

Laboratory assessment of the motion behaviour of intertidal gastropods

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Abstract: The motion behaviour of three coexisting species of intertidal gastropods, *Bembicium melanostomum*, *Austrocochlea porcata* and *Nerita atramentosa*, was quantitatively studied in the laboratory in the absence of any abiotic and biotic cues. The behavioural properties used to assess movement pathways were the speed of the displacements and two measures of path complexity, the net to gross displacement ratio (NGDR) and the turning angle. *B. melanostomum* displacements were significantly slower than *A. porcata* and *N. atramentosa*, and significantly more complex than those of *N. atramentosa*. These differences cannot be explained by abiotic (e.g. topographic complexity) or biotic factors (e.g. competition for food, space). The movement patterns observed in the laboratory are, however, consistent with the feeding patterns previously reported for these species. The origin of these similarities is discussed in relation to inborn and acquired behaviours. The importance of the differences in the displacements between closely-related species is finally discussed in relation to the niche differentiation process.

Keywords: *gastropods, motion behaviour, innate, acquired*

1. Introduction

Dispersal behaviour is a key process influencing the structure and function of ecosystems (CHAPMAN, 2000b; MORALES and ELLNER, 2002). Understanding the factors affecting motion behaviour is then important to improve our knowledge of the distributions (STAFFORD and DAVIES, 2005), abundances and dispersion patterns of coexisting species (CHAPMAN, 2000b) as well as community diversity (KERR *et al.*, 2002; DAVIDSON *et al.*, 2004). Most animal movement studies have essentially investigated the role of environmental factors (e.g. changing tidal regime, time of immersion, pneumatophore density, DAVIES *et al.*, 2006; SEURONT *et al.*, 2007; BISHOP *et al.*, 2007) on motion behaviour within different species. Particularly, intraspecific variability has received increasing attention over the last decade (MARSHALL and KEOUGH, 1994; ERLANDSSON

and KOSTYLEV, 1995; CHAPMAN, 1998; PARDO and JOHNSON, 2004, 2006; NG and WILLIAMS, 2006; RAJASEKHARAN and CROWE, 2007). Quantitative comparative studies about intraspecific motion behaviour have been investigated in different habitats (CHAPMAN and UNDERWOOD, 1994; CROWE, 1999; PARDO and JOHNSON, 2006; RAJASEKHARAN and CROWE, 2007) to assess the relative importance of intrinsic characteristics (e.g. sex, body size; PARDO and JOHNSON, 2004) and the flexibility of the behaviour (CHAPMAN, 2000b). Only a few quantitative comparative studies of movement patterns have, however, been done between species (CHAPMAN, 2000a; MICHEL *et al.*, 2007) although interspecific variability can be large even among ecologically similar species (LEVINGS and GARRITY, 1983; CHAPMAN, 2000a).

Intertidal rocky shores are particularly suited to compare closely-related species which exploit the same resource and occupy the same area (CHAPMAN, 2000a). Herbivorous grazing gastropods inhabiting rocky intertidal shores typically compete for resources and space (ESPINOSA *et al.*, 2006). Dispersal and different

movement patterns have been shown to be a short term response to competition (TILMAN, 1994; WILSON *et al.*, 1999; CROWE and UNDERWOOD, 1998; BYERS, 2000; ESPINOSA *et al.*, 2006). However, it is still not well understood whether these differences in motion behaviour are innate or caused by acquired experiences (PYKE, 1984).

In this context, this work investigates the motion behaviour of three ecologically-related species of intertidal gastropods, *Nerita atramentosa*, *Bembicium melanostomum* and *Austrocochlea porcata*, which are found at the same level of intertidal rocky shores in South Australia. More specifically, to improve our understanding of the determinism of the motion behaviour of coexisting species, the aims of this study are (i) to quantify the motion behaviour of three coexistent species observed from continuous measurements at small spatial-scales, (ii) to assess whether interspecific variability in movement pattern is maintained in the absence of any environmental cues, and (iii) to investigate the part of innate and acquired in the motion behaviour.

2. Materials and methods

2.1. Sampling site and individuals collection

Snails were collected in February 2007 at low tide on a moderately exposed rocky shore situated at Marino Rocks, South Australia (35°02'40"S-138°30'30"E). Individuals were sampled at the mid-level shore on a platform characterized by a simple topography (i.e. flat, smooth rocky substrate with a few shallow pits and grooves). The salinity and temperature at the time of sampling were 35 and ~25 °C respectively. Three species of snails coexisting on this platform were collected, a species found in Australia and New Zealand, *Nerita atramentosa* (REEVE, 1855), and two exclusively Australian species, *Bembicium melanostomum* (GMELIN, 1791) and *Austrocochlea porcata* (ADAMS, 1851). Individuals of each species are herbivorous grazers (EDGAR, 1997) and as such are expected to compete for food and space. Ten individuals were investigated for each species. It was ensured that each individual belonged to the same body size class (15.5 ± 0.9 mm; x ± SE). Prior to the behavioural experiments,

individuals were acclimatized in aquaria under experimental conditions, where temperature = 19 °C and salinity = 38, for 36 h.

2.2. Behavioural observations and analysis

Experiments were conducted in an opaque tank (2 × 1.10 m) to avoid the potential bias of phototaxis (PETRAITIS, 1982; HAMILTON and WINTER, 1982), a dim light positioned above the centre of the tank was used to provide a steady light intensity (0.32 μE m⁻² s⁻¹). Between each trial, the tank was emptied and washed to remove the mucus of the previous individual, then refilled with seawater of constant salinity and temperature (S = 38, T ~ 19°C) to a depth of 4 cm to completely submerge individuals. Trajectories of each active individual were recorded for one hour using a digital camera (DV Sony DCR-PC120E) placed above the tank. Movements were subsequently plotted onto tracing paper attached to a TV screen by carrying forward the successive positions every 15 seconds. Then, trajectories were computerised in order to quantify the motion behaviour.

Motion behaviour was assessed using the motion speed as well as two indexes of complexity, namely the net-to-gross displacement rate (NGDR) and the turning angle (TA). The speed v (cm min⁻¹) was calculated as $v = d \times f$ where f is the frequency of observation (15 seconds) and d is the displaced distance estimated from the plotted coordinates (x_t, y_t) , (x_{t+1}, y_{t+1}) , at time t and $t+1$, respectively, as $d = [(x_{t+1} - x_t)^2 + (y_{t+1} - y_t)^2]^{1/2}$. The NGDR (SEURONT *et al.*, 2004b) was calculated as $NGDR = ND/GD$, where ND (Net Displacement) represents the linear distance between the first and the last positions of an individual, and GD (Gross Displacement) the actual distance travelled and calculated by the sum of the distances of the successive moves (Fig. 1). NGDR gives information about the linearity of a trajectory; higher values of NGDR show a straight displacement, while smaller values indicate the presence of curviness in the path. Finally, the turning angle θ_e is defined as the change in direction from one vector of movement to the next (JERDE and VISSCHER, 2005) and calculated as $\theta_e = 180 - ((180 * \pi) \times \theta)$, where $\theta = \arccos(\vec{A} \cdot \vec{B} / \|\vec{A}\| \|\vec{B}\|)$, \vec{A} is the

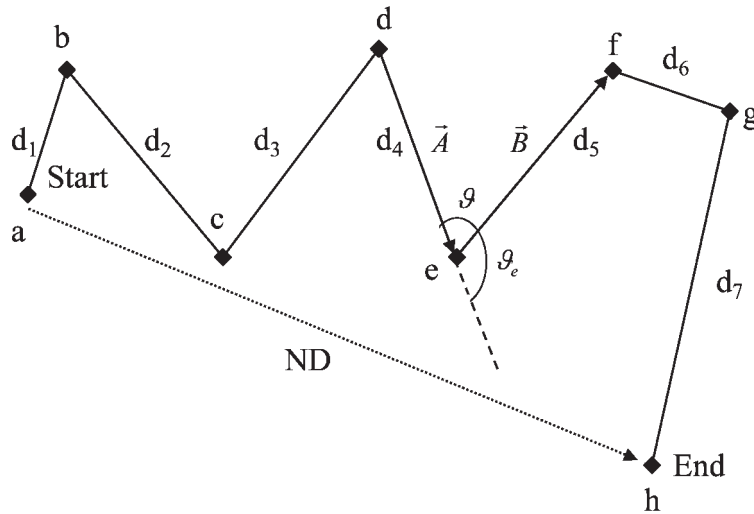


Fig. 1. Schematic illustration of the principles to estimate turning angle and NGDR. The turning angle θ_e corresponds to the change in direction between the successive vectors of movement \vec{A} and \vec{B} . The NGDR is the ratio between the net displacement ND (i.e. the straight line between the start and the end of the trajectory) and the actual distance GD, the gross displacement (i.e. the sum of the distances d_i).

vector between location d and location e , \vec{B} is the vector between location e and location f (Fig. 1). The norms $\|\vec{A}\|$ and $\|\vec{B}\|$ are the lengths of the vectors \vec{A} and \vec{B} (Fig. 1). Low mean turning angles indicate weaker changes in the direction between successive moves than the high mean turning angles.

2.3. Statistical analyses

The distribution of speed and complexity indexes were non-normally distributed, accordingly we used non-parametric statistical analyses. Interspecific comparisons of the parameters were done with the Kruskal-Wallis test followed by a multiple comparison procedure based on the Tukey test to identify distinct groups of measurements.

3. Results

A two-dimensional illustration of the typical paths exhibited by the three species of gastropods is given in Fig. 2. Clear dissimilarities in the movement patterns of the three species were apparent. More specifically, at a qualitative level, *B. melanostomum* appeared most dissimilar amongst the 3 species. *B. melanostomum* individuals displacements were tortuous with frequent changes in direction,

resulting in paths typically formed by the presence of small loops and a relatively restricted search area (Fig. 2). In contrast, the motion patterns of *N. atramentosa* and *A. porcata* were similar (Fig. 2), with a larger area typically explored than by *B. melanostomum* over the same time of observation. They travelled rectilinearly with large curves and loops around the whole field of view (Fig. 2).

Statistically significant differences were observed between the three species for speed, NGDR and turning angle (KW test, $p < 0.05$). *B. melanostomum* was significantly ($p < 0.05$) slower than the two others species (Fig. 3a, b), averaging $3.66 \pm 0.21 \text{ cm min}^{-1}$ ($\bar{x} \pm \text{SE}$). The speed of *N. atramentosa* and *A. porcata* were not significantly different ($p > 0.05$), however, on average *N. atramentosa* ($8.7 \pm 0.5 \text{ cm min}^{-1}$) was faster than *A. porcata* ($7.8 \pm 0.8 \text{ cm min}^{-1}$). The movements of *B. melanostomum* were significantly ($p < 0.05$) less linear and more sinuous (NGDR = 0.3 ± 0.1 , TA = 26.7 ± 1.0 degrees; $\bar{x} \pm \text{SE}$) than *N. atramentosa* (NGDR = 0.7 ± 0.1 , TA = 17.6 ± 1.8 degrees; Fig. 3c). The complexity of *A. porcata* trajectories (NGDR = 0.4 ± 0.1 , TA = 20.2 ± 1.3 degrees) did not differ significantly from those of the two others species.

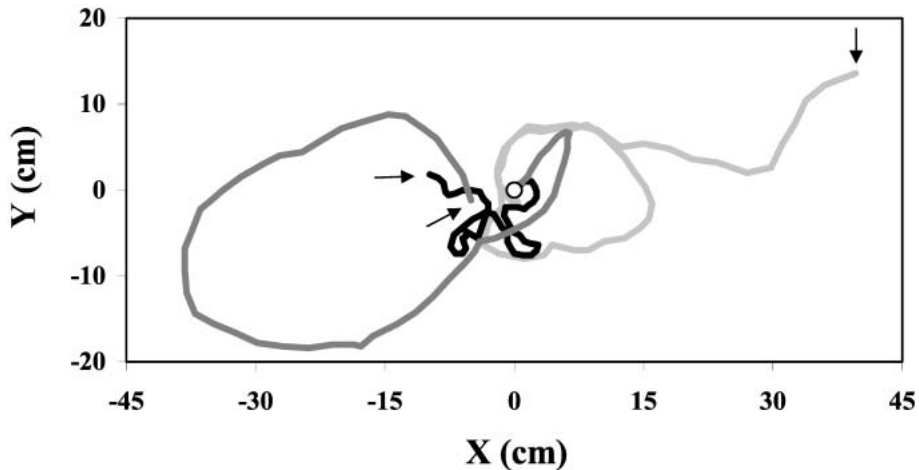


Fig. 2. Motion behaviour of *A. porcata* (dark grey), *N. atramentosa* (light grey) and *B. melanostomum* (black). Time of observation : 14 minutes. The initial and final locations are respectively represented by the white point and the black arrows.

4. Discussion

Nerita atramentosa, *Austrocochlea porcata* and a congeneric species of *Bembicium melanostomum* (i.e. *B. nanum*) have also been found to move differently in the field over different periods of time (i.e. two 24 h periods, UNDERWOOD, 1977; 24 h, 1 and 2 weeks; CHAPMAN, 2000a). UNDERWOOD (1977) found that *N. atramentosa* and *A. porcata* moved similar distances but significantly further than *B. nanum*. In contrast, CHAPMAN (2000a) found that over 24 h, *A. porcata* dispersed further than the two others species. These differences have been related to topographic complexity, specific characteristics, interspecific interactions and feeding activities (CHAPMAN, 2000a). These differences could also be related to the different scales of observations, i.e. 48 and 24 h respectively in UNDERWOOD (1977) and CHAPMAN (2000a), as the distance travelled has been acknowledged as a scale-dependent metric (SEURONT *et al.*, 2004a). The patterns observed here cannot be thought as a behavioural response to abiotic factors as the complexity of the topography (CHAPMAN, 2000a) or biotic factors as the feeding (UNDERWOOD, 1977), since the experiments were done in controlled conditions in the absence of any cues after 36 h of starvation.

It is suggested that the observed behaviours

are instead (i) a reminiscence of the previous trophic conditions encountered in the field, i.e. an acquired behaviour and/or (ii) an innate behaviour inherited through natural selection at the evolutionary scale. The differences observed in the motion behaviour of *N. atramentosa*, *A. porcata* and *B. melanostomum* in the laboratory are consistent with their feeding ecology. *N. atramentosa* and *A. constricta*, a congeneric species of *A. porcata*, graze preferentially on microalgae (UNDERWOOD, 1978; QUINN and RYAN, 1989). In contrast, *B. nanum*, a congeneric species of *B. melanostomum* is more suitable to graze on macroalgae (QUINN and RYAN, 1989). *N. atramentosa* and *A. porcata*, and *B. melanostomum* are then expected to have developed foraging extensive and intensive search strategies, respectively. This is consistent with both the highly convoluted paths exhibited by *B. melanostomum*, and the more rectilinear paths of *N. atramentosa* and *A. porcata* that cover larger areas over the same duration (Figs. 2 and 3). This resource partitioning (WILSON and RICHARDS, 2000) constitutes a niche differentiation which favours coexistence (LEIBOLD and MCPHEEK, 2006) between the consumers of microalgae (i.e. *A. porcata* and *N. atramentosa*) and those of macroalgae (*B. melanostomum*).

It is also likely that the motion patterns

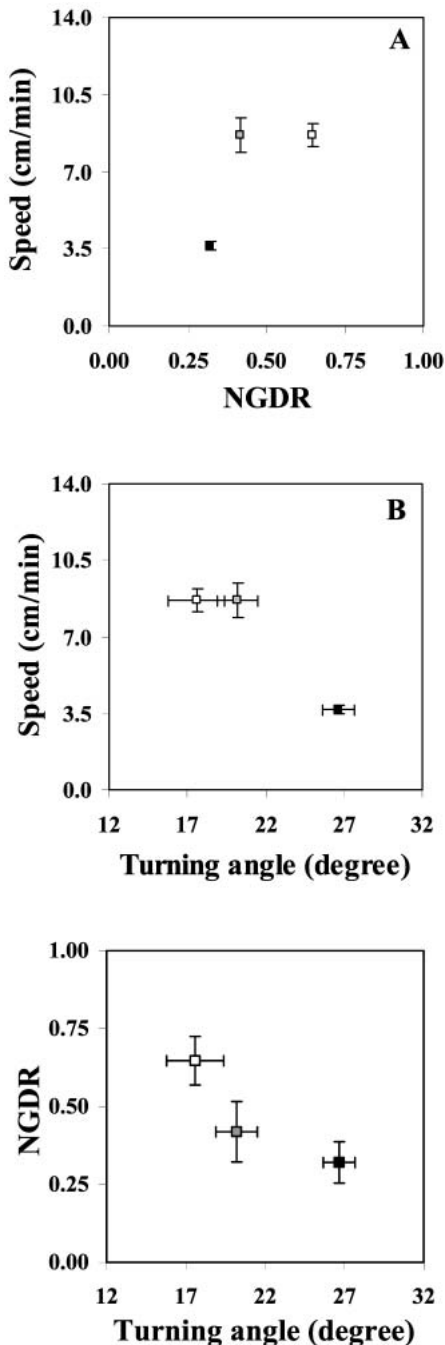


Fig. 3. Fig. 3. Speed as a function of net-to-gross displacement ratios (A) and turning angle (B). Net-to-gross displacement ratios as a function of turning angle (C) observed in *A. porcata* (grey), *N. atramentosa* (white) and *B. melanostomum* (black). Values are means and errors bars are standard errors.

observed in the laboratory are related to the spatial distribution of the preferential resources. Food items, notably microalgae, are heterogeneously distributed throughout the environment (SEURONT and SPILMONT, 2002; KLAASSEN *et al.* 2006). The related optimal foraging strategy would be to move linearly and to travel rapidly over long distances to maximize the chance of encounter with high food densities (HUGUES, 1980; ERLANDSSON and KOSTYLEV, 1995). We observed this typical motion behaviour in *A. porcata* and *N. atramentosa* (Fig. 2) which consume preferentially microalgae. Resource abundance can also influence the movement patterns of consumers. If the food is abundant at one location (e.g. the blade of a macroalgae), the forager will concentrate effort in this area (PYKE, 1984), thus moving tortuously. This is consistent with the area restricted displacements of *B. melanostomum* (Fig. 2). Finally, the differences observed between the motion behaviour of *A. porcata* and *N. atramentosa* may suggest an additional level of niche differentiation through specific behavioural adaptation. While these two species are both microphytobenthos grazers, they might have coevolved to exploit different levels of food patches, thus to minimise resource competition. However, our knowledge of gastropod spatial memory, learning performance and individuals abilities to collect and store information is still poor, and suggests that this area of research is still in its early age.

5. Conclusion

Quantitative comparisons of the motion behaviour of coexisting intertidal gastropods are still scarce in the literature. The present work complements the few studies conducted in the field which showed interspecific differences in the motion behaviour in response to abiotic and biotic factors. We found that interspecific differences in movement patterns still exist in three species of intertidal gastropods coexisting on the same rocky shore, even after 36 h of acclimation in the laboratory in the absence of any cues. The motion behaviour observed in the laboratory for *N. atramentosa*, *A. porcata* and *B. melanostomum* is consistent with their

feeding ecology and the recognised spatial properties of their resource. It is then consequently hypothesised that the observed patterns may be the result of acquired and/or innate properties driven by the history of the tested individuals and by natural selection, respectively. A thorough understanding of the determinism of gastropod motion behaviour is, however, still lacking, and the complexities highlighted by these experiments stress the need for further experiments to assess the relative part of innate and acquired in gastropod motion behaviour.

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References

- BISHOP, M.J., B.P. KELAHER, S.M. SHARP and M. VERHOEVEN (2007): Dispersal of the estuarine gastropod *Pyrazus ebeninus* is only weakly influenced by pneumatophore density. *J. Exp. Mar. Biol. Ecol.*, **340**, 62–69.
- BYERS, J.E. (2000): Effects of body size and resource availability on dispersal in a native and a non-native estuarine snail. *J. Exp. Mar. Biol. Ecol.*, **248**, 133–150.
- CHAPMAN, M.G. (1998): Variability in trail-following and aggregation in *Nodilittorina unifasciata* Gray. *J. Exp. Mar. Biol. Ecol.*, **224**, 49–71.
- CHAPMAN, M.G. (2000a): A comparative study of differences among species and patches of habitat on movements of three species of intertidal gastropods. *J. Exp. Mar. Biol. Ecol.*, **244**, 181–201.
- CHAPMAN, M.G. (2000b): Poor design of behavioural experiments gets poor results: examples from intertidal habitats. *J. Exp. Mar. Biol. Ecol.*, **250**, 77–95.
- CHAPMAN, M.G. and A.J. UNDERWOOD (1994): Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *J. Exp. Mar. Biol. Ecol.*, **179**, 145–169.
- CROWE, T.P. (1999): Limits to generality: seasonal and temporal variation in dispersal of an intertidal gastropod. *J. Exp. Mar. Biol. Ecol.*, **232**, 177–196.
- CROWE, T.P. and A.J. UNDERWOOD (1998): Testing behavioural “preference” for suitable microhabitat. *J. Exp. Mar. Biol. Ecol.*, **225**, 1–11.
- DAVIDSON, I.C., A.C. CROOK and D.K.A. BARNES (2004): Quantifying spatial patterns of intertidal biodiversity: is movement important? *Mar. Ecol.*, **25**, 15–34.
- DAVIES, M.S., M. EDWARDS and G.A. WILLIAMS (2006): Movement patterns of the limpet *Cellana grata* (Gould) observed over a continuous period through a changing tidal regime. *Mar. Biol.*, **149**, 775–787.
- EDGAR, G.J. (1997): Australian Marine Life: the plants and animals of temperate waters. Reed Books, Kew, 240–245.
- ERLANDSSON, J. and V. KOSTYLEV (1995): Trail following, speed and fractal dimension of movement in a marine prosobranch, *Littorina littorea*, during a mating and a non-mating season. *Mar. Biol.*, **122**, 87–94.
- ESPINOSA, F., J.M. GUERRA-GARCIA, D. FA and J.C. GARCIA-GOMEZ (2006): Effects of competition on an endangered limpet *Patella ferruginea* (Gastropoda: Patellidae): Implications for conservation. *J. Exp. Mar. Biol. Ecol.*, **330**, 482–492.
- HAMILTON, P.V. and M.A. WINTER (1982): Behavioural responses to visual stimuli by the *Littorina irrorata*. *Anim. Behav.*, **30**, 752–760.
- HUGUES, R.N. (1980): Optimal foraging theory in the marine context. *Oceanogr. Mar. Biol. Ann. Rev.*, **18**, 423–481.
- JERDE, C.L. and D.R. VISSCHER (2005): GPS measurement error influences on movement model parameterization. *Ecol. Appl.*, **15**, 806–810.
- KERR, B., M.A. RILEY, M.W. FELDMAN and B.J.M. BOHANNAN (2002): Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature*, **418**, 171–174.
- KLAASSEN, R.H.G., B.A. NOLET, J.A. van GILS and S. BAUER (2006): Optimal movement between patches under incomplete information about the spatial distribution of food items. *Theor. Popul. Biol.*, **70**, 452–463.
- LEIBOLD, M.A. and M.A. MCPEEK (2006): Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, **87**, 1399–1410.
- LEWINGS, S.C. and S.D. GARRITY (1983): Diel and tidal movement of two co-occurring neritid snails; differences in grazing patterns on a tropical rocky shore. *J. Exp. Mar. Biol. Ecol.*, **67**, 261–278.
- MARSHALL, P.A. and M.J. KEOUGH (1994): Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* (sowerby). *J. Exp. Mar. Biol. Ecol.*, **177**, 121–138.
- MICHEL, E., P.B. MCINTYRE and J. CHAN (2007): A snail’s space sets a snail’s pace: movement rates of *Lavigeria* gastropods in Lake Tanganyika, East Africa. *J. Mollus. Stud.*, **73**, 195–198.
- MORALES, J.M. and S.P. ELLNER (2002): Scaling up

- animal movements in heterogeneous landscapes: the importance of behavior. *Ecology*, **83**, 2240–2247.
- NG, J.S.S. and G.A. WILLIAMS (2006): Intraspecific variation in foraging behaviour: influence of shore height on temporal organization of activity in the chiton *Acanthopleura japonica*. *Mar. Ecol. Progr. Ser.*, **321**, 183–192.
- PARDO, L.M. and L.E. JOHNSON (2004): Activity and shelter use of an intertidal snail: effects of sex, reproductive condition and tidal cycle. *J. Exp. Mar. Biol. Ecol.*, **301**, 175–191.
- PARDO, L.M. and L.E. JOHNSON (2006): Influence of water motion and reproductive attributes on movement and shelter use in the marine snail *Littorina saxatilis*. *Mar. Ecol. Progr. Ser.*, **315**, 177–186.
- PETRAITIS, P.S. (1982): Occurrence of random and directional movements in the periwinkle, *Littorina littorea* (L.). *J. Exp. Mar. Biol. Ecol.*, **59**, 207–217.
- PYKE, G.H. (1984): Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.*, **15**, 523–575.
- QUINN, G.P. and N.R. RYAN (1989): Competitive interactions between two species of intertidal herbivorous gastropods from Victoria, Australia. *J. Exp. Mar. Biol. Ecol.*, **125**, 1–12.
- RAJASEKHARAN, M. and T.P. CROWE (2007): Intrinsic differences in dispersal between populations of gastropods separated by a few metres: Evidence from reciprocal experimental transplantation. *J. Exp. Mar. Biol. Ecol.*, **341**, 264–273.
- SEURONT, L., M. BREWER and J.R. STRICKLER (2004a): Quantifying zooplankton swimming behaviour: the question of scale. In: SEURONT, L. and P.G. STRUTTON (eds.), *Handbook of scaling methods in aquatic ecology: measurement, analysis, simulation*. CRC Press, Boca Raton, 333–359.
- SEURONT, L., A.C. DUPONCHEL and C. CHAPPERON (2007): Heavy-tailed distributions in the intermittent motion behaviour of the intertidal gastropod *Littorina littorea* (Linnaeus). *Physica A*, **385**, 573–582.
- SEURONT, L., J-S. HWANG, L-C. TSENG, F.G. SCHMITT, S. SOUISSI and C-K. WONG (2004b): Individual variability in the swimming behavior of the subtropical copepod *Oncaea venusta* (Copepoda: Poecilostomatoida). *Mar. Ecol. Progr. Ser.*, **283**, 199–217.
- SEURONT, L. and N. SPILMONT (2002): Self-organized criticality in intertidal microphytobenthos patch patterns. *Physica A*, **313**, 513–539.
- STAFFORD, R. and M.S. DAVIES (2005): Spatial patchiness of epilithic biofilm caused by refuge-inhabiting high shore gastropods. *Hydrobiologia*, **545**, 279–287.
- TILMAN, D. (1994): Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.
- UNDERWOOD, A.J. (1977): Movements of intertidal gastropods. *J. Exp. Mar. Biol. Ecol.*, **26**, 191–201.
- UNDERWOOD, A.J. (1978): An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia*, **33**, 185–202.
- WILSON, W.G., C.W. OSENBURG, R.J. SCHMITT and R.M. NISBET (1999): Complementary foraging behaviors allow coexistence of two consumers. *Ecology*, **80**, 2358–2372.
- WILSON, W.G. and S.A. RICHARDS (2000): Evolutionarily stable strategies for consuming a structured resource. *Am. Nat.*, **155**, 83–100.

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