J. Mar. Biol. Ass. U.K. (1999), **79**, 459–465
Printed in the United Kingdom

Preliminary observations on the timing and geometry of foraging activity in the intertidal pulmonate limpet *Siphonaria pectinata*

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Siphonaria pectinata (Mollusca: Gastropoda) at Gibraltar foraged when exposed continuously or intermittently to air, when the relative humidity at the rock surface exceeded 75%. The paths followed by individual limpets were either single or compound loops beginning and ending at a home scar. In the main, outward and inward tracks were independent and there was little evidence of trail following. *Siphonaria pectinata* exhibited a range of crawling speeds but spent much of the excursion stationary or moving very slowly. Both duration of excursion and maximum foraging distance were very variable. No correlation between the size of *S. pectinata* and the duration of the excursion was apparent. The timing of activity may reflect an adaptive response designed to provide enough time to forage while avoiding predation, desiccation and dislodgement by waves.

INTRODUCTION

Many gastropods exhibit clear patterns of activity and the possible underlying reasons for these have been discussed by Underwood (1979), Branch (1981), Hawkins & Hartnoll (1983) and Little (1989). As these patterns appear to be very labile rigid classification is very difficult. However, all these reviews agreed that foraging behaviour strategies were designed to avoid physical stress, predation and dislodgement by wave action.

Siphonarian limpets exhibit variation in the timing of foraging activity (Iwasaki, 1995). Most siphonarians feed during both ebb and flood phases of the tidal cycle, mainly when emersed and awash, although others feed during flood and ebb tides when awash and submerged. A few species feed only during ebb tides when emersed and awash. The final pattern of activity is movement during ebb tides when emersed. This is shown by only two species of siphonarians.

The paths followed by foraging siphonarians vary considerably but may play an important part in maximizing food intake. Abe (1939) and Cook & Cook (1981) considered that movement patterns in siphonarians were designed to avoid covering recently grazed areas.

Despite the assumption that many patterns of foraging are controlled by physical conditions, there is little information on the effect of micro-climate on foraging. A notable exception is the study carried out by Verdeber et al. (1983) in which they correlated the level of foraging activity of *Siphonaria alternata* (Say) with the wetness of the home scar. They concluded that foraging excursions mainly took place when the home scar was continuously or intermittently covered by water. However, in this study a purely arbitrary scale based on visual observations was used to determine scar wetness and there was no indication of the dampness of the rock surface over which the limpets foraged.

Foraging activity in *Siphonaria pectinata* has been previously studied in Florida by Thomas (1973). This author showed that the limpet travelled rather short distances (less than 15 cm) and that the outward trail was frequently used to return to the home scar. He also found that large snails tended to travel further away from their home scars during foraging excursions than small ones, but there was considerable variation.

Preliminary observations (T.M.J.O., unpublished data) indicated that at Gibraltar, many *S. pectinata* behaved differently and did not use the outward trail to return to the home scar. The aim of the study was, therefore, to establish whether *S. pectinata* does behave differently in the conditions prevailing at Gibraltar and to obtain data to describe initiation and inhibition of activity by physical conditions.

MATERIALS AND METHODS

Study site

This study was undertaken at North Mole, Gibraltar (36°07′N 05°21′W). This is a sheltered site consisting of an artificial breakwater 100 m long constructed in 1987. The shore is composed of medium-sized limestone boulders regularly deposited with an overall slope seawards of 34°. As the site is adjacent to two marinas the rocks are subjected to periodic wetting from the wake of passing vessels. Strong westerly winds generate some wave action, but because of the fetch to adjacent land these do not exceed 1 m and very strong easterly winds may generate a swell of approximately 1 m.

Measurement of limpet activity

Ten individuals located between 0.5 and 0.75 m above mean low water (MLW) on similar north-facing boulders with a slope of ±50°, were individually labelled using paper tags numbered with waterproof ink and attached to the shell with Loctite Super-glue. Each boulder was relatively homogeneous in topography with no cracks or crevices and with a barnacle cover of approximately 30%. Observations were made over six hour periods during ebb and flood phases of the tidal cycle thus including all phases of the tide and at different times of the day.

The temperature and relative humidity at the substrate level were taken using a Kane–May 8001 Thermohygrometer at the start and end of the observation period. When foraging activity was commenced from the home scar, the following data were collected for every active animal at 10 min intervals: time, substrate temperature immediately beside limpet, relative humidity of air immediately beside limpet, distance from home scar in centimetres, main axis of limpet orientation from scar, tidal phase (ebb or flood) and exposure status (whether the animal was exposed, submerged or awash).

The period of observation ended after six hours unless an animal was still away from its scar in which case readings were continued until it had returned. Sampling was carried out between winter 1994/95 and autumn 1995. At night observations were made using red light only as white light has been shown to cause clamping in foraging limpets (M.S. Davies, personal communication; Gray & Naylor, 1996). The degree of trail overlap was assessed using the technique described by Chelazzi et al. (1987).

Table 1. *Number of completed foraging excursions undertaken by individual limpets under different exposure conditions. Total number of observation periods per limpet = 35.*

Limpet number	Movement while exposed	Movement while awash	Inactive
1	3	11	21
2	2	1	32
3	1	1	33
4	2	20	13
5	0	5	30
6	0	3	32
7	0	2	33
8	1	3	31
9	0	3	32
10	1	3	31

RESULTS

Foraging excursions were initiated only when the relative humidity of the air immediately beside the limpet was high (75–100%) and the substrate very damp or wet. Table 1 shows that limpets foraged mainly when awash, at times when they were periodically splashed by wave action or by ebb and flood tides. Movement was also recorded when animals were exposed to air but on all these occasions the substratum was very damp or wet. There was some intra- and interindividual variation, but the results indicate a preference towards foraging while awash (Table 1). No activity was recorded during immersion.

On one occasion the relative humidity of the rock surface fell below 75% while the animal foraged. The limpet stopped moving almost immediately and clamped firmly onto the rock surface 3 cm away from its home scar. No further movement was recorded before observations were concluded at low tide when the relative humidity had fallen to 55%. Within the next 24 h the limpet returned to its home scar. A similar clamping response was observed in two foraging limpets when it started to rain heavily. All movement ceased for the duration of the observation period. Both limpets returned to their scars within the following tidal cycle. With these exceptions, limpet excursions always began and ended at the home scar within the period of observation.

The paths followed by individual limpets during foraging activity showed considerable variation (Table 2) but can be classified into five distinct types: single loops, with no overlap of outward and homebound trails (Figure 1A); single loops with partial overlap of outward and homebound trails (Figure 1B); compound loops with no overlap of outward and homebound trails (Figure 1C); compound loops with partial overlap of outward and homebound

Table 2. *Number and type of foraging paths followed by individual limpets. Total number of observations per limpet = 35.*

Limpet number	Single loop, no overlap	Single loop, partial overlap	Compound loop, no overlap	Compound loop, partial overlap	Complete overlap	Inactive
1	7	1	3	3	0	21
2	2	1	0	0	0	32
3	1	0	1	0	0	33
4	12	0	9	1	0	13
5	2	1	1	0	1	30
6	1	1	0	1	0	32
7	1	0	1	0	0	33
8	2	0	1	1	0	31
9	2	0	1	0	0	32
10	2	0	2	0	0	31

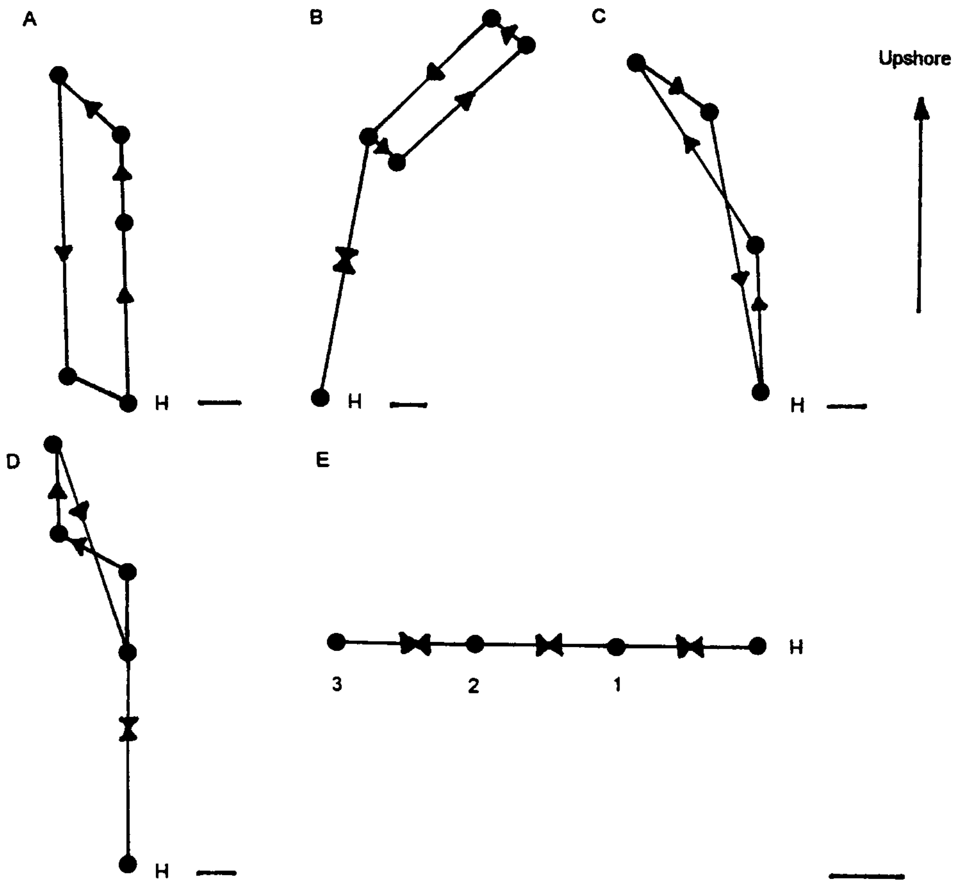

Figure 1. Representative sample of foraging excursions undertaken by *Siphonaria pectinata* at Gibraltar. Points/numbers represent the position of the limpet at 10 min intervals. H denotes the position of the home scar. (A) Single loop, no overlap of outward and homebound paths; (B) single loop, partial overlap; (C) double loop, no overlap; (D) double loop, partial overlap; (E) complete overlap. Scale bars: 1 cm.

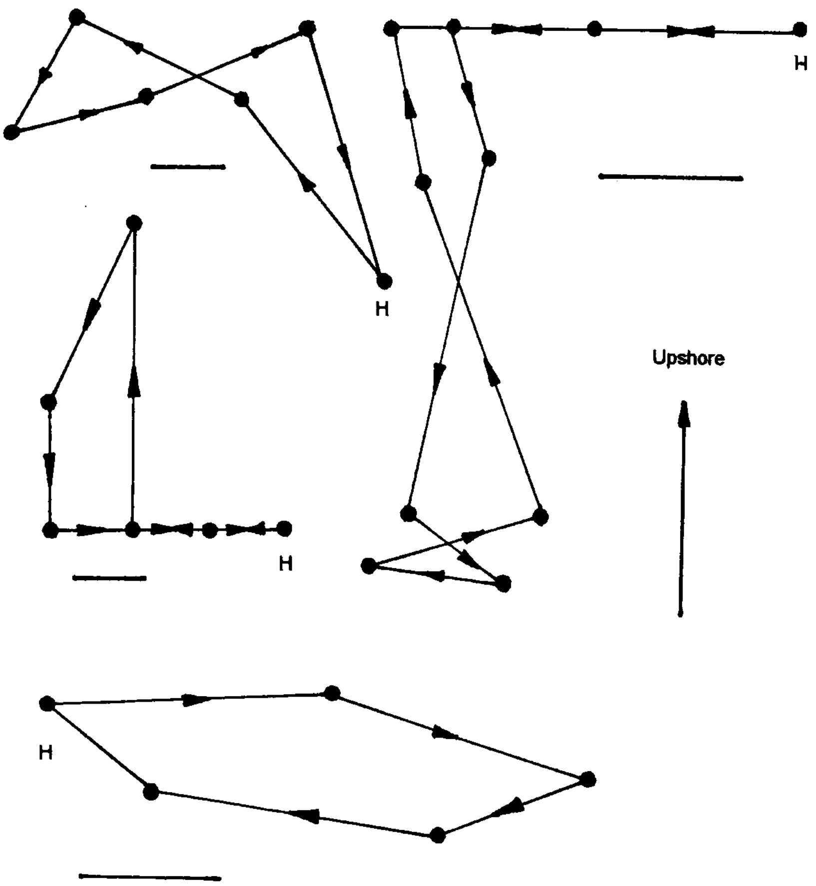

Figure 2. Diversity of foraging paths undertaken by a single individual (limpet 1). Points represent the position of the limpet at 10 min intervals. H denotes the position of the home scar. Scale bars: 1 cm.

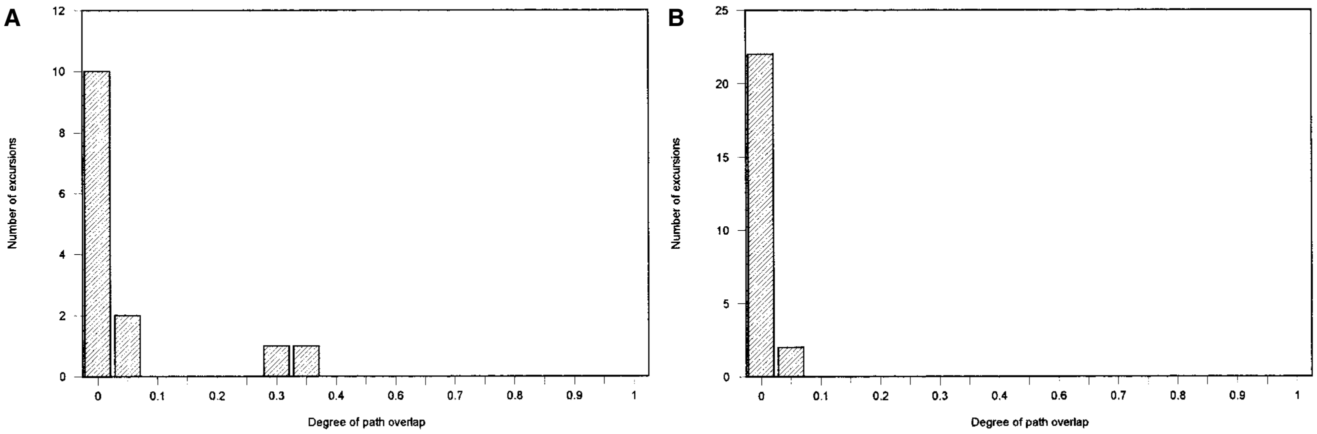

Figure 3. Frequency distribution of trail following performed by individual limpets during return branch of the route. x=0, no overlap; x=1, complete overlap between outgoing and return path. (A) limpet 1; (B) limpet 4.

trails (Figure 1D); and complete overlap, where outward and homebound trails were identical (Figure 1E).

Path morphology exhibited some intraindividual variation. The diversity of tracks followed by a single individual is illustrated in Figure 2. These foraging paths vary in form and direction. However, the results show a predominance of single or compound loops where outward and homebound tracks were independent (Table 2). Only a single individual, on only one occasion, undertook a foraging excursion where outward and homebound paths

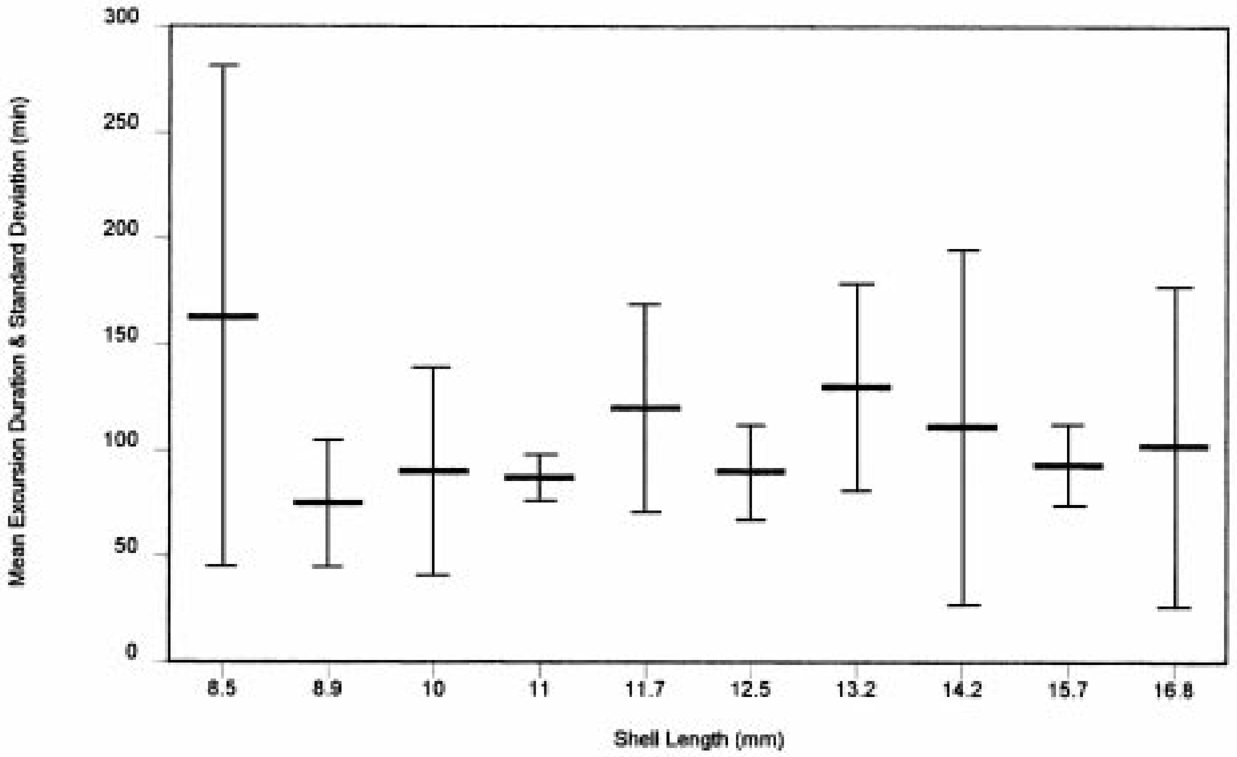

Figure 4. Relationship between size of limpet (as determined by shell length) and mean excursion duration (±SD). Correlation co-efficient: 0.58 ($P > 0.05$).

overlapped completely. The low incidence of trail following is further illustrated in Figure 3A&B which show the frequency distribution of trail following performed by limpets 1 and 4 (chosen because these two animals provided greatest replication). This parameter was computed as the fraction of steps (5 mm long) of the return path (i.e. the route from the point at the maximum distance from home to the home scar) overlapped to at least one step of the outgoing path (see Chelazzi et al., 1987).

Crawling speeds recorded during foraging showed considerable variation and ranged from 0 to 1.36 cm min^{-1}. During foraging many limpets exhibited periods of inactivity or very slow movement, but occasionally showed bouts of very rapid movement.

The duration of excursion also varied ranging from 30 min to 8 h and 20 min. Maximum foraging distance ranged from 2.3 to 38 cm. Figure 4 shows that there was no significant correlation between the size of the animal (as determined by the shell length) and the mean excursion duration (r=0.58; $P>0.05$) although the sample size was small (N=10).

DISCUSSION

These results show that foraging in *Siphonaria pectinata* at Gibraltar is restricted to times when the limpet is exposed either continuously or intermittently to damp air. This conforms to the pattern seen in Branch (1988) for *S. thersites* (Carpenter) and Iwasaki (1995) for 11 species of *Siphonaria*. A similar pattern was reported by Thomas (1973) for *S. pectinata* in Florida. This tendency to forage when exposed to air may be physiologically determined. Siphonarians have a large buccal mass rich in myoglobin which can only be properly saturated when it is exposed to air in which the partial pressure of oxygen is high (Wells & Wong, 1978). It appears likely that the oxygen demands during feeding can only be met when exposed to air. Thus the lack of activity of *S. pectinata* when submerged, despite its amphibious nature, may be because the low partial pressure of oxygen in water inhibits activity.

Desiccation can undoubtedly pose a serious problem for high level mollusc species (Garrity, 1984; Branch & Cherry, 1985; Little, 1989) and may influence the behaviour of *S. pectinata*. When emersed it appears that the main physical factor determining foraging activity of *S. pectinata* is the relative humidity close to the rock surface. Inhibition of activity observed when the relative humidity near the rock surface fell below 75%, suggests that this may be a critical value below which foraging is unlikely due to increased risk of desiccation. The timing of foraging activity has also been suggested as a mechanism to reduce evaporative water loss by Thomas (1973) for *S. pectinata* in Florida and Cook & Cook (1978) for *S. alternata* and *S. normalis* in Bermuda.

The clamping response observed in a limpet caught away from its home scar on a rapidly drying rock surface may be evidence of an adaptive mechanism for limiting water loss until the animal is able to return to its home scar. A similar clamping response was observed in limpets away from their home scars during periods of rain. Here, low salinity may pose an osmotic threat. Clamping down in *S. pectinata* appears to be a response to adverse conditions. Similar behaviour has been reported by Hawkins & Hartnoll (1982) and Little (1989) for *Patella vulgata* (L.). Heavy rain suppressed all activity and individuals clamped tightly onto their home scars so that they were effectively isolated from dilution.

There was some variation in the foraging path followed by *S. pectinata*. Most often *S. pectinata* performed foraging loops originating and ending at the home scar. These observations are in sharp contrast to other findings for *Siphonaria*, as all other published studies report direct trail-following as the most common or only pattern of behaviour (Abe, 1939, 1940; Cook, 1969, 1971; Thomas, 1973; Cook & Cook, 1978; Verdeber et al., 1983).

Thomas (1973) reported that the most common movement pattern exhibited by *S. pectinata* in Florida was movement out in a straight line and a return journey along this line. On the few occasions when individuals returned home using a path different to that on which they started out, movement was commonly in the form of loops or circles. Similar findings were reported by Verdeber et al. (1983). This contrasts with the present study, which showed a very low incidence of trail following. Foraging loops where outward and homebound trails are different may be a mechanism to avoid passing over previously grazed areas thus maximizing food intake as suggested by Abe (1939) for *S. atra* and Cook & Cook (1981) for two species of *Siphonaria*. Thomas (1973) and Verdeber et al. (1983) concluded, however, that siphonariid limpets could not use clues other than mucus trails in homing behaviour and the occasional failure to return along the outbound paths meant only that the animals preferred trails laid out on previous excursions. They based these assumptions on findings reported by Cook (1970) that under laboratory conditions, trails could remain effective for at least 48 h.

It has been suggested, (Davies et al., 1992), that for grazers a cost-effective way of using deposited mucus would be to reingest it, especially if its adhesive properties serve to concentrate the organic particles upon which these animals feed. The pedal mucus of prosobranch limpets has been shown to adhesively trap microalgal particles in this way, has been found to increase the rate of microalgal growth (Connor & Quinn, 1984; Connor, 1986) and may be reingested (Connor, 1983). The tendency for many siphonarians to home using mucus trails laid down during the outbound part of the excursion may be a mechanism designed to maximize food intake or minimize energy expenditure by using prepared trails. Why *S. pectinata* at Gibraltar does not seem to take advantage of mucus trail following is unknown. Clearly more information about mucus production and fate in siphonarians is required.

The crawling speeds exhibited by *S. pectinata* during foraging trips were very variable. It was not possible to determine when any animal was actually feeding, but it was evident that the animal spends a considerable part of its foraging excursion stationary or moving very slowly. These periods may represent periods of intensive grazing activity. Variation in crawling speeds may reflect different levels of grazing intensity which are related to microalgal availability. This hypothesis is supported by the findings of Little & Stirling (1985) and Della Santina et al. (1995). These authors concluded that *Patella vulgata* fed for almost the entire time they were active, since rasping commenced as the individual began turning on its home scar and often continued without pause until the limpet had returned. Chelazzi et al. (1994) concluded that the spatial organization of foraging activity in *P. vulgata* was not due to temporal modulation of rasping rate, but only to changing travel speeds along the path. Access to automatic motographic and sonographic techniques as described by Chelazzi et al. (1994) and Parpagnoli & Chelazzi (1995) would be necessary to further assess temporal and spatial organization of foraging activity in *S. pectinata* at Gibraltar.

Larger *S. pectinata* did not necessarily forage for longer. There was no significant correlation between limpet size and duration of excursion. Similar findings were reported by Cook & Cook (1981) for *Siphonaria* populations at Bermuda but contrasts with the findings reported by Thomas (1973) for *S. pectinata* at Florida and by Levings & Garrity (1984) for *S. gigas* (Sowerby).

In conclusion, this study shows both intra- and inter-individual variability in the spatial and temporal organization of foraging activity in *S. pectinata*. In addition the data strongly suggests that foraging activity is limited to times when the substrate is very damp or wet and when the animal is periodically or totally exposed to air. There is little evidence of direct trail following during homing as reported for other siphonarians and for this species in Florida. The timing of activity may reflect an adaptive response to secure enough time to forage while avoiding predation, desiccation and dislodgement by waves.

This work was partly financed by the Gibraltar Government Cultural Fund, Wildlife Gibraltar Ltd, Riggs Valmet Ltd and Minster Management Services Ltd. Our thanks go to Dr John Cortes and Eric Shaw for their helpful comments and to Darren Fa for his assistance during fieldwork.

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Received 14 January 1998. Accepted 23 June 1998.