

Movement patterns in the green sea urchin, *Strongylocentrotus droebachiensis*

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Time-lapse video was used to record movement paths of *Strongylocentrotus droebachiensis* on a rocky bottom at 8 m depth, both at a grazing front and in recently formed barrens in the wake of the front. Urchins did not exhibit strong directionality in movement and we did not detect any differences in movement variables between the front and barrens. Density of conspecifics had a negative effect on the speed, move length (distance), and daily displacement of urchins, but did not significantly affect the proportion of time spent moving, the linearity index and the number of moves taken per day. The frequency distributions of turning angles between moves and steps were non-uniformly distributed, indicating directionality in individual paths. A correlated random walk model was used to predict the displacement of urchins through time and provided a good fit with observed data. Our results provide insight into the foraging behaviour of *S. droebachiensis* and are consistent with previous observations of small-scale movement in this species.

INTRODUCTION

The path followed by an animal in search of food affects its foraging efficiency (Kareiva & Shigesada, 1983). Theoretical studies have examined the fitness consequences of foraging movement in context of optimality theory (Viswanathan et al., 1999; Wilson & Richards, 2000); however, empirical data available to test models remain scarce. Some intrinsic difficulties associated with the study of movement may explain this lag between theoretical and empirical work (Turchin, 1998). Many animals have movements that appear erratic and irregular, which complicates the analysis of pattern. The use of random walk models provides a theoretical framework to quantify succinctly these movement patterns (Kareiva & Shigesada, 1983). Levin (1992) views the use of random walk and diffusion models as the most successful applications of mathematics to an ecological phenomenon. This is reflected by the applicability of these models to a wide range of animal taxa (e.g. insects, Kareiva & Shigesada, 1983; caribou, Bergman et al., 2000; seals, Austin et al., 2004).

Aside from their importance in determining individual fitness (Turchin, 1998), movement patterns also are key to understanding ecological processes that regulate community structure, such as predation and grazing (Lubchenco & Gaines, 1981). A prime example is the switch from productive kelp beds to less productive barrens that results from a change in the foraging behaviour of sea urchins (Scheibling & Hatcher, 2001). In the north-west Atlantic, destructive grazing by the green sea urchin, *Strongylocentrotus droebachiensis* (Müller), is preceded by the formation of dense feeding aggregations or ‘fronts’ (Scheibling et al., 1999; Gagnon et al., 2004). In the absence of these aggregations, urchins have little impact

Table 1. Date of sampling, location and density of urchins in nine time-lapse video samples from Little Duck Island, Nova Scotia.

Sample	Date	Location	Density (urchin m ⁻²)
A	30 June 1993	Front	272
B	14 July 1993	Front	121
C	30 August 1993	Front	150
D	11 July 1995	Front	113
E	13 July 1995	Front	172
F	09 August 1995	Front	153
G	24 August 1993	Barrens	53
H	29 June 1995	Barrens	206
I	14 August 1995	Barrens	41

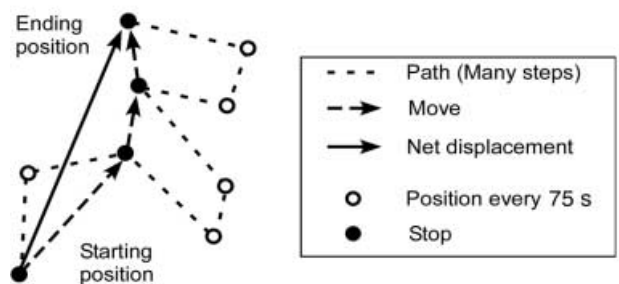


Figure 1. Schematic representation of an urchin's path showing successive positions (at 75 s intervals), steps between positions, stops, moves between stops, and net displacement (see Materials and Methods for further explanation of path descriptors).

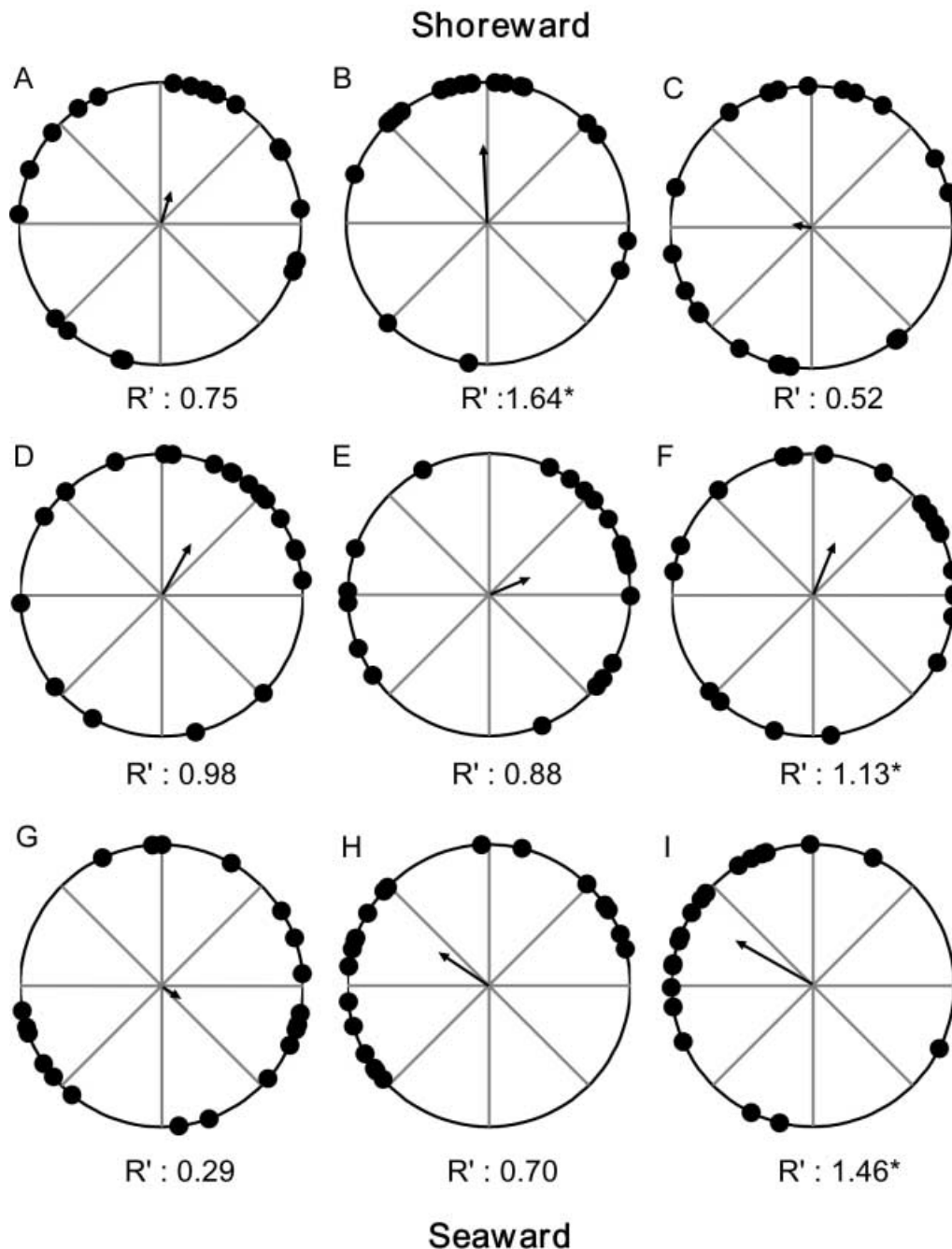


Figure 2. Direction of displacement for 20 urchins per video sequence. Arrows indicate the direction and magnitude of the mean vector (r). Top of plots is directed toward shore. Moore's modification of Rayleigh's test weighted by distance (R') is given under each plot and values marked by an asterisk (*) are statistically significant ($P < 0.05$). (A–F) Front samples; (G–I) barrens samples (see Table 1 for details).

on kelp beds, which persist for many years. Given the impact of such profound habitat shifts on the benthic community, it is important to understand how movement patterns can lead to the formation and maintenance of feeding fronts.

Previous studies of movement in urchins have measured distance and direction travelled over intervals ranging from hours to days (James, 2000; Duggan & Miller, 2001; Dumont et al., 2004; Tuya et al., 2004). In this study, we use time-lapse video to measure movement patterns of *S. droebachiensis* at smaller temporal scales (minutes to hours), and to examine the effect of conspecific density on

movement. We use these empirical measures to parameterize a correlated random walk model that adequately describes the observed patterns. To our knowledge, our study is the first to examine the fine-scale movements of urchins, which underlie larger-scale patterns such as the formation of feeding aggregations.

MATERIALS AND METHODS

Study site

This study was conducted at Little Duck Island (44°22'N 64°11'W), at the mouth of Mahone Bay on the

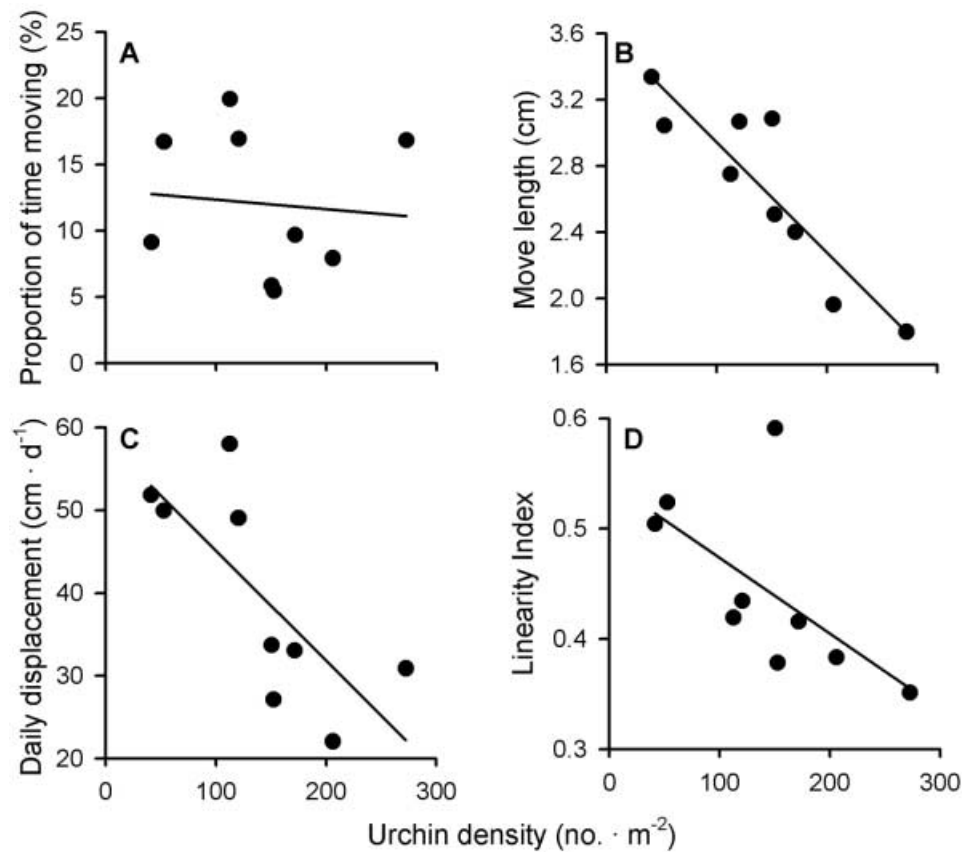


Figure 3. Linear regressions of (A) proportion of time spent moving; (B) move length; (C) daily displacement; and (D) linearity index (see Table 2) per video sample on urchin density.

Table 2. Linear regression analysis of movement variables (video sample means, $N=20$ urchins) on urchin density. Net square displacement and daily displacement are calculated using the correlated random walk model. Significant regression coefficients ($P < 0.05$) are shown in bold.

Variable	Intercept (SE)	Slope (SE)	t	P	r^2
Proportion of time moving (%)	13.063 (4.541)	-0.007 (0.029)	-0.247	0.812	0.009
Speed (cm h ⁻¹)	15.126 (2.573)	-0.041 (0.016)	-2.532	0.039	0.478
Move length (cm)	3.608 (21.983)	-0.007 (0.001)	-5.393	0.001	0.806
Daily displacement (cm d ⁻¹)	58.437 (6.940)	-0.133 (0.044)	-3.021	0.019	0.566
Linearity index	0.542 (0.051)	-0.001 (3×10^{-4})	-2.132	0.070	0.394
Step length (cm)	3.749 (0.194)	-0.008 (0.004)	-2.181	0.066	0.405
Number of moves h ⁻¹	3.192 (0.916)	-0.001 (0.006)	-0.208	0.841	0.006
Number of steps move ⁻¹	1.934 (0.562)	-0.002 (0.001)	-1.805	0.114	0.317
Net square displacement (cm ² d ⁻¹)	3218.241 (570.116)	-10.629 (3.616)	-2.939	0.022	0.552

SE, standard error.

Atlantic coast of Nova Scotia, Canada. The site is located in the lee of the island and protected from the prevailing south-westerly swells in summer. The substratum is characterized by broad ridges of heavily grooved basaltic bedrock. During our study, a kelp bed consisting mainly

of *Laminaria longicuris* (De La Pylaie) extended from the shore to a depth of 5–8 m (below chart datum). An active grazing aggregation (or front) of sea urchins (*Strongylocentrotus droebachiensis*) was advancing shoreward along the lower margin of the bed at rates of 1–4 m per

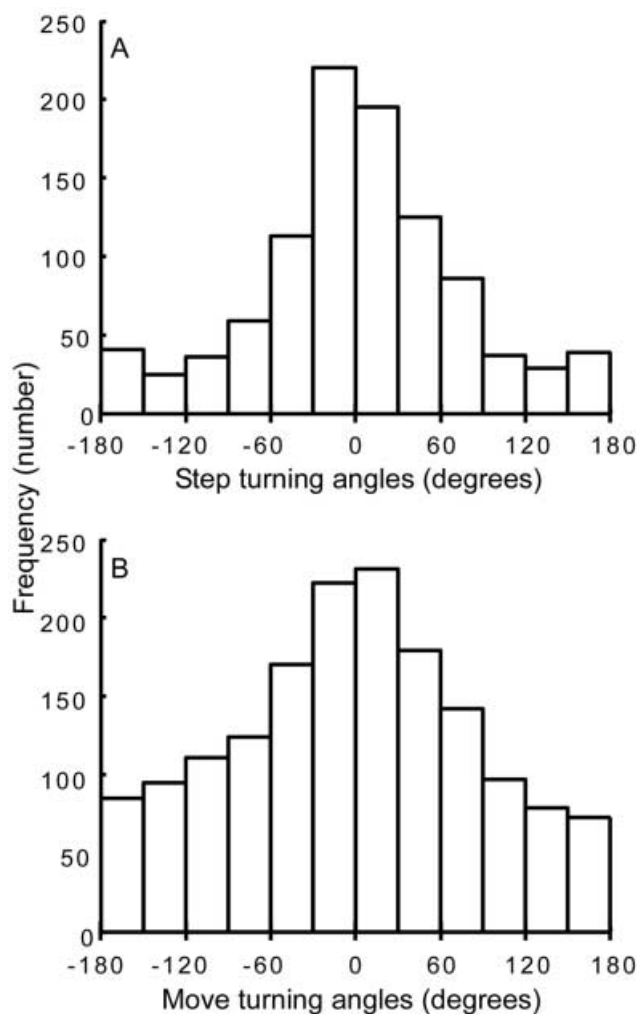


Figure 4. Frequency distribution of turning angles (A) between steps and (B) between moves for data pooled over all video samples.

month by destructively grazing all kelps and erect, non-corralline algae. The front was mainly composed of large adult urchins (38 to 51 mm in test diameter) at densities ranging from 200 to 350 urchins m^{-2} . In the wake of the front, corallines were the only remaining algae and the density of urchins in the barrens was lower than in the front, with mean density ranging from 56 to 108 urchins m^{-2} . For a more detailed description of the study site and the urchin population, see Scheibling et al. (1999).

Movement analysis

Urchin movement was recorded in nine time-lapse video sequences between 6 June 1993 and 14 August 1995 (Table 1): six along the trailing edge of the grazing front and <1 m from kelp bed, and three in the barrens habitat > 5 m from the front (Table 1). A video camera (Sony WPC 140) attached to a supporting framework was deployed by SCUBA divers. The camera was connected to a time-lapse (1 s of video was recorded every 15 s) video recorder (Fuhrman Diversified, Inc., Seabrook, TX) set to record for a period of ~5 h. The area photographed was ~0.9 m^2 as estimated using a graduated 1-m pole placed

on the bottom within the field of view. Videos were digitized for analysis of urchin movement.

A sample of 20 urchins was obtained for each video sequence by projecting a set of 20 random points onto the initial frame and selecting urchins closest to each point. The position of each urchin was recorded as Cartesian coordinates every 75 s for the entire sequence or until the urchin left the field of view. From these coordinates we were able to reproduce the path followed by an urchin through time, and record the location and duration of stops. A stop is defined as an interval when an urchin remains stationary during at least 75 s (two successive frames). The path of each urchin could then be divided into moves and steps (Figure 1) (Turchin, 1998). A step is defined by the vector connecting two successive positions (75 s apart). A move is the vector connecting two successive stops and can be composed of one or more steps. The direction and length of each move and step vector, and the turning angle between two successive steps (θ_s) or moves (θ_m), were recorded for each of the sampled urchins in a video sequence. The step (or move) direction is the direction of the displacement relative to the shore (0° being shoreward, 180° being seaward), and the turning angle is the difference between two successive step (or move) directions. The presence of a directional bias was evaluated using Moore's modification of Rayleigh's test, which is weighted by distance for a uniform distribution (Zar, 1999). Based on the urchin's paths, we also calculated the mean speed (total distance travelled divided by total time), the mean step and move length, the proportion of time spent travelling, the linearity index (net displacement divided by the total distance travelled), and the direction and length of the mean vector (\bar{r}) describing the distribution of angles (Zar, 1999) for each video sequence.

Urchin density was estimated for each video sequence by averaging counts of urchins in the first and last frame and dividing by the area in the field of view (Table 1; the difference in counts between the first and last frame in all cases was small). We examined the relationship between movement variables (mean speed, mean daily displacement, mean proportion of time spent moving, mean step length, mean move length, and mean linearity index) and urchin density by linear regression. We pooled data from urchin front and barrens sequences because no significant differences in movement variables were detected between locations (*t*-test, $P > 0.05$). Homoscedasticity and linearity assumptions were assessed by visual inspection of residuals (Draper & Smith, 1998). The distribution of turning angles between steps and between moves was tested against a uniform distribution using Rayleigh's z statistic (Zar, 1999).

Overall, 67% of urchins remained in the camera's field of view until the end of the video sequence and the mean period of observation per urchin was 3.70 h (± 0.31 , SE), giving 664 urchin hours of observation (sum of observation times over all urchins).

Movement simulations

To test whether the movement of urchins can be accurately described using a correlated random walk (CRW) model (Kareiva & Shigesada, 1983), we simulated 1000 paths, each composed of N moves (after Turchin, 1998).

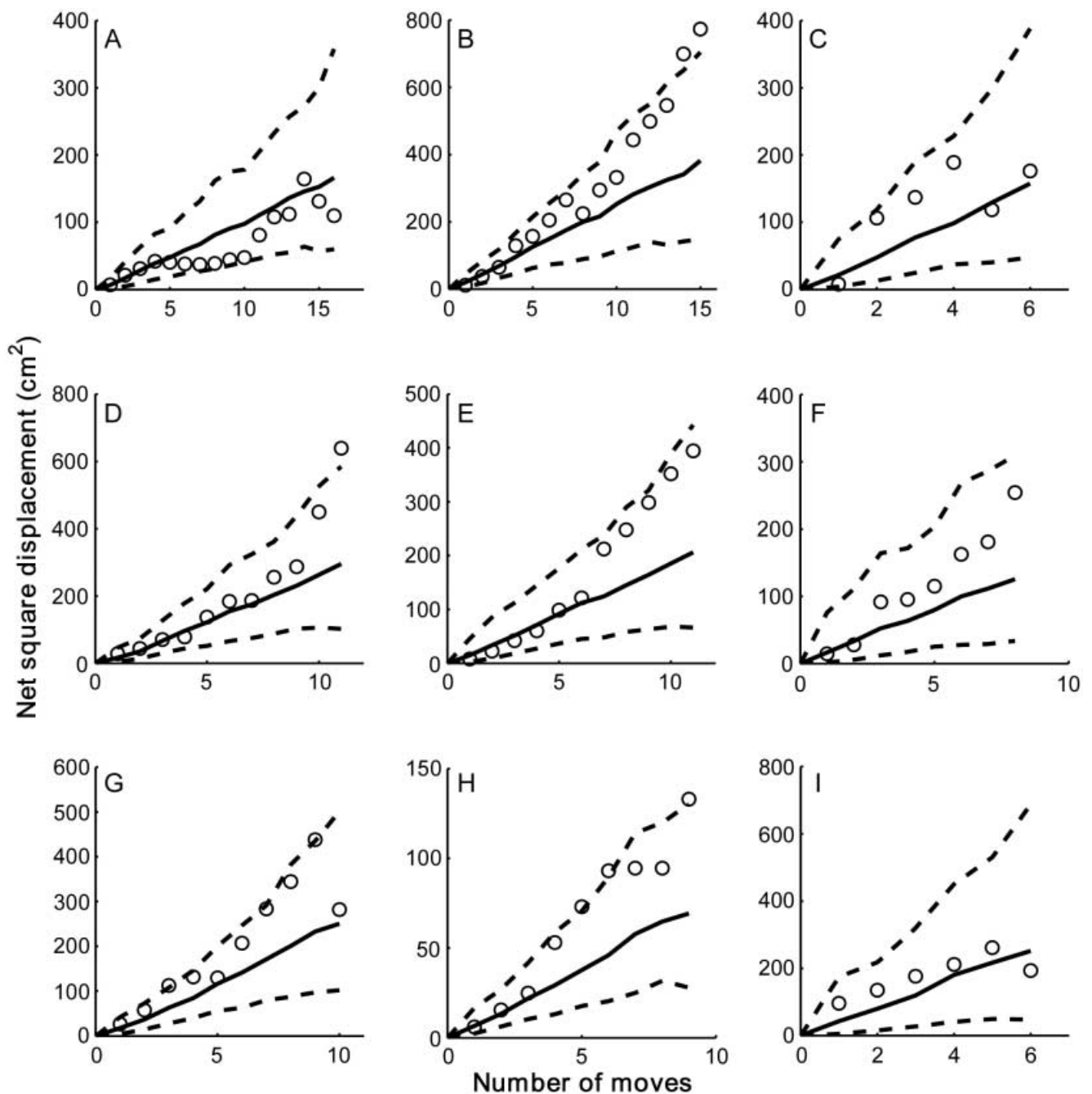


Figure 5. Mean net square displacement (solid line) and 95% CI (dashed line) over 6–15 moves predicted by a correlated random walk model and that observed (open circles) for each video sample. (A–F) Samples from front; (G–I) samples from barrens (see Table 1 for details).

The total number of moves per path simulated by the model varied among video sequences and was equal to the largest number of moves taken by at least five urchins in a sequence. Each of the 1000 paths was simulated by randomly selecting N turning angles between moves and N move lengths from the respective empirical distributions for each video sequence. Once the paths were obtained, the mean net square displacement was calculated as the mean of the squared distance displaced for all simulated paths and the 95% confidence interval (CI) was estimated by the percentile method (Manly, 1997). We then compared the mean net square displacement observed in our video sequences to the values predicted by the CRW

model. We used the I-statistic developed by Austin et al. (2004) to assess the overall fit of the model. This statistic provides an index of the proportion of observations that lie outside of the CIs of the model predictions.

Prior to generating correlated random walks, we tested our data for autocorrelation between subsequent move lengths as well as for autocorrelation between subsequent turning angles for each urchin followed (Turchin, 1998). We did not detect any autocorrelation in turning angles between subsequent moves. We detected autocorrelation of movement distance in no more than 1 individual per sample, which is to be expected using a probability of

type-I error equal to 0.05 (1 urchin out of 20), and decided to proceed with the CRW model. Furthermore, in the presence of adequate fit, small deviations from the auto-correlation assumption of a CRW model can be dismissed (Turchin, 1998).

Mean daily displacements were estimated by running the correlated random walk simulations for the expected number of moves made by an urchin during 24 hours (number of moves $h^{-1} \times 24$ h).

Image analysis and simulations were done in MATLAB (The MathWorks, Natick, MA, USA).

RESULTS

Observed densities of urchins ranged from 41 to 272 urchins m^{-2} . Although urchin densities were generally higher in the front (163.5 ± 23.5 urchins m^{-2}) than in the barrens (100 ± 37.6 urchins m^{-2}), they did not differ significantly between locations ($t_7=1.299$, $P=0.235$). This is attributable to the low sample size (3) in the barrens, which included one sample (video sequence H) with a higher density than most of the front samples (Table 1).

Urchins appeared to travel in a common direction in three of our nine video sequences: two in the front, one in the barrens (Figure 2). In each of these cases, the mean direction was oriented shoreward, but the mean vector was relatively small ($r=0.4$ to 0.6), indicating a weak correlation among individuals in movement direction. In the remaining six video sequences the distribution of directions was not significantly different from a uniform distribution, indicating a random movement direction (Figure 2).

The proportion of time urchins spent moving was not significantly related to their density (Table 2 and Figure 3A), and averaged 10% (± 1.4 , SE) of the recorded time. Speed varied between 4 and 16 $cm\ h^{-1}$ and decreased with increasing urchin density (Table 2). The mean move length and mean daily displacement also decreased with urchin density (Table 2 and Figure 3B,C). The linearity index varied between 0.35 and 0.60, indicating an intermediate level of directionality in individual paths. Although the linearity index tended to decrease with urchin density (Figure 3D), this trend was marginally non-significant (Table 2). As well, step length (mean \pm SE: 2.69 ± 0.25 cm) tended to decrease with urchin density, although this was marginally nonsignificant. Number of moves per hour (3.02 ± 0.37) and number of steps per move (1.69 ± 0.07) were not significantly related to urchin density (Table 2).

The distributions of turning angles between steps (θ_s : Rayleigh's $z_{1012}=226.7$, $P<0.001$) and between moves (θ_m : Rayleigh's $z_{1610}=113.2$, $P<0.001$) are clearly non-uniform and concentrated around 0° (mean turning angle \pm angular deviation: $\theta_s=3.7^\circ \pm 58.8$; $\theta_m=0.5^\circ \pm 69.5$) (Figure 4). Both distributions are symmetrical as indicated by the low values for the sum of sines of the turning angles ($\Sigma \sin \theta_s=0.030$, $\Sigma \sin \theta_m=0.002$). Because of the non-uniform distributions, a simple random walk model would not provide a good estimate of population spread because it would underestimate the net square displacement (Turchin, 1998).

Figure 5 shows the mean net square displacement observed after one to N moves as well as the mean net

square displacement predicted by the CRW model with the 95% CI. In all nine video sequences, observed net square displacements generally fall within the 95% CI. Although in some sequences (e.g. Figure 5B,E,G,H), observations approached (but rarely exceeded) the upper confidence limit at greater move numbers, the I-statistic was significant in all cases, indicating a good fit of the model. The net square displacement predicted by the CRW model decreased with urchin density (Table 2).

DISCUSSION

Strongylocentrotus droebachiensis did not exhibit strong directionality in foraging movement in our study. Movement was oriented in a predominantly shoreward direction in one-third (3 out of 9) video samples, but the concordance in individual directions in these samples was weak. Dumont et al. (2004) observed directionality in five of six trials with *S. droebachiensis* released in an urchin barrens, although the mean direction differed between trials. In a subsequent study, however, these authors found no evidence of directionality in urchins in barrens either near or far from a kelp bed (C. Dumont, J.H. Himmelman and M.P. Russell, personal communication). Duggan & Miller (2001) also failed to detect any directional movement towards or away from an adjacent kelp bed in a tagging experiment with *S. droebachiensis* released on a cobble bottom. Numerous studies have shown that *S. droebachiensis* is induced to move in response to the presence of food or predators by detecting water-borne cues that attract or repel urchins (e.g. Garnick, 1978; Scheibling & Hamm, 1991). The presence of nearby kelp may have influenced the directionality of movement that we observed. However, directionality was not simply related to distance from the kelp bed, since the same proportion of samples in both an urchin front and barrens showed directional movement.

In this study, we did not observe any significant difference in movement patterns between urchins along a grazing front or a few metres away in recently formed barrens. This is likely due to the overlap in the range of density observed between these two locations, given the strong effect of density on movement. At high density, urchins moved at a slower speed and their move length and net displacement were reduced. Our estimates of density at the front and in its wake (Table 1) are within the range concurrently measured at these locations over a larger scale at the same study site (Scheibling et al., 1999).

If aggregation is the result of associative behaviour (Bernstein et al., 1983), then we would expect urchins to reduce movement at high density in order to maintain the aggregation. Alternatively, reduced movement may simply be a consequence of interference between individuals in an aggregation. We observed that urchins contacting a conspecific remained stationary for a few seconds and then changed direction. This would tend to decrease distance displaced and limit dispersal. Thus, once aggregation is initiated (e.g. by the presence of food), the decrease in movement with increased density may have a stabilizing effect on a grazing front. This may explain the formation of fronts with extremely high densities of urchins (up to 500 urchins m^{-2} ; Gagnon et al., 2004).

This positive feedback mechanism alone provides a simple explanation for the persistence of feeding fronts, which does not necessitate associative behaviour.

The movement of urchins was characterized by a degree of linearity in successive moves, as indicated by the distribution of turning angles and the linearity index. Therefore, a simple random walk model would not be appropriate to describe urchin movement because it would underestimate the net square displacement of individuals. The high frequency of turning angles between steps (θ_s) centred on zero suggests that urchins tend to move more or less unidirectionally until their next stop, as opposed to a random search pattern which would tend towards a uniform distribution of turning angles. Possibly, urchins that detect food by chemoreception travel in a somewhat convoluted path until they reach the source of the signal. Small changes in direction between each step may be a mechanism to ensure that the direction of movement is appropriate. If the chemical signal decreases as an urchin changes direction, then the individual can realign accordingly. Similar behaviours were observed in the blue crab *Callinectes sapidus* (Weissburg & Dusenbery, 2002) and the sea star *Asterias vulgaris* (Drolet & Himmelman, 2004), and could be common in animals using tropotaxis (spatial comparisons of chemical stimulus using different receptors) as an orientation mechanism.

The trend towards a constant direction between successive moves could be explained by two mechanisms. Either urchins can somehow keep track of their previous move direction and are more likely to start the next move in a similar direction, or they respond to some large-scale environmental cue (e.g. kelp bed, current, slope, etc.). The latter seems unlikely given the absence of overall directionality observed in two-thirds of the video sequences. If movement direction was affected by a large-scale environmental cue, we might expect all urchins to exhibit a similar response to this cue and therefore have a similar movement direction.

The CRW model provides an adequate estimate of urchin displacement over periods of 3–5 h and up to 16 moves. Observed net square displacements generally fell within the 95% CI of model predictions, although observations at higher move numbers tended towards the upper confidence limit in some cases, suggesting the model could underestimate dispersal over longer periods. The predicted net square displacements obtained from our CRW model are correlated with urchin density. This suggests that urchins can disperse more rapidly at low density than when aggregated. Our estimates of daily displacement at low density (0.5–0.6 m d⁻¹) are within the lower range observed for this species and conspecifics. Dumont et al. (personal communication) measured movement rates of 0.4 to 1.7 m d⁻¹ and Garnick (1978) observed net displacements of up to 3 m d⁻¹ for *S. droebachiensis*. Mattisson et al. (1977) recorded a mean movement of 0.5 m d⁻¹ in *S. fransiscanus* in barrens located 15 to 100 m from a California kelp bed.

Displacement data can also be used to calculate a diffusion coefficient which, when combined with an estimate of the intrinsic rate of population growth, could be used to predict the spread of a population (Shigesada & Kawasaki, 1997). This could be used to predict the time required for a deep population to re-colonize the shallow

subtidal zone following a mass mortality of urchins (Scheibling et al., 1999) and estimate the flux of urchins moving across barrens to a feeding front. This type of information could prove useful in management plans aimed at controlling the harvest of urchins in fronts to maintain a commercially viable urchin population (Miller & Nolan, 2000). However, extrapolation from small-scale foraging movement to larger-scale displacement may be misleading, and experiments designed to compare movement patterns across a range of temporal and spatial scales are needed.

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