

Predator-induced shell plasticity in mussels hinders predation by drilling snails

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ABSTRACT: Sessile invertebrate prey that detect waterborne predator cues often respond by strengthening their structural defenses. Experimental evidence of the functional significance of such modifications using field-raised organisms is lacking. This study addresses that gap using intertidal mussels and predatory dogwhelks from Atlantic Canada. During the spring and summer of 2016, we ran a field experiment that manipulated dogwhelk presence to test their nonconsumptive effects on mussel traits. Dogwhelk cues elicited thickening at the lip, centre, and base of mussel shells while simultaneously limiting shell growth in length. As shell mass was unaffected by dogwhelk presence, a trade-off between shell thickening and elongation was revealed. Thickening was most pronounced at the thinnest parts of the shell. Using the field-raised organisms, a lab experiment found that dogwhelks took, on average, 55% longer to drill and consume mussels previously exposed to dogwhelk cues than mussels grown without such a cue exposure. Dogwhelks drilled at the thinnest parts of the shell, but, nonetheless, the consumed cue-exposed mussels had thicker shells at the borehole than the consumed mussels not previously exposed to cues, which likely explains the observed difference in handling time. As handling time normally decreases predation success, this study indicates that the plastic structural modifications in mussels triggered by dogwhelk cues in the field hinder predation by these drilling predators.

KEY WORDS: Dogwhelk · Intertidal · Mussel · *Mytilus edulis* · *Mytilus trossulus* · Nonconsumptive predator effect · *Nucella lapillus* · Phenotypic plasticity · Predation risk

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INTRODUCTION

Nonconsumptive effects (NCEs) of predators on prey mediated by chemical cues are ubiquitous in aquatic systems (Ferrari et al. 2010, Brönmark & Hansson 2012). For example, when aquatic prey detect waterborne predator cues, short-term responses often include behavioural changes such as moving away or reducing feeding activities to decrease predation risk (Keppel & Scrosati 2004, Molis et al. 2011, Hossie et al. 2017). Longer-term responses include the phenotypically plastic strengthening of morphological defenses, especially in prey with little or no escape capabilities, such as slow-moving and sessile species (Leonard et al. 1999, Nakaoka 2000, Freeman & Byers 2006). Predator NCEs may ultimately influence prey demography (Ellrich et al. 2015) and, indirectly, the abundance of other species in the commu-

nity (Weissburg et al. 2014, Matassa et al. 2016). Thus, NCE research has become an important part of ecology. The present contribution investigates the functional significance of structural changes in sessile prey that are triggered by waterborne predator cues.

Morphological changes in shell-bearing invertebrate prey can be induced by waterborne cues from predatory snails, crabs, and sea stars (Reimer & Tedengren 1996, Smith & Jennings 2000, Cheung et al. 2004, Freeman 2007, Newell et al. 2007, Lord & Whitlatch 2012, Lowen et al. 2013, Robinson et al. 2014, Babarro et al. 2016, Gosnell et al. 2017). For some cases, experimental evidence indicates that such modifications increase the prey's resistance to predation (Boulding 1984, Norberg & Tedengren 1995, Reimer & Tedengren 1996, Freeman 2007, Newell et al. 2007, Robinson et al. 2014). Mussels have been useful model systems in this regard. For ex-

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ample, when exposed to cues from sea stars, mussels develop thicker and more rounded shells, stronger adductor muscles, and more byssal threads (Côté 1995, Reimer & Tedengren 1997, Leonard et al. 1999, Reimer & Harms-Ringdahl 2001, Freeman & Byers 2006, Freeman 2007, Shin et al. 2009, Lowen et al. 2013). Live-feeding experiments have shown that those responses improve mussel survival and increase the time and energy required for sea stars to pry open mussels (Norberg & Tedengren 1995, Reimer & Tedengren 1996, 1997, Freeman 2007, Lowen et al. 2013). When exposed to crab cues, mussels increase shell thickness, sometimes at the expense of shell elongation (Leonard et al. 1999, Caro & Castilla 2004, Cheung et al. 2004, Freeman & Byers 2006, Freeman 2007, Shin et al. 2009, Lowen et al. 2013, Naddafi & Rudstam 2014), and reinforce attachment to the substrate (Wang et al. 2010, Lowen et al. 2013). Shell thickening increases the handling time and force required for crabs to crush and consume a mussel (Boulding 1984, Leonard et al. 1999, Freeman 2007).

Drilling predators, such as many snail species, are also common predators of mussels worldwide. When exposed to cues from such predators, mussels also respond by thickening their shells (Smith & Jennings 2000, Cheung et al. 2004, Freeman 2007, Babarro et al. 2016). However, whether such modifications improve the ability of mussels to cope with drilling predators has not been experimentally evaluated yet. Moreover, the studies that have shown that predator-induced morphological plasticity in bivalves hampers predation were done using lab-reared organisms, which is a less realistic approach than using organisms raised under natural conditions (Weissburg et al. 2014). To address these knowledge gaps, we conducted experiments using intertidal mussels and dogwhelks from the Atlantic coast of Canada. First, we tested the hypothesis that, in the presence of waterborne dogwhelk cues in the field, mussels would thicken their shells but grow less in length. Then, assuming the predicted shell thickening, we tested the hypothesis that the handling time required by dogwhelks to prey on mussels would be higher when consuming mussels that were previously exposed to dogwhelk cues in the field.

MATERIALS AND METHODS

Effects of dogwhelk cues on mussel traits

To evaluate the effects of dogwhelk cues on mussel traits, we did a field experiment during the spring and

summer of 2016 in rocky intertidal habitats from Deming Island (300 m of shoreline between 45° 12' 41" N, 61° 10' 50" W and 45° 12' 45" N, 61° 10' 26" W), located near Whitehead, Nova Scotia, Canada. The substrate of the studied habitats is stable bedrock. Maximum water velocity measured with dynamometers (Bell & Denny 1994) in these habitats was $6.0 \pm 0.4 \text{ m s}^{-1}$ (mean \pm SE, $n = 24$), indicating that wave exposure was moderate, as values can reach 12 m s^{-1} at wave-exposed sites in Nova Scotia (Hunt & Scheibling 2001). Intertidal temperature measured every 30 min during the study period with submersible loggers attached to the substrate was $14.2 \pm 0.1^\circ\text{C}$ ($n = 9$ loggers), while coastal seawater salinity measured with a handheld refractometer was 35‰. We used *Nucella lapillus*, which is the only local intertidal dogwhelk (Scrosati & Heaven 2007), and *Mytilus edulis* and *M. trossulus*, which are the 2 local intertidal mussels and important prey items for dogwhelks (Largen 1967). It is difficult to visually differentiate between these 2 mussel species because of morphological similarities. However, recent genetic studies have revealed that *M. trossulus* predominates over *M. edulis* in moderately exposed habitats on this coast (Tam & Scrosati 2014). Thus, given that we collected mussels at random for this study, our samples likely exhibited a predominance of *M. trossulus* over *M. edulis*. Mussels are filter feeders, their main food item being phytoplankton. MODIS-Aqua satellite data indicated that the concentration of chlorophyll *a* (a proxy for phytoplankton abundance) on the studied shore was 1.7 to 2.2 mg m^{-3} during the study period (National Aeronautics and Space Administration 2017).

We evaluated dogwhelk cue effects on mussel traits by manipulating dogwhelk presence in cages attached to the intertidal substrate. Each cage (Fig. 1) was made with a PVC ring (25 cm in diameter and 2.5 cm tall) and plastic mesh (0.5 \times 0.5 cm opening size). Each cage was divided by mesh into a central compartment (area = 144 cm^2) and a peripheral compartment (area = 347 cm^2). The peripheral compartment was used to create 2 dogwhelk treatments by enclosing either 10 dogwhelks ($2.23 \pm 0.02 \text{ cm}$ in length, measured from the shell apex to the opposite distal extreme at the edge of the shell aperture, $n = 104$) or none. The used dogwhelk density (ca. 3 ind. dm^{-2}) was representative of the studied coast (Ellrich & Scrosati 2016). The central compartment of each cage contained 18 mussels ($3.5 \pm 0.1 \text{ cm}$ in shell length, $n = 30$) to simulate a natural mussel patch. The central compartment also contained a conical mesh compartment (6 cm in base diameter and 2.5 cm tall). Each conical compartment enclosed 2

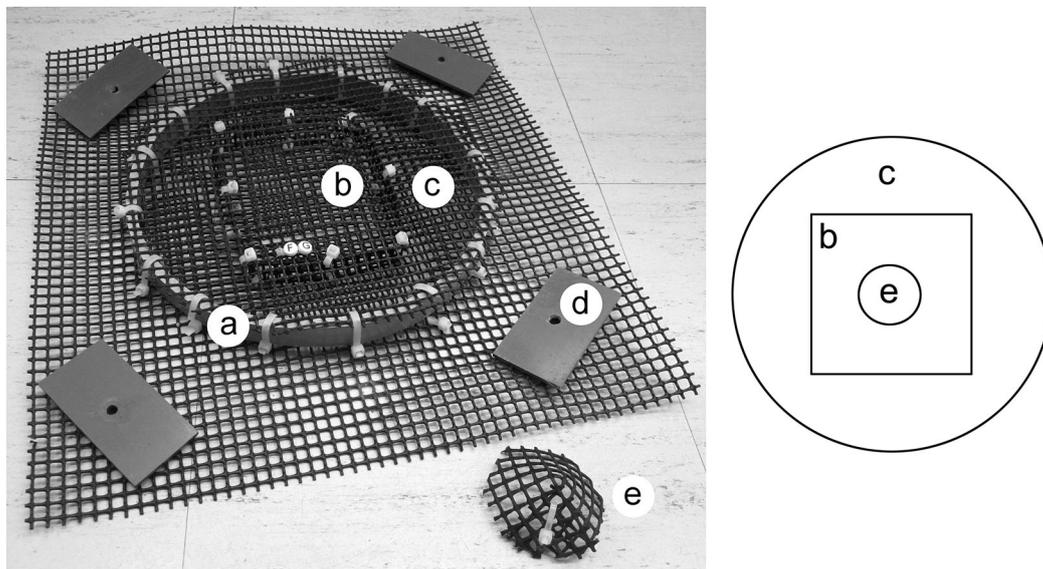


Fig. 1. Experimental cage, showing the outer PVC ring (a), the central compartment (b), the peripheral compartment (c), the 4 PVC tiles used to keep the cage attached to the intertidal substrate (d), and the conical compartment that during the experiment was kept inside the central compartment (as shown in the diagram to the right) holding the 2 experimental mussels (e). The PVC ring is 25 cm in diameter and 2.5 cm tall

mussels (1.86 ± 0.01 cm in shell length, $n = 120$). One of these 2 mussels was eventually used to take the growth measurements as influenced by dogwhelk cues (the goal of the field experiment), while the other mussel was used for the lab experiment on handling time described in the next subsection. The size of the mussels placed inside the conical compartment was selected to ensure that those mussels would remain within the preferred prey size range of dogwhelks (Hughes & Dunkin 1984) during the experiment, thus likely facilitating NCE detection. In general, mussels of a moderate size are vulnerable to predation (Czarnolewski et al. 2006) and react strongly to predation risk (Kobak & Ryńska 2014), whereas bivalves that achieve a size refuge from predators do not exhibit induced responses (Kobak & Kakareko 2009, Scherer et al. 2016). Thus, evaluating NCEs on the selected size of mussels is also relevant to understand how mussels deal with predation before reaching a size refuge.

For the field experiment, we attached the cages to the intertidal substrate with screws and PVC tiles. We previously removed all seaweeds and invertebrates from the study area to prevent their potential influences on water flow, shading at low tide, or undesired cues (Beermann et al. 2013). Because of the lack of macroalgal cover, almost no dogwhelks were found near the cages during the experiment (checked weekly). Nonetheless, the very few dogwhelks that were found were also readily removed to

ensure a virtual lack of influences from free-living dogwhelks, as achieved by previous field experiments that manipulated dogwhelk abundance using similar cages (Ellrich et al. 2015, 2016).

The experiment was arranged as a randomized complete block design with replicated treatments within blocks (Quinn & Keough 2002). We established 15 blocks at an intertidal elevation of 1 m above chart datum (the full intertidal range is 1.8 m). Each block was ca. 5 m² in extent and included 2 replicates of each of the 2 dogwhelk treatments, thus yielding 60 cages (30 cages per dogwhelk treatment). Replicate cages within a block were separated by at least 50 cm. We started the experiment on 6 June 2016. During the experiment, we did not feed the caged dogwhelks, but, to prevent their starvation, we replaced them every 10 d with mussel-fed dogwhelks that were kept in separate cages tens of metres away from the experimental area. We used mussel-fed dogwhelks to elicit strong responses in the experimental mussels, as prey often react most strongly to cues from predators fed conspecific prey (Hagen et al. 2002, Schoeppner & Relyea 2005, Weissburg & Beauvais 2015). We ran the experiment for 71 d until 16 August 2016, when we transported the mussels from the conical mesh compartments to the laboratory.

In the laboratory, we randomly selected 1 of the 2 mussels from each conical compartment for measurements. For each selected mussel, we measured shell

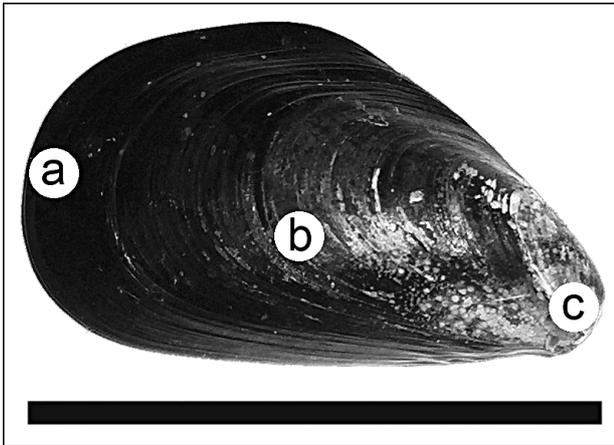


Fig. 2. Right valve of a mussel, indicating the places where shell thickness was measured at the end of the field experiment: lip (a), centre (b), and base (c). Scale bar = 2 cm

length to the nearest 0.01 mm using a digital vernier caliper. Since we had also measured shell length at the beginning of the experiment, we calculated relative length increment as $[(L_f - L_i)/L_i]$, where L_f was final length and L_i was initial length. Using a vernier caliper modified with metal extensions attached to the tip of each caliper jaw, we also measured shell thickness at the lip (1 mm from the posterior edge of the shell), centre, and base (1 mm from the anterior edge of the shell) of the right valve (looking from a dorsal view) of each mussel (Fig. 2). Then, we dried the mussels at 50°C for 72 h. After that, we separated the soft tissues from the shells and measured shell mass and soft tissue dry mass to the nearest 0.1 mg.

Effects of mussel shell thickness on dogwhelk handling time

To evaluate the effects of mussel shell thickness on dogwhelk handling time, we did a lab experiment based on the finding (see 'Results') that shells thickened in the presence of dogwhelk cues in the field. For the lab experiment, we used from each conical compartment the mussel that was not used for the measurements described in the previous subsection. Because 10% (12 of 120) of the mussels kept in the conical compartments died during the field experiment (seemingly from natural causes), we used 26 mussels from the dogwhelk-presence treatment and 22 mussels from the no-dogwhelk treatment. We started the lab experiment on 17 August 2016, having kept the mussels overnight after collection from the field in a culture room at 17°C (water temperature on the studied coast in August). We placed each of the 48

mussels in a separate container with 250 ml of seawater. We then secured with epoxy glue the left valve of each mussel to a PVC tile at the bottom of each container, leaving the right valve facing upwards, exposed to predation. We selected the right valve because whelks bore the right valve more often than the left (Alexander et al. 2015). We allowed the glue to harden overnight and then placed 1 dogwhelk (2.22 ± 0.01 cm in shell length, $n = 48$) in each container. The dogwhelks had been previously starved for 10 d to standardize starvation level, which could have otherwise affected their feeding rate (Bayne & Scullard 1978, Hughes & Drewett 1985). We attached a GoPro Hero4 Black camera to the ceiling of the culture room to take pictures of the entire set of containers every 30 s. We checked the containers every 2 h and changed their seawater (collected on the studied coast) daily using a pipette to minimize disturbance. We ran the experiment for 18 d until 3 September 2016, although no dogwhelks fed after the 13th day. We measured handling time from the moment when a dogwhelk mounted its prey to the moment when the dogwhelk moved away from the formed borehole (or, in 1 case, when the mussel shell was empty; see 'Results'). To confirm that shell thickening was higher in the consumed cue-exposed mussels than in the consumed mussels not exposed to cues, we measured shell thickness around the borehole of each consumed mussel. Finally, to evaluate if dogwhelks bore into a shell at points of reduced thickness, for each consumed mussel we also measured shell thickness at 5 random intact points on the shell.

Data analyses

We tested the effects of dogwhelk cues (fixed factor with 2 levels: dogwhelk presence and absence) on shell thickness at the lip, centre, and base of mussel shells, on mussel relative length increment, on mussel shell mass, and on mussel soft tissue dry mass through separate ANOVAs appropriate for a randomized complete block design with replicated treatments within blocks (random factor with 15 levels). The assumptions of normality and homoscedasticity were tested for each variable with the Kolmogorov-Smirnov test and Cochran's *C*-test, respectively (Quinn & Keough 2002). Such assumptions were met using the raw data for relative length increment, shell mass, and thickness at the centre of the shell and using square-root-transformed data for thickness at the lip and base of the shell and soft tissue dry mass. Since neither the blocking factor nor

the interaction term affected shell thickness for the field experiment (see 'Results'), for the lab experiment we compared dogwhelk handling time and mussel shell thickness at the borehole between cue-exposed mussels and mussels without a previous cue exposure through independent-samples *t*-tests. Separately for each cue treatment, we compared shell thickness between the borehole area and intact shell areas (mean of the 5 measurements per mussel) through a paired-samples *t*-test. We did these analyses with Statistica 12.5 (Statsoft).

RESULTS

The field experiment indicated that waterborne dogwhelk cues elicited an increase in the thickness of the lip, centre, and base of mussel shells but a slower growth in terms of length (Table 1, Fig. 3). Relative to the no-cue treatment, mean thickness in

Table 1. Results of the ANOVAs conducted to evaluate the effects of dogwhelk cues on various mussel traits through a field experiment

	SS	df	MS	<i>F</i>	<i>p</i>
Shell thickness (lip)					
Dogwhelks	0.696	1	0.696	61.56	<0.001
Blocks	0.173	14	0.012	1.47	0.185
Dogwhelks × Blocks	0.158	14	0.011	1.34	0.240
Residual	0.252	30	0.008		
Shell thickness (centre)					
Dogwhelks	0.267	1	0.267	10.11	0.007
Blocks	0.334	14	0.024	1.31	0.258
Dogwhelks × Blocks	0.370	14	0.026	1.45	0.190
Residual	0.545	30	0.018		
Shell thickness (base)					
Dogwhelks	0.300	1	0.300	21.00	<0.001
Blocks	0.094	14	0.007	0.59	0.853
Dogwhelks × Blocks	0.200	14	0.014	1.25	0.292
Residual	0.342	30	0.011		
Relative length increment					
Dogwhelks	0.019	1	0.019	18.53	<0.001
Blocks	0.142	14	0.010	2.37	0.023
Dogwhelks × Blocks	0.015	14	0.001	0.25	0.996
Residual	0.128	30	0.004		
Shell mass					
Dogwhelks	0.020	1	0.021	1.02	0.329
Blocks	0.284	14	0.020	0.99	0.483
Dogwhelks × Blocks	0.285	14	0.020	1.00	0.479
Residual	0.612	30	0.020		
Soft tissue dry mass					
Dogwhelks	0.001	1	0.001	0.87	0.368
Blocks	0.014	14	0.001	0.86	0.603
Dogwhelks × Blocks	0.015	14	0.001	0.95	0.526
Residual	0.034	30	0.001		

the presence of cues increased more (87%) in thinner areas of the shell (lip) than in thicker areas (32% increase at the shell centre and 47% increase at the shell base; Fig. 3). Neither the mass of mussel shells nor the dry mass of mussel soft tissues was affected by dogwhelk cues (Table 1, Fig. 3). The blocking factor was only significant in 1 case (relative length increment, Table 1), but that result merely indicates that relative length increment varied among blocks. The important result is that the interaction between the dogwhelks factor and the blocking factor was not significant for any case, indicating that the presence or absence of NCEs, depending on the case as described in this paragraph, was spatially consistent.

In the lab experiment, 16 dogwhelks (9 fed cue-exposed mussels and 7 fed non-exposed mussels) consumed their respective mussel by drilling a hole in the mussel's shell. One dogwhelk waited for its mussel to gape to then insert its proboscis through the opening, while the remaining dogwhelks did not feed. For the dogwhelks that drilled a borehole, handling time was higher when consuming a mussel previously exposed to dogwhelk cues than when consuming a mussel without a previous cue exposure (independent-samples *t*-test, $t_{12} = 1.91$, $p = 0.040$; Fig. 4). Data for 2 drilling dogwhelks fed cue-exposed mussels could not be used for that *t*-test because such dogwhelks started to handle their respective mussel during a short initial period when the camera did not record images. Handling time was accurately calculated for all of the other 14 drilling dogwhelks, on which that *t*-test was based.

Based on the 7 cue-exposed mussels and the 7 non-exposed mussels that were drilled by dogwhelks (and for which handling time data were available), shell thickness at the borehole was higher in cue-exposed mussels than in non-exposed mussels (independent-samples *t*-test, $t_{12} = 7.19$, $p < 0.001$; Fig. 4). Shell thickness at the borehole was lower than at intact parts of the shell regardless of previous cue exposure (paired-samples *t*-tests, $t_6 = 3.84$, $p = 0.009$ for cue-exposed mussels and $t_6 = 4.89$, $p = 0.003$ for mussels not previously exposed to cues; Fig. 4). Six mussels released gametes to the water soon after a dogwhelk was introduced in the container.

DISCUSSION

The present study has revealed that mussels in natural environments respond to dogwhelk cues by thickening their shells while simultaneously limiting linear shell growth. Since the mass of mussel shells

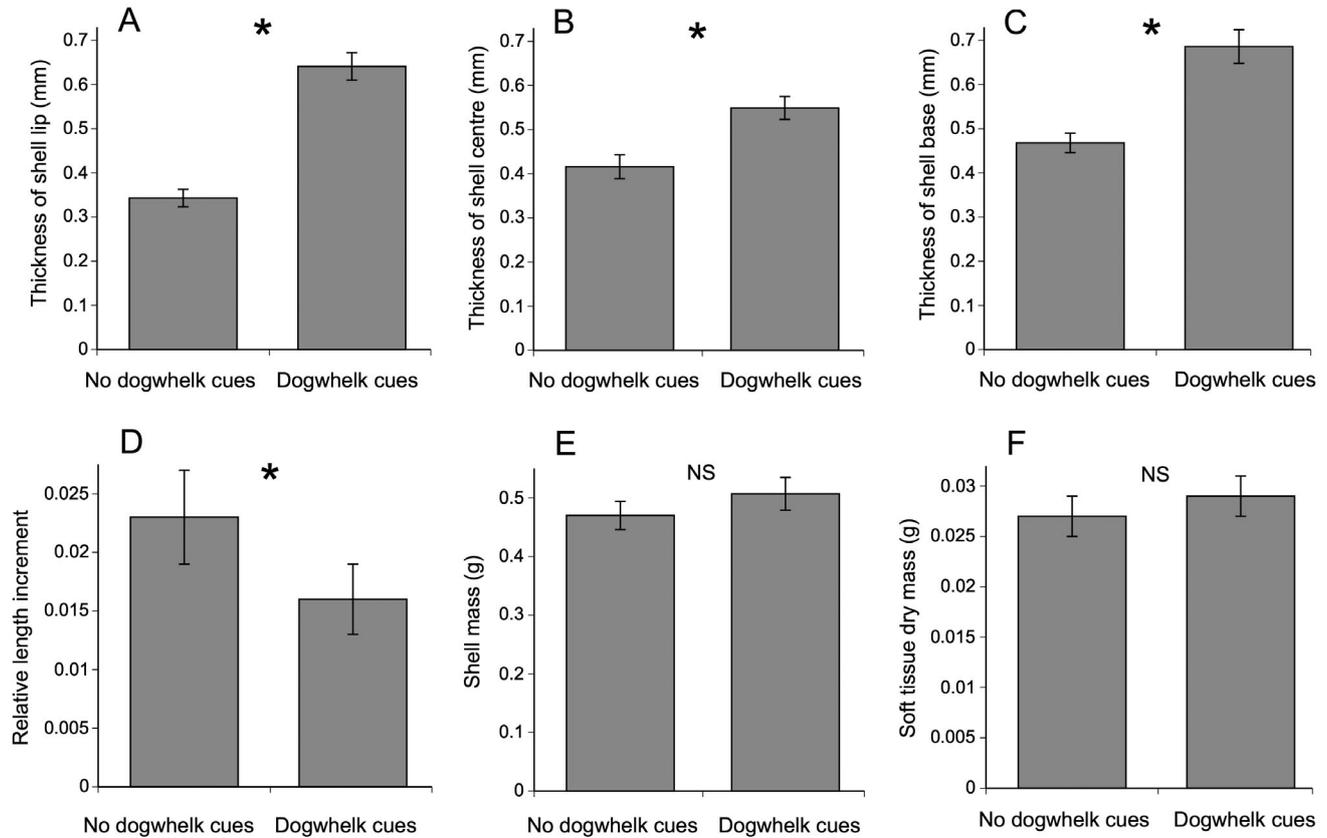


Fig. 3. Mussel traits (mean \pm SE; $n = 30$ for all cases) depending on the presence or absence of dogwhelk cues: thickness at the (A) lip, (B) centre, and (C) base of mussel shells, (D) relative length increment of shells, (E) shell mass, and (F) soft tissue dry mass. Asterisks indicate a significant difference ($p < 0.05$) between both treatments; NS indicates a nonsignificant result

was not affected by dogwhelk presence, a trade-off between shell thickening and elongation became evident. Such a plastic trade-off has been observed for mussels in general in response to crab cues (Reimer & Tedengren 1997, Leonard et al. 1999, Freeman 2007, Shin et al. 2009, Lowen et al. 2013, Naddafi & Rudstam 2014) and cues from other whelks (Smith & Jennings 2000, Freeman 2007). For other bivalves (i.e. oysters), changes in shell thickness come at a cost to soft tissue growth (Robinson et al. 2014). However, there has been no indication of such a trade-off for mussels (Reimer & Tedengren 1997, Cheung et al. 2004, Babarro et al. 2016), and the lack of dogwhelk effects on mussel soft tissue mass in our study supports that notion. Besides their NCEs on mussel shells, dogwhelks also triggered short-term responses, as some mussels exhibited a broadcast reproductive response to direct predatory threat in the lab experiment. Such a response may have been a last attempt by mussels to spawn, which aligns with findings that *Mytilus edulis* reacts to predator cues by escalating short-term investments in reproductive output (Reimer 1999).

This study also confirms that induced shell thickening in mussels occurs throughout the entire shell (Leonard et al. 1999), although it shows for the first time that the degree of thickening varies across the shell. Thickening resulting from exposure to dogwhelk cues was most pronounced in thinner areas of the shell, which are potentially most vulnerable to drilling by predators (Hughes & Dunkin 1984). Despite the overall thickening of mussel shells, however, dogwhelks were still able to find the thinnest part to drill, as shell thickness at the borehole was lower than at intact parts of the shell.

The functional significance of the plastic response in mussels observed in the field was revealed by the lab experiment, because it took 55% longer, on average, for dogwhelks to drill and consume mussels that had been exposed to dogwhelk cues and, hence, had thicker shells. These results show for the first time that predator-induced shell thickening in mussels hinders the feeding of drilling predators. Induced morphological defenses in mussels also increase handling time for predatory crabs (Boulding 1984, Reimer & Tedengren 1997, Freeman 2007) and sea stars (Norberg &

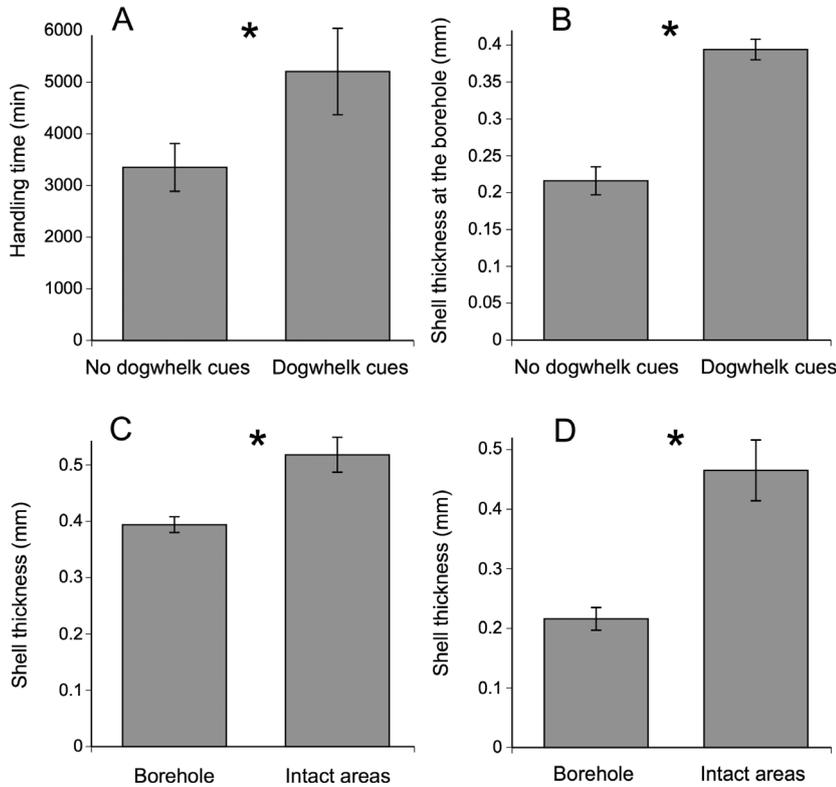


Fig. 4. (A) Handling time by dogwhelks (mean \pm SE) and (B) shell thickness at the borehole of mussels previously exposed to dogwhelk cues and mussels not exposed to such cues. Shell thickness at the borehole and at intact shell areas of (C) mussels previously exposed to dogwhelk cues and (D) mussels not exposed to such cues. Asterisks indicate a significant difference ($p < 0.05$) between both treatments ($n = 7$ for all cases)

Tedengren 1995, Freeman 2007). However, comparable proportional increases in handling time may be more detrimental for dogwhelks. The handling time required for dogwhelks to drill into mussels is considerably longer than for crabs and sea stars to crush or pry open a mussel (Freeman 2007, Miller 2013). Thus, a similar proportional increase in handling time would expose dogwhelks for longer periods of time than crabs and sea stars to desiccation stress when feeding during low tides (Hughes & Dunkin 1984, Davenport & MacAlister 1996), to competitors that can displace a feeding dogwhelk (Hughes & Dunkin 1984, Chattopadhyay & Baumiller 2007, Quinn et al. 2012, Hutchings & Herbert 2013), to predators (Vadas et al. 1994), to entrapment by neighboring mussels (Davenport et al. 1996, Farrell & Crowe 2007), or to dislodgement by waves when feeding during high tides (Denny 1988). Thus, the morphological alterations that increase the time a mussel is handled by a dogwhelk should increase the likelihood that the mussel survives a predation attempt.

Future research could investigate if the dogwhelk-induced responses differ to some extent between *M. edulis* and *M. trossulus*. Recent research has found that *M. trossulus* exhibits weaker morphological responses to crab and sea star cues than *M. edulis* (Lowen et al. 2013), but species-specific responses to slower-moving predators such as dogwhelks remain unknown. Given the observed responses to crab and sea star cues (Lowen et al. 2013) and that *M. trossulus* likely predominated over *M. edulis* in our samples (Tam & Scrosati 2014), our results do suggest that both species alter their shell morphology in response to dogwhelk cues. In addition, the potential influence of seawater conditions, as altered by climate change, on the ability of mussels to thicken their shells (Gestoso et al. 2015) in response to dogwhelk cues might also be a relevant area of future research.

Overall, this is the first study that has used organisms raised in the field, rather than in the lab, to demonstrate that predator-induced morphological responses in bivalve prey hinder predation. The complex abiotic and biotic conditions of intertidal environments, almost impossible to replicate in a lab,

conferred a high degree of realism to the results from the field experiment and the organisms used for the feeding assay. This approach is thus in line with recent studies that have highlighted the need to understand NCEs under realistic conditions to improve theory development (Weissburg et al. 2014, Babarro et al. 2016).

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