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Trail following, speed and fractal dimension of movement in a marine prosobranch, *Littorina littorea*, during a mating and a non-mating season

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Abstract We quantitatively studied movement behaviour in the gastropod *Littorina littorea* in laboratory experiments during periods of their non-mating season (November 1992) and their mating season (April–May 1993). Snails were collected in 1992 and 1993 from one boulder shore on the north west coast of Sweden. In a comparison between the two seasons (one non-mating and one mating) we measured trail complexity of unsexed snails using fractal dimension, the degree of mucus trail following (coincidence index of marker and tracker trails) and average movement speed of marker and tracker snails. We found no differences in fractal dimension and coincidence index of trails between the two seasons. Tracker snails moved, however, significantly faster than marker snails during both seasons. This could not be explained by trackers, when locomoting, using the mucus trail deposited by the marker to increase their speed, since there was no correlation between coincidence index and tracker speed. During the mating season we also conducted trail complexity, trail following and speed experiments comparing the behaviour of males and females. There was no difference between males and females in the fractal dimension of movement, nor was there any difference between the mean speed of male and female snails, although male marker snails tended to move faster than female marker snails. Males tracking other males, females tracking other females and females tracking males followed trails about equally long distances (i.e., coincidence indices did not differ). In contrast, males following female mucus trails showed a significantly higher degree of trail following than the other sex combinations. This new finding may suggest that females of *L. littorea* release pheromones in their mucus trails and that males are able to identify them.

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Introduction

Chemoreception in gastropods occurs in most species, and it is considered to be of importance in feeding and homing behaviour, in escaping from predators and also in social and mating behaviour (see review by Croll 1983). Water-borne chemicals have been reported as important for herbivorous gastropods in locating and choosing different food items, and also for many intertidal gastropods that may detect chemical substances for the purpose of escaping from predators. Water-borne chemicals, such as pheromones, may also be a reason for the aggregation of sexually mature snails in some marine species (Croll 1983). Trail following has been shown to be the main mechanism of the homing behaviour observed in many limpets (Wells and Buckley 1972; Townsend 1974). A limpet may identify its trail by chemical cues in the mucus.

In species of the marine prosobranch family *Littorinidae*, trail following is also common, e.g. in *Littoraria irrorata* (Stirling and Hamilton 1986; Tankersley 1989), *Littorina keenae* (=*planaxis*, Raftery 1983) and *Littorina littorea* (Gilly and Swenson 1978). Imrie (1992) showed in the laboratory that *L. littorea* grazed much more on a surface with deposited mucus trails than on one without. He also reported that individuals of *L. littorea* grazed more on mucus trails deposited by themselves than by other individuals of their own and other species. Imrie (1992) concluded that this behaviour allowed *L. littorea* to feed not only on the mucus but also on the algae attached to the mucus and that tasting of the mucus may facilitate the snails in finding their way back to their zonation area if dislodged on the shore.

In *Littorina littorea*, experiments have also been performed on the mechanism for detecting mucus trail polarity, and Gilly and Swenson (1978) found that snails followed each other in the same direction (with polarity). As in *L. irrorata* (Stirling and Hamilton 1986), chemical concentration gradients are concluded to be one but not the only mechanism involved. Structural elements in the mucus may have a greater influence on the detection of trail

polarity (Bretz and Dimock 1983; Stirling and Hamilton 1986).

There have been suggestions that chemoreception may be involved in the mating behavior of littorinids. Dinter (1974) suggested that a water-borne sex pheromone is involved in the mating behaviour of *Littorina littorea* such that males attract other males and females, but her experiments have been criticized (Fretter and Graham 1980). In *L. keenae* (=*planaxis*), Raftery (1983) could not show in the laboratory that this species had any sexual preferences in trail following. There are indications of either water-borne or trail-borne pheromones in two littorinid species of Hawaii, since no copulations between males (male-male pairs) were noted on the shores (Struhsaker 1966). However, in another Hawaiian species (Struhsaker 1966) and in *Littorina saxatilis* (Raffaelli 1977; Saur 1990) intrasexual copulations between males are common. Male-male copulations in *L. littorea* can be seen on Swedish shores but not in such large proportions as in *L. saxatilis* (Saur 1990; personal observation). Saur (1990) observed that males of *L. littorea* discriminate between male and female mates during copulation, since male-male copulations lasted a much shorter time than male-female copulations.

On the Swedish west coast (an almost atidal region), *Littorina littorea* is found frequently on cliff and boulder shores from about mean water level to a few metres depth. It is a promiscuous species which has separate sexes, internal fertilization and a reproductive period that is most intense from March to early July in Sweden. During the mating season, males mount most of the snails they encounter (Saur 1990; personal observation). However, large females of *L. littorea* are favoured over small ones, and males prefer to mate with these more fecund females (Erlandsson and Johannesson 1994). *L. littorea* moves most actively when submerged (Newell 1958), probably since locomotion, dependent on mucus deposition, is more costly on a dry substratum (Davies et al. 1992). The purpose of the present study of movement behaviour in *L. littorea* was to describe, in a quantitative way, the movement complexity, the persistence of trail following and the average speed in this species in relation to the season of the year and the sex of the snails.

Movement complexity and fractal dimension

In a recent study, fractal dimension was used as a new descriptor of animal trails by describing movement tortuousity of spider mites (Dicke and Burrough 1988). The complexity of a spatial trail, like the complexity of a geometrical shape may be described by means of fractal geometry (Mandelbrot 1982). Instead of a description of geometrical objects in Euclidian space with integer topological dimensions (0 for point, 1 for line, 2 for plane and 3 for volume), one may describe complex geometrical shapes with another descriptor, the fractional Hausdorff-Besicovitch dimension, that need not be an integer. For very tortuous curves, for example the track of a particle in a random walk, the Hausdorff-Besicovitch dimension exceeds the topological dimension. This means that the line covers space very intensively, changing to something which is no longer a line but not yet a plane. A fractal is defined as a geometrical set, for which the Hausdorff-Besicovitch dimension strictly exceeds the topological dimension (Mandelbrot 1977), and an ideal mathematical fractal has the same structure (is self-similar) on an infinite range of scales.

For self-similar mathematical fractals, the Hausdorff-Besicovitch dimension coincides with the fractal dimension (D) and is calculated as

$$D = \frac{\ln(N)}{\ln(k)} \quad (1)$$

where one element is divided into N self-similar ones, whose linear size is k times smaller. The fractal dimension is related to the fractional Brownian motion function developed by Mandelbrot (1982), where $D = 1.5$ corresponds to the usual random Brownian motion, $D < 1.5$ describes persistent, directional spatial behaviour, while $D > 1.5$ corresponds to antipersistent, very tortuous curves. This property of the fractal dimension is used in the present paper for the analysis of mucus trail complexity of *Littorina littorea*, which can explain whether or not some snails (e.g. males compared to females) move more tortuously than others.

Materials and methods

All experiments were conducted in the laboratory within a plastic tank (~1 m^3). The outer walls of the tank were covered with black plastic so that no disturbing light could enter. We put a glass plate on the bottom surface to make the experimental surface flat. The same glass plate (~80×80 cm) was used in all experimental trials. It was washed with 95% ethanol so that all mucus was removed between every pair of snail combinations and between treatments. The water level in every experimental trial was ca. 3 cm deep, thus submerging the snails. The background was white, and between every pair of marker and tracker the tank was emptied and refilled with new seawater.

The light condition was constant, with a light intensity of 1.5×10^{-8} Einsteins s^{-1} m^{-2} and no shading. A videocamera (placed over the centre of the glass plate in orthogonal projection) was used to record the movements of the snails. Only active snails were recorded, and the videocamera was not started until the tentacles were fully visible. Snails that did not move within 5 min were not used. The trails were plotted onto overhead sheets, when showing the taped sequencies on a screen. Then, fractal dimension and/or length of the trails were measured.

All snails used in the experiments were collected from one population on a boulder shore at the island of Tjärnö in the north west coast of Sweden in 1992 and 1993. The snails were kept in aquaria, with running water, prior to all experiments. In the experiments where we were interested in possible sexual differences, males and females were in separate aquaria, and thus no copulating male-female pairs were formed from the time of collection to the time of experiment. We used snails with a size of ca. 20 mm in the experiments. Each snail was used only once.

Movement complexity of *Littorina littorea*

Comparison between non-mating and mating season

One set of experiments was performed in the last two weeks of November 1992 (non-mating season) and one set between 4 and 14 April 1993 (mating season), both in the same manner. Twenty snails were used each season, and each snail was used within 5 d of the day of collection. In this test we did not sex the randomly collected snails, because a male's penis does not usually develop in the non-mating season (Fretter and Graham 1980). We assumed that males and females were represented in roughly equal numbers (Saur 1990).

The sizes of the snails were between 19 and 22 mm. The salinity was 34 to 35‰, the temperature in the November experiments was 8 to 10 °C, and in the April experiments 6 °C. There was no treatment applied, i.e., the glass plate was washed between each snail trial. One snail at a time was put in the centre of the arena (the glass plate) facing in random directions and left free to move.

Analyses of fractal dimension of movement

Analyses were made on trails deposited by snails moving for 20 min, and the complexity of the trails was described with fractal dimension using the "divider" method (in the mating period also the "box-counting" method).

With the "divider" method, different "stick" sizes are used for measuring trail length. Simple estimation of D is based on log-log regression of obtained length of a trail vs "stick" size. D is estimated as

$$D = 1 - a \quad (2)$$

where a is a slope of the power function of trail length vs "stick" size (Frontier 1987).

For curves on a plane, the fractal dimension is bounded between the values of 1 and 2. Plotted trails were measured on overhead sheets with a pair of compasses using the steps ("stick" sizes) 2, 4, 8 and 16 mm corresponding to 1.12, 2.24, 4.48 and 8.96 cm of real scale (Fig. 1).

By using the "box-counting" method, the area occupied by a trail is estimated with a series of "counting squares" spanning a range of areas down to some small fraction of the entire area (Fig. 1). D is calculated from

$$B = t^D \quad (3)$$

where t is 1/(box size), (box size is the length of one side of a box), and B is the number of boxes occupied by the trail. For all topological dimensions from point to volume the same method may be used, giving $0 < D < 3$ (Loehle 1990). In trail complexity measurements in a two dimensional space, D may not exceed 2. The plotted trails were digitised in a computer and analysed with a program written by V.K.

The results were analysed with a one-factor analysis of variance (ANOVA) comparing the two seasons and with a correlation analysis comparing the trail length dependency of both methods of measuring fractal dimension. In addition, the obtained fractal dimensions were tested for deviations from fractal dimension of 1 (linear movement) and 1.5 (Brownian motion) with a two-tailed t-test.

Comparison between males and females during mating season

This experiment was conducted between 22 April and 27 May 1993. The snails were sexed alive by letting them crawl out a little bit from the shell to determine whether the snails had a penis or not. A total of 20 males and 20 females were tested. Each snail was used within 4 d of collection. Each experimental snail was chosen randomly during the day. Trails of 15 min were used instead of 20 min, because the snails were more active at the beginning of this experiment. This was probably due to the fact that we covered the bottom of the "waiting aquaria" with small cover glasses onto which snails were attached. The snail, attached to the cover glass, was then moved to the experimental arena. Thus, the soft body was already extended from the shell and the snail therefore became active immediately. This procedure was done to avoid directional movement as much as possible, since Petraitis (1982) found indications that *Littorina littorea* moves directionally if it is dislodged from the surface and randomly if not dislodged.

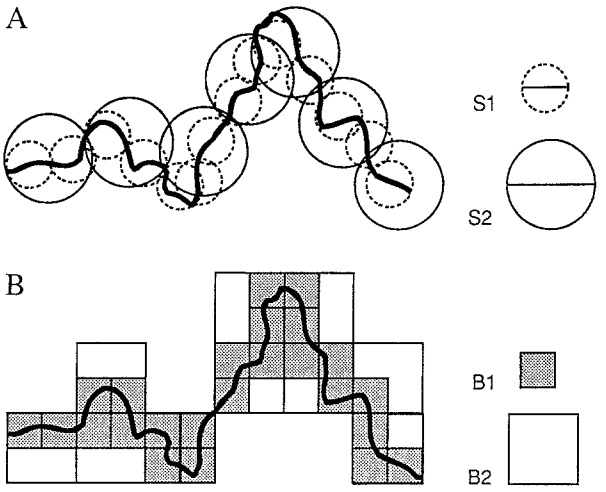

Fig. 1 Illustration of the **A** "divider" and the **B** "box-counting" methods used to describe trail complexity with fractal dimension. Two steps of the analyses are shown. (S_1 "stick" size 1; S_2 "stick" size 2; B_1 box size 1; B_2 box size 2). For the "divider" method $L_{(s)} = s \times N_{(s)}$, where L is measured trail length, s is "stick" size, and N is number of "sticks"

The size range used was 17 to 24 mm, which in another study (Erlandsson and Johannesson 1994) was considered to be one size category, namely large snails. In the experiments, salinity was 34 to 35‰, and temperature was 6 to 10 °C in the first weeks and 10 to 13 °C in the last weeks.

Except for these differences, this experiment was conducted in the same way as the movement complexity experiments comparing seasons.

The trails were described with fractal dimension by using the "divider" method. The results were analysed with a one-factor ANOVA, comparing the fractal dimension of male and female trails. The fractal dimensions of the trails were also compared to a fractal dimension of 1, i.e., linear movement, and to a fractal dimension of 1.5, i.e., Brownian motion, and deviations were tested with a two-tailed t-test.

Mucus trail following in *Littorina littorea*

Comparison between non-mating and mating season

These experiments were carried out over the same period of time in each season as the movement complexity experiments comparing non-mating and mating period. All snails in this case were also used within 5 d. Twenty marker snails and 20 tracker snails were tested each season using one snail at a time. The 20 snails used in the movement complexity experiments each season served as markers in these experiments. The glass plate was not washed between marker and tracker snails, so as to retain the mucus trail deposited by the marker. The tracker was put down in the centre, on the deposited trail facing in its starting direction. Both the marker and the tracker were allowed to crawl until they reached the edge of the arena or for no long-

er than 30 min, since polarity information of the mucus in an ageing trail older than 30 min has been shown to be unreliable (Gilly and Swenson 1978). In each trial, marker and tracker trails were analysed over the same time.

Sexes were assumed to be represented in equal numbers among trackers, whose size range was between 19 and 22 mm. The salinity and the temperature were 34 to 35‰, 8 to 10 °C (November) and 6 °C (April).

We measured the length of the marker's trail (L_m), the length of the tracker's trail (L_t), and the portion of the tracker's trail coincident with the marker's trail (L_c) with a curvimeter. Coincidence was defined as a complete overlap between the marker's and the tracker's trails, (i.e., the tracker following the marker's trail exactly). The degree of trail following was quantified by use of a coincidence index (C.I.) suggested by Townsend (1974):

$$\text{C.I.} = L_c/(L_m \times L_t)^{1/2} \quad (4)$$

The range of the C.I. lies between 0 and 1, where 0 indicates no coincidence and 1 complete coincidence.

The probability of coincidence by chance or due to the materials used was calculated by measuring the C.I. for 20 pairs of randomly chosen marker trails, which served as controls. The results of the C.I.s were analysed using a one-factor ANOVA comparing the two seasons, and comparing control and treatment.

Comparison between all four sex combinations during mating season

The present experiment was conducted over the same period of time during the mating season 1993 as the movement complexity experiment comparing males and females. The individuals were sexed alive, and four different sex combinations were tested, i.e., male marker–male tracker, male marker–female tracker, female marker–female tracker, female marker–male tracker. In each combination, 20 markers and 20 trackers were used, and the different pairs of sex combination were chosen randomly during the day. The 20 males and the 20 females in the movement complexity experiment were used as markers in this experiment, but also an additional 20 individuals of each sex were markers. The snails were used in the experiments within 4 d of collection day, and, to test if the amount of time spent waiting in separate aquaria had any effect on trail following for males and females, "Day" was introduced as a factor. Four pairs of marker and tracker snails for each sex combination were recorded for each "Day", from Day 0 to 4, where Day 0 was the same day as the snails were collected, and Day 4 was 4 d after collection.

Cover glasses were also used for the trackers, to avoid (as much as possible) snails, dislodged from the surface, from following trails for the purpose of "homing" back to their zonation area by tasting the mucus and in that way identifying other conspecifics (Imrie 1992).

The size range here was also 17 to 24 mm (size category: large snails), the salinity 34 to 35‰, the temperature 6 to 10 °C in the first weeks and 10 to 13 °C in the last weeks.

Apart from the differences mentioned, this experiment was carried out in the same way as the trail following experiments comparing both seasons, except that the probability of coincidence by chance was not calculated. All markers and trackers in this experiment were dissected afterwards to estimate the degree of infection of trematode cercaria in the gonads. Parasitic infection like this may cause sterility of *Littorina littorea* snails (Hughes and Answer 1982) and could therefore influence the mating behaviour of *L. littorea* and act as a confounding factor in the present experiment. Less than 8% of the snails used in the experiments were actually infected, which we consider too low to affect the outcome of the experiments.

The C.I.s obtained were analysed with a three-factor ANOVA to see if there were any effects of male and female markers and trackers and/or "Day".

Movement speed of *Littorina littorea*

Comparison between marker and tracker snails, and between seasons

Since we knew both the distance moved by the snails and the time it took, a calculation of the average speed was possible. This was done for the marker and tracker snails in the trail following experiments comparing both seasons. A two-factor ANOVA was used to analyse and compare the marker and tracker speeds in the non-mating and in the mating season.

In addition a correlation analysis was done between C.I. and tracker speed. This was analysed in order to estimate if there is an increase in locomotive speed of a tracker snail with a higher degree of trail following, e.g. by gliding on the mucus trail. Tankersley (1989) showed that the metabolic cost of locomotion is reduced when snails are locomoting over old trails.

Since the water temperature increased 0.5 °C after 30 min due to the lamps that were used, this could influence the movement speed of tracker snails, as Newell (1958) found a positive correlation between temperature of water and speed of *Littorina littorea*. One of the most generally accepted methods for comparing the magnitude of the effect of temperature on the velocity of different rate processes such as chemical reactions, physical or biological processes is Van't Hoff's Q_{10} approximation, which is the factor by which the velocity of a rate process is increased for a rise in temperature of 10 °C (Duncan and Klekowski 1975). We used this method to calculate the theoretical effect of the rise in temperature (0.5 °C) on the speed differences between marker and tracker snails during the experiments in both seasons. Thus,

$$V_t \approx V_m \times Q_{10}^{(t_2-t_1)/10} \quad (5)$$

where V_t is the tracker speed, V_m is the marker speed, and t_2-t_1 is the temperature rise. The temperature interval 5 to 10 °C has a Q_{10} value of 3.5, which was the case for our experiments (T: 6 ° and 8 to 10 °C).

Comparison between males and females

To investigate if male and female movement speed differed in the experiments, calculations were done for 40 male and 40 female markers, and 40 male and 40 female trackers in the experiment comparing male and female movement during the mating season. In addition the speed of male and female tracker snails tracking either a deposited male or female trail was calculated. In each case, the results were analysed with a one-factor ANOVA to compare male and female marker and tracker speeds.

Results

Movement complexity of *Littorina littorea*

Both methods of describing trail complexity with fractal dimension were tested for trail length dependency. The results show that the "box-counting" method yields values of fractal dimension that are positively correlated to the trail lengths ($R=0.60$, $P=0.0048$, df = 19), while the "divider" method does not show trail length dependency ($R=0.25$, $P=0.30$, df = 19). This means that the "divider" method is more reliable when measuring the complexity of an animal trail using fractal dimension, since the distance travelled is not necessarily associated with the tortuosity of an animal trail.

The differences in the fractal dimension of movement ("divider" method) between the non-mating and the mating season were not significant ($F=1.48, P=0.23$, df=39). The average fractal dimension during the non-mating season in November was 1.11 ± 0.041 (SE) and 1.19 ± 0.048 (SE) during the mating period. Variances were homogeneous ($C=0.58$, $C_{crit}=0.72$) according to Cochran's test (see e.g. Underwood 1981).

During the mating season, there were no significant differences of complexity between male and female trails ($F=0.45, P=0.51$, df=39). The average fractal dimension (which was measured with the "divider" method) of a male trail was 1.11 ± 0.024 (SE) and of a female trail 1.14 ± 0.036 (SE). Variances here were also homogeneous ($C=0.68$, $C_{crit}=0.72$).

Significant deviations from a fractal dimensions of 1.5 (Brownian motion: $P<0.001$) and of 1 (linear movement: $P>0.02$) were found for the two seasons and the two sexes.

Table 1 *Littorina littorea.* Three factor analysis of variance of the degree of trail following (coincidence index) comparing male and female markers and trackers during a mating season and in relation to the time males and females spent in separate aquaria (max. 4 d) before used in experiments

Source of variation	df	MS	F	P
♂ + ♀ markers	1	0.50	7.98	0.0064
♂ + ♀ trackers	1	0.55	8.74	0.0044
Day	4	0.023	0.36	0.84
♂ + ♀ markers × ♂ + ♀ trackers	1	0.88	14.03	0.0004
♂ + ♀ markers × Day	4	0.048	0.76	0.56
♂ + ♀ trackers × Day	4	0.051	0.81	0.53
♂ + ♀ markers × ♂ + ♀ trackers × Day	4	0.13	2.02	0.10
Residual	60	0.063		

Mucus trail following in *Littorina littorea*

C.I.s between control (i.e., randomly chosen marker–marker pairs) and treatment (i.e., marker–tracker pairs) in each season were clearly different (non-mating season: $F=16.2$, $P=0.0003$, df=39; mating season: $F=39.5$, $P=0.0001$, df=39), which means that the probability of trail following by chance was low. Variances became homogeneous after double square root transformation (non-mating season: $C=0.68$; mating season: $C=0.56$, $C_{crit}=0.72$).

A comparison of trail following of marker–tracker pairs between the seasons did not reveal any significant differences of the C.I.s ($F=1.84, P=0.18$, df=39). The average C.I. was 0.36 ± 0.079 (SE) during November and 0.23 ± 0.054 (SE) during the mating period. Variances were homogeneous ($C=0.69$, $C_{crit}=0.72$).

The trail following experiments with different sex combinations (male marker–male tracker, male marker–female tracker, female marker–female tracker, female marker–male tracker) during the mating season 1993 suggest that the factor "Day" had no influence on the distance a tracker followed a marker (Table 1) (i.e., the time snails were kept in aquaria before the experiments did not seem to affect the results). In contrast, the type of sex and sex combination had a great significant influence on the degree of trail following, i.e., the C.I. (Table 1). The C.I.s were largest with females as markers and males as trackers, which shows that males followed females clearly longer distances than males followed males and than females followed either females or males (Fig. 2). Variances were homogeneous ($C=0.14$, $C_{crit}=0.22$).

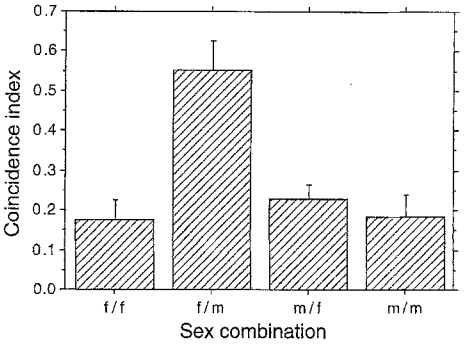

Fig. 2 *Littorina littorea.* Coincidence index (degree of trail following) of four sex combinations of marker and tracker snails during the mating season 1993. (*f/f* female marker–female tracker; *f/m* female marker–male tracker; *m/f* male marker–female tracker; *m/m* male marker–male tracker.) SE bars shown

Movement speed of *Littorina littorea*

In this test the snails moved faster in the non-mating period compared to the mating period, and trackers' speeds were greater than markers' in each season (Fig. 3; non-mating season: average marker speed = 3.55 cm min^{-1}, average tracker speed = 4.47 cm min^{-1}; mating season: average marker speed = 2.88 cm min^{-1}, average tracker speed = 3.42 cm min^{-1}). These differences in snail speed between the two seasons (one non-mating and one mating) and between marker and tracker snails were highly significant (Table 2). Variances were slightly heterogeneous ($C=0.427$, $C_{crit}=0.422$), but no data transformation could make variances homogeneous.

There was no correlation between C.I. and speed for the trackers tested, either in the non-mating season ($R=0.21$, $P=0.37$, df=19) or in the mating season ($R=0.28$, $P=0.23$, df=19). That is, those trackers that followed marker trails for a long period of time did not crawl at different rates compared to those following other trails just for a short time.

The obtained results of the movement speed of the tracker snails were compared to the theoretical value of tracker speed, if speed differences between marker and tracker snails were caused by the rise in water temperature

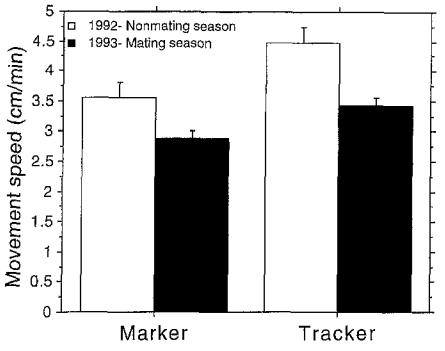

Fig. 3 *Littorina littorea.* Movement speed comparing marker and tracker snails and a non-mating season with a mating season. SE bars shown

Table 2 *Littorina littorea.* Two factor analysis of variance of average movement speed comparing marker and tracker snails and a non-mating season with a mating season

Source of variation	df	MS	*F*	*P*
Season	1	14.61	17.36	0.0001
Marker/Tracker	1	10.66	12.68	0.0006
Season×Marker/Tracker	1	0.75	0.90	0.35
Residual	76	0.84		

alone. Deviations were analysed with two-tailed *t*-tests. The obtained tracker speeds were higher than the theoretical tracker speed ($t=2.53$ in both seasons, $P<0.05$). That is, the temperature rise alone could not explain all of the increase in tracker speed compared to marker speed.

The average female marker speed was 3.32 cm min^{-1} ±0.15 (SE), and the average male marker speed 3.74 cm min^{-1} ±0.15 (SE), while the average female and male tracker speeds (irrespective of marker snail) were 3.90 cm min^{-1} ±0.16 (SE) and 3.84 cm min^{-1} ±0.16 (SE), respectively. Female tracker and male tracker speeds differed significantly from female marker speed [$F=2.86$, $P=0.04$, df = 159; Student-Newman-Keuls (SNK)-posthoc test, $P<0.05$]. The difference between female marker and male marker speed was not significant, although there was a trend towards males moving faster than females (SNK-posthoc test, $0.05<P<0.10$). Variances were shown to be homogeneous ($C=0.27$, $C_{crit}>0.31$).

Females had an average speed of 3.85 cm min^{-1} ±0.24 (SE) when following females and 3.96 cm min^{-1} ±0.20 (SE) when following males. There was a trend (SNK-posthoc test: diff. = 0.55, crit. diff. = 0.83 at $P=0.05$) towards males moving faster when following females [average speed of 4.12 cm min^{-1} ±0.22 (SE)] compared to when males followed males [average speed: 3.57 cm min^{-1} ±0.22 (SE)]. None of these differences, however, were significant ($F=1.10$, $P=0.36$, df = 79). Variances were homogeneous ($C=0.30$, $C_{crit}=0.42$).

Discussion

The movement complexity experiments could not reveal any differences in fractal dimensions of trails, either between the two seasons or between males and females. Nor did males and females differ in movement speed, even though males tended to move faster than females in untreated experiments. If snails cover a larger area by moving more tortuously or if they disperse over a longer distance by moving faster, they may be more able to find mates or food items that are randomly or patchily distributed on the shore. The foraging movements of many non-homing, intertidal grazers are random or independent in distance and direction of movement within a population (see review by Chapman and Underwood 1992), although directionality and length of the actual path moved by a foraging gastropod has not been studied. Hughes (1980) has suggested that if algal food items are spatially patchy on a shore, a gastropod that moves randomly and thus in a tortuous way would be unlikely to come into contact with its food. Instead, the optimal foraging would be to move in a directional way and traverse longer distances, perhaps by moving faster, between the algal patches. The present experiments in *Littorina littorea* suggest that the males do not increase their movement complexity for the purpose of finding more female mates. In addition, since males and females did not clearly differ in speed, this may suggest that movement for the purpose of finding food is more important than for finding mates.

The trails did not reach the complexity of Brownian motion (fractal dimension of 1.5), which suggests that the snails had low dimensional chaotic behaviour, i.e., they moved non-randomly and in a directional way. Had the experimental area (i.e., the glass plate) been larger, the complexity of the trails might have been higher since these snails are slow-turning animals and since the snails did not move in a completely directional way. In addition, a bilateral symmetry and an anterior and a posterior end, which create tendencies to move forward (Bovet and Benhamou 1988), may play a role in the directional movement found on the studied scale in *Littorina littorea*. Some general observations in the present experiments were that snails often rotated on their starting point and then began to move with a circular tendency. We also observed that the snails often explored the surrounding surface with their tentacles very much apart and separated, which may result in the snails moving straighter if nothing of interest is found in the neighbouring area.

Dicke and Burrough (1988) claimed that the original random walk model considers infinitesimally small subtrails and that the parameters required for this method cannot be determined experimentally, and therefore this model is not useful for analysing actually observed trails. The fractal dimension as a measure of tortuosity of animal trails, on the other hand, takes into account the complete structure of the trail. A disadvantage with the fractal dimension method, however, is that it cannot give information about the direction of turning at different intervals.

The lack of a significant difference in C.I.s between the non-mating and the mating season may suggest that there are many explanations for mucus trail following in *Littorina littorea*. Energy loss from mucus deposition in *L. littorea* is very high (Davies et al. 1992). However, Imrie (1992) found that trail following in *L. littorea* included feeding on the mucus or algae attached to the mucus, and in that way they could regain some of the energy lost in the mucus deposition. Imrie (1992) also discussed the idea that this behaviour might be a way for a snail to find its way back to its zonation area, i.e., by tasting and identifying the mucus, since the *L. littorea* snails grazed on the trails of their conspecifics more than on trails of other intertidal species and even grazed more on their own individual trails than on trails deposited by other individuals. These suggestions may explain why 10% of the snails followed their own trails for some distance in our trail following experiments comparing the two seasons.

The most important result of our experiments was that the C.I.s of the sex combination female marker/male tracker were much higher than the coincidence indices of the rest of the sex combinations (i.e., male marker/male tracker, male marker/female tracker, female marker/female tracker). The absence of food and separation of males and females in different aquaria before the experiments for different lengths of time do not seem to influence the degree of trail following. Thus, the males are able to discriminate between male and female mucus trails, which suggests a new functional role for trail following in *Littorina* spp. snails. This finding implies that females of *L. littorea* do release pheromones in their mucus trails, even though pheromones may also be water-borne, which may increase the encounter rate of males and females.

Even though males of *Littorina littorea* can discriminate between male and female mucus trails, males can still be seen copulating with other males on the shore (Saur 1990; personal observation). Saur (1990) found nine male–male copulations out of a total of 129 copulating pairs on a boulder shore on the north west coast of Sweden. According to our experiments, 1/5 of the males tracking a female had a C.I. of less than 0.25, which may suggest that males might have different abilities to recognize a female trail. Maybe a male when following a female comes across multiple layered trails, which will result in lost structural information in the trail. This may lead to trail following against the polarity and to copulation between males, even though pheromones may still be detected through the layers. Nevertheless, the frequency of male–male copulations in *L. littorea* on the shore is clearly lower than the frequency of intersexual male–female copulations (Saur 1990: $\chi^2 = 56.5$, df = 1, $P = < 0.001$), which Saur (1990) explained by the fact that male–female copulations last about four times longer than male–male copulations. We suggest that not only differences in the duration of a copulation, but also in the ability of males to identify female mucus trails explain why such a high portion (93%) in Saur's (1990) study are copulating male–female pairs.

In a related species, *Littorina saxatilis*, which is also very common on North Atlantic shores, a higher portion of intrasexual male–male copulations have been observed. Raffaelli (1977) found only 57 male–female copulations (the rest were either intrasexual male–male pairs or interspecific pairs) out of 109 copulating pairs on a boulder shore in North Wales. Of 124 copulating pairs of *L. saxatilis* collected on a boulder shore in the northwest of Sweden, 33 pairs were found to be male–male copulations (Saur 1990). This may reflect a low ability of males for precopulatory sex recognition or indicate that there is no difference between male and female mucus in *L. saxatilis*. A comparison of trail following in *L. saxatilis* to that done for *L. littorea* in our experiments is, therefore, of great interest (Erlandsson in preparation).

Only four out of 20 pairs in the sex combination female marker–male tracker had a C.I. lower than 0.25 in our experiments. In one of these four pairs the female marker was severely infected by trematode parasites, and the male tracker stopped following this female's trail after a few centimetres. Curtis (1993) showed that abundant cercariae can be found in the mucus trails deposited by migrating host snails of *Ilyanassa obsoleta*. Saur (1990) reported a slight tendency for male *Littorina littorea* to copulate for a shorter duration with parasitized females than with uninfected females. Since these snails become sterile when their gonads are infected (Hughes and Answer 1982), it would be an advantage for healthy males to avoid parasitized females. If males are able to detect infected females and avoid matings with them, for example by detecting cercariae in the mucus trails, this would have very important evolutionary and ecological consequences. However, further experiments have yet to show if males have this ability.

The differences in average snail speed between the non-mating season and the mating season may be caused by the water temperature being 2 to 4 °C higher in the non-mating season. Activity and movement speed of *Littorina littorea* have been shown to increase with increases in water temperature (Newell 1958). A temperature rise of 0.5 °C in 30 min could not alone, however, according to Van't Hoff's Q_{10} coefficient, explain why tracker snails moved faster than marker snails in our experiments. Speed was not correlated to the degree of trail following, i.e., the tracker snails seem to increase their speed actively without, for example, gliding on the mucus, even though they can still save energy by moving over other mucus trails as suggested by Tankersley (1989) and Davies et al. (1992). A possible reason for the increase of tracker speed could be that water-borne chemicals may be released by marker snails, which could perhaps attract or repel the tracker snails.

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