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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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Keywords: Grazing front; Movement pattern; Random walk; *Strongylocentrotus droebachiensis*; Urchin barrens; Video recording

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,

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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

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