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Predator-inducible defences and local intra-population variability of the intertidal mussel *Semimytilus algosus* in central Chile

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ABSTRACT: Predator-inducible defences have a strong influence on the expression of morphological traits of intertidal invertebrates. For instance, mussels exposed to predators often have thicker shells than non-exposed. On the intertidal rocky shores of Chile, the mussel *Semimytilus algosus* is a preferred prey of many carnivorous invertebrates, including the snails *Nucella crassilabrum* and *Concholepas concholepas*, and the crab *Acanthocyclus gayi*. Preliminary observations indicated that *S. algosus* exists as 2 morphotypes: a thick, smooth shell and a thinner, ringed shell. The thick-shell morphotype was found mostly on compact, rocky platforms, whereas the thin one was found on emergent rocks. We examined the role of invertebrate predators in determining the morphological differences observed in *S. algosus* as a process of defence induction. The density and size of mussel predators showed significant differences between habitats: *A. gayi* dominating the platforms and *N. crassilabrum* emergent rocks. *C. concholepas* did not show differences between habitats. Waterborne cue experiments demonstrated that the mussel shell thickness is increased by the presence of predators, especially *A. gayi.* Furthermore, in contrast to the other predators, *A. gayi* preferentially selects mussels of the thin-shell morphotype. We demonstrate the cause and effect connection between variation in mussel shell morphology in the laboratory and their associated spatial distribution in the field, as well as the ecological role played by predators. We propose that, at local scales, the distribution and abundance of predators in the field explain the inter-population morphological differences of the mussel *S. algosus*.

KEY WORDS: Predator-inducible defences · Shell thickness · Growth · Predator–prey interaction · Mussel · *Semimytilus algosus*

INTRODUCTION

Predator-inducible defences, which are present in numerous taxonomic groups (vertebrates, invertebrates, plants, bacteria), are caused by cues associated with predators, and may diminish the effects of subsequent predator attacks (Adler & Harvell 1990, Harvell 1990, Tollrian & Harvell 1999). Predators can affect a diverse array of traits in their prey: behaviour, physiology, morphology and life-history (Dodson 1989, Adler & Harvell 1990, Lima & Dill 1990, Skelly & Werner 1990, Kats & Dill 1998, Lima 1998). When predation is patchy and unpredictable, the prey may benefit from possessing defences that can be induced when needed, rather than being permanently expressed (Tollrian & Harvell 1999). The induction of defences requires an external signal for activation and is thought to be favoured over constitutive defences when (1) the cues associated with predators are non-lethal; (2) the fitness costs are less than the benefits of the defence; (3) the probability of encountering a predator is high, but unpredictable; (4) the prey have reliable cues for detecting the presence of a predator; and (5) the presence of the predator in time and space

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is intermittent (Harvell 1986, 1990, Lively 1986a, Havel 1987, Adler & Harvell 1990, Riessen 1992).

In marine, rocky, intertidal systems, morphological defences lowering predation success can be produced by invertebrate prey, for example gastropods (Appleton & Palmer 1988, Palmer 1990, Trussell 1996), bryozoans (Yoshioka 1982), barnacles (Lively 1986b) and mussels (Reimer & Tedengren 1996, Leonard et al. 1999, Reimer & Harms-Ringdahl 2001). Mussels are prey for a variety of predators, including gastropods, crustaceans, seastars, fishes, shorebirds and mammals (Seed 1976, Menge 1978a,b, Suchanek 1978, Castilla 1981, Bahamondes & Castilla 1986, Meire & Ervnyck 1986, Ojeda & Dearborn 1991). Regardless of the predation mode, these predators are able to breach the mussel's protective shell to reach the soft tissue in a variety of ways: (1) whole-animal ingestion, (2) invasion through the shell aperture, (3) breakage and (4) drilling. Whilst most marine gastropod predators drill holes through mussel shells using a combination of chemical and mechanical procedures (Castilla et al. 1979, Serra et al. 1997), crabs use their chelae and/or their mandibles to break shells (Castilla 1981, Hughes & Seed 1981, Navarrete & Castilla 1988). For each of the methods employed to consume mussels, there is an associated handling time, depending on (1) the morphological or behavioural resistance of the prey (e.g. the ability of the shell to resist penetration or being opened), and (2) the efficiency of the predator in overcoming the prey's resistance. Optimal foraging theory predicts that predators should prefer medium-sized mussels to smaller or larger ones, since the ratio of handling time to reward is minimised (Elner & Hughes 1978, Hughes & Seed 1981).

Many mussel species show considerable intra-population variation in morphological traits (i.e. shell thickness and growth) that have been explained by wave exposure (Raubenheimer & Cook 1990, Steffani & Branch 2003), population density, food supply (Seed 1968) and intertidal height (Franz 1993). Furthermore, classical studies have addressed this kind of variability in terms of predator–prey interactions (Kitching et al. 1959, Ebling et al. 1964). For instance, many mussels develop defence mechanisms, such as increased shell thickness (Leonard et al. 1999, Smith & Jennings 2000), strong adductor muscles (Hancock 1965), and increased byssus thread production (Day et al. 1991, Côté 1995), to reduce the efficiency of their predators.

The mussel *Semimytilus algosus* (Gould, 1850) is a common inhabitant of the low rocky intertidal fringe in central Chile, distributed between Ecuador and Chiloe Island (approximately 42° S). In central Chile (around 33° S), this mussel is one of the preferred prey for a guild of intertidal carnivorous predators, including the gastropods *Concholepas concholepas* (Bruguière,1789), *Nucella crassilabrum* (Pallas, 1774) and *Crassilabrum crassilabrum* (Sowerby, 1834); the echinoderms *Heliaster helianthus* (Lamarck, 1816) and *Stichaster striatus* (Müller & Troschel, 1840); and the crustaceans *Acanthocyclus gayi* (Milne Edwards & Lucas, 1844) and *A. hassleri* (Rathbun, 1898) (Castilla 1981, Méndez & Cancino 1990, Soto 1996, 2001). At Matanzas (central Chile), 2 contrasting habitats can be distinguished: (1) extensive, compact, rocky platforms, and (2) small, emergent, disconnected rocks, surrounded by sand. Preliminary observations have shown that there are morphological differences in *S. algosus* from the 2 habitats (S. Navarrete pers. comm.). Mussels on emergent rocks have thick, uniformly yellow shells with a smooth surface, while those on platforms have thinner, uniformly brown shells with a ringed surface. However, these differences are not evident in juvenile specimens (shell length < 10 mm). Although *S. algosus* shows these strikingly different morphologies, no studies in Chile have addressed the ecological causes. The objective of this work was to evaluate the effect of predation risk on the growth and shell thickness of *S. algosus*, and to address the interaction between this mussel and its main predators. Based on laboratory experiments, we hypothesise that intra-population differences in the shell thickness of *S. algosus* are caused by sub-lethal predator–prey interactions, via a process of defence induction. Therefore, differences in the density and spatial distribution of the mussel's predators between habitats may constitute an important factor influencing the pattern of shell thickness in the field. We propose that the production of defensive morphotypes has an adaptive value for this mussel, since predators have a preference for mussels with thinner shells.

MATERIALS AND METHODS

Locality. The study was conducted in Matanzas (33° 58′ S, 71° 53′ W), an exposed rocky shore on the coast of central Chile. Matanzas has a fragmented intertidal zone with 2 different habitats, extending approximately 2 km along the shore. One is characterised by emergent rocks of relatively small area (~1 to 3 m^2), separated from each other by sand. The second habitat is characterised by compact and extensive rocky platforms (~15 to 30 m^2). The mussel *Semimytilus algosus* inhabits the low intertidal fringe in both habitats, forming dense monolayer patches. Sand scour difference between habitats was not tested.

We worked at 3 sites, each containing both habitats, and characterised their wave exposure, registering maximum wave velocity over a 4 d period (July 12 to 15, 2003). Five dynamometers (Bell & Denny 1994) per

habitat were screwed down in the low intertidal zone at each site. Daily maximum wave force was registered in the field, as drag force (N), using a line spring scale (PESOLA®, accuracy = 0.075 N). Drag force data were transformed to values of velocity (m s^{-1}) using the calibration curve previously obtained from a power fit (see Castilla et al. 1998). A 2-way ANOVA for maximum wave velocity data was performed on ln(x)-transformed data. Days were considered as a blocking factor.

Morphological analysis. We evaluated the existence of shell morphological differences in *Semimytilus algosus* through the collection of mussels during 4 seasonal sampling events over a 1 yr period. During each sampling, three 10 × 10 cm quadrats were thrown haphazardly in each habitat (n = 1 quadrat per habitat per site) in the low intertidal fringe (maximum tidal range: 1.7 m). Mussels within each quadrat were collected by scraping the rock with a metal spatula. Samples were frozen (–18°C) prior to analysis. To evaluate mussel shell thickness and compare mussel characteristics between habitats, we haphazardly sub-sampled 30 mussels (shell length >10 mm) per quadrat. Mussel shell mass was evaluated by dissecting the mussels into shell and flesh components; shells were oven-dried at 70°C for 48 h, and weighed (precision: ±0.001 g). Shell thickness was calculated using a thickness index (Ti): Ti = weight of right valve (g) / planar valve surface (mm^2) (Guiñez 1996). To measure the planar valve surface area, we took high-resolution pictures of the right mussel valve for 30 individuals per quadrat, using a digital camera (Kodak™ digital science model DC210 Zoom Camera). Pictures were converted to binary files and the surface area of each valve was measured separately using SigmaScan® Pro 5.0 software (SPSS 1999). We decided not to make direct measurements of valve thickness, because there is interdependence among the multiple measurements for a single valve. The calculated thickness index solved this problem and allowed us to perform parametric statistical tests. For mussel shell thickness data we performed a 3-way, blocked, mixed ANCOVA (analysis of covariance), with Season and Habitat Type as fixed factors and Site as a random factor. We used shell weight as the dependent variable and shell surface area as a covariate. Differences in the Ti were analysed using a 3-way, blocked, mixed ANOVA, with Season and Habitat Type as fixed factors and Site as a blocking factor. Mussel thickness index data were ln(x) transformed to meet assumptions of normality and homoscedasticity of variances. For both analyses, we assumed no interaction effects between blocks and the other factors.

Predator density and size. Through bi-monthly determinations (May 1999 to May 2000), we evaluated the density of intertidal invertebrate predators. For each sample we recorded the number and sizes of predators (body size >10 mm) in the low intertidal fringe in 18 haphazardly placed 50 × 50 cm quadrats (i.e. 3 replicates in each habitat per site). Site was considered as a blocking factor. Body sizes were measured only twice (November 1999 and March 2000) to minimise potential effects of disturbance on the system. For gastropods, we measured maximum shell length and for crabs, the maximum carapace width, using vernier callipers. Measurements were made in the field and specimens returned to their habitat.

Multiple-choice feeding preference. Feeding preferences of 3 *Semimytilus algosus* predators, i.e. *Nucella crassilabrum*, *Concholepas concholepas* and *Acanthocyclus gayi*, were investigated via multiple-choice laboratory experiments, using thin and thick mussel morphotypes. Both morphotypes were held in the same aquarium and offered simultaneously to the predators. We hypothesised that predators would prefer mussels with thin shells. The predators and mussels used in the experiments were collected from the study locality on May 15, 2000. Prior to experimentation, predators and mussels were maintained under laboratory conditions for a 1 wk period in separate aquaria. Experiments were run simultaneously for 10 consecutive d using the 3 predators. Each experimental unit consisted of a plastic aquarium (2 l), containing 1 predator and 10 adult mussels (shell length 25 to 27 mm) of each morphotype (n = 10 aquaria per predator species). Aquaria received constant, continuously flowing seawater and air during the experiment and the temperature ranged between 14 and 16°C. We recorded the number of mussels per morphotype consumed per predator per day in each aquarium. To maintain a constant probability of predators encountering a prey, the consumed mussels were replaced daily by fresh mussels of the same morphotype. To evaluate predator-independent mortality, control mussels were kept in aquaria without predators (controls). Several authors have described deficiencies in the design and analysis of multiple-choice feeding-preference experiments (Peterson & Renaud 1989, Roa 1992, Manly 1993, Lockwood 1998, Jeffrey et al. 2004). In this work, we followed Roa's (1992) methodology and used a 1-sample Hotelling's T-squared test for statistical analysis.

Predator water-borne cues. To test the hypothesis that *Semimytilus algosus* shell thickness is the result of sub-lethal predator–prey interactions, we exposed juvenile mussels (shell length 7.0 to 10.0 mm) to water-borne cues from the crab *Acanthocyclus gayi* and the gastropods *Concholepas concholepas* and *Nucella crassilabrum* over a 5 mo period, and evaluated the effect on *S. algosus* shell growth and thickness. On December 24, 2000 we collected 720 juvenile *S. algo-*

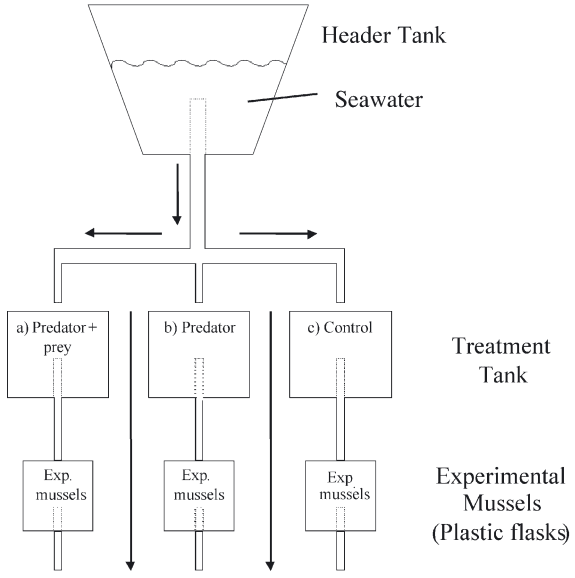

Fig. 1. Simplified scheme of the system designed for experiments on predator water-borne cues. Each plastic flask is an experimental unit (=20 juvenile *Semimytilus algosus*). The complete design included 36 experimental units (n = 4 per treatment per predator species)

sus from the study locality and marked them with a coloured and numbered bee tag (C. Graze, Germany), glued to the right valve with cyanoacrylate glue (Poxipol™). Prior to experimental treatments, we recorded the maximum shell length of mussels using digital callipers. The experimental mussels were held in plastic flasks and exposed to effluent arriving from 1 of 3 treatments: (1) tank with predator + mussels (i.e. 1 predator with 5 mussels as prey, replaced daily according to consumption); (2) tank with predator alone (i.e. 1 predator specimen); and (3) tank with mussels (i.e. 5 adult mussels and no predator) (Fig. 1). Experiments were performed simultaneously for the 3 predator species (n = 4 replicated plastic flasks per effluent treatment per predator species; total of 36 independent flasks). Treatments were spatially arranged at random. Each flask received flowing seawater (filtered through a coarse sand filter) at a rate of 0.25 l min^{-1} and water flow was verified every 12 h. Each plastic flask (volume = 0.4 l) contained 20 mussels and was connected to the treatment tank by a PVC tube (length = 7 cm; diameter = 2 cm) (Fig. 1). Mussels were not artificially fed. Every 15 d we replaced the predator and prey specimens in the tank treatments with freshly collected specimens from Matanzas. Predators were fasted for 1 wk prior to their introduction into the experimental system. After 5 mo of exposure to the treatments we measured the mussels' maximum shell length, width and height. We also calculated the thickness index (Ti) and evaluated the effect of each treatment on Ti and growth using a 3-way nested ANCOVA, considering Predator species (3 levels), Effluent (3 levels) and Replica as fixed factors, and the initial shell length as a covariable.

RESULTS

Exposure

The maximum average daily wave velocity registered in the platform habitats was 3.26 ± 0.30 m s^{-1}, and in the emergent rock habitats was 3.22 ± 0.23 m s^{-1} (mean ±1 SE). Wave velocity was not significantly different between habitats (Table 1).

Morphological analysis

Mussels from the platform habitat had a greater weight per unit surface area than mussels from the emergent rocks (Fig. 2). Shell weight was not signifi-

Table 1. Three-way nested ANOVA for maximum wave velocity at 3 sites in Matanzas (df = degrees of freedom, MS = mean square, *F* = value of the *F*-statistics, p = p-value)

Source of variation	df	MS	*F*	p
Day	3	0.7141	58.83	0.004
Site	2	0.1282	10.56	0.044
Habitat (Site)	3	0.0121	0.27	0.847
Day × Site	6	0.0455	1.47	0.197
Residual	105	0.0310		

Table 2. *Nucella crassilabrum*, *Concolepas concholepas* and *Acanthocyclus gayi*. Monthly average density (ind. m^{-2}) of predators in each habitat (ER = emergent rock habitat; P = platform habitat) in Matanzas during May 1999 to May 2000. Mean (SE)

	N. crassilabrum		*C. concholepas*		*A. gayi*	
	ER	P	ER	P	ER	P
May 99	7.5 (1.0)	3.2 (0.8)	2.1 (0.8)	4.0 (0.1)	0.0 (0.0)	5.5 (0.4)
Jul 99	9.1 (0.1)	5.9 (0.6)	3.0 (1.2)	2.6 (1.8)	0.8 (0.2)	7.6 (1.0)
Sep 99	12.8 (0.3)	8.4 (1.0)	5.1 (0.1)	4.1 (0.2)	0.8 (0.4)	8.0 (1.5)
Nov 99	12.6 (0.9)	11.8 (0.1)	5.2 (1.1)	3.9 (0.6)	0.6 (0.2)	8.4 (1.9)
Jan 00	12.2 (0.6)	10.8 (1.2)	4.2 (0.9)	6.5 (1.6)	0.0 (0.0)	5.5 (0.4)
Mar 00	11.0 (0.8)	6.8 (1.0)	3.2 (1.1)	3.2 (1.1)	0.6 (0.2)	5.9 (0.2)
May 00	7.2 (0.8)	4.2 (0.1)	2.1 (1.2)	3.0 (0.2)	0.0 (0.0)	3.0 (0.2)

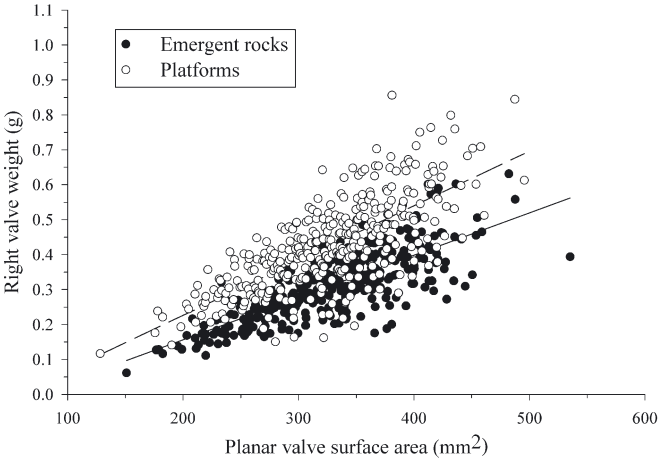

Fig. 2. *Semimytilus algosus*. Shell thickness. Right valve weight (g) versus planar valve surface area (mm^2) relationship of mussel shell (n = 360 mussels per habitat). The continuous line represents the linear regression for mussels associated with emergent rock habitat (equation: valve weight = 0.001211 × planar valve surface area – 0.0855; $r^2 = 0.58$) and the segmented line represents the linear regression for mussels in the platform habitat (equation: valve weight = 0.001567 × planar valve surface area – 0.0870; $r^2 = 0.52$)

cantly affected by the principal effect of Site or its interactions ($p > 0.5$), but was significantly affected by Habitat Type (ANCOVA, $F_{1, 2} = 722.53$, $p = 0.001$; Fig. 2). The thickness index was significantly greater (by about 37%) for mussels from the platform habitat compared with those on emergent rocks (ANOVA, $F_{1, 2} = 695.79$, $p = 0.001$).

Predator density and size

The density of *Nucella crassilabrum* was significantly greater on the emergent rock habitat than on the platforms ($F_{1, 2} = 58.36$, $p = 0.017$; Table 2). The density of *Concholepas concholepas* did not show significant differences between habitats ($F_{1, 2} = 0.245$, $p = 0.670$; Table 2), reaching densities of about 4 individuals m^{-2} at both habitats. *Acanthocyclus gayi* had a different pattern, being 10 times more abundant on the platform habitat than on the emergent rocks, reaching average densities of 6 individuals m^{-2} on the former ($F_{1, 2} = 73.662$, $p = 0.013$; Table 2).

For *Nucella crassilabrum*, the largest individuals were associated with the emergent rock habitat (ANOVA, $F_{1, 52} = 9.39$, $p = 0.0035$). *Concholepas concholepas* sizes did not differ significantly between habitats (ANOVA, $F_{1, 22} = 3.17$, $p = 0.089$) or between sampling dates (ANOVA, $F_{1, 22} = 3.55$, $p = 0.072$). During the sampling of predator size, we did not record sufficient numbers of *Acanthocyclus gayi* individuals in the emergent rock habitat to allow a comparison between habitats; in the platform habitat, *A. gayi* did not differ significantly among sampling dates (ANOVA, $F_{1, 15} = 0.10$, $p = 0.750$).

Multiple-choice feeding preference

Out of the 3 predators studied, the crab *Acanthocyclus gayi* had the fastest total (thick and thin morphotypes) daily mussel consumption rate , averaging 1.99 individuals per day. The average rates for *Concholepas concholepas* and *Nucella crassilabrum* were 1.86 and 0.99 mussels, respectively. The crab *A. gayi* showed a selective foraging behaviour, indicated by the highly significant differences between the consumption rates of the different *Semimytilus algosus* morphotypes (Hotelling's T-squared = 140.00, $p < 0.001$; Fig. 3). *C. concholepas* and *N. crassilabrum* were less selective, consuming morphotypes of both mussels at similar rates (Fig. 3).

Predator water-borne cues

Fig. 4 shows the effect of each predator on the shell thickness of juvenile *Semimytilus algosus*. Thickness indexes showed significant differences for the interaction Predator × Effluent ($p < 0.001$; Table 3A). This interaction precludes an analysis of main effects. Therefore, for each Effluent, we compared the differential effects among predator treatments, using the

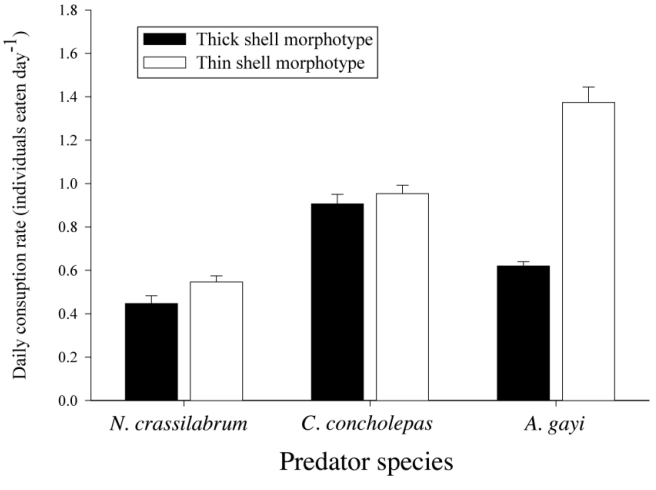

Fig. 3. *Nucella crassilabrum*, *Concolepas concholepas* and *Acanthocyclus gayi*. Daily consumption rates in the multiple-choice feeding-preference experiment on the 2 mussel morphotypes: thick-shell morphotype (black bars) and thin-shell morphotype (white bars). The bars represent means + 1 SE for 10 independent experimental units

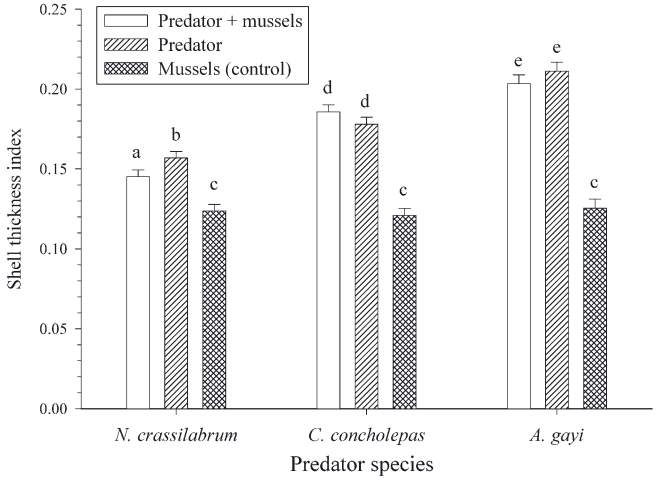

Fig. 4. *Semimytilus algosus*. Shell thickness of juveniles in predator water-borne cue experiment. The bars represent means + 1 SE for 4 independent experimental units. Treatments sharing the same letter are not significantly different ($p > 0.05$, Tukey's HSD test adjusted for multiple comparisons)

SLICE option of PROC GLM (SAS 1996). The predator + mussels and predator treatments showed significant differences among Predator ($p < 0.001$; Table 3B), but the mussels treatment (control) did not ($p = 0.784$; Table 3B). Of the 3 predators tested, the crab *Acanthocyclus gayi* induced the largest increase in *S. algosus* shell thickness. Experimental mussels exposed to effluents from this crab developed shells with a thickness index greater than 0.20 g mm^{-2}. In contrast, *Nucella crassilabrum* induced the least morphological defence from its prey. *A posteriori* analyses indicated that there were significant differences between the predator + mussels treatment and the predator treatment for *N. crassilabrum* ($p = 0.012$, Tukey's HSD test adjusted for multiple comparisons; Fig. 4). For *Concholepas concholepas* and *A. gayi* treatments, however, there were no statistical differences between these 2 effluent treatments ($p = 0.321$ and $p = 0.109$, respectively, Tukey's HSD test; Fig. 4). For all predators, we detected significant differences in *S. algosus* shell thickness among the treatments that contained predators (Treatments 1 and 2) versus the treatment without predator (Treatment 3).

The presence of water-borne cues from the 3 predator and predator + mussel treatments produced a decrease in *Semimytilus algosus* shell growth (Fig. 5). Since the Predator × Effluent interaction was statistically significant ($p < 0.001$; Table 4A), we again compared the differential effects of each effluent treatment among Predator, using the SLICE option of PROC GLM (SAS 1996). The predator + mussels and predator treatments showed significant differences among Predator ($p < 0.001$; Table 4B), but the mussel (control) treatment did not ($p = 0.438$; Table 4B). *S. algosus* exposed to the *Acanthocyclus gayi* + mussels treatment had the smallest shell growth (Fig. 5). *A posteriori* analyses indicated that, for *A. gayi* treatments, there were statistical differences among the 3 effluents treatments ($p < 0.01$, Tukey's HSD test; Fig. 5). *Concholepas concholepas* effluent produced only a small decrease in the growth of *S. algosus* in comparison with the control treatment; but there was a significant difference between the predator and control treatments ($p = 0.015$, Tukey's HSD test; Fig. 5). For *Nucella crassilabrum* and *C. concholepas*, the results did not show significant differences between the predator + mussels and predator treatments ($p > 0.1$, Tukey's HSD test; Fig. 5).

DISCUSSION

In laboratory experiments, the mussel *Semimytilus algosus* developed different morphological traits when exposed to different predator effluents. *S. algosus* exposed to water-borne cues from 3 predators, *Acanthocyclus gayi*, *Concholepas concholepas* and *Nucella crassilabrum*, showed a significant increment in shell thickness, accompanied with a reduction in growth. An increase in mussel shell thickness in response to preda-

Table 3. *Semimytilus algosus*. Three-way nested ANCOVA for shell thickness (Thickness index) in predator water-borne cue experiment. Initial shell length was used as the covariate (df = degrees of freedom, SS = sums of squares, MS = mean square, *F* = value of the *F*-statistics, p = p-value)

A) Source of Variation	df	MS	*F*	p[a]
Predator	2	2.7861	3.47	0.134 (a)
Effluent	2	10.3691	12.92	0.018 (a)
Predator × Effluent	4	0.8024	9.78	<0.001 (b)
Replicate (Predator × Effluent)	27	0.0820	1.17	0.249 (c)
Initial length	1	0.0015	0.02	0.883 (c)
Residual	683	0.0698		

B) Predator × Effluent effect sliced by Effluent for shell thickness (thickness index)

Effluent	df	SS	MS	*F*	p
Predator + mussels	2	5.3151	2.6576	32.64	<0.001
Predator	2	3.4281	1.7140	20.9	<0.001
Mussels (control)	2	0.0402	0.0201	0.2	0.784

[a]Error term: (a) = Predator × Effluent; (b) = Replicate (Predator × Effluent); (c) = Residual

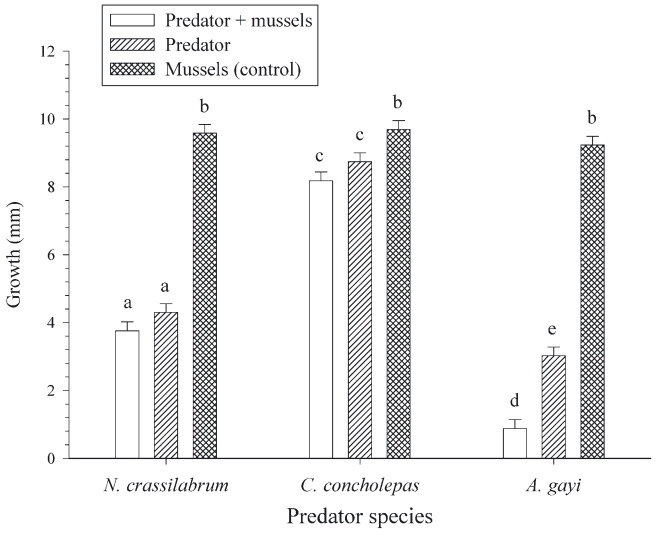

Fig. 5. *Semimytilus algosus*. Growth of juveniles in predator water-borne cue experiment. The bars represent means + 1 SE for 4 independent experimental units. Treatments sharing the same letter are not significantly different ($p > 0.05$, Tukey's HSD test adjusted for multiple comparisons)

tor effluents has been demonstrated for *Mytilus edulis* exposed to water-borne cues from crabs (Leonard et al. 1999, Smith & Jennings 2000, Reimer & Harms-Ringdahl 2001), whelks (Smith & Jennings 2000) and starfishes (Reimer & Tedengren 1996, Reimer & Harms-Ringdahl 2001). Mussel shell-thickness variation is a common defence response to predation risk, independent of predator type or their mode of attack (Smith & Jennings 2000). Furthermore, it is noticeable that mussel defence responses are induced even by predators that do not break or perforate the mussel shell to gain access to the soft tissue (e.g. starfish). *M. edulis* produces thicker shell lips in response to drilling and crushing predators, but increases in shell thickness are greater in the presence of a perforating gastropod predator (Smith & Jennings 2000). In the same vein, *S. algosus* developed different shell thickness responses depending on the kind of predator tested. Water-borne cues from the shell-crushing crab *Acanthocyclus gayi* caused the greatest increases, while the smallest increment was caused by cues from the whelk *Nucella crassilabrum*.

Our results thus show that the attack modes of predators on mussels may modify the magnitude of the mussel defence response. In the laboratory, the thin-shell morphotype of *Semimytilus algosus* was preferred by the crab *Acanthocyclus gayi*; however, the other 2 predators ate both shell morphotypes indiscriminately (Fig. 3). This difference may be related to the predator's mode of attack. For those that break mussel shells, the thickness may be an important factor determining handling time. In fact, laboratory experiments show that the crab *A. gayi* handles its prey for several minutes while trying to break its shell, and if the manipulation period lapses without success, the crab searches for another mussel. *A. gayi*'s handling time is positively correlated with shell thickness (A.C. pers. obs.). Thus, the phenotypic plasticity of mussel shell morphological traits (e.g. thickness) may constitute a strong source of intra-populational variation, since it may increase survival under field conditions. Mussels in the population which produce thicker shells when faced with predation risk should have a higher survival probability than those not able to do so or that are slow responders. On the other hand, if predators are distributed unequally in the field (i.e. due to the availability of different microhabitats), it can be hypothesised that their induction of defences in *S. algosus* would explain the inter-population phenotypic differences in mussel shell thickness observed in the field. In fact, in the platform habitat at Matanzas, where the crab *A. gayi* is abundant (Table 2), the mussel population is dominated by the thick-shell morphotype; whereas emergent rock habitats, where the crabs are scarce, are dominated by the thin-shell *S. algosus* morphotype.

Inter-habitat differences in shell morphology may also result from different local-scale physical processes, such as the effect of wave exposure (Rauben-

Table 4. *Semimytilus algosus*. Three-way nested ANCOVA for shell growth in predator water-borne cue experiment. Initial length was used as the covariate. Abbreviations as in Table 3

A) Source of Variation	df	MS	*F*	p[a]
Predator	2	1254.1315	4.54	0.093 (a)
Effluent	2	1823.0272	921.24	0.054 (a)
Predator × Effluent	4	275.9654	51.12	<0.001 (b)
Replicate (Predator × Effluent)	27	5.3988	1.68	0.016 (c)
Initial length	1	141.9615	44.16	0.001 (c)
Residual	683	3.2147		

B) Predator × Effluent effect sliced by Effluent for shell growth

Effluent	df	SS	MS	*F*	p
Predator + mussels	2	2155.6615	1077.8307	199.6	<0.001
Predator	2	1435.4942	717.7471	132.9	<0.001
Mussels (control)	2	9.1867	4.5934	0.8	0.438

[a]Error term: (a) = Predator × Effluent; (b) = Replicate (Predator × Effluent); (c) = Residual

heimer & Cook 1990, Guiñez 1996). However, our results demonstrate that the wave exposure at Matanzas did not vary significantly between habitats (Table 1); therefore, the most plausible cause for *Semimytilus algosus* inter-habitat shell morphology differences appears to be biotic variables. Life-history trade-offs in growth (Leonard et al. 1999) and reproductive rates (Lively 1986b) may accompany predator-inducible defences. For instance, our results show one such trade-off in the presence of predators, i.e. an increase in *S. algosus* shell thickness is accompanied by a decrease in shell growth. Apparently, predation risks provoke changes in resource partitioning of mussel shell production, giving a heavier weight to shell thickness than to linear growth, therefore diminishing the efficiency of predators.

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