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Impact of predators and resource abundance levels on physiological traits of *Fissurella crassa* (Archeogastropoda)

Impacto de depredadores y niveles de recursos sobre rasgos fisiológicos de *Fissurella crassa* (Archeogastropoda)

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ABSTRACT

The effects of predators on the density of prey and their resources have been widely studied; however, there is little evidence on the effects of the predators in conjunction with the availability of resources on the traits of the prey, which could affect foraging activities. In this study, the physiological state and the escape response of the intertidal herbivore *Fissurella crassa* were evaluated in two sites which differ in terms of the abundance of its predator *Heliaster helianthus*. The results suggest that the escape response of *F. crassa* in the site with greater predator density and lower resource availability could require a better body condition that is compensated with increments in foraging. The results highlight the need to address the physiological perspective in community ecology in order to understand the interactions within these communities.

Key words: Foraging activity, *Heliaster helianthus*, intermareal, measured through traits, scape response.

RESUMEN

Los efectos de los depredadores sobre la densidad de presas y sus recursos ha sido ampliamente estudiado, sin embargo existe escasa evidencia sobre los efectos de los depredadores en combinación con la disponibilidad de recursos relacionados con los rasgos de las presas que pueden afectar la actividad de forrajeo. En este estudio se evaluó el estado fisiológico y la respuesta de escape del herbívoro intermareal *Fissurella crassa* en dos sitios con diferencias en la abundancia de su depredador *Heliaster helianthus*. Los resultados sugieren que la respuesta de escape de *F. crassa* en el sitio de mayor densidad del depredador y baja disponibilidad de recursos, podría requerir una mejor condición corporal que se compensé con un incremento en el forrajeo. Los resultados destacan la necesidad de abordar la perspectiva fisiológica en ecología de comunidades para entender mejor las interacciones dentro de estas comunidades.

Palabras clave: Actividad de forrajeo, *Heliaster helianthus* intermareal, mediada por rasgos, intermareal, respuesta de escape.

INTRODUCTION

The indirect effects of carnivores on primary producers, as mediated by herbivores, can control community dynamics in a number of ways (Terborgh *et al*., 2001; Shurin *et al*., 2002; Trussell *et al*., 2004). Traditionally, it has been suggested that the consumption of herbivores by carnivores translates into a lower impact on primary producers (e.g. Rosenzweig, 1973; Oksanen *et al*., 1981), a situation referred to as a density-mediated indirect interaction (DMII) (Abrams, 1995; Werner & Peacor, 2003). More recently, it has been suggested that predators can induce changes in the phenotypic traits of their prey that reduce or eliminate the risk of predation. Evading carnivores could diminish the foraging activities of herbivores and therefore reduce their impact on primary producers (Abrams, 1995; Lima, 1998; Sih *et al*., 2000; Lima, 2002), an effect known as a trait-mediated indirect interaction (TMII) (Abrams, 1995; Werner & Peacor, 2003).

In the marine environment, the morphological and behavioral plasticity of prey in response to predators has been widely reported (Trussell & Smith, 2000; Trussell & Nicklin, 2002; Dill *et al*., 2003; Trussell et al., 2004). Within the marine environment, rocky intertidal shores can be used to evaluate the relative importance of non-lethal effects due

to variations in predator density and prey recruitment, variations that lead to uncertainty in predation risk between sites (Navarrete & Manzur, 2008; Wieters *et al*., 2008).

The sun-star *Heliaster helianthus* (Lamarck, 1816) is the most notable rocky intertidal predator along the central-northern coasts of Chile and southern coasts of Peru (Castilla & Paine, 1987; Tokeshi, 1989). In central Chile, *H. helianthus* is a generalist predator that increases its consumption of limpets when the availability of its primary prey, the mussel *Perumytilus purpuratus* (Lamarck, 1819), is diminished (Paine *et al*., 1985; Navarrete & Manzur, 2008; Barahona & Navarrete, 2010). Limpets (*Fissurella* spp.) play a key role in the community structure of the mid-intertidal zone through the consumption of the dominant corticated algae *Mazzaella*, and this can entirely modify the intertidal landscape, especially when there is a high abundance of large *Fissurella* limpets (Oliva & Castilla, 1986; Moreno & Jaramillo, 1983; Jara & Moreno, 1984; Aguilera, 2011).

In general, the activity patterns, foraging modes, and habitat use of intertidal limpets are altered by predation risk from diverse taxa (Branch, 1981; Phillips & Castori, 1982; Hahn & Denny, 1989; Sorensen & Lindberg, 1991; Iwasaki, 1993). Studies concerning the behavioral ecology of *Fissurella* spp. highlight predation risk as a determinant for higher activity levels during nocturnal low tide (Franz, 1990; Pino *et al*., 1994; Serra *et al*., 2001). More recently, Escobar & Navarrete (2011) evaluated the escape responses of *Fissurella crassa* (Lamarck, 1822) and *Fissurella limbata* (Sowerby, 1835) when faced with changes in predation risk and considering contact history with the predator *H. helianthus*. However, this study presented major weaknesses in its evaluations; one being that the resources available to prey were not considered and the other being that the physiological significance of the escape response on *F. crassa* trait variations was not considered.

The aim of the present research was to evaluate the body condition and escape response of the intertidal herbivore *Fissurella crassa* in natural habitats differing in predation risk and in resource availability, as estimated through the abundance of the predator *H. helianthus* and algae, respectively. It was hypothesized that higher algae abundance and body conditions would be found in zones with a greater *H. helianthus* predation risk.

MATERIALS AND METHODS

Study sites. In the autumn of 2009, two sites (El Litre and Playa Chica) located at Quintay, Valparaíso, Chile (33° 11´ S; 71° 1´ W) were selected for observations. Both sites are characterized as upwelling areas (Pulgar *et al*., 2011), in addition to belonging to a Management and Exploitation Area for Benthic Resources where the catch of certain invertebrate species, such as *Fissurella* spp., is regulated. El Litre and Playa Chica were selected because prior evidence indicates that El Litre has a higher density of predators as compared to Playa Chica (Molina *et al.,* 2014), with a distance of 3.8 km between sites. However, both sites have a high abundance of *F. crassa*. For site evaluations, sectors were chosen with moderately sloped (< 45°) rocky substrates and with semi-exposure to waves. In each of these sectors, the abundance of the predator *H. helianthus*, the mussel *P. purpuratus*, and of the limpet *F. crassa* were determined along with the richness and abundance of algae and the body condition and escape response of *F. crassa*.

Table I. Taxonomic groups and algal taxa recorded at the study sites (Quintay, Valparaiso, Chile).

Taxonomic group	Algal taxa	El Litre	Playa Chica
Chlorophyta	*Chaetomorpha firma* Levring		X
	Codium dimorphum Svedelius	X	X
	Ulva sp.	X	X
Rhodophyta	*Centroceras clavulatum* (C. Agardh) Montagne		X
	Ceramium sp.		X
	Chondrus sp.		X
	Schottera nicaeensis (J.V. Lamouroux ex Duby) Guiry *et* Hollenberg		X
	Corallina officinalis var. chilensis (Decaisne) Kützing	X	X
	Gelidium sp.	X	X
	Mazzaella sp.	X	X
	Lithothamnium sp.	X	X
	Polysiphonia sp.	X	X
	Porphyra sp.	X	X
Phaeophyceae	*Colpomenia sinuosa* (Mertens ex Roth) Derbès *et* Solier	X	
	Lessonia trabeculata Villouta *et* Santelices	X	
	Colpomenia phaeodactyla M.J. Wynne *et* J.N. Norris		X
	Lessonia nigrescens Bory de Saint-Vicent		X
	Scytosiphon lomentaria (Lyngbye) Link	X	X
	TOTAL	11	16

Determining predator (*H. helianthus*), prey (*P. purpuratus* and *F. crassa*), and algae abundance. At each site, the abundances of *H. helianthus,* the mussel *P. purpuratus*, and the limpet *F. crassa* were determined by using two horizontal transects located in the low- and mid-intertidal zones of the coast. A minimum of 16 and a maximum of 40 quadrats of 0.25 m^2 were located at intervals of 2-3 meters along each transect. In each quadrat, the number of *H. helianthus* and the intertidal limpets *F. crassa* were recorded along with the coverage percentage of *P. purpuratus*. The coverage percentage of mussels was determined with the help of a grid containing 25 squares of 10x10 cm, with each square accounting for 4% coverage. Likewise, the coverage percentage and number of algae species per site were estimated using a minimum of 10 and maximum of 50 quadrats along each of the two transects. The taxonomic identification of algae, at least to the genus level, was performed using conventional techniques (Womersley, 1984) according to Ramírez and Santelices (1991) and Hoffmann and Santelices (1997).

Physiological state of *F. crassa*. Specimens of *F. crassa* were manually collected from the intertidal zone at each study site (El Litre n= 271, Playa Chica n= 205). All specimens were deposited in plastic bags, labeled, and transported to the laboratory where they were frozen (-20°C). In the laboratory, the maximum shell length was measured, and the intestine and muscular foot of each limpet were isolated and weighed. Additionally, the body condition was estimated from the residuals of the relationship between soft tissue biomass and maximum shell length (Jakob *et al.*, 1996).

Escape response of *F. crassa*. The characterization and quantification of the escape response of *F. crassa* was performed at both sites during low tide, at similar hours of the day, and on limpets located on moderately sloped (< 45°) rocky substrates with similar textures and humidity and without algal cover or seawater flushing. Specimens of *F. crassa* were identified according to the morphological traits described by Oliva and Castilla (1992).

In predator trials, the sun-star *H. helianthus* was manually deposited, while moist, on the apical orifice of the limpet's shell (El Litre n= 57 and Playa Chica n= 29) (modified from Espoz & Castilla, 2000). To validate the ability of the limpet to detect and escape from *H. helianthus*, control trials were performed via the direct stimulation of the apical orifice of *F. crassa* with a plastic tube (n= 15 individuals per site) (Escobar & Navarrete, 2011). The sun-stars were collected *in situ* before the trials and were changed every three assays.

The time, in seconds, was recorded from the moment of contact until the manifestation of behaviors associated with escape or permanence in place (movement or inaction, respectively) using a digital chronometer (CASIO *Frogman,* DW 9900). All trials continued until the entire limpet's body was out of stimulus range or, in the case of inaction, until 15 minutes (approximately double the response time recorded by Espoz & Castilla, 2000). The assays were performed only one time per individual limpet. In order to assess the relative speed of the limpet in exhibiting distinct behavioral responses, the percentage of total time taken by the limpet to express each behavior was calculated.

Data analyses. A two-way analysis of variance (ANOVA) (General Lineal Models) test was used to compare the abundances of the predator *H. helianthus*, the mussel *P. purpuratus*, the limpet *F. crassa*, and of algae between sites (El Litre and Playa Chica) and between intertidal zones (mid and low). The site was considered a random factor, and the intertidal zone was a fixed factor (Mixed Model). The site was considered a random factor given the study's aim of understanding how variations in predator abundance and resource availability for the prey influence the behavior and physiological state of the prey. The intertidal zone was considered a fixed factor because tidal zones have a physical basis for definition (see Bennington & Thayne, 1994). As a response variable, the abundance of each taxon was considered, and, in the case of algae, the coverage of dominant functional groups was also taken into account.

Given that gut biomass, body condition, and muscular foot biomass are affected by a limpet's body size, the residual of these relationships were compared between study sites using one-way ANOVA (General Lineal Models). The total response time and the percentage of total time used by F. crassa in expressing any response were evaluated between sites by one-way ANOVA (General Lineal Models). Finally, repeated measures ANOVA was used to evaluate the temporal sequence of the limpets' behavioral responses by considering the sites and the lapsed time between behaviors (Sokal & Rohlf, 1981; Zar, 1996).

RESULTS

Predator and prey abundance and algae richness and abundance. The predator abundance of the sun-star *H. helianthus* was greater at El Litre than at Playa Chica (ANOVA, $F_{1,126} = 8.84$, $p = 0.003$; Fig. 1a), without differences between intertidal zones. In contrast, the abundance of its principal prey, the mussel *P. purpuratus,* was lower at El Litre than at Playa Chica and greater in the mid-intertidal zone than in the low-intertidal zone (ANOVA, site: $F_{1,72} = 32.15$, $p < 0.001$; intertidal zone: $F_{1,72} = 5.33$, $P = 0.024$; Fig. 1b). Additionally, the abundance of Fissurella *spp.* did not show significant differences between sites, and at both sites, abundance was higher in the low-intertidal zone (ANOVA, $F_{1,126} = 10.65$, $p = 0.001$; Fig. 1c).

A total of 18 algae species were recorded, of which 11 were found at El Litre and 16 at Playa Chica (Table I). The low-intertidal zone of Playa Chica showed a higher total coverage of algae than the mid-intertidal zone and as compared to the two intertidal zones of El Litre. (ANOVA, $F_{1,273} = 15.11$, $p < 0.001$, Fig. 1d, Tukey *a-posteriori* test, $p < 0.05$). Analysis of the coverage percentage of common algae species indicated that some species varied between sites depending on the intertidal zone, with *Ulva* sp. specifically showing greater coverage in the mid-intertidal zone at El Litre as compared to Playa Chica (Fig. 2a). In contrast, in the low-intertidal zone, *Ulva* sp., *Porphyra* sp., *Polysiphonia sp.*, and *Mazzaella* sp showed a higher coverage at Playa Chica than at El Litre (ANOVA, $F_{7,728} = 15.87$, $p < 0.001$,Tukey, *a-posteriori* test $p < 0.05$; Fig. 2a and b). Evaluation of the dominant functional groups indicated that ephemeral algae were more abundant at El Litre in the mid-intertidal zone, while at Playa Chica these were more abundant in the low-intertidal zone (ANOVA, $F_{1,467} = 10.89$, $p = 0.001$; Fig. 2a and b).

Physiological state of *F. crassa*. The gut biomass, body condition, and muscular foot biomass of *F. crassa* were at least two times greater at El Litre than at Playa Chica (ANOVA, gut biomass: $F_{1,430} = 36.54$, $p < 0.001$; body condition: $F_{1,469} = 13.25$, $p < 0.001$; muscular foot biomass: $F_{1,435} = 11.12$, $p < 0.001$; Fig. 3a-c).

Escape response of *F. crassa*. In the trials, 29 *H. helianthus* individuals of 15 cm in diameter were used; 19 of which were from El Litre and 10 of which were from Playa Chica. Limpets with a shell length of 6.59 ± 2.08 cm (mean ± SD) for El Litre and of 6.24 ± 0.99 cm for Playa Chica were obtained with no significant differences between sites (ANOVA, $F_{1,}$

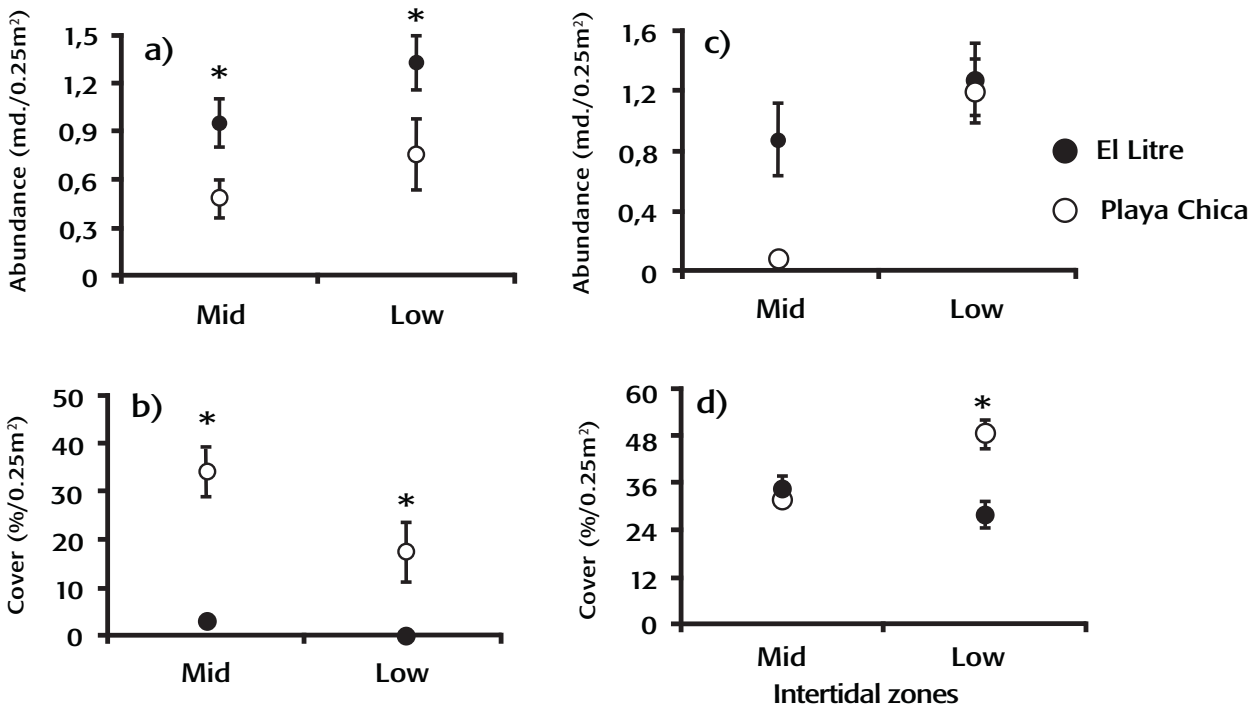


Figure 11a-d. Average abundance of predator, prey, and algae at the different study sites and intertidal zones. (a) Sun-star *H. helianthus*. (b) Mussels *P. purpuratus*. (c) Limpets *Fissurella* spp. (d) Algae. Bars indicate ± standard error. * indicates significant differences between sites.

$_{114}$ = 0.586; p = 0.448). All *F. crassa* in the control trials responded by firmly fixing to the substrate (Fig. 4a). On the contrary, limpets subjected to contact with the sun-star *H. helianthus* showed at least one or all of the following behaviors associated with escape in a temporal sequence of occurrence: display of the mantle and pallial tentacles, projection of cephalic tentacles, and/or active displacement of individuals away from the point of contact (Repeated measures ANOVA, $F_{2,128}$ = 17.53, p< 0.001; Figs. 4b and 5). The total time used for these successive behaviors did not show significant differences between sites (ANOVA, $F_{1,84}$ = 0.74, p = 0.393; Fig. 5), as was also found for the percentage of time spent on the first two responses (ANOVA, display of the mantle and pallial tentacles: $F_{1,79}$ = 0.73, p = 0.394; cephalic tentacles projection: $F_{1,71}$ = 0.21, p = 0.650; Fig. 6). However, the proportion of time used by *F. crassa* to start displacement was lower at El Litre, the site with the highest density of predators and, in general, lower algal resources (ANOVA, $F_{1,74}$ = 8.03, p = 0.006; Figs. 1d and 6).

DISCUSSION

The obtained results showed a higher abundance of *H. helianthus* and lower abundance of *P. purpuratus* at El Litre, which suggest that probability of predator encounters could be greater for the limpet population at El Litre. Moreover, *F. crassa* at this site showed an intense escape response to the presence of a predator and higher body conditions than at Playa Chica. Considering this, the lower algae coverage at El Litre could be related to higher algae consumption at this site as compared to Playa Chica, with differences between sites at the genus-level in association with algae important to the diet of *F. crassa*. In this regard, some studies suggest that the per capita predation pressure of *H. helianthus* on limpets is negatively associated with the environmental availability of the mussel *P. purpuratus* (Navarrete & Manzur, 2008; Barahona & Navarrete, 2010). Thus, the probability of a predator encounter could be more important for the limpet population at El Litre, especially when considering that the recognition of and escape from predators are characteristics retained by limpets that would be favored by a contact history between predator and prey (Escobar & Navarrete, 2011).

On the other hand, the total level of resources available to *F. crassa* showed differences between sites only in the low-intertidal zone, where the greatest abundance of limpets was found (Fig. 1c). In general, the total algae coverage was lower at El Litre than at Playa Chica (Fig. 1d), and a genus-level assessment showed that the differences between sites were associated with the importance of each algae in the *F. crassa* diet. Identified algae included ephemeral forms such as *Ulva* sp., *Porphyra* sp. and *Polysiphonia* sp. and corticated forms such as *Mazzaella* sp. and *Gelidium* sp. (Moreno & Jaramillo, 1983; Santelices *et al.*, 1986; Osorio *et al.*, 1988; Aguilera, 2011). Most of these taxa were less abundant at El Litre compared to Playa Chica (Fig. 2b), with the exception of *Ulva* sp. that presented a higher abundance in the mid-intertidal zone, where the abundance of *F. crassa* was low (Fig. 2a). Thus, El Litre was characterized by low food availability for limpets and a greater probability of encountering predators.

According to evidence that incorporates the trade-off between mortality risk and resource acquisition (Lima & Dill, 1990; McNamara & Houston, 1994; Werner & Anholt, 1993; Anholt & Werner, 1995), a

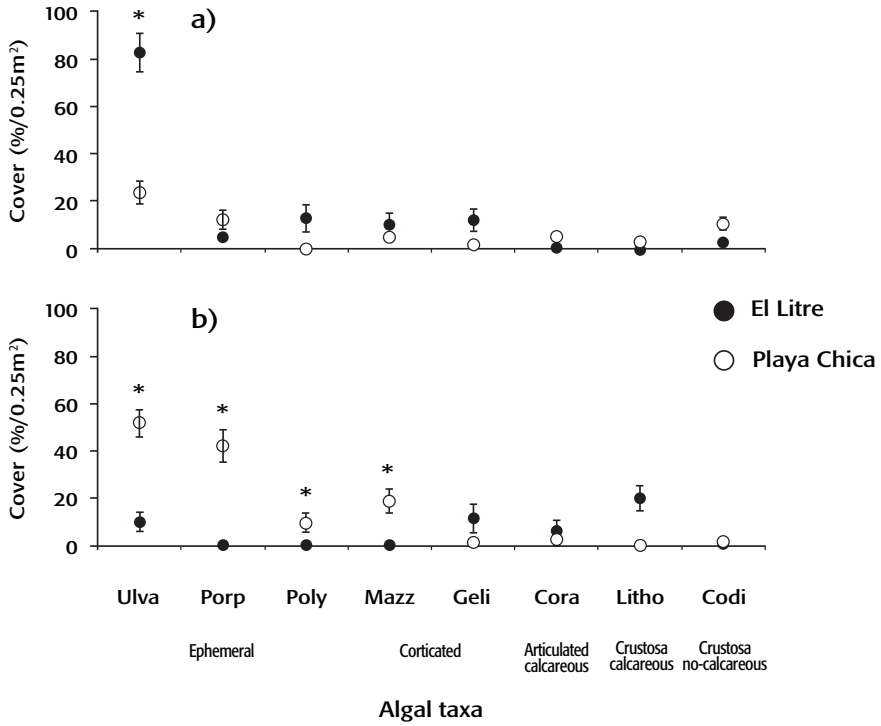


Figure 2a-b. Average coverage of algal taxa at the different study sites and intertidal zones. (a) Mid-intertidal zone. (b) Low-intertidal zone. Bars indicate ± standard error. Ulva= *Ulva* sp., Porp= *Porphyra* sp., Poly= *Polysiphonia* sp., Mazz= *Mazzaella* sp., Geli= *Gelidium* spp., Cora= *Corallina officinalis var. chilensis*, Litho= *Lithothamnion* sp., and Codi= *Codium dimorphum*. Eph: Ephimeral, Cort: Corticated, Artic calc: Articulated calcareous, Crust calc: Crustosa calcareous, and Crust no-calc: Crustosa no-calcareous.

lower abundance of important algae for the *Fissurella* spp. diet at the site with higher predator density (Fig. 1a) could be expected to lead to less foraging activity by limpets. In this sense, the greater gut biomass of limpets at El Litre (Fig. 3a) suggests more foraging activity. Moreover, the body condition and muscular foot biomass recorded for limpets at this site suggest a better nutritional state (Fig. 3b-c).

Additionally, similar densities of *F. crassa* between El Litre and Playa Chica (Fig. 1c) suggest that the differential abundance of *H. helianthus* between sites did not affect limpet mortality. In this sense, reducing the probability of predator encounters or reducing the probability of prey death in predator encounters through escape responses are survival strategies (Sih, 1984; Miner *et al*., 2005). The present data indicated that there was greater foraging activity and a better nutritional state for *F. crassa* at El Litre (Fig. 3), therefore suggesting a more developed escape response of *F. crassa* at El Litre than at Playa Chica (Fig. 6). This is consistent with other studies at these research sites (Pulgar *et al*., 2012a; Pulgar *et al*., 2012bThe effectiveness of escape responses in reducing predation rates by *H. helianthus* is supported by field observations along the coast of Chile (Castilla, 1981; Gaymer & Himmelman, 2008; Escobar & Navarrete, 2011). The present results indicated that at both sites *H. helianthus* induced behavioral responses in *F. crassa* associated with escape from predation (Fig. 4a), including the following three sequential behaviors: display of the mantle and pallial tentacles,

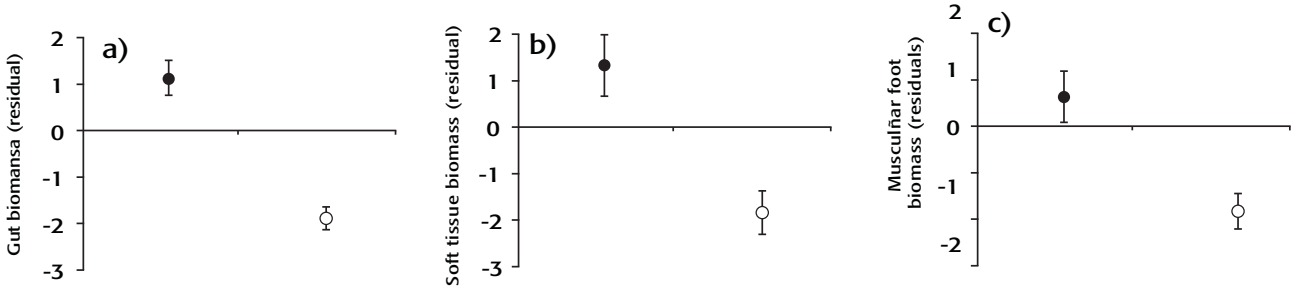


Figure 3a-c. Residuals from the regression between (a) gut biomass, (b) soft biomass, and (c) muscular foot biomass of *Fissurella crassa* individuals at El Litre and Playa Chica. ● El Litre; ○ Playa Chica. Bars indicate ± standard error.

cephalic tentacle projection, and, finally, displacement (Fig. 5). However, limpets at the site with higher predator density and fewer algae resources (Fig. 1, El Litre) were quicker to displace and escape (Fig. 6). The absence of these behaviors during control trials, where the limpets stayed firmly fixed to the substrate (Fig. 4a), suggests that *F. crassa* is able to discriminate between different stimuli. Variations in the escape response could result from contact history between prey and predator at a given site (Sih, 1992; Schmitz *et al*., 2004).

In general, all of the processes involved in the capture and allocation of energy when in the presence of a predator have been related to behavioral changes (Lima & Bednekoff, 1999; Werner & Peacor, 2003; Schmitz *et al*., 2004). More specifically, it has been suggested that physiological restrictions could be related to temporal and spatial activity patterns of *Fissurella* spp. (Franz, 1990; Serra *et al*., 2001). In this sense, the escape response of *F. crassa* to a predator at the site with higher *H. helianthus* density (Figs. 1, 4, and 5) would require a better body condition and greater muscular foot development that could be obtained by increased foraging (Fig. 3). In this regard, the development of the muscular foot in *F. crassa* is an important attribute against the risks of dislodgement and predation (Serra *et al*., 2001). Thus, the increase in foraging activity at the site with higher predator density could be associated with increased energy demands imposed by the escape

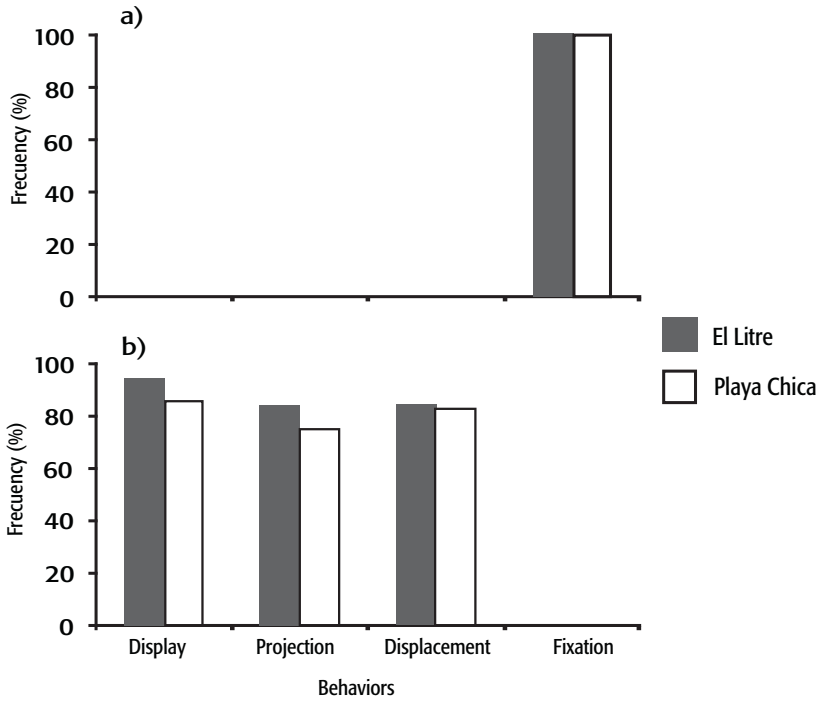


Figure 4a-b. Percentage of limpets showing the following behaviors: display of the mantle and pallial tentacles, projection of cephalic tentacles, active displacement, and fixation to the substrate; during (a) the control trials and (b) the predator trials.

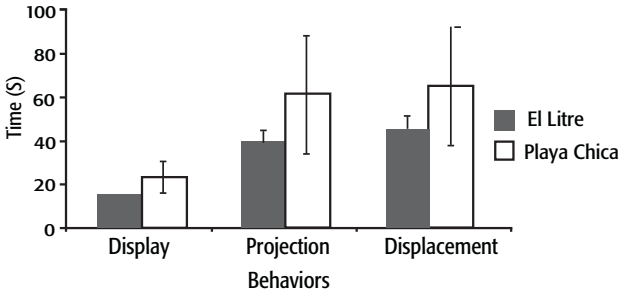


Figure 5. Time used by *F. crassa* to initiate the following behaviors recorded in response to the presence of *H. helianthus*: display of the mantle and pallial tentacles, projection of cephalic tentacles, and active displacement. Bars indicate ± standard error.

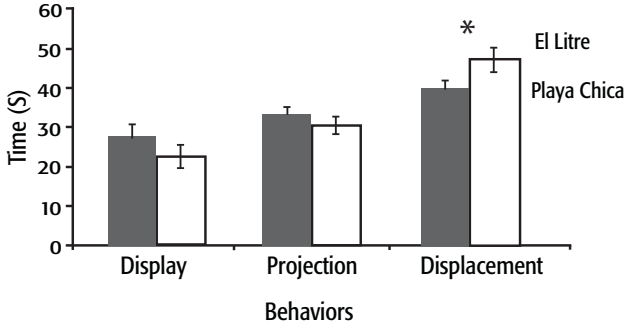


Figure 6. Percentage of total time used by *F. crassa* to initiate the following registered behaviors: display of the mantle and pallial tentacles, projection of cephalic tentacles, and active displacement. Bars indicate ± standard error. * indicates significant differences between sites.

response (e.g. faster displacement), with subsequent effects on food abundance (e.g. algae coverage) (Figs. 1d and 6).

Studies on the processes that structure communities have typically focused on density-dependent perspectives, such as lethal effects (Begon *et al*., 2006), and have not considered behavioral changes and the consequences of these for community structure (Espoz & Castilla, 2000; Werner & Peacor, 2003; Trussell *et al*., 2004; Schmitz *et al*., 2004). In the present study, the predator appears to affect the behavioral traits of the prey, which in turn would impact the algae consumption needed to meet the energy demands associated with these behaviors. The current results emphasize the need to consider a physiological perspective when studying indirect, trait-mediated effects, which could help elucidate how environmental variation is expressed through physiological characteristics and ecological processes (Dahloff *et al*., 2002; Menge *et al*., 2002; Pulgar *et al*., 2011; Pulgar *et al*., 2012a; Pulgar *et al*., 2012b).

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