

RESEARCH ARTICLE

Adult Prey Neutralizes Predator Nonconsumptive Limitation of Prey Recruitment

Julius A. Ellrich^{1*}, Ricardo A. Scrosati¹, Katharina Romoth^{1,2}, Markus Molis³

1 Department of Biology, St. Francis Xavier University, Antigonish, Nova Scotia, Canada, **2** Department of Chemistry and Biology of the Marine Environment, Carl von Ossietzky Universität, Oldenburg, Niedersachsen, Germany, **3** Section Functional Ecology, Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Bremen, Germany

* jellrich@stfx.ca



OPEN ACCESS

Citation: Ellrich JA, Scrosati RA, Romoth K, Molis M (2016) Adult Prey Neutralizes Predator Nonconsumptive Limitation of Prey Recruitment. PLoS ONE 11(4): e0154572. doi:10.1371/journal.pone.0154572

Editor: Ross Coleman, The University of Sydney, AUSTRALIA

Received: November 26, 2015

Accepted: April 15, 2016

Published: April 28, 2016

Copyright: © 2016 Ellrich et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files ([S1 Dataset](#)).

Funding: Research was funded through grants by Canada Research Chairs (grant number: 210283, <http://www.chairs-chaires.gc.ca/home-accueil-eng.aspx>), the Canada Foundation for Innovation (grant number: 202034, <http://www.innovation.ca/>) and the Natural Sciences and Engineering Research Council (grant number: 311624, http://www.nserc-crsng.gc.ca/index_eng.aspx) received by RAS. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Abstract

Recent studies have shown that predator chemical cues can limit prey demographic rates such as recruitment. For instance, barnacle pelagic larvae reduce settlement where predatory dogwhelk cues are detected, thereby limiting benthic recruitment. However, adult barnacles attract conspecific larvae through chemical and visual cues, aiding larvae to find suitable habitat for development. Thus, we tested the hypothesis that the presence of adult barnacles (*Semibalanus balanoides*) can neutralize dogwhelk (*Nucella lapillus*) nonconsumptive effects on barnacle recruitment. We did a field experiment in Atlantic Canada during the 2012 and 2013 barnacle recruitment seasons (May–June). We manipulated the presence of dogwhelks (without allowing them to physically contact barnacles) and adult barnacles in cages established in rocky intertidal habitats. At the end of both recruitment seasons, we measured barnacle recruit density on tiles kept inside the cages. Without adult barnacles, the nearby presence of dogwhelks limited barnacle recruitment by 51%. However, the presence of adult barnacles increased barnacle recruitment by 44% and neutralized dogwhelk nonconsumptive effects on barnacle recruitment, as recruit density was unaffected by dogwhelk presence. For species from several invertebrate phyla, benthic adult organisms attract conspecific pelagic larvae. Thus, adult prey might commonly constitute a key factor preventing negative predator nonconsumptive effects on prey recruitment.

Introduction

Predators control prey populations by killing prey, but they also have nonconsumptive effects (NCEs) on prey [1]. NCEs are often triggered by chemical or visual predator cues that are detected by prey [2,3]. Upon cue detection, immediate prey responses often include moving away or decreasing feeding activities to minimize predation risk [4–9]. Such responses occur in aquatic and terrestrial predator–prey systems [10,11]. As predator cues may reach many prey individuals at the same time, NCEs may have larger consequences for prey populations than

Competing Interests: The authors have declared that no competing interests exist.

consumptive effects, as indicated by theoretical [12,13] and empirical [14–17] studies. For this reason, currently an important aim in ecology is to identify what factors affect the intensity of predator NCEs on prey [18].

Studies on invertebrate predator–prey systems have found that predator cues can limit prey larval settlement [3,19–21] and subsequent recruitment [22], as a number of settling larvae move away when predator cues are detected to reduce future predation risk [23–25]. However, studies using species from several groups, including molluscs, polychaetes, echinoderms, arthropods, and tunicates, have found that benthic adult organisms chemically attract conspecific pelagic larvae that are seeking habitat for settlement [26–31]. Such a behavior is thought to enhance the long-term persistence of populations, as the attraction exerted by adults guides larvae to locate adequate conditions for development [30,32,33]. Therefore, for species in which adults attract conspecific larvae, the presence of adult organisms might reduce, or even eliminate, predator NCEs on the recruitment of such prey species. This study experimentally investigates this notion using marine predators (dogwhelks) and prey (barnacles) as a model system.

Barnacles are sessile organisms with pelagic larvae and are common in intertidal habitats worldwide [34]. Dogwhelks are benthic predatory snails that frequently feed on intertidal barnacles [35,36]. Barnacle larvae often react negatively to chemical cues released by dogwhelks (e.g., pedal mucus [19]). Recent field experiments have shown that, in the absence of adult barnacles, waterborne chemical cues from dogwhelks can limit barnacle larval settlement [21] and, ultimately, barnacle recruitment [22]. However, adult barnacles attract conspecific larvae that are seeking settlement [37–40] through chemical [41–45] and visual [46] cues, in that way enhancing barnacle recruitment [47–49]. Therefore, we conducted a factorial field experiment that simultaneously manipulated the presence of dogwhelks and adult barnacles to test the hypothesis that adult barnacles can neutralize the negative NCEs that dogwhelks have on barnacle recruitment. To examine the generality of this prediction, we replicated the experiment in two years.

Material and Methods

Study System

For barnacles, settlement is the permanent contact with the substrate established by pelagic cyprid larvae [50], while recruitment is the appearance of new benthic individuals that have metamorphosed after larval settlement and have reached a size that allows them to be counted [51]. We did the experiment in rocky intertidal habitats on Deming Island (45° 12' 45" N, 61° 10' 26" W), near Whitehead, on the Atlantic coast of Nova Scotia, Canada. The experiment spanned two barnacle recruitment seasons (2012 and 2013), that is, the period during which recruits appeared on the shore. Daily maximum water velocity (an indication of wave exposure) determined with dynamometers (see design in [52]) was $5.0 \pm 0.7 \text{ m s}^{-1}$ (mean \pm SE, range = 3.5–6.6 m s^{-1} ; $n = 5$) in the 2012 recruitment season and $4.2 \pm 0.1 \text{ m s}^{-1}$ (range = 3.0–6.9 m s^{-1} ; $n = 94$) in the 2013 recruitment season. 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} [53]. Intertidal temperature measured every 30 minutes throughout consecutive high and low tides with submersible loggers (HOBO Pendant Logger, Onset Computer Corp., Pocasset, MA, USA) was $9.2 \pm 0.2^\circ\text{C}$ (mean \pm SE; $n = 6$ loggers) during the 2013 recruitment season (no data are available for 2012), with temperatures not exceeding 20°C during low tides. Coastal seawater salinity was 30 ppt in both years [54]. The abundance of coastal phytoplankton (food for barnacle nauplius larvae and recruits [34, 55]) measured as chlorophyll-*a* concentration was $1.50 \pm 0.49 \text{ mg m}^{-3}$ (mean \pm SE; $n = 3$) during the 2012

recruitment season and $3.22 \pm 0.02 \text{ mg m}^{-3}$ ($n = 2$) during the 2013 recruitment season (MODIS-Aqua satellite data [56]).

On this coast, *Semibalanus balanoides* (L. 1767) is the only intertidal barnacle species [57]. It is a cross-fertilizing hermaphrodite [34,58] that broods once per year [59,60]. In Atlantic Canada, *S. balanoides* mates in early autumn, breeds in winter, and releases pelagic larvae in spring [59,61]. Larvae develop over 5–6 weeks in the water column [59]. In northern Nova Scotia, barnacle recruits appear in intertidal habitats in May and June [49]. The dogwhelk *Nucella lapillus* (L. 1758) is the main predator of *S. balanoides* on this coast. Movement and feeding in *N. lapillus* start at 3–5°C of water temperature and increase up to 20°C [62]. On the Atlantic coast of Nova Scotia, *N. lapillus* becomes active in April [35,63], when it can be found preying on barnacles. Under the environmental conditions described above, *N. lapillus* cues limit *S. balanoides* recruitment [22] by limiting larval settlement [21]. *Nucella lapillus* releases pedal mucus during locomotion [64].

Field Experiment

To test our hypothesis, we did a manipulative field experiment. Both in 2012 and 2013, we used "dogwhelks" and "adult barnacles" as crossed factors, each with two levels (presence and absence), arranged following a randomized complete block design with each of the four treatments replicated twice within each block. We established six blocks each year on relatively horizontal intertidal areas, totalling 24 experimental units (12 per year) for each of the four treatments involving the "dogwhelks" and "adult barnacles" factors. We used different blocks in each year. The vertical intertidal range is 1.8 m on this coast and the blocks were established at an elevation range of 0.7–1.4 m above chart datum (lowest normal tide in Canada). Block size was $15.3 \pm 3.0 \text{ m}^2$ (mean \pm SE; $n = 12$ blocks), with experimental units being at least 0.5 m apart within blocks.

The experimental unit (Fig 1) included a cage made of a PVC ring (25 cm in diameter and 2.5 cm tall) and plastic mesh (0.5 cm x 0.5 cm of opening size). Each cage was subdivided by mesh into a central compartment (12 cm x 12 cm) and a peripheral compartment (area = 347 cm^2). We used the peripheral compartment to manipulate dogwhelk presence by either enclosing 10 dogwhelks (2.1–2.3 cm long) collected locally or by excluding dogwhelks. These values of dogwhelk density represent the natural density range on the studied coast (0–3 dogwhelks dm^{-2}), which we determined using 60 random quadrats (40 cm x 40 cm). The central compartment included two contiguous PVC tiles (each one measuring 8.9 cm x 4.6 cm x 0.4 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. A pilot study indicated that such tiles are representative of natural rates of barnacle larval settlement, as the density of settled larvae during May did not differ between tiles (3 ± 1 individuals dm^{-2} ; mean \pm SE, $n = 12$ tiles) and the natural rocky substrate (5 ± 2 individuals dm^{-2} , $n = 12$ quadrats) ($t_{22} = 0.809$, $P = 0.427$). We also used the central compartment to manipulate adult barnacle presence. Each adult-present cage had four substrates (each one being 4- cm^2 in area and 0.3–0.5 cm in height) hosting a total of 15 adult barnacles (0.5–1.5 cm in basal shell diameter and 0.3–0.5 cm in height) in the central compartment. These substrates were attached to the tiles with marine epoxy (A-788 Splash Zone Compound, Z-Spar, Los Angeles, CA, USA). An adult-absent cage had four such substrates without adult barnacles to eliminate the epoxy as a possible confounding factor. Because of the small size of the adult barnacles relative to the substrates and of the moderate wave exposure in the habitats, no major effects of adult barnacles on water motion were expected. We created these substrates by cutting out wood pieces with and without barnacles from a nearby dock. The density of adult

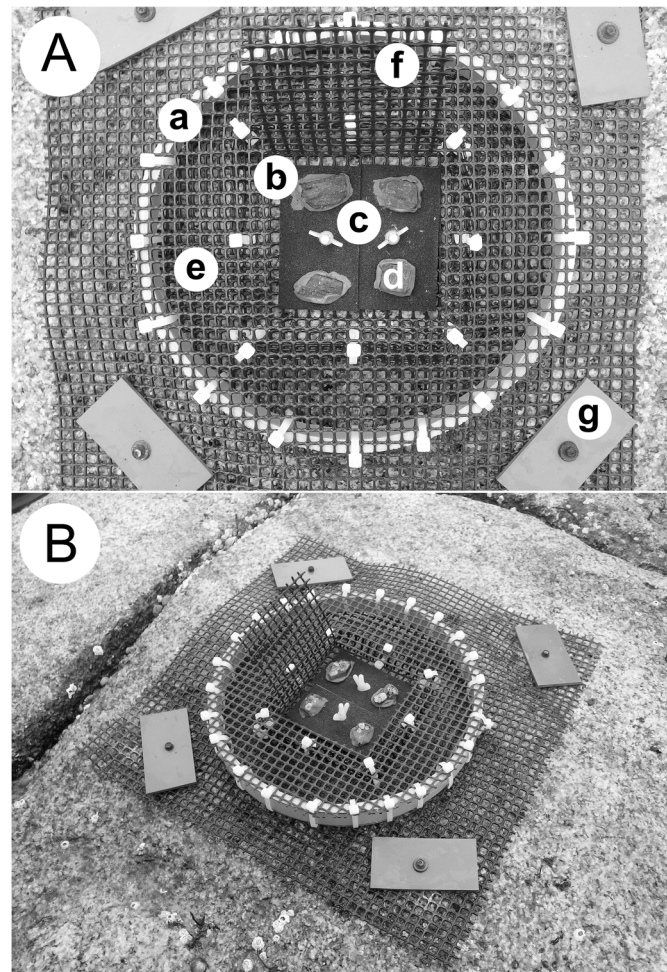


Fig 1. Experimental unit. (A) Top view of a cage, showing (a) the PVC ring of 25 cm in diameter, (b) the central compartment with (c) two barnacle recruitment tiles and (d) four small substrates (shown without adult barnacles), and (e) the peripheral compartment (shown without dogwhelks). The (f) top mesh of the central compartment is shown open to improve viewing of its internal components, 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 a cage (showing adult barnacles in the four substrates in the central compartment), exhibiting its limited height (2.5 cm) (Picture credits: Julius A. Ellrich).

doi:10.1371/journal.pone.0154572.g001

barnacles in the central compartment (calculated based on the area of the two tiles) was representative of the studied shore. We secured the cages to the substrate with screws, washers, and plastic anchors placed into holes drilled into the substrate. We tightened the tiles to the bottom mesh of the cages with plastic screws, wing nuts, and washers. In our study habitats, dogwhelks were naturally feeding on a barnacle diet, as mussels (another possible prey for dogwhelks) [65] were largely absent.

Cues from adult barnacles [45,46] and dogwhelks [21] affect nearby cyprid settlement within centimeters. The caged dogwhelks could freely move inside the peripheral compartment and approach the recruitment tiles up to 1.5 cm. Thus, cyprids settling on the tiles were exposed to cues from adult barnacles and dogwhelks but not to physical contact with these predators. To exclude cyprid attraction by adult barnacles found outside the cages, we removed all adult barnacles from 40 cm x 40 cm areas around the center of each cage. We did not feed the caged dogwhelks during the experiment but, to prevent starvation, we replaced the dogwhelks every two

weeks, releasing the removed individuals hundreds of meters away. We also removed any free-living dogwhelks found around the cages periodically. To exclude potential influences of seaweed mucus [19], canopy flow barriers [66] and canopy thermal and humidifying effects [49] on barnacle recruitment, we removed all seaweeds (mainly *Fucus vesiculosus* and some *Asco-phylllum nodosum*) found around the cages. We started the experiment by setting up all treatments on the shore on 16 April 2012 and on 24 April 2013.

Barnacle recruits appeared for the first time on 30 April 2012 and on 9 May 2013. We measured barnacle recruit density on the tiles on 25 May 2012 and on 26 June 2013. On those dates, recruits had a basal diameter of 1–2 mm. No recruits appeared afterwards, so we sampled at the end of the 2012 and 2013 recruitment seasons, when maximum recruit densities were reached (S1 Dataset).

Statistical Analysis

We conducted a nested, four-way analysis of variance (ANOVA) to test for the effects of dogwhelk cues (fixed factor with two levels: presence and absence), adult barnacles (fixed factor with two levels: presence and absence), year (random factor with two levels), and block (random factor with six levels, nested within year) on barnacle recruit density. We confirmed the homoscedasticity and normality assumptions using Cochran's *C*-test and Shapiro-Wilk test, respectively, after square-root transformation of the data. When nonsignificant results occurred for interactions involving random and fixed factors at $P \geq 0.25$, we eliminated the corresponding sources of variation and pooled their sum of squares with the residual sum of squares to increase statistical power to test the remaining factors [67]. After running the final ANOVA following this procedure, we compared treatments using Tukey's Honestly Significant Difference (HSD) tests. We conducted the analyses with SPSS 18.

Ethics Statement

We did the experiment in public-access marine intertidal habitats. The species that we used for the study, dogwhelks (*Nucella lapillus*) and barnacles (*Semibalanus balanoides*), are very abundant and not endangered or protected. Thus, neither a permit nor ethics approval was required for our research.

Results

The "year x dogwhelks", "year x adult barnacles", "dogwhelks x block(year)" and "dogwhelks x adult barnacles x block(year)" interactions exhibited *P* values higher than 0.25 in the first ANOVA (S1 Table). After pooling the sum of squares of those sources of variation with the residual sum of squares, the second ANOVA revealed that the "dogwhelk x adult barnacles x year" interaction then showed a *P* value higher than 0.25 (S2 Table). After a second step of sum-of-squares pooling, the final (third) ANOVA indicated that the presence of dogwhelks and adult barnacles significantly affected barnacle recruit density (Table 1). As the interaction between those two factors was also significant (Table 1), Tukey HSD tests compared the four corresponding treatments. Regardless of the nearby presence or absence of dogwhelks, adult barnacles significantly enhanced barnacle recruit density, by 44% on average combining both dogwhelk treatments (Fig 2). In turn, adult barnacle presence affected the expression of dogwhelk NCEs on barnacle recruitment. In the absence of adult barnacles, the nearby presence of dogwhelks significantly limited (Tukey HSD test, $P < 0.001$) barnacle recruit density (by 51% on average), but the presence of adult barnacles prevented dogwhelks from having any NCEs on barnacle recruit density (Tukey HSD test, $P = 0.571$; Fig 2), supporting this study's hypothesis. The factor "year" and the "adult barnacles x block(year)" interaction were not significant

Table 1. Summary results of the final ANOVA on barnacle recruit density.

Source of variation	df	MS	F	P
Dogwhelks	1	210.102	14.954	<0.001
Adult barnacles	1	536.024	20.560	0.001
Dogwhelks x Adult barnacles	1	59.218	4.215	0.044
Year	1	0.170	0.002	0.964
Block(Year)	10	78.309	3.001	0.043
Adult barnacles x Block(Year)	11	26.093	1.857	0.061
Pooled	69	14.050		

doi:10.1371/journal.pone.0154572.t001

(Table 1). The factor "block(year)" was significant, but this result merely tells that barnacle recruit density differed among blocks, the important result being that blocks did not interact with other factors, indicating that the interactive effects of dogwhelks and adult barnacles summarized above were spatially consistent on the shore.

Results of the final (third) ANOVA that tested the effects of dogwhelk presence ("Dogwhelks"), adult barnacle presence ("Adult barnacles"), year ("Year"), and blocks nested within year ("Block(Year)") on barnacle recruit density on the Atlantic coast of Nova Scotia, Canada,

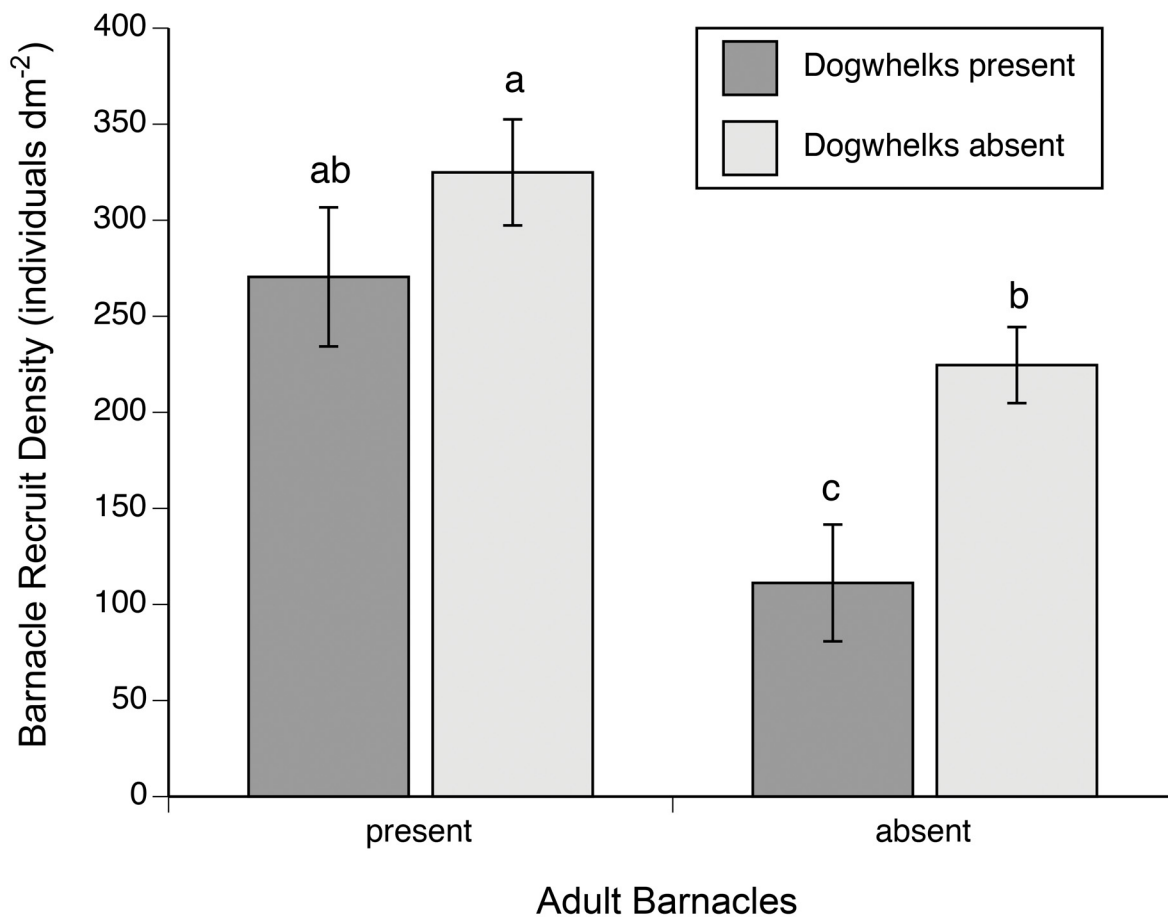


Fig 2. Barnacle recruit density (mean ± SE) in the presence and absence of nearby dogwhelks and adult barnacles. Significant differences between treatments ($P < 0.05$) are indicated when the two corresponding bars do not share the same letter.

doi:10.1371/journal.pone.0154572.g002

at the end of the 2012 and 2013 recruitment seasons. The term "Pooled" refers to the residual source of variation in the first ANOVA plus the variation for the sources that were nonsignificant with $P \geq 0.25$ in the first and second ANOVA, which are summarized in the [S1](#) and [S2](#) Tables. Significant P values ($P < 0.05$) are highlighted in boldface.

Discussion

This study has revealed that the presence of adult barnacles prevents the nonconsumptive limitation that dogwhelks would otherwise exert on barnacle recruitment. This is an important finding because, as predator NCEs may influence prey populations more than consumptive effects [[12–17](#)], it is relevant to unravel the factors that influence the occurrence of NCEs [[18](#)]. Our results may be explained by considering the known role of dogwhelk and adult barnacle cues. On the one hand, in the absence of adult barnacles, dogwhelk cues have been found to limit barnacle larval settlement [[19,21](#)] and subsequent recruitment [[22](#)], as such cues are an indication of predation risk in benthic habitats. However, adult barnacles attract conspecific larvae that are seeking settlement [[37–40](#)] through chemical [[41–45](#)] and visual cues [[46](#)]. Correspondingly, our experiment has shown that adult barnacle presence increases barnacle recruitment, which was the case regardless of the presence or absence of dogwhelks. Therefore, the lack of dogwhelk NCEs on barnacle recruitment in the presence of adult barnacles likely resulted from the influence of the attractive cues from the adult barnacles. In the presence of barnacle adults, cyprid larvae possibly did sense dogwhelk cues when these predators were present, but the adult barnacle cues seemingly had a more prominent role in the settlement behavior of barnacle larvae. Adult barnacle cues may have indicated to larvae that abiotic and biotic conditions were suitable for post-settlement growth and reproduction [[33](#)].

Future research could investigate if the relative density of dogwhelks and adult barnacles may influence the occurrence of dogwhelk NCEs on barnacle recruitment. For example, a higher dogwhelk density than used in our experiment might trigger NCEs on barnacle recruitment under the adult barnacle density we used. This could be so because studies with other species have shown that predator NCEs on prey behavior may intensify with predator density through the increase of predator cues in the environment [[68–70](#)]. Dogwhelk density has already been found to influence the occurrence of NCEs on barnacle recruitment in the absence of adult barnacles [[71](#)]. On the other hand, a lower adult barnacle density than used in our experiment might limit, but not neutralize, dogwhelk NCEs on barnacle recruitment for the dogwhelk density we used. This could be the case because microcosm experiments with other species have found that, for a given predator density, the intensity of predator NCEs on prey activity and growth is negatively related to prey density [[72,73](#)]. Because of the convenient body size of dogwhelks and barnacles for field experimentation, this model predator—prey system could help to further advance the theory about density influences on predator NCEs on prey demography.

Besides barnacles, many invertebrate species show attraction of conspecific larvae by adult organisms, including other arthropod species and species of molluscs, polychaetes, echinoderms, and tunicates [[26–31](#)]. Thus, reduced or absent predator NCEs on the recruitment of those species in the presence of adult conspecifics could be a common phenomenon. Exceptions could be cannibalistic species in which adults or juveniles consume conspecific larvae. For instance, in cannibalistic crabs, conspecific presence may have neutral [[20](#)] or negative [[3](#)] NCEs on larval settlement, suggesting that conspecific presence would not neutralize negative NCEs from heterospecific predators on prey recruitment. A thorough understanding of the interactive effects of predator and adult prey density on prey recruitment could be gained

through field experiments using prey species spanning a range of adult influences on larval settlement behavior.

Supporting Information

S1 Dataset. Barnacle recruit density (individuals dm^{-2}) in the presence and absence of dogwhelks and adult barnacles.

(XLSX)

S1 Table. Results of the first ANOVA that preceded the second ANOVA that is summarized in the [S2 Table](#). The first ANOVA tested the effects of the nearby presence of dogwhelks (denoted as "D"), presence of adult barnacles ("A"), year ("Y"), and block nested within year ("B(Y)") on barnacle recruit density on the Atlantic coast of Nova Scotia, Canada, at the end of the 2012 and 2013 barnacle recruitment seasons.

(DOCX)

S2 Table. Results of the second ANOVA that preceded the final ANOVA that is summarized in [Table 1](#). The second ANOVA tested the effects of the nearby presence of dogwhelks (denoted as "D"), presence of adult barnacles ("A"), year ("Y"), and block nested within year ("Block(Year)") on barnacle recruit density on the Atlantic coast of Nova Scotia, Canada, at the end of the 2012 and 2013 barnacle recruitment seasons. The term "Pooled" refers to the residual source of variation in the first ANOVA plus the variation for the sources that were nonsignificant with $P \geq 0.25$ in the first ANOVA.

(DOCX)

Acknowledgments

We thank Arne Beermann, Elise Keppel, and Willy Petzold for field assistance, David Risk, Steven MacDonald, and Vince Arsenault for laboratory assistance, and Ross Coleman, Ana Silva, and an anonymous reviewer for their constructive comments on earlier versions of this paper.

Author Contributions

Conceived and designed the experiments: JAE RAS MM. Performed the experiments: JAE KR. Analyzed the data: JAE MM. Contributed reagents/materials/analysis tools: RAS. Wrote the paper: JAE RAS. Commented on earlier drafts of the manuscript: KR MM.

References

1. Holt RD. Predation and community organization. In: Levin SA, editor. *The Princeton guide to ecology*. Princeton: Princeton University Press; 2009. p. 274–281.
2. Ferrari MCO, Wisenden BD, Chivers DP. Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. *Can J Zool*. 2010; 88:698–724.
3. Tapia-Lewin S, Pardo LM. Field assessment of the predation risk—food availability trade-off in crab megalopae settlement. *PLoS ONE*. 2014; 9:e95335. doi: [10.1371/journal.pone.0095335](https://doi.org/10.1371/journal.pone.0095335) PMID: [24748151](https://pubmed.ncbi.nlm.nih.gov/24748151/)
4. Trussell GC, Ewanchuk PJ, Bertness, MD. Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. *Ecology*. 2003; 84:629–640.
5. Keppel E, Scrosati R. Chemically mediated avoidance of *Hemigrapsus nudus* (Crustacea) by *Littorina scutulata* (Gastropoda): effects of species coexistence and variable cues. *Anim Behav*. 2004; 68:915–920.
6. Large SI, Smee DL, Trussell GC. Environmental conditions influence the frequency of prey responses to predation risk. *Mar Ecol Prog Ser*. 2011; 422:41–49.
7. Molis M, Preuss I, Firmenich A, Ellrich J. Predation risk indirectly enhances survival of seaweed recruits but not intraspecific competition in an intermediate herbivore species. *J Ecol*. 2011; 99:807–817.

8. Johnston BR, Molis M, Scrosati RA. Predator chemical cues affect prey feeding activity differently in juveniles and adults. *Can J Zool.* 2012; 90:128–132.
9. Orrock JL, Preisser EL, Grabowski JH, Trussell GC. The cost of safety: refuges increase the impact of predation risk in aquatic systems. *Ecology.* 2013; 94:573–579. PMID: [23687883](#)
10. Hermann SL, Thaler JS. Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia.* 2014; 176:669–676. doi: [10.1007/s00442-014-3069-5](#) PMID: [25234373](#)
11. Matassa SM, Trussell GC. Effects of predation risk across a latitudinal temperature gradient. *Oecologia.* 2015; 177:775–784. doi: [10.1007/s00442-014-3156-7](#) PMID: [25433694](#)
12. Preisser EL, Bolnick DI, Benard MF. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology.* 2005; 86:501–509.
13. Peacor SD, Peckarsky BL, Trussell GC, Vonesh JR. Costs of predator-induced phenotypic plasticity: a graphical model for predicting the contribution of nonconsumptive and consumptive effects of predators on prey. *Oecologia.* 2013; 171:1–10. doi: [10.1007/s00442-012-2394-9](#) PMID: [22851163](#)
14. Peacor S, Werner EE. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc Natl Acad Sci U S A.* 2001; 98:3904–3908. PMID: [11259674](#)
15. Trussell GC, Ewanchuk PJ, Matassa CM. Habitat effects on the relative importance of trait- and density-mediated indirect interactions. *Ecol Lett.* 2006; 9:1245–1252. PMID: [17040327](#)
16. Pangle KL, Peacor SD, Johannsson OE. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology.* 2007; 88:402–412. PMID: [17479758](#)
17. Matassa CM, Trussell GC. Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. *Ecology.* 2011; 92:2258–2266. PMID: [22352165](#)
18. Weissburg M, Smee DL, Ferner MC. The sensory ecology of nonconsumptive predator effects. *Am Nat.* 2014; 184:141–157. doi: [10.1086/676644](#) PMID: [25058276](#)
19. Johnson LE, Strathmann RR. Settling barnacle larvae avoid substrata previously occupied by a mobile predator. *J Exp Mar Biol Ecol.* 1989; 128:87–103.
20. Welch JM, Rittschof D, Bullock TM, Fordward RB. Effects of chemical cues on settlement behaviour of blue crab *Callinectes sapidus* postlarvae. *Mar Ecol Prog Ser.* 1997; 154:143–153.
21. Ellrich JA, Scrosati RA, Bertolini C, Molis M. A predator has nonconsumptive effects on different life-history stages of a prey. *Mar Biol.* 2016; 163:5.
22. Ellrich JA, Scrosati RA, Molis M. Predator nonconsumptive effects on prey recruitment weaken with recruit density. *Ecology.* 2015; 96:611–616. PMID: [26236858](#)
23. Boudreau B, Bourget E, Simard Y. Behavioural responses of competent lobster postlarvae to odor plumes. *Mar Biol.* 1993; 117:63–69.
24. Banks J, Dinnel P. Settlement behavior of Dungeness crab (*Cancer magister* Dana, 1852) megalopae in the presence of the shore crab, *Hemigrapsus* (Decapoda, Brachyura). *Crustaceana.* 2000; 73:223–234.
25. Metaxas A, Burdett-Coutts V. Response of invertebrate larvae to the presence of the ctenophore *Bolinopsis infundibulum*, a potential predator. *J Exp Mar Biol Ecol.* 2006; 334:187–195.
26. Qian PY. Larval settlement of polychaetes. *Hydrobiologia.* 1999; 402:239–253.
27. Hadfield MG, Paul VJ. Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. In: McClintock JB, Baker JB, editors. *Marine chemical ecology.* Boca Raton: CRC Press; 2001. p 431–460.
28. Manríquez PH, Castilla JC. Roles of larval behaviour and microhabitat traits in determining spatial aggregations in the ascidian *Pyura chilensis*. *Mar Ecol Prog Ser.* 2007; 332:155–165.
29. Takeda S. Mechanisms maintaining dense beds of the sand dollar *Scaphechinus mirabilis* in northern Japan. *J Exp Mar Biol Ecol.* 2008; 363:21–27.
30. Vásquez HE, Hashimoto K, Yoshida A, Hara K, Imai CC, Kitamura H, et al. A glycoprotein in shells of conspecifics induces larval settlement of the Pacific oyster *Crassostrea gigas*. *PLoS ONE.* 2013; 8: e82358. doi: [10.1371/journal.pone.0082358](#) PMID: [24349261](#)
31. Puglisi MP, Sneed JM, Sharp KH, Ritson-Williams R, Paul VJ. Marine chemical ecology in benthic environments. *Nat Prod Rep.* 2014; 31:1510–1553. doi: [10.1039/c4np00017j](#) PMID: [25070776](#)
32. Rodríguez SR, Ojeda FP, Inestrosa NC. Settlement of benthic marine invertebrates. *Mar Ecol Prog Ser.* 1993; 79:193–207.
33. Clare AS. Toward a characterization of the chemical cue to barnacle gregariousness. In: Breithaupt T, Thiel M, editors. *Chemical communication in crustaceans.* New York: Springer Science; 2011. p. 431–450.

34. Anderson DT. Barnacles. Structure, function, development, and evolution. London: Chapman & Hall; 1994.
35. Hughes RN. Annual production of two Nova Scotian populations of *Nucella lapillus* (L.). *Oecologia*. 1972; 8:356–370.
36. Palmer AR. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *J Exp Mar Biol Ecol*. 1983; 73:95–124.
37. Raimondi PT. Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology*. 1988; 69:400–407.
38. Bertness MD, Gaines SD, Stephens EG, Yund PO. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J Exp Mar Biol Ecol*. 1992; 156:199–215.
39. Thompson RC, Norton TA, Hawkins SJ. The influence of epilithic microbial films on the settlement of *Semibalanus balanoides* cyprids—a comparison between laboratory and field experiments. *Hydrobiologia*. 1998; 375/376:203–216.
40. Wright JR, Boxshall AJ. The influence of small-scale flow and chemical cues on the settlement of two congeneric barnacle species. *Mar Ecol Prog Ser*. 1999; 183:179–187.
41. Crisp DJ, Meadows PS. The chemical basis of gregariousness in cirripedes. *Proc R Soc B*. 1962; 156:500–520.
42. Gabbott PA, Larman VN. The chemical basis of gregariousness in cirripedes: a review (1953–1984). In: Schram R, Southward AJ, editors. *Barnacle biology*. Rotterdam: A. A. Balkema; 1987. p. 377–388.
43. Matsumura KJ, Hills M, Thomason PO, Thomason JC, and Clare AS. Discrimination at settlement in barnacles: laboratory and field experiments on settlement behaviour in response to settlement-inducing protein complexes. *Biofouling*. 2000; 16:181–190.
44. Dreanno C, Kirby RR, Clare AS. Involvement of the barnacle settlement-inducing protein complex (SIPC) in species recognition at settlement. *J Exp Mar Biol Ecol*. 2007; 351:276–282.
45. Elbourne PD, Clare AS. Ecological relevance of conspecific, waterborne settlement cue in *Balanus amphitrite*. *J Exp Mar Biol Ecol*. 2010; 392:99–106.
46. Matsumura K, Qian P-Y. Larval vision contributes to gregarious settlement in barnacles: adult red fluorescence as a possible visual signal. *J Exp Biol*. 2014; 217:743–750. doi: [10.1242/jeb.096990](https://doi.org/10.1242/jeb.096990) PMID: [24574388](https://pubmed.ncbi.nlm.nih.gov/24574388/)
47. Chiba S, Noda T. Factors maintaining topography-related mosaic of barnacle and mussel on a rocky shore. *J Mar Biol Assoc U. K.*. 2000; 80:617–622.
48. Kent A, Hawkins SJ, Doncaster CP. Population consequences of mutual attraction between settling and adult barnacles. *J Anim Ecol*. 2003; 72:941–952.
49. Beermann AJ, Ellrich JA, Molis M, Scrosati RA. Effects of seaweed canopies and adult barnacles on barnacle recruitment: the interplay of positive and negative influences. *J Exp Mar Biol Ecol*. 2013; 448:162–170.
50. Jenkins SR, Åberg P, Cervin G, Coleman RA, Delany J, Della Santina P, et al. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *J Exp Mar Biol Ecol*. 2000; 243:209–225.
51. Cole SWB, Scrosati RA, Tam JC, Sussmann AV. Regional decoupling between NW Atlantic barnacle recruit and adult density is related to changes in pelagic food supply and benthic disturbance. *J Sea Res*. 2011; 65:33–37.
52. Bell EC, Denny MW. Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. *J Exp Mar Biol Ecol*. 1994; 181:9–29.
53. Hunt HL, Scheibling RE. Patch dynamics of mussels on rocky shores: integrating process to understand pattern. *Ecology*. 2001; 82:3213–3231.
54. Fisheries and Oceans Canada. Oceanography and scientific data branch; 2015. Database: Oceanographic data [Internet]. Accessed: <http://www.meds-sdmm.dfo-mpo.gc.ca>
55. Vargas CA, Manríquez PH, Navarrete SA. Feeding by larvae of intertidal invertebrates: assessing their position in pelagic food webs. *Ecology*. 2006; 87:444–457. PMID: [16637369](https://pubmed.ncbi.nlm.nih.gov/16637369/)
56. National Aeronautics and Space Administration; 2015. Database: Ocean color radiometry online visualization and analysis [Internet]. Accessed: http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day
57. Scrosati R, Heaven C. Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. *Mar Ecol Prog Ser*. 2007; 342:1–14.
58. Rainbow PS. An introduction to the biology of British littoral barnacles. *Field Stud*. 1984; 6:1–51.

59. Bousfield EL. The distribution and spawning seasons of barnacles on the Atlantic coast of Canada. *Bull Natl Mus Can.* 1954; 132:112–154.
60. Pineda J, Riebensahm D, Medeiros-Bergen D. *Semibalanus balanoides* in winter and spring: Larval concentration, settlement, and substrate occupancy. *Mar Biol.* 2002; 140:789–800.
61. Bouchard GM, Aiken RB. Latitudinal variation in the reproductive cycle and size of the northern rock barnacle *Semibalanus balanoides* (L.) (Cirripedia, Archaeobalanidae) in the Bay of Fundy. *Crustaceana.* 2012; 85:779–787.
62. Largen MJ. The influence of water temperature upon the life of the dog-whelk *Thais lapillus* (Gastropoda: Prosobranchia). *J Anim Ecol.* 1967; 36:207–214.
63. Hunt HL, Scheibling RE. Effects of whelk (*Nucella lapillus* (L.)) predation on mussel (*Mytilus trossulus* (Gould), *M. edulis* (L.)) assemblages in tidepools and on emergent rock on a wave-exposed rocky shore in Nova Scotia, Canada. *J Exp Mar Biol Ecol.* 1998; 226:87–113.
64. Davies MS, Hawkins SJ. Mucus from marine molluscs. *Adv Mar Biol.* 1998; 34:1–71.
65. Largen MJ. The diet of the dog-whelk, *Nucella lapillus* (Gastropoda Prosobranchia). *J Zool.* 1967; 151:123–127.
66. Jenkins SR, Norton TA, Hawkins SJ. Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of furoid canopy algae. *J Exp Mar Biol Ecol.* 1999; 236:49–67.
67. Underwood AJ. *Experiments in ecology: their logical design and interpretation using analysis of variance.* Cambridge: Cambridge University Press; 1997.
68. Silberbush A, Blaustein L. Mosquito females quantify risk of predation to their progeny when selecting an oviposition site. *Funct Ecology.* 2011; 25:1091–1095.
69. Bowler DE, Yano S, Amano H. The non-consumptive effects of a predator on spider mites depend on predator density. *J Zool.* 2012; 289:52–59.
70. Hill JM, Weissburg MJ. Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. *Oecologia.* 2013; 172:79–91. doi: [10.1007/s00442-012-2488-4](https://doi.org/10.1007/s00442-012-2488-4) PMID: [23250631](https://pubmed.ncbi.nlm.nih.gov/23250631/)
71. Ellrich JA, Scrosati RA, Petzold W. Predator density affects nonconsumptive predator limitation of prey recruitment: field experimental evidence. *J Exp Mar Biol Ecol.* 2015; 472:72–76.
72. Turner AM. Non-lethal effects of predators on prey growth rates depend on prey density and nutrient additions. *Oikos.* 2004; 104:561–569.
73. Van Buskirk J, Ferrari M, Kueng D, Näpflin K, Ritter N. Prey risk assessment depends on conspecific density. *Oikos.* 2011; 120:1235–1239.