flow and turbulence. Dilution of predator

Table 1

Summary results of the ANOVA done to evaluate the nonconsumptive effects of dogwhelk density on barnacle recruit density at the end of the 2013 recruitment season.

Source of variation	df	SS	MS	F	P
Dogwhelk density	3	222.21	74.07	9.61	0.001
Block	5	477.23	95.45	12.39	<0.001
Dogwhelk density \times block	15	115.58	7.71	0.28	0.993
Residual	24	664.69	27.70		

cues with water movement can decrease the ability of prey to detect predators and therefore weaken NCEs, but calm waters may also weaken NCEs by limiting the dispersal of predator cues (Smee and Weissburg, 2006b; Large et al., 2011). Replication of the dogwhelk–barnacle study under higher and lower levels of wave exposure than considered in this study could evaluate whether water movement can modify dogwhelk density influences on dogwhelk NCEs on barnacle recruitment.

Studies focusing on predator NCEs on prey behavior and morphology have found that either NCEs intensify continuously with predator density or that NCEs occur only when a certain predator density is reached, showing little change under higher densities (the underlying causes are under debate; Van Buskirk and Arioli, 2002; Schoeppner and Relyea, 2008; Hill and Weissburg, 2013). The present study focusing on prey recruitment suggests a combination of responses. On the one hand, a threshold predator density was obviously needed for NCEs to occur, as one dogwhelk per cage did not limit barnacle recruitment but ten dogwhelks did. On the other hand, the comparisons done among the one-, five-, and ten-dogwhelk treatments suggest that NCEs might intensify more or less continuously with dogwhelk density for that density range. Establishing the precise shape of the NCE functional response to dogwhelk density was beyond the scope of this study, but it could be determined using several density treatments in a future field experiment.

Overall, this field study shows that predator density matters for the occurrence of negative predator NCEs on a demographic rate of prey. Studies using other predator–prey systems focusing on recruitment as well as on other demographic rates should help to build a general understanding of how predator density modulates the intensity of NCEs on prey populations.

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