Random movement pattern of the sea urchin *Strongylocentrotus droebachiensis*

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Abstract

We describe the fine-scale movement of the sea urchin *Strongylocentrotus droebachiensis* based on analyses of video recordings of undisturbed individuals in the two habitats which mainly differed in food availability, urchin barrens and grazing front. Urchin activity decreased as urchin density increased. Individuals alternated between moving and being stationary and their behaviour did not appear to be affected by either current velocity (within the range from 0 to 15 cm s^{-1}) and temperature (2.3 to 6.0 °C). Movement of individuals at each location was compared to that predicted by a random walk model. Mean move length (linear distance between two stationary periods), turning angle and net squared displacement were calculated for each individual. The distribution of turning angles was uniform at each location and there was no evidence of a relationship between urchin density and either move length or urchin velocity. The random model predicted a higher dispersal rate at locations with low urchin densities, such as barrens habitats. However, the movement was sometimes greater or less than predicted by the model, suggesting the influence of local environmental factors. The deviation of individual paths from the model revealed that urchins can be stationary or adopt a local (displacement less than random), random or directional movement. The net daily distance displaced on the barrens, predicted by a random walk model, was similar to the observed movement recorded in our previous study of tagged urchins at one site, but less than that observed at a second site. We postulate that the random dispersal of urchins allows individuals on barrens to reach the kelp zone where food is more abundant although the time required to reach the kelp zone may be considerable (months to years). Urchins decrease their rate of dispersal once they reach the kelp zone so that they likely remain close to this abundant food sources for long periods.
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1. Introduction

Quantifying movement is fundamental to elucidating temporal and spatial changes in populations. Most animals move in search of food and shelter and to avoid predation and environmental stress (Swingland and Greenwood, 1982; Bell, 1991). Studying movement patterns at a fine-scale may provide information on foraging strategies and on the ability of individuals to exploit different habitats. Individual-based models are an attractive tool for characterizing small-scale movement patterns and for studying changes in behavioural decisions (movement rules) over time (Lima and Zollner,

1996; Turchin, 1998). For example, the random walk model describes the movement as a series of perfectly random moves in which the direction of each move is independent of the previous move (e.g., uniform distribution of turning angles). In contrast, in the correlated random walk model (Kareiva, 1983), individuals tend to move in a particular direction (i.e., nonuniform distribution of turning angles). Such simple models are frequently used as a first approach in characterizing the foraging behaviour in a homogeneous space. It is only necessary to develop more complex models if the random walk model is rejected (Turchin, 1991; Lima and Zollner, 1996; Turchin, 1998).

The movement of an individual can be continuous or periodically interrupted by stops. Studies of movement usually approximate the movement pattern by breaking the trajectory down into individual moves (from one stop to the next) and calculating the duration of moves and straight-line distances covered between stops (even if the actual trajectory between the stop points is tortuous). Some animals naturally move in discrete steps that start and end at specific positions (e.g., insects visiting flowers, Kareiva, 1983) whereas many others show stops that appear to be erratic and this results in unrelated moves referred to as saltatory searching (O'Brien et al., 1990). If an animal does make successive random moves, then a random walk model is appropriate for describing its pattern of movement.

Studies of fine-scale movement may also help to elucidate the movement of individuals at a larger scale and the degree of connectivity among habitats (Wiens et al., 1993). Extrapolation of movement from a random walk model to a longer period assumes that individuals do not change their behaviour during the period and that the distance moved from the starting position increases linearly over time. However, these assumptions often fail to describe foraging behaviour on a larger time scale as individuals can change their behaviour over time. Then, more complex models that incorporate behavioural states and environmental factors are required to describe the pattern of movement (Lima and Zollner, 1996; Zollner and Lima, 1999; Morales and Ellner, 2002; Morales et al., 2004). One way to examine if the information observed at a fine-scale can be used to understand movement at larger scales is to compare the extrapolation from fine-scale observations with observed movements at a larger scale (Samu et al., 2003; Bowne and White, 2004).

For many marine benthic invertebrates, the long-distance dispersal of planktonic larvae is likely the primary factor that determines the structure of local populations (Young, 1995). In this case, movement of individuals with a low mobility after settlement is assumed to be less important in determining population dynamics. In temperate coastal regions, sea urchins are often the dominant herbivore and they can strongly limit the distribution of macroalgae (Lawrence, 1975). For example, urchins often form dense aggregations at the lower limit of the kelp beds that can advance into the kelp zone a rate up to 4 m month^{-1} (Scheibling et al., 1999; Gagnon et al., 2004). Also, the intensive grazing by urchins often maintains extensive denuded zones called urchin barrens (Lawrence, 1975; Chapman, 1981; Johnson and Mann, 1982). We recently reported that the green sea urchin, *Strongylocentrotus droebachiensis*, shows an ontogenetic change in its foraging behaviour, as individuals smaller than 15–20 mm are sedentary and cryptic, whereas larger individuals actively move about to forage (Dumont et al., 2004, 2006). Adult urchins move up to 5 m d^{-1} on barrens, where food is rare, but tend to move less when close to the kelp bed, where food is more abundant (Dumont et al., 2006). Sea urchins are able to locate food sources (i.e., drift algae) using chemodetection and this often leads to the formation of feeding aggregations (Sloan and Campbell, 1982; Bernstein et al., 1983). However, their pattern of movement, and how it is adapted to such activities as locating food, remains unclear. For example, individuals often change their displacement direction on successive days (Dumont et al., 2006).

The objective of the present study is to describe the fine-scale movement patterns of the sea urchin *S. droebachiensis*. We do this by observing the movement of urchins which were recorded in the field using a video system, in two habitats that mainly differed in food availability. We extracted the quantitative parameters of the movement paths from the recordings and used them to determine if movement patterns fitted a random walk model. Finally, to validate the predictions of the model, we extrapolated our fine-scale movement data to a one day period and compared these values to the daily movements we recorded for tagged urchins in a previous study (Dumont et al., 2006).

2. Methods

Our study was conducted during June 2003 in the Mingan Islands in the northern Gulf of St. Lawrence, eastern Canada (50°13.6″N, 63°41.12″W). We used video filming to quantify the movement of urchins in two habitats, on urchin barrens and in grazing fronts, at each of four locations, Corbeau, Havre South, Goéland West and Marteau. One 6–10 h filming bout was made at each habitat. The habitats sampled at each location were on gently sloped bedrock, mainly covered with encrusting

coralline algae, except for the barrens habitat at Corbeau where there was a plateau of pebbles overlaying mud and sand (see Dumont et al., 2006 for further description). Scattered patches of fleshy macroalgae (mainly *Alaria esculenta*) and drift algae were present at the grazing front at all locations. We used a vector current meter (Nortek, Norway) to record the current velocity and water temperature at 5-min intervals over the periods when urchin movement was being filmed, except on the barrens at Goéland West where the current meter malfunctioned (Table 1).

2.1. Video recording

The filming was done with an underwater video camera (Sony DCR TRV900) that was positioned 1 m above the bottom so that field of view was 95×71 cm. The camera was attached to a rack that was supported by feet (steel rods) that were 1.2 m from the center of the field (so the structure did not to interfere with the urchins or water flow). The video camera was set in time-lapse mode to record for 2 s every 30 s. Images were then transferred from the video to a computer using the image analysis software Optimas 6.2 (Media Cybernetics Ltd.). To avoid over-sampling (Bell, 1991; Turchin, 1998), we re-sampled the video recordings at 2-min intervals. To examine the time spent moving and the movement path, we used the image analysis software UTHSCSA Image Tool 3.0 freeware (http://ddsdx.uthscsa.edu/dig/itdesc.

html). We determined the spatial position (x and y coordinates) of 15 randomly-chosen urchins at 2-min intervals over the duration of the filming bout. When an individual left the field of view, we substituted it with another randomly chosen individual. The mean size of urchins tracked was larger at the grazing front (mean± SE, 48 ± 0.09 mm) than on the barrens (34.6 ± 0.08 mm), however there was no correlation between velocity and urchin size in either the barrens or grazing front habitats (linear regression, $p>0.34$ at all four locations). Further, our previous study (Dumont et al., 2006) showed that there was no effect of size on the movement rate for individuals measuring 25–69 mm. To provide a comparative measure of urchin abundance in the habitats and locations sampled, the urchin density was estimated by counting individuals in the field of view for each video sequence (<20 mm urchins were not included in this count as they were often covered or hidden) and we also calculated the nearest neighbour distance, the net distance to the closest >20-mm conspecific.

2.2. Movement path characteristics

As urchins only moved from time to time, we first examined the proportion of individuals that were moving over time and related this to urchin density, temperature and current velocity (except on the barrens at Goéland West where the current meter malfunctioned) using linear regressions (homoscedasticity and linearity of residuals

Table 1
Characteristics (abiotic, biotic and movement pattern) for the urchin barrens and grazing front habitats at the four locations where we made video observations of the sea urchin *S. droebachiensis*

Characteristics	Corbeau		Goéland West		Havre South		Marteau	
Habitat	Urchin barrens	Grazing front	Urchin barrens	Grazing front	Urchin barrens	Grazing front	Urchin barrens	Grazing front
Sampling date in June 2003	9	13	6	7	11	14	16	15
Depth (m)	10	3	7	2	7	2	8	2
Current velocity (cm s^{-1})	6	8	11	11	9	8	6	15
Temperature (°C)	5.3	3.3	4.2	4.3	5.2	6.0	2.3	2.6
Urchin density (number m^{-2})	25	74	44	180	32	65	40	114
Proportion moving (%)	34.0	33.5	37.0	3.7	43.0	23.9	21.7	8.6
Number of observed paths >3 moves	17	10	13	3	11	18	16	4
Velocity (cm min^{-1})	0.47 (0.03)	0.48 (0.06)	0.31 (0.02)	0.25 (0.02)	0.71 (0.06)	0.44 (0.05)	0.42 (0.04)	0.35 (0.06)
Length of move (cm)	5.6 (0.6)	4.8 (0.8)	3.8 (0.5)	2.4 (0.4)	11.4 (1.7)	3.8 (0.4)	5.2 (0.7)	5.4 (1.7)
Cosine of the turning angle (°)	−0.04	0.01	0.04	0.02	−0.03	0.01	0.04	0.02
Duration of move (min)	7.3 (1.14)	5.8 (1.0)	6.15 (0.68)	3.8 (0.9)	17.4 (3.1)	4.2 (0.4)	6.3 (1.0)	9.5 (2.7)
Residence time (min)	14.0 (0.9)	15.2 (3.0)	15.6 (0.6)	19.3 (9.9)	7.3 (0.6)	22.4 (2.4)	12.6 (0.9)	36.0 (11.9)
Extrapolated NDD (cm)	83.8 (12.4)[ns]	64.1 (10.8)	46.1 (9.7)*		190.3 (59.8)		44.6 (10.1)	76.7 (19.2)
Daily NDD (cm) as observed by Dumont et al. (2006)	119.2 (23.1)		101.3 (13.2)					

Extrapolated daily net distance displaced (NDD) based on the video observations in the barrens were compared with daily distance displaced as previously observed by Dumont et al. (2006) on the barrens at two of the locations. * indicates a significant difference (Kolmogorov–Smirnov test, $p<0.05$) and *ns* no difference between expected and observed NDD. Numbers in parenthesis are standard errors.

were evaluated visually). We considered that an individual was stationary if it was observed in the same position for 2 or more consecutive observations (the observations were made at 2-min intervals). We then determined the proportion of time during which individuals were moving over the duration of the filming bout. In this analysis, urchins tracked for <30 min were eliminated to avoid potential bias because of a short observation period. For each urchin, we calculated its velocity (cm min^{-1}) at fixed steps of 2 min, move lengths (net distance moved between 2 stop periods) and turning angles (angular difference between 2 consecutive moves). A path incorporated a series of moves that varied in length and duration (Fig. 1). To avoid image noise when analysing the tracks, the minimal displacement (step) was set at 3 mm.

We used linear regressions to examine the relationship between the proportion of time spent moving (urchin activity) and urchin movement characteristics, velocity and move length. We also examined the linearity of displacement during a move (the path between two stops) using an index of straightness (I) calculated by dividing the net displacement during the move by the sum of the distances travelled for the 2-min intervals during the move. A value of 1 would indicate straight line movement and a value of 0 tortuous movement (Batschelet, 1981). In comparing the linearity of displacement for the barrens habitat at different locations, we excluded moves of <6 steps, as at least 6 steps are required for statistical comparisons. We could not compare the linearity of movement at the different locations at the grazing front because the number of steps moved was too low for most individuals.
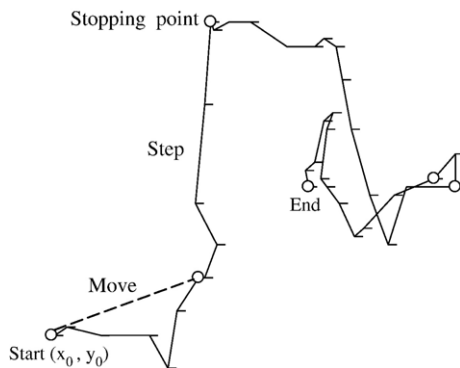

Fig. 1. An example of the relative position of a sea urchin *S. droebachiensis* as recorded at 2 min intervals (steps) using video filming. The circles indicate positions where an urchin stopped, here defined as not moving for 2 or more consecutive 2-min intervals. The length of a move, defined as the straight-line distance between two consecutive stopping points, was used in our calculations for the random walk model.

2.3. Random walk model

To interpret urchin movement, we compared the observed paths with the net squared displacement predicted by a random walk model (Turchin, 1998). The mean net squared displacement ($\overline{R_n^2}$) was calculated for up to 6 moves to characterize the movement pattern of individuals at each location in the two habitats (urchin barrens and grazing front). We calculated the predicted net squared displacement (R_n^2) using the correlated random walk equation (Kareiva and Shigesada, 1983):

$$R_n^2 = nm_2 + 2m_1^2 \frac{\psi}{1-\psi}\left(n - \frac{1-\psi^n}{1-\psi}\right) \tag{1}$$

where n is the number of moves, m_2 is the mean of the squared move length, m_1 is the mean of move length and ψ is the mean cosine turning angle. Moves of <1 cm were considered as repositioning and were excluded from the analyses. We only retained paths which included 3 moves or more. When the distribution of turning angles is uniform (mean cosine of turning angles equal 0), the Eq. (1) is reduced to a random walk:

$$R_n^2 = nm_2 \tag{2}$$

Because the random walk assumes there is no autocorrelation between the length or direction of movement from one move to the next, we tested the first-order autocorrelation using Spearman rank tests for the length of successive moves (Zar, 1999) and circular–circular correlation coefficients for the turning angles (Batschelet, 1981). To determine if the distribution of turning angles was uniform at each location, we used the Rayleigh test (Batschelet, 1981).

For the barrens and grazing front at each location, we tested if the observed net squared displacements differed significantly from the model, by simulating paths of 1000 individuals moving according to the empirical distribution of move lengths of the individuals observed and a uniform distribution of turning angles (Bootstrap method, Turchin, 1998). For every iteration of the simulation, a move length and a turning angle were randomly drawn (with replacement). The simulation continued until the number of moves (6 in most cases) was the same for the observed and simulated paths. The net squared displacement from the starting point was calculated after the nth move as:

$$R_n^2 = \chi_n^2 + y_n^2 \tag{3}$$

We then randomly drew as many R_n^2 values as there were observed paths with at least n moves, and

calculated the $\overline{R}^2_n$ for this set. This procedure was repeated 1000 times and then the 95% confidence interval was determined. For each move n, we tested for departure of the observed net squared displacement from the expected values (a departure was declared significant if the value was not located within the confidence interval). A path was considered significantly different from the model when at least half of moves fell outside the confidence intervals. We examined the overall movement of pooled paths at each location using the technique recommended by Turchin (1998). The paths of individual urchins were also examined to determine the paths that fit the corresponding model of each location (Fortin, 2003; Austin et al., 2004). Individual paths within the confidence interval of the model were considered as random movement. Paths that were overestimated by the model were identified as local movement and those underestimated by the model as directed movement.

2.4. Scaling up fine-scale observations to daily movements

We extrapolated fine-scale observations to a daily scale by applying the random walk as the scaling function. The net distance displaced (NDD) of each urchin observed at a fine-scale was calculated from their individual descriptive parameters (mean move length, mean move time and mean turning angle) using the Eq. (1). To estimate the number of moves within a day, we calculated the mean duration of a move and the mean stationary time between 2 successive moves for each individual. The distributions of extrapolated and observed net daily distance displaced were compared using the nonparametric Kolmogorov–Smirnov test. The observed daily movement data was obtained for 2 locations, Goéland West and Corbeau, on barrens from a previous tagging experiment (Dumont et al., 2006).

3. Results

Urchin density was higher in the grazing front habitat than in the barrens habitat (*t*-test, $t_6=2.45$, $p=0.017$, Table 1). Also, the distance to the nearest neighbor was greater in the barrens habitat (mean±SE, 3.2±0.2 cm) than in the grazing front habitat (0.75±0.19 cm) (2-way ANOVA, Habitat: $F_{1,\,130}=65.7$, $p=0.004$, Location and Location×Habitat: $p>0.15$).

In the two habitats at the four locations, urchins were stationary most of the time, as the proportion of time spent moving (over the observation period of 6 to 10 h)

was 4 to 43% (Fig. 2). Although time spent moving decreased with increasing urchin density (Fig. 2), neither urchin velocity ($y=-0.002x+0.55$, $r^2=0.29$, $p=0.09$) or move length ($y=-0.031x+13.47$, $r^2=0.01$, $p=0.38$) varied with urchin density. Further, time spent moving did not appear to vary with changes in current velocity between 0 and <15 cm s^{-1} ($y=-295.94x+50.19$, $r^2=0.21$, $p=0.17$) or with changes in temperature between 2.3 and 6.0 °C ($y=7.88x+3.91$, $r^2=0.01$, $p=0.38$). However, the time spent moving seemed to be unusually high (>60% of individuals were moving) during the period of low current velocity on barrens at Havre South.

Most moves (82% to 100%) were over short distances (<10 cm) at all locations except on the barrens at Havre South where 40% of the moves were by >10 cm. The index of straightness (I) for urchins on the barrens which were observed for 6 or more steps revealed linear displacement at three locations, Corbeau (I±SE, 0.77±0.03), Havre South (0.74±0.04) and Marteau (0.68±0.05), but not at Goéland West (0.44±0.08) where the index was lower than at the other locations (1-way ANOVA applied to arcsine transformed data, $F_{3,\,60}=5.50$, $p=0.002$).

We detected an autocorrelation in the length of successive moves for urchins on the barrens at Havre South (Spearman rank correlation, $r_s=0.28$, $p=0.03$), but not in the other habitats and locations ($p>0.15$). Also, there was no autocorrelation in subsequent turning angles for urchins in the two habitats at the four locations (circular–circular correlation, $r_-=0.07$ to $r_+=0.08$). The mean cosine of turning angles was close to zero at all locations (Table 1), which indicates a lack of directional persistence. Also, in the two habitats at the four locations the angles chosen by the urchins did not differ from a uniform distribution (Rayleigh tests, $r<0.04$, $p>0.1$).
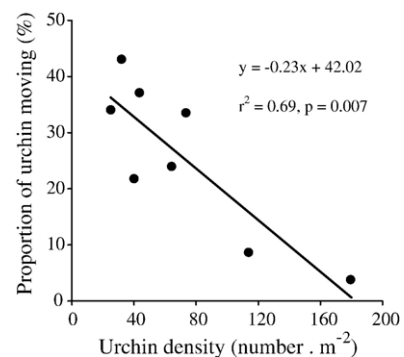

Fig. 2. Relation of mean proportion of urchins *S. droebachiensis* moving over the filming period ($n=15$ for each point) to urchin density.
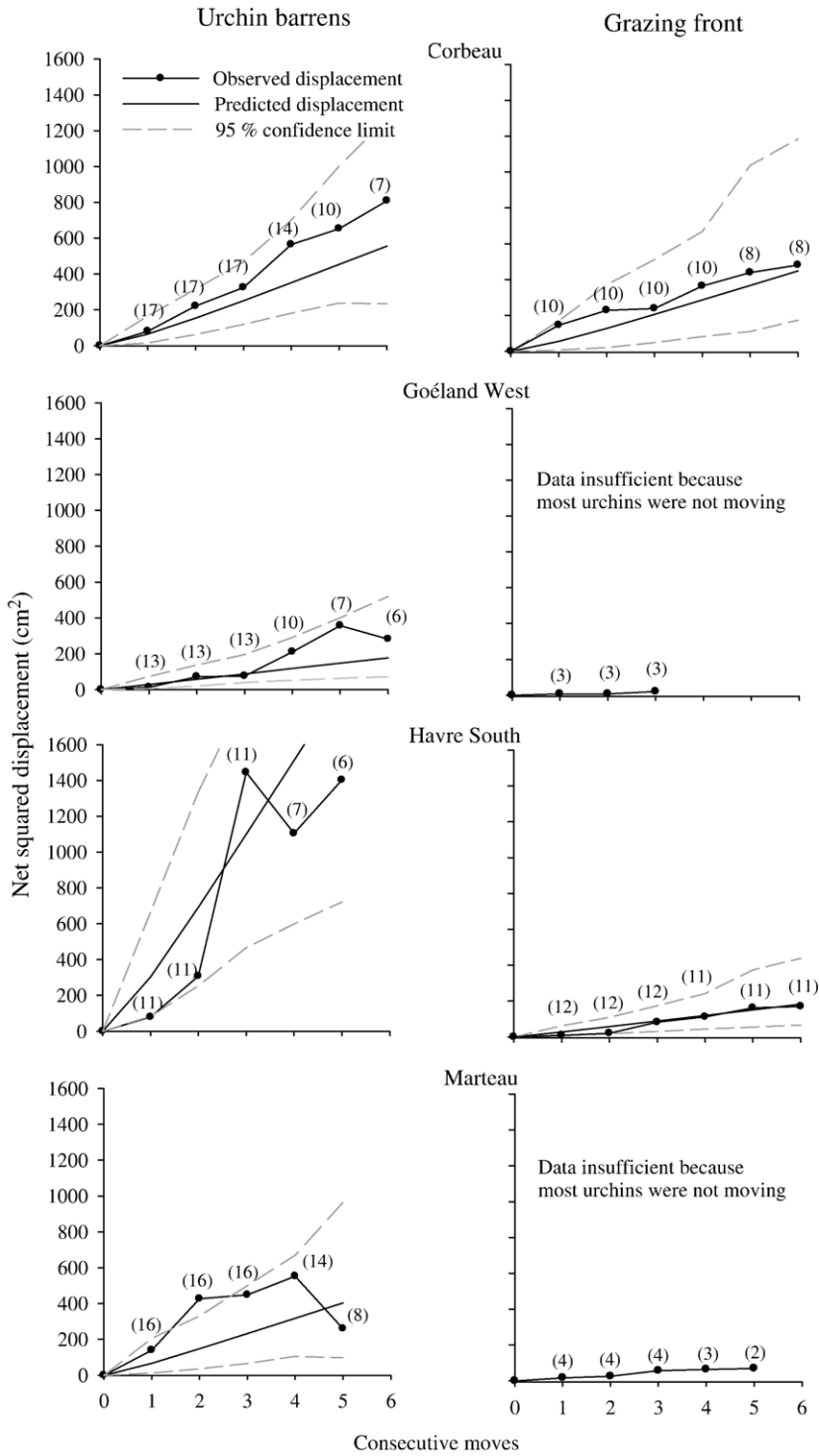
Fig. 3. Relationship between the predicted and the observed average net squared displacement for consecutive moves of the sea urchin *S. droebachiensis* in two habitats, urchin barrens and at the grazing front, at each of the four study locations. The dashed lines indicate the 95% confidence intervals for the net squared displacement as calculated with the empirical distribution of move lengths and a uniform distribution of turning angles. Numbers in parenthesis indicate the number of individuals observed.

The average net squared observed displacement varied in both habitats at the different locations (Fig. 3). With increasing moves, net squared displacement diverged between the barrens and grazing front habitats and urchins generally moved further on the barrens than in the grazing front. The uniform distribution of turning angles reduced the correlated random walk model to a random walk model. We could not apply a random walk model to the data for urchins in the grazing fronts at Goéland West and Marteau due low proportion of urchins that were moving (most were stationary during the filming bouts). In these situations where we could apply the model, the observed net squared displacement was similar to the predicted displacement for most moves. However, the random walk model tended to underestimate the net squared displacement in the second move for urchins on the barrens at Marteau: the observed displacements in the second move exceeded the upper confidence interval of the model (Fig. 3). Further, the model overestimated the observed net squared displacement in the first move for urchins on the barrens at Havre South. At each habitat and location, the examination of individual paths indicated that urchins frequently moved short distances

Table 2

Relative frequency of four types of movement by the sea urchin *S. droebachiensis* in two habitats, urchin barrens and the grazing front, at each of four locations

Location	Habitat	n	Movement type (%)			
			Stationary	Local	Random	Directed
Corbeau	Urchin barrens	18	5.6	61.1	16.7	16.7
	Grazing front	11	9.1	45.5	27.3	18.2
Goéland West	Urchin barrens	13	0.0	53.8	30.8	15.4
	Grazing front	11	72.7	27.3	0.0	0.0
Havre South	Urchin barrens	11	0.0	36.4	63.6	0.0
	Grazing front	14	14.3	35.7	50.0	0.0
Marteau	Urchin barrens	18	11.1	44.4	33.3	11.1
	Grazing front	10	60.0	40.0	0.0	0.0

The movement type of each urchin was identified with the corresponding random walk model. The observed paths within the confidence intervals of the random walk model were identified as random movement. Observed paths that were overestimated by the model were classified as local movement and those underestimated by the model as directed movement. Individual that did not move at all during the filming bouts were identified as stationary. Number of urchins observed is indicated.

within a restricted area (displacement less than random) or randomly but occasionally showed directed movement (Table 2). A large proportion of urchins were stationary in the grazing fronts at Goéland West and Marteau, where urchin density was the highest (Table 2).

We used the parameters of the random walk model to extrapolate the displacement of each individual observed on a fine scale on the barrens and compared this with urchins tracked on a daily scale in our previous study (Dumont et al., 2006). The extrapolation of the fine-scale observations resulted in a mean net daily distance diplaced that varied from 44.6 (SE± 10.1) to 190 (±59.8) cm and the maximum extrapolated movement rate was 678 cm at Havre South (Table 1). Whereas the distribution of observed daily displacement at Corbeau and that extrapolated by the model were similar (Kolmogorov–Smirnov test, $D = 0.25$, $n_{extrapolated} = 17$, $n_{observed} = 28$, $p > 0.1$), observed daily displacement at Goéland West was greater than that extrapolated from the model ($D = 0.50$, $n_{extrapolated} = 13$, $n_{observed} = 32$, $p < 0.02$).

4. Discussion

We show that the movement pattern of the sea urchin *S. droebachiensis* can be adequately described by the random walk model. The agreement between our observations of urchins moving in the field and the movement pattern predicted by a random walk model indicates that urchins move about at random. One prediction of the model is that urchins disperse at a higher rate (e.g., net squared displacement) on barrens than in the grazing front. The increased movement on the barrens is likely because of the scarcity of food. The random dispersal of urchins in the barrens habitat likely means that individuals remain for extended periods of time in this habitat, which had low food availability. Urchins show numerous adaptations for tolerating long periods of starvation, including the ability to decrease their metabolic rate and to use reserves stored in the gonads (Lawrence and Lane, 1982; Andrew, 1989). Further, they can switch from being herbivores to feeding on alternative foods such as detritus, conspecifics or other invertebrates (Himmelman and Steele, 1971; Briscoe and Sebens, 1988; Drolet et al., 2004). A recent study described the movement pattern of *S. droebachiensis* in a similar manner but did not observe a change in distance moved between grazing front and barrens and better describe the movement patterns of *S. droebachiensis* with a correlated random walk model (Luazon-Guay et al., 2006).

Although the overall movement pattern at our study sites was at random, the movement of some individuals

fell outside the confidence limits of the model. We observed several different movement types (Table 2), with some individuals showing more sinuous paths than predicted by the model (they tended to remain in the same area), and others showing more directional movement that predicted by the model. Hence, urchins can be stationary or adopt a local, random or directed movement. Movement within a restricted area is likely the main search strategy of urchins. Most urchins in grazing fronts, where densities were high, were more or less stationary, whereas at sites with lower densities, some individuals moved about randomly and others showed directional movement.

Such deviations from the random walk model likely indicate that local environmental factors influence the movement of urchins, and these factors may include both the distribution of patches of food and physical environmental conditions. The most striking deviation was the period of increase activity for urchins on the barrens at Havre South (move 3, Fig. 3), in which individuals moved faster and in a more directional manner than for individuals at the same site during a different time. Although sequential moves during this period of high activity were autocorrelated, and this violates one assumption of the random walk model (Root and Shigesada, 1983; Turchin, 1998), the overall movement remained within the confidence intervals of the model. Possibly, the increased activity was due to some local stimulus, such as the presence of food within a detectable range. In this instance, movement towards some stimulus was also indicated by the increased orientation (straightness index > 0.7). In separate trials, in which we studied urchin movement in the vicinity of a piece of preferred algae (anchored to the bottom), we similarly observed increased activity and directional movement towards the algae (Dumont et al., unpublished data). Hence, urchins appear to move in random directions most of the time but at certain times (as when food is detected), they may shift to more directional movement.

The uniform distribution of turning angles showed that urchins generally move in random directions. Previous studies also failed to detect directionality in urchin movement (Dumont et al., 2004, 2006; Luazon-Guay et al., 2006). Nevertheless, we still have a limited understanding of the advantages of this type of movement, particularly in respect to obtaining food resources. Although it is possible that stationary urchins were feeding, the low mobility of urchins in the grazing front may also have been because their movements were limited by the large numbers of conspecifics in this habitat. This hypothesis is suggested by the inverse relationship we documented between urchin activity and urchin density

and also the lower displacement of urchins at high urchin density observed by Luazon-Guay et al. (2006). Hayakawa and Kittaka (1984) studied the feeding behaviour of the sea urchin *Strongylocentrotus nudus* in a laboratory experiment and compared the observations with several movement models. Their simulations of feeding behaviour suggested that starved urchins move randomly to uniformly distributed patches of food. Studies adapting their approach would likely be useful in elucidating (1) how green sea urchins search for food relative to the distribution of food patches and (2) the role of chemodetection in locating food sources.

Our extrapolation of daily movement, based on our fine-scale observations of movement, indicated a daily displacement that would be similar to that which we previously recorded for tagged urchins at one site, but less than that recorded for tagged urchins at a second site. The difference in the two estimations at the second site could have been due temporal changes at this site, for example appearance of drift algae or changes in temperature or current. The environmental data obtained while we were filming urchin movement provided no evidence of an effect of either temperature (2.3 to 6 °C) or current velocity (0 to 15 cm s^{-1}) on urchin activity. Kawamata (1998) previously showed that the movement of the sea urchin *S. nudus* is not affected by low current velocities, but movement does decrease once velocities exceed 20 cm s^{-1}. Finally, our observations were made during calm conditions and wave surge does reduce urchin movement, at least when a certain level is reached (Gagnon, 2003). A major limitation of our study was that all observations were made during daylight hours, so that we could not explore whether movement patterns change between day and night. Such changes have been reported for several echinoids (Carpenter, 1984; Dance, 1987; Tertschnig, 1989; Jones and Andrew, 1990). Our extrapolations of the individual paths to a daily movement are limited to individuals that moved during the filming bouts. However, on barrens, almost all urchins did move (see Table 2). Consequently, the exclusion of non-moving urchins had a negligible effect on mean daily movement. On the other hand, the daily movement estimated for the two locations in the grazing front overestimated the distance moved.

The simulations of Zollner and Lima (1999) predict that a strongly correlated random walk type of movement (e.g. a nearly straight movement path) is appropriate for animals that can perceive things over a long distance and that can move long distances, as it should increase the likelihood of successful dispersal. However, a tortuous displacement is more appropriate for organisms with limited perception of the landscape, as this behaviour

should increase the chance of finding a food patch. A random search strategy is probably most appropriate for sea urchins, since they move slowly and can likely only detect food sources over a limited distance.

An important question is whether the dispersal rate of urchins allows them to migrate from deeper water to the kelp zone in shallow water. We postulate that urchins move randomly from the barrens to the kelp zone and the probability of reaching the kelp zone will decrease with the distance from the kelp. Once urchins reach the kelp zone, their dispersal rate should decrease so that individuals may remain in the same area for long periods. They likely move short distances within a restricted area (local movement). Several previous workers postulate that large urchins migrate shoreward to form the aggregations at the lower limit of kelp bed (Propp, 1977; Meidel and Scheibling, 1998; Scheibling et al., 1999; Vadas et al., 2002), but in these studies movement data were lacking so the hypothesis could not be evaluated. In the present study, we quantified and modelled urchin dispersal with observations made during the summer. Our data likely cannot be used to estimate dispersal over the year as movement behaviour likely changes with season. Konar (2000) observed that urchins moved little throughout the year in the kelp zone whereas on barrens movement was decreased during the winter compared to in the summer. Gagnon et al. (2004) recorded large seasonal fluctuations of urchin densities in the kelp zone in the Mingan Islands, and there were much higher densities in summer than in spring and fall. Abiotic factors such as wave surge and ice formation may be important factors affecting the movement rate of urchins, and both factors may dislodge urchins in shallow water (Gagnon et al., 2004). These factors may thus lead to periodic exchanges between the kelp and barrens habitats. Our model provides an estimate of the dispersal rate of urchins at a scale over which urchins from barrens are likely to interact with individuals in the kelp zone.

In a context of fishery management, our results provide insights into the rate of recolonization in harvested areas. Urchins collected adjacent to the kelp zone (e.g. where individuals have larger gonads than on the barrens) will likely be replaced by adult urchins from the barrens that come into contact with the kelp zone through their random movements. However, an intensive harvesting in the kelp zone may lead to a rapid depletion of surrounding adult urchins and an expansion of the kelp zone. The growth of juveniles on barrens may then be necessary to provide a new generation of adults. The time required for juveniles on barrens to attain the size (15–20 mm) at which they actively move about in open areas will likely depend on food availability and any expansion of the kelp zone

should increase kelp litter and thus the growth of juveniles on the barrens.

References

Andrew, N.L., 1989. Contrasting ecological implications of food limitation in sea urchins and herbivorous gastropods. Mar. Ecol. Prog. Ser. 51, 189–193.

Austin, D., Bowen, W.D., McMillan, J.I., 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. Oikos 105, 15–30.

Batschelet, E., 1981. Circular Statistic in Biology. Academic Press, New York.

Bell, W.J., 1991. Searching Behaviour: the Behavioural Ecology of Finding Resources. Chapman and Hall, London.

Bernstein, B.B., Schroeter, S., Mann, K.H., 1983. Sea urchin (Strongylocentrotus droebachiensis) aggregating behavior investigated by a subtidal multifactorial experiment. Can. J. Fish. Aquat. Sci. 40, 1975–1986.

Bowne, D.R., White, H.R., 2004. Searching strategy of the painted turtle Chrysemys picta across spatial scales. Anim. Behav. 68, 1401–1409.

Briscoe, C.S., Sebens, K.P., 1988. Omnivory in Strongylocentrotus droebachiensis (Müller) (Echinodermata: Echinodea): predation on a subtidal mussels. J. Exp. Mar. Biol. Ecol. 115, 1–24.

Carpenter, R.C., 1984. Predator and population density control of homing behavior in the Caribbean echinoid Diadema antillarum Phillippi. Mar. Biol. 82, 101–108.

Chapman, A.R.O., 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's bay, Eastern Canada. Mar. Biol. 62, 307–311.

Dance, C., 1987. Patterns of activity of the sea urchin Paracentrotus lividus in the Bay of Port-Cros (Var, France, Mediterranean). PSZN I: Mar. Ecol. 8, 131–142.

Drolet, D., Himmelman, J.H., Rochette, R., 2004. Trade-off in the use of refuges by the ophiuroid Ophiopholis aculeata related to contrasting effects of substratum complexity on the risk of predation from two predators. Mar. Ecol. Prog. Ser. 284, 173–183.

Dumont, C., Himmelman, J.H., Russell, M.P., 2004. Size-specific movement of green sea urchins Strongylocentrotus droebachiensis on urchin barrens in eastern Canada. Mar. Ecol. Prog. Ser. 276, 93–101.

Dumont, C., Himmelman, J.H., Russell, M.P., 2006. Daily movement of the sea urchin Strongylocentrotus droebachiensis in different subtidal habitats in eastern Canada. Mar. Ecol. Prog. Ser. 317, 87–99.

Fortin, D., 2003. Searching behavior and use of sampling information by free-ranging bison (Bos bison). Behav. Ecol. Sociobiol. 54, 194–203.

Gagnon, P., 2003. Dynamique de répartition et mécanismes de défense des macrophytes de la zone infralittorale rocheuse dominée par l'oursin vert, *Strongylocentrotus droebachiensis*. PhD thesis. Laval University. Canada.

Gagnon, P., Himmelman, J.H., Johnson, L.E., 2004. Temporal variation in community interfaces: kelp bed boundary dynamics adjacent to persistent urchin barrens. Mar. Biol. 144, 1191–1203.

Hayakawa, Y., Kittaka, J., 1984. Simulation of feeding behavior of sea urchin *Strongylocentrotus nudus*. Bull. Jpn. Soc. Sci. Fish 50, 233–240.

Himmelman, J.H., Steele, D.H., 1971. Foods and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. Mar. Biol. 9, 315–322.

Johnson, C.R., Mann, K.H., 1982. Adaptations of *Strongylocentrotus droebacheinsis* for survival on barren grounds in Nova Scotia. In: Lawrence, J.M. (Ed.), International Echinoderms Conference. Balkema, A.A., Tampay Bay, pp. 277–283.

Jones, G.P., Andrew, N.L., 1990. Herbivory and patch dynamics on rocky reefs in temperate Australasia: the roles of fish and sea urchins. Aust. J. Ecol. 15, 505–520.

Kareiva, P.M., 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. Oecologia 57, 322–327.

Kareiva, P.M., Shigesada, N., 1983. Analysing insect movement as a correlated random walk. Oecologia 56, 234–238.

Kawamata, S., 1998. Effect of wave-induced oscillatory flow on grazing by a subtidal sea urchin *Strongylocentrotus nudus* (A. Agassiz). J. Exp. Mar. Biol. Ecol. 224, 31–48.

Konar, B., 2000. Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. Oecologia 125, 208–217.

Luazon-Guay, J.-S., Scheibling, R.E., Barbeau, M.A., 2006. Movement patterns in the green sea urchin, *Strongylocentrotus droebachiensis*. J. Mar. Biol. Assoc. UK 86, 167–174.

Lawrence, J.M., 1975. On the relationships between marine plants and sea urchins. Oceanogr. Mar. Biol. Annu. Rev. 13, 213–286.

Lawrence, J.M., Lane, J.M., 1982. The utilization of nutrients by postmetamorphic echinoderms. In: Jangoux, M., Lawrence, J.M. (Eds.), Echinoderm Nutrition. Balkema, Rotterdam, pp. 331–372.

Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11, 131–135.

Meidel, S.K., Scheibling, R.E., 1998. Size and structure of the sea urchin *Strongylocentrotus droebachiensis* in different habitats. In: Mooi, R., Telford, M. (Eds.), Echinoderms. A.A. Balkema, Rotterdam, San Francisco, pp. 737–742.

Morales, J.M., Ellner, S.P., 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. Ecology 83, 2240–2247.

Morales, J.M., Haydon, D.T., Frair, J., Holsiner, K.E., Fryxell, J.M., 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85, 2436–2445.

O'Brien, W., Browman, H., Evans, B., 1990. Search strategies of foraging animals. Am. Sci. 78, 152–160.

Propp, M.V., 1977. Ecology of the sea urchin *Strongylocentrotus droebachiensis* of the Barrents Sea: metabolism and regulation of abundance. Sov. J. Mar. Biol. 3, 27–37.

Samu, F., Sziranyi, A., Kiss, B., 2003. Foraging in agricultural fields: local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. Anim. Behav. 66, 939–947.

Scheibling, R.E., Hennigar, A.W., Balch, T., 1999. Destructive grazing, epiphytism, and disease: the dynamics of sea urchin–kelp interactions in Nova Scotia. Can. J. Fish. Aquat. Sci. 56, 2300–2314.

Sloan, N.A., Campbell, A.C., 1982. Perception of food. In: Jangoux, M., Lawrence, J.M. (Eds.), Echinoderm Nutrition. Balkema A.A, Rotterdam, pp. 3–24.

Swingland, I.R., Greenwood, P.J., 1982. The ecology of animal movement. Clarendon Press, Oxford University Press, New York.

Tertschnig, W.P., 1989. Diel activity patterns and foraging dynamics of the sea urchin *Tripneustes ventricosus* in a tropical seagrass community and a reef environment (Virgin Islands). PSZNI: Mar. Ecol. 10, 3–21.

Turchin, P., 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72, 1253–1266.

Turchin, P., 1998. Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Sinauer Associates, Sunderland.

Vadas, R.L., Smith, B.D., Beal, B., Dowling, T., 2002. Sympatric growth morphs and size bimodality in the green sea urchin (*Strongylocentrotus droebachiensis*). Ecol. Monogr. 72, 113–132.

Wiens, J.A., Stenseth, N.C., Van Horne, B., Ims, R.A., 1993. Ecological mechanisms and landscape ecology. Oikos 66, 369–380.

Young, C.M., 1995. Behavior and locomotion during the dispersal phase of larval life. In: McEdward, L.R. (Ed.), Ecology of Marine Invertebrates Larvae. CRC Press, pp. 249–277.

Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.

Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movements. Ecology 80, 1019–1030.