

# Predator nonconsumptive effects on prey recruitment weaken with recruit density

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**Abstract.** We investigated the nonconsumptive effects (NCEs) of predatory dogwhelks (*Nucella lapillus*) on intertidal barnacle (*Semibalanus balanoides*) recruitment through field experiments on the Gulf of St. Lawrence coast and the Atlantic coast of Nova Scotia, Canada. We studied the recruitment seasons (May–June) of 2011 and 2013. In 2011, the Gulf coast had five times more nearshore phytoplankton (food for barnacle larvae and recruits) during the recruitment season and yielded a 58% higher barnacle recruit density than the Atlantic coast at the end of the recruitment season. In 2013, phytoplankton levels and barnacle recruit density were similar on both coasts and also lower than for the Gulf coast in 2011. Using the comparative–experimental method, the manipulation of dogwhelk presence (without allowing physical contact with prey) revealed that dogwhelk cues limited barnacle recruitment under moderate recruit densities (Atlantic 2011/2013 and Gulf 2013) but had no effect under a high recruit density (Gulf 2011). Barnacle recruits attract settling larvae through chemical cues. Thus, the highest recruit density appears to have neutralized dogwhelk effects. This study suggests that the predation risk perceived by settling larvae may decrease with increasing recruit density and that prey food supply may indirectly influence predator NCEs on prey recruitment.

**Key words:** intertidal habitats; nonconsumptive effect; *Nucella lapillus*; predation risk; predator cue; recruitment; *Semibalanus balanoides*.

## INTRODUCTION

Recruitment is a key process affecting population persistence. Many marine invertebrates have a complex life cycle that includes a benthic adult phase and pelagic dispersal of larvae. The pelagic phase ends with settlement, the moment when larvae make contact with the substrate and metamorphose. Recruitment is the appearance of new individuals that have developed after settlement and have reached an arbitrary size that allows them to be counted (Pineda et al. 2009).

The recruitment rate is often affected by the consumption of developing settlers by benthic predators (Buschbaum 2002, O'Connor et al. 2008). Predators, however, may also have nonconsumptive effects (NCEs) on prey. Through the detection of waterborne chemical cues released by predators, adult prey may decrease feeding or move away to avoid predation (Trussell et al. 2003, Keppel and Scrosati 2004, Molis et al. 2011, Johnston et al. 2012, Orrock et al. 2013). As NCEs from nearby predators can influence many prey organisms simultaneously, such effects may have larger consequences for prey populations than consumptive effects (Preisser et al. 2005, Trussell et al. 2006, Matassa and

Trussell 2011). Knowledge of predator NCEs on the recruitment of benthic prey, however, is still limited. Predator NCEs decrease settlement in crabs, for example (Welch et al. 1997), but only daily effects were evaluated, so recruitment responses over weeks or months remain unknown. Johnson and Strathmann (1989) found that cues from dogwhelk (*Nucella lamellosa*) pedal mucus decrease settlement and early recruitment in barnacles (*Balanus glandula*). However, recruitment was evaluated only up to four days after settlement, so possible effects throughout the entire recruitment season (the months-long period during which recruits appear) also remain unknown.

During the recruitment season of a prey species, conspecifics often accumulate. Positive intraspecific interactions could potentially alter the perception of predation risk in settling larvae and, hence, predator NCEs on prey recruitment. For example, barnacle larvae that are seeking settlement (cyprids) are attracted to recently settled conspecifics (Wetley 1984, Hills and Thomason 1998) and recruits (Knight-Jones 1953, Shanks 2009) through chemical cues. This behavior, thought to aid cyprids in finding conditions favoring survival, growth, and reproduction (Clare 2011), leads to gregarious settlement (Crisp and Meadows 1962, Matsumura et al. 2000) and, thus, the gradual accumulation of attractive conspecific cues. Furthermore, while exploring the substrate, cyprids leave proteinaceous footprints consisting of a temporary adhesive (Walker

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and Yule 1984) that lasts up to three weeks and attract more cyprids (Yule and Walker 1985). Therefore, the accumulation of attractive conspecific cues during the recruitment season might lessen predator NCEs on prey recruitment.

Using a predator–prey system from NW Atlantic rocky shores, we tested the hypotheses that (1) predatory dogwhelks (*Nucella lapillus*) have negative nonconsumptive effects on barnacle (*Semibalanus balanoides*) recruitment and that (2) relatively high recruit densities at the end of the recruitment season weaken predator NCEs. We applied the comparative–experimental method (Menge et al. 1994, Vinuela et al. 2014) and performed a manipulative experiment on two coasts that were expected to differ in barnacle recruit density based on previous findings (Cole et al. 2011). In search for generality, we repeated the experiments in another year.

#### METHODS

We worked in rocky intertidal habitats on the Gulf of St. Lawrence coast and the Atlantic coast of Nova Scotia, Canada, in 2011 and 2013. In 2011, we conducted the Gulf experiment at Sea Spray (45°46' N, 62°08' W) and the Atlantic experiment at Glasgow Head (45°12' N, 61°10' W). In 2013, we did the Gulf experiment between Sea Spray and Oceanview (45°46' N, 62°07' W) and the Atlantic experiment between Halfway Cove (45°20' N, 61°22' W) and Half Island Cove (45°21' N, 61°11' W). On both coasts, the intertidal substrate is stable bedrock. The studied habitats are subjected to limited wave action. Maximum water velocity measured in situ with dynamometers (see design in Bell and Denny 1994) during the barnacle recruitment season (May and June) was  $2.16 \pm 0.05$  m/s (mean  $\pm$  SE) for the Gulf habitats (range, 1.89–2.50 m/s;  $N = 25$ ) and  $2.07 \pm 0.04$  m/s for the Atlantic habitats (range, 1.83–2.56 m/s;  $N = 25$ ), confirming their wave-sheltered nature, as habitats facing the open ocean directly in Nova Scotia can experience values of 12 m/s (Hunt and Scheibling 2001). Sea surface temperature during the barnacle recruitment season was similar between both coasts:  $7.6^\circ \pm 1.2^\circ\text{C}$  (mean  $\pm$  SE) on the Gulf coast and  $5.9^\circ \pm 1.1^\circ\text{C}$  on the Atlantic coast in 2011, and  $8.8^\circ \pm 1.9^\circ\text{C}$  on the Gulf coast and  $8.4^\circ \pm 1.6^\circ\text{C}$  on the Atlantic coast in 2013 (MODIS-Aqua satellite data; data available online).<sup>4</sup> Coastal seawater salinity was approximately 30 ppt on both coasts (data available online).<sup>5</sup>

*Semibalanus balanoides* is the only intertidal barnacle species on these coasts. It is a cross-fertilizing hermaphrodite (Pineda et al. 2002) with one brood per year (Bousfield 1954). In Atlantic Canada, *S. balanoides* mating occurs in autumn, breeding in winter, and larval release in spring (Bousfield 1954). Development of larval stages in the water takes 5–6 weeks (Bousfield 1954),

cyprid larvae being abundant until late spring (Minchinton and Scheibling 1991). Recruits (1–2 mm of basal diameter) appear on the studied coasts during May and June (MacPherson and Scrosati 2008, Beermann et al. 2013). The dogwhelk *Nucella lapillus* is a major predator of *S. balanoides* on these coasts. Movement and foraging of *N. lapillus* starts around 3–5°C of water temperature and increases up to 20°C (Largen 1967). In Nova Scotia, adult dogwhelks can be found preying on barnacles as early as April.

We selected the Gulf and Atlantic coasts because the former was expected to yield a higher barnacle recruit density than the latter. A study in 2007 found that the Gulf coast had higher nearshore phytoplankton abundance than the Atlantic coast and that *Semibalanus balanoides* recruit density was 75% higher on the Gulf coast at the end of the recruitment season (Cole et al. 2011). The positive association between barnacle recruitment and phytoplankton abundance likely reflects benthic–pelagic coupling, since phytoplankton is a major food source for barnacle nauplius larvae (stages preceding the cyprids) and recruits (Anderson 1994, Vargas et al. 2006). Cyprids do not feed, but live on reserves accumulated during nauplius stages. To see if differences in barnacle food supply between coasts persisted in our study, we evaluated nearshore phytoplankton abundance during the 2011 and 2013 recruitment seasons (May and June) using MODIS-Aqua satellite data on chlorophyll-*a* concentration as a proxy. Chlorophyll-*a* concentration was five times higher on the Gulf coast ( $7.14 \pm 1.58$  mg/m<sup>3</sup>; mean  $\pm$  SE) than on the Atlantic coast ( $1.19 \pm 0.18$  mg/m<sup>3</sup>) in 2011, but similar between the Gulf ( $4.68 \pm 0.01$  mg/m<sup>3</sup>) and Atlantic ( $4.30 \pm 0.66$  mg/m<sup>3</sup>) coasts in 2013 (see footnote 4).

Using the comparative–experimental method, we ran the same experiment on each coast and year to test if barnacle recruit density weakens dogwhelk NCEs on barnacle recruitment. We used two dogwhelk treatments (presence vs. absence) arranged as a randomized complete block design, replicating each treatment twice within each block (Quinn and Keough 2002). We established six (2011) or eight (2013) blocks on each coast at random along the shoreline. Our experiments used context-dependent differences in recruit density as opposed to in situ density manipulations because mechanical recruit removals are imperfect and would have likely left barnacle cues and previous footprints that could have attracted new larvae seeking settlement.

Each experimental unit (see Appendix A) included a cage made up of a PVC ring (25 cm in diameter, 2.5 cm high) and plastic mesh (0.5 cm of opening size). The cage was subdivided with mesh into a central compartment (12  $\times$  12 cm) and a peripheral compartment (area = 347 cm<sup>2</sup>). We used the peripheral compartment to manipulate dogwhelk occurrence by either enclosing 10 dogwhelks or by excluding them. Caged dogwhelks could move freely inside the peripheral compartment but

<sup>4</sup> [http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance\\_id=ocean\\_month](http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month)

<sup>5</sup> <http://www.meds-sdmm.dfo-mpo.gc.ca>

TABLE 1. Results of ANOVAs testing the effect of dogwhelk (*Nucella lapillus*) cues on barnacle (*Semibalanus balanoides*) recruit density at the end of the recruitment seasons of 2011 and 2013 on the Gulf of St. Lawrence coast and the Atlantic coast of Nova Scotia, Canada.

Coast and year	Source of variation	df	SS	MS	F	P
Gulf, 2011	Dogwhelks	1	10 993	10 993	1.37	0.295
	Blocks	5	78 930	15 786	1.96	0.238
	Dogwhelks $\times$ blocks	5	40 213	8 043	1.12	0.400
	Residual	12	86 107	7 176		
Atlantic, 2011	Dogwhelks	1	178.08	178.08	33.33	<b>0.002</b>
	Blocks	5	246.36	49.27	9.22	<b>0.015</b>
	Dogwhelks $\times$ blocks	5	26.71	5.34	0.34	0.880
	Residual	12	189.85	15.82		
Gulf, 2013	Dogwhelks	1	1.88	1.88	22.55	<b>0.002</b>
	Blocks	7	8.98	1.28	15.42	<b>0.001</b>
	Dogwhelks $\times$ blocks	7	0.58	0.08	0.49	0.826
	Residual	16	2.70	0.17		
Atlantic, 2013	Dogwhelks	1	7.17	7.17	37.22	<b>0.001</b>
	Blocks	7	9.88	1.41	7.33	<b>0.009</b>
	Dogwhelks $\times$ blocks	7	1.35	0.19	0.21	0.976
	Residual	16	14.37	0.90		

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

could not access the central compartment. In the central compartment, we included a PVC recruitment tile ( $8.9 \times 4.6 \times 0.35$  cm) covered with safety-walk tape (Farrell et al. 1991) to offer a homogeneous surface for barnacle recruitment. The tile was attached to the bottom mesh of the cage using a plastic screw, a wingnut, and a washer. 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 tidal range on both coasts is 1.8 m. We installed the cages at an elevation of 61–65% of the highest elevation at which barnacles occurred naturally above each block on each coast. By keeping such a relative elevation of blocks nearly constant, and given that the local upper boundary of barnacle distribution indicates potential local differences in water splash caused by local topography, we ensured that settling larvae and recruits across replicate cages were subjected to similar periods of dogwhelk cue exposure and (for recruits) food availability. To avoid cyprid attraction by adult barnacles (Chabot and Bourget 1988, Bertness et al. 1992), we removed all barnacle adults from  $40 \times 40$  cm areas around the center of each cage. We also removed seaweeds (mainly *Ascophyllum nodosum* and secondarily *Fucus vesiculosus*) around the cages 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. We attached the cages to the substrate with plastic anchors, screws, and washers. The average block size was  $7.2 \pm 1.4$  m<sup>2</sup> (mean  $\pm$  SE), and the replicate cages were separated by at least 0.5 m in each block.

We used adult dogwhelks 21–23 mm in shell length. We started the experiments by placing the recruitment tiles and dogwhelks into the cages in April 2011 and 2013. To minimize potential NCEs from free-living dogwhelks, we

removed any dogwhelks found around the cages initially and every two weeks afterwards. We did not feed the dogwhelks inside the cages during the experiments but, to prevent their starvation, we replaced the dogwhelks every two weeks with individuals collected locally, releasing the removed individuals hundreds of meters away. We left the tiles in place until the end of the recruitment season. Periodic observations indicated that recruits started to appear during the first week of May. We evaluated predator NCEs on barnacle recruitment at the end of the recruitment season, when the highest recruit densities were reached. We measured recruit density using pictures of the tiles (see Appendix B) taken on 15 June 2011 (Atlantic) and 16 June 2011 (Gulf) and on 27 June 2013 (Atlantic) and 28 June 2013 (Gulf). No new recruits appeared afterward. Thus, the recruitment season lasted about six weeks in 2011 and eight weeks in 2013.

For each coast and year (in agreement with Moran 2003), we tested for predator NCEs (fixed factor with two levels: dogwhelk presence and absence) on barnacle recruit density through analysis of variance (ANOVA) for a randomized complete block design with replicated treatments within blocks (random factor with six levels in 2011 and eight levels in 2013; Quinn and Keough 2002). We tested the homoscedasticity and normality assumptions with Cochran's *C* test and Shapiro Wilk's test, respectively. All analyses were done with Statistica 10.

## RESULTS

In the four experimental trials, barnacle recruits reached their highest abundance at the end of the recruitment season. Dogwhelk presence had significantly negative NCEs on barnacle recruitment in three cases (Table 1), limiting recruitment (compared with control tiles) by 51% on the Gulf coast in 2013 and by 60% (2011) and 83% (2013) on the Atlantic coast (Fig. 1). Dogwhelk presence, however, did not affect barnacle recruitment on the Gulf coast in 2011 (Table 1). There were significant differences

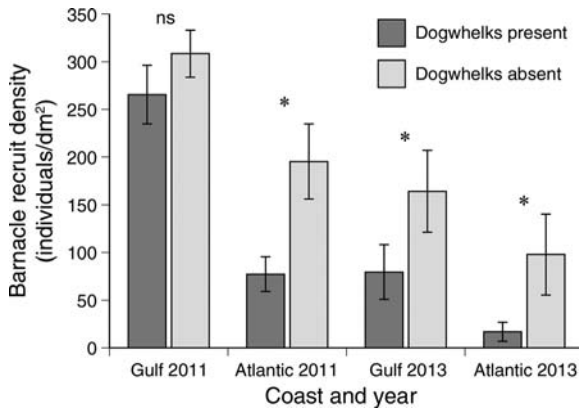


FIG. 1. Barnacle (*Semibalanus balanoides*) recruit density (mean  $\pm$  SE) at the end of the recruitment seasons of 2011 and 2013 on the Gulf of St. Lawrence coast and the Atlantic coast of Nova Scotia, Canada, depending on nearby presence or absence of dogwhelks (*Nucella lapillus*). Asterisks (\*) indicate a significant difference ( $P < 0.05$ ) between both dogwhelk treatments, while ns indicates a nonsignificant result.

among blocks in three cases (Table 1), but such results only indicate that overall recruitment (combining both dogwhelk treatments) differed among some blocks. The important result about blocks is that the dogwhelks  $\times$  blocks interaction was never significant (Table 1), indicating that the occurrence (Gulf coast in 2013 and Atlantic coast in 2011 and 2013) or absence (Gulf coast in 2011) of dogwhelk NCEs on barnacle recruitment were spatially consistent on the shore for each corresponding case. The lack of dogwhelk NCEs occurred under the highest recruit density of barnacles. In control tiles, the average recruit density on the Gulf coast in 2011 was 58% (2011) and 215% (2013) higher than on the Atlantic coast and 88% higher than on the Gulf coast in 2013 (Fig. 1). In turn, the highest barnacle recruit density in control tiles occurred when phytoplanktonic food supply for barnacles was highest (see *Methods*). Lower values of food supply were related to more moderate recruit densities and, ultimately, to the occurrence of negative dogwhelk NCEs on barnacle recruitment.

#### DISCUSSION

As found in 2007 (Cole et al. 2011), in 2011 the Gulf coast was more productive in terms of phytoplanktonic food supply and exhibited greater barnacle recruit density than the Atlantic coast in Nova Scotia. In turn, our experiments revealed that dogwhelks had negative NCEs on barnacle recruitment on the Atlantic coast, but on the Gulf coast they had no effect. These results are consistent with a lessening of the predation risk perceived by cyprid larvae seeking settlement under relatively high conspecific densities. Recently settled cyprids and recruits are known to attract settling cyprids through chemical cues (Knight-Jones 1953, Crisp and Meadows 1962, Wethey 1984, Hills and Thomason 1998). Thus, the relatively high conspecific densities on

the Gulf coast may have provided enough attractive cues to neutralize the influence of dogwhelk cues. This interpretation is reinforced by the results of 2013. In that year, barnacle recruit density was similar on the Gulf and Atlantic coasts (likely because of their similarity in barnacle food supply) and comparable to values for the Atlantic coast in 2011. Consistent with the idea of stronger NCEs due to lower recruit densities and weaker chemical cues, dogwhelks had negative NCEs on barnacle recruitment on both studied coasts in 2013.

The absence of NCEs on the Gulf coast in 2011 cannot be explained by a hypothetical decrease of dogwhelk cues. In all cases, we replaced the caged dogwhelks every 14 days with dogwhelks of similar size from the same coast. Regular inspections during the experiments indicated that the activity of caged dogwhelks was similar to that of free dogwhelks. Inside and outside of the cages, dogwhelks crawled freely while submerged during rising tides and were firmly attached to the substrate during low tides. Also, no caged dogwhelks died. Moreover, dogwhelks deposited egg capsules inside the cages, as seen in areas near the blocks. *Nucella lapillus* deposits egg capsules in locations of low desiccation (Crothers 1985). These observations were consistent on both studied coasts, suggesting that dogwhelk activity and fitness were not affected by the experimental conditions. No dogwhelk hatchlings emerged from the egg capsules inside the cages during the experiments, as development of *N. lapillus* embryos takes about four months (Fretter and Graham 1985). Likewise, dogwhelk recruits ( $\sim 1$  cm in shell length) did not occur on the coast until early August, coinciding with the onset of *N. lapillus* recruitment in Nova Scotia (Hunt and Scheibling 1998). Lastly, no dogwhelks escaped from the cages, crawled on top of the cages, or invaded them from the outside. Thus, predator chemical cues should have been consistently present in cages with dogwhelks throughout both recruitment seasons on both coasts.

The setup of our four experiments was the same, and the two studied coasts were similar in terms of temperature, salinity, and wave exposure. This further supports the notion that high barnacle recruit density was behind the absence of dogwhelk NCEs on the Gulf coast in 2011. The observed links between phytoplankton abundance, barnacle recruitment, and presence or absence of dogwhelk NCEs suggest that, through the regulation of recruit density, pelagic food supply for barnacles may influence the occurrence of predator NCEs on barnacle recruitment.

Johnson and Strathmann (1989) found that pedal mucus of *Nucella lamellosa* limited daily settlement and early recruitment (monitored up to four days) of *Balanus glandula*. The recruitment season of *B. glandula*, however, lasts several months (Menge and Menge 2013). Thus, mean *B. glandula* recruit density did not exceed 38 recruits/dm<sup>2</sup> with dogwhelk cues and 65 recruits/dm<sup>2</sup> without dogwhelk cues in the study by Johnson and Strathmann (1989). Such values are similar

to those we found for *Semibalanus balanoides* early in its recruitment season. Therefore, current evidence indicates that dogwhelk NCEs limit barnacle recruitment under low recruit densities in these species. Since *B. glandula* recruits attract cyprids at the density attained by *S. balanoides* recruits on the Gulf coast in 2011 (Shanks 2009), it is worth testing if higher recruit densities than considered for *B. glandula* by Johnson and Strathmann (1989; i.e., as the recruitment season advances) could also neutralize dogwhelk NCEs on *B. glandula* recruitment.

When dogwhelks do not preferentially feed on a barnacle species, predator NCEs on barnacle recruitment may not occur. For example, *Nucella lamellosa* pedal mucus did not decrease *Semibalanus cariosus* settlement or recruitment in a four-day study (Johnson and Strathmann 1989). The large size and thatched shell of *S. cariosus* are thought to protect this barnacle from dogwhelk predation (Palmer 1983, Carroll and Wethey 1990). In fact, *N. lamellosa* prefers *Balanus glandula* when given the choice (Palmer 1983, Carroll and Wethey 1990). As *B. glandula* and *S. cariosus* co-occur in NE Pacific intertidal habitats, the lack of *N. lamellosa* NCEs on *S. cariosus* recruitment could be a consequence of *N. lamellosa* feeding preferences. On Gulf of California rocky shores, pedal mucus of the dogwhelk *Acanthina angelica* actually increased settlement in the barnacle *Chthamalus anisopoma* after one day of testing (Raimondi 1988). On the one hand, *C. anisopoma* can plastically develop a shell form that decreases predation (Lively 1986), suggesting that *A. angelica* may have had little influence on the evolution of settlement behavior in *C. anisopoma*. On the other hand, *C. anisopoma* cannot survive the intense abiotic stress at high intertidal elevations, so cyprids use chemical cues from organisms (including dogwhelks) from lower elevations to settle in benign habitats (Raimondi 1988). As *B. glandula* and *Semibalanus balanoides* can tolerate harsh high-intertidal conditions (Connell 1970, Scrosati and Heaven 2007), it would not be particularly advantageous for them to follow cues from benthic mollusks, including their predators, for settlement.

Overall, this study provides field experimental evidence indicating that barnacle recruit density can weaken the negative NCEs of predatory dogwhelks on barnacle recruitment. The replication of our experiment on different coasts and years suggests that pelagic food supply for barnacles may indirectly influence predator NCEs on barnacle recruitment through the increase of recruit density. It is possible that, in prey species exhibiting positive intraspecific interactions at settlement, increasing recruit densities may contribute to decreasing predator NCEs on prey recruitment. Future tests should evaluate this possibility using other predator-prey systems.

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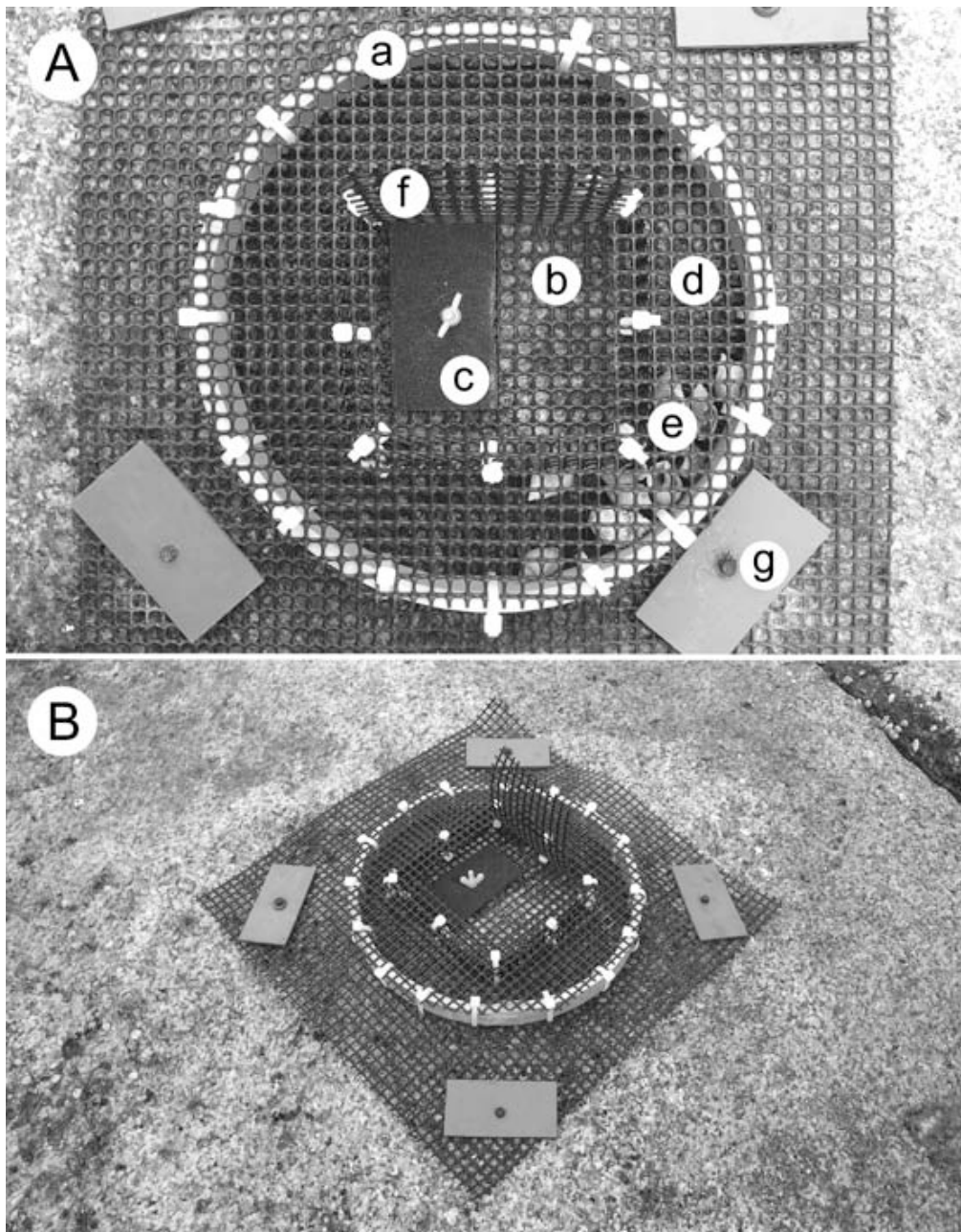
## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-1856.1.sm>

Julius A. Ellrich, Ricardo A. Scrosati, and Markus Molis (2015). *Predator nonconsumptive effects on barnacle recruitment weaken with recruit density. Ecology* 96 (3): 611–616.

**APPENDIX A.** Experimental unit. (A) Top view of a cage, showing (a) the PVC ring of 25 cm in diameter, (b) the central compartment containing (c) the barnacle recruitment plate, and (d) the peripheral compartment containing (e) the dogwhelks. The (f) top mesh of the central compartment appears open in this picture to improve viewing of the recruitment plate, but it remained closed with plastic cable ties during the experiments. The cage was secured with (g) screws to the substrate. (B) Side view of the cage, showing its limited height (2.5 cm). Photo credits: Julius A. Ellrich.



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**APPENDIX B.** Top view of a recruitment plate (8.9 cm x 4.6 cm) exhibiting barnacle recruits at the end of the recruitment season and the central screw and wingnut that kept the plate attached to the bottom mesh of the corresponding cage. Photo credit: Julius A. Ellrich.

