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Site fidelity and homing behaviour in the intertidal species *Chiton granosus* (Polyplacophora) (Frembly 1889)

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ABSTRACT

Homing behaviour is frequently observed in marine intertidal invertebrate species. This behaviour may help species to deal with the environmental variability of the intertidal, providing shelter during low tides and areas to explore and search for food during high tides. The capacity of individuals to show fidelity behaviour should be an adaptive trait, due to the uncertainty that finding a new shelter in each tidal cycle implies. *Chiton granosus* is a common polyplacophora of the Southeastern Pacific rocky intertidal zone. During high tides, individuals move throughout the substratum in search of food; meanwhile, they are found within crevices in groups of variable sizes during low tides. According to previous works, this species shows some degree of fidelity to these shelters. Using field and laboratory experiments, we herein evaluate the factors determining the degree of site fidelity in *C. granosus*, taking into account the distance travelled from the shelter and food availability. Also, we evaluated the importance that chemical signs from the pedal mucus have in aiding *C. granosus* to return to its refuge. Field observations showed that *C. granosus* presents variable levels of site fidelity covering a maximum distance of 50 cm from its shelter. Laboratory results suggested that fidelity to shelters is related to the proximity of food sources. Chemical cues from the pedal mucus could be used to find the shelter after exploratory activities during high tides.

1. Introduction

Site fidelity, the behaviour to return to the same shelter previously occupied, is commonly observed in intertidal species as response to tidal cycles (Papi, 1992; Ruiz-Sebastián et al., 2002; Stafford, 2010). This behaviour supposes the ability of individuals to localize the way back after each excursion period. Homing behaviour, as the mechanism of site fidelity, may be related to chemical and/or topographic signs as navigation mechanisms to leave and return to the refuge (Chelazzi et al., 1988). For example, the gastropod *Onchidium verruculatum* shows group homing behaviour, emerging from crevices and holes during low tide on rocky shores, leaving trails behind them that contain directional information in order to return to the refuges (McFarlane, 1981). Trails are also used by individual homers, such as the limpet *Patella vulgata* (Funke, 1968), suggesting that trail-following is pivotal in the homing behaviour of several intertidal mollusk species (Ng et al., 2013).

Chitons are one of the most abundant mollusks in the rocky intertidal (Latyshev et al., 2004), and they have been identified as key structuring species of intertidal communities (Camus et al., 2008; Aguilera and Navarrete, 2007). Several works suggest that some chiton species show site fidelity behaviour (e.g. Aguilera and Navarrete, 2011; Yoshioka and Fujitani, 2006). In this group, a variety of sensor organs provide accurate information on the surrounding environment; these organs are embedded within the porous outer layer of the aragonite-made shell plates. In some species, small eyes are interspersed among these sensor organs, and a variety of light-influenced behaviours have been reported (Kingston et al., 2018). Yoshioka and Fujitani (2006) observed that the geographic cognition of the environment is supported by the homing behaviour in chitons. In non-manipulative experiments these authors found that “departure” and “arrival” tracks home did not overlap; hence, the departure track is not the only key for homing. However, it has also been argued that eyed chitons use principally chemosensory cues for homing rather than vision (Chelazzi et al., 1987). Furthermore, a “cooperative homing” behaviour has been reported for intertidal species. This pattern consists of the use of paths generated by conspecific individuals or those belonging to other species to find the way back to the refuge (Edwards and Davies, 2002).

On the Southeastern Pacific coast, one of the most abundant chiton species is *Chiton granosus* (Frembly, 1889), which has a broad distributional range from Paita, Perú, to the Aysén Region in southern

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Chile (Araya and Araya, 2015). Although this species is commonly found on rocky walls and crevices in exposed intertidal shores (Otaíza and Santelices, 1985; Ibáñez et al., 2019), there is scarce information about its behaviour (Otaíza and Santelices, 1985; Otaíza, 1986; Aguilera, 2005; Aguilera and Navarrete, 2007; Camus et al., 2008; Aguilera et al., 2013). Similar to other chitons, *C. granosus* is mostly a strict herbivore (micro- and macroalgae), although small invertebrates have been reported in its diet, e.g. cirriped larvae, that may sometimes constitute its main food source (Aguilera, 2005). During high tides, *C. granosus* actively searches for food and during low tides it remains in crevices to reduce environmental stress (Basáez and Zamorano, 1997). According to Aguilera and Navarrete (2011), *C. granosus* shows a 'moderate' homing behaviour with approximately 60% of individuals returned to their original position after foraging. Although the factors determining fidelity level to specific shelters and the mechanisms utilised for shelter localization are unclear, the association between foraging activity and homing behaviour suggests that food availability would play a significant role in the site fidelity of *C. granosus*.

We herein aim to identify the factors that determine the homing behaviour of *C. granosus*, specifically those that influence site fidelity and the principal mechanisms utilised to find the same shelters, with special emphasis on the existence of chemical signs from the pedal mucus. We hypothesized that: (1) site fidelity would be negatively correlated to the distance from food sources, and (2) chemical signs in the mucus from the pedal muscle would aid in finding the way back to refuges. In addition, we evaluated the persistence of the fidelity behaviour of *C. granosus* in landscapes with different topographic complexity.

2. Materials and methods

2.1. Study area and field experiments

The field experiment was conducted in the rocky intertidal of the locality Punta de Hualpén (36°46′S; 73°12′W) in Concepción, Chile. To determine the percentage of site fidelity and the travelled distance of *C. granosus*, a total of 36 individuals with 2–2.5 cm of the fifth plate width were collected during low tide from six crevices (refuges) and epoxy-marked with a correlative number (Fig. 1). The narrowness of the crevices that *C. granosus* uses as refuges made marking the individuals in situ impossible. Marked individuals were then returned to the same refuge from which they were collected, recording six individuals per refuge. In any case, the factor "manipulation" was present in all treatments carried out in the field, subsequently, comparisons between them is valid and potential differences observed may be attributed to the treatments essayed. Marked individuals were monitored in each refuge during low tides for weeks 1, 2, 3, 5, 8, 9, and 10. Weeks 6 and 7 were not monitored due to bad weather conditions during diurnal low tides. Site fidelity was considered when the individuals remained at the same refuge throughout the study period, and the site fidelity percentage per refuge was estimated for each monitoring time. Also, the travelled distance was recorded as the distance from the refuge to the point where individuals were found during the first half hour after the low tide period started.

2.2. Laboratory experiments

Laboratory experiments were run to evaluate the relationship between food availability and site fidelity, and the potential role that the pedal mucus could play by providing chemical signs to find the refuge. Consequently, individuals of *C. granosus* (2–2.5 cm of fifth plate width) were collected from the same locality where field experiments were run and transported to the laboratory. To standardize experimental conditions, after three weeks of exposition to running unfiltered seawater, food was provided on microscope slides covered by biofouling; microorganisms, microalgae, incrusting algae and invertebrate settlers covered the plates. Refuges and slope variation were considered in the experiment using PVC panels in order to discard potential bias in the behaviour of the individuals due to differences in micro complexity, temperature, biofouling presences, etc. that exist in natural substrates, such as rocks. (Fig. 2). Cycle tides were simulated in the aquaria using a water pump connected to a timer to control emptying and filling cycles of 6 h. In addition, desiccation stress was simulated by light bulbs at the upper level of the aquaria. The temperature oscillated between 13 and 14 °C during submersion and 19 and 20 °C during emersion. These conditions were used in all of the experiments described below.

2.3. Site fidelity and proximity to food source

The relationship between food availability and site fidelity was evaluated considering the proximity of the individuals to the food source. For that, three food availability treatments were essayed according to the distance in a straight line from the refuge to five microscope slides provided with biofouling as food: "beside", with immediate access to food (0 cm); "near" with 60 cm of distance; and "far", 100 cm apart. Each essay consisted of five individuals (2.0–2.5 cm of fifth plate width) aggregated in an artificial refuge located at the start of a lane within a channel (Fig. 2A). Daily, the slides with food were changed and the channel cleaned to remove biofouling. The number of individuals that remained in the refuge was recorded weekly during the second low daily tide for a period of eight weeks. Finally, the site fidelity percentage was calculated as previously explained in the field experiments. There were four replicates for each treatment.

In addition, to evaluate site fidelity behaviour of *C. granosus* in a

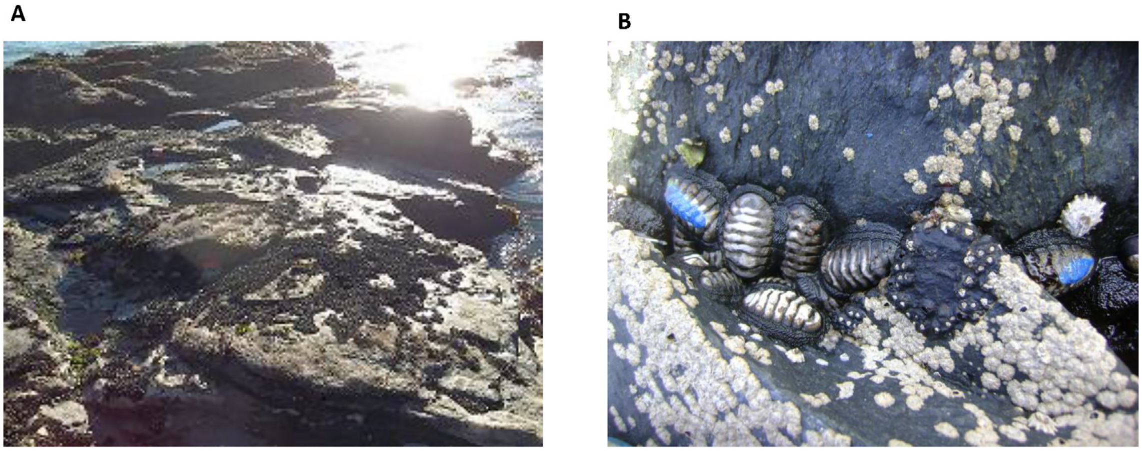

Fig. 1. Study site in the locality of Punta Hualpén (A) and individuals of *C. granosus* marked with epoxy resin for movement monitoring in the field (B).

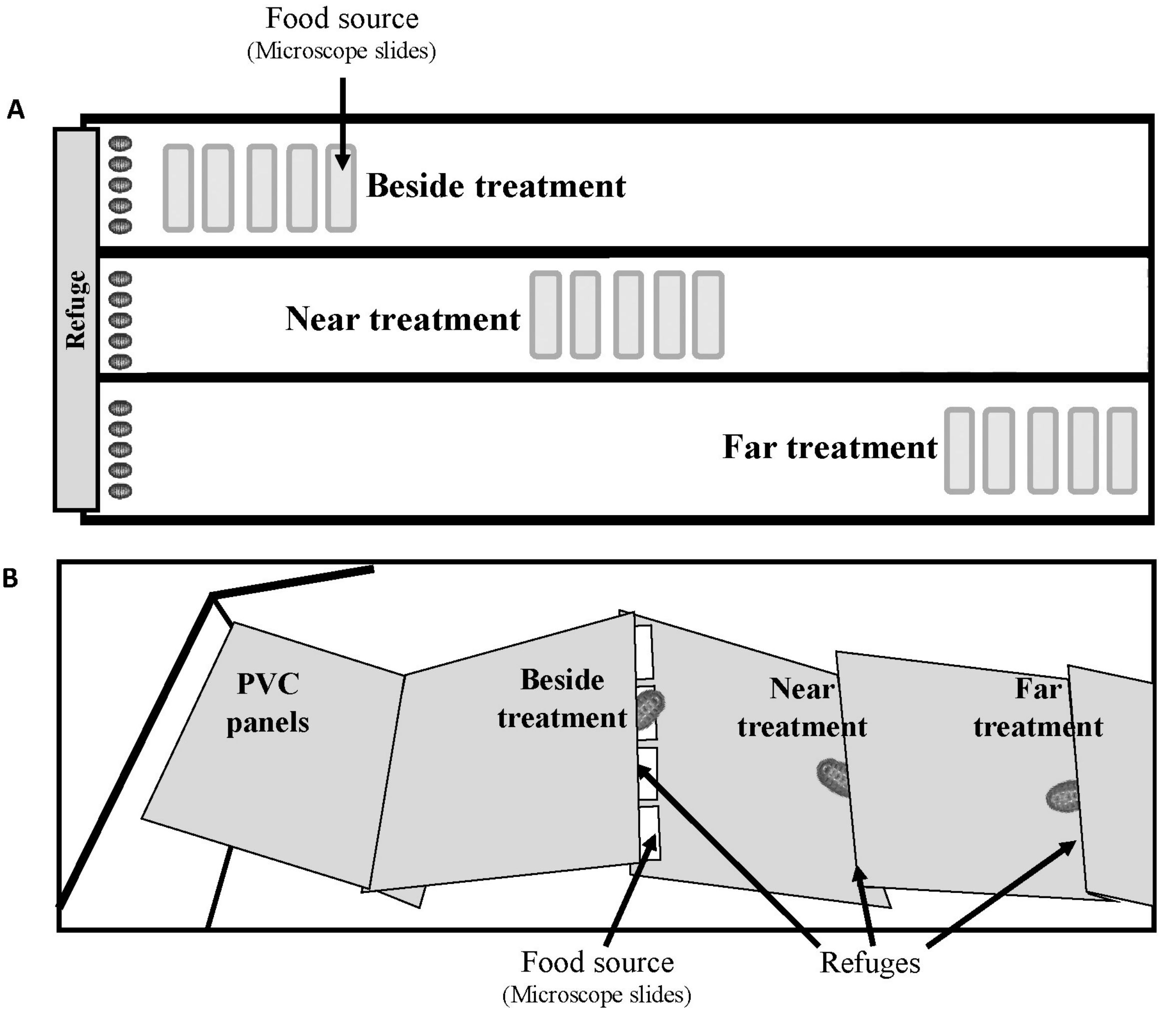

Fig. 2. Experimental design to evaluate the site fidelity percentage considering the proximity to food sources in low (A) and high spatial complexity (B).

landscape with higher topographic complexity, multiple alternative refuges were provided using PVC panels (Fig. 2B). Food was provided on microscope slides as described above at the three distance treatments (beside, near and far). Individuals were located in the refuge of reference and their positions were then recorded after two days of the experiment. For each treatment, 13 different individuals (replicates) of *C. granosus* were used.

2.4. Chemical mechanisms of site fidelity

The mucus trail was evaluated as a mechanism for site fidelity behaviour in *C. granosus*. Subsequently, each individual of *C. granosus* was gently stimulated with forceps to move to the food source (microscope slide with biofouling) and the mucus trail was traced on a plate (Fig. 3). Posteriorly, the same specimen was exposed to low tide conditions to record how it returned to the refuge. The number of individuals that followed their own mucus trail were counted. A total of 52 replicates were conducted in this experiment, corresponding to 52 different individuals.

2.5. Data analysis

Percentage of site fidelity and the travelled distance in the field through time was analysed using Repeated Measures ANOVAs with refuge and time as factors. To evaluate the effect of the distance of the food source on site fidelity in the scenario of low spatial complexity, two independent one-way ANOVAs were used to compare the mean percentage of fidelity between distance treatments (beside, near and far) in weeks 1 and 8. Normality and homoscedasticity assumptions were tested using Shapiro-Wilk and Cochran tests, respectively. The Tukey *a posterior* test was used when significant differences were found (Zar 1996). As data in the scenario of high spatial complexity was recorded as frequency of fidelity in the three distance treatments, Chi-square tests were performed with an expected proportion of 1:1. A significant departure from the expected proportion indicates a bias in the observed frequency of faithful and unfaithful individuals. A Chi-square test was also used to examine the frequency of *C. granosus* individuals that actively moved to the food source following a chemical pathway generated by their own feet. If the return behaviour were biased by the mucus trail, a significant departure from 1:1 towards the mucus trail would be observed. All statistical analyses were conducted using STATISTICA 13.0.

3. Results

3.1. Site fidelity in the field

In the field, the site fidelity of *C. granosus* decreased on average from 85% for the first week to 39% at the end of the experiment, after eight weeks (Fig. 4A). The repeated measures ANOVA showed a significant effect of the time factor ($F_{6,180} = 85.7$; $P < 0.05$). The a posteriori analysis determined a decrease in the mean percentage of site fidelity from week 1 to 3 (Tukey test: $P < 0.05$); then, fidelity remained roughly constant between 40% and 50% until week 10 (Tukey test:

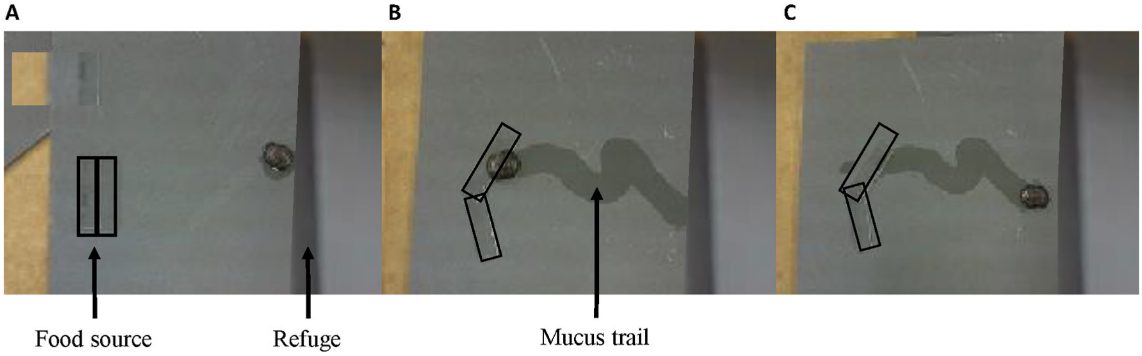

Fig. 3. Experimental design to evaluate the role of pedal mucus in the site fidelity behaviour of *C. granosus*. The individuals were gently dragged across the plates from the original position (A) to the slides covered with biofouling (food) (B). After that, the movement of the individual was observed and the final position recorded. In photo (C) the individual followed the same route to return to the original position.

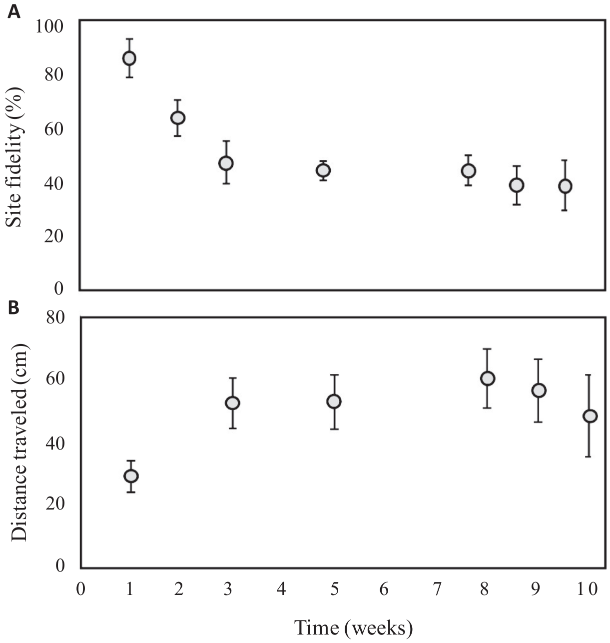

Fig. 4. Percentages of site fidelity (A) and distance travelled (B) by marked individuals of *C. granulosus* in the field. Movement of individuals was recorded for 10 weeks. Each data corresponds to the mean ± SE.

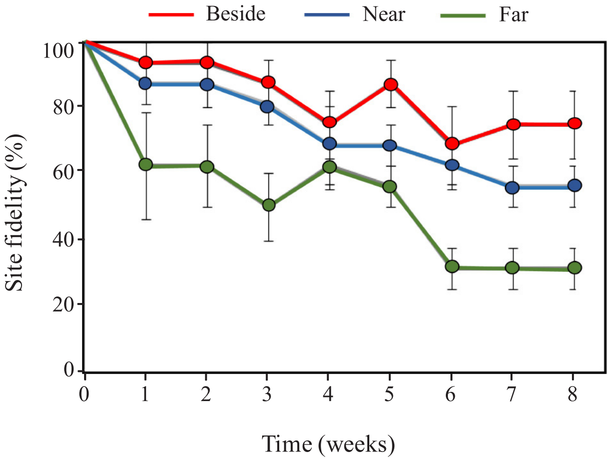

Fig. 5. Percentages of site fidelity of *C. granulosus* considering the proximity of food source in laboratory conditions of low spatial complexity.

$P > 0.05$). Concerning the distance travelled by individuals from their refuges, the repeated measures ANOVA evidenced significant differences among times ($F_{6,180} = 13.3$; $P < 0.05$). The a posteriori test showed that the shortest distance recorded was during the first week, with a mean value of 29 cm (Tukey test: $P < 0.05$; Fig. 4B). For the rest of the time, mean distance oscillated between 55 and 60 cm with no significant differences among weeks (Tukey test: $P > 0.05$; Fig. 4B).

3.2. Laboratory experiments

In all treatments evaluating the relationship between food availability and site fidelity, individuals were observed positioned on the slides provided with biofouling. Moreover, a closer inspection of slides denoted radular teeth marks revealing grazing activity. Site fidelity according to proximity of food source showed that in conditions of low spatial complexity, the percentage of site fidelity decreased throughout time in all treatments (Fig. 5). In week 1, average values were 93%, 87% and 62%, for the beside, near and far treatments, respectively, and no significant differences were found among the three treatments ($F_{2,9} = 2.88$, $p = 0.107$). In week 8, the statistical analysis showed significant differences among distance treatments ($F_{2,9} = 7.92$; $p = 0.0103$). These differences were mainly due to the dissimilarity of the far treatment (31%) compared to the other two treatments of food source distance, beside (75%) and near (56%) (Tukey test $p < 0.05$).

In conditions of high spatial complexity, the fidelity frequency of *C. granosus* greatly varied among the three treatments (beside, near and far). Thus, at the end of the experiment 92% of individuals showed site fidelity in the beside treatment, with lower levels in the near (53.8%) and far (38.5%) distance treatments to food sources. The Chi-square test showed a significant departure from the 1:1 proportion between faithful and unfaithful individuals in the beside treatment ($\chi^2_{(0,05;1)} = 9.3$; $p = 0.002$), but no dissimilar departure was detected in the near ($\chi^2_{(0,05;1)} = 0.076$; $p = 0.781$) and far ($\chi^2_{(0,05;1)} = 0.692$; $p = 0.405$) treatments.

3.3. Chemical mechanism of site fidelity

A total of 65% of individuals followed the path previously generated by their foot mucus, and 35% followed a different path to reach the food source. Significant differences were observed in the frequency of individuals that followed or did not follow their previous path with chemical signs ($X^2_{(0,05;\ 1)} = 4.923$; $p = 0.026$).

4. Discussion

The intertidal imposes important restrictions and challenges to species inhabiting this habitat; therefore, adaptive responses should arise to increase survival. We herein showed that behavioural mechanisms are fundamental traits in the intertidal species *Chiton granosus*. Thus, homing behaviour associated with refuges (crevices) was commonly observed in this species. Moreover, site fidelity was determined by food availability, measured as the distance between the refuge and the food source. Also, we herein observed that chemical signs from foot mucus may help *C. granosus* to find the path back to its refuge. The combination of all of these features would help *C. granosus* respond to the cyclic intertidal environment during low and high tides; these characteristics would act as a selective force in species inhabiting these habitats.

Site fidelity is a relatively common behavioural strategy in species from different taxonomic groups, and in particular in several marine invertebrates such as mollusks (e.g. the limpet *Cellana toreuma*; (Hirano, 1981), crustaceans (e.g. the crab *Hemigrapsus sanguineus*) (Brousseau et al., 2002), or echinoderms (e.g. the seastar *Parvulastra exigua* (Martínez et al., 2017). Specifically, in the present study, *Chiton granosus* showed a site fidelity oscillating ca. 40% after 10 weeks of field observations. The reasons that produce site fidelity in intertidal assemblages vary between sedentary and vagile organisms. In the later, homing behaviour is associated with foraging events where animals move out from their shelter to search for food during high tide and return before the low tide to a safe place in order to avoid being exposed to air during low tide (Gibson, 1999). Recent studies have shown that highly mobile species, e.g. intertidal fish, resident species have stronger site fidelity than secondary resident species that spend part of their life history in the intertidal, and this homing success was regardless of the displacement distance from where they were rellocated (White and Brown, 2013).

In sedentary species, site fidelity may vary as a response to different factors depending on species interactions, their life history, environmental conditions, refuge quality, among others (Davies et al., 2006). Among those factors associated with refuge quality, food availability is one of the most important features promoting site fidelity behaviour, as has been observed in a wide range of species from terrestrial (Kozakai et al., 2017) and marine vertebrates (Passadore et al., 2018) to intertidal limpets (Núñez et al., 2014). In *C. granosus*, site fidelity depended on the proximity of food sources to the refuge, with an inverse relationship between the percentage of site fidelity and distance to food. Thus, while site fidelity reached around 80% after eight weeks when food was located immediately next to the refuge (beside treatment), it decreased to around 30% in the far treatment. Similar results were observed when individuals were exposed to a more topographically complex environment, with higher fidelity recorded in the beside treatment. Moreover, the distance covered by individuals of *C. granosus* in the field increased significantly with time which could be related to an exploration effort to access food. The distances recorded in our study, i.e. ca. 55–60 cm at the end of the experiment, are slightly larger than those reported by Aguilera and Navarrete (2011) (30–45 cm). We must take into account that some specimens moved > 60 cm from their refuges; they could most likely get refuge on adjacent cracks or crevices with higher food availability or better environmental conditions.

It is clear that food availability is an important attribute of refuge quality and could explain site fidelity in *C. granosus*. However, on a temporal scale, site fidelity decreased with time, regardless of the field or laboratory conditions, and habitat complexity. This pattern suggests that *C. granosus* may change its refuge throughout its lifetime. Other factors not considered in the present study, may have a pivotal influence on the site fidelity of this intertidal species. For example, the crevice position may affect microhabitat conditions, such as humidity and temperature during low tides (e.g. Denny et al., 2011; Aguilera et al., 2019). In the limpet *Patella flexuosa*, site fidelity has proven to be affected by intraspecific competition, and the percentage of emigrants also varied with the season (Iwasaki, 1999). Refuge choice in the amphipod *Peramphithoe tea* was related to the provision of protection against wave energy or predation risk (Sotka, 2007). Intertidal chitons have shown physiological adaptations to tolerate air exposure by using air-exposed gills for O2 uptake (e.g. McMahon et al., 1991, Schill et al., 2002). Therefore, it is possible that habtitat exploration by individuals of *C. granosus* may not only be limited to periods of high tides. This capacity opens a wider temporal window for refuge searching if habitat conditions change. It is clear that field and laboratory multifactorial experiments should be carried out to understand the temporal and intraspecific variations of site fidelity in *C. granosus*.

The ability of the individual to find its way back to its refuge is a key mechanism of site fidelity. Some mollusks are able to return to their refuge by taking the same path. This implies that when the refuge has been modified, they are no longer able to find it. This behaviour is explained by the existence of a muscular and tactile topographic memory (Baumgardt, 2009). The results presented herein suggest that site fidelity in *C. granosus* is mainly based on chemical signs from foot mucus. Chelazzi et al. (1987) suggested that chemical signs of the chiton *Acanthopleura gemmata* are not limited to those originated by the same individual, but signs from other specimens could also be useful to find the way back. However, the secretion of mucus has a high energy cost, and certain species, such as *Littorina littorea,* can re-ingest the mucus to recover the energy expended in its production (Edwards and Davies, 2002). Additional studies are needed to determine the energetic cost of mucus production and the specificity of the pedal chemical sign in *C. granosus*.

Site fidelity in variable and stressful environments, such as the intertidal habitat, could be an important driver of intra and interspecific interactions, influencing distributional patterns and community structure. Under this scenario, our study suggests that long-term site fidelity monitoring and experiments are essential to elucidate physical, biological and ecological factors determining refuge choice and site fidelity in *C. granosus*.

Declaration of Competing Interest

None.

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