

Temporal shifts in motion behaviour and habitat use in an intertidal gastropod

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*Animal movements in heterogeneous environments shape most ecological processes from individuals to ecosystems. The identification of the processes underlying animal movements thus has critical implications in a wide range of fields. Changes in the motion behaviour of free-ranging species have mainly been reported across different spatial scales but have been less investigated over time. Here the processes potentially triggering temporal changes in movement, microhabitat occupation and distribution patterns of the intertidal herbivorous gastropod *Nerita atramentosa* were examined on a south Australian rocky shore during 8 successive daytime low tides considered in four different months. The observed temporal shift in microhabitat occupation and aggregation behaviour was likely an adaptation to both abiotic and biotic stressors such as temperature and food distribution. In contrast, the temporal changes observed in *N. atramentosa* motion behaviour are consistent with optimal foraging strategies driven by the presumed variability in both microalgal density and distribution. Individuals seemed to switch from an extensive foraging strategy in February and May to an intensive strategy in August and October. Specifically, *N. atramentosa* seemed to adopt two different foraging strategies, a Lévy-like foraging strategy in May and a ballistic foraging strategy in February when the resources are expected to be respectively non-depleted and depleted. The Brownian foraging strategy theoretically expected under high food density conditions was however not observed. The potential role of the behavioural flexibility observed in *N. atramentosa* motion behaviour is discussed in relation to the persistence of this species under disrupted environmental conditions.*

Keywords: motion, foraging behaviour, Lévy flight, distribution, herbivorous snails, intertidal environment

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INTRODUCTION

Movements in heterogeneous environments structure many ecological processes ranging from the organism to the ecosystem levels (Bowler & Benton, 2005; Nathan *et al.*, 2008). In particular, understanding the movements of organisms provides insight into the mechanistic links between behaviour and physiology (Matthews & Rodewald, 2010), environment (Barahona & Navarrette, 2010) and biological interactions between trophic levels (Rochette & Dill, 2000). Therefore, the comprehension of the determinism of movements across a range of spatial and temporal scales may critically advance fields such as behavioural ecology (Owen-Smith *et al.*, 2010), population dynamics (Morales *et al.*, 2010), conservation biogeography and biodiversity (Franklin, 2010; Agudo *et al.*, 2011), and climate change (Feder *et al.*, 2010; Franklin, 2010). However, empirical data on individual displacements are still required to reach a complete understanding of what factors and processes lead to the observed dispersion and distribution patterns (Buchanan, 2008; Humphries *et al.*, 2010; Viswanathan, 2010). Ultimately, this information is fundamental to generate dynamic models of movements such as

the recently developed space–state models that incorporate both the organism behaviour and environmental variables (see Patterson *et al.* (2008) for a review).

Animals primarily move to find food and mates while avoiding predators in order to maintain individual fitness and potentially ensure the persistence of populations in changing environments (Bowler & Benton, 2005). Organisms thus exhibit innate and acquired motion behavioural strategies to optimize the search for resources (Owen-Smith *et al.*, 2010; Chapperon & Seuront, 2011a), mates (Shane, 2001) and refuges from environmental (e.g. thermal stress; Dubois *et al.*, 2009; Chapperon & Seuront, 2011b, c) and biological constraints (e.g. predation: Orrock *et al.*, 2010). Specifically, the optimal foraging strategies adopted by a range of terrestrial and aquatic herbivores to maximize resource intake while minimizing energy expenditure (Pyke, 1984; Williams & Little, 2007) are intrinsically defined by: (i) their ability to detect the resources and to move accordingly (Nathan *et al.*, 2008); and (ii) the spatial distribution of primary producers as well as both their quality and quantity (Owen-Smith *et al.*, 2010). Besides, other constraints such as the presence of predators and desiccation stress potentially generate trade-offs between the different fitness components of herbivores (Jones & Boulding, 1999; Schmitz *et al.*, 2008). Behavioural changes in the displacements and distribution of individual organisms may thus be required to adapt to new environmental conditions while ensuring basic needs. Movements

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in spatially structured habitats, especially in the intertidal, are determined by the interaction of multiple abiotic (e.g. habitat complexity: Coffin *et al.*, 2008), biotic (e.g. food: Seuront *et al.*, 2007) and intrinsic factors (e.g. reproductive status: Pardo & Johnson, 2006). The displacements of intertidal organisms are therefore highly variable in space and time as they result from the behavioural responses of organisms to the space–time heterogeneity of the surrounding environment (Chapman, 2000a; Patterson *et al.*, 2008). This specifically implies that intertidal invertebrates must have enough flexibility in their motion behaviour to adjust their movements and their distributions over different spatial (i.e. microhabitats to habitats) and temporal scales (i.e. minutes to seasons). Recent studies have focused upon the changes in the statistical properties of animal motion behaviour as a response to complex landscapes (Sims *et al.*, 2008) and food density (Humphries *et al.*, 2010) over a wide range of spatial scales. Temporal changes in the statistical properties of animal displacements are, however, still poorly investigated. In this context, this study aimed to: (i) quantify the temporal variability in the displacements and the distribution of the gastropod *Nerita atramentosa* on a south Australian temperate rocky shore over four distinct study periods, i.e. May (autumn), August (winter) and October (spring) 2009, and in February 2010 (summer); (ii) identify what environmental and/or biotic factors potentially drove the observed patterns; and (iii) examine the extent of snail motion behavioural flexibility. This work has been motivated by previous evidence that the motion behaviour of a range of animals is primarily constrained by the distribution and abundance of their resource (e.g. Seuront *et al.*, 2007; Seuront & Vincent, 2008; Sims *et al.*, 2008; Humphries *et al.*, 2010), and the assumption that microalgae in south Australian rocky shores distribute and abound similarly to other studied temperate rocky shores, where resources are more abundant at low shore levels than at high

shore levels and during winter months than during summer months (Underwood, 1984; Thompson *et al.*, 2004; Jackson *et al.*, 2010). We consequently expected to observe: (i) Brownian movements when the food is likely to be the most abundant (i.e. August); (ii) ballistic movements when the food is depleted (i.e. summer); (iii) Lévy-like movements when the food is anticipated to be scarce but non-depleted (i.e. May and October); and (iv) seaward movements especially when the food abundance is predicted to be low (i.e. summer).

MATERIALS AND METHODS

Field site and species studied

The displacements and the distribution patterns of 240 *Nerita atramentosa* individuals (Reeve, 1855) were monitored on a temperate intertidal rocky shore in Marino Rocks (South Australia, Australia) during morning and midday low tides (i.e. 9 am to 2 pm) at four different periods of the year in May (autumn), August (winter) and October (spring) 2009, and in February 2010 (summer). Seawater and air temperature data during the monitored periods are summarized in Table 1. The study site was located at the upper bound of the intertidal zone of a moderately exposed boulder field (35°2'38.04"S–138°30'30.13"E) characterized by a variety of microhabitats such as pools and crevices. The rocks of the study site were consistently nearly bare all over the year although macroalgae such as *Ulva* sp. were occasionally observed. This site was chosen due to the presence of herbivorous gastropods such as *Bembicium* sp., *Nodilittorina* sp. and the predominance of the Neritidae *N. atramentosa*. The studied species is a superior competitor for microalgae on intertidal rocky shores (Underwood, 1984), active when immersed and show aggregative tendencies at low tide throughout the year (Underwood, 1976).

Table 1. Snail body size, meteorological data and metrics used to quantify the motion behaviour of *Nerita atramentosa* in four different periods in 2009–2010. Values are means. Circular statistics run in ORIANA version 3 (RockWare Inc., 2010, CO USA) were used to calculate mean angles and standard deviation of the mean (Zar, 2010). Minimum and maximum values are also provided for meteorological data (AT, air temperature; WT, sea water temperature). d_i and θ_i are the daily distances displaced and the orientation angles taken between successive daytime low tides. The skewness (g_1) and the kurtosis (g_2) of the distributions of daily distances displaced d_i are also indicated. All d_i and θ_i values were pooled at each study period. Meteorological data source: Bureau of Meteorology of Australia (Port Stanvac).

		May 2009	August 2009	October 2009	February 2010
Length (cm)	Mean	21	21.61	21.13	17.92
Height (cm)	Mean	13.95	14.66	14.57	14.49
AT (°C)	Mean	11.53	14.59	17.72	21.79
	N	48	240	240	216
	Minimum	4.9	10.9	11	15.5
WT (°C)	Maximum	18.4	20.7	29.4	31.2
	Mean	18.73	14.55	16.06	23.01
	N	216	240	240	216
	Minimum	18.3	14.2	15.3	22.6
	Maximum	19.6	14.9	18.1	23.6
	Mean	162.03	114.21	131.56	172.46
d_i (cm/day)	N	360	204	100	166
	Minimum	1	3	1	2
	Maximum	1055.46	415.21	376.016	490
	g_1	1.98	1.078	0.277	0.588
	g_2	5.125	0.714	−1.32	−0.396
	Mean	91.58	95.28	87.88	109.71
θ_i (°)	N	271	94	43	90
	Min	0.55	4.39	1.71×10^{-6}	1.21×10^{-6}
	Max	180	180	180	180

Snail collection, tagging and release

For each study period, 60 adult individuals were randomly collected during the low tide using a random number table. The size (i.e. shell length and height) of each individual was measured using a calliper and the mean individual size was calculated for each study period (Table 1). Individuals were tagged with glue-on shellfish tags (8 × 4 mm, Hallprint, Hallprint Pty Ltd, Hindmarsh, South Australia). Tagging has previously been shown not to affect the motion behaviour of gastropods (e.g. Chapman, 2000b; Henry & Jarne 2007; Seuront *et al.*, 2007). Each individual was subsequently randomly placed within a 25 × 25 cm area surrounding a release point situated on the top of the centre of a flat boulder (90 × 40 × 40 cm). Note that all the individuals used in the present work were collected from flat rocks on the studied boulder field to minimize the behavioural impact of the dislodgement and relocation on the release site. Marked snails were left undisturbed from the release day. The distribution and the displacements of each individual were recorded during the 8 subsequent daytime low tides. Whilst many littoral herbivorous molluscs can remain active during emersion when the rocks are damp (e.g. Little, 1989), all *N. atramentosa* individuals were immobile during the monitored low tides. Note that the relative uniformity of boulder size on the release site ensures that snail displacements were not constrained by topographic complexity.

Distribution of *N. atramentosa*: microhabitat occupation and status

Microhabitat distribution and individual status (i.e. aggregated versus solitary) of *N. atramentosa* was assessed at each low tide. Microhabitats were classified into 4 categories: flat rock, crevice, rock bottom and pool (Table 2). An individual was considered aggregated when there was a direct shell contact with the shell of at least another conspecific (Chappon & Seuront, 2011b).

Activity, dispersion and motion behaviour of *N. atramentosa*

ACTIVITY INDEX

An individual was defined as active when a change in position between two successive daytime low tides was detected. An activity index was calculated as:

$$N_i/N \times 100 \tag{1}$$

where N_i is the total number of mobile individuals between two successive daytime low tides and N is the total number of recorded individuals. Some individuals were, however, found at the exact same location between successive daytime low tides. Since individuals were monitored at daytime low tide, it was impossible to determine whether the lack of movement corresponded to a lack of activity during the high tide or an indication of homing behaviour. However, we never observed any sign of homing behaviour in *N. atramentosa* during our field observations, which to our knowledge has also not been reported in the literature. As a consequence, an individual located at the exact same location over consecutive daytime low tides was considered as a lack of activity throughout this work.

FORAGING BEHAVIOUR

Nerita atramentosa individual displacements were monitored by measuring the orientation angle θ and the distance displaced d , i.e. the angle and distance displaced by each individual from the release point to the monitored snail position at each daytime low tide. The orientation angle θ was estimated from the release point using the magnetic North as a reference. The distance displaced d was measured by a plastic tape measure laid down the substratum topography from the release point to the snail's position. The x and y coordinates were estimated from the distance displaced d and orientation angle θ as:

$$\begin{cases} x = d \times \cos \theta \\ y = d \times \sin \theta \end{cases} \tag{2}$$

The daily orientation angle θ_i was defined as the angle taken by an individual between two successive daytime low tides and was calculated as:

$$\theta_i = 180 - [(180/\pi)] \times \theta_e \tag{3}$$

with θ_e defined as:

$$\theta_e = \arccos \left[\frac{(p_1 p_2)^2 + (p_2 p_3)^2 - (p_1 p_3)^2}{2(p_1 p_2)(p_2 p_3)} \right] \tag{4}$$

where $(p_1 p_2)$, $(p_1 p_3)$ and $(p_2 p_3)$ are respectively the distances between the positions p_1 and p_2 , p_1 and p_3 , and p_2 and p_3 (Jerde & Visscher, 2005). Likewise, the daily distance displaced d_i was defined as the distance displaced by an individual between two successive daytime low tides and was

Table 2. Definitions and roles of the four microhabitats considered in this study.

Microhabitat	Definition	Role
Flat rock	Smooth surface	Direct exposure to local environmental conditions (e.g. solar radiations, breaking waves) and predation
Crevice	Dry depression deep and wide enough to fit at least one individual from small cracks, pits and fissures to wider depressions	Shelter from local environmental conditions and predation
Rock bottom	Bottom of a rock, i.e. substrate underneath a rock to which individuals attached and underside of a rock from which individuals hung	Shelter from local environmental conditions and predation
Pool	Deep depression (a few cm up to 70–80 cm) filled with water during emersion	Reduction of desiccation and thermal stresses Potential activation of feeding activities

calculated as:

$$d_i = \sqrt{(x_{t+1} - x_t)^2 + (y_{t+1} - y_t)^2} \quad (5)$$

Finally, as intermittent motion behaviour has recently been identified in another species of intertidal snail, *Littorina littorea* (Seuront *et al.*, 2007), the potential intermittency arising in the displacements of *N. atramentosa* (i.e. a few very large displacements over a wide range of small displacements) was investigated by comparing the probability density function $P(d_i)$ of the daily distance displaced d_i to a power-law distribution of the form:

$$P(d_i) = kd_i^{-\mu} \quad (6)$$

where μ is the slope of the log-log plot of $P(d_i)$ versus d_i , and k is a constant. When $1 < \mu \leq 3$, the displacements comprise many small steps connected by longer relocations that characterize Lévy processes; in the special case $\mu = 2$, the movements correspond to a Lévy flight that has been identified in the movement behaviour of a range of organisms ranging from invertebrates to large fish, birds and mammals (e.g. Mårell *et al.*, 2002; Bartumeus *et al.*, 2003; Seuront *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010), and considered to be an optimal foraging strategy in places where preys are scarce and randomly distributed (Viswanathan *et al.*, 1999). When $\mu = 1$, the displacements are ballistic (i.e. nearly linear displacements), and values $\mu \leq 1$ correspond to probability distribution that cannot be normalized. In contrast, when $\mu \geq 3$, the distribution of daily distance displaced is Gaussian and the movement is equivalent to a Brownian motion (i.e. normally distributed successive displacements occurring in random directions); see Seuront (2010) and Viswanathan *et al.* (2011) for more details. More generally, the smaller the exponent μ , the more intermittent is the distribution of the distances d_i . Because an objective criterion is needed to decide upon an appropriate range of values of the daily distances d_i to include in the regression analysis, we used the values of d_i which satisfied two statistically sound criteria. First, a regression window of a varying width that ranges from a minimum of 5 data points to the entire data set was considered. The smallest window was slid along the entire data set at the smallest available increments, with the whole procedure iterated ($n-4$) times, where n is the total number of available data points. Within each window and for each width, the coefficient of determination (r^2) and the sum of the squared residuals for the regression were estimated. Note that parametric regression analysis was used throughout this work instead of non-parametric regression analysis because the residuals were consistently normally distributed (Zar, 2010). The values of d_i (Equation 6), which maximized the coefficient of determination and minimized the total sum of the squared residuals, a procedure referred to as the R^2 -SSR criterion (Seuront *et al.*, 2004), were subsequently used to define the scaling range and to estimate the exponent μ .

DISPERSION

The ability of *N. atramentosa* individuals to disperse from a release point was investigated using the net travel angle and the net distance travelled, i.e. orientation angle and distance

displaced between the release point and the last monitored low tide position for each snail.

Statistical analyses

As some individuals were not retrieved between two consecutive daytime low tides, daily distances and daily orientation angles were monitored for a minimum of 3 successive days since a minimum of three coordinates are required to calculate them. Note that this has been done to avoid any bias stemming from the use of observations conducted at different scales; see e.g. Seuront (2010). Since the data were not normally distributed (Kolmogorov–Smirnov test, $P < 0.05$), the Kruskal–Wallis test (KW test hereafter) was run to analyse the temporal variations in individual distribution (aggregation and microhabitat occupation) and displacements (net distance displaced, daily distance displaced d_i). A multiple comparison procedure based on the Tukey test was subsequently used to identify distinct groups of measurements (Zar, 2010). In addition, the non-parametric Watson's U^2 test was used to test for temporal differences in the net orientation angles and the daily orientation angles θ_i .

While a range of goodness of fit procedures exists in the literature to evaluate which distribution best fits experimental data (e.g. Edwards *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010), we followed Turchin's procedure (Turchin, 1998) to assess the quantitative nature of *N. atramentosa* daily displacement. Specifically, the distributions of daily orientation angles θ_i and net orientation angles were compared to a von Mises distribution using the Watson's U^2 test, to a normal distribution using the Kolmogorov–Smirnov test (Zar, 2010) and to a uniform distribution by using both tests.

The distributions of daily distances displaced d_i were tested for uniformity with the Kolmogorov–Smirnov test. 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). All statistical analyses were run in PASW Statistics 18 (SPSS Inc., 2009, IL USA) and ORIANA version 3 (RockWare Inc., 2010, CO USA).

RESULTS

Temporal variability in *N. atramentosa* distribution pattern

AGGREGATION BEHAVIOUR (TABLE 3; FIGURE 1A)

The proportions of aggregation were significantly different between the study periods. In particular, the proportions of aggregation in May and August were significantly lower than in October and February. No significant difference was found between August and May, neither between October and February. Individuals aggregated more frequently within crevices in May (69%) and August (67%) and in pools in October and February (63% of aggregates).

MICROHABITAT OCCUPATION (TABLE 3; FIGURE 1B)

No significant difference in the proportions of individuals found under rocks was detectable between the four study periods. In contrast, significant temporal differences were

Table 3. Kruskal–Wallis test and subsequent multiple comparisons (*post-hoc* based on the Tukey test) to investigate the temporal variation (M, May 2009; A, August 2009; O, October 2009; F, February 2010) in the parameters used to quantify *Nerita atramentosa* distribution and movement patterns between the four microhabitats. Results of the tests are indicated in the last column (NS, non-significant).

Parameters		df	χ^2	P	Post-hoc
Distribution patterns	Aggregation	3	26.745	<0.001	M = A < O = F
	Under rock occupation	3	0.674	0.879	NS
	Crevice occupation	3	92.108	<0.001	M > A > O = F
	Pool occupation	3	107.568	<0.001	M < A < F = O
	Flat rock occupation	3	83.339	<0.001	M = A > O = F
Movement patterns	Net distance displaced	3	54.725	<0.001	A = O < M = F
	Daily distance displaced d_i	3	23.306	<0.001	M = A = O < F

found in the proportions of individuals occupying crevices, pools and flat rocks. More specifically, the proportions of individuals occupying crevices were significantly higher in May than in the other periods. Similarly, higher percentages of organisms were distributed in crevices in August than in October and February. In contrast, the percentages of individuals in pools were significantly greater in February and October than in the two others periods. Likewise, individuals were significantly more frequently observed in pools in August than in May. No significant difference in the percentages of occupation of crevices and pools was found between October and February. Finally, the proportions of individuals resting on flat rocks were significantly lower in February and October, than in August and May. No significant difference in the percentages of individuals on flat rocks was found between May and August and, October and February.

Temporal variability in *N. atramentosa* dispersion and foraging behaviour

ACTIVITY INDEX

In total, 99%, 91% and 45% of individuals were respectively active in May and August, February, and October. The proportions of missing data due to unobserved individuals were higher in the warm months (56% in February, and 41% October) than in the cooler months (32% in August, and 18% in May).

DISPERSION (FIGURE 2)

Net orientation angles θ were $267.56^\circ \pm 3.40^\circ$ ($\bar{x} \pm SE$), $231.64^\circ \pm 13.44^\circ$, $216.75^\circ \pm 21.05^\circ$ and $208.04^\circ \pm 16.89^\circ$ in May, February, August and October, respectively. They were significantly higher in May than in the three others study periods ($U_{May-Febr}^2 = 0.248$, $P < 0.05$; $U_{May-Aug}^2 = 0.817$, $P < 0.001$; $U_{May-Oct}^2 = 0.849$, $P < 0.001$). No significant difference was, however, obtained between February, August and October ($U_{Feb-Aug}^2 = 0.052$, $P > 0.05$; $U_{Feb-Oct}^2 = 0.128$, $P > 0.1$; $U_{Aug-Oct}^2 = 0.142$, $P > 0.05$). Net orientation angles distributions were not significantly uniformly distributed ($U_{May}^2 = 2.414$, $P < 0.005$; $U_{Aug}^2 = 0.271$, $P < 0.01$; $U_{Oct}^2 = 0.489$, $P < 0.005$; $U_{Feb}^2 = 0.396$, $P < 0.005$).

The net distance displaced (d) by *N. atramentosa* individuals was greater in May (621.50 ± 45.85 cm, $\bar{x} \pm SE$), than in February (474 ± 51.37 cm), October (263.41 ± 12.74 cm) and August (201.58 ± 21.58 cm). Significant differences in the net distance displaced were found ($P < 0.001$: Table 3). In particular, the net distances displaced were significantly greater in February and May than in August and October

($Q_{Feb-Aug} = 3.946 > Q_{0.05,4}$, $Q_{0.05,4} = 2.639$; $Q_{Feb-Oct} = 3.044 > Q_{0.05,4}$; $Q_{May-Aug} = 6.446 > Q_{0.05,4}$; $Q_{May-Oct} = 5.580 > Q_{0.05,4}$). No significant difference in the net distances displaced was observed between February and May ($Q = 0.628 < Q_{0.05,4}$), and August and October ($Q = 1.494 < Q_{0.05,4}$).

FORAGING BEHAVIOUR

The daily orientation angles θ_i (Table 1) taken by individuals between two successive daytime low tides did not significantly differ between study periods ($U_{May-Aug}^2 = 0.057$, $P > 0.5$; $U_{May-Oct}^2 = 0.135$, $0.2 > P > 0.1$; $U_{May-Feb}^2 = 0.161$, $0.1 > P > 0.05$; $U_{Aug-Oct}^2 = 0.147$, $0.2 > P > 0.1$; $U_{Aug-Feb}^2 = 0.14$, $0.2 > P > 0.1$; $U_{Oct-Feb}^2 = 0.175$, $0.1 > P > 0.05$). More specifically, whatever the study period, the distributions of daily orientation angles θ_i did not fit a von Mises distribution ($U_{May}^2 = 0.619$, $P < 0.005$; $U_{Aug}^2 = 0.277$, $P < 0.005$; $U_{Oct}^2 = 0.095$, $P < 0.05$; $U_{Feb}^2 = 0.317$, $P < 0.005$). Distributions were best fitted by a uniform distribution in May ($Z = 0.785$, $P = 0.569$), August ($Z = 0.796$, $P = 0.550$) and October ($Z = 1.006$, $P = 0.264$) and by a Normal distribution in February ($Z = 1.328$, $P = 0.059$).

Significant differences in the daily distances displaced d_i between successive daytime low tides were observed between the different study periods (Table 3). Specifically, organisms moved over greater distances in February than at the three others periods ($Q_{Feb-May} = 3.422 > Q_{0.05,4}$; $Q_{Feb-Aug} = 4.525 > Q_{0.05,4}$; $Q_{Feb-Oct} = 3.550 > Q_{0.05,4}$). No significant differences in d_i were found between the three others periods ($Q_{May-Aug} = 1.735 < Q_{0.05,4}$; $Q_{May-Oct} = 1.136 < Q_{0.05,4}$; $Q_{Oct-Aug} = 0.193 < Q_{0.05,4}$).

The daily distances d_i were not normally distributed ($Z_{May} = 3.435$, $P < 0.001$; $Z_{Aug} = 1.868$, $P = 0.002$; $Z_{Oct} = 1.856$, $P = 0.002$; $Z_{Feb} = 1.599$, $P = 0.012$) and neither uniformly distributed ($Z_{May} = 10.421$, $P < 0.001$; $Z_{Aug} = 5.619$, $P < 0.001$; $Z_{Oct} = 2.867$, $P < 0.001$; $Z_{Feb} = 3.680$, $P < 0.001$). Instead, they were positively skewed for all study periods, leptokurtic in May and August and platykurtic in October and February (Table 1). The log-log linear regressions of the frequency distributions of daily distance displaced were highly significant in May ($R^2 = 0.858$, $df = 8$, $t = -6.964$, $P < 0.001$), August ($R^2 = 0.956$, $df = 5$, $t = -10.403$, $P < 0.001$) and February ($R^2 = 0.617$, $df = 7$, $t = -3.359$, $P = 0.012$) but not in October ($R^2 = 0.439$, $df = 3$, $t = -1.533$, $P = 0.223$). More specifically, the distribution of daily distances displaced was close to a Lévy distribution in May ($\mu = 1.90$) which contrasted with the power-law behaviours observed during the others study periods, with $\mu = 1.35$ in August and $\mu = 1.10$ in February. The exponent μ observed

in May ($\mu = 1.90$) cannot be statistically distinguished from the theoretical exponent expected for a Lévy flight (i.e. $\mu = 2.00$, $P > 0.05$; modified t -test, Zar 2010), while they were significantly lower in August and February ($P < 0.05$). No autocorrelation in distances displaced between successive daytime low tides was found in all periods ($P > 0.05$), except in one individual in May, October and February, and two individuals in August ($P < 0.05$).

DISCUSSION

Nerita atramentosa distribution patterns as an adaptation to exogenous and endogenous stressors

The clear temporal shift in *N. atramentosa* microhabitat occupation (i.e. a gradual increase in pool occupation and decrease in both crevice and flat rock occupation from May to February; Figure 1B) likely results from the behavioural selection of a favourable microhabitat related to the three major environmental stressors found in the intertidal that are temperature, desiccation and hydrodynamism. In October and February, *N. atramentosa* preferentially selected and aggregated within pools (63% of total aggregation: Figure 1) that reduce both thermal and desiccation stresses (Coffin *et al.*, 2008) more than the underneath of rocks or crevices (Bates & Hicks, 2005). In contrast, in May and August, aggregation within crevices (and pools in August: Figure 1) likely reduced dislodgement risk caused by breaking waves (Miller *et al.*, 2007).

The temporal variability in microhabitat use and aggregation may also be explained by biological factors such as

predation, reproduction and feeding. In particular, snails likely aggregated in February as a response to predation risk (as indicated by the consistent observations of crushed and empty shells; Chapperon & Seuront, personal observation) also observed in others invertebrates (Coleman, 2008). Breeding aggregation prior to *N. atramentosa* spawning season peak (September to April: Przeslawski, 2008) could also explain the 55% aggregation rate in October (Figure 1A).

The trail and/or odour following behaviour observed in *N. atramentosa* (Chapperon & Seuront, personal observation) may also contribute to the formation of aggregates (Stafford *et al.*, 2007; Chapperon & Seuront, 2009, 2011b). Finally, *N. atramentosa* distribution could be primarily determined by the abundance and the small-scale patchiness of microphytobenthos (Seuront & Spilmont, 2002; Murphy *et al.*, 2008). More specifically, individuals may remain aggregated whilst the tide is retreating in the microhabitat that abounds the most with microalgae (i.e. crevices in August and May, and rockpools in October and February), and in which grazing activities are undertaken during immersion (Berger & Weaver, 2004). Although no movement was observed in *N. atramentosa* during the monitored day-time low tides, the observed individual distribution could also result from the potential trail following and/or grazing movements of snails on wet rocks during emersion (due to rainfall or awash conditions: Little, 1989).

Nerita atramentosa dispersion as an adaptation to environmental stress and food availability

Nerita atramentosa displacements in August and October (Figure 2C–F) suggest maintenance of individuals at their shore level (Williams, 1995). Individuals remained in the vicinity up and mainly down the release point (Figure 2C–F). This limited dispersion indicates that snail activities were restricted to a small area, i.e. within a 3 m radius around the release point (Figure 2C–F). Snails might have intensively fed upon microalgae previously identified to be particularly abundant during this period of the year (i.e. winter) on other temperate rocky shores in New South Wales and the United Kingdom (Underwood, 1984; Thompson *et al.*, 2004; Jackson *et al.*, 2010). This low dispersion is also consistent with the lower seawater temperature (Table 1; Seuffert *et al.*, 2010) and the increase in wave action (Pardo & Johnson, 2006) observed over the study site in August and October (Chapperon & Seuront, personal observation) that may have constrained organisms to adhere to the substratum in order to reduce dislodgement risk (Barahona & Navarrete, 2010). Further investigations are, however, required to assess the eventual relationship between wave action force (non-measured in the present study) and *N. atramentosa* movements.

In February and May, *N. atramentosa* moved farther seaward (i.e. within a 6 to 9 m radius from the release point: Figure 2A, B, G, H), as observed in others neritids (Garrity & Levings, 1981). Seaward displacements (Figure 2A, B, G, H) were possibly driven by more suitable feeding and/or environmental conditions prevailing at lower shore levels (Williams, 1994; Gibson, 2003). Particularly, *N. atramentosa* likely foraged extensively to increase the likelihood of encountering microphytobenthos resources that have been demonstrated to be scarce during this period of the year especially

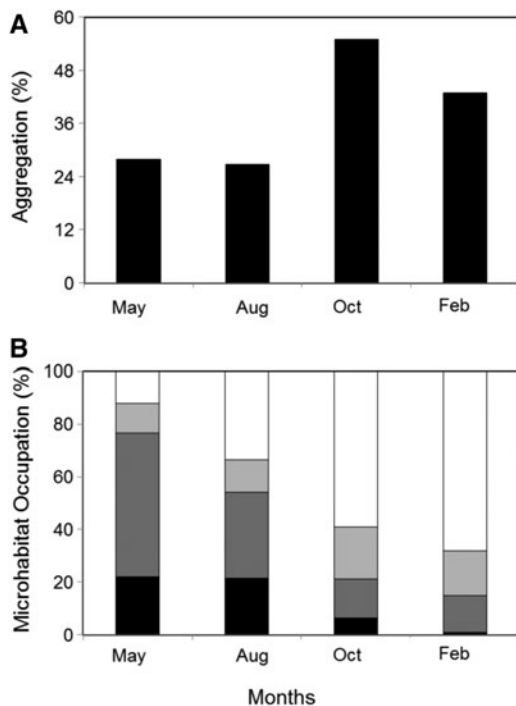


Fig. 1. Proportion of *Nerita atramentosa* individuals aggregated (A) and microhabitat occupation (B) at daytime low tide over 8 days in May 2009 (May), August 2009 (Aug), October 2009 (Oct) and February 2010 (Feb). The four microhabitats considered were pool (white bars), under rock (light grey bars), crevice (dark grey bars) and flat rock (black bars).

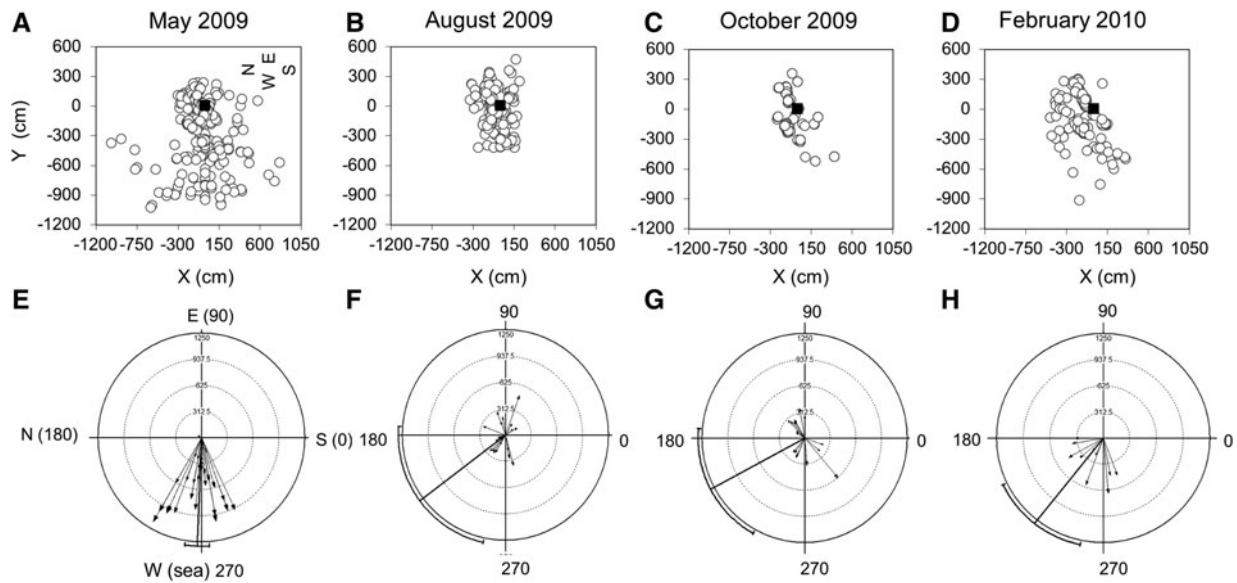


Fig. 2. Two-dimensional positions (cm) of *Nerita atramentosa* individuals (white dots) from the release point (A, C, E, G, black square) recorded at 8 daytime low tides in May 2009 (A, N = 396), August 2009 (C, N = 285), October 2009 (E, N = 285) and February 2010 (G, N = 212). Net directions and distances displaced from the release point (B, D, F, H, centre of circle) in May 2009 (B, N = 42), August 2009 (D, N = 24), October 2009 (F, N = 37) and February 2009 (H, N = 11). Each vector indicates the net direction taken by each individual. The concentric circles represent the distance displaced (increments of 312.5 cm from 0 to 1250 cm). The length of a vector is indicative of the individual distance travelled from the release point. The solid lines and the arcs are representative of the mean direction and its 95% confidence interval. The bottom of the graphs is oriented seaward.

at the high shore level on other temperate rocky shores in New South Wales and the United Kingdom (Underwood, 1984; Thompson *et al.*, 2004; Jackson *et al.*, 2010). Finally, the increase in seawater temperature (Table 1) may have increased *N. atramentosa* locomotor performance (e.g. Barahona & Navarrete, 2010), hence increased their dispersion abilities. In order to validate the hypothesis that snail movements are directed by the space–time variability in microalgal resources, further experiments are however required to investigate the abundance, distribution and availability of microphytobenthos on south Australian rocky shores, that were not measured in the present study. Interpretations of the present results were solely based on the assumption that the space–time variability in the abundance, distribution and availability of south Australian microalgal resources is comparable to that observed on other temperate rocky shores (i.e. New South Wales and the United Kingdom: Underwood, 1984; Thompson *et al.*, 2004; Jackson *et al.*, 2010).

Intermittency in foraging behaviour: an adaptive response to resource distribution

The foraging behaviour of *N. atramentosa*, further assessed through the probability density function of their successive daily displacements d_i , was found to exhibit intermittent properties, i.e. their probability density functions $P(d_i)$ follow a power-law behaviour $P(d_i) = kd_i^{-\mu}$ (see Equation (6)) in May, August and February. This indicates that the successive displacements of *N. atramentosa* belong to a family of distributions defined according to the value of the exponent μ . This is consistent with an adaptive response of *N. atramentosa* to the Lévy-like patterns previously identified in the spatial distribution of microphytobenthos biomass over a range of intertidal environments (Seuront & Spilmont, 2002; Seuront, 2010). A similar response to resource distribution has also

been identified in the foraging behaviour of top predators (Sims *et al.*, 2008). In addition, the increase in the exponent μ observed from $\mu = 1.10$ in February, $\mu = 1.35$ in August, and $\mu = 1.90$ in May, may be indicative of a concomitant increase in foraging activity as seen from the foraging behaviour of *Littorina littorea* (Seuront *et al.*, 2007).

More specifically, the exponent μ was not significantly distinguished (modified *t*-test, $P > 0.05$; Zar, 2010) from the value $\mu = 2$ in May, as expected for a Lévy flight. Under the Lévy flights foraging hypothesis, Lévy flights are considered as an optimal foraging strategy where prey is scarce and randomly distributed, while Brownian motion ($\mu = 3$) is expected in environments where prey is abundant (Viswanathan *et al.*, 1999). This is consistent with the low density but non-depleted resource expected in our sampling site in May if microalgal resource abundance follows that observed in others temperate rocky shores of New South Wales and the United Kingdom (Underwood, 1984; Thompson *et al.*, 2004; Jackson *et al.*, 2010), and with the Lévy flights identified in the foraging behaviour of *Littorina littorea* on a low food density rocky shore during European winter (Seuront *et al.*, 2007). This contrasts, however, with the nearly ballistic movements (i.e. exponent μ close to unity) observed in February and previously found in *N. atramentosa* in the absence of food, i.e. depleted resource (Chapponon & Seuront, 2011a). This suggests that under similar conditions of low food density, *N. atramentosa* may behaviourally optimize its foraging behaviour depending on both the spatial patterns and the level of food depletion, i.e. depleted versus non-depleted. The optimal Brownian foraging strategy ($\mu = 3$) anticipated under conditions of abundant resources (Humphries *et al.*, 2010), as expected in winter and spring months (Underwood, 1984; Thompson *et al.*, 2004; Jackson *et al.*, 2010), was not observed. Instead, organisms were confined to the surroundings of the release point, and exhibited Lévy-like properties in August but not in

October. This suggests that the intermittent properties observed in August and October may not be solely related to food foraging, but also impacted by other environmental processes such as hydrodynamism or predation (Bartumeus, 2009).

Technical limitations in movement studies: a challenge for intertidal ecologists

These results were obtained from a mark–release–capture method that provides discontinuous spatial observations of individuals, i.e. a ‘capture history’ (Patterson *et al.*, 2008). Snails were thus implicitly, and over-simplistically, assumed to displace linearly during immersion between two successive day–time low tides. *Nerita atramentosa* individuals, however, have previously exhibited convoluted trajectories and elevated individual speed up to 10.7 cm min^{-1} when observed at high temporal resolution (i.e. 15 seconds: Chapperon & Seuront, 2011a). Mean *N. atramentosa* distance travelled during each study period was therefore likely underestimated. In addition, some individuals were not observed over either short periods (e.g. one day) or until the end of the monitoring. This absence of information also constitutes a potential bias in the data set since it is not clear whether those individuals were: (i) alive but out of sight hidden in deep depressions; (ii) far beyond the prospection area; (iii) dead due to predation, thermal or desiccation stresses; or (iv) dislodged and exported from the studied area by breaking waves. This highlights the difficulties faced by intertidal ecologists in studying movement and distribution patterns in the intertidal that are most often based solely on the interpretations of indirect observations. An increase in the awareness of intertidal ecologists for new technologies, multi-expertise and the development of new biotelemetric devices adapted to small size organisms (Cooke *et al.*, 2004) is hence essential to achieve a more thorough understanding of the patterns of distribution, dispersion and movement in order to implement species conservation and management plans in the changing world.

Conclusion

This study highlights that *N. atramentosa* individuals have enough motion behavioural flexibility to adapt: (i) their microhabitat occupation and aggregation patterns to the various environmental and biological conditions encountered in different periods of the year; and (ii) their foraging strategy to the predicted stochastic patterns of their landscape (e.g. Lévy-like food distribution) based on the hypothesis that south Australian microalgal resources have similar space–time variability in their distribution, abundance and availability than other temperate rocky shores (New South Wales and the United Kingdom: Underwood, 1984; Thompson *et al.*, 2004; Jackson *et al.*, 2010). Under this hypothesis, our results also support the fact that the Lévy flights previously observed in *Littorina littorea* (Seuront *et al.*, 2007) might occur among a range of intertidal grazers, but also suggests that Lévy behaviour may not be the universal rule in heterogeneous and fluctuating environments (Humphries *et al.*, 2010). Further investigations are also required to identify the factors triggering the observed switch between different foraging strategies. Although snails are able to detect food sources by chemoreception and to adapt their movements

accordingly (Croll, 1983), the presumed switch observed between different searching strategies may also: (i) be reminiscent of innate properties in *N. atramentosa* motion behaviour (see also Chapperon & Seuront, 2011a); (ii) resume from an internal clock (e.g. endogenous rhythm: Williams & Little, 2007; Gray & Williams, 2010); or (iii) be activated by other environmental factors specific to each season (e.g. water temperature). Finally, the observed behavioural flexibility in *N. atramentosa* might constitute a strong evolutionary advantage in stressful and fluctuating environments such as the intertidal which are likely to be heavily impacted by the fast changing world climate.

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