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Littorina littorea show small-scale persistent tidal height and habitat partitioning that is resilient to dislodgement through specific movement rates

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ABSTRACT

Dislodgment, in particular by breaking waves, is a widely acknowledged source of stress, if not mortality, in rocky shores intertidal gastropods. This raises the question of understanding if snails dislodged from a specific habitat have the ability to navigate back to their original substrate, and how this is achieved. In this context, we investigated the consequences of dislodgement on a population of *Littorina littorea* inhabiting two proximate habitats (a seawall ranging from the low to the high intertidal zone and the related low intertidal rocky platform) located on an isolated offshore reef over a three-month period. Using tagged undisturbed, disturbed, translocated and transplanted *L. littorea*, we assessed a potential tidal height preference and found that *L. littorea* showed a clear tendency to remain on their original tidal height, with recapture rates ranging between 100% and 88%, respectively 1 and 78 days after dislodgment. We subsequently measured the recapture rates of individuals dislodged from three distinct tidal levels on the seawall and from a horizontal platform. Dislodged *L. littorea* showed a clear tendency to return to their original tidal level, with return rates ranging between 32 and 48% 78 days after dislodgment; snails from the horizontal platform were never found on the proximate seawall. In addition, high frequency observations conducted on individually tagged dislodged *L. littorea* during the first 8 successive low tides of our survey indicate that individuals originating from the seawall consistently showed higher movement rates and directionality to wards the seawall, while individuals usubstrate and tidal height. Putative processes include a combination of geotaxis, chemotaxis, and rheotaxis. At relatively short time scales (i.e. days to months), *L. littorea* how both tidal and habitat partitioning that is distinct from the movement patterns previously reported in littorinids over a range of temporal scales.

1. Introduction

Life in the intertidal zone is heavily constrained by a range of stressors including thermal and desiccation stresses, wave exposure and the related risk of dislodgement by wave action (Denny and Gaines, 2007). Understanding the direct and indirect effects of wave exposure, force and activity on the structure and function of intertidal populations and communities has been a prolific area of research over four decades (Dayton, 1971; Wolcott, 1973; Menge and Sutherland, 1976, 1987; Sousa, 1979, 1984; Pain and Levin, 1981; Helmuth and Hofmann, 2001; Harley and Helmuth, 2003; Finke et al., 2007; Scrosati et al., 2010). Specifically, waves can dislodge intertidal organisms by imparting lift, acceleration reaction, and drag forces (Denny et al., 1985). Measuring or predicting these forces makes it possible to estimate the risk of dislodgement from the substratum under various wave conditions for a range of organisms such as macroalgae (Carrington, 1990; Gaylord

et al., 1994; Blanchette, 1997), crustaceans (Martinez, 2001; Lau and Martinez, 2003), and various molluscs (Denny, 1985, 1987, 1995; Bell and Gosline, 1997; Denny and Blanchette, 2000; Carrington, 2002; Wyeth and Willows, 2006; Brenner and Buck, 2010), including littorinids (Trussell et al., 1993).

Snails on exposed shores tend to express traits that increase dislodgement resistance such as longer, broader feet and greater tenacity (Miller, 1974; Etter, 1988; Trussell et al., 1993; Trussell, 1997a, 1997b; Parsons, 1997a, 1997b), though some exceptions exist (Hohenlohe, 2003; Prowse and Pile, 2005). The ability of intertidal gastropods to survive on wave-swept environments is hence partially determined by their ability to resist dislodgement by breaking waves, which are also likely to reduce foraging efficiencies and reproductive success (Denny et al., 1985; Etter, 1989; Trussell et al., 1993). The consequences of dislodgement have, however, been far less studied (Miller et al., 2007; Chapperon and Seuront, 2009), and there is still seldom information on

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how dislodged intertidal gastropods may navigate back to their original (or more generally suitable) habitat or tidal height despite decades of investigations of littorinid sensory abilities (Evans, 1951, 1961; Charles, 1961; Newell, 1965; Warburton, 1973; Hamilton, 1976; Petraitis, 1982; Hamilton and Winter, 1982; Thain et al., 1985; Seyer, 1992; Land and Nilsson, 2002; Chapperon and Seuront, 2009; Seuront and Spilmont, 2015).

In this context, the aim of this study is to improve our understanding of littorinids behavioural ecology and navigational capabilities following a dislodgment from a preferred resting site or tidal height. Specifically, the present work uniquely focuses on a population of L. *littorea* inhabiting two proximate habitats (*i.e.* a seawall ranging from the low to high intertidal zone and the proximate low intertidal rocky platform). We first assessed whether L. littorea exhibit both tidal height and habitat partitioning through a temporal survey of the location of undisturbed, disturbed and translocated individuals from three distinct tidal levels on the seawall, and the horizontal platform. Specifically, if L. littorea exhibit tidal height and habitat partitioning, we would expect to consistently observe the same individuals on distinct tidal levels and on the horizontal platform. We further investigate the robustness of this partitioning following simulated wave dislodgement through the ability of dislodged L. littorea to navigate back to their original habitat whether they were dislodged from the horizontal platform or the seawall for time scales ranging from 1 to 90 days. In an attempt to assess whether the movement of dislodged individuals is directed or random, we also monitored the successive positions of individually tagged individuals sampled from both the horizontal platform and the three distinct tidal levels considered on the seawall during 8 consecutive low tides.

2. Materials and methods

2.1. Study site

Littorina littorea experiments were carried out on the landward side of the Fort de l'Heurt (50°42'29"N, 1°33'35"E; Fig. 1), where their abundance typically ranges from 15 to 250 individuals m⁻² (Seuront, unpublished data). Note that L. littorea are consistently absent from the seaward wave-exposed side of the Fort (Seuront, personal observation), which is directly exposed to the main SSW swell direction that characterizes this area. The landward side of the Fort, though less exposed to the dominant swell regime, is nevertheless heavily wave-swept under stormy conditions. This consistently results in massive L. littorea dislodgment with 2- to 5-fold decrease in abundance observed during the low tide immediately following a storm (L. Seuront, personal observation). The Fort de l'Heurt is located 650 m away from the Mean High Water Spring (MHWS) line, on an intertidal rocky reef south of Boulogne-sur-Mer on the French side of the eastern English Channel (Fig. 1A-D). This coastal area is characterised by the amplitude of its tidal range (between 3 and 9 m), and both the strength of the tidal circulation with strong (1 to 2 m s^{-1}) tidal currents parallel to the coast, and the shallow water generate extremely high levels of mixing, with turbulence intensities ranging from 10^{-7} to 10^{-4} m² s⁻³ (Seuront, 2005). Once a massive structure covering nearly 1800 m² (50 m \times 35 m), the Fort de l'Heurt has been heavily damaged by wave impacts and its original walls made of large stones (190 cm \times 130 cm \times 40 cm) have been destroyed and scattered around the remaining inner core, which is about 25 m long, 10 m wide and 10 m tall. Nowadays, each side of the Fort similarly consists of vertical walls made of stones of various sizes and shapes bounded with a mortar of cement or lime (Fig. 1E). The landward wall of the Fort de l'Heurt ranges from a height of 3 metres above the Mean Lower Low Water (MLLW) to the supratidal zone. L. littorea were sampled from 3 tidal levels on the seawall, i.e. 3 to 5 metres, 5 to 7 metres and 7 to 9 metres above MLLW that are hereafter referred to as low, intermediate and high tidal levels. L. littorea individuals were also sampled from the proximate horizontal platform (20 m long, and 10 m wide) located 2 meters above MLLW, and



Fig. 1. The study area is located on the French coast of the eastern English Channel (a), south of Boulogne-sur-Mer (b). The study site, the Fort de l'Heurt, is situated 650 m away from the Mean High Water Spring on an intertidal rocky reef (c, d). Experiments were conducted on the landward wall of the Fort and the proximate horizontal reef (e). The dashed lines separate the three 2-m high tidal levels used in this work, the rectangles identify the sampling bands where *Littorina littorea* were sampled, and the double pointed arrows represent 2 m. The red dashed ovals identify the studied horizontal platform, and the asterisk the flat section of the reef where the transplanted control snails where sampled form.

dominated by small-scale topographic features such as crevices, pits and small boulders, and hosting a bed of the blue mussel *Mytilus edulis*. Note that *L. littorina* were never observed in aggregations or trail-following on this site, in sharp contrast with nearby rocky platforms devoid of topographic features (L. Seuront, unpublished data).

2.2. Experimental design

The existence of tidal height and habitat partitioning in *L. littorea* was investigated using a combination of experiments involving (i) undislodged marked snails, (ii) snails that were dislodged, marked and replaced in the location they were taken from, (iii) translocated snails that were dislodged, marked and moved to another location in their habitat, and (iv) transplanted snails that were dislodged, marked and

transplanted to a different habitat. These experiments have been specifically chosen to ensure that the effect of transplantation in a new habitat (here following a manual dislodgement) can be distinguished from the effects of disturbance and translocation; see Chapman (1986); Chapman and Underwood (1994a, b) and Chapman and Underwood (1992). The corresponding experimental procedures are detailed hereafter.

2.2.1. Control experiment

L. littorina tidal height and habitat preference was investigated through experiments conducted by marking in situ during the same low tide 4 groups of 40 undisturbed snails (i.e. '*control snails*') — one from the horizontal platform and 3 from each tidal level along 1.5-m wide sampling bands on the landward wall (Fig. 1E) — with acrylic nail polish of distinct bright colours to facilitate subsequent location in the field.

2.2.2. Disturbance experiment

During the same low tide, we also manually dislodged individual snails (i.e. '*disturbed snails*') from the horizontal platform (N = 35) and each tidal levels (N = 40 per level), subsequently marked them as done with the control snails, and replaced them in the exact position they were taken from.

2.2.3. Translocation and transplantation experiments

Four control groups of 100 snails were haphazardly collected from the horizontal platform and each tidal level, and returned to the laboratory for tagging. The shells of these individuals were coated with acrylic nail polish of distinct bright colours. After marking the snails, we allowed the nail polish to dry for three hours and then kept the snails in flowing seawater overnight before returning them to the field. Snails were judged unaffected by the handling, painting and drying process since they attached to the sides of the aquaria and crawled out of the seawater, as unmanipulated *L. littorea* do (L. Seuront, personal observation). This criterion is consistent with previous evidence that tagging does not affect the motion behaviour of gastropods (*e.g.*Chapman, 1986, 2000a, 2000b; Henry and Jarne, 2007; Seuront et al., 2007; Chapperon and Seuront, 2012).

During the next daytime low tide, 50 individuals of each group (i.e. 'translocated snails') were transported in distinct aerated plastic containers to the Fort de l'Heurt, haphazardly placed back in their initial habitat (i.e. horizontal platform and tidal level on the seawall) and gently sprayed with in situ seawater to allow them to reattach with their foot on the substratum. During the subsequent high tide, the remaining 4 groups of 50 individuals (hereafter referred to as 'transplanted snails') were mixed together in aerated plastic containers, brought back to the Fort de l'Heurt using a Stand-Up Paddle (Lokahi Aka Entry 10'6), and haphazardly dropped into the water over a 10 m \times 10 m area facing the seawall and located directly above the horizontal platform. This procedure was used (i) to simulate snails being dislodged from their vertical substratum, with no opportunity for quick reattachment before falling into lower intertidal levels, and (ii) to guarantee that all snails were released in the same habitat, hence will experience similar stressors and cues.

Finally, because the horizontal platform is located below the low tidal level considered on the seawall (i.e. 2 metres and 3 to 5 metres above MLLW, respectively), we conducted an additional control experiment to ensure that the return rates observed on the seawall were driven by an actual preference for the seawall rather than by a tidal level preference. We sampled 50 *L. littorea* individuals (i.e. 'control transplanted snails') from a nearby flat section of the reef surrounding the Fort de l'Heurt that is located 3.5 meters above MLLW (Fig. 1D). These snails were subsequently manipulated as described above before being released at high tide above the horizontal platform.

2.3. Behavioural experiments

Four groups of 50 snails were sampled from the horizontal platform and the three tidal levels, coated with acrylic nail polish of distinct bright colours and individually tagged with glue-on shellfish tags (4 × 2 mm, Hallprint, Hallprint Pty Ltd, Hindmarsh, South Australia). Each group of 50 individuals was subsequently randomly placed within a 25 × 25 cm area surrounding a release point haphazardly situated on the horizontal platform, sprayed with *in situ* seawater to allow them to reattach with their foot on the substratum, and left undisturbed from the release day. The position of marked snails was subsequently monitored during 8 consecutive low tides to assess whether the movement of dislodged individuals is directed or random.

2.4. Morphologic traits and dislodgement resistance

Because resistance to dislodgment may be habitat-related and driven by specific differences in shell size and morphology (Miller, 1974; Etter, 1988; Trussell et al., 1993; Trussell, 1997a, 1997b; Parsons, 1997a, 1997b), the height, width and length of all snail shells considered in the present work were systematically measured. We additionally measured the foot surface area of L. littorea for individuals (n = 10) sampled from the horizontal platform and the three tidal levels of the seawall. In the laboratory, snails were allowed to crawl over a glass plate in air (T = 22° C) until they became stationary and attached (typically after 60 to 75 s). The foot was then photographed (Nikon V1 mounted with a Nikkor 10-30 mm lens) from below, the foot area A (cm²) measured using the software Image J (Schneider et al., 2012; Schindelin et al., 2015), and expressed as a function of shell length L (cm) following $A_i = a_i L_i^{b_i}$, where a_i and b_i are empirical parameters related to the snail habitat *i* (i.e. horizontal platform and the three tidal levels on the seawall).

2.5. Environmental variables

Air and water temperature, and wind speed were considered as environmental variables that are most likely to affect *L. littorea* navigation and tenacity as (i) *L. littorea* speed has been shown to significantly covary with temperature (Newell, 1958a, 1958b; Erlandsson and Kostylev, 1995) and (ii) the risk of dislodgment of intertidal organisms, including gastropods, increases with wave force, that is essentially driven by wind speed in coastal seas (Wright et al., 1999). Air and water temperatures were measured every 5 minutes using HOBO* Tidbit v2 Temperature Data Logger (Onset Computer Corporation, Bourne, MA, USA), that were glued on the horizontal platform and each tidal level on the seawall. Hourly wind speed recorded at the Boulognesur-Mer weather station were obtained from Météo-France.

2.6. Census

The three seawall tidal levels and the horizontal platform were surveyed at low tide 1, 2, 8, 17, 27, 37, 45, 57, 67, 78 and 90 days after the control, disturbed, translocated and transplanted snails were tagged. The censuses of each seawall level and the horizontal platform were implemented through a total of twenty person-minutes of searching per site per day (Miller et al., 2007). To avoid potential biases related to additional disturbances, snails were never manipulated during counts.

2.7. Behavioural analysis

To determine the nature of the daily individual displacements of *L*. *littorea*, we monitored the orientation angle α_t and the distance displaced d_t by each individual from the release point to the monitored snail position during 8 successive low tide, i.e. t = 1 to 8. The orientation angle α_t was estimated from the release point using the



Fig. 2. Temporal patterns of (a) daily averaged air temperature (grey dots) and seawater temperature (...), and (b) daily maximum wind speed observed over the course of our survey. The open symbols in (a) and (b) indicate the sampling days.

direction of the landward wall of the Fort de l'Heurt as a reference. The distance displaced d_t was measured by a plastic tape measure (resolution 0.1 cm) laid down the substratum topography from the release point to the snail's position. The (x_t, y_t) coordinates were subsequently estimated from the distance displaced d_t and orientation angle α_t as $x_t = d_t \cos \alpha_t$ and $y_t = d_t \sin \alpha_t$. The daily orientation angles α_i were subsequently defined as the angle taken by an individual between two successive low tides and calculated as $\alpha_i = 180 - \alpha_e (180/\pi)$, where $\alpha_e = \arccos (D_1^2 + D_2^2 + D_3^2)/(2D_1D_2) D_1, D_2 \text{ and } D_3 \text{ are the distances}$ between positions $(x_{t=1}, y_{t=1})$ and $(x_{t=2}, y_{t=2})$, $(x_{t=2}, y_{t=2})$ and $(x_{t=3}, y_{t=3})$, and $(x_{t=1}, y_{t=1})$ and $(x_{t=3}, y_{t=3})$ (Jerde and Visscher, 2005). The daily distance displaced d_i was estimated as the distance displaced by an individual between two successive low tides as $d_i = [(x_{t+1} - x_t)^2 + (y_{t+1} - y_t)^2]^{1/2}$. The net orientation α_{net} and distance d_{net} were finally estimated from the final position of the tagged snails, i.e. $\alpha_{net} = \alpha_{t=8}$ and $d_{net} = d_{t=8}$. We also quantified the level of activity of dislodged L. littorea individuals through using the ratio N_i/N_i where N_i is the total number of mobile individuals between two successive low tides (i.e. the number of individuals that changed position between two successive low tides) and N is the total number of individuals.

2.8. Data analysis

Because L. littorea abundance, size and successive displacements were non-normally distributed (Kolmogorov-Smirnov test, p < 0.05), nonparametric statistics were used throughout. Multiple comparisons between sampling sites (i.e. three tidal levels on the seawall and the horizontal platform) and both net and daily displacements were conducted using the Kruskal-Wallis test (KW test hereafter), and a subsequent multiple comparison procedure based on the Tukey test was used to identify distinct groups of measurements (Zar, 2010). The Mardia's extension of the non-parametric Wheeler and Watson test (WW test hereafter; Zar (2010)) was used to infer (i) differences in the net orientation angles α_n for snails originating from different habitats, and (ii) temporal differences in the daily orientation angles α_i for snails originating from the same habitat. The distributions of daily orientation angles and net orientation angles were further compared to a uniform distribution using the Watson one-sample U² test (Zar, 2010). The autocorrelation functions (ACF) and the Box-Ljung statistic were used to test for autocorrelation in the successive displaced distances for all lags up to 7 moves (Turchin, 1998). Differences in the empirical parameters a_i and b_i of the allometric relationships $A_i = a_i L_i^{b_i}$ were respectively assessed on log-transformed data with a *F* test and an analysis of covariance which were respectively used to infer regression intercepts and slopes (Zar, 2010). It is finally stressed that because *L. littorina* individuals have never been observed forming aggregations or trail-following on our study site, we rule out the possibility of trail-following to occur subsequently to our transplantation experiment, hence we consider that *L. littorea* individuals were independent in their movements and each recapture has been considered an independent event.

3. Results

3.1. Littorina littorea abundance on the study site

At the beginning of our study, significant differences were found in the abundance of *L. littorea* between the seawall tidal levels and the horizontal platform (Kruskal-Wallis test, p < 0.05). No significant differences were, however, found in the abundance of *L. littorea* between the three tidal levels (Tukey test, p > 0.05). Seawall abundance, which ranged between 10 and 134 ind m⁻² were significantly lower than on the horizontal platform (Tukey test, p < 0.05), where they reached up to 200 ind m⁻² (69-202 ind m⁻²).

3.2. Environmental conditions

Over the course of our 90 days experiment, air temperature ranged between 26.6°C and 8.9°C, and significantly decreased (Pearson test, p < 0.01) from August 24 to November 24. No significant difference in temperature where observed between the horizontal platform and the three tidal levels of the seawall (KW test, p > 0.05). Seawater temperature increased from 18.7 to 20.3°C over the first 16 days of our survey, and subsequently steadily decreased down to 11°C at the end of the survey (Fig. 2A). Daily averaged wind speed ranged from 1.0 to 7.2 m s⁻¹, with daily maximum ranging from 5 to 43 m s⁻¹ (Fig. 2B). Note that the maximum averaged and instantaneous wind speeds were observed two days before the end of our experiments.

3.3. Morphologic traits

No significant differences were found in snail size between the

Table 1

Best nonlinear fits describing the temporal evolution of the recapture rates of control (R_c), disturbed (R_c), translocated ($R_{transplanted}$) and transplanted ($R_{transplanted}$) *Littorina littorea* depending on their initial habitat, i.e. a horizontal platform 2 metres above the Mean Lower Low Water, a flat reef 3.5 metres above MLLW and the proximate vertical wall at tidal levels ranging from 3 to 5 metres (Level 1), 5 to 7 metres (Level 2) and 7 to 9 metres (Level 3) above MLLW. To assess whether the relationship between the recapture rates and time *t* was best fitted by a linear, power-law, logarithmic, or an exponential function, we used the theory of model selection based on Akaike's information criterion (AIC: Edwards, 2008).

Recapture rate	Habitat	Model	r^2
R _c	Platform	Rc = -11.6ln(t) + 99.0	0.99
	Level 1	Rc = -2.2ln(t) + 99.9	0.96
	Level 2	Rc = -2.1ln(t) + 98.5	0.96
	Level 3	Rc = -2.4ln(t) + 99.2	0.95
R _d	Platform	Rc = -11.9ln(t) + 98.6	0.99
	Level 1	Rc = -2.5ln(t) + 98.7	0.98
	Level 2	Rc = -2.4ln(t) + 99.2	0.96
	Level 3	Rc = -2.6ln(t) + 97.7	0.95
Rtranslocated	Platform	$Rc = -12.1\ln(t) + 97.8$	0.98
	Level 1	$R_{translocated} = -2.7\ln(t) + 100.7$	0.87
	Level 2	$R_{2translocated} = -2.5\ln(t) + 97.9$	0.96
	Level 3	$R_{translocated} = -2.5\ln(t) + 99.9$	0.95
R _{transplanted}	Platform	$R_{\text{transplanted}} = -12.8\ln(t) + 98.0$	0.99
	Flat reef	$R_{transplanted} = -13.1\ln(t) + 97.8$	0.98
	Level 1	$R_{\text{transplanted}} = 78.9 e^{-0.02t}$	0.99
	Level 2	$R_{transplanted} = 81.1e^{-0.027t}$	0.99
	Level 3	$R_{transplanted} = 92.4e^{-0.027t}$	0.99
		-	

seawall tidal levels and the horizontal platform (KW test, p > 0.05), with *L. littorea* consistently ranging in length between 11.2 and 17.8 mm. *L. littorea* foot area A_i did not significantly differ between habitats (KW test, p > 0.05), with *A* ranging from 0.9 to 1.3 cm². More specifically, A_i consistently significantly (p < 0.05) scaled as a power function of shell length L_i , *i.e.* $A_i = a_i L_i^{b_i}$, irrespective of the sample location. No significant differences were found between the empirical parameters a_i (*F*-test, p > 0.05) or b_i (analysis of covariance, p > 0.05) for snails originating from the horizontal platform and from the seawall three tidal heights; overall, foot area scales as a function of shell length as $A = 0.12L^{0.84}$.

3.4. Control, disturbance and translocation experiments

The recapture rates of control snails (i.e. undisturbed snails marked in situ), disturbed snails (i.e. snails manually dislodged, marked in situ and replaced to their initial position) and translocated snails (i.e. snails manually dislodged, marked and moved to another location in their habitat) on the horizontal platform significantly (p < 0.01) decayed logarithmically with time t (Table 1). The decay typically occurred from 98% to 42% respectively 1 and 78 days after snails were marked, and an additional drop to 25-21% consistently occurred after 90 days (Fig. 3A). These rates were non-significantly different from each other (*F*-test, p > 0.05). On the seawall, the recapture rates of control, disturbed and translocated snails also decayed logarithmically with time t (Table 1), from 100 to 90%, 98 to 88% and 99 to 88% at tidal levels 1, 2 and 3 respectively over the first 78 days of the experiment (Fig. 3B). These rates did not significantly differ between tidal levels (F-test, p > 0.05), but were significantly slower than on the horizontal platform (*F*-test, p < 0.01). After 90 days, recapture rates drastically dropped to 44, 48 and 46% at tidal levels 1, 2 and 3, respectively (Fig. 3B). Note that the decrease in recapture rates observed both on the platform and the seawall is likely to be related to the massive storm that hit the French shores of the eastern English Channel from November 17 till November 20 (Fig. 2B). Noticeably, snails originating from different tidal levels were never observed outside of their original tidal level over the course of the experiment.

3.5. Transplantation experiments

The recapture rates of snails transplanted from the horizontal platform (i.e. snails sampled from the horizontal platform, tagged and released on the horizontal platform at high tide) and control transplanted snails (i.e. snails sampled from an elevated flat section of the reef, tagged and released on the horizontal platform at high tide) both significantly decayed logarithmically with time *t* (Table 1) from 96% to 42% respectively 1 and 78 days after being released over the horizontal platform, and an additional drop to 20% occurred after 90 days (Fig. 3C). These rates did not significantly differ from each other (*F*-test, *p* > 0.05), and were not significantly different from the recapture rates observed for control, disturbed and translocated snails (Fig. 3A, Table 1).

The recapture rate of snails transplanted from the seawall to the horizontal platform decayed exponentially, irrespective of the tidal level they were sampled from (Fig. 3D, Table 1). More specifically, these rates decayed from 82 to 12%, 84 to 7%, and 88 to 7% over the course of the 90 days survey for snails originating from tidal levels 1, 2 and 3, respectively. No significant differences were found between the 3 groups of snails in the decay of their recapture rates (*F*-test, *p* > 0.05). These rates decayed highly significantly faster (*F*-test, *p* < 0.01) than the recapture rate of snails transplanted from the horizontal platform and the flat section of the reef (Table 1).

Experimentally dislodged L. littorea concomitantly returned to the seawall at rates increasing from 8 to 54%, 6 to 58% and 4 to 54% respectively for snails originating from tidal levels 1, 2 and 3 (Fig. 4); these rates were best described by a logarithmic increase (Table 1), which did not significantly differ with the origin of the snails (F-test, p > 0.05). Note the decrease in return rates from 54 to 40%, 58 to 42% and 54 to 43% observed 90 days after dislodgment (Fig. 4). Noticeably, transplanted snails originating from the horizontal platform and the flat section of the reef were only rarely (0 to 6%) found on the seawall, and when present they were typically observed over the first few centimetres of the lowest limit of the tidal level 1. These observations suggests that the return rates observed on the seawall were habitat-driven (i.e. snails originating from the seawall tend to return to the seawall), and not driven by a tidal height preference. In the latter case, the snails originating from the flat section of the reef located 3.5 metres above MLLW and transplanted on a horizontal platform located 2 metres above MLLW should have exhibited a tendency to return to a similar tidal height on the seawall. Though the temporal patterns of the overall return rates of L. littorea on the seawall did not significantly differ between the experimental groups of snails (Fig. 4), these rates were clearly dependent from the tidal level they were dislodged from (Fig. 5).

Snails dislodged from the low tidal level (Fig. 5C) essentially returned to their tidal level, with a maximum return rate (48%) reached 45 days after dislodgement, which remained stable, until it dropped down to 26% at the end of the survey. This pattern indicates that these snails progressively come back to the tidal level they originate from. The plateau observed from 45 to 78 days after dislodgment further suggests that the return rates of these snails compensate the natural losses occurring over this period, which typically range from 0.1 to 0.3 snails per day (see Fig. 3A). Some of these snails marginally (2 to 6%) reached the intermediate tidal level 17 days after dislodgement.

L. littorea dislodged from the intermediate tidal level first returned to the low tidal level until they reached a maximum (36%) 27 days after dislodgement, and subsequently decayed down to 8% at the end of the survey. The proportion of snails reaching the intermediate tidal level consistently increased from 4% eight days after dislodgement to 40% seventy-eight days after dislodgement (Fig. 5B).

Finally, the return rate of snails dislodged from the high tidal level exhibited a more complex temporal pattern (Fig. 5A), that indicates a continuous upward movement of these snails though low and intermediate tidal levels toward the high tidal level. Specifically, dislodged



Fig. 3. Recapture rate (%) of *Littorina littorea* on the horizontal platform of the Fort de l'Heurt after being (a, b) translocated (i.e. manually dislodged, marked and moved to another location in their habitat) and (c, d) transplanted (i.e. manually dislodged, marked and moved to a different habitat), shown for snails sampled from the horizontal rocky platform (a, c) and the (b, d) the high tidal level on the Fort de l'Heurt.



Fig. 4. Return rates of *Littorina littorea* dislodged from low (dark grey), intermediate (light grey) and high (white) tidal levels of a vertical wall that returned to the vertical wall, irrespective of original tidal height.

L. littorea reached a maximum of 26% twenty-seven days after dislodgement, and consistently decreased afterwards. In turn, these snails reached the intermediate and high tidal levels respectively 8 and 17 days after dislodgement. Their return rate reached a maximum on the intermediate tidal level (16%) 32 days after dislodgement and steadily

decreased afterward down to 6% at the end of the experiment. The return rate observed on the high tidal level kept increasing up to 32% seventy-eight days after dislodgement. Note that the sharp decrease in return rates observed 90 days after dislodgement similarly affects the three experimental groups of dislodged snails, with a 2- to 3-fold decay in return rates (Fig. 5).

3.6. Motion behaviour of dislodged L. littorea

The number n_i of individually tagged *L. littorea* that were recaptured on the horizontal platform over our 8 successive low tide surveys was consistently high (i.e. 86 to 96%) for individuals originating from the low, intermediate and high tidal levels of the seawall, with n_1 , n_2 and n_3 ranging respectively between 47 and 44, 48 and 45, and 48 and 43. In contrast, the number *N* of individuals originating from the horizontal platform significantly decreased with time t ($r^2 = 0.99$, p < 0.01) from 50 to 38 as N = 51.5 - 1.7t. Note that in contrast to previous reports (Chapperon and Seuront, 2012), no individual was ever observed at the exact same location between two successive low tides, nor between any low tides over our 8-days survey. This resulted in an activity index of 1 for all the *L. littorea* considered in this work, irrespective of their habitat (platform or seawall) or tidal height.

The daily orientation angles α_i followed by *L. littorea* originating from the horizontal platform did not significantly differ between low tides (WW test, p > 0.05), and were consistently best fitted by a uniform distribution (U² test, p > 0.05; Fig. 6). In contrast, α_i followed by



Fig. 5. Percentage of *Littorina littorea* dislodged from (a) high, (b) intermediate and (c) low tidal levels of the Fort de l'Heurt that returned to low (black bars), intermediate (dark grey bars) and high (light grey bars) tidal levels.

L. littorea originating from the seawall were highly directional (Fig. 7) and consistently significantly diverged from a uniform distribution (U² test, p < 0.01), irrespective of the tidal height considered. The daily distances d_i did not significantly differ between successive low tides (KW test, p < 0.05), for both *L. littorea* originating from the horizontal platform (Fig. 6) and the seawall (Fig. 7). These distances ranged from 23 to 85 cm for *L. littorea* originating from the horizontal platform 16 to 212 cm for snails originating from the seawall. These figures resulted in daily displacement rates of 49 cm and 75 cm for *L. littorea* originating from the horizontal platform (Fig. 6H). In contrast, *L. littorea* individuals originating from the vertical wall were highly directional, and consistently travelled preferentially towards the seawall (Fig. 7H).

Significant differences were found in the daily distances d_i between the four groups of *L. littorea* (KW test, p < 0.05). The distances d_i did not significantly differ between the three groups of snails originating from the seawall (Tukey test, p > 0.05), and ranged between 0.6 and 2.1 metres. These distances were significantly greater (Tukey test, p < 0.05) than those travelled by snails originating from the horizontal platform (d_i ranged between 0.3 and 0.9 metres). No significant autocorrelation in d_i was found between successive low tides (p > 0.05).



Fig. 6. Locations of *L. littorea* originating from the horizontal platform, subsequently individually tagged (n = 50), released on the platform and resampled (n) daily during 8 successive low tides (a to h). At each date, the polygon joins the *N* snails that were found on the platform. The black scale bar represents 2 metres, and the grey bars the landward seawall of the Fort de l'Heurt. Note that the distribution of angles and distances shown in the final distribution (h) are the net orientation α_{net} and distance d_{net} .

Finally, the net distance d_{net} significantly differed between the four groups of snails (KW test, p < 0.05). Specifically, d_{net} did not significantly differ between individuals from different tidal heights (Tukey test, p > 0.05), and ranged from 7.1 to 11.8 metres. These distances were highly significantly greater (Tukey test, p < 0.01) than those observed for individuals originating from the horizontal platform, which ranged between 3 to 7 metres.

4. Discussion

This work investigated the return rates of *L. littorea* individuals over a 90-day period after they were manually dislodged from proximate horizontal and vertical habitats. Specifically, our results show that *L. littorea* exhibit both habitat selection and tidal height partitioning, as undisturbed, disturbed, translocated and transplanted individuals show a clear preference for both the habitat (*i.e.* horizontal or vertical surfaces) and the tidal level they originate from. In addition, the high frequency resampling of individually tagged dislodged *L. littorea* during the first 8 successive low tides of our survey indicates that individuals originating from the seawall consistently showed higher movement rates and directionality towards the seawall, while individuals originating from the platform showed no directionality and reduced migration rate. It is acknowledged that this study suffers from what may be seen as a complete lack of spatial replication. Our conclusions would



Fig. 7. Locations of *L. littorea* originating from the high tidal level of the seawall, subsequently individually tagged (n = 50), released on the horizontal platform and resampled (*N*) daily during 8 successive low tides (a to h). At each date, the polygon joins the *N* snails that were found on the platform. The black scale bar represents 2 metres, and the grey bars the landward seawall of the Fort de l'Heurt. Note that the distribution of angles and distance shown in the final distribution (h) are the net orientation α_{net} and distance d_{net} .

have undeniably been stronger through site replication (i.e. different locations with rock platforms and seawalls) and using 'site' as a random factor in subsequent analyses. This limitation is, however, intrinsically driven by the unique nature of our study site, i.e. a seawall located on an isolated intertidal reef, and the absence of similar structures in the region that could have been used to replicate our experiments and assessed *e.g.* how the observed differences among tidal levels compare to differences among sites, regardless they are (or not) at different levels.

4.1. Tidal height and habitat partitioning in L. littorea

A significant fraction (88-90%) of *L. littorea* individuals manually dislodged from three distinct tidal heights on a seawall, tagged and subsequently placed back to their original location remained in their tidal height over our 3-month survey (Fig. 3B). These results suggest a vertical partitioning of a *L. littorea* population as a function of tidal height. This hypothesis is further supported by (i) the low capture rate (0-6%) of control snails originating from the horizontal platform on the seawall, (ii) the relatively high return rates (54 to 58%) of experimental individuals dislodged from the seawall to their vertical substratum within 45 days (Fig. 4), and (iii) the fact that snails dislodged from a given tidal level on the seawall showed a clear tendency to return to that specific level (Fig. 5). The absence of mixing between undisturbed, disturbed and translocated snails of distinct tidal height over a 3-month

period, further suggests the temporal persistence of the observed pattern. This observation is consistent with previous work showing that L. saxatilis did not migrate out of their microhabitat, but if moved to another habitat they showed a tendency of returning to their intertidal zone (Erlandsson et al., 1998). Our results are also consistent with and generalised both to several tidal levels and to longer time scales previous work conducted on the high shore littorinid Littorina keenae that showed a high retention rate (92-100%) of marked control snails within $1m^2$ high-shore sites over a 3-week period (Miller et al., 2007). More generally, our results are consistent with previous studies showing (i) movement up the shore for a range of intertidal gastropod species transplanted lower on the shore during low tide periods (Evans, 1961: Bock and Johnson, 1967: Gendron, 1977: Thain et al., 1985: Erlandsson et al., 1998), (ii) the ability of L. littorea to navigate back towards their original habitat following dislodgment from a localised rocky substrate to the surrounding tidal flat (Chapperon and Seuront, 2009), and (iii) more directionality and higher movement rates in L. saxatilis released at an alien shore level (Erlandsson et al., 1998).

The distinct temporal decays observed in the recapture rates of undisturbed, disturbed and translocated *L. littorina* originating from the horizontal platform and the seawall (Table 1, Fig. 3) may be an indication of the different processes at play in the behaviour of *L. littorea* in distinct habitats.

The slower decay of recapture rates on the seawall of undisturbed, disturbed and translocated snails may indicate a stronger attachment of L. littorea to vertical surfaces, hence a lower risk of dislodgment. While this hypothesis is not consistent with the lack of significant differences observed in shell morphology and foot surfaces for snails sampled on the horizontal platform and the seawall three tidal heights, it is supported by preliminary results suggesting a stronger tenacity of L. littorea on vertical than horizontal surfaces (L. Seuront, unpublished data). This observation is consistent with previous work showing that periwinkles out of water for longer periods use a stronger mucus attachment, which may result in greater recapture rates for snails, which are out of the water for longer periods (Smith and Morin, 2002). This observation also indicates that beyond the expression of traits that increase dislodgement resistance on exposed shores (e.g. longer, broader feet and greater tenacity; see Miller, 1974; Etter, 1988; Trussell et al., 1993; Trussell, 1997a, 1997b; Parsons, 1997a, 1997b), intertidal snails may also tend to express habitat-specific traits that modulate attachment strength depending on the horizontal or vertical nature of their substratum, but also on their tidal height.

Alternatively, the tidal height partitioning observed in L. littorea on the seawall suggests that snails attached to the seawall are likely to be spatially constrained in their movement by the limited size of their habitat. This hypothesis is consistent with both the high recapture rates over our 3-month survey and the slow decrease in the recapture rate of undisturbed, disturbed and translocated snails with time (typically between 100 and 88%), which indicates a persistent presence of L. littorea on the seawall. This is not the case, however, on the horizontal platform where movements are not limited spatially (i.e. horizontally). It is then likely that the stronger logarithmic decay of the recapture rate of undisturbed, disturbed and translocated snails on the horizontal platform (Fig. 3A) reflects faster movement rates of L. littorea on the horizontal platform than on the seawall. The exponential decay observed in the recapture rate of seawall snails transplanted on the horizontal platform (Fig. 3D) indicate, in turn, a faster diffusion via a directed movement towards the seawall. This observation is consistent with the behavioural observations conducted during 8 successive low tides on individually tagged individuals originating from the horizontal platform (Fig. 6) and the seawall (Fig. 7), which showed higher movement rates and directionality towards the seawall in the latter, and no directionality and lower movement rates in the former. Note that these behavioural observations are also consistent with both theoretical and experimental studies showing faster movement rates in directed diffusion than in pure diffusion; see e.g.Berg (1993) and Viswanathan

et al. (2011).

Finally, it is stressed that one may argue that because there is no horizontal habitat on the mid- to high-shore levels, the nature of the study does not allow disentangling whether the snails are selecting a shore-level or a habitat. However, this contradicts (i) the lack of difference between the recapture rates of control transplanted snails (i.e. snails sampled from a flat section of the reef located 1.5 meters above the horizontal platform, tagged and released on the horizontal platform at high tide) and the return rates of control, disturbed, transplanted and translocated snails (Fig. 3A, Table 1) and (ii) the fact that control transplanted snails did not show any tendency to climb the seawall. These results indicate that the return rates observed on the seawall were driven by an actual preference for the seawall rather than by a tidal level preference. This more generally suggests that dislodged L. littorea may be more prone to navigate back to their initial habitat (i.e. a vertical or a horizontal substrate) than their initial tidal height in an alien habitat. Tidal height partitioning may also be habitat-specific and/or occur on shorter time scales on vertical substrates that on horizontal ones as suggested by the widely reported ontogenetic and seasonal preferences in shore height (Underwood, 1977, 1979; Gendron, 1977; Hamilton, 1978; Petraitis, 1982; Takada, 1996; Warner, 2001; Bishop et al., 2007). Further work is, however, needed to disentangle what may be a complex relationship between habitat and tidal level in the ecology of intertidal gastropods through e.g. the translocation of snails from different tidal levels of a vertical wall to a 'horizontal' reef offering the same range of tidal height.

4.2. On the horizontal navigational abilities of L. littorea

More fundamentally, our results indicate that L. littorea dislodged from a seawall have the ability to navigate back to that surface, and subsequently to return to their original vertical position. These observations are consistent with previous work on L. littorea short-term migratory behaviour (Gendron, 1977) and imply that these snails can determine their relative position on the shore, and orient in the direction of their preferred habitat. This implies that L. littorea use a variety of directional cues to accomplish such directed movements. Numerous directional cues have been found in intertidal snails, including phototaxis (Charles, 1961; Evans, 1961; Warburton, 1973; Petraitis, 1982; Thain et al., 1985), geotaxis (Evans, 1961; Petraitis, 1982; Thain et al., 1985), chemotaxis towards both water-borne and air-born infochemicals from food sources and conspecifics (Fratini et al., 2001; Shearer and Atkinson, 2001; Fink et al., 2006; Chapperon and Seuront, 2009; Seuront and Spilmont, 2015), and rheotaxis, i.e. a movement either towards or away from the stimulus induced by a flow (Overholser, 1964; Neale, 1965; Crisp, 1969; Duch, 1971; Gendron, 1977).

Specifically, the horizontal platform where dislodged snails were released does not exhibit a significant slope towards the seawall, suggesting that navigation towards the seawall cannot be driven by geotaxis. Navigation towards the seawall may, however, be driven by phototaxis as littorinids have image-forming eyes with relatively greater resolving capabilities than many other molluscs (Newell, 1965; Seyer, 1992; Land and Nilsson, 2002), which may allow them to pick out the silhouette of the 10 metre high landward side of the Fort de l'Heurt rising above them. This hypothesis is consistent with empirical results conducted on a range of intertidal gastropods (including littorinids) showing oriented responses to plastic black walls in Gibbula umbilicalis (Thain et al., 1985), to shore-line topographic features and nocturnal silhouettes of vegetation in Littorina punctata (Evans, 1961), Nerita textilis (Chelazzi and Vannini, 1976) and N. atramentosa (L. Seuront, unpublished data) and to large areas of vegetation and individual plant stems in Littorina irrorata (Hamilton, 1977, 1978) and Littoraria scabra (Seuront, unpublished data). Note that these responses contrast with the oriented responses to the light (i.e. positive phototaxis) of the sun in L. littorea (Newell, 1958a, 1958b), L. punctata (Evans, 1961) and *Nerita plicata* (Warburton, 1973) and unidentified celestial objects in *Aplysia brasiliana* (Hamilton and Russell, 1982). As such if the navigation of *L. littorina* towards the Fort de l'Heurt relies on visual cues, the processes involved are *sensu stricto* more likely to be related to positive scototaxis (i.e. a movement towards dark targets; Alverdes, 1930) than negative phototaxis (i.e. a movement in the direction of decreasing light intensity). Though little is still know on the role of scototaxis in the development of complex oriented behaviour in intertidal gastropods, scototaxis has been shown to involve several derived behaviour in arthropod orientation behaviour (Lehrer, 1997) including perigrammotaxis (orientation towards contrasting edges), photohorotaxis (a tendendy to follow continuous contrasting edges) and hypsotaxis (attraction to the highest outline at the horizon) that may all be relevant to gastropods.

The infochemicals present on the seawall may also differ from those on the horizontal platform due to clear faunistic differences between the two habitats, hence generate a concentration gradient that snails can navigate to. In particular, the abundance of the blue mussel *Mytilus edulis* was significantly higher on the horizontal platform $(6,225 \pm 1,050 \text{ ind m}^{-2})$ than on the seawall $(4,050 \pm 725 \text{ ind m}^{-2})$, and both annelids and nematods reached densities that are up to 1 to 2 orders of magnitude greater on the platform than on the seawall (C. Hennion, unpublished data). Note that the infochemicals related to the presence of conspecific and epilithic biofilm can act synergistically in *L. littorea* horizontal migration (Chapperon and Seuront, 2009). The resolution of this specific issue warrants further work, as we did not attempt to assess the nature of the distribution (i.e. uniform vs. patchy), the concentration nor the specific composition of the epilithic biofilm present on the horizontal platform and the seawall.

The landward side of the Fort de l'Heurt lies in the wake of the main SSW swell direction that characterizes this area. As such, infochemicals are likely spread away from the rock through odour plumes (Zimmer and Butman, 2000) heading landward during incoming tide, hence creating a gradient of concentration towards the seawall. The potential turbulence dampening effect of the Fort de l'Heurt may also induce a rheotatic response in L. littorea as several species of gastropod have long been known to respond to unidirectional currents (e.g. Overholser, 1964; Neale, 1965; Crisp, 1969; Duch, 1971; Rochette et al., 1997). In addition, the presence of chemical cues have been shown to trigger and enhance positive rheotaxis (Seuffert and Martin, 2012), suggesting that odour cues from the seawall and the current pattern characterizing our study site may act synergistically in L. littorea navigation. Even in high Reynolds number flow, where diffusive odour gradients are eroded if not destroyed, a behavioural strategy referred to as odour-gated rheotaxis (Vickers, 2000; Weissburg, 2000) still allows an organism to find attractive odour sources. This strategy is particularly efficient for slow moving organisms, hence L. littorea, that follow relatively straight paths towards an odour source even in fast turbulent flows (Webster and Weissburg, 2009; Ferner and Weissburg, 2005). Specifically, a slower pace allows a temporally integrated chemosensation (typically through the klinotactic behaviour — i.e. a movement either towards or away from the stimulus induced by a physical contact - exhibited by gastropod in response to a source of stimulation; Audesirk and Audesirk, 1985; Chelazzi, 1990) that in turn might lead to some measurement of average odour concentrations, possibly creating circumstances when the animals could follow the time-averaged chemical gradients found in odour plumes (Ferner and Weissburg, 2005; Wilson and Weissburg, 2012; Wyeth and Willows, 2006; Wyeth et al., 2006). Further work is, however, needed to quantify the nature of the flow at our study site under various tide and swell conditions to infer the potential role of flow in L. littorea navigation.

4.3. On the vertical navigational abilities of L. littorea

Once they reached the seawall, *L. littorea* showed a clear preference for their original tidal level (Fig. 5). While this observation may suggest

a negative geotactic response of L. littorea on vertical surfaces, it contradicts the results of our control transplantation experiments where snails from a flat section of the reef located 1.5 meters above the horizontal platform did not show any tendency to climb the seawall. The observed vertical partitioning (Fig. 3B) instead suggests that individuals migrating upward know when to stop once they reached their initial habitat. Each tidal level may then be characterized by specific airborne and/or waterborne infochemicals that L. littorea use in their navigation (Seuront and Spilmont, 2015). The three tidal levels considered in this work are also intrinsically characterized by different hydrostatic pressures at high tide. L. littorea may then use changes in hydrostatic pressure to adjust their vertical position on the seawall. This ability has been suggested to help L. littorea to navigate up and down the shore using the maximum and minimum pressures associated with shoreward and seaward currents, respectively (Gendron, 1977). However, to our knowledge, no evidence exists for this behaviour in either L. littorea, littorinids, or more generally in prosobranchs. Finally, as littorinids typically show some seasonality in their preferred shore height (Gendron, 1977; Hamilton, 1978; Petraitis, 1982; Warner, 2001), further work is needed to generalised the observed tidal height preference through the consideration of (i) the potential seasonal vertical migration of L. littorea on the studied seawall, and (ii) the seasonal fluctuations in the abundance and diversity of the fauna and flora characterizing each tidal level as they are likely to drive the nature and quantity of infochemicals available to navigation.

5. Conclusion

These results suggests that at relatively short time scales (i.e. days to months), L. littorea show both tidal height and habitat partitioning that is distinct from the range of movement patterns previously reported in littorinids over a range of temporal scales such as (i) ontogenetic migration (Underwood, 1977, 1979; Takada, 1996; Bishop et al., 2007), (ii) seasonality in preferred shore height (Gendron, 1977; Hamilton, 1978; Petraitis, 1982; Warner, 2001), (iii) migration to preferred shore height following dislodgment or transplantation (Evans, 1961; Bock and Johnson, 1967; Gendron, 1977; Thain et al., 1985; Miller et al., 2007), eventually in relation to different ecotypes (Rolán-Alvarez et al., 1997; Erlandsson et al., 1998), (iv) navigation back to a preferred resting site (Chapperon and Seuront, 2009), and (v) daily displacement rates related to tidal height, surface topography and food distribution of microhabitats, prey availability and shelter, and trail-following (Fairweather, 1988; Underwood and Chapman, 1989, 1992; Chapman, 1998, 2000a, 2000b; Byers, 2000; Chapman and Underwood, 1994a, 1994b; Seuront et al., 2007; Chapperon and Seuront, 2012). Additional factors such as parasitism are also known to affect the short-term movements of littorinids through either movements higher on the shore depending on the parasite present (Curtis, 1987; McCarthy et al., 2000) or reduced movement (Williams and Ellis, 1975; Miller and Poulin, 2001; O'Dwyer et al., 2014). Note, however, that this is unlikely to have affected our results as preliminary work conducted on our study site showed that L. littorea did not exhibit either patent or non-patent parasitic infections, as no swimming cercariae were found in 100-ml seawater jars that held individual snails overnight and no parasites were microscopically observed in dissected visceral mass tissue (Seuront and Spilmont, 2015). The potential effect of parasitism on L. littorea movements nevertheless remains an issue that needs to be considered with caution in any behavioural study of this species.

More fundamentally, our results unambiguously show that *L. littorea* has a strong ability to navigate back to their original habitat and tidal height following dislodgment. It is nevertheless stressed that despite decades of investigations of littorinid sensory abilities little is still known on the actual mechanisms involved, which is in deep contrast with the state of knowledge related to the sensory ecology of other invertebrates, especially crustaceans (Vickers, 2000; Webster and Weissburg 2001; Ferner and Weissburg, 2005; Wyeth and Willows,

2006; Wyeth et al., 2006; Wilson and Weissburg, 2012). The relative paucity of information available on the mechanisms driving littorinid navigation in the literature and the strong evidence provided in this work of the ability of *L. litorrea* to navigate back to a preferred habitat and/or tidal height warrants further work to decipher the relative contribution of various cues and the related taxes to the field of littorinid sensory ecology. Our journey to understand intertidal ecosystems through the lens of gastropod chemical ecology may hence still be in its infancy.

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