

Temporal and spatial activity of the key-hole limpet *Fissurella crassa* (Mollusca: Gastropoda) in the eastern Pacific

Gianluca Serra*, Guido Chelazzi* and Juan C. Castilla†

*Dipartimento di Biologia Animale e Genetica, Università di Firenze, 50125 Firenze, Italia. †Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda 340, Casilla 114, Santiago de Chile, Chile.

*E-mail: gianlu@fbcc.it

An automated photographic technique was used to collect quantitative information on the activity patterns of *Fissurella crassa* under heavy-exposed sea conditions. The activity of this key-hole limpet was confined to nocturnal low tides. Total length of excursions was significantly greater during spring tides than neap tides, as was the maximum distance reached from the refuge. Total duration of excursions and their average speed did not vary significantly according to the spring/neap cycle. While the direction angle of excursions relative to the refuge was not influenced significantly by the spring/neap cycle, the lowest zone within the intertidal was reached by *F. crassa* during spring low tides only.

Fissurella crassa showed a spatial activity pattern fluctuating intra/inter-individually between a central place foraging and a ranging strategy, with a marked propensity for the former. Looped excursions were characterized by higher speed for the movements away and toward the limpet's refuge, than the movements at maximum distance from the refuge. As the outward and inward branches of looped excursions often overlapped extensively, trail-following is suggested as the main mechanism of orientation used by *F. crassa* to relocate the refuge.

INTRODUCTION

The combined adoption of specific temporal and spatial activity patterns enhances the morpho-physiological adaptive potential of benthic invertebrates to intertidal rocky shores (Underwood, 1979; Little, 1989). A variety of activity patterns relative to the spring/neap and night/day cycles have been recorded in intertidal chitons and gastropods, resulting in a wide inter/intraspecific variability (see Underwood, 1979; Little, 1989; Raffaelli & Hawkins, 1996). Several intertidal benthic molluscs exhibit central place foraging patterns, based on homing to a personal and constant refuge (for reviews on the homing behaviour of intertidal molluscs, see Newell, 1979; Chelazzi et al., 1988; Chelazzi, 1990). Most of the previous studies on homing patterns in prosobranch limpets refer to Patellidae and Acmaeidae (Branch, 1981; Della Santina et al., 1995; Chelazzi et al., 1998). The only previous field study on the homing behaviour and activity patterns of fissurellid limpets was that of Franz (1990) on three intertidal Caribbean species.

Fissurellid gastropods are represented by 13 species along the rocky shores of Chile (Oliva & Castilla, 1992), but only three are strictly intertidal: *Fissurella crassa*, *F. limbata* and *F. picta*. The first two species are relatively abundant at very exposed sites in central Chile where they show different patterns of distribution. *Fissurella crassa* is typical of the mid-intertidal, while *F. limbata* occurs more frequently in the lower-intertidal (Santelices, 1989). Both species are large dominant grazers, very relevant to the organization of the intertidal communities of rocky shores (Oliva & Castilla, 1986; Santelices, 1989). Despite the economic and ecological

relevance of these fissurellids (Oliva & Castilla, 1986; Santelices, 1989), information on their behavioural ecology is scant. The aim of this study was to describe the temporal and spatial activity patterns of *F. crassa* relative to the spring/neap and day/night cycles using *in situ* field recording.

MATERIALS AND METHODS

Study area and data collection

The study was conducted within the marine reserve Estación Costera de Investigaciones Marinas (ECIM, Pontificia Universidad Católica de Chile), located on the central Chilean coast at Las Cruces (33°30'S 71°38'W). Data were collected from November 1994 to February 1995, and from December 1995 to March 1996. Coastal topography, climate and the structure of littoral and sublittoral communities of the Chilean coast is described by Oliva & Castilla (1986) and Santelices (1989). *Fissurella crassa* usually inhabits vertical and subvertical inshore-oriented surfaces of large granite boulders. The coast of Las Cruces is severely exposed to prevailing winds (south-west to north-west, depending on season) (Dayton et al., 1977; Santelices, 1989), and tides are semidiurnal, with a range between high and low tide of approximately 1.5 m at spring tides. The minimum of spring low tides occurs at about 0600 and 1800, while that of neap low tides occurs at about 1200 and 0000, respectively.

The automated field technique described by Chelazzi et al. (1983) was used for collecting data. Six vertical and subvertical rocky walls of separated boulders, with a smooth surface, were selected within the study area, and

at each location 5–10 adult *F. crassa* individuals (7–13 cm total shell length) were selected randomly from a 3–5 m² area. During diurnal low tides, each limpet had an LED (light emitting diode) attached to the posterior section of the shell using a non-toxic, water resistant epoxy resin. Each LED, emitting a red flashing light, was supplied with a lithium micro-battery whose longevity was about three months. Once surrounded by the epoxy resin and mounted on the shell, the LED marker had a size of 25×15×20 mm (length, width, height) and a weight of about 6 g. Once marked, each limpet was repositioned at its exact former location. Although the LED emitting light ceased functioning after three months of continuous operation, the ID number mark lasted more than 12 months for several individuals. Two green LED markers were glued to the rocky substrate, at each motographic location, within the spatial activity range of marked *F. crassa*. The distance between these two reference markers was measured and recorded.

A camera (either a Pentax 90 WR or an Hasselblad 500 ELM) was firmly attached on a separate boulder facing each group of marked limpets at a distance ranging from 5–10 m. Cameras maintained a constant framing during the whole recording session at each motographic location (ML), always comprising the two reference green markers within the frame of the photo. The focal axis of the camera was approximately perpendicular to the rock surface with marked limpets. The movements of LED-equipped limpets were continuously recorded throughout the night (from about 2000 to 0600) by programming cameras to

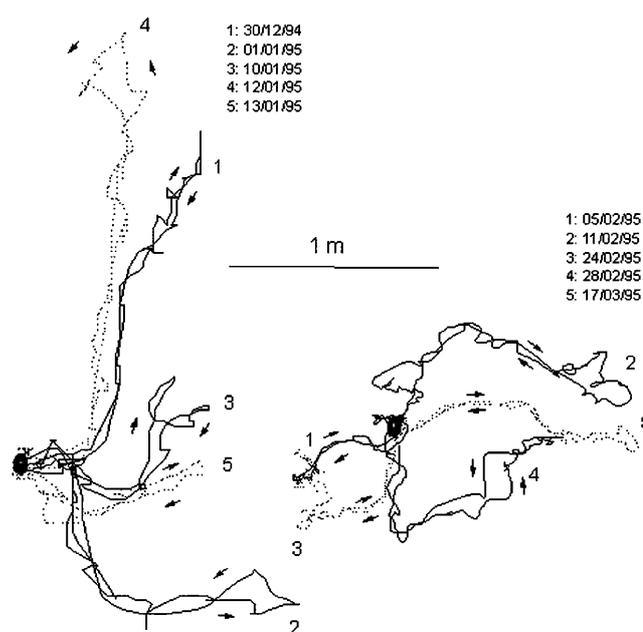


Figure 1. Examples of looped excursions performed by two *Fissurella crassa* at ECIM.

take consecutive B-pose exposures of constant duration (15 min each). Cameras were activated manually at dusk, and the starting time recorded. One 36-pose 100-ASA film was sufficient to cover an entire night of recording.

The locomotory behaviour of 36 marked *F. crassa*, located at six independent motographic locations

Table 1. Definition of motographic indices extracted by individual excursions.

Motographic Index	Definition	Measurement Unit
Homing Precision (HP) ^a	the linear distance between the starting and the ending point of the individual excursion	cm
Total Length (TL)	the total length of the excursion	cm
Maximum Distance From Home (MDH)	the linear distance between the starting point and the furthest point of the excursion	cm
Segmental Maximum Distance From Home (SMDH)	the linear distance between the starting point and the mid-point of each of 10 spatially equivalent fractions by which the excursion was partitioned	cm
Time of Departure From Home (TDH)	the time corresponding to the starting point of the excursion	h
Total Duration (TD)	the total time passed between TDH and the ending point of the excursion	min
Average Speed (AS)	TL/TD	cm min ⁻¹
Segmental Average Speed (SAS)	the average speed performed during each of 10 temporally-equivalent fractions by which the excursion was partitioned	cm min ⁻¹
Direction Angle (DA)	the angle between the vertical line through the starting point and the line passing through the starting point and the MDH point (for instance, to a precise upward movement DA = 0 or 360, and to a precise downward movement DA = 180)	
Trail Overlap (TO) ^b	the ratio between the number of overlapped points (= those pair of points, separated by at least ten consecutive other ones, whose linear distance was < 7.0 cm) and the total number of points of an excursion	pure number

^a, We regarded an occurrence of an homing performance, or an excursion was regarded as looped, whenever an excursion scored an HP ≤ 18.0 cm. This spatial threshold was selected by the estimation of the maximum error possible, resulting from the sum of two types of errors: (i) the measurement error (i.e. the inaccuracy of the photo-recording technique and that of the digitization process) estimated to range between 0 and 8.0 cm, and (ii) the variability of positioning of a single limpet at the same refuge by the end of different foraging excursions. As the LED was mounted in proximity to one of the shell's poles, the maximum value for this error corresponded approximately to the average shell length of *F. crassa* (i.e. 10 cm); ^b, this index was only calculated for excursions with HP ≤ 18.0 cm (i.e. looped excursions); ^c, looped excursions with evident overlapped outward and inward branches (like those showed in Figure 1) were used to select this arbitrary threshold distance.

(ML-1=12 marked ind, ML-2=8 ind, ML-3=7 ind, ML-4=5 ind, ML-5=2 ind, ML-6=2 ind) was recorded continuously throughout variable temporal intervals, ranging from 10 to 79 consecutive nights. A total of 13,000 exposures were taken during 216 nights of data collection.

Data analysis

Once the 216 films were developed, each frame was digitized and processed by an image analysis program (CRIAP Co., Firenze, Italia). Connecting the individual red tracks recorded on subsequent frames of each film, the whole individual excursion could be traced precisely and reconstructed. The coordinates, relative to an arbitrary reference X–Y axis, of the most conspicuous points or steps of each individual excursion (i.e. the minimum number of points sufficient to render a detailed trajectory of the excursion) were automatically determined, and saved as individual/night-specific files. The linear distance between the two green reference markers was used to assess the spatial scale of the excursions, while the starting time of each film was used to determine the timing of every point of each excursion. Examples of reconstructed excursions of two lapa individuals are showed in Figure 1.

Coordinates of individual excursions were then processed by means of self-written Q-Basic programs, to assess quantitatively synthetic spatial and temporal indices related to the locomotory activity of limpets (hereinafter referred as to motographic indices). The definition of motographic indices considered in our analysis are reported in Table 1.

The frequency–distribution of each motographic index was plotted using 36 individual excursions, at both spring and neap tides. These were selected randomly among the whole set of excursions undertaken by each of the 36 marked individuals during spring and neap tides. Mean SD was calculated for each motographic index. A Wilcoxon–Mann–Whitney test for unpaired data (Siegel & Castellan, 1988) was used to test for differences of motographic indices between spring and neap tides. The Wilcoxon–Mann–Whitney test for paired data (Siegel & Castellan, 1988) was performed to compare the values of motographic indices throughout a time interval of 12 months. The significance level selected for all statistical comparisons was 0.05.

RESULTS

Long-term recording of foraging excursions of *Fissurella crassa* revealed that most activity was nocturnal. Diurnal inspections of motographic locations, conducted daily during the whole study and randomly throughout the day, clearly showed that all limpets were inactive during the day. With few exceptions the nocturnal motographic recording was sufficient to cover the entire foraging activity of the limpets. The Time of Departure from Home (TDH) of 12 marked individuals on 79 consecutive nights (Figure 2) shows that activity in *F. crassa* could be correlated to the spring/neap cycle. At spring tides (ST), when the low tide occurs in the early night, limpets started to move around 2100–2200. As low tide became later, throughout the spring/neap cycle, TDH was delayed

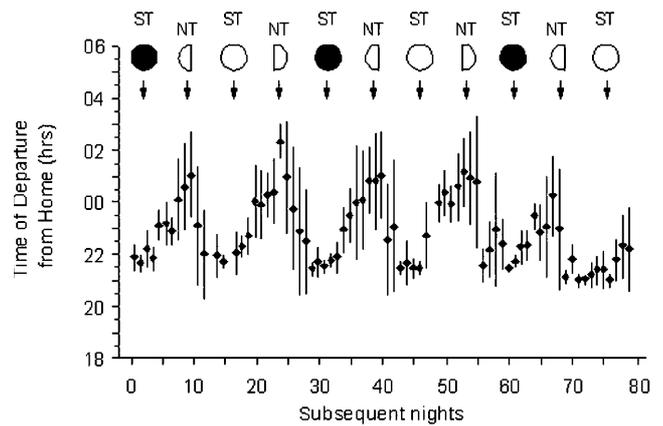


Figure 2. Variation of the Time of Departure from Home (TDH) of 12 marked *Fissurella crassa* throughout five spring/neap cycles (i.e. 79 subsequent nights). ♦, average TDH; bars, standard deviations; ST, spring tides; NT, neap tides; white circles, full moons; black circles, black moons.

correspondingly. At neap tides (NT), when the low tide occurs at midnight, limpets started their activity on average at about 0000–0200. Inter-individual variability of TDH was higher during NT than during ST (Figure 2).

Homing Precision (HP) did not differ significantly between ST and NT, averaging 15.6 ± 9.8 cm and

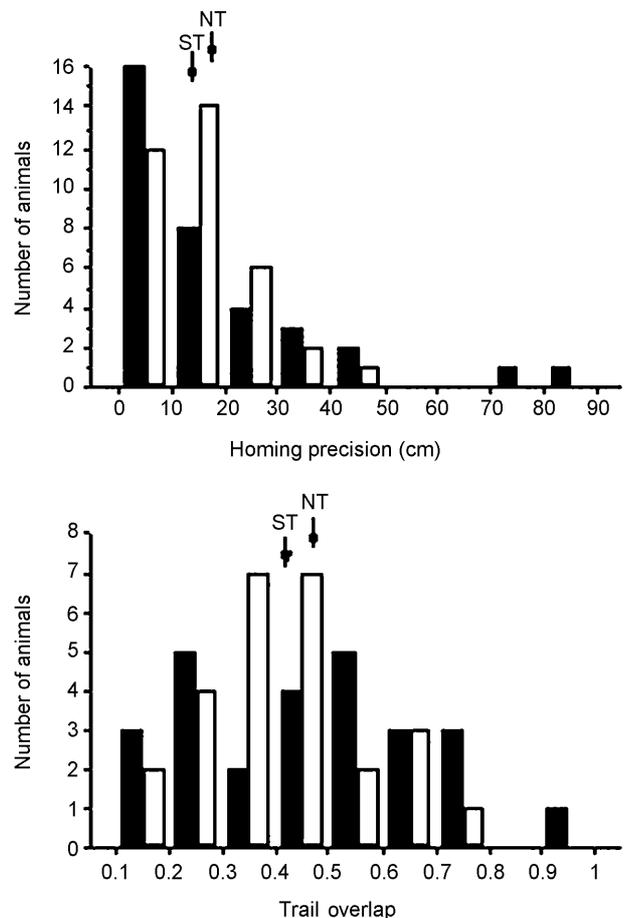


Figure 3. Frequency distribution of Homing Precision (HP) and Trail Overlap (TO) at spring and neap tides. N=36; black bars, spring tides (ST=mean); white bars, neap tides (NT=mean).

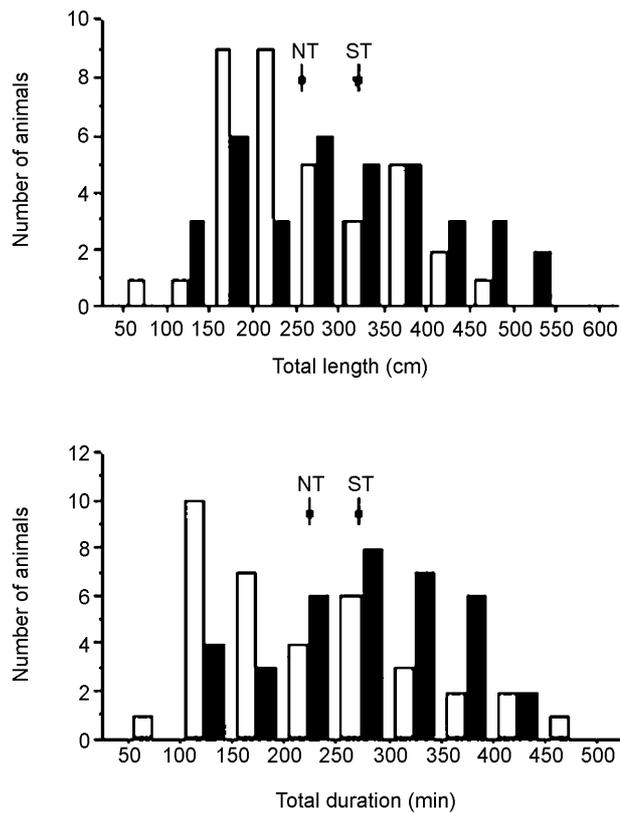


Figure 4. Frequency-distribution of Total Length (TL) and Total Duration (TD) at spring and neap tides. $N=36$; black bars, spring tides (ST=mean); white bars, neap tides (NT=mean).

19.6 ± 18.8 cm, respectively ($Z=0.021$, $P>0.05$) (Figure 3). More than 70% of individual foraging excursions, selected randomly irrespective of the spring/neap cycle, scored HP values 18.0 cm. At ST, occasional HP values >80 cm corresponded to limpets relocating. The Trail Overlap

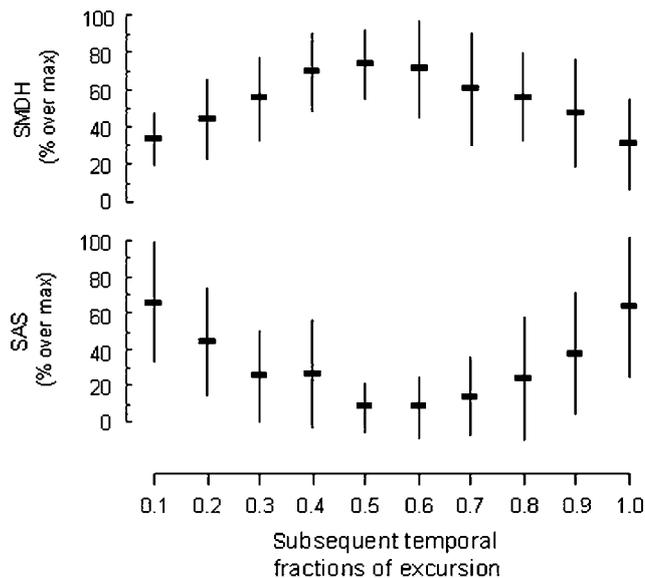


Figure 5. Variation of Segmental Maximum Distance from Home (SMDH) and Segmental Average Speed (SAS) throughout 10 subsequent fractions of the foraging excursion. Y-axis, percentage relatively to max values; vertical bars, standard deviation (SD).

(TO) varied among individuals (Figure 3), but no significant difference was found between ST and NT (0.42 ± 0.15 , and 0.47 ± 0.20 , respectively; $Z=0.590$, $P>0.05$).

The Total Length (TL) and the Total Duration (TD) of excursions were also variable among the 36 marked individuals (Figure 4). Average TL was significantly larger during ST (308.6 ± 116.8 cm) than NT (257.4 ± 94.4 cm) ($Z=3.172$; $P<0.05$). Accordingly, the Maximum Distance from Home (MDH) was greater at ST than at NT (60.3 ± 30.1 cm and 48.8 ± 24.5 cm, respectively; $Z=2.173$; $P<0.05$). Average TD was higher at ST (277.7 ± 83.2 min) than at NT (228.2 ± 104.8 min), with modal values around 275 and 125 min, respectively ($Z=1.521$; $P>0.05$). Consistent with the frequency-distribution of TL and TD, the Average Speed (AS) was not significantly different between ST and NT (0.8 ± 0.3 and 0.7 ± 0.3 cm min^{-1} , respectively; $Z=0.501$ $P>0.05$). The values for TL, TD, MDH and AS did not differ significantly for eight marked individuals at a single motographic location throughout 12 months ($Z=0.634$, 0.987 , 0.432 , 1.674 , respectively, $P>0.05$). The Direction Angle (DA) of excursions was also variable among the 36 marked individuals. No significant difference was found between ST and NT, with the majority of excursions approximately heading downwards at both times: the resultant DA was 141 and 164 at ST and NT, respectively. Variation of Segmental Average Speed (SAS) and Segmental Maximum Distance from Home (SMDH) throughout ten subsequent excursion fractions (Figure 5) shows a tri-phasic organization of *F. crassa* excursions, with a relatively fast outward phase, a slow-moving phase around the MDH point, and a relatively fast returning phase.

DISCUSSION

Fissurella crassa was active during nocturnal low tides and inactive in sheltered refuges during high tides, irrespective of the day/night cycle. Crevices and depressions of the rock are used as refuges by this limpet. A similar activity pattern have been reported for several other intertidal molluscs (e.g. Wells, 1980; Hawkins & Hartnoll, 1982; Della Santina & Chelazzi, 1991). Tide cycles in combination with local factors, like the risk of dislodgement by waves, the risk of dehydration and that of predation, affect the activity rhythm of intertidal gastropods (Little, 1989). In particular, diurnal low tides present marine molluscs with the risk of dehydration (Levings & Garrity, 1983, 1984; Little & Stirling, 1985; Branch & Cherry, 1985). Franz (1990) suggested the differential dehydration risk on three *Fissurella* spp. as the major cause of their different activity rhythms. This physiological constraint may be particularly important to *F. crassa*. This species has a large foot extensively uncovered by the shell, as well as the hole at the apex of the shell. The fact that inter-individual variability of the Time of Departure from Home was significantly lower during spring tides (when the low tide occurs at the beginning of the night) than at neap (when low tides are at midnight), suggests the importance of complete darkness in controlling activity in *F. crassa* (average TDH is around 2100–2200 at spring). Since central Chilean rocky shores are ranked as heavy exposed (Dayton et al., 1977; Santelices, 1989), hydrodynamics are regarded as the major abiotic factor inducing

inactivation of *F. crassa* and tenacity of attachment to substrate during high tides, either diurnal as nocturnal ones, as also showed for *Cellana* spp. (Underwood, 1976) and for *Acanthopleura granulata* (Focardi & Chelazzi, 1990). Moreover, during the marking process *F. crassa* efficiency was directly experienced in firmly attaching by their large foot to the refuge. This appears to be a considerable adaptation to the risk of dislodgement and predation. In synthesis, the temporal window corresponding to nocturnal low tides appears to present the most favourable conditions of stressing factors for *F. crassa* under heavy sea exposure. A comparison of these results with an independent assessment of activity rhythm in populations inhabiting less exposed rocky shores would be important to test hypotheses on abiotic factors influencing activity patterns of this species.

Regarding the spatial behavioural patterns, this key-hole limpet showed an isozonal spatial strategy (Chelazzi, 1990), fluctuating on a continuum between a central place foraging and a ranging strategy. However, homing behaviour was dominant over the ranging strategy among the marked individuals studied. Central place foraging strategy has been described in a number of intertidal chitons and gastropods (Underwood, 1979; Chelazzi et al., 1988; Chelazzi, 1990). Flexibility of spatial strategies of *F. crassa* was observed at an inter/intraindividual level. Franz (1990) also found that the spatial activity patterns of three Caribbean *Fissurella* spp. were a combination of distinct spatial strategies.

The present study provides strong indications about the mechanism of orientation enabling lapas to relocate home. A conspicuous percentage of steps of the inward branch of individual excursions was overlapped with those of the outward branch, consistently with a trail-following hypothesis (Chelazzi et al., 1988). Trail-following is well documented within intertidal molluscs, always in strict association with homing behaviour (Chelazzi et al., 1987; 1993; Focardi & Chelazzi, 1990; Santini et al., 1991).

Analysis of Segmental Average Speed (SAS) and Segmental Maximum Distance from Home (SMDH) suggests that individual excursions are tri-phasic in their organization. The first and the third part are characterized by high values for SAS, while the second part has high values for SMDH associated with low values of SAS. This suggests that during the outward and inward part of the excursion the forager moves rapidly (away from and toward home, respectively), while during the second part it moves slowly to search for food and to feed (Evans & Williams, 1991; Santini et al., 1991). Interestingly, despite excursions did not differ significantly in their Direction Angle (DA) between spring and neap (the resultant DA was downward directed in both cases), our data show that *F. crassa* spent more time in the lowest intertidal belt during spring than during neap low tides, when this fringe remains normally submerged.

Finally, a long-term stability of temporal and spatial patterns of foraging excursions was revealed by the 12-months comparison of four motographic parameters (Total Length, Maximum Distance from Home, Total Duration, Average Speed) relatively to eight *F. crassa* at a single motographic location. Consistently, the average grazing areas of three Caribbean *Fissurella* spp. did not

differ significantly in the course of different seasons (Franz, 1990).

This study was funded by the European Union (contract no. CT1*CT93-03). G.S. was supported by a grant from the Università degli Studi di Firenze (Dottorato in Biologia animale—Etologia).

REFERENCES

- Branch, G.M., 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanographic Marine Biology Annual Review*, **19**, 236–380.
- Branch, G.M. & Cherry, M.I., 1985. Activity rhythms of the pulmonate limpet *Siphonaria capensis* (Q. & G.) as an adaptation to osmotic stress, predation and wave action. *Journal of Experimental Marine Biology and Ecology*, **87**, 153–168.
- Chelazzi, G., 1990. Eco-ethological aspects of homing behaviour in molluscs. *Ethology, Ecology and Evolution*, **2**, 11–26.
- Chelazzi, G., Della Santina, P. & Parpagnoli, D., 1987. Trail-following in the chiton *Acanthopleura gemmata*: operational and ecological problems. *Marine Biology*, **95**, 539–545.
- Chelazzi, G., Focardi, S. & Deneubourg, J.L., 1983. Competition for the home and aggressive behaviour in the chiton *Acanthopleura gemmata* (Blainville) (Mollusca: Polyplacophora). *Behaviour Ecology and Sociobiology*, **14**, 15–20.
- Chelazzi, G., Focardi, S. & Deneubourg, J.L., 1988. Analysis of movement patterns and orientation mechanisms in intertidal chitons and gastropods. In *Behavioural adaptation to intertidal life* (ed. G. Chelazzi and M. Vannini), pp. 173–184. New York: Plenum Press.
- Chelazzi, G., Santini, G. & Della Santina, P., 1998. Route-selection in the foraging of *Patella vulgata* (Mollusca: Gastropoda). *Journal of the Marine Biological Association of the United Kingdom*, **78**, 1223–1232.
- Chelazzi, G., Santini, G., Della Santina, P. & Focardi, S., 1993. Does the homing accuracy of intertidal chitons rely on active trail-following? A simulation approach. *Journal of Theoretical Biology*, **160**, 165–178.
- Dayton, P.K., Rosenthal, R.J., Mahen, L.C. & Antezana, T., 1977. Population structure and foraging biology of the predaceous Chilean asteroid *Meyenaster gelatinosus* and the escape biology of its prey. *Marine Biology*, **39**, 361–370.
- Della Santina, P. & Chelazzi, G., 1991. Temporal organization of two Mediterranean limpets, *Patella rustica* and *P. coerulea*. *Journal of Experimental Marine Biology and Ecology*, **153**, 75–85.
- Della Santina, P., Santini, G. & Chelazzi, G., 1995. Factors affecting variability of foraging excursions in a population of *Patella vulgata* (Mollusca: Gastropoda). *Marine Biology*, **122**, 265–270.
- Evans, M. & Williams, G.A., 1991. Time partitioning of foraging in the limpet *Patella vulgata*. *Journal of Animal Ecology*, **60**, 563–575.
- Focardi, S. & Chelazzi, G., 1990. Ecological determinants of bioeconomics in three intertidal chitons (*Acanthopleura* spp.). *Journal of Animal Zoology*, **59**, 347–362.
- Franz, C.J., 1990. Seasonal, diurnal, and nocturnal activity patterns of three species of Caribbean intertidal key-hole limpets (Mollusca: Gastropoda: *Fissurella*). *The Veliger*, **33**, 155–165.
- Hawkins, S.J. & Hartnoll, R.G., 1982. The influence of barnacle cover on the numbers, growth and behaviour of *Patella vulgata* on a vertical pier. *Journal of the Marine Biological Association of the United Kingdom*, **62**, 855–867.
- Levings, S.C. & Garrity, S.D., 1983. Diel and tidal movements of two co-occurring neritid snails: differences in grazing patterns on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology*, **67**, 261–278.

- Levings, S.C. & Garrity, S.D., 1984. Grazing patterns in *Siphonaria gigas* (Mollusca: Pulmonata) on the rocky Pacific coast of Panama. *Oecologia*, **64**, 152–159.
- Little, C., 1989. Factors governing patterns of foraging activity in littoral marine herbivorous molluscs. *Journal of Molluscan Studies*, **55**, 273–284.
- Little, C. & Stirling, P., 1985. Patterns of foraging activity in the limpet *Patella vulgata* L.—a preliminary study. *Journal of Experimental Marine Biology and Ecology*, **89**, 283–296.
- Newell, R.C., 1979. *Biology of intertidal animals*. Faversham: Marine Ecological Survey Ltd.
- Oliva, D. & Castilla, J.C., 1986. The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. *Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecology*, **7**, 201–217.
- Oliva, D. & Castilla, J.C., 1992. Recognition guide and morphometry of ten species of genus *Fissurella* (Bruguere) (Mollusca: Gastropoda) common in fishery and indigenous shellmidden from central and southern Chile. *Gayana Zoologia*, **56**, 77–108.
- Raffaelli, D. & Hawkins, S.J., 1996. *Intertidal ecology*. London: Chapman & Hall.
- Santini, G., Della Santina, P. & Chelazzi, G., 1991. A motographic analysis of foraging behaviour in intertidal chitons (*Acanthopleura* spp.). *Journal of the Marine Biological Association of the United Kingdom*, **71**, 759–769.
- Santelices, B., 1989. *Algas marinas de Chile*. Ediciones Pontificia Universidad Católica de Chile.
- Siegel, S.N.J. & Castellan, Jr, 1988. *Nonparametric statistics for the behavioral sciences*. New York, NY: McGraw-Hill Inc.
- Underwood, A.J., 1979. The ecology of intertidal gastropods. *Advances in Marine Biology*, **16**, 111–210.
- Wells, R., 1980. Activity pattern as a mechanism of predator avoidance in two species of acmaeid limpet. *Journal of Experimental Marine Biology and Ecology*, **48**, 151–168.

Submitted 8 June 2000. Accepted 20 October 2000.