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Predator-induced defenses differ between sympatric *Mytilus edulis* and *M. trossulus*

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ABSTRACT: This is the first study to compare defenses to predation in closely related species of *Mytilus* and draws attention to the role of predation in determining their distribution, abundance and co-existence. We experimentally determined whether 2 blue mussel species, *Mytilus edulis* and *M. trossulus*, that co-exist within a hybrid zone in Newfoundland, Canada, differ in their predator-induced responses. Both species recognized cues from predators, although the magnitude of the responses to these cues varied with the predator (*Asterias rubens* or *Cancer irroratus*) and the traits measured (growth, attachment strength, shell thickness and adductor muscle mass) after 122 d of exposure. Both mussel species showed decreased growth following exposure to sea stars. Both predator species induced an increase in attachment strength in both mussel species (*M. edulis* > *M. trossulus*). *M. edulis* displayed plasticity in partitioning resources among defensive traits in the presence of sea stars (growth in adductor muscle) or crabs (increased shell thickness). These responses were not observed in *M. trossulus*, which is therefore likely more susceptible to these predators than is *M. edulis*. The preference of sea stars for *M. trossulus* supports this conclusion. Differences in predator-inducible defenses increase the likelihood of *M. edulis* succeeding *M. trossulus* in mussel aggregations, which in turn explains the often abrupt increase in the proportion of *M. edulis* among larger mussels. Such predator-induced defenses, and the resultant predator–prey interactions, affect the temporal and spatial distributions of mussel species and their potential to coexist and hybridize.

KEY WORDS: Predator-induced defenses · Sibling species · *Mytilus edulis* · *Mytilus trossulus* · Hybrid zone · *Asterias rubens* · *Cancer irroratus* · North Atlantic

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INTRODUCTION

The optimal resource allocation strategy adopted by an organism is based on how it adapts to the threat of mortality (Boggs 1992). Sessile organisms, unable to escape from predators, rely on morphological or chemical defenses (Vermeij 1987), habitat heterogeneity (Eggleston 1990) or aggregation behaviour (Bertness & Grosholz 1985) as refuges. Defenses are likely to be induced where predation pressure is variable and unpredictable and the cues are reliable (Harvell 1990), otherwise fixed defenses may be optimal as long as the costs of permanent expression do not decrease fitness (Clark & Harvell 1992).

Many organisms, particularly aquatic species, have evolved predator-inducible defenses (Lively 1986, Harvell 1990, McCollum & Van Buskirk 1996), that in turn shape predator and prey interactions and community structure. Yet, despite their ubiquity, few studies have focused on comparing predator-inducible defenses among co-existing congeners, particularly in the species-rich intertidal. For example, none of the numerous studies on predator-induced morphological defenses in blue mussels *Mytilus* spp. have incorporated genetic markers to distinguish species and hybrids (Reimer & Tedengren 1996, Leonard et al. 1999, Smith & Jennings 2000, Reimer & Harms-Ringdahl 2001, Freeman &

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Byers 2006, Freeman 2007, Freeman et al. 2009). Closely related *Mytilus* species competing for space and other resources are also more likely to inter-breed because of spatial overlap. In this context, determination of the extent to which predators induce defenses in each species is important when trying to explain their potential to coexist and hybridize in environments with varying predation pressure.

Predation, then, may play an important but poorly understood role in determining the distribution and abundance of the closely related blue mussels *Mytilus edulis* (Linnaeus, 1758) and *Mytilus trossulus* (Gould, 1850), which compete for space and other resources in the North Atlantic hybrid zone. In cohort analyses, smaller mussels (20 to 40 mm shell length) were more abundant than larger ones (i.e. >40 mm shell length) throughout insular Newfoundland, Canada. Moreover, there was a concurrent and marked decrease in the proportion of *M. trossulus* in larger size classes (>40 mm) (Miranda 2004). This in turn implies that there are interspecific differences in growth or survival (Comesaña et al. 1999, Toro et al. 2002, 2004, Lowen 2008). One important aspect of mortality that has received less attention in co-existing mussel species is the relative importance of predator-induced defenses and the associated decrease in susceptibility to predation.

After exposure to sea stars, crabs, or other predators with similar attack modes, these predators generally induce defenses in mussels in one or more of 3 ways. (1) They produce more and stronger byssal threads, resulting in increased attachment strength (Reimer & Tedengren 1996, 1999, Farrell & Crowe 2007). This is an effective defense when predators try to dislodge individual mussels from a clump (Reimer & Harms-Ringdahl 2001). (2) To counteract the crushing claws of crabs, mussels can develop thicker shells (Leonard et al. 1999). Sea stars, on the other hand, pry apart the valves and can induce mussels to develop stronger adductor muscles and occasionally thicker shells (Reimer & Harms-Ringdahl 2001). The latter adaptation may be effective where the strength of the adductor exceeds that of the shell. (3) The presence of sea stars or crabs may induce a reduction in shell growth, which in combination with increased adductor, shell or attachment strength further enhances the defense response (Reimer & Harms-Ringdahl 2001). Alternatively, as the benefits from reproduction begin to outweigh the costs of the predator-induced defense, mussels may increase reproductive allocation (Riessen 1992, Cote 1995, Reimer & Tedengren 1996, 1999).

In a field experiment, sited in close proximity to sea stars and crabs feeding on rope-cultivated mussels, *Mytilus edulis* developed a thicker shell and a heavier adductor muscle than *M. trossulus* (Lowen 2008). Differences in adductor muscle mass and shell thickness between *M. edulis* and *M. trossulus* could arise from a divergent response to cues from sea stars, crabs, or other predators with similar attack modes. Predator-induced defenses may thus partially explain differences in shell thickness between *M. edulis* and *M. trossulus* grown on or off the bottom (Mallet & Carver 1995, Miranda 2004, Lowen 2008).

The objective of our study was to compare the predator-induced defenses of *Mytilus edulis* and *M. trossulus*. Laboratory-cultured *M. edulis* and *M. trossulus* were exposed to sea stars *Asterias rubens* and crabs *Cancer irroratus*, and the subsequent allocation to absolute growth, adductor mass, shell thickness and attachment strength was quantified, thereby providing information on the relative susceptibility of each mussel species to predation. This is the first study on *Mytilus* spp. predation to compare closely related species and draws attention to the role of predators in determining the distribution and abundance of co-existing blue mussel species.

MATERIALS AND METHODS

Mussel rearing and conditioning

Mytilus edulis and *M. trossulus* were obtained in Newfoundland, Canada, from Salmonier Cove (47.6784437° N, 55.6736662° W), Reach Run (49.496 482° N, 54.796875° W) and Cap Cove (48.379166° N, 53.375004° W). They were identified with 2 allozyme genetic markers (MPI and EST-D), 4 nuclear DNA markers (ME, ITS, MAL and PLIIa) and 1 mitochondrial DNA marker (COIII) (Miranda et al. 2010). Pure-species families (5 families per species, from 5 sites), each spawned from multiple parents, were then produced in the laboratory in July 2001 as outlined in Miranda et al. (2010).

Mussels were initially reared for 18 mo in the laboratory, where they were fed a standard hatchery diet consisting of mixtures of 10^5 cells ml^{-1} *Isochrysis galbana*, *Chaetoceros muelleri* and *Tetraselmis suecica* (5:3:2 ratio) and raw seawater in a partial recirculation system. They were transferred in November 2001 to a mussel farm in Notre Dame Bay and returned to the laboratory in November 2002, where they were maintained as described above. Mussels from all families for each species were pooled and reared in pearl nets for a further 9 mo at a mussel farm in Trinity, Newfoundland. Thus, all mussels used in the laboratory experiments were exposed to the same conditions from the larval stage to age 3 yr. Of each species, 9 groups of 30 mussels were subsequently sampled from the pearl nets in May 2004, and individuals were labelled with an engraving tool.

Byssal attachment, morphometric measurements and dissection

Groups of 30 mussels of each species were allocated to 1 of 2 separate compartments in nine 1 mm mesh trays each suspended in a 10 l aquarium from July to November 2004 (Fig. 1). Three replicate aquaria were used for each of the crab *Cancer irroratus*, sea star *Asterias rubens* and control (no predator) treatments. Mussels were conditioned in an aerated continuous flow-through system containing Shellfish Diet 1800 (Reed Mariculture) mixed with unfiltered natural seawater at a daily ration of ~3% of the estimated total soft tissue biomass of the mussels in each tray. From a holding tank containing 20 crabs and 30 sea stars, 2 crabs or 3 sea stars, depending on the treatment, were rotated into and out of each experimental aquarium every 3 d. Predators in each aquarium were separated from the mussels by a mesh that prevented physical contact but allowed the passage of water. At any given time each experimental aquarium contained approximately the same predator biomass. Mussels were held in the trays for 2 wk before predators were introduced. Observations of other mussels reared in identical aquaria with the same conditioning diet suggested that mussels had spawned by September 2004 and were recovering until the end of the experiment in late November 2004.

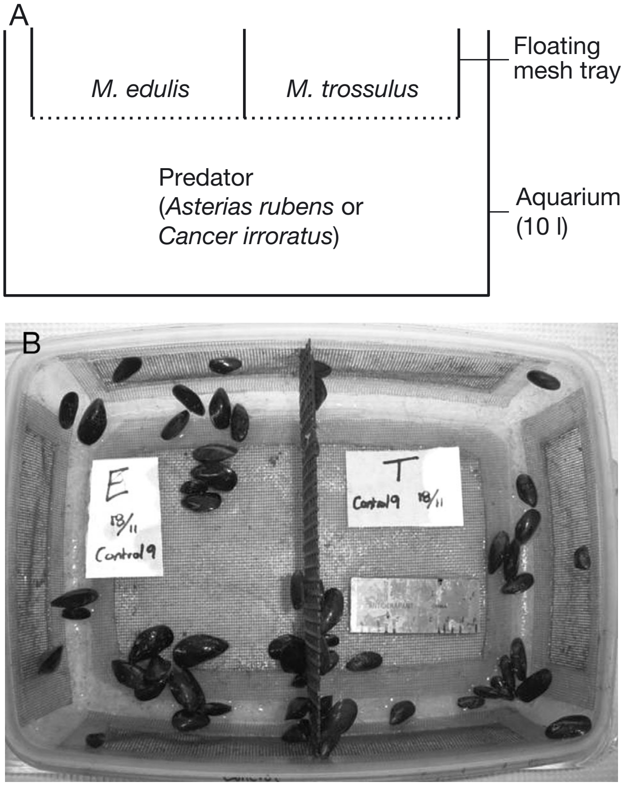

Fig. 1. Aquarium plan used for predation experiments. (A) Schematic side view, (B) top view. One tray was suspended in each of nine 10 l aquaria (3 aquaria for each treatment: crab, sea star, control). Each tray had 2 compartments, one containing 30 *Mytilus edulis* (E), the other containing 30 *M. trossulus* (T)

Attachment force (*g*), measured with modified forceps and a force gauge, was determined for each mussel in late November (after 122 d of the predation experiment). The forceps, connected to the force gauge with inflexible braided fishing line (100 lb breaking strain), were modified such that they would clamp or hook around the mussel without applying undue pressure to it or altering its position. Once the forceps were attached to the mussel, the force gauge was carefully elevated until the mussel detached from the substrate, at which point the gauge reading was recorded. Only individuals attached directly to the mesh trays were included in the analyses, mussels attached to each other being excluded. Shell length (anterior–posterior axis), height (dorso–ventral axis) and width (lateral axis) were measured (±0.1 mm) with vernier calipers at the beginning (August 2004) and end (November 2004 or 122 d) of the predation experiment. The surface area of the shell was approximated using the formula:

$$A = 0.5\pi l(h^2 + w^2)^{0.5} \tag{1}$$

where A is surface area (cm^2), l is length (cm), h is height (cm) and w is width (cm) (Beadman et al. 2003). Because shell surface area is strongly correlated with shell volume, A is a reliable measure of body size (Freeman & Byers 2006).

After termination of the experiment, the remaining individuals were stored at −20°C. The adductor muscle, remaining soft body tissues and shell were subsequently removed and dried separately to constant weight at 80°C, then weighed to the nearest 0.1 mg.

Rate of attack by sea stars

Sixty *Mytilus edulis* were placed in 1 of 2 identical compartments of a mesh tray suspended in a 10 l aquarium, and 60 *M. trossulus* were placed in the other compartment. This setup was duplicated in an identical aquarium. The rate at which sea stars attacked the mussels was recorded during July and August 2004 for 60 d. To minimize feeding bias among individual sea stars, ~35 sea stars taken from a holding tank were rotated into and out of the aquaria every 3 to 5 d. Sea stars were physically separated from the mussels by the 1 mm mesh screen. To prevent position effects, the trays were randomly reorientated within the aquaria every 3 d. Mussels were conditioned as described in 'Mussel rearing and conditioning', and observed at ~15 min intervals from 09:00 to 17:00 h Monday to Friday for 60 d. An attack was recorded when a sea star had settled under a mussel and begun to evaginate its stomach through the mesh of the tray. At this point the sea star was gently removed from the bottom or sides of the mesh tray and placed at the bottom of the aquarium.

Statistical analyses

All analyses were conducted in the R-statistical environment version 2.5.0 (R Development Core Team 2012). Shell growth was calculated for marked individuals as the difference between final and initial shell length. Only mussels that could be accurately identified by their labels were included in the analyses of shell length growth (i.e. 36 of 461 individuals were excluded). Furthermore, only individuals attached to mesh trays were included in the analyses of attachment force (i.e. 88 of 461 individuals were excluded).

Adductor muscle mass and shell deposition were determined in all individuals remaining at the end of the experiment. Data for byssal attachment force, shell length growth, adductor muscle mass and shell deposition were analyzed by 2-way MANCOVA, followed by separate univariate ANCOVAs, with species and treatment as fixed effects, final shell area as a covariate, and aquaria nested within both treatment and species × treatment as random effects. To accommodate the unbalanced design in the MANCOVA and subsequent ANCOVAs, Type III sum of squares were used to estimate all *F*-ratios. Pair-wise contrasts between treatments within each species or between species within each treatment were adjusted by the Bonferroni method (Sokal & Rohlf 1995). All tests met the assumptions of normality and homogenous distribution of residuals required by the generalized linear model. Additionally, sea star attack rates between species were contrasted using chi-squared tests of goodness-of-fit, with Yates corrections.

RESULTS

Attachment force

Exposure of *Mytilus trossulus* and *M. edulis* to predators resulted in significantly increased attachment in both species (crab treatment > sea star treatment > control), although predator treatments were significantly different (Fig. 2A, Table 1). Relative to the control, *M. trossulus* required 450 % (*M. edulis*: 903 %) more force to detach from the substrate in the presence of crabs and 189 % (*M. edulis*: 571 %) more force following exposure to sea stars. The attachment force of *M. edulis* was significantly greater than that of *M. trossulus* in both predator treatments, but did not differ between mussel species in the control (Fig. 2A, Table 1).

Shell growth

Increase in shell length of *Mytilus trossulus* was greater in the control than in the predation treatments (control treatment > crab treatment > sea star treatment), while in *M. edulis* shell growth was lower only in the sea star treatment (control treatment = crab treatment > sea star treatment) (Fig. 2B, Table 1). In both the control and crab treatments, shell length measurements increased significantly more in *M. edulis* than in *M. trossulus*. In the sea star treatment, however, the shell length increment was not significantly different between the species (Fig. 2B).

Shell and adductor mass

Exposure of mussels to the crab treatment resulted in a significant increase in shell weight for *Mytilus edulis* (crab treatment > sea star treatment = control treatment) but not for *M. trossulus* (crab = sea star = control) (Fig. 2C, Table 1). For example, *M. edulis* shell mass, standardized to a shell surface area of 3.2 cm^2, was 34 % greater in the crab treatment than in the control. Furthermore, there was a large increase in adductor mass in *M. edulis* in the presence of sea stars but not in the presence of crabs (sea star treatment > crab treatment = control treatment), whereas there were no treatment effects in *M. trossulus* (Fig. 2D, Table 1).

Sea star attack rate

During the observation period of 60 d, *Mytilus trossulus* was attacked by sea stars significantly more

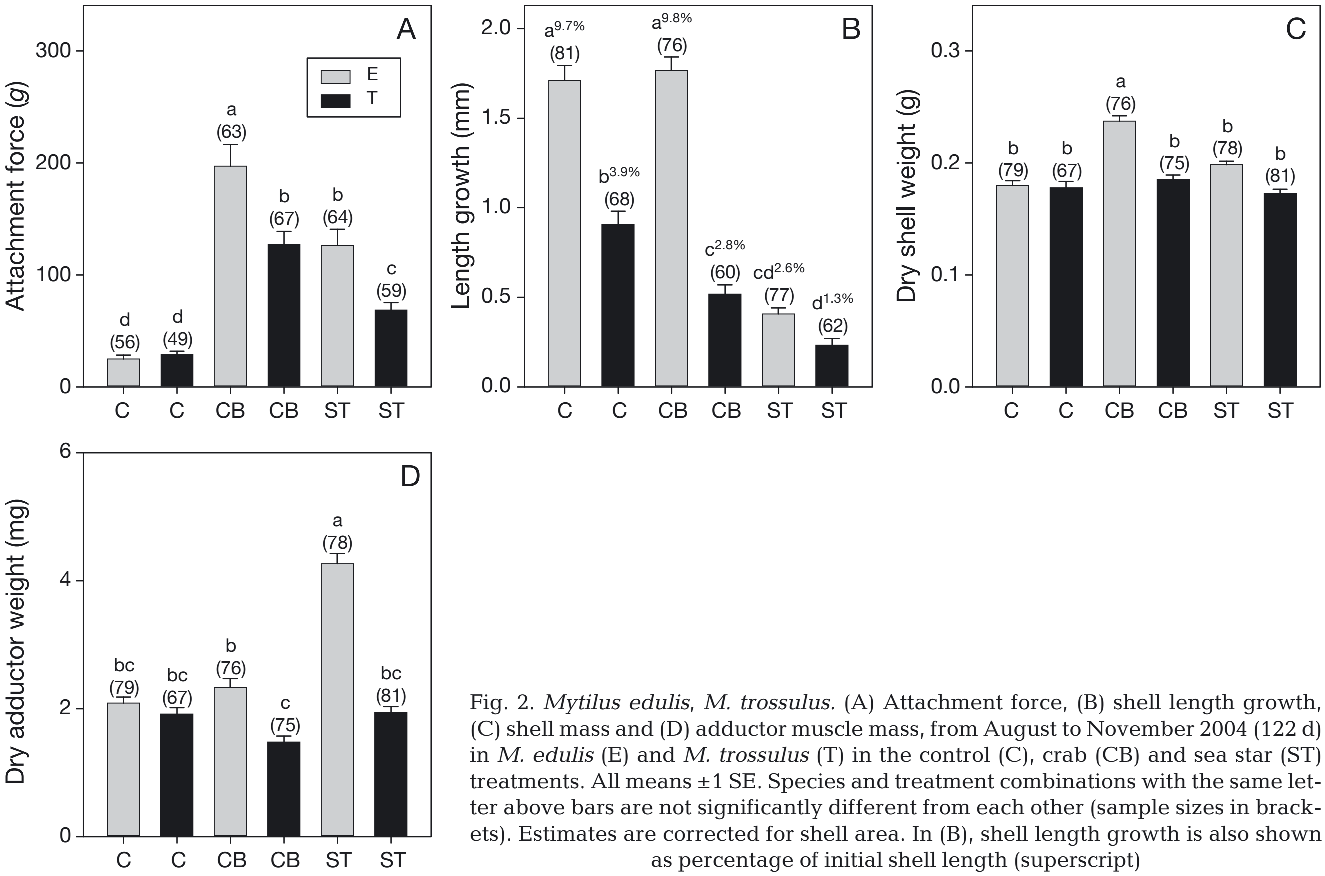

Fig. 2. *Mytilus edulis*, *M. trossulus.* (A) Attachment force, (B) shell length growth, (C) shell mass and (D) adductor muscle mass, from August to November 2004 (122 d) in *M. edulis* (E) and *M. trossulus* (T) in the control (C), crab (CB) and sea star (ST) treatments. All means ±1 SE. Species and treatment combinations with the same letter above bars are not significantly different from each other (sample sizes in brackets). Estimates are corrected for shell area. In (B), shell length growth is also shown as percentage of initial shell length (superscript)

Table 1. Two-way MANCOVA followed by univariate ANCOVAs (both MANCOVA and ANCOVA are unbalanced, Type III sum of squares, general linear model) for attachment force (*g*), growth (mm), shell mass (g) and adductor mass (mg), from August to November 2004 (122 d). Main effects: univariate ANOVA (Univ.) for each dependent variable (attachment, growth, shell mass, adductor); treatment: crab, sea star, control; species: *Mytilus edulis*, *M. trossulus*. Covariate: shell area [ln(x + 1)]. Random effects (error terms for split plot design): aquaria nested within treatment (error term for 'species'); aquaria nested within species × treatment (error term for 'treatment × species'). *p < 0.05; **p < 0.01; ***p < 0.001; ns: non-significant

Effect	Multivariate		Univ. Attachment		Univ. Growth		Univ. Shell mass		Adductor
	df	*F*	df	*F*	df	*F*	df	*F*	*F*
Treatment	8	144.82***	2	409.91***	2	40.20***	2	97.43***	19.62***
Species	4	88.91***	1	0.54 ns	1	51.55***	1	91.77***	86.60***
Treatment × Species	8	16.00***	2	11.94***	2	3.10*	2	17.78***	13.88***
Aquaria$^{\text{(Treatment)}}$	24	1.68*	6	0.92 ns	4	2.37*	6	0.63 ns	7.05*
Aquaria$^{\text{(Species × Treatment)}}$	24	1.55*	6	1.20 ns	6	1.34 ns	6	1.978 ns	3.03*
Shell area [ln(x + 1)]	4	1488.93	1	262.89***	1	0.29 ns	1	11417.36***	155.17***
Residuals	1256		354		402		442		

often than *M. edulis* (total number of attacks recorded = 101, 75 of which were on *M. trossulus*, with the remaining 26 attacks on *M. edulis*: chi-squared tests of goodness-of-fit, df = 1, chi-squared = 22.8, p < 0.0001).

DISCUSSION

The predator-induced defenses observed here, to resist the crushing claws of crabs or increase the effort required for sea stars to pry open the shell valves, are generally consistent with other studies on *Mytilus* spp. (Leonard et al. 1999, Reimer & Harms-Ringdahl 2001, Caro & Castilla 2004, Freeman & Byers 2006, Freeman 2007, Freeman et al. 2009). None of these studies, however, compared coexisting species exposed to the same predators. An induced response in a prey organism can arise after exposure to 'infochemicals' either from the predator itself (enemy-avoidance kairomones; Ruther et al. 2002) or from damaged and ingested prey conspecifics (alarm pheromones; Smith 1992), or simply as a result of non-lethal physical contact with the predator (Leonard et al. 1999). The predator-induced phenotypes (i.e. enhanced byssal attachment, heavier adductor muscle and shell thickening) observed in the current experiment were probably attributable to a combination of 'enemy-avoidance kairomones' or, on occasions where crabs or sea stars had moved onto the underside of the mesh tray supporting the mussels in each aquarium, physical contact with the predators.

Shell thickening provides increased protection from the crushing action of crab claws and is common in bivalves and gastropods (Leonard et al. 1999). Following exposure to crabs, *Mytilus edulis* developed a thicker shell, while *M. trossulus* did not. In response to sea star exposure, *M. edulis* developed a greatly enlarged adductor muscle, which is in agreement with other studies (Reimer & Harms-Ringdahl 2001, Freeman 2007), but *M. trossulus* did not. The observed predator-induced increase in byssal attachment in both mussel species is probably an efficient defense against both sea stars and crabs, since the mussel becomes more difficult to remove from the substrate (Auster 1986, Reimer & Harms-Ringdahl 2001, Farrell & Crowe 2007). The attachment of *M. edulis* in the predator treatments was much stronger than that of *M. trossulus*. Differences between the 2 species in key defensive traits (increases in shell and/or adductor muscle mass) were only apparent in the presence of sea stars or crabs. Consequently, observed differences in shell weight or thickness (Mallet & Carver 1995, Miranda 2004, Lowen 2008) or adductor muscle weight (Lowen 2008) are at least partly attributable to predator-induced phenotypic plasticity.

Allometric increases in important components of predator-induced defenses such as attachment, adductor weight and shell thickness are often associated with depressed shell length growth in blue mussels (Leonard et al. 1999, Freeman & Byers 2006). These findings are generally consistent with allocation models of induced defenses that incorporate fitness costs arising primarily from shifts in allocation from growth in body size to enhanced present defense or reproduction (Lively 1986, Clark & Harvell 1992). The costs associated with diverting resources from growth to inducible defenses in turn keep the expression of defenses in check and are therefore a central component of red queen or arms race models, because costs prevent the prey's defenses from easily outrunning the exploitative capabilities of the predator (Futuyma & Moreno 1988, Fry 1996).

In our study, the relationship between the expression of induced defenses and shell length growth was not straightforward. The costs of morphological defenses, especially growth, can be offset by a compensatory increase in feeding (Paige 1992), or enhanced if feeding decreases (Harvell 1990). *Mytilus* spp. feeding behaviour, however, is unaffected by predator cues (Freeman 2007). Thus, the lack of change in feeding behaviour, together with the relatively low costs of shell deposition, could explain why *M. edulis* shell length growth remains constant during shell accretion after exposure to crabs. *M. edulis*, then, can both defend against the threat of crab predation, while at the same time growing towards a potential size refuge from crab predation (Seed & Suchanek 1992). Increasing the size of the adductor muscle, on the other hand, is energetically costly, and when *M. edulis* was exposed to sea stars this additional cost was reflected in an apparent trade-off between shell length growth and deposition of adductor muscle tissue. Interpreting the costs of predator-induced defenses in *M. trossulus* is more difficult given the data in the current experiment, although increasing reproductive allocation, which was not measured in this experiment, also strongly reduces growth. Consistent with Toro et al. (2002) and Lowen (2008), it is likely that *M. trossulus*, in the presence of predators, was diverting resources to reproduction to a greater extent than *M. edulis*.

The adaptive significance of predator-induced defenses is well documented for *Mytilus edulis* (Leonard et al. 1999, Smith & Jennings 2000, Freeman 2007). The predator-induced increases in shell and adductor mass of *M. edulis* and in attachment strength in both species in the present experiment are consistent with the findings of Leonard et al. (1999) and Freeman (2007). Miranda (2004) also demonstrated a clear relationship between shell thickness or mass and a greater resistance to breakage in *M. edulis* than in *M. trossulus*. Data from our study therefore suggest that *M. trossulus* is more susceptible than *M. edulis* to predation by sea stars and crabs. Consequently, periods of selective predation on *M. trossulus* (~20 to 40 mm shell length, as in this experiment) could explain, at least in part, the decrease in the proportion of *M. trossulus* in larger size classes (>40 mm) (Comesaña et al. 1999, Miranda 2004, Toro et al. 2004).This in turn would increase the likelihood of *M. edulis* displacing *M. trossulus*, resulting in the dominance of *M. edulis* in patches that have not experienced indiscriminate disturbance.

The preference of sea stars for *Mytilus trossulus* also supports the conclusion that *M. trossulus* is more susceptible than *M. edulis* to predation by sea stars. However, it does not imply a direct correlation between the observed predator-induced defenses and the likelihood of being predated; as the sea stars were prevented from prying open the shell by the tray mesh. Thus, sea stars may be distinguishing among morphologically similar mussel species by relying on 'odours' rather than tactile cues (e.g. Gaymer et al. 2004), but would do so only if they had learned (e.g. Mercier & Hamel 2008) to feed on the species that is more susceptible to their attack mode (i.e. *M. trossulus*). Further work, is required to test these assumptions.

The observed interspecific differences in the extent to which predators induce defenses in *Mytilus* spp. may be part of a broader life-history allocation strategy (Lowen 2008). The lesser degree to which predators induced defenses in *M. trossulus* supports the argument that it prioritizes resource allocation to reproductive rather than somatic functions earlier in life, unlike *M. edulis* (Lowen 2008). Relative to *M. edulis*, increased allocation to reproduction (Toro et al. 2002) in turn enhances the ability of *M. trossulus* to recolonize disturbed patches, thereby increasing its resilience rather than its resistance to disturbance (Toro et al. 2002, Lowen 2008). Differences between *M. edulis* and *M. trossulus* in resilience or resistance to disturbance arising from divergent resource allocation patterns (Lowen 2008) could theoretically reinforce the stabilizing mechanisms that maintain their coexistence (Chesson 2000).

Furthermore, because of differences in the way predators induce defenses in *Mytilius edulis* and *M. trossulus*, the interpretation of studies on predator-induced defenses where the 2 species co-occur but are not uniquely identified could be confounded. Freeman & Byers (2006), for example, suggested that there has been rapid evolution of an inducible morphological response in *M. edulis* to the crab *Hemigrapsus sanguineus* within 15 yr of its introduction to southern New England (USA) (but see Rawson et al. 2007). Freeman & Byers (2006) originally assumed, however, that the study population was exclusively *M. edulis*, whereas in fact it was a mixture of *M. edulis* and *M. trossulus*. Following the discovery that both species may have been present in Freeman & Byers' (2006) study, tissues from the experimental mussels were subsequently genotyped. The number of *M. trossulus* sampled in Freeman & Byers (2006), however, was small relative to *M. edulis* so that the results were similar whether or not *M. trossulus* was included in the analyses (Freeman & Byers 2007). In contrast, the present experiment was carried out under well-controlled conditions in the laboratory using much larger numbers of mussels of known species composition and thus provides reliable estimates of interspecific predator defenses.

An important caveat of the current experiment is that mussel growth rates were lower than in field experiments over a similar time period (Lowen 2008), implying that mussels were food limited in the laboratory. Due to bio-fouling of the supply pipes, raw seawater pumped to the experimental aquaria contained relatively little suspended organic material, and the mixed-species algal concentrate used to feed the mussels was likely an imperfect substitute for naturally occurring algae. Therefore, our experiment most closely simulated situations in which predator density is high or mussels are food limited but not starved.

Moreover, food limitation may induce shell thickening in gastropods (but see Tung & Alfaro 2011) such that the predator-induced response is indirectly mediated by prey behaviour (i.e. reduced feeding) rather than directly cued by predators (Bourdeau 2010, Bourdeau & Johansson 2012). Currently there is no such precedent in sessile bivalves, and further work on *Mytilus* spp. is needed to disentangle the cause and effect of shell thickening in this context. If shell accretion in *Mytilus* spp. is also mediated by a reduction in feeding rate, then, because mussels were food limited in this experiment, the predator (i.e. crab) effect on shell accretion rate could potentially be reduced, or even negated (see Bourdeau 2010). Nonetheless, crabs still induced a thicker shell in *M. edulis*, but did not in *M. trossulus*. This in turn highlights underlying differences in shell accretion rates among the 2 species that leave *M. edulis* better defended than *M. trossulus* against the threat of predation by crabs.

Overall, predator-induced morphological defenses are weaker under low resource conditions because the diversion of limited resources is more costly (Harvell 1990, Chivers et al. 2008). If *Mytilus trossulus* is not food limited, predators may induce defenses more effectively once the requirements of reproductive investment have been met. *M. trossulus* was certainly able to recognize cues from sea stars or crabs and increase attachment strength accordingly. Presumably the reproductive costs in such circumstances are lower than the costs of the defense associated with exposure to the predator (Harvell 1990). Nevertheless, it is likely that with a better food supply *M. edulis* would still prioritize defense to a greater degree than *M. trossulus*. Evidence for this comes from a field experiment where invertebrate predator cues were present (Lowen 2008), whereby *M. edulis* developed thicker shells and larger adductor muscles than *M. trossulus*, consistent with the laboratory experiment discussed here.

In conclusion, the current experiment supports growing evidence that predation risk alone (i.e. nonlethal effects) can drive trophic interactions and play an important role in shaping community structure and dynamics (Turner et al. 2000, Werner & Peacor 2003). For example, predators may induce adaptive changes in the phenotype of their prey, thereby influencing the interactions between predator and prey. This experiment also demonstrated that co-existing sibling species may differ in their predator-induced response, such that one species (*Mytilus edulis*) is more resistant to predators than the other (*M. trossulus*), which is potentially more resilient through a greater investment in reproduction (Toro et al. 2002). Such predator-induced defenses and the resultant predator–prey interactions, together with differences in species resistance or resilience to predation impact in turn the temporal and spatial distribution of the species and their subsequent potential to coexist through successional dynamics.

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