



A geographic comparison of the resting site fidelity behaviour in an intertidal limpet: Correlation with biological and physical factors



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ABSTRACT

Many organisms vary their behaviour in response to environmental change. In stressful habitats motile organisms often exhibit behavioural patterns that are consistent with stress-minimizing strategies. In the present study we analysed the proportions of individuals with strong site fidelity and distances travelled by “unfaithful” individuals from their home scar at different temporal and spatial scales in the intertidal gastropod *Siphonaria lessoni*. We also assessed the behavioural response of *S. lessoni* to biological pressures such as conspecific population density and food availability (assessed by measures of chlorophyll *a*). The experiments were carried out in the arid climate of Patagonia on the rocky intertidal of Las Grutas (LG), and in the humid climate of The Pampas on the rocky intertidal of Mar del Plata (MDP) Argentina. At each site, shells of five hundred animals were marked with epoxy paint. Movement was measured as distance to a reference point after periods of one, five and ten days. Our results showed a positive relationship between food availability, site fidelity and distance to home scar for almost all observation days, but no relationship between population density and behavioural variables. Limpets in LG were more “faithful” than in MDP. Unfaithful limpets had the same mean displacement for all days and seasons except for Spring day-1 where MDP was higher than in LG and in Autumn day-10 where MDP was smaller than LG. The present results thus show differential response behaviour in intertidal limpets probably driven by the environmental conditions in which they live.

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1. Introduction

Behavioural plasticity provides the potential for organisms to respond rapidly and effectively to environmental heterogeneities. Behavioural plasticity involves a large spectrum of behavioural mechanisms and properties that depend on physiological processes (Mery and Burns, 2010). In stressful habitats such as the intertidal environments motile organisms often exhibit behavioural patterns that are consistent with stress-minimizing strategies (Heath, 1970). For example, during periods of suitable conditions they can increase activity (Chapman and Underwood, 1992; Little, 1989), while during unfavourable periods they can reduce activity so it prevents detachment by waves (Mackay and Underwood, 1977). Moreover, this reduced activity prevents stress by dehydration (Branch and Cherry, 1985; Cook and Cook, 1981), thermal stress (Garrity, 1984), and even minimizes negative biotic interactions such as competition and predation (Branch and Cherry, 1985; Levings and Garrity, 1984).

A widely studied case of behavioural plasticity is the resting site fidelity (also known as homing behaviour) that some limpet and chiton

species display as a strategy to minimize stress and/or to maximize exploitation of food (e.g. Chapman and Underwood, 1992; Chelazzi, 1990; Nishihama and Nojima, 1990). Individuals displaying site fidelity behaviour depart and return periodically from a fixed resting site, called the “home scar”. However, not all individuals within or among populations of a species display this behaviour. The proportion of “faithful” and “unfaithful” individuals within a population can vary greatly depending on habitat, tidal height, humidity (e.g. Little, 1989; Little and Stirling, 1985; Ng and Williams, 2006; Takada, 2001), coastal energy (e.g. Branch, 1981, 1985; Gray and Hodgson, 1997), food resources (e.g. Iwasaki, 1994; Jenkins and Hartnoll, 2001), density of co-occurring competitors (e.g. Chelazzi et al., 1983), population density (e.g. Iwasaki, 1995; Mackay and Underwood, 1977), intra-specific antagonism (e.g. Shanks, 2002), and predators (e.g. Branch, 1981; Iwasaki, 1993). Thus, biotic as well as abiotic factors can strongly influence homing behaviour. However, there is little information on how the combination of these two types of factors works together (but see Jenkins et al., 2001).

In the South West Atlantic (SWA) region one of the most abundant limpets is *Siphonaria lessoni* (Pulmonata, Siphonariidae). Its distribution in South America extends from Peru to Cape Horn in the Pacific Ocean and to the north of Uruguay in the Atlantic Ocean (Castellanos et al., 1993), where it inhabits intertidal crevices and tide pools of rocky

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shores (Penchaszadeh, 2004). However, its homing behaviour has not been consistent at different latitudes: while in the highest latitudes of the Argentinean coast it did not exhibit site fidelity (López Gappa et al., 1996; Olivier and Penchaszadeh, 1968), in the mean latitudes of the Chilean coast it was described as a moderate homing species (Aguilera and Navarrete, 2011).

Along the extensive coast of Argentina (~2,500 km) there are four well-defined climate types, humid temperate climate (from 36° to 38° approximately), semi-arid climate (from 38° to 42° approximately), arid climate (from 42° to 52° approximately) and humid cold climate (from 52° to 54° approximately). With the different climatic areas biotic variable such as food availability also vary (Nuñez et al. Unpublished data). Thus, differences in homing behaviour within the SWA region could be driven by differences in the biotic and abiotic factors within each site.

In this sense, three alternative and non-mutually exclusive hypotheses could explain differences in the pattern of movements in species displaying resting site fidelity. First, the “environmentally stressful response” hypothesis predicts that individuals make behavioural decisions to reduce desiccation risk (see Chapman and Underwood, 1992; Raffaelli and Hawkins, 1996). If this hypothesis holds true, both a higher proportion of “faithful” limpets together with a minor displacement of “unfaithful” individuals would be expected at higher environmental desiccation rates. Second, the “denso-dependent response” hypothesis assumes on the one hand a negative relationship between population density and the proportion of “faithful” individuals, and on the other a positive relationship between population density and displacement of “unfaithful” individuals. For example, past studies observed a negative relationship between the number of “faithful” limpets and local density in *Cellana tramoserica* and *Patella flexuosa* (Iwasaki, 1999; Underwood, 1988). Finally, the “food availability response” hypothesis predicts that site fidelity depends on the availability of nutritional resources since a high proportion of “unfaithful” individuals potentially improves the chances of finding new patches of food when food is scarce (e.g. Calow, 1974; Iwasaki, 1992). This hypothesis predicts a positive relation between food abundance and proportion of “faithful” individuals, as well as a negative relationship between food abundance and displacement of “unfaithful” individuals.

In the present study we analyse site fidelity behaviour and the distance to home scar of “unfaithful” individuals in the limpet *S. lessoni* in relation to the above hypotheses. To achieve this goal, we selected two geographic sites (separated by 1000 km) which differ in their desiccation rates. Each site was sampled in two contrasting seasons (spring

and autumn) to span the greatest natural variability possible. Moreover, for all this data set we analyse the relationship between food availability and conspecific population density with the above mentioned behavioural variables.

2. Methods

2.1. Study sites

This study was conducted in Mar del Plata (MDP; 38° 02' S 57° 31' W) and Las Grutas (LG; 40° 48' S 64° 53' W), which differ in climatological characteristics (Fig. 1). Average tidal amplitude in MDP is 0.80 m (maximum 1.69 m) and at low tide the beach is 10–30 m wide. Mean water temperature ranges from 7.5 °C in August (austral winter) to 20.6 °C in January (austral summer). In contrast, the average tidal amplitude in LG is 6.46 m (maximum 9.38 m) and consequently at low tide the beach is 450–600 m wide. Mean water temperature ranges from 4.4 °C in August to 25.2 °C in January (Servicio Argentino Hidrografía Naval, <http://www.hidro.gov.ar/>).

The intertidal shore of MDP and LG is characterized by the presence of a compact sedimentary rock called “compact loess” which is sometimes cemented by crystalline calcium carbonate. *Siphonaria lessoni* occurs on loess rocks at LG and MDP is dominated by barnacles (*Balanus glandula*) and mussels (*Brachidontes rodriguezii*). Loess rocks support a diverse community of patchily distributed algae, e.g., native Ceramiales algae (*Ceramium* sp.), Rhodomelaceae (*Ralfsia* sp. and *Polysiphonia* sp.) and some Ulvaceae (*Ulva* spp.).

2.2. Data collection and analyses

At each site all observations focused on the uppermost horizon of the intertidal rocky rock. Observations were conducted using only the vertical surface of rocks to control for potential intra-population behaviour variations associated with different orientation of substrate (see Santini et al., 2004). In addition, the observed rocks were always leeward the sea to minimize differences in sun exposure.

“Faithful” limpets are those that returned to their home scar at the point of our measurement and “unfaithful” individuals are those that were displaced, or found away from the home scar at the point of our measurement.

During low tides in Autumn and Spring 2009 we marked 1000 animals of 12–14 mm in shell length, distributed across 30 rocks in each site, with epoxy paint on their shell without detaching them from the

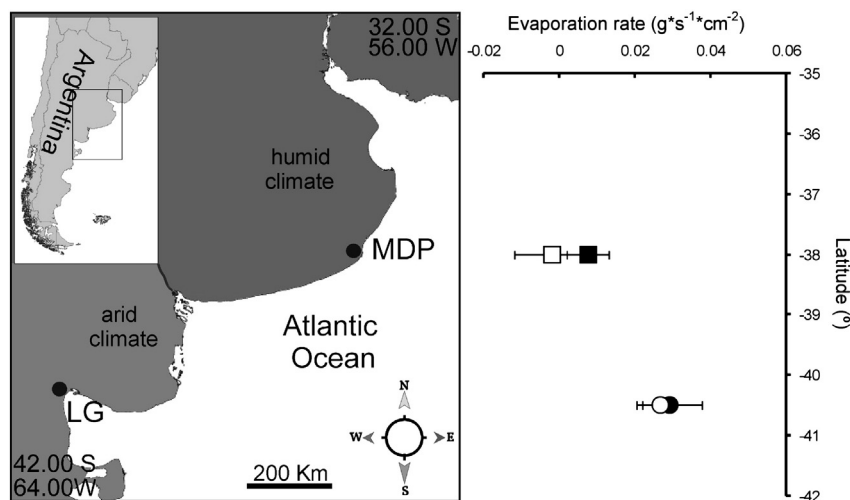


Fig. 1. Map of observation locations in Argentinean coast, MDP (Mar del Plata), LG (Las Grutas). Different colours indicate the different climatic regions. The graph shows the evaporation rate for each site in different seasons calculated sensu Bertness et al. (2006). Different point types show different sites (circle = LG; square = MDP). Different colours indicate different seasons (white = spring, black = autumn).

Table 1

Descriptive data of “faithful” limpets returning to home-scars in different seasons and geographic sites.

Season	Site	Day of observation	Number of rocks observed	Number of marker limpets per rock	Number of marker limpets per day of observation	“Faithful” limpets	“Unfaithful” limpets	Limpets lost	Recorded limpets
Spring	MDP	1st	10	10	100	52	38	10	90
		5th	5	10	50	21	22	7	43
		10th	10	10	100	35	51	14	83
		Total	25	–	250	108	111	31	219
	LG	1st	10	10	100	79	18	3	97
		5th	5	10	50	39	9	2	48
		10th	10	10	100	62	34	4	96
		Total	25	–	250	180	61	9	241
Autumn	MDP	1st	10	10	100	52	39	9	91
		5th	5	10	50	17	26	7	43
		10th	10	10	100	30	52	18	82
		Total	25	–	250	99	117	34	216
	LG	1st	10	10	100	72	26	2	98
		5th	5	10	50	37	12	1	49
		10th	10	10	100	60	35	5	95
		Total	25	–	250	169	73	8	242

substrate in order to minimize disturbance sensu Chapman (1986). After marking (day 0), measurements were carried out at day 1, day 5 and day 10 (see Table 1). Ten different rocks (of the 30 previously chosen) were randomly selected for each day of observation at each site, and not re-used in subsequent measurements, thus avoiding data “auto-correlation”. During the observation period, the position of marked limpets was recorded by measuring the distances from the apex of each limpet to each of the two fixed reference points, and by recording the position of the limpet in relation to a line between the reference points (Mackay and Underwood, 1977; Underwood, 1977). Prior to the observational measurements, in order to determine the error of the measuring method, laboratory simulations were performed by placing four empty limpet shells at different distances and angles from two reference points. The positions of these shells were changed at random to obtain five observations each. Direct measurements of position were compared to the distances calculated by triangulation. The mean difference between measured and estimated distance was 5 mm (SD 11.5 mm) and the maximum difference was 20.6 mm. Distances less than 21 mm are thus considered not to differ from zero. Calculations based on the displacement of limpets over time intervals will always

underestimate the actual displacement distances because they do not trace the paths of movement (Erlandsson et al., 1999). In this sense, the method used ensures the discrimination between “faithful” and “unfaithful” limpets.

2.3. Data analysis

Given that the proportion of “faithful” limpets and the distance to the home scar of “unfaithful” limpets at each observation was based on relatively small samples and therefore subject to sampling error, we used a Bayesian approach in all analyses to retain the appropriate degree of uncertainty in this estimate. Bayesian methods are preferred over classic statistics for this type of analysis because the results can easily be interpreted in terms of relative probability, unlike conventional confidence intervals or P values (Hilborn and Mangel, 1997; Quinn et al., 2006; Wade, 2000).

We used models based on binomial distribution to describe the fidelity behaviour of *S. lessoni* on each observation day (see Appendix A1 in the supplementary material) and an analysis of the distance to

Table 2

Mean and credibility intervals for posterior distribution probability obtained with Bayesian analysis of site fidelity of “faithful” limpets, and displacement of “unfaithful” limpets in different seasons and geographic sites.

	Site	Season	Day of observation	Credibility interval		
				lower	mean	upper
Posterior probability distribution of fidelity limpets (Θ)	MDP	Spring	1st	0.475	0.576	0.676
			5th	0.345	0.488	0.633
			10th	0.30	0.4	0.511
		Autumn	1st	0.469	0.567	0.669
			5th	0.26	0.4	0.542
			10th	0.267	0.369	0.472
	LG	Spring	1st	0.73	0.808	0.883
			5th	0.692	0.80	0.898
			10th	0.547	0.643	0.736
		Autumn	1st	0.643	0.73	0.814
			5th	0.625	0.745	0.859
			10th	0.532	0.723	0.63
Estimated mean of displacement (τ)	MDP	Spring	1st	3.983	8.414	12.86
			5th	7.518	13.38	19.26
			10th	17.74	21.61	25.48
		Autumn	1st	9.735	14.13	18.52
			5th	9.056	14.45	19.79
			10th	21.97	25.84	29.63
	LG	Spring	1st	14.09	20.62	27.04
			5th	−3.9	5.178	14.33
			10th	9.57	14.27	18.99
		Autumn	1st	12.27	17.69	23.01
			5th	−0.24	7.68	15.66
			10th	9.93	14.6	19.27

the home scar based on a normal distribution for “unfaithful” specimens (see Appendix A2 in the supplementary material).

We examined the potential influence of food availability and limpet density on *S. lessona* movement. Limpet density was quantified by counting the number of individuals in a 50 × 50 cm quadrat on each rock at every observation. As a proxy estimation of food supply, we determined the abundance of epilithic microalgae as concentration of chlorophyll *a* (Chl *a*; Jenkins and Hartnoll, 2001) by collecting 4 cm² rock chips from each rock with every observation and placing them in acetone to extract Chl *a* (Jeffrey and Humphrey, 1975). Chl *a* extract was quantified by fluorescence spectrophotometry. Although the acetone technique extracts less than 50% (Thompson et al., 1999) of the total epilithic biofilm, it is considered satisfactory for the extraction of diatoms and algal propagules (Thompson et al., 1999), which are the main items in the diet of *S. lessona* (Bastida et al., 1971).

Bayesian regression models were developed with the combination of food availability (Chl *a*), limpet density (Den), season and site as independent variables, and “faithful” limpets and the displacement of “unfaithful” limpets as dependent variables. We used Bayesian regression models based on binomial distribution for “faithful” limpets and on normal distribution for “unfaithful” limpets, to describe behaviour on each observation day. Prior to analysis, multicollinearity among predictors in the Bayesian regression models was tested using variance inflation factor (VIF). The estimated VIF showed low levels of collinearity among predictors (VIF < 10 for all the cases). Thus all the predictors were included in the Bayesian regression models.

The importance of each explanatory factor in the minimum adequate model was assessed by comparing a reduced model (with all terms involved and the factor of interest removed) against the full model, using deviance information criterion (DIC) developed by Spiegelhalter et al. (2002), which evaluates model fit and complexity such that smaller values are preferable. Models with smaller DIC were selected, where differences between 3 and 5 DIC units are typically assumed to be relevant (Spiegelhalter et al., 2002, 2003).

3. Results

A total 1000 *Shiphonaria lessona* were tagged, of which 918 were recaptured after 10 observation days. Recovery rates were higher at the LG site than at the MDP site (97 and 87% respectively), but similar between seasons (87% in spring and 86% in autumn in MDP and 96% in spring and 97% in autumn in LG) (Table 1). Table 2 shows the mean proportion of site fidelity and the credibility intervals for the displacement of “unfaithful” limpets.

S. lessona did not respond to seasonality at either study site (on a time macro-scale), but differed in response to environmental variables in each habitat. LG had a higher proportion of “faithful” limpets than MDP. The Bayesian analysis showed that all posterior probabilities of “faithful” limpet behaviour were higher in LG than in MDP (Fig. 2a–c). The confidence intervals (CI) were different in all cases, thus showing that the posterior probabilities were different (Table 2). The macro-scale (seasonality) comparison had no evident effect within each site, since the CI overlapped in both seasons for each site (Table 2). In the micro-scale comparison (during the 10 days of experimentation) the fidelity to a site decreased with time elapsed (Fig. 2a–c).

The displacement of “unfaithful” *S. lessona* limpets and resting site fidelity showed no effect for seasonality at either study site (time macro-scale) but did show differences related to geography. Between sites (on a spatial macro-scale), estimated mean displacement (μ) differed in some cases (Fig. 3). While in spring on observation day 1, mean displacement was higher in MDP than LG, in autumn on observation day 10 it was lower (see Table 2).

The macro-scale (seasonality) comparisons did not show any differences in displacement within sites because all CI overlapped (Table 2). However, on the micro-scale (during the 10 days of experimentation), in general terms, displacement increased with elapsed time (Fig. 3).

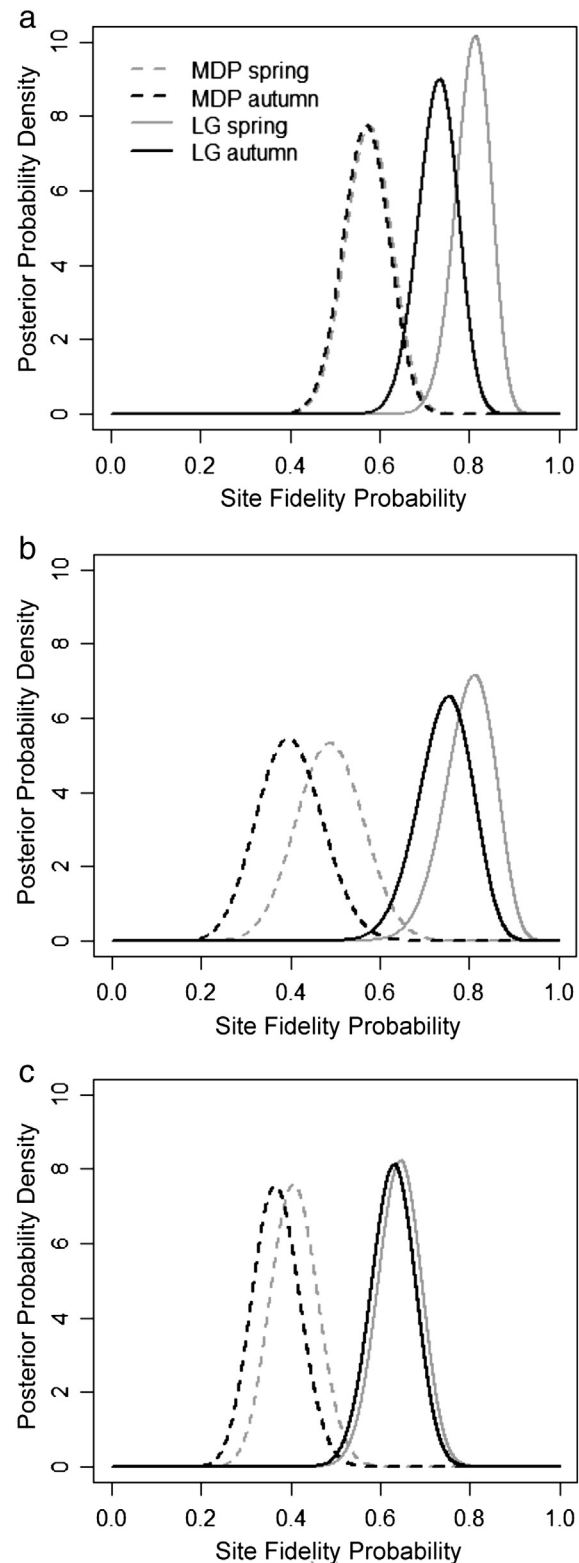


Fig. 2. Graph of Bayesian analysis of the proportion of site fidelity limpets at different seasons and geographic sites. The y axis shows the density of posterior probability distribution and the x axis the probability of site fidelity (Θ). (Dashed line = MDP; full line = LG) (grey = spring, black = autumn). a: observation day 1, b: observation day 5, c: observation day 10.

Fidelity to home scar did not change with season at either site (DIC < 5, Table 3). Food availability (Chl *a*) had an effect only for experimentation day 1 (DIC > 5, Table 3), and the effect was negative (Fig. 4).

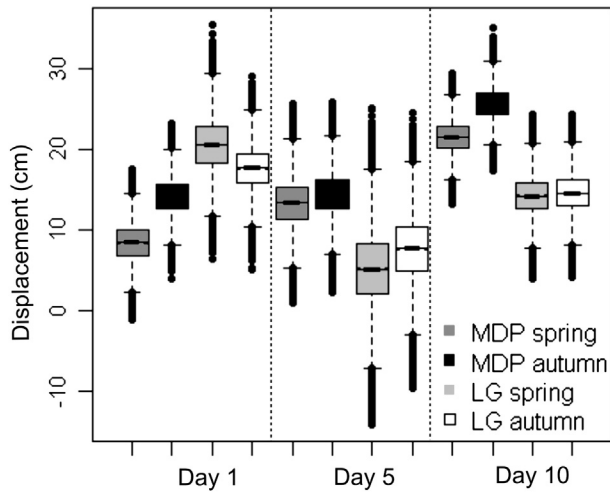


Fig. 3. Box-plot of the displacement of “unfaithful” limpets in different seasons and geographic sites. The y axis shows the mean estimated displacement (μ) and the x axis days of observations. Different box types show different sites (light grey box = MDP site in spring; black box = MDP site in autumn; grey box = LG site in spring; white box = LG site in autumn).

There was no effect on fidelity response for the other observation days (5 and 10) or for the density of limpets (Den) (DIC < 3, Table 3).

Displacement of “unfaithful” limpets, was not affected by density (Den) (DIC < 3, Table 3), although it did depend on Chl *a* on experimentation days 5 and 10 (DIC > 5, Table 3), with a negative relationship in both cases (Fig. 5a, b).

4. Discussion

Our results show that the limpet *S. lessona* displays different behavioural strategies regarding movement between the two geographic sites analysed. The proportion of “faithful” limpets is higher in LG than in MDP, where the climate is less harsh in terms of desiccation. Therefore, and considering the “environmentally stressful response”

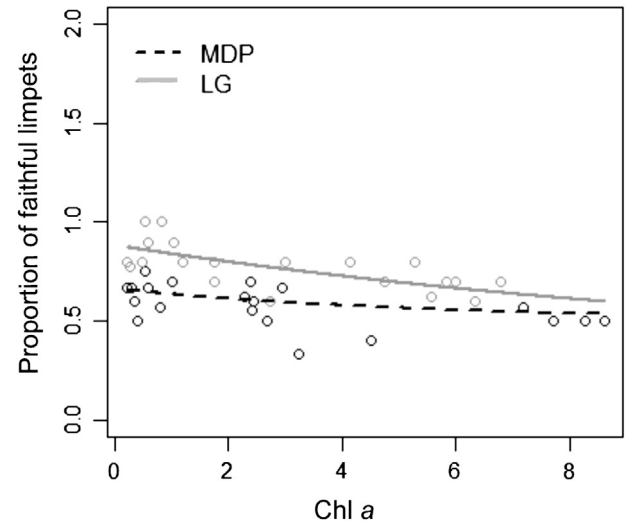


Fig. 4. Bayesian regression model graph of “faithful” limpets and food availability. The y axis shows the mean proportion estimated of “faithful” limpets and the x axis concentration of Chl *a*. (black dashed line and circles = MDP; grey full line and circles = LG) in experimentation day 1.

hypothesis (see Introduction), the different desiccation rates could drive differences in homing behaviour. In this regard, two other limpets (*Siphonaria capensis* and *Cellana grata*) differed in homing behaviour resulting from different desiccation rates in day/night cycles. Both species had a preference for nocturnal activity (when the desiccation rate is lower) suggesting clear avoidance of stressful environmental conditions (Branch and Cherry, 1985; Santini et al., 2011). Thus, there is evidence to support the “environmentally stressful response”, and the addition of new observation sites with different desiccation rates could help strengthen our conclusions.

Limpet behaviour is known to be affected not only by spatial variations, but also by seasonal influences (Gray and Hodgson, 1997; Santini et al., 2004), probably due to intrinsic changes in energy metabolism such as gonad development (e.g. Blackmore, 1969; Morais et al.,

Table 3

Summary of Bayesian regression analysis model fits to behavioural data in different seasons and geographic sites for each observation day. In bold, the best fitting model including the main effects with less Deviance information criteria (DICs). The effective number of parameters (pD).

Day of observation	Site fidelity			Displacement		
	Model	DIC	pD	Model	DIC	pD
1st	Season + Chl <i>a</i> + density	137.4	12.1	Season + Chl <i>a</i> + density	972.2	6.6
	Chl <i>a</i> + density	125.9	5.9	Chl <i>a</i> + density	972.4	5.3
	Season + Chl <i>a</i>	130.2	8	Season + Chl <i>a</i>	972.6	6.7
	Season + density	135	8.1	Season + density	971.5	6.5
	Chl <i>a</i>	122.5	4	Chl <i>a</i>	972.9	4.9
	Density	128.5	3.9	Density	971.4	4.9
	Season	128.3	4	Season	969.9	4.7
	Minimal	126.1	2	Minimal model	970.4	3
5th	Season + Chl <i>a</i> + density	78.3	12.1	Season + Chl <i>a</i> + density	517.5	7
	Chl <i>a</i> + density	68.9	6.2	Chl <i>a</i> + density	511.7	6.4
	Season + Chl <i>a</i>	70.6	8.1	Season + Chl <i>a</i>	512.4	6.4
	Season + density	72.8	8.1	Season + density	518.8	6.3
	Chl <i>a</i>	65.6	4	Chl <i>a</i>	508.1	4.7
	Density	65.7	4	Density	516.4	4.6
	Season	65.6	4	Season	518.5	4.6
	Minimal	62.8	2	Minimal model	514.7	3
10th	Season + Chl <i>a</i> + density	148.1	12.2	Season + Chl <i>a</i> + density	1442.5	9.5
	Chl <i>a</i> + density	143	6	Chl <i>a</i> + density	1441.3	6.9
	Season + Chl <i>a</i>	143.7	8.2	Season + Chl <i>a</i>	1442.9	7.1
	Season + density	141.7	8.2	Season + density	1443.1	8.6
	Chl <i>a</i>	139.1	4	Chl <i>a</i>	1440.1	4.8
	Density	139.7	4	Density	1446.3	5
	Season	139.8	4	Season	1446.1	4.8
	Minimal	136.2	2	Minimal model	1444	3

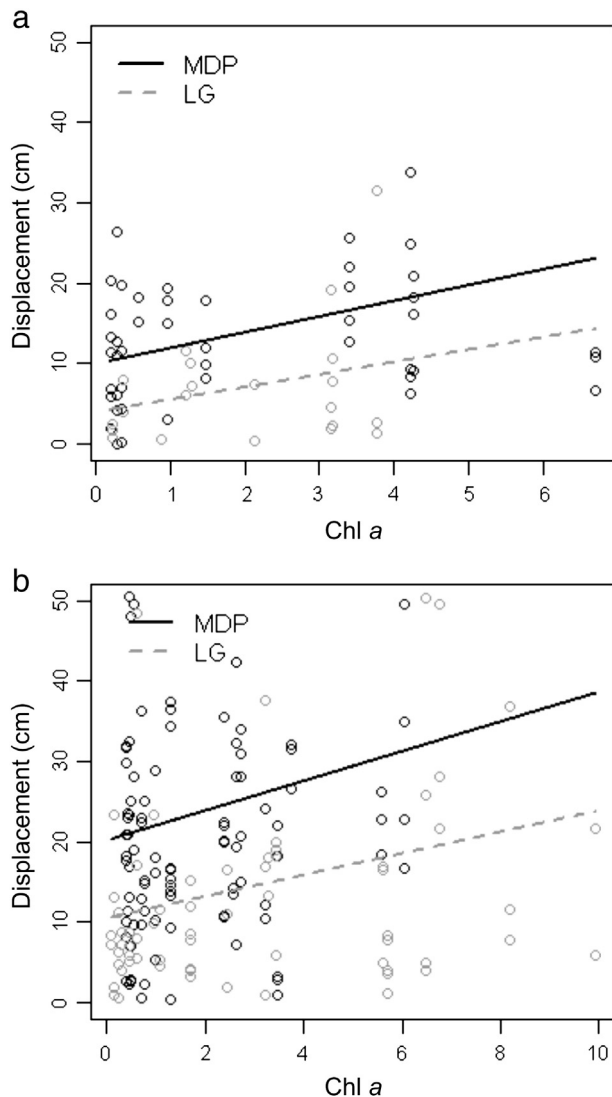


Fig. 5. Bayesian regression model graph of displacement of “unfaithful” limpets and food availability. The y axis shows the mean estimated displacement and the x axis concentration of Chl *a*. (black dashed line and circles = MDP; grey full line and circles = LG) in a: experimentation day 5, b: experimentation day 10.

2003) or changes in food availability (Hill and Hawkins, 1991; Nagarkar and Williams, 1999). However, in our study the two seasons analysed did not influence the behaviour of *S. lessoni*, even though *S. lessoni* individuals were at different gonad stages in the two seasons (Nuñez et al., unpublished results). Moreover, we found no relationship between seasonal food availability and the behavioural characters analysed. Therefore, in this study model, the differences between seasons do not appear to be an important factor in modulating homing behaviour.

In our 10-day analysis (longest period analysed at micro-scale), this species behaved with different degrees of site fidelity and displacement of “unfaithful” limpets. These results contrast with Bulleri et al. (2004) for the limpet *Cellana tramoserica*, where the differences for displacement were only recorded at macro-scale. Therefore, the resting site fidelity behaviour response of *S. lessoni* on a small timescale seems to be more sensitive than on a large timescale and probably depend on the sum of influential events that may occur during the day such as rainfall, wave action, wind or atmospheric pressure (e.g. Della Santina and Chelazzi, 1991; Little et al., 1991).

Density-dependent dispersal is mainly thought to represent a response to avoid extreme desiccation rates or to increase the possibility of finding new food resources (Iwasaki, 1995). Several authors have

reported a negative density-dependent effect on the proportion of homing individuals either in experimental or natural conditions (e.g., Mackay and Underwood, 1977; McClintock and Lawrence, 1986; Stimson and Black, 1975), while others did not show such patterns (Breen, 1971; Iwasaki, 1992). In *S. lessoni*, the Bayesian regression did not show associations between population density and site fidelity and distance to home scar. The plastic behavioural responses of the same species on the Pacific coast of Chile (32° S) were related to agonistic interspecific interactions (Aguilera and Navarrete, 2012). However, at our study sites, *S. lessoni* has no competitor, and thus at natural density, with no interspecific competition, there is no significant effect on its behaviour.

The success of a grazer depends on the trade-off between the energy gained from foraging (i.e. the energy ingested and assimilated) and the energy expended to obtain the food (Stephens and Krebs, 1986). A periodic return to a reference spot (i.e. the home scar) might facilitate the spatial organisation of foraging, improving exploitation of radially distributed food patches. In this context, molluscs are known to adapt their behaviour (Bell, 1991; Stephens and Krebs, 1986). The resting site fidelity behaviour and distance to home scar were related to Chl *a* availability for *S. lessoni* grazing. On day 1 the displacement and site fidelity at both study sites was related positively with Chl *a*, while on days 5 and 10, the distance to the home scar was related negatively with Chl *a*. Therefore, food availability likely induces changes in behavioural response, but the direction of change depends on the temporal scale analysed. For example, while food availability promotes short-term homing behaviour, over a longer period it promotes longer excursions of “unfaithful” limpets, probably driven by exploration of places with more food abundance.

To conclude, our study suggests that the homing behaviour of *Siphonaria lessoni* can be sensitive to some biotic variables such as food, as well as to different climate contexts (e.g. desiccation rate). However, we also found that this sensitivity can change over the different time scales evaluated (days or seasons). Thus, further experiments are needed to unravel the role of the different environmental and biotic factors involved and understand more precisely which variables affect the variability in *S. lessoni* behaviour.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2014.01.014>.

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