

Heavy-tailed distributions in the intermittent motion behaviour of the intertidal gastropod *Littorina littorea*

Laurent Seuront^{a,b,*}, Anne-Charlotte Duponchel^b, Coraline Chapperon^b

^aSchool of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001, SA, Australia

^bEcosystèmes Littoraux et Côtiers, CNRS FRE 2816 ELICO, Station Marine de Wimereux, Université des Sciences et Technologies de Lille-Lille 1, 62930 Wimereux, France

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Abstract

The two-dimensional motion behaviour of the common intertidal gastropod *Littorina littorea* is investigated as a function of the immersion time from three sampling sites on an exposed rocky shore. A total of 90 individuals have been individually marked and tracked over 14 consecutive daylight low tide. Successive displacements show very intermittent behaviour, with a few localised large displacements over a wide range of small displacements. We show that successive displacements are described by flight length l_d heavy-tailed distributions with $P(l_d) \sim l_d^{-\mu}$. The very low values of the exponent μ ($\mu \approx 2.22, 2.43$ and 2.67) indicate that *L. littorea* flights fall into the category of super-diffusive processes. These exponents were significantly higher than the special value $\mu \approx 2$ analytically and theoretically predicted to be the most advantageous in optimising long-term encounter statistics, especially for low-prey-density scenario. As natural selection should favour flexible behaviour, leading to different optimum searching statistics, under different conditions, our results support the idea that the differences in food concentration and distribution encountered at the different sites by *L. littorea* led to different heavy-tailed distributions observed for the most extreme displacements.

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1. Introduction

Animal locomotion is a critical area of research where the interests of physiologists, functional morphologists, animal behaviourists, biologists, ecologists and evolutionary biologists meet. Most of previous behavioural studies have focused on steady-state movements, assuming that most locomotion occurs at constant speeds or that the variation in speed is unimportant. This intrinsically neglects the most extreme fluctuations such as Lévy flights in which increments are distributed according to a heavy-tailed distribution [1]. In the past 10 years an increasing interest has been devoted to these super-diffusive processes in physics [2–4]. Realisations of Lévy flights in natural phenomena are plentiful and range from fluid dynamics and

*Corresponding author. School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001, SA, Australia.
Tel.: +61 8 8201 5080; fax: +61 8 8201 3015.

E-mail address: laurent.seuront@flinders.edu.au (L. Seuront).

dynamical systems [5] to econophysics [6–8]. In biological systems, Lévy flights have first been proposed to describe the behaviour of foraging ants [5]. They have later been identified in marine microzooplankton [9], flies [10], parasitic protozoa [11], deer [12], wandering albatrosses [13], rat [14], gilt [15], reindeer [16], jackal [17], heterotrophic dinoflagellate [18] and seal [19].

The extreme fluctuations related to Lévy flights, or more generally heavy-tailed distributions, are particularly relevant in ecosystem studies as they might provide insights on the interplay between the spatial heterogeneity of the environment and the behavioural response of organisms to their need to locate resources in complex and unpredictable environments. In particular, quantitative models reveal how behaviour can mediate individual movement, such that deviations from a random walk or a Lévy flight may reveal specific foraging strategies. The assessment of how living organisms perceive and interact with their biotic and abiotic environment is thus critical to understand how they adapt to highly variable conditions [20,21], especially in the marine environment where intermittent fluctuations rule in the open water [22–28] and on the bottom [29,30].

Intertidal ecosystems localised in the seashore area defined by the highest and lowest tides are particularly well suited to the study of biophysical interactions and related behavioural processes. Organisms living in these environments must indeed survive wave action, exposure to air and heat during low tide and severe predation and competition for space [31,32]. In this context, we focus on the intertidal gastropod *Littorina littorea* (Fig. 1). This species plays a critical ecological role in many rocky, sandy and muddy coastal habitats of Western Europe through the control of algal growth and sediment dynamics, and the drastic alteration of the native intertidal communities of Eastern North America where it has been introduced in the early 18th century. The behaviour of such a key species can have a fundamental role in structuring benthic assemblages and it is, therefore, necessary to assess how it is affected by the biotic and abiotic properties of the environment. As motion behaviour is a fundamental lynch-pin in the overall ecological success of a species [33] and intertidal gastropods forage primarily under water, during cool, low tides or when ocean spray moistens the rocks [34], the objective of this work is to assess the potential effect of immersion time on the motion behaviour of *L. littorea* through the analysis of successive displacements recorded during 14 consecutive low tides at three sites characterized by increasing distances from the low tide limit and related immersion times. We demonstrate that successive displacements are highly intermittent and their probability density function exhibit a power-law behaviour indicative of heavy-tailed dynamics that differ according to the location. The abiotic and biotic processes that might have contributed to the observed dynamics are critically discussed, and the intermittent behaviour observed for *L. littorea* is compared with the Lévy flights behaviour previously identified in other biological systems.

2. Motion behaviour of the intertidal gastropod *L. littorea*

2.1. Study organism: the intertidal gastropod *L. littorea*

The edible or common periwinkle, *L. littorea*, is among the most abundant herbivorous gastropod molluscs of the Western and Northern European coasts. *L. littorea* was introduced to North America from Europe in the mid 1800s to Nova Scotia either through ballast waters or for food [35]. Since their arrival they have managed to out compete most local species to become the dominant herbivore in the rocky intertidal from New England to Chesapeake Bay [35]. Their spread was limited to most of the east coast of North America which is only compatible with the temperature ranges that exist in Europe [31].

L. littorea normally grow to about 2–3 cm in length [35] and have an average life span of 5–10 years [36]. The general morphology differs from region to region, but they have a dark grey or black conical shell (Fig. 1a) with spiral ridges that evolves towards a smooth surface with age. *L. littorea* is widely distributed on most rocky shores from the upper shore into the sublittoral, except in the most exposed areas. It can also be found in sandy and muddy habitats such as estuaries and mud-flats, and is fairly tolerant of brackish water. Like its land relative, the snail, *L. littorea* move on a muscular, ciliated foot secreting a film of slimy mucus on which they can slide and move [37]. They forage primarily under water or during cool, low tides or when ocean spray moistens the rocks [34] (Fig. 1b). When not walking and/or exposed to the sun for a long time, *L. Littorea* often seek shelter in a shaded crevice and seals the gap between its shell and the rock with mucus to

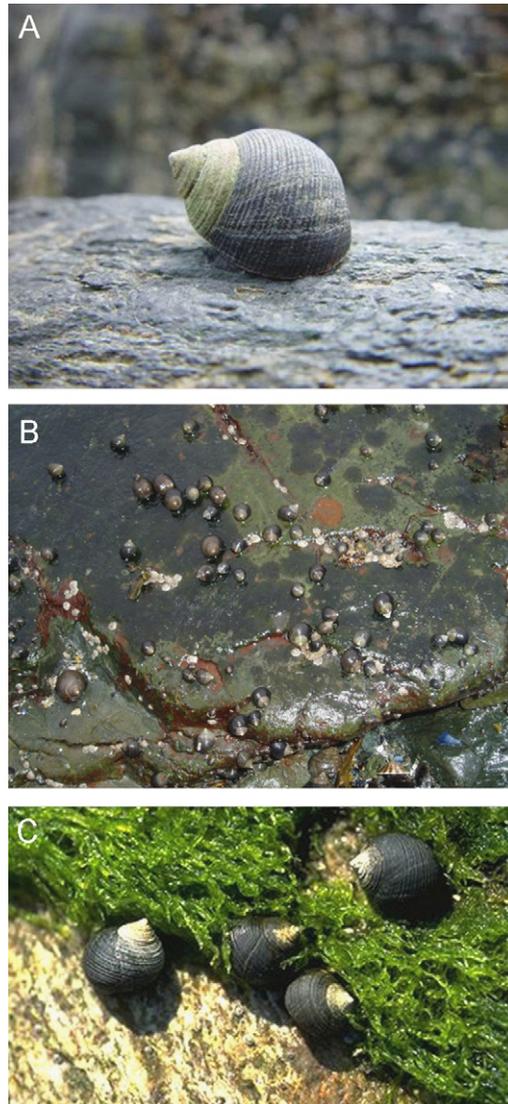


Fig. 1. The intertidal gastropod *Littorina littorea* shown in its typical rocky environment while sealed to a dry rock (a), foraging on a moistened rock platform (b) and grazing on the green alga *Enteromorpha intestinalis* (c).

avoid desiccation or being swept away by currents and breaking waves [38]. Periwinkles eat a wide range of food items from non-siliceous microalgae over diatoms to leathery and coralline macroalgae [39]. *L. littorea*, however, graze preferentially on periphyton (i.e., a complex matrix of microalgae, cyanobacteria, heterotrophic bacteria and detritus attached to submerged surfaces such as rocks) and ephemeral macroalgae [34] such as *Enteromorpha* sp. (Fig. 1c). This species is a very important grazer in intertidal ecosystems, as at high densities (i.e., up to 600–1000 m²; [35]), it will consume all ephemeral algae [40].

2.2. Recording successive displacement of *L. littorea*

We investigated the motion behaviour of *L. littorea* on a rocky platform typical of the rocky habitats found along the French coast of the Eastern English Channel. This platform ranges over the whole intertidal zones, bounded between the upper and lower limits reached by the tidal flow at high and low tide, respectively. The topography of the platform was homogeneous, dominated by bare rocks partially covered by the common barnacle *Balanus balanoides* with few cracks and crevices occupied by the blue mussel *Mytilus edulis*. Three

sites were chosen for their decreasing immersion time during high tide at 50 m (site A), 90 m (site B) and 130 m (site C) from the lower limit of the low tide, and were all submersed at high tide. At each site, a preliminary study investigated the density and the size of *L. littorea* from the observations conducted using five randomly spaced 1 m² quadrats. No significant differences were found in *L. littorea* abundances between sites (Kruskal–Wallis *H*-test, $p < 0.05$) leading to an average density of 152 ± 21 ind m⁻². In contrast, the sizes s of *L. littorea* were, however, significantly different between sites (Kruskal–Wallis *H*-test, $p > 0.01$, $N = 500$) with $s = 15.32 \pm 0.08$ mm ($\bar{x} \pm$ SD) at site A, $s = 14.71 \pm 0.07$ mm at site B and $s = 13.61 \pm 0.10$ mm at site C. This increase in size with the distance from the limit of the lowest tide is related to the ontogenic migration performed by a variety of intertidal gastropod to reduce predation and intraspecific competition [41–43]. At each of the three locations, 30 specimens *L. littorea* were captured, individually measured and marked with numbered plastic tags (2 mm \times 3 mm) fixed to the dorsal part of the shell with inert glue and released from a single point. The shell size of the three groups of individuals were significantly different (Kruskal–Wallis *H*-test, $p < 0.01$) with 15.27 ± 0.15 mm at site A, 14.68 ± 0.17 mm at site B and 13.69 ± 0.18 mm at site C; these measurements are consistent with our preliminary observations. After the release of individuals on 20 March 2006, the three release sites were searched on 14 successive daylight low tides. The direction of a sighted *L. littorea* from the release stake was measured with a compass and distance (nearest centimetre) with a tape. The actual distances travelled from one low tide to the next were actually estimated as

$$\sqrt{(d_{t+1} \sin \alpha_{t+1} - d_t \sin \alpha_t)^2 + (d_{t+1} \cos \alpha_{t+1} - d_t \cos \alpha_t)^2}, \quad (1)$$

where α_{t+1} and α_t , and d_{t+1} and d_t are the angle and distances measured from the release stake on two consecutive daylight low tides. Each site thus provided 420 measurements of distance travelled. No movements were observed at low tide during the distance measurements.

3. Intermittency and heavy-tailed foraging in *L. littorea*

The successive displacements of *L. littorea* (Fig. 2) are consistently characterized by a very intermittent behaviour, with a few localised large displacements over a wide range of small displacements (Fig. 3). The corresponding displacements ranged from 1 to 1558 cm (81.1 ± 161.1 cm) in site A, 1 to 858 cm (73.2 ± 93.8 cm) in site B, and 1 and 1084 cm (71.6 ± 96.7 cm) in site C. These intermittent distributions result in significantly non-normal distribution ($p < 0.01$) with elevated positive skewness g_1 , $g_1 = 6.1$, 3.4 and 5.1 in sites A, B and C, respectively. None of the distributions were statistically different from each other (Kruskal–Wallis *H*-test, $p > 0.05$).

To further quantify the property of the extreme displacements leading to the observed positively skewed distributions, we considered the probability density function of *L. littorea* successive displacements, and focused on the tail of the distribution which can be expressed using the hyperbolic form:

$$P(l_d = l) = kl^{-\mu}, \quad (2)$$

where l_d is the displacement length, l a threshold value, k a constant and μ ($1 < \mu \leq 3$) characterize the power-law behaviour of the tail of the distribution. Eq. (2) corresponds to a family of distributions defined according to the values of μ . These distributions mean that extremely long movements occurred more often than would be expected if the forager exhibited movement lengths with a normal distribution. For $\mu \geq 3$, the distribution is Gaussian (which according to the central-limit theorem has a finite variance) and the motion is equivalent to Brownian motion walks. For $2 \leq \mu < 3$, the scaling is super-diffusive [2], while the value $\mu = 2$ indicates that the scaling becomes quadratic in time, and corresponds to the lower extreme of super-diffusive processes, i.e., Lévy flight [2]. In contrast, values $\mu \leq 1$ do not correspond to probability distribution that can be normalised [2]. The smaller μ is, the more intermittent is the distribution. When $\mu \leq 3$, the variance of the process diverges, and when $\mu \leq 2$ the mean is not defined.

The parameters μ were estimated for sites A, B and C as the slope of $P(l_d)$ versus l_d in log–log plots (Fig. 4). We used linear regression on the log-transformed data instead of nonlinear regression on the raw data as the residual error will be distributed as a quadratic and the minimum error is not guaranteed. This is not the case with nonlinear regression [29]. Finally, because an objective criterion is needed for deciding upon the

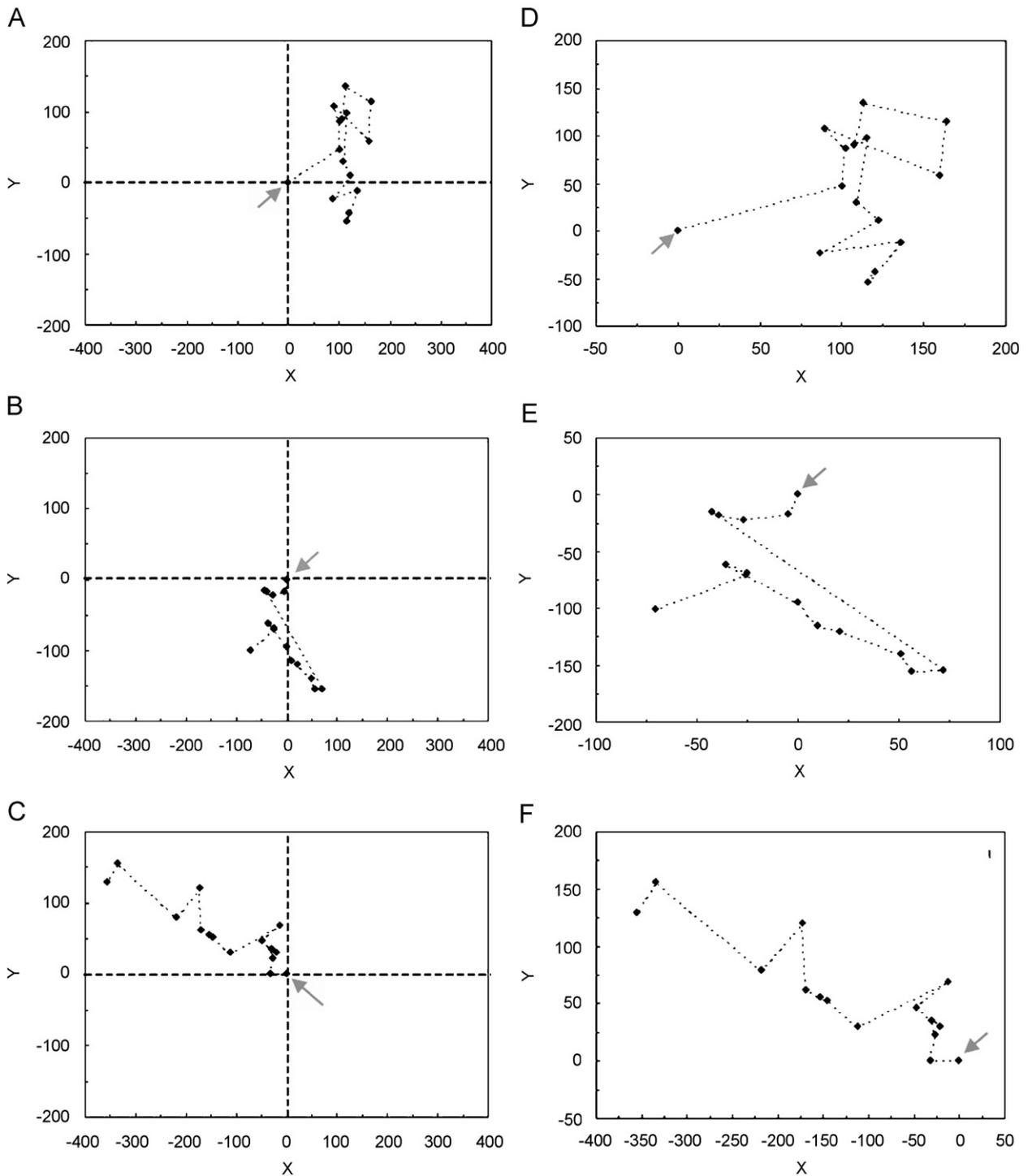


Fig. 2. Illustration of *Littorina littorea* motion behaviour on the same referential (a–c) and after enhancement (d–f). The grey arrows indicate the release stake, and units are given in centimetre.

appropriate range of l_d values to be included in the regression, we used $P(l_d)$ and l_d values which maximised the coefficient of determination and minimised the total sum of the squared residuals for the regression. The values of μ estimated from *L. littorea* displacements were all significantly higher than 2 ($p < 0.01$), and

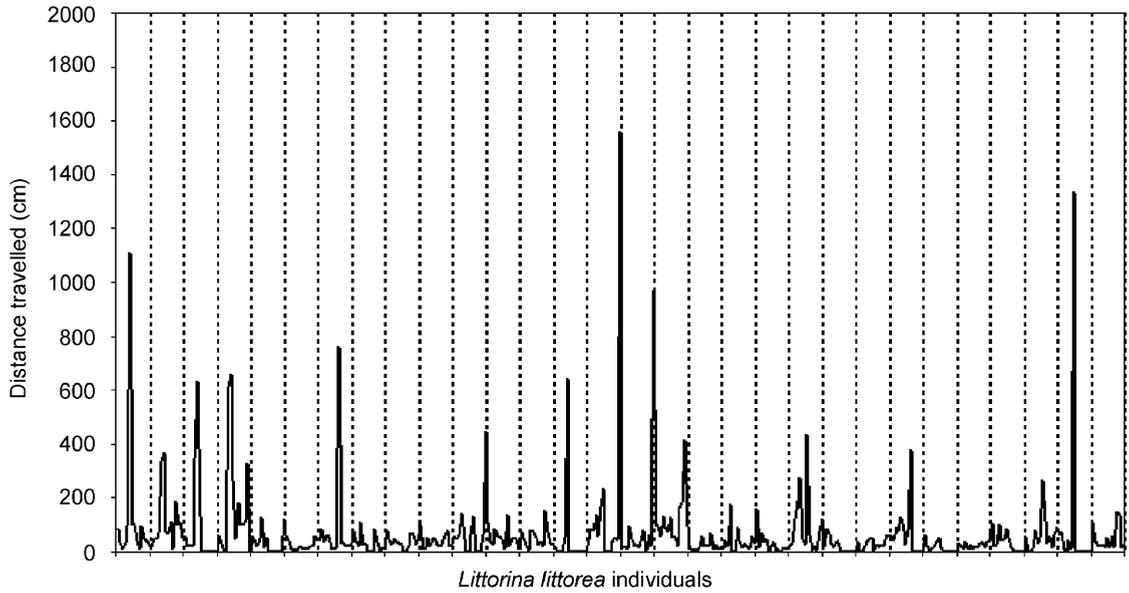


Fig. 3. Illustration of the intermittent character of successive displacements in *Littorina littorea* motion behaviour observed at site A located 50m away from the lower limit of low tide. Each dotted line separates the 14 successive records of each of the 30 tracked individuals.

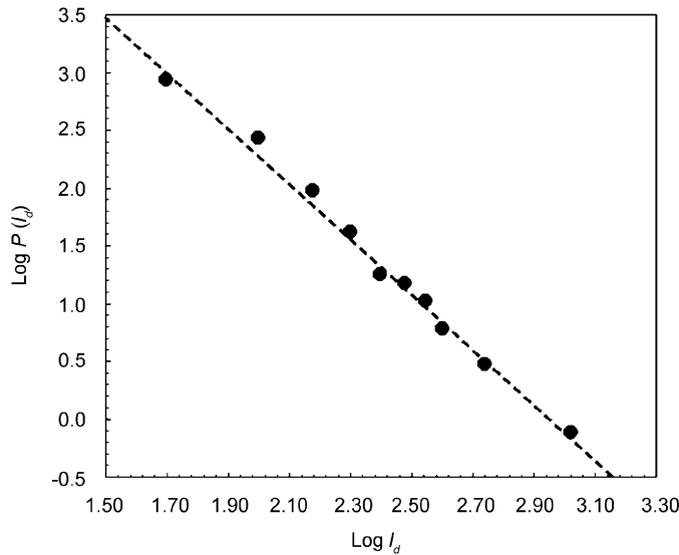


Fig. 4. Log–log plot of the probability distribution function of *Littorina littorea* successive displacements investigated at site B located 70m away from the lower limit of low tide. The dotted lines correspond to the best linear fit of $P(l_d)$ versus $P(l_d)$, leading to estimate the exponent μ as $\mu = 2.43 \pm 0.05$.

significantly different from each other ($p < 0.01$) with $\mu = 2.22 \pm 0.02$ for site A, $\mu = 2.43 \pm 0.05$ for site B and $\mu = 2.67 \pm 0.04$ for site C. The scaling then falls into the category of super-diffusive processes, i.e., $\mu \leq 3$. These values are very low and indicate that the variance of the distribution diverge. This has direct and practical implications as μ can be conveniently used as an estimate of the critical order of divergence of moments, as moments of order μ will diverge as

$$\langle l_d^\mu \rangle = \int l^\mu P(l) dl \geq k \int \frac{dl}{l} \rightarrow \infty, \tag{3}$$

where ‘ $\langle \rangle$ ’ indicate ensemble averaging. In practice, this means that the value of the variance of the displacement length depends on the number of successive displacements taken into account. Increasing the number of observations will simply lead to increase the variance of the displacement length, which is similar to the second-order phase transition related to sampling limitations [44]. However, because the distances we have considered here have an upper bound (i.e., the maximum possible displacements is the maximum possible speed of a gastropod multiplied by 24 h), Eq. (3) produces finite moments.

4. Discussion

4.1. Intermittency in *L. littorea* motion behaviour

The increase in the parameter μ with increasing distances from the lower limit of the low tide suggests that the intermittency of movement patterns increases with increasing immersion time. This is consistent with reported increase in periwinkles foraging activity when underwater at high tide [34]. The maximum displacements observed here (1558, 858 and 1084 cm for sites A, B and C, respectively) are also consistent with the movement speed found in the literature for *L. littorea*, ranging from 3 to 5 cm min⁻¹ [45]. Considering that between two successive daylight low tides (ca. 24 h), the three sites were submersed between 30% and 50% of the time (i.e., 8–12 h), the expected displacements ranged from 1440 to 3600 cm. Finally, despite the significantly different sizes of the test organisms considered at sites A, B and C, no significant differences were found between the average distances travelled during the 14 days of the survey. This indicates that the significant differences in the immersion time encountered at sites A, B and C did not affect the mean distance travelled. This is consistent with the significant increase observed in *L. littorea* speed v from site C to A, i.e., $v = 3.2 \pm 0.1$ cm s⁻¹ at site C ($N = 20$), $v = 3.9 \pm 0.1$ cm s⁻¹ at site B ($N = 16$) and $v = 4.4 \pm 0.2$ cm s⁻¹ at site A ($N = 18$; Seuront, unpublished data). As *L. littorea* forage primarily under water or during cool, low tides [34], it is likely that the observed differences in motion velocity balanced the decrease in immersion time between sites.

4.2. Heavy-tailed distributions in *L. littorea* motion behaviour

We also investigated the potential causal relationships between *L. littorea* successive displacements and the main abiotic forcing factors characterizing the sampling sites. Immersion time, seawater temperature and sea conditions are thus likely to impact *L. littorea* motion behaviour as these organisms increase their activity when underwater [34] or when temperature is raising [45,46]. In turn, increased hydrodynamic conditions such as tidal currents and breaking waves may dislodge them and advect them far away. However, no significant correlations were observed with immersion time, seawater temperature or sea conditions (approximated by wind speed as winds are the main factor responsible for the formation of breaking waves in this area, [47]). As no wave breaking events were recorded on the sampling site over the duration of our experiments, the main source of dislodgments might have been related to the strong tidal currents occurring in the area, i.e., 5–120 cm s⁻¹ [48]. To assess the strength of *L. littorina* attachment to the substrate under strong current conditions, a set of 50 individuals from each sampling site were immersed in a circular flume and acclimatised for 20 min, a duration necessary for *L. littorina* individuals collected in the field to re-attach to the substrate [45]. A steady flow ranging from 10 to 150 cm was then generated by surface friction of rotating circular PVC plates. Each group of *L. littorina* individuals was submitted for 30 min to flow velocities of 10, 25, 50, 100 and 150 cm s⁻¹, and for each flow velocity the number of individuals dislodged by the current was recorded. None of the 150 individuals considered (i.e., 50 per sampling site) got dislodged by the simulated flows, supporting the fact that the observed intermittency in *L. littorea* motion behaviour is very unlikely related to the transport of dislodged individuals along the bottom by tidal currents.

As *L. littorea* successive displacements exhibit heavy-tailed distributions, it is hypothesised that similar driving processes, expectedly biotic, are driving the dynamics of distance travelled by *L. littorea*. In particular, the structure of *L. littorea* motion behaviour is likely to be driven by the spatial distribution of resource. In the absence of any macroalgae on the study sites, the only food source available to *L. littorea* was the microflora attached to the substrate surface. We are not aware of any attempt to quantify the spatial distribution of

microflora on rocky substrate at scales relevant to the behavioural ecology of *L. littorea*. However, recent studies have illustrated the heavy-tailed properties of the spatial distribution of microflora on sandy and muddy substrates [29,30]. Assuming similar properties of microflora on rocky surfaces, the heavy-tailed properties observed in *L. littorea* motion behaviour could be related to the spatial distribution of their food. These distributions are intrinsically characterised by a few dense patches occurring over a background of low-density patches [29,30]. The intermittent distribution observed in *L. littorea* motion behaviour (cf. Fig. 3) may then reflect the alternation between periods when the organisms feed within food patches (intensive search with small successive displacements) as opposed to the search for new patches (extensive search with large displacements) as previously illustrated for the foraging behaviour of beetles [49]. This type of behaviour is also consistent with the chemical cues associated by the mucus trails of conspecific that may accelerate the utilisation of patchy food resources [50,51], but also aid navigation [52–54], homing [55], aggregation behaviour [56] and mating [45].

4.3. Heavy-tailed behaviour in other biological systems and its ecological relevance

By simulating a limiting generalised searcher–target model (e.g., predator–prey, mating partner, pollinator–flower and parasite–host), recent theoretical results indicate that Lévy walks confer a significant advantage over the usual Gaussian (i.e., Brownian) motion for increasing encounter rates when the searcher is larger or moves rapidly relative to the target, and when the target density is low [57–59]. More specifically, among heavy-tails distributions, a Lévy flight foraging strategy is advantageous when resources are randomly distributed because the probability of returning to a previously visited site is smaller than for a normal distribution [59,60]. The behaviour of organisms that fits a Lévy distribution thus suggests that food patches used by these organisms are randomly distributed. In addition, a Lévy distribution is preferable because the number of new sites visited is greater than for simple random walkers under typical Brownian motion [61]. A range of organisms, both invertebrate [9–11,18] and vertebrate [12–17,19], have thus been shown to perform Lévy flights, i.e., $\mu = 2$. A few studies have investigated the effect of food density on the stochastic properties of foraging behaviours [18,60], and demonstrated a shift from a Lévy flight foraging strategy at low food concentration to a random walk (i.e., Brownian motion) at high food concentration for selected marine and terrestrial invertebrate, mammal and bird species. The heavy-tailed distributions observed here (i.e., with $\mu = 2.22, 2.43$ and 2.67) significantly diverges from Lévy walks where $\mu = 2$. According to optimal foraging theory [62], evolution through natural selection should favour flexible behaviour, leading to different optimum searching strategies (i.e., searching statistics) under different conditions. Our results then suggest that the biotic conditions encountered at each of our three sites might have been different, leading to different (heavy-tailed) distributions for the most extreme displacements. In particular, the increase in the value of μ in *L. littorea* motion behaviour at sites characterised by increased immersion times suggests that (i) the food concentration is higher, and/or (ii) the food is more patchy at locations immersed for longer periods. These two hypotheses are consistent with recent work demonstrating an increased in both microflora biomass and patchiness under conditions of increased immersion [63].

It is finally stressed that while an inverse square probability density distribution $P(l_d) \sim l_d^{-2}$ of step lengths l_d leads to an optimal random strategy for organisms searching for randomly located objects that can be revisited any number of times [57,62], we are not aware of any attempt to investigate this issue when prey items are heterogeneously distributed as previously reported for the sampling site [29,30]. While this is not an easy task, future work should concentrate their effort in getting simultaneous measurements of predator motion behaviour and prey concentration and distribution. As the main biotic factors driving organism motion behaviour is the presence/absence, abundance and distribution of prey items, predators and mates, further investigations on the interplay between motion behaviour statistics and the qualitative and quantitative nature of the biotic environments are critical to gain new insights into the origin of heavy-tailed distributions in biological systems.

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