

Variability in the motion behaviour of intertidal gastropods: ecological and evolutionary perspectives

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The variability in motion behaviour properties was investigated for three species of intertidal gastropods at the inter-specific, inter-individual and individual levels in the absence of abiotic and biotic cues. Interspecific differences in movement patterns were reminiscent of the optimal searching behaviours expected for Austrocochlea porcata, Nerita atramentosa and Bembicium melanostomum in their natural environment. Specifically, N. atramentosa, A. porcata and B. melanostomum respectively displayed extensive and intensive foraging strategies consistent with their feeding ecology. The related inter-individual variability within each species highlights the potential ability of species to adapt their movement patterns to new environmental conditions and to persist over long-term changes. Finally, the strong variability observed in the speed and turning angle of individuals of the three species and the resulting behavioural plasticity may be an adaptive strategy to optimize energy expenditure and to react to an environmental fluctuation. Specifically, it is suggested that the lack of significant differences in individual behavioural variability between the three species indicates that despite clear inter-specific differences in motion behaviour, at the individual level A. porcata, N. atramentosa and B. melanostomum have similar abilities to face environmental fluctuations. This work stresses that individual variability in the motion behaviour of intertidal gastropods constitutes a fundamental evolutionary advantage when facing heterogeneous environmental conditions.

Keywords: marine gastropods, variability, behaviour, movement

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INTRODUCTION

Animal movement is a key determinant of population viability and species dynamics in response to spatially and temporally structured habitats (Tilman, 1994; Chapman, 2000a; Morales & Ellner, 2002). The assessment of animal movement requires an understanding of how animal behaviour is affected by fluctuations in the abiotic and biotic properties of the environment and how animals make decisions about moving across different habitats (Chapman, 2000a). For instance, in fluctuating habitats (e.g. influenced by diel, tidal and seasonal cycles) animals often alternate space use patterns in a predictable way. On a seasonal scale, responses often include switching between localized resource utilization and large-scale movements driven by migration (Bergman *et al.*, 2000; Laidre *et al.*, 2004). Behavioural responses may also be driven by local processes such as habitat heterogeneity (Tews *et al.*, 2004), intra- and inter-specific competition (Fausch, 1998; Craig *et al.*, 2000; Bolnick, 2001), predation (Lima, 2002), endogenous rhythms, physiological states and gender (Seuront *et al.*, 2004). Behavioural changes resulting in differential movement patterns may also be a response to habitat structure (Morales & Ellner, 2002; Haynes & Cronin, 2006)

and maintain physiological performance particularly in ectothermic organisms (Bennett & Huey, 1990).

Intertidal invertebrates are particularly well suited to study the impact of abiotic and biotic processes on behavioural patterns as they must survive wave action (Helmuth & Denny, 2003; Ríos-Jara *et al.*, 2004; Pardo & Johnson, 2006; Chapperon & Seuront, 2009), desiccation during low tide (Bazterrica *et al.*, 2007; Przeslawski & Davis, 2007), predation (Dix & Hamilton, 1993; Fernandes *et al.*, 1999) and competition for space (Byers, 2000; Rajasekharan & Crowe, 2007). Each of these factors may determine the activity patterns of species such as gastropod herbivorous grazers, which have a strong influence on community structure and function (Chapman, 2000a). Their behavioural responses to a wide range of cues (i.e. chemical cues; Chapperon & Seuront, 2009) influence their patterns of distribution and dispersion (Chapman, 2000a; Stafford & Davies, 2005), as well as their local abundance and diversity (Chapman, 2000a; Kerr *et al.*, 2002; Davidson *et al.*, 2004). However, to our knowledge little is still known about what determines gastropod behaviour and whether it is: (i) an acquired behaviour, such as the use and development of spatial memory (Rajasekharan & Crowe, 2007); or (ii) an innate behaviour, which might be more related to mechanisms needed for directional and complex movements exhibited during annual migration and food foraging (Byers, 2001). In addition, the causes and consequences of individual variability have barely been explored as most behavioural studies have been conducted at discrete

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scales (e.g. Chapman, 2000b; Seuront *et al.*, 2007) that are not compatible with the behaviour of individual organisms. A better understanding of the individual variability can occur only if we investigate behavioural properties at an appropriate scale, more precisely at the scale individuals perceive and react to their immediate environment (Nams, 2005). These issues are particularly pertinent for understanding the ecology of gastropod species that share the same environment and food resource but exhibit different behaviours (Chapman, 2000b). In this context, we investigated the properties of the motion behaviour and the potential for innate behavioural properties of three species of intertidal grazers that commonly co-occur on South Australian intertidal rocky shores: *Nerita atramentosa*, *Austrocochlea porcata* and *Bembicium melanostomum*. More specifically, the objectives of this study were: (i) to assess if these species resume a common behaviour in the absence of any abiotic and biotic cues; (ii) to infer potential differences between species; and (iii) to investigate the nature and extent of the observed individual variability.

MATERIALS AND METHODS

Studied species and sampling area

This study focused on three species of intertidal prosobranch gastropods; two species found only in Australia, *Austrocochlea porcata* (Adams, 1851) and *Bembicium melanostomum* (Gmelin, 1791), and one species that occurs both in Australia and New Zealand, *Nerita atramentosa* (Reeve, 1855). These herbivorous grazers are commonly found from the mid to the high intertidal levels on most Australian rocky shores (Edgar, 1997), and as such are expected to potentially compete for food and space.

All the individuals tested were collected in February 2007 at low tide from the midshore levels of a moderately exposed rocky shore located in Marino Rocks, South Australia (35°02'40S–138°30'30E). The individuals used in the experiments were sampled on a platform characterized by a relatively simple topography with a flat, smooth rocky substrate with a few shallow pits and crevices. The potential effect of size on behavioural properties (Byers, 2000; Pardo & Johnson, 2004) was avoided using snails belonging to the same size-class for each species, i.e. 14.1 ± 0.38 mm (mean ± standard deviation), 17.1 ± 0.31 mm and 14.1 ± 0.38 mm in *N. atramentosa*, *A. porcata* and *B. melanostomum*, respectively.

Experimental procedures and behavioural observations

Individuals were acclimatized for 36 hours as preliminary experiments only showed statistical differences ($P < 0.01$) in the motion behaviour of individuals acclimatized for less than 36 hours. Individuals were kept in different aquaria with aerated seawater in the temperature and salinity conditions of the behavioural experiments.

All the experiments were conducted under controlled conditions of temperature (19°C) and salinity (38 PSU) in an opaque tank (2 × 1.10 m) in order to eliminate the potential bias related to phototaxis (Petraitis, 1982; Rossetti & Cabanac, 2006). The only light source was a dim light (0.32 μE s⁻¹ m⁻²) positioned above the tank. The water level

was consistently kept at a depth of 4 cm to completely submerge the individuals and simulate high tide conditions, when they are more active (Chapman, 2000a). Between each test, the tank was emptied, washed with a scraper, thoroughly rinsed and refilled with fresh seawater in order to remove the mucus trails and chemical cues of the tested individual, which could bias the motion behaviour of the next individual tested (Erlandsson & Kostylev, 1995; Edwards & Davies, 2002).

For each species, the movements of 10 individuals were individually recorded for one hour using a digital camera (DV Sony DCR-PC120E) placed above the centre of the tank. Each individual was placed in the centre of the field of view, and videorecording started when the individual started to move. Each snail was only used once. Displacements were recorded while individuals were present in the field of view, viewed on a TV screen, the positions of the individuals were plotted every 15 seconds on tracing paper attached to the TV screen and the trajectories were subsequently computerized using a scaling factor of 2 which corresponds to the ratio between the distances observed in the tank and on the screen. Note that the resolution was specifically chosen as this is the highest resolution at which direction changes relate to actual motion behaviour, and are not contaminated by local re-orientation of the shell performed at very low velocity and did not relate to the direction of travel.

Quantifying gastropod motion behaviour

The motion behaviour of gastropods has previously been investigated using a wide range of parameters (e.g. speed, direction, tortuosity and sinuosity of motion). In this study, we considered a series of parameters that quantify both the level of activity of individual gastropods and the complexity of their motion behaviour.

ACTIVITY INDEX

The level of activity of a gastropod was estimated as the percentage of time allocated to movements. The activity index A_i was subsequently defined as:

$$A_i = 100 \times \frac{t_{\text{video}}}{t_{\text{move}}} \quad (1)$$

where t_{video} and t_{move} are the duration of the video observation and the time a gastropod spent moving, respectively.

SPEED

The distance d (cm) between two successive positions was calculated from the x and y coordinates as:

$$d = [(x_{t+1} - x_t)^2 + (y_{t+1} - y_t)^2]^{1/2} \quad (2)$$

where (x_t, y_t) and (x_{t+1}, y_{t+1}) are the positions of a gastropod at time t and $t + 1$, respectively. The movement speed v (cm min⁻¹) was subsequently estimated as:

$$v = d \times f \quad (3)$$

where f is the frequency of observation (15 sec). Mean speeds and standard deviations were calculated for each individual and each species.

NGDR (NET-TO-GROSS DISPLACEMENT RATE)

The NGDR provides a measure of the relative linearity of a gastropod path as:

$$NGDR = ND/GD \quad (4)$$

where ND is the net displacement (cm), i.e. the linear distance between the beginning and end of the observed displacement and GD is the gross displacement (cm), corresponding to the actual distance travelled by the individual. A NGDR value of 1 indicates a linear displacement, and the NGDR decreases as the path tortuosity increases.

TURNING ANGLE

The turning angle θ_e is defined as the net direction between two successive moves following (Jerde & Visscher, 2005):

$$\theta_e = 180 - \left(\frac{180}{\pi} \times \theta \right) \quad (5)$$

where θ is given by:

$$\theta = \arccos\left(\frac{(p_1p_3)^2 - (p_1p_2)^2 - (p_2p_3)^2}{2(p_1p_2)(p_2p_3)}\right) \quad (6)$$

where (p_1p_3) , (p_1p_2) and (p_2p_3) are respectively the distances between the positions p_1 and p_3 , p_1 and p_2 , and p_2 and p_3 . A low mean turning angle indicates that the general individual displacement is smooth and the successive moves are straight. In contrast, a higher mean angle show strong direction changes between the successive moves.

Statistical analyses

Non-parametric statistical tests were used as all the parameters did not follow a normal distribution (Lilliefors test, $P < 0.05$). Intraspecific and interspecific comparisons of speed and turning angle were done with the Kruskal–Wallis test (KW test hereafter). Interspecific differences in NGDRs values were carried out with the KW test, and a subsequent multiple comparison procedure based on the Tukey test was used to identify distinct groups of measurements (Zar, 1996). Correlations between the parameters were tested using Spearman's coefficient of rank correlation. The individual variability in speed, NGDR and turning angle was expressed using the coefficient of variation CV ($CV = SD/\bar{x}$), where SD is the standard deviation and \bar{x} the mean of the distribution. Skewness (i.e. measure of symmetry of the distribution) and kurtosis (i.e. measure of flatness of a distribution compared to a normal distribution) were calculated to characterize the variability. Coefficient of variation, skewness and kurtosis of speed and turning angle values were compared between species using the KW test. The Kolmogorov–Smirnov test was used to compare speed and turning angle coefficients of variation, skewness and kurtosis between individuals.

RESULTS**Inter-specific variability in motion behaviour**

The displacements of *A. porcata*, *N. atramentosa* and *B. melanostomum* consistently exhibited different levels of

complexity, for both short observations (Figure 1A) and long observations (Figure 1B–D). *Austrocochlea porcata* and *N. atramentosa* trajectories (Figure 1A–C) were mainly rectilinear and characterized by the presence of large loops. In contrast, the movement pathways of *B. melanostomum* (Figure 1A, D) were much more convoluted and characterized by small loops. As a consequence, *N. atramentosa* and *A. porcata* moved farther than *B. melanostomum* over shorter or similar durations (Figure 1).

Nerita atramentosa, *B. melanostomum* and *A. porcata* were found to be very active and respectively moved during 99.4%, 98.3% and 93.7% of the observation periods. No significant differences were found between species (KW test, $P > 0.05$). Mean movement speeds were, however, significantly different between species ($P < 0.01$). More specifically, *B. melanostomum* moved significantly slower ($P < 0.05$) than *N. atramentosa* and *A. porcata* (Figure 2A). Significant differences between species were also found between NGDR values ($P < 0.05$). The trajectories of *B. melanostomum* were significantly ($P < 0.05$) less rectilinear than those of *N. atramentosa*. The NGDR of *A. porcata* was not significantly different from the other species ($P > 0.05$; Figure 2B). The three gastropods also exhibited significant interspecific differences in turning angles ($P < 0.01$). Changes in direction were significantly higher in *B. melanostomum* trajectories than those of *N. atramentosa* and *A. porcata* ($P < 0.05$). Turning angles of *A. porcata* were not significantly different from those of *N. atramentosa* (Figure 2C). Mean speeds of species were positively correlated with NGDR values ($P < 0.05$) and negatively correlated with turning angle values ($P < 0.05$).

Inter-individual variability in motion behaviour

Besides the interspecific differences observed in their movement pathways (Figure 1) and behavioural properties (Figure 2),

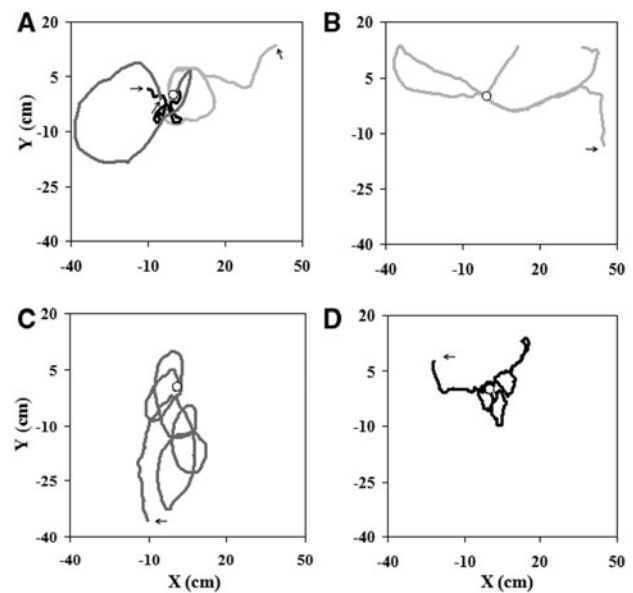


Fig. 1. Individual movement pathways of *Nerita atramentosa* (A: light grey; B), *Austrocochlea porcata* (A: dark grey; C) and *Bembicium melanostomum* (A: black; D). Time of observation: 14 minutes (A), 36 minutes (B), 52 minutes (C), 55 minutes (D). The start and the end of trajectories are respectively represented by a white dot and a black arrow.

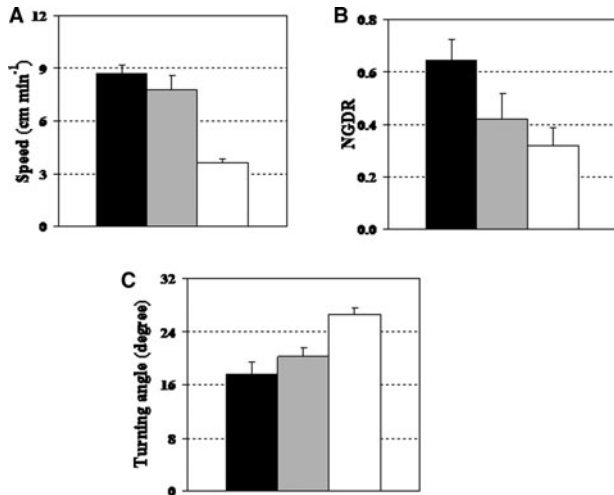


Fig. 2. Mean speed (A), NGDR (B) and turning angle (C) of the motion behaviour of *Nerita atramentosa* (Na, black), *Austrocochlea porcata* (Ap, grey) and *Bembicium melanostomum* (Bm, white). The error bars are the standard errors, $N = 10$.

N. atramentosa, *B. melanostomum* and *A. porcata* individuals exhibited a strong inter-individual variability (Figure 3). Speed and turning angle were significantly different between conspecifics (KW test, $P < 0.05$; Figure 3). More specifically, the variability observed in movement speed was higher for *A. porcata* ($CV = 0.32$) than for both *B. melanostomum* ($CV = 0.18$) and *N. atramentosa* ($CV = 0.19$). This results in the speed of *A. porcata* individuals ranging on average from 4.7 cm min^{-1}

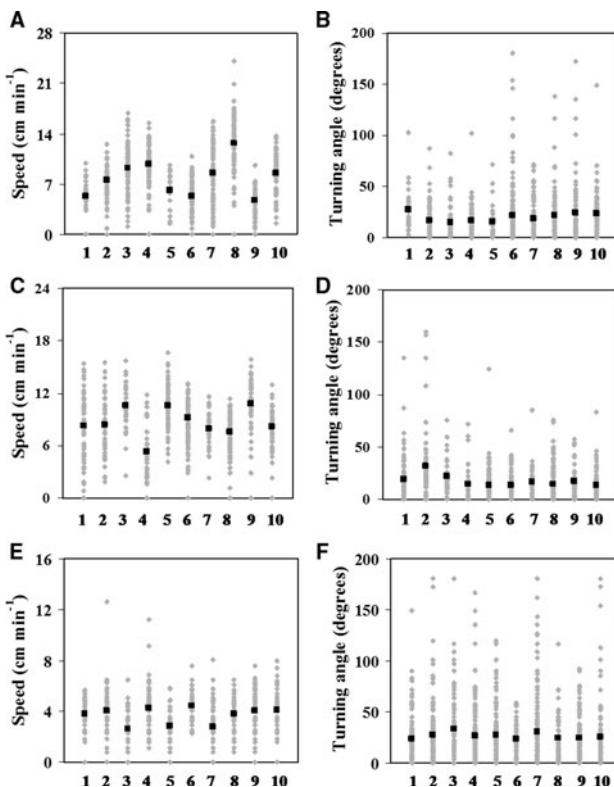


Fig. 3. Inter-specific variability in speed (A, C, E) and turning angle (B, D, F) for *Austrocochlea porcata* (A, B), *Nerita atramentosa* (C, D) and *Bembicium melanostomum* (E, F). The grey and black points are the observed and mean values, respectively.

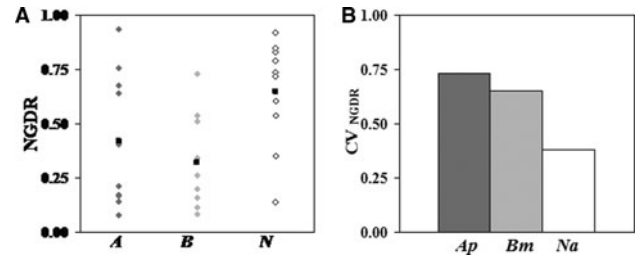


Fig. 4. Inter-specific variability in NGDR observed for *Austrocochlea porcata* (Ap, grey), *Bembicium melanostomum* (Bm, light grey) and *Nerita atramentosa* (Na, white) (A) and coefficient of variation of NGDR (CV_{NGDR}) per species (B). Grey, light grey and white points are the observed values per individual, black points are the mean values observed per species.

to 12.7 cm min^{-1} (Figure 3A). In contrast, the speed of *N. atramentosa* and *B. melanostomum* individuals ranged on average from 5.3 cm min^{-1} to 10.7 cm min^{-1} , and from 2.6 cm min^{-1} to 4.4 cm min^{-1} , respectively. In contrast, turning angles were more variable for *N. atramentosa* ($CV = 0.32$) than for *A. porcata* ($CV = 0.20$) and *B. melanostomum* ($CV = 0.12$). Mean turning angles ranged from 13.4 to 31.8 degrees for *N. atramentosa*, 15.2 to 27.3 degrees for *A. porcata*, and 23.5 to 33.6 degrees for *B. melanostomum*.

Finally, NGDR values were highly variable between individuals (Figure 4A). The strongest variability was observed for *A. porcata* ($CV = 0.73$; Figure 4B), with NGDR values ranging from 0.08 (i.e. highly convoluted) to 0.93 (i.e. highly linear; Figure 4A).

Intra-individual variability in motion behaviour

Successive individual moves (i.e. recorded every 15 seconds) were characterized by strong fluctuations in speed (Figure 5A, C, E) and turning angle (Figure 5B, D, F). This variability resulted in individual speed varying from 0.8 to 10.9 cm min^{-1} for *A. porcata* (Figure 5A), 1.1 to 10.7 cm min^{-1} for *N. atramentosa* (Figure 5C) and 0.8 to 8.0 cm min^{-1} for *B. melanostomum* (Figure 5E). Similarly, individual turning angles ranged between 0 and 180 , 0 and 76 and 0 and 180 degrees for *A. porcata* (Figure 5B), *N. atramentosa* (Figure 5D) and *B. melanostomum* (Figure 5F), respectively.

More specifically, movement speeds were characterized by marked long-term fluctuations in the baseline values of *A. porcata* and *N. atramentosa* (Figure 5A, C), and resulted in elevated mean speeds. *Bembicium melanostomum* speeds were more symmetrically distributed around the mean and mainly exhibited short-term fluctuations (Figure 5E). In contrast, turning angles were consistently characterized by very intermittent distributions, i.e. a few high values greater than the mean over a wide range of low density values smaller than the mean (Figure 5B, D, F).

The quantitative nature of these distributions has further been assessed using the coefficient of variation CV , and the skewness and kurtosis coefficients g_1 and g_2 (Table 1). The coefficients of variation estimated for both speed and turning angle were not significantly different between species ($P > 0.05$; Figure 6). The CV s estimated from the distribution of turning angles were, however, significantly higher ($P < 0.01$) than the speed variation for the three species (Figure 6). On average, the speed distributions of *A. porcata*

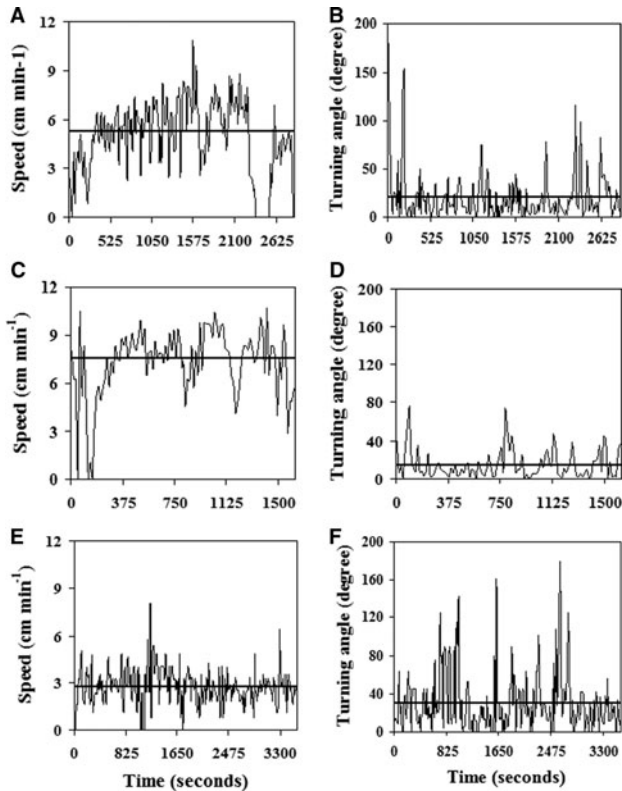


Fig. 5. Intra-individual variability in speed (A, C, E) and turning angle (B, D, F) observed in *Austrocochlea porcata* (A, B), *Nerita atramentosa* (C, D) and *Bembicium melanostomum* (E, F). Durations of observations were respectively 53, 27 and 62 minutes for *A. porcata*, *N. atramentosa* and *B. melanostomum*. The black lines represent mean values.

and *N. atramentosa* were negatively skewed while those of turning angle were positively skewed. Both distributions were positively skewed for *B. melanostomum* (Table 1). Speed distributions were generally characterized in each species by a few fast moves over a wide range of slow moves and turning angle distributions showed a few sharp turning angles over a wide range of smoother turning angles (Figure 5). Positive kurtosis values observed for turning angle and speed are indicative of distributions with more peaks than expected in the case of normality. However, the much higher g_2 values observed for turning angles (Table 1) indicated that sharp changes in direction were far more frequent than sharp changes in speed. Furthermore, significant differences ($P < 0.05$) were found between the skewness and kurtosis of speed and turning values in the three species. Most turning angle distributions were characterized by significantly ($P < 0.05$) more elevated skewness and kurtosis values (Table 1) than those of speed distributions. No inter-specific differences were found for the skewness and the kurtosis values of speed and turning angle distributions.

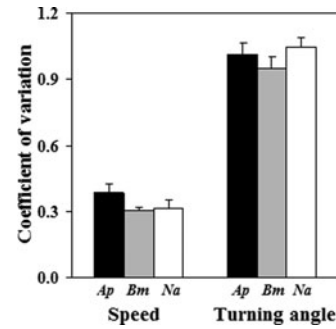


Fig. 6. Mean coefficient of variation of speed and turning angle observed in *Austrocochlea porcata* (black bars), *Bembicium melanostomum* (grey bars) and *Nerita atramentosa* (white bars). The error bars are the standard errors.

DISCUSSION

Inter-specific variability in motion behaviour as an adaptation to the spatial distribution of the food

Inter-specific differences in the motion behaviour of intertidal gastropod species (i.e. *A. porcata*, *N. atramentosa* and *B. nanum*) have previously been found in the field over different periods of time (48 hours, Underwood, 1977; 24 hours, 1 and 2 weeks, Chapman, 2000b) and have mainly been related to topographic complexity (Chapman, 2000b) and feeding activities (Underwood, 1977). However, the inter-specific differences identified here cannot be related to any environmental factors, since the experiments were conducted in controlled conditions in the absence of any cues after 36 hours of starvation. Instead, this suggests that the processes driving the observed motility pattern continue to operate in the absence of sensory cues, hence involving the presence of an innate determinant to motion behaviour (Bell, 1991). While this issue has still barely been investigated in gastropod ecology, it has been previously shown that innate information can be genetically determined and/or transferred through heredity or derived from exogenous sources (Bell, 1991). This is consistent with the inter-specific behavioural differences observed in this study which can be thought as a reminiscence of the previous trophic conditions encountered in the field.

Feeding activity patterns are influenced by the distribution of resource items and their space-time availabilities. *Nerita atramentosa* and *A. constricta* (a congeneric species of *A. porcata*) mainly graze on microalgae (Underwood, 1978; Quinn & Ryan, 1989), a resource typically distributed in small-scale patches (Seuront & Spilmont, 2002; Seuront & Leterme, 2006; Klaassen *et al.*, 2006). In contrast, *B. nanum* (a congeneric species of *B. melanostomum*) typically feeds on macroalgae (Quinn & Ryan, 1989), a resource intrinsically

Table 1. Skewness (g_1) and kurtosis (g_2) mean values of speed and turning angle distributions of *Nerita atramentosa*, *Austrocochlea porcata* and *Bembicium melanostomum*. Values are means \pm standard errors (SE), $N = 10$ individuals.

	<i>A. porcata</i>		<i>B. melanostomum</i>		<i>N. atramentosa</i>	
	g_1	g_2	g_1	g_2	g_1	g_2
v	-0.30 ± 0.15	0.06 ± 0.31	0.09 ± 0.20	2.43 ± 0.95	-0.61 ± 0.20	0.92 ± 0.49
θ	2.38 ± 0.20	8.30 ± 1.57	1.74 ± 0.24	4.60 ± 1.18	2.23 ± 0.29	7.44 ± 2.55

limited in space to the surface of macroalgae blades. *Nerita atramentosa* and *A. porcata* are then expected to have developed extensive foraging strategies. In contrast, *B. melanostomum* is likely to have developed intensive foraging strategies. This is consistent with both the highly convoluted paths of *B. melanostomum*, and the more rectilinear paths of *N. atramentosa* and *A. porcata*, as more rectilinear paths will cover larger areas over the same duration (Figures 1 & 2). In addition, when an animal does not get any information from the environment, like in our experiments, it should adopt a strategy which optimizes the probability to encounter food and reduces the chance to move in an area already explored (Bell, 1991). This is in concordance with *N. atramentosa* and *A. porcata* behaviours as they were found to exploit rapidly and extensively the experimental arena using successive randomly orientated straight long moves as well as big loops. This foraging pattern, previously qualified as transecting (Bell, 1991), is considered as the most efficient strategy to locate food patches such as microalgae (Hugues, 1980; Erlandsson & Kostylev, 1995). In contrast, *B. melanostomum* was slower and explored the area more intensively and tortuously, which can be considered as a restricted area search strategy optimised to exploit spatially-localized food items (Pyke, 1984; Bell, 1991). This strategy is consistent with the feeding ecology of *B. melanostomum* which concentrates its effort *in situ* on the spatially limited surface of macroalgae blades; mechanisms such as looping, zigzag motion patterns and short move length then constitute an efficient strategy (Bell, 1991).

Inter-specific differences in motion behaviour suggest that each species has its own behavioural repertoire, a repertoire being constituted by the range of speed and turning angle values observed (Figure 2A, C). This can likely be the result of natural selection through the selection of the searching strategy that is best adapted to the ecological niche of each species. To some extent, the motion behavioural patterns observed in this study might be related to the optimal searching foraging that the different species could exhibit in an ideal environment (e.g. absence of intraspecific competition). The differences observed in the motion behaviour of *A. porcata* and *N. atramentosa*, both grazers of microalgae, even in the absence of biotic and abiotic cues might constitute a niche differentiation that favours coexistence through resource partitioning and the subsequent reduction of resource competition.

Inter-individual variability in motion behaviour as an adaptation to long-term environmental fluctuations

Besides the inter-specific variability discussed above, we identified a strong inter-individual variability in the motion behaviour of *A. porcata*, *N. atramentosa* and *B. melanostomum* (Figure 3). Phenotypic differentiation, which gives information about the potential behavioural ability of a species to respond and react to long-term changes, may have caused the observed differences in motion property and performance within a given species. This is consistent with the assumption that animal fitness is generally associated to the foraging behaviour and the assumption of a heritable component in foraging behaviour (Pyke, 1984). The inter-individual variability observed in the three species investigated here then may

relate to different phenotypes, and be thought of as an evolutionary adaptation to fluctuating environmental conditions to increase the chances of species persistence throughout a period of changes.

Intrinsic characteristics of individuals such as body size, sex, parasite load but also reproductive, nutritional and physiological states (Pardo & Johnson, 2004) may also explain the observed intra-specific differences as individuals belonging to different categories do not favour the same fitness components (i.e. survival and reproduction). Albeit body size and starvation cannot influence the motion behaviour observed in our experiments since individuals belong to the same size-class and were not starved, further investigations are nevertheless still required to determine the effect of gender, maturity and parasitism on the motion patterns of the studied species.

In this study, variability among individuals could not be related to abiotic (i.e. temperature, humidity) and biotic (i.e. food quality and quantity, competition) factors since our experiments were conducted in the absence of any cues. However, the innate properties of the motion behaviour could be altered by the history of each individual considered. Individuals may gather distinct information directly from the same environment or indirectly through social influence (Keppel & Scrosati, 2004). This may have influenced the behaviour of distinct individuals and cause a deviation from the inborn behaviour common to the species. Nevertheless, the impact of past experiences on the present behaviour is dependent on the individual's ability to learn (e.g. social learning; Keppel & Scrosati, 2004), store (i.e. long term memory) and process information (Pyke, 1984; Vásquez *et al.*, 2002; Turner *et al.*, 2006). At this stage, still little is known about learning and memory abilities of gastropods (Turner *et al.*, 2006).

Intra-individual variability in motion behaviour as an adaptation to short-term environmental fluctuations

Individuals of *A. porcata*, *N. atramentosa* and *B. melanostomum* exhibited an ability to drastically change their speed and direction at very short time scales (i.e. 15 seconds). Each individual used a different repertoire of speed and turning angle values (Figures 3 & 5) within the species repertoire (Figure 2). However, the extent to which the repertoire was used was not significantly different between individuals of the three species. This suggests a strong and similar flexibility in the motion behaviour within the three species that may be seen as an adaptation to short-term environmental changes.

This behavioural flexibility is essential to the survival of gastropods inhabiting extreme habitats such as intertidal rocky shores since they have to respond to rapid environmental fluctuations that are either predictable (i.e. tide) or unpredictable (i.e. weather conditions, predators) in both space and time (Underwood & Chapman, 2000). In addition, individuals were more flexible when it comes to a change of direction rather than a change of speed. This is consistent with the optimal foraging theory (Pyke, 1984) that predicts that optimal movements (i.e. optimal speed and directionality) minimize the rate of energy expenditure, mainly due to the mucus produced to crawl (which can be about twenty

times more costly than the muscular mechanical work (Denny, 1980a, b; Lauga & Hosoi, 2006)) while searching for food and maximize the energy gained by its consumption.

CONCLUSION

The movement patterns and the related behavioural variability observed in the intertidal gastropods *Austrocochlea porcata*, *Nerita atramentosa* and *Bembicium melanostomum* in the absence of abiotic and biotic cues were shown to reflect both innate and acquired properties related to both: (i) the optimal foraging strategies for each species; and (ii) an adaptation to both short- and long-term space–time environmental fluctuations. This work has stressed the need to identify which component of behavioural variability is innate and/or acquired through heritability and past history. Bridging this gap in intertidal gastropod behavioural ecology is, however, critical to increase our understanding of how these organisms can survive into a continually changing environment. This may be particularly relevant in predicting whether they may be able adjust to long-term ecological changes, such as global climate fluctuations.

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