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Research Article

Responses of the mussel *Perumytilus purpuratus* (Bivalvia, Mytilidae) to hydrodynamic conditions and the presence of predators

Mabel A. Carvallo[1], Rodrigo Riera[2] & Antonio Brante[1,3]
[1]Departamento de Ecología, Facultad de Ciencias
Universidad Católica de la Santísima Concepción (UCSC), Concepción, Chile
[2]IU-ECOAQUA, Biodiversity and Conservation Research Group
Universidad de Las Palmas de Gran Canaria, Islas Canarias, España
[3]Centro de Investigación en Biodiversidad y Ambientes Sustentables (CIBAS)
Universidad Católica de la Santísima Concepción (UCSC), Concepción, Chile
Corresponding author: Antonio Brante (abrante@ucsc.cl)

ABSTRACT. The intertidal mussel *Perumytilus purpuratus* exhibits phenotypic plasticity in response to predation threats, with these responses influenced by the mussels' perception of predation risk. These adaptations, however, are constrained by energy costs and interactions with environmental factors that may trigger synergistic effects or trade-offs among different fitness traits. In particular, this study focuses on the anti-predatory responses of *P. purpuratus* against the sea star *Meyenaster gelatinosus*, examining how the presence of the predator and water flow strength influence these responses. The research was conducted through laboratory experiments, comparing mussels from two distinct localities with varying predation risks posed by *M. gelatinosus*: Punta Hualpén, where the predator is naturally present, and Coliumo, where it is absent. The anti-predatory responses were assessed by measuring attachment strength, byssus production, and adductor muscle mass in the presence of predator cues. Additionally, potential costs associated with these responses were estimated using the gonadosomatic index as a measure of reproductive investment. The findings indicate that the anti-predatory responses of *P. purpuratus* are contingent on the mussel's origin, with adhesion strength and byssus production negatively impacting reproductive investment. Moreover, the study highlights the intricate interplay of multiple factors, as evidenced by the complex adaptive mechanisms observed in *P. purpuratus*. The interaction between predator presence and water flow strength and their combined effects on various traits underscores the need for comprehensive multifactorial experiments to understand these adaptive processes. In conclusion, this study provided valuable insights into the nuanced and site-specific nature of anti-predatory responses in *P. purpuratus*. The research emphasizes the importance of considering multiple factors and conducting comprehensive experiments to unravel the intricacies of adaptive mechanisms in prey species.

Keywords: *Perumytilus purpuratus*; chemical cue; intertidal zone; *Meyenaster gelatinosus*; plastic responses; predation risk; water flow strength

INTRODUCTION

Anti-predatory responses are used to avoid predators or reduce the probability of being consumed once the encounter has occurred, decreasing the success of the predator while increasing prey survival (Caro et al. 2008). Many marine species have developed plastic mechanisms that can be deployed in short periods, depending on the duration of the predatory event and their previous experience with the predator (Hossie & Murray 2012, Brown et al. 2013). On the other hand, anti-predatory responses may demand a high amount of energy from the prey, limiting its response capacity and affecting other fitness traits (Lind & Cresswell 2005).

Prey can perceive predator odor or chemical cues from damaged conspecifics, triggering anti-predatory

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responses (Fassler & Kaiser 2008, Guerra et al. 2012, Lowen et al. 2013). In addition, prey may improve their responses when exposed to the predator during their lifetime or through successive generations (West et al. 2018). For example, in natural systems, the whelk *Buccinum undatum* shows higher escape efficiency in localities with the presence of its main predator, the sea star *Leptasterias polaris*, in comparison to localities where the predator is absent (Rochette et al. 1996). In hatchery-reared species, predation escape responses can be lost or minimized after some generations due to the absence of predators. Brokordt et al. (2006) found that cultured individuals of the scallop *Argopecten purpuratus* are less sensitive to predators and escape more slowly than specimens from wild populations.

Similarly, the presence of sea stars may produce anti-predatory morphological responses in sessile species, such as mussels. Thicker or larger shells, adductor muscles with longer sizes and biomass, in addition to higher attachment force due to the production of more and thicker byssus, would increase the resistance of mussel individuals to the opening force of sea stars (Norberg & Tedengren 1995, Reimer & Tedengren 1996, Sommer et al. 1999, Kamermans et al. 2009). For example, *Mytilus edulis*, with longer height and higher muscle size and attachment, shows lower mortality rates due to *Asterias rubens* predation (Norberg & Tedengren 1995). In concordance, *M. edulis* exposed experimentally to *A. rubens* shows significantly larger posterior adductor muscle, a thicker shell, and more flesh per shell volume (Reimer & Tedengren 1996). From an optimal foraging approach, mussels of small and medium sizes are preferred by *A. rubens*, given the higher flesh/manipulation time rate (Sommer et al. 1999).

Anti-predatory responses can be highly energy expensive, triggering complex trade-offs between fitness traits (Creel 2018). Under the energetic budget model, developing and maintaining anti-predatory traits may affect other organism functions associated with fitness, such as growth and reproduction (Begum et al. 2010, Guerra et al. 2012). For example, when the bivalve *Argopecten ventricosus* is exposed to predatory crabs, the gonad maturation is delayed, and the gonadosomatic index is reduced, resulting in a lower reproductive performance (Guerra et al. 2012). The overproduction of byssus in the mussel *M. edulis* exposed to predators requires high tissue carbon and nitrogen production, significantly affecting its growth rate (Coté 1995). During gonadal maturation and spawning, adults of the scallop species *Chlamys islandica* show a diminished capacity for physiological recovery after escaping from predators (Brokordt et al. 2000).

Anti-predatory responses are also affected by environmental factors that cause responses in the same traits (e.g. Sui et al. 2015). Intertidal sessile organisms depend on their ability to resist wave strength (Trussell et al. 1993, Le Pennec et al. 2017). For example, mussels may produce larger and stronger byssus when exposed to strong wave action to avoid detachment from the substrate (Bell & Gosline 1997). In *Mytilus* sp., the attached strength varies seasonally, with an increase of 17% in winter (Carrington 2002). Therefore, traits associated with anti-predator responses could be constrained or overexpressed depending on the environmental conditions that individuals experience during their lifespan.

Perumytilus purpuratus is a common mussel on the southeast Pacific coast and an important intertidal ecosystem engineer (Alvarado & Castilla 1996). In the presence of predators, as observed in other mussels, this species increases byssus production and strength, in addition to its adductor muscle mass and strength, which hinders the manipulation by the predator (Coté 1995, Caro & Castilla 2004, Fassler & Kaiser 2008). Additionally, it has been reported that byssus production increases in habitats with high wave strength, reducing detachment (Alvarado & Castilla 1996). Despite the vast literature on this topic, no studies evaluate the cost of anti-predatory responses on other fitness traits, such as fecundity, or the potential interactions between factors affecting the same traits. In Chile, *P. purpuratus* is a frequent component of rocky intertidal communities and other mobile and sessile invertebrates such as barnacles, anemones, gastropods, crabs, and other mussels. These habitats are characterized by fluctuating temperatures and desiccation conditions associated with tidal cycles; wave-exposed coasts are characteristics along Chile. The natural predators of *P. purpuratus* in this area are some carnivorous gastropods such as *Concholepas concholepas* and *Acanthina monodon*, crabs such as *Acanthocyclus gayi* and *A. hassleri*, and the echinoderms *Heliaster helianthus*, *Stichaster striatus* and *Meyenaster gelatinosus*. However, these predators' presence and abundance vary across their distributional ranges. Then, prey such as *P. purpuratus* may experience different intensities and predator-type predation pressures that may affect anti-predatory responses.

M. gelatinosus is an important predator of *P. purpuratus*, and its abundance varies greatly between sites along the Chilean coast, with localities presenting high abundances. In contrast, in others, it is absent. This study aims to evaluate the anti-predatory response of *P. purpuratus* individuals from two sites differing in predation risk by the sea star *M. gelatinosus* (presence *vs*. absence). The interaction of these responses with different water flow strength conditions and their potential reproductive costs was also evaluated. An interaction effect between predation risk experience and water flow strength on the anti-predatory response of *P. purpuratus*, affecting fitness traits at different levels, is expected.

MATERIALS AND METHODS

Sample collection

To evaluate the anti-predatory responses of *P. purpuratu*s, individuals of 20-34 mm length were collected from the mid-level of the rocky intertidal of two sites 37 km apart: Punta Hualpén (36º48'19.9"S, 73º10'42.6"W), where *M. gelatinosus* is present with a mean abundance of 0.2 ind m^{-2}, and Coliumo (36º31'31.1"S, 72º57'14.2"W) where this predator was not observed during any of the several visits made in the year prior to sampling (A. Brante *pers. obs.*). Measurements using a dynamometer installed for one month at the intertidal level in the middle of the *P. purpuratus* bed recorded a similar maximal wave strength in both sites (Punta Hualpén = 8.5 N and Coliumo = 8 N). We followed the work by Bell & Denny (1994) for the dynamometer design and the wave strength method used. This dynamometer is designed to accurately measure the forces exerted by waves on marine structures, providing valuable data for understanding wave dynamics and their effects on the coast. The device typically consists of precision sensors, such as strain gauges, strategically positioned within the dynamometer structure to capture the complex forces generated by waves. Predators (*M. gelatinosus* ca. 20 cm in diameter) were collected from Punta Hualpén. Mussels (prey) and sea stars (predators) were transferred in coolers to the Estación de Biología Marina "Abate Juan Ignacio Molina", Universidad Católica de la Santísima Concepción, Chile. Before experiments, predator and prey were acclimated to a water temperature of 14-15ºC and salinity of ~34 (similar to those observed in the collection sites) for seven days, and *M. gelatinosus* specimens were maintained under starvation for four days to standardize hunger level. Each individual of *P. purpuratus* was cleaned, and the byssus was gently removed with a scraper under a binocular to standardize initial conditions. The experiments were carried out between November and December, before the spawning periods in January at this latitudinal level (Oyarzún et al. 2018).

Experiment design

A multifactorial experiment was carried out to evaluate the interaction effect between sites and water flow strengths on the anti-predatory responses of *P. purpuratus* (Fig. 1). For that; experiments considered three experimental factors: site (Punta Hualpén (presence of predators) and Coliumo (absence of predators)) × predator chemical stimuli (present and absent) × water flow strength (low and high). Low and highwater flow was differentiated using reference values from the literature. As experimental units, plastic boxes containing 24 ind of *P. purpuratus* each were exposed to the combination of predator stimuli and water strength factors. One individual of the predator *M. gelatinosus* was maintained in a 220 L container connected to a second container containing 16 plastic boxes of 4 L each with *P. purpuratus* individuals (8 for Punta Hualpén and 8 for Coliumo) to mimic predator presence; thus, an open system with a constant seawater current (20 cm s^{-1}) with predator odor flowed from the first (with the predator) to the second containers. Small holes (3 mm diameter) were drilled into each plastic box to allow unfiltered seawater circulation and ensure optimal experimental conditions to keep good quality water, constant oxygenation and temperature, and constant food provision for mussels. For the high-flow treatment, in 8 of the 16 plastic boxes (4 for Punta Hualpén and 4 for Coliumo), small water pumps were installed on one side of each box to direct a pressurized water current at 80 cm s^{-1} on the mussels. In another 220 L container with constant seawater circulation (20 cm s^{-1}) without predator odor, 16 drilled plastic boxes with *P. purpuratus* individuals (8 for Punta Hualpén and 8 for Coliumo) were placed. Four boxes from Punta Hualpén and four from Coliumo received the high-flow treatment as we described above. The remaining boxes were considered controls, with no predator odor and no water flow effects. In summary, 32 boxes were installed, with four boxes (replicates) for each treatment combination (locality × predator odor × flow strength). For all cases, individuals of *P. purpurtaus* were assigned haphazardly to different treatments.

P. purpuratus may trigger anti-predator responses in minutes or hours regarding byssus production and attachment strength (Caro et al. 2008). In addition, to test longer anti-predator responses in mussels, experimental times of two to six weeks are commonly used in other studies (Reimer & Tedengren 1996,

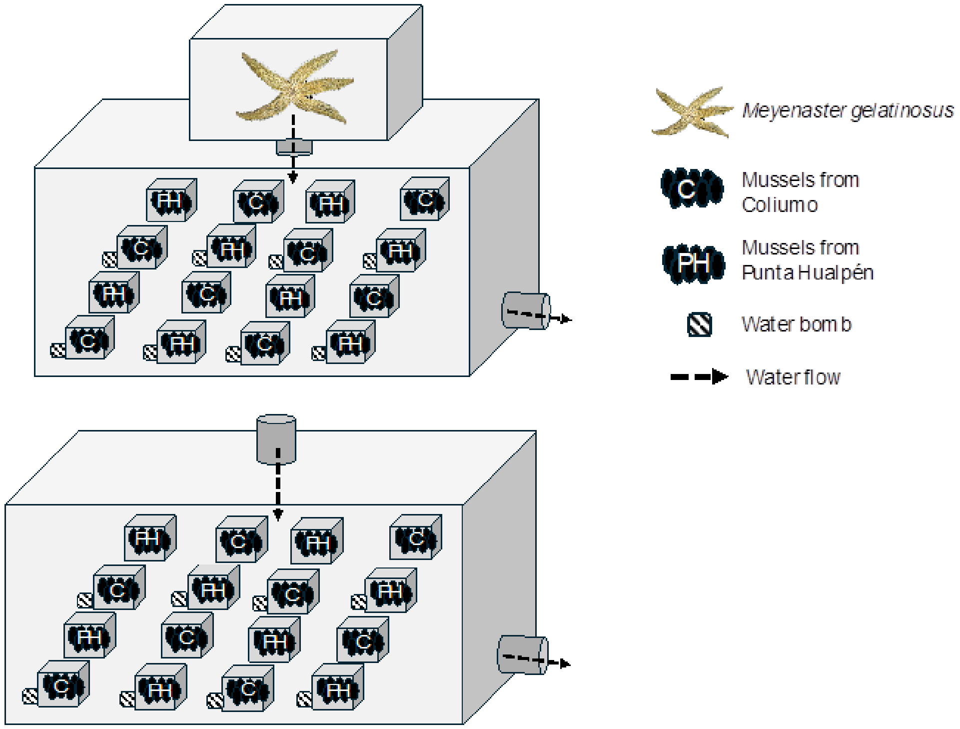

Figure 1. Diagram of the experimental design used to test the effect of the predator's odor, *M. gelatinosus*, and the strength of the water flow on individuals of *P. purpuratus* from the sites of Coliumo and Punta Hualpén.

Naddafi & Rudstam 2013, Hirsch et al. 2014, Jahnsen-Guzmán et al. 2022). Thus, in the present work, after 39 days of experimentation, adhesion strength, byssus production, and adductor muscle mass were measured in *P. purpuratus*. The costs of these responses were measured in terms of reproductive investment as the gonadosomatic index (GSI). Experiments were conducted at 14-15ºC with a natural photoperiod and unfiltered seawater to ensure a constant food supply to mussels. Individuals of *M. gelatinosus* were maintained in starved conditions and changed every five days for a new individual to prevent mortality. No differences (material, environmental conditions) between plastic containers and boxes, more than the experimental factors essayed, were evident.

Attachment strength was estimated using the methodology described by Denny (1987) and Bell & Gosline (1997). For that, a spring scale (Pesola™) was implemented with a hook fixed to the mussel through a small hole (1.5 mm) drilled in the posterior end of the shell. A vertical force was applied until the individual detached from the surface, and the attachment strength was expressed in Newtons (N). Individuals were kept submerged during measurements. The byssus was removed with a scalpel from individuals already used to measure the adhesion force to estimate byssus production. Also, the byssus remaining in the plate was removed and considered for estimations.

Given that we are interested in the potential energetic trade-off between traits associated with fitness, byssus production was expressed in g cm^{-1} of shell length. Thus, each byssus was placed on a labeled aluminum foil and dried in an oven at 80ºC for 2 h. The dry weight was then recorded using an analytic balance (0.00001 g precision).

The adductor muscles (as a proxy of closing force) and gonads were separated with a scalpel from the rest of the soft body and shell to evaluate the effect of experimental treatments on the closing force of valves and reproductive investment and dried at 80°C. After drying, the gonads, adductor muscles, and the rest of the body were weighed on an analytic balance (0.00001 g precision). Finally, the data obtained from the total mass and gonads of each individual were used to obtain the GSI, using the equation: GSI = (gonad weight / body weight) × 100. This index was used to estimate the reproductive cost of the anti-predatory responses. Seven hundred sixty-eight individuals were dissected (24 ind per plastic box × 32 boxes) and randomly selected from the same area with similar body sizes.

The variables attachment force and byssus production were standardized by shell length (cm). The adductor muscle mass was corrected for the overall weight of soft tissue.

Data analysis

Mixed ANOVAs were performed considering three fixed factors: site (Punta Hualpén and Coliumo), predator chemical stimuli (present and absent), and water flow strength (low and high). The response variables were the attachment strength (N cm^{-1} of body length), byssus production (g of byssus cm^{-1} of body length), adductor muscle mass (g of muscle g^{-1} of mussel), and reproductive investment (GSI%). Plastic boxes were considered a nested factor within the interaction of the three previous factors (site × predator presence × flow strength). When no effect was observed in the box nested factor, data were pooled at this level, and *P. purpuratus* individuals were considered replicates. Tukey *a posteriori* tests were performed when significant effects were detected in any of the factors or their interactions. Before the statistical analysis, ANOVA assumptions were evaluated using the Shapiro-Wilk test to evaluate normality distribution, and the Cochran test was utilized to evaluate homoscedasticity. The Software Statistica v.10 was used to run all analyses.

RESULTS

Attachment strength

The ANOVA analysis showed that the box nested factor was significant ($F_{56,1472} = 3.2$, $P < 0.05$) for the attachment strength variable. A more detailed analysis showed that the differences were explained by only two boxes within the interaction Punta Hualpén site × high water flow strength × no stimulus from the predator. Considering the significant full interaction term (site × predator chemical stimuli × water flow strength), the Tukey test showed that the strongest attachment in *P. purpuratus* is observed in the treatment with high water flow (Tukey test: $P < 0.05$), expecting for individuals from Coliumo without predators (Fig. 2a). Within the highwater flow treatment, individuals from Punta Hualpén showed higher attachment strength than those from Coliumo (Tukey test: $P < 0.05$; Fig. 2a). A significantly higher attachment strength was observed in individuals from Coliumo exposed to predator chemical stimuli than those without stimuli (Tukey test: $P < 0.05$), while no response was detected in individuals from Punta Hualpén (Tukey test: $P > 0.05$; Fig. 2a). In the low water flow treatment, neither the site factor nor predator stimuli showed significant effects on the attachment strength measured in individuals of *P. purpuratus* (Tukey test: $P > 0.05$; Fig. 2a).

Byssus production

A three-way ANOVA was performed for byssus production since the box nested factor was non-significant ($F_{56.1472} = 0.21$, $P > 0.05$). A significant effect of the interaction term was detected (site × predator chemical stimuli × water flow; $F_{1,152} = 3.52$, $P < 0.05$). As a general pattern, the Tukey test showed that the byssus production in *P. purpuratus* is higher in individuals from Punta Hualpén, compared to those from Coliumo, except in the treatment high flow × predator (Fig. 2b). Individuals from Coliumo responded with higher byssus production in the treatment with high water flow strength (Tukey test: $P < 0.05$; Fig. 2b). Individuals from Punta Hualpén only showed significantly higher values in the treatment with no chemical predator stimuli (Tukey test: $P < 0.05$; Fig. 2b).

Adductor muscle mass

A three-way ANOVA was performed for the adductor muscle mass variable since the box nested factor was non-significant ($F_{56,1472} = 0.42$, $P > 0.05$). Although a trend of greater adductor muscle development was observed in individuals from Punta Hualpén, the overall adductor muscle mass production was non-significantly affected by any of the factors or the evaluated interactions in this study (Tukey test: $P > 0.05$; Fig. 3a).

Gonadosomatic index (GSI)

Data for the GSI were pooled in a three-way ANOVA since the box nested factor was non-significant ($F_{56,1472} = 0.53$, $P > 0.05$). A significant interaction between the site and water flow strength factors was observed ($F_{1,1528} = 6.45$, $P < 0.001$). The Tukey test showed that individuals from Coliumo have higher GSI values in the treatment with low water flow compared to those exposed to a higher water flow (Tukey test: $P > 0.05$; Fig. 3b). None of the treatments resulted in significant differences in individuals from Punta Hualpén (Tukey test: $P < 0.05$).

DISCUSSION

In the intertidal, predation and wave action may trigger important morphological changes in *P. purpuratus*, increasing its survival probability (Moeser et al. 2006,

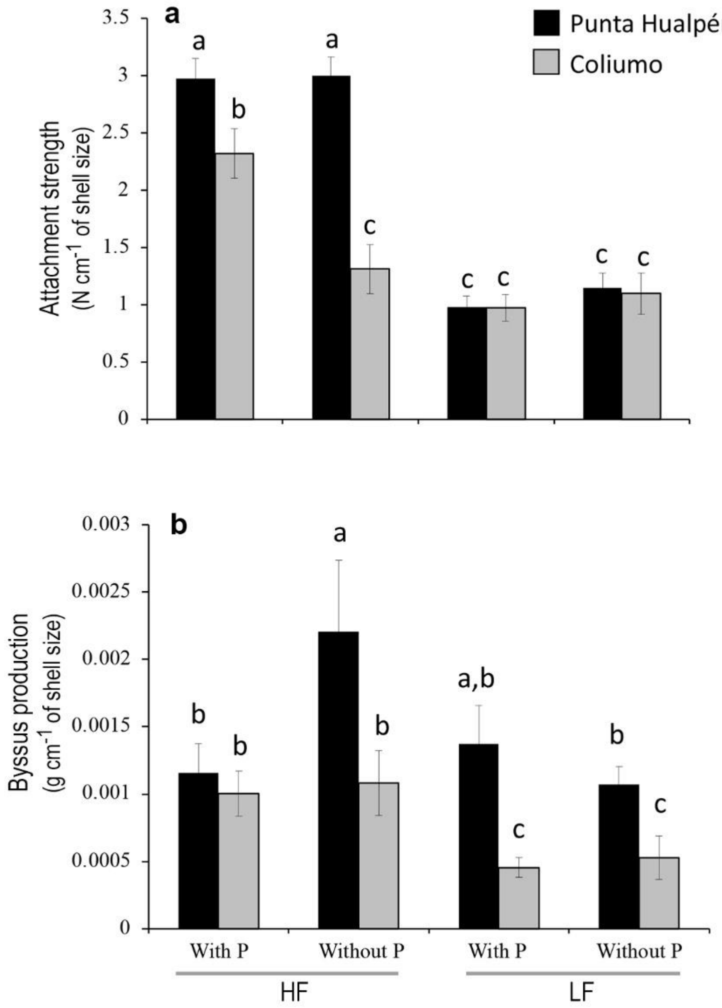

Figure 2. Responses in a) attachment strength and b) byssus production of individuals of *P. purpuratus* from Coliumo and Punta de Hualpén exposed to the presence (with P) and in the absence (without P) of the predator *M. gelatinosus* at high (HF) and low water (LF) flows. Lines on bars correspond to standard errors, and letters represent the results of the ANOVA. Different letters denote significant differences ($P < 0.05$).

Barahona & Navarrete 2010). However, responses to combined selective factors do not always have predictable magnitudes and directions. In this study, individuals of *P. purpuratus* from the site where the predator *M. gelatinosus* showed a higher byssus production in laboratory experiments than individuals from the locality where the predator is absent. However, this response was not directly related to a higher adhesion force, which only varied under high water flow conditions. Greater production of byssus negatively correlated with the GSI of *P. purpuratus*, which could be associated with this response's potential reproductive cost. In contrast, the investment in the adductor muscle was not affected. In this way, our results suggest complex interactions between anti-predatory responses and local environmental conditions in *P. purpuratus*, which energetic trade-offs and previous experience with the predator may drive.

Adhesion strength and byssus production have been reported as anti-predatory responses in mussel species (Castilla & Crisp 1970, Barahona & Navarrete 2010, Lowen et al. 2013). As a general pattern, the byssus production of *P. purpuratus* varied between specimens from the two localities. A higher byssus production was observed in individuals from the site where *P. purpuratus* naturally cohabits with the predator *M. gelatinosus* (Punta Hualpén). Several works have noted the importance of the experience of the prey with the predator in the anti-predatory response. Individuals of *Mytilus* sp. from the North Sea, where crab and sea star predators are present, showed a higher byssus adhesion

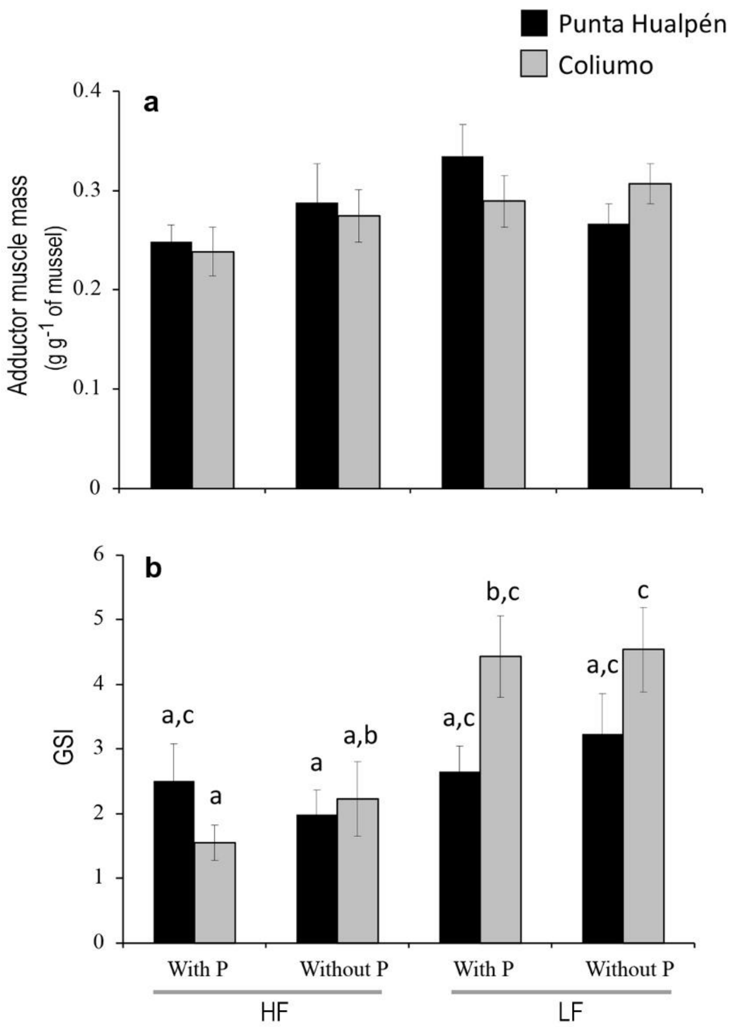

Figure 3. Responses in a) adductor muscle mass and b) gonadosomatic index (GSI) of individuals of *P. purpuratus* from Coliumo and Punta de Hualpén exposed to the presence (with P) and in the absence (without P) of the predator *M. gelatinosus* at high (HF) and low water (LF) flows. Lines on bars correspond to standard errors, and letters represent the results of the ANOVA. Different letters denote significant differences ($P < 0.05$).

force than individuals from the Baltic Sea, where predators are absent (Reimer & Harms-Ringdahl 2001). Thus, Baltic mussels could recognize the predator but did not respond as well as mussels from populations naturally exposed to the predator (Reimer & Harms-Ringdahl 2001), which could be explained by the previous exposition of the individuals to predator cues in their natural habitat, resulting in faster and more efficient anti-predatory responses. The lower efficiency in individuals from populations inhabiting habitats without predators could be explained by the high energy cost of maintaining anti-predatory responses in conditions where they do not report a benefit in biological fitness (Blumstein & Janice 2005).

Hydrodynamics is another important selective force in the intertidal. As a general pattern, we observed that individuals of *P. purpuratus* exposed to a higher water flow exhibited a greater adhesion force. This plastic adaptative response through adhesion strength has been observed in other mussels exposed to contrasting wave conditions. For example, the byssus adhesion strength of *Mytilus edulis* shows a significant increase during winter due to seasonal changes in wave force (Coté 1995, Carrington 2002, Moeser et al. 2006). In our experiments, although the greatest strength of byssus adhesion was obtained in specimens exposed to a highwater flow, this pattern did not correlate with byssus production. Moeser et al. (2006) demonstrated that byssus production increases at flow rates of 10 cm

s^{-1} and decreases at velocities >18 cm s^{-1}, explained by the mechanical constraints that mussels face when extending the foot where the gland that secretes byssus is located, due to the high hydrodynamic load exerted on the retractor byssus muscle. In our experiments, individuals in the higher water flow treatment were exposed to a current of 80 cm s^{-1}, which could be limiting the byssus production of *P. purpuratus* and triggering alternative mechanisms, such as an increase in the byssus adhesion force through byssus thickness. It has been reported that the 40% increase in attached strength during winter in the mussels *Perna perna* and *Mytilus galloprovincialis* is mainly explained by the production of a thicker byssus (Zardi et al. 2007). Unfortunately, no measurements of the byssus thickness were carried out in our experiments, so it should be tested in future works.

In several bivalve species, individuals exposed to predators increase their muscle mass and strength to difficult the valve opening by the predator (e.g. Norberg & Tedengren 1995, Reimer & Tedengren 1996, Reimer & Harms-Ringdahl 2001). In our experiments, the adductor muscle mass of *P. purpuratus* did not show significant differences among the different treatments. Thus, no effect of the predator odor was observed on this trait. One hypothesis to explain these results is that byssus production could be the main and faster anti-predatory response of *P. purpuratus* against its predator, *M. gelatinosus*, instead of strengthening the adductor muscle. Alternatively, the response of the adductor muscle to the predator may take longer than the duration of the experiment performed in this study.

The GSI of *P. purpuratus*, as a proxy of reproductive investment, did not show a clear pattern among experimental treatments. However, the highest values of GSI were observed in individuals from Coliumo at the low water flow, with and without predator stimuli, and the lowest values were recorded in the treatments where individuals from the same site were exposed to the combination of highwater flow and predator odor. These results suggest that the synergic combination of highwater strength and predator presence may impose important physical and physiological stress on individuals of *P. purpuratus* from Coliumo that are not naturally exposed to the predator in the field, affecting reproductive output. Adaptive mechanisms and plastic responses may have important energetic costs for individuals. For example, Zardi et al. (2007) outlined that during gonadal maturation, mussels invest up to 90% of their energy budget in gametes, limiting byssus production. On the other hand, *P. purpuratus* exposed to the carnivorous snail *Acanthina monodon* reduces valve gape size, clearance rate, and oxygen consumption rate (Büchner-Miranda et al. 2024). In this way, a combination of ecological and environmental stressful variables may have important costs for prey.

Here, we showed that plastic anti-predatory responses of *P. purpuratus* could depend on local environmental conditions that individuals experience in their natural habitats, and trade-offs and complex interactions among different fitness traits could drive them. Also, this study did not consider other factors that would change the intensity and direction of antipredator responses. For example, several works in intertidal species have suggested that maximum performances are reached in emersion and immersion cycles (Gillmor 1982, Widdows & Shick 1985). Here, all experiments were carried out under constant immersion of mussels, which could have biased (over or underestimated) some responses. In addition, different predators are present in natural environments, and synergic or antagonistic responses could arise (Smith & Jennings 2000, Caro et al. 2008). This way, more complex experimental scenarios should be essayed to test adaptive responses to fluctuating environments, such as intertidal habitats.

Credit author contribution

M.A. Carvallo: methodology, data acquisition, writing-original draft; R. Riera: formal analysis, review, and editing. A. Brante: funding acquisition, project administration, editing and supervision. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no potential conflict of interest in this manuscript.

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