Post-settlement movement as response to interspecific competition between the bioengineer mussels *Semimytilus algosus* and *Perumytilus purpuratus*

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ABSTRACT

Post-settlement movement has been reported mainly in marine species with low or reduced adult mobility, where distribution varies in accordance with ontogeny, thus avoiding or reducing environmental stress or biological interactions. Mussels show high dispersal at the larval stage, and settlement is a highly complex process in which larvae must choose an appropriate site to attach. Although adults are mainly sedentary, it has been shown that they move on a local scale during the benthic phase in response to physical and biological factors. *Semimytilus algosus* and *Perumytilus purpuratus* are two bioengineer mussel species cohabiting most of the Chilean rocky shores. While *S. algosus* occurs in the low intertidal zone, *P. purpuratus* dominates the mid and mid-high zones. Field and laboratory experiments have shown that *S. algosus* is a weak competitor with respect to *P. purpuratus*, and post-settlers present high mobility to relocate in the intertidal. Under this scenario, we evaluated the dispersal behavior of juveniles and adults of *S. algosus* as a potential response to competition with *P. purpuratus*. We also measured the attachment strength of *S. algosus* in the presence of its competitor, as a measure of its escape response ability. Our results showed that the presence of *P. purpuratus* increased the movement activity of juveniles and adults of *S. algosus* and decreased their attachment strength. Field experiments carried out with marked individuals in a Chilean rocky shore, showed that *S. algosus* exhibits higher local dispersion in the zone where *P. purpuratus* is present. Mussels' high dispersal ability throughout the whole benthic phase may not only serve to reach the optimal physiological position in the intertidal, but also to reduce competition interaction.

1. Introduction

Competition is an important ecological and evolutionary force, which models individual and ecological traits of species, as well as determining their abundance and distributional patterns (Jones et al., 2012; Pfennig and Pfennig, 2012). In the intertidal zone, food and space are limited resources, especially for sessile and sedentary filter feeder species, resulting in some cases in complex competitive interactions (Connell, 1961; Martínez and Montecino, 2000; Aguilera and Navarrete, 2012). However, species may show physiological and behavioral adaptations to reduce or avoid competition, which also may vary in time according to specific ecological conditions that they experience in ontogeny (Connell, 1970; Buss, 1986; Fairfull and Harriot, 1999; Richards, 2011).

Mussels are the dominant species along the rocky shores of many coastal areas worldwide, and may play an important role for community structure as bioengineers and as preys for other species (Guiñez, 2005; Koivisto and Westerbom, 2010; Valdivia et al., 2014). Individuals

attach to the substratum with byssus, a tuft of filaments secreted by a gland on the foot, and are generally considered sedentary with reduced mobility (Dinesen and Morton, 2014; Aguilera et al., 2017). Many species form extensive beds, which may cover from the mid-high level of the intertidal to shallow waters and may cohabit in the same area (Trovant et al., 2013; Adami et al., 2018). In particular, intertidal species have several physiological and morphological adaptations to resist the extreme environmental conditions in this habitat, such as wave strength and temperature fluctuations (Iwasaki, 1995; Montecinos et al., 2009; Nicastro et al., 2010).

The high abundance that mussels may reach and the limited space available for recruitment in the intertidal may intensify interspecific competition, determining hierarchical interactions among species according to their competitive abilities (Harger, 1968; Folmer et al., 2014; de Paoli et al., 2015). Mytilids may compete directly, *i.e.* by physical interference triggering agglomeration and suffocation, but also indirectly, *i.e.* more efficient resource exploitation (Shinen and Morgan, 2009). These behaviors may negatively affect both the growth and

survival of competitors and explain vertical distribution patterns in coastal areas (Benedetti-Cecchi and Cinelli, 1997; Shinen and Morgan, 2009; Chappuis et al., 2014). Moreover, the stressful physical conditions that characterize intertidal habitats may intensify competitive interactions and selective pressures (Tomanek and Helmuth, 2002). Under this scenario, it is expected that different responses arise in intertidal organisms to reduce and even avoid competitive interactions, confronting the spatial and temporal variability of these habitats. For example, juveniles and adults of mussel species commonly show movements on a small and medium spatial scale as response to competition (Harger, 1972; Kennedy, 1984; Schneider et al., 2005; Nicastro et al., 2008). These movements are facilitated by the muscular foot while the individual release and reattach byssal filaments during crawling, allowing mussels to move to better environmental conditions (Hunt and Scheibiling, 2002). Moreover, several studies have shown that movement capacity is an important trait to improve fitness in mussels and a determinant factor for the structure and functioning of ecosystems (Schneider et al., 2005; Van de Koppel et al., 2008; Shinen and Morgan, 2009).

Perumytilus purpuratus and *Semimytilus algosus* are the most abundant mussel species along rocky shores of the SE Pacific Ocean. *P. purpuratus* is considered a highly-competitive species and dominates the mid intertidal, with a high capacity to outcompete other sessile species (Alvarado and Castilla, 1996; Guzmán et al., 1998; Caro et al., 2008). This species forms dense multi-stratified matrices to increase protection against wave action and to reduce desiccation and temperature during low tides (Alvarado and Castilla, 1996). *S. algosus* mainly dominates the low intertidal, forming mono-stratified matrices with disperse distribution (Guzmán et al., 1998). Also, small individuals of this species can be found within the *P. purpuratus* belt in the mid intertidal (Caro and Castilla, 2004; Caro et al., 2008). Both of these species undergo an intermediate larval stage, recruiting in shallow waters between 2 and 4 weeks after having been in the plankton (Ramorino and Campos, 1979; Garrido, 1996). According to Navarrete et al. (2015) recruitment of both of these species starts with metamorphosis on offshore benthic habitats while post-settlement-relocation occurs as they migrate to the intertidal zone in the case of *P. purpuratus* or to shallow habitats in *S. algosus*. At the juvenile stage, individuals still have the capacity to move around on the mussel bed, and although adults may crowd at short distances (personal observations), their relocation capacity becomes progressively reduced as they grow (Navarrete et al., 2015).

Previous studies have shown that *S. algosus* is a weak competitor against *P. purpuratus* (Fuentes and Brante, 2014). In combined field and experimental works, Fuentes and Brante (2014) found that *S. algosus* may occupy most of the intertidal zone in absence of *P. purpuratus*, showing a high colonizing potential and capacity to settle in the primary substrate or low complexity habitats. However, the greater competitive ability of *P. purpuratus* could displace *S. algosus* to lower levels of the rocky shore due to its greater capacity to resist "crowding", higher filtration rate and higher physiological performance at mid levels of the intertidal (Fuentes and Brante, 2014; Pinochet et al., 2018). Hence, this complex of mussel species is an interesting model to test alternative adaptive behavioral mechanisms to reduce competition in a highly variable environment.

We herein tested the escape ability of *S. algosus* at juvenile and adult stages as a response to its competitive interaction with *P. purpuratus*. Specifically, we tested the following hypotheses: (i) The escape response in *S. algosus* is triggered by the presence of *P. purpuratus*; (ii) Higher dispersion of *S. algosus* is observed in the field in the co-occurrence area with *P. purpuratus*; and (iii) Escape ability decreases as individuals spend more time attached to the substrata. Response variables included the relocation distance from the original position, time until the first escape movement occurred, and attachment strength.

2. Materials and methods

For laboratory experiments, individuals of *S. algosus* and *P. purpuratus* were collected from the intertidal shore of Playa Bellavista, Tomé, in the Biobío Region (36°37′S, 72°57′W). After collection, specimens were transported to the Marine Biological Station Abate Juan Ignacio Molina of the Universidad Católica de la Santísima Concepción to run the experiments. According to Navarrete et al. (2015), the size distribution of settlers of *P. purpuratus* ranges between 0.2 cm and about 2.7 cm. In the case of *S. algosus*, the settler size oscillates between 0.2 cm and 2.3 cm in shell length. Thus, in our work, we considered juveniles as those individuals ranging between 1.0 and 1.5 cm, and adults as those between 3.5 and 4.0 cm. We then considered these size ranges for all of the laboratory and field experiments. All individuals, before laboratory experiments, were acclimated for 7 days at a constant unfiltered seawater flow and aeration. The temperature oscillated between 13 and 14 °C. Field experiments were carried out in the same locality where individuals were collected for laboratory experiments.

2.1. Escape behavior of S. algosus in the presence of P. purpuratus

In order to evaluate the escape behavior of *S. algosus* as a response to its interaction with *P. purpuratus*, two cultivation treatments forming artificial clumps were carried out for both juvenile and adult stages, separately: (1) monocultures of *S. algosus* consisted of 20 individuals of this species aggregated in a clump; and (2) polycultures of a mix of 10 individuals of each mussel species aggregated in a clump. Clumps were submerged and enclosed in a piece of PVC tube to force the aggregation until attachment. Holes were drilled in each tube to allow constant aeration and water flow. After two days, once the aggregations were settled, the time (minutes) until the first individual left the aggregation was recorded. Also the distance (cm) from the initial position was measured after 2 h Fig. 1. A total of 5 replicates per treatment were carried out.

Statistical comparisons of both variable responses were run using two-way ANOVAs with life stage (juvenile and adult) and culture condition (mono- and polyculture) as fixed factors. Shapiro-Wilk and Cochrane-Levene tests were conducted to check normality and homoscedasticity assumptions, respectively.

2.2. Attachment strength of S. algosus in the presence of P. purpuratus at different cultivation times

The effect of the presence of *P. purpuratus* on the attachment strength of juveniles and adults of *S. algosus* was evaluated in the laboratory using monoculture and polyculture treatments for three different cultivation times, 2, 5 and 7 days. A similar protocol as that described above was used to carry out monoculture and polyculture treatments. After each cultivation time treatment, the attachment strength of the mussels was recorded with a dynamometer. For this, a hook was glued to each individual to connect the dynamometer and a vertical force was applied until detachment occurred and the maximum strength (Newton) was recorded. One individual per clutch was selected each time to record the attachment strength. A total of 5 replicates per treatment combination (life stage and cultivation time) were carried out.

Two-way ANOVAs were performed using culture conditions (mono- and polyculture) and time (2, 5, and 7 days) as fixed factors. Shapiro-Wilk, and Cochrane and Levene tests were conducted to check normality and homocedasticity assumptions, respectively. Juvenile and adult stages were analyzed separately.

2.3. Post-settlement dispersal of S. algosus in the field

A total of 20 adult individuals of each mussel species, *S. algosus* and *P. purpuratus*, were haphazardly selected and marked in-place in one of

Monoculture of *S. algosus*

Polyculture of *S. algosus* and *P. purpuratus*
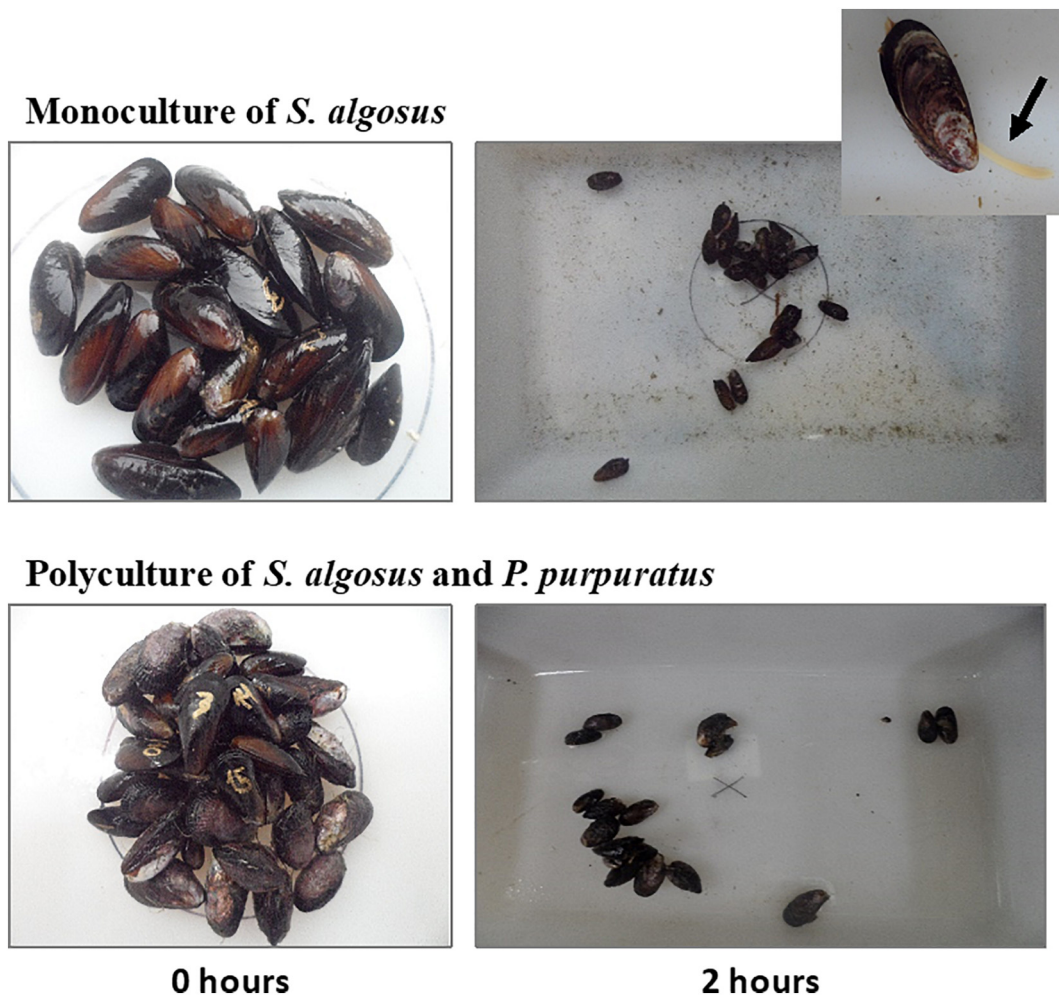
Fig. 1. Photographs showing experiments with monoculture and polyculture of *S. algosus* and *P. purpuratus* aggregations. The movement of individuals can be appreciated at the end of the experiment (after 2 h) in both treatments. The arrow in the inset photo shows the foot of *S. algosus,* which is used to crawl along the substrate.

their valves, without removal. Individuals were numerated sequentially with indelible ink. This procedure was carried out in the co-occurrence zone (mid intertidal), as well as the single-species zone for both species, *i.e.* mid-high intertidal for *P. purpuratus* and low intertidal for *S. algosus*. Although we tried to mark and follow juvenile individuals, it was impossible to find them on the following days given their small sizes and tiny marks.

The capture and recapture method was applied to monitor the dispersion of adult individuals. Every 4 days for the course of a month, the position of each individual was recorded and the final dispersion distance (cm) was estimated using epoxy putty as initial reference marks. The non-parametric Kruskal-Wallis test was used to evaluate significant differences in the dispersal distance between zones, since ANOVA assumptions were not fulfilled.

3. Results

### 3.1. Escape behavior of S. algosus in the presence of P. purpuratus

In monocultures of *S. algosus*, the mean dispersion distance of juveniles and adults was 8.3 ± 2.7 SD cm and 5.5 ± 2.3 SD cm, respectively (Fig. 2A). In the polyculture, the mean distance dispersed by *S. algosus* was 4.1 ± 0.2 SD cm for juveniles and 11.4 ± 3.4 SD cm for adults (Fig. 2A). The two-way ANOVA showed significant interactions among cultivation type and life stage factors ($F_{8,2} = 112.75$; $p < .01$).

The *a posteriori* Tukey test showed significant differences among all treatment combinations ($p < .05$).

The mean escape response time of *S. algosus* in the monoculture was 4.1 ± 1.6 SD min for juveniles and 7.1 ± 1.7 SD min for adults. In the polyculture, the response was faster with 2 ± 1.4 SD min for juveniles and 0.8 ± 0.6 SD min for adults (Fig. 2B). The two-way ANOVA showed significant interactions among cultivation type and life stage factors ($F_{5,3} = 53.08$; $p < .01$). The *a posteriori* Tukey test showed that all groups significantly differed among them ($p < .05$).

3.2. Attachment strength of S. algosus in the presence of P. purpuratus at different cultivation times

Attachment strength of *S. algosus* differed among treatments showing significant interactions between cultivation type and cultivation time factors in juveniles (Two-way ANOVA: $F_{2,14} = 30.24$; $p < .01$) and adults (Two-way ANOVA: $F_{2,14} = 3.21$; $p < .01$). The Tukey *a posteiori* test revealed a general pattern of the attachment strength increasing with time in both life stages (Fig. 3). Also, a weaker attachment was recorded in individuals of *S. algosus* cohabiting with *P. purpuratus* in polycultures as compared to the monoculture treatment (Fig. 3).
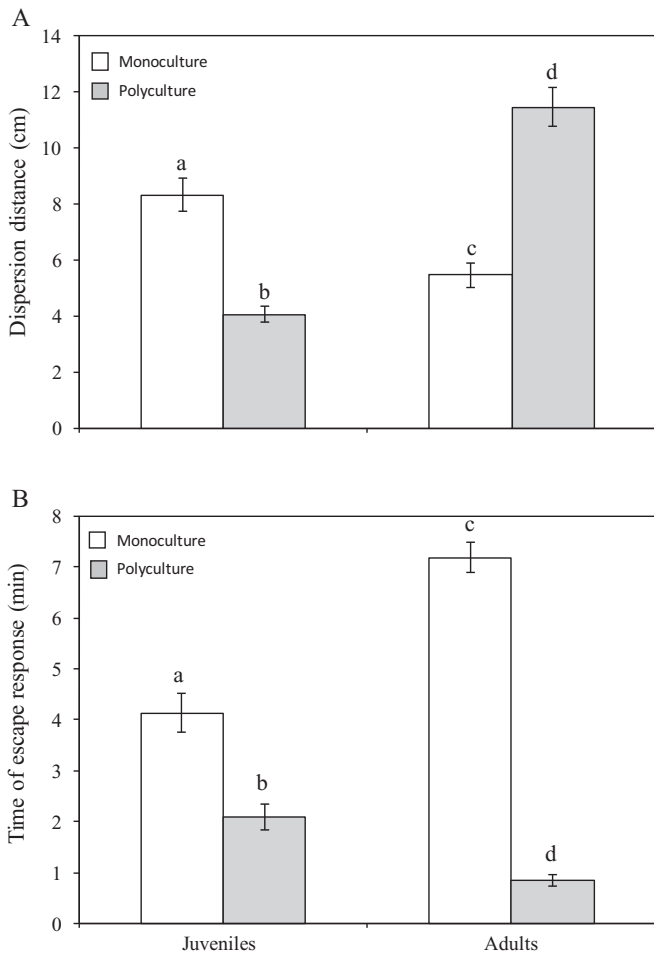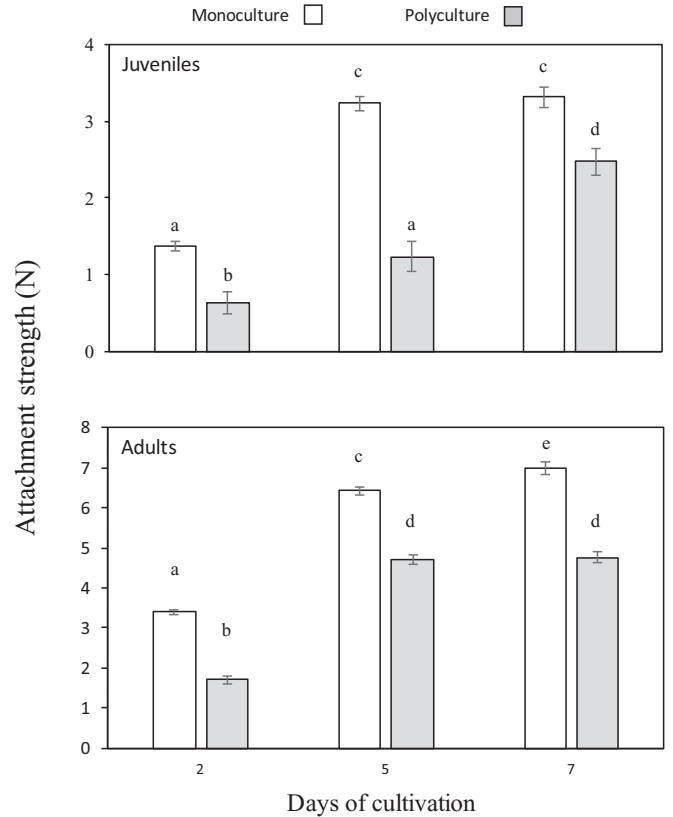
Fig. 2. (A) Distance (cm) moved by juveniles and adults of *S. algosus* in monoculture and polyculture (with *P. purpuratus*) treatments. (B) Time (minutes) until the first escape movement response of juveniles and adults of *S. algosus* was recorded in monoculture and polyculture (with *P. purpuratus*) treatments. Letters on the top of each bar represent the results of the pairwise comparisons after the *a posteriori* Tukey test. Vertical error bars correspond to ± 1 SD.

3.3. Post-settlement dispersal of S. algosus and P. purpuratus in the field

Different patterns of movement behavior were observed between species and zones in the intertidal. Of the total of the marked individuals, 80% of *S. algosus* and 85% of *P. purpuratus* individuals were recaptured after one month of observation. Mean distance moved by individuals of *S. algosus* in the single-species zone was significantly lower than that recorded in the co-occurrence zone, with 3.8 ± 3.5 SD cm and 35.4 ± 10.8 cm, respectively (Kruskal-Wallis: p < .01; Fig. 4). Individuals of *P. purpuratus* showed reduced movements with mean values oscillating between 1.2 ± 1.7 SD in the single-species zone and no movement in the co-occurrence zone (Fig. 4).

4. Discussion

Mussels are the dominant bioengineer species on SE Pacific coasts, showing characteristic vertical distributional patterns as a consequence of hierarchical interspecific interactions. Former studies have found that the mussel *S. algosus* is a weak competitor with respect to the dominant species *P. purpuratus*, being negatively affected in growth and survival rates (Fuentes and Brante, 2014). In the present work, we showed that the lower competitive ability of *S. algosus* triggers escape behaviors in juveniles and adults when confronted with *P. purpuratus* in

Fig. 3. Attachment strength (N) of juveniles and adults of *S. algosus* after 2, 5 and 7 days of cultivation in monoculture and polyculture (with *P. purpuratus*) treatments. Letters on the top of each bar represent the results of the pairwise comparisons after the *a posteriori* Tukey test. Vertical error bars correspond to ± 1 SD.
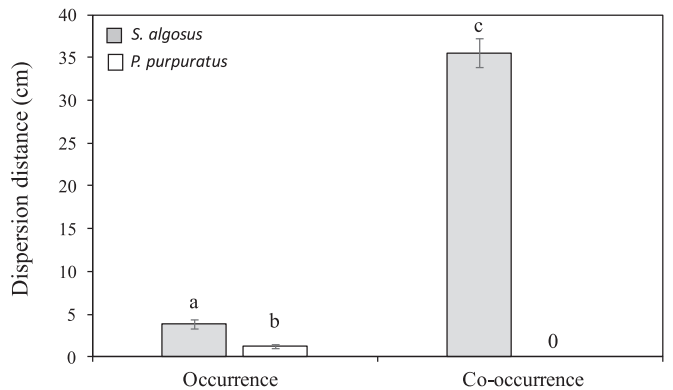
Fig. 4. Distance (cm) moved by adults of *S. algosus* and *P. purpuratus* in the areas they inhabit without their competitor in the intertidal and in those areas they cohabit. Letters on the top of each bar represent the results of the pairwise comparisons after the *a posteriori* Tukey test. Vertical error bars correspond to ± 1 SD.

both laboratory and field conditions. The attachment strength was also found to be lower in the presence of its competitor, which may facilitate escaping. Our findings, together with previous evidence on vertical dispersion of post-settlers along rocky shores of both species, suggest that small spatial scale dispersal and escape behavior as response to competition play an important role in explaining abundance and distributional patterns in intertidal communities.

We herein evaluated the dispersion of *S. algosus* under interspecific competitive pressure in both controlled and field conditions. Adults showed higher mobility (dispersal distance) and faster escape responses

when cohabiting with *P. purpuratus* in artificial clumps. In contrast to our results, previous findings have shown that the mussels *Mytilus trossulus* and *Xenostrobus securis* reduced their capacity to escape when cultivated with *M. galloprovincialis* in a clump (Shinen and Morgan, 2009; Babarro and Abad, 2013). According to these authors, this may be explained by the higher competitive ability of *M. galloprovincialis,* which smothers and limits the movement of the weaker competitors resulting in reduced growth and survival rates (Shinen and Morgan, 2009; Babarro and Abad, 2013). Interestingly, although juveniles of *S. algosus* responded and escaped faster when *P. purpuratus* was present, they moved longer distances in monoculture as compared to polyculture conditions. Fuentes and Brante (2014) observed in experimental mussel clumps that small individuals of *P. purpuratus* attached to the top of *S. algosus* shells, potentially reducing the movement of the latter. Alternatively, intraspecific competition could be a greater stressor in *S. algosus*. This stressor may also help to explain the lack of multi-stratified aggregations in *S. algosus,* unlike *P. purpuratus,* which forms dense clumps of several layers that provide complex microenvironments for other species (Briones and Guiñez, 2005).

Mussels' post-settlement movement ability has also been highlighted as an important trait in strong competitor and invader species. *Mytilus galloprovincialis*, a successful invader, uses dispersive mechanisms at juvenile and adult stages to efficiently occupy the intertidal space available on the rocky shore (Ruis and McQuaid, 2006; Shinen et al., 2009). Similarly, *M. edulis* also uses movement and dispersion as an advantageous strategy to adhere to different substrates, increasing byssus production when competing with other species (Khalaman and Lezin, 2015).

Our field experiments were in accordance with the behavioral patterns of *S. algosus* that we observed in the laboratory. Thus, juveniles and adults of this species showed higher mobility in areas where they co-occurred with *P. purpuratus*. In contrast, the competitor, *P. purpuratus,* showed scarce mobility in the intertidal. Mussels' escape behavior capacity could depend on their capacity to detach from the substrata. In our experiments, the adhesion strength of *S. algosus* increased with attachment time, however, it was weaker in the polyculture treatment with *P. purpuratus*. Previous studies have shown that the byssus production rate is influenced by biotic and abiotic factors (Carrington et al., 2015; Aguilera et al., 2017), such as hydrodynamic conditions (Lee et al., 1990; Bell and Gosline, 1997; Hunt and Scheibiling, 2001), predation level (Leonard et al., 1999) or physiological processes (Clarke, 1999; Carrington, 2002; Babarro et al., 2008; Gilbert and Sone, 2010). Attachment strength also varies spatially and temporally, with an increase of byssal filaments during harsher conditions (Moeser and Carrington, 2006). Unfortunately, scarce information currently exists on biological and ecological aspects of *S. algosus*. However, when comparing the attachment strength recorded for *S. algosus* in this study, and that reported for *P. purpuratus* by Aguilera et al. (2017), important differences can be observed. Adults of *P. purpuratus* may reach up to 50 N of attachment strength, while a maximum of 7.8 N was recorded for *S. algosus*. These data suggest there is a trade-off between the ability for dispersal and attachment strength in mussels, which is consistent with other, reported trade-offs between life history traits and production of byssus in other mussel species (Zardi et al., 2007; Carrington, 2002). Consequently, although *S. algosus* showed a high dispersal capacity, it may be constrained to inhabit lesser wave-exposed habitats, in comparison to *P. purpuratus*, given its low attachment strength.

The distribution of *S. algosus* along rocky shores has proven to be restricted to the low intertidal when *P. purpuratus* is present (Fuentes and Brante, 2014). However, the vertical segregation in the distribution of these two mussel species is not only explained by interspecific competition. Established populations of *S. algosus* have been observed in sites with a high influence of sand (Caro and Castilla, 2004; Caro et al., 2008). Experimental works have found that *S. algosus* cultivated with sand in suspension has significantly higher filtration rates than *P. purpuratus* exposed to similar conditions (Pinochet et al., 2018). In

addition, field data have shown that the highest growth and survival rates of *S. algosus* were observed in the medium-low level, while, *P. purpuratus* has shown its highest performance in the medium-high level, which could be related to differences in tolerance to air exposure and/or temperature (Pinochet et al., 2018). These results indicate that the distribution patterns of *P. purpuratus* and *S. algosus* in the intertidal can be explained by a combination of differences in physiological tolerances and competition abilities.

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