

Variation in foraging activity of *Acanthochitona garnoti* (Mollusca: Polyplacophora) from different habitats

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Foraging activity of *Acanthochitona garnoti* was studied during spring and neap tides in three different habitats: an aeolian sandstone platform, a permanent high-shore rock pool (aeolian shore) and a quartzitic sandstone boulder shore. On exposed rock, *A. garnoti* was active only during nocturnal low tides, although some individuals were active during early morning low tides when in shade. Chitons from upper-shore pools were active during both day and night low tides. At all sites chitons foraged for longer (\bar{x} = 5.5 h) and travelled further (\bar{x} = 313 mm) during a spring tide new moon and least on a spring tide full moon (\bar{x} = 4.0 h; \bar{x} = 182 mm). Chitons on the boulder beach travelled greater distances (\bar{x} = 367 mm) during foraging than those from aeolian shores (\bar{x} = 105 mm). It is suggested that this is a result of boulder beach chitons having further to travel to find a grazing patch. Finally, *A. garnoti* was found to have a ranging pattern of activity on boulder shores and a homing pattern on aeolian shores.

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The role of grazers in structuring intertidal rocky shore communities is well documented (Branch 1981, 1985; Hawkins & Hartnoll 1983; Branch & Barkai 1988). This pivotal importance of grazers has prompted numerous studies of their ecology, including detailed examinations of their activity and foraging behaviour. Gastropod molluscs have been the most closely studied (see Underwood 1979; Branch 1981; Chelazzi, Focardi & Deneubourg 1988; Little 1989 for reviews of literature) but chitons can also be very abundant on rocky shores (Bode 1989). Detailed investigations into their activity have been the subject of more recent studies (e.g. Chelazzi, Focardi & Deneubourg 1983; Chelazzi & Parpagnoli 1987; Chelazzi, Della Santina & Parpagnoli 1987; Deneubourg, Focardi & Chelazzi 1988; Focardi & Chelazzi 1990; Chelazzi, Della Santina & Parpagnoli 1990; Santini, Della Santina & Chelazzi 1991).

Studies on the foraging behaviour of limpets have shown that habitat can influence the timing of activity within a species (Branch & Cherry 1985; Little 1989; Gray & Naylor 1996). Whereas movement patterns between species of chiton from similar habitats have been studied (Chelazzi, Focardi & Deneubourg 1983; Chelazzi, Della Santina & Parpagnoli 1990), there have been no investigations of how habitat may influence movement within a species.

Acanthochitona garnoti (Blainville, 1825) is one of the commonest chitons in the mid- to upper intertidal regions of rocky shores of South Africa, being distributed from Saldanha Bay to southern Natal (Kilburn & Rippey 1982; Branch, Griffiths, Branch & Beckley 1994). Furthermore, *A. garnoti* is ubiquitous on rocky shores with different geomorphologies (Hodgson pers. obs.), being found on platforms, vertical rocky reefs and boulder shores as well as in rock pools. Although very abundant, very little is known about its influence in intertidal communities. As a first step towards an understanding of the role played by *A. garnoti* on rocky shores, we compared the activity patterns and behaviour of this chiton on shores with different geomorphologies. In addition, the behaviour of individuals which are permanent inhab-

itants of rock pools was also investigated.

Materials and methods

Study sites and habitats of chitons

Activity of *Acanthochitona garnoti* was studied on an exposed horizontal platform of aeolian sandstone (Kenton-on-Sea — 33°41'S; 26°40'E) and a quartzitic sandstone boulder shore (Cannon Rocks — 33°44'S; 26°35'E), during 1994. In addition, the activity rhythms of chitons which were permanent inhabitants of high shore rock pools at Kenton-on-Sea were observed. All sites experienced semi-diurnal tides, the tidal range being about 1.9 m on mean spring tides, and 0.9 m on mean neap tides, with highest spring tides phased around 04:00 and 16:00 (S.A. Navy tide tables).

At all sites foraging activity of chitons was studied during different lunar regimes: spring tide full moon (SFM), neap tide quarter moon (NQM) (except aeolian platform), and spring tide new moon (SNM). The observations at Cannon Rocks were carried out between late March to early May 1994, whereas those at Kenton-on-Sea were between late July to early September 1994 (see Figure 1 for dates).

Foraging activity: aeolian platform and rock pools, Kenton-on-Sea

During daytime low tides many chitons on aeolian sandstone inhabit small depressions or holes which we believe are actively excavated by the chitons, as has been previously suggested for *Ceratozona angusta* (Schmidt-Effing 1980) and *Acanthopleura gemmata* (Chelazzi, Focardi, Deneubourg & Innocenti 1983; Chelazzi & Parpagnoli 1987). Twenty chitons, each at least 20 mm in length, were labelled with small plastic numbers (Dymo tape) attached to one of the central valves with epoxy resin 24 h prior to observations. The position of the chitons was determined by triangulation (Cook, Bamford, Freeman & Tiedman 1969) every hour from when the chitons were uncovered by the tide to re-submergence. The triangulation points consisted of three steel nails embed-

ded into the rock equi-distant from one another (50 cm) in an equilateral triangle. Measurements were not taken during high tide since intense wave activity in the intertidal zone made observations impossible. However, it was assumed that chitons remained inactive during immersion, as preliminary observations of *A. garnoti* have shown them to be inactive when submerged by high tides (Reddy 1993).

Chitons were recorded as 'inactive' when they were in a depression/hole and as 'active' when away from this position. At night, observations were made using only red light, since previous studies have shown that white light causes limpets to cease foraging (Cook *et al.* 1969; Little & Stirling 1985; Gray & Naylor 1996).

Foraging activity: boulder shore, Cannon Rocks

During the daytime low tides at Cannon Rocks the chitons retreated beneath boulders. The topography of the shore made it impossible to use triangulation to monitor their position. Instead, 30 chitons (20 to 30 mm length) and their resting positions were each marked with a small coloured dot using non-toxic paint. Twenty-four hours later the animals were observed every hour from when they were first exposed to re-submergence, during daytime and night-time low tides. At each observation, a small dot of paint was placed next to the

new position of each chiton. Thus it was possible to track the position of each animal, calculate the distance moved and estimate the speed of movement.

Results

Acanthochitona garnoti from the horizontal platform of aeolian sandstone (Kenton-on-Sea) and boulder beach (Cannon Rocks) had a daily rhythm of activity. On both spring and neap tides, chitons only foraged during the nocturnal low tides, with 80 to 100% of the marked chitons being active (Figure 1). However, we observed that in other areas of the shores, some chitons were active during early morning low tides if they were in the shade. Those chitons inhabiting the rock pools were active during both day and night low tides although the number of chitons active was always less during the day (50–70%) than by night (70–90%) (Figure 1). Therefore, calculations of time spent foraging and distance travelled by the rock-pool chitons include data from both day and night excursions.

On all occasions, activity of *A. garnoti* commenced as the tide receded and the chitons were emersed, and homeward movement commenced well before the rising tide covered the chitons. Throughout the study 92% of the marked chitons from the aeolian platform and 90% of the marked animals in

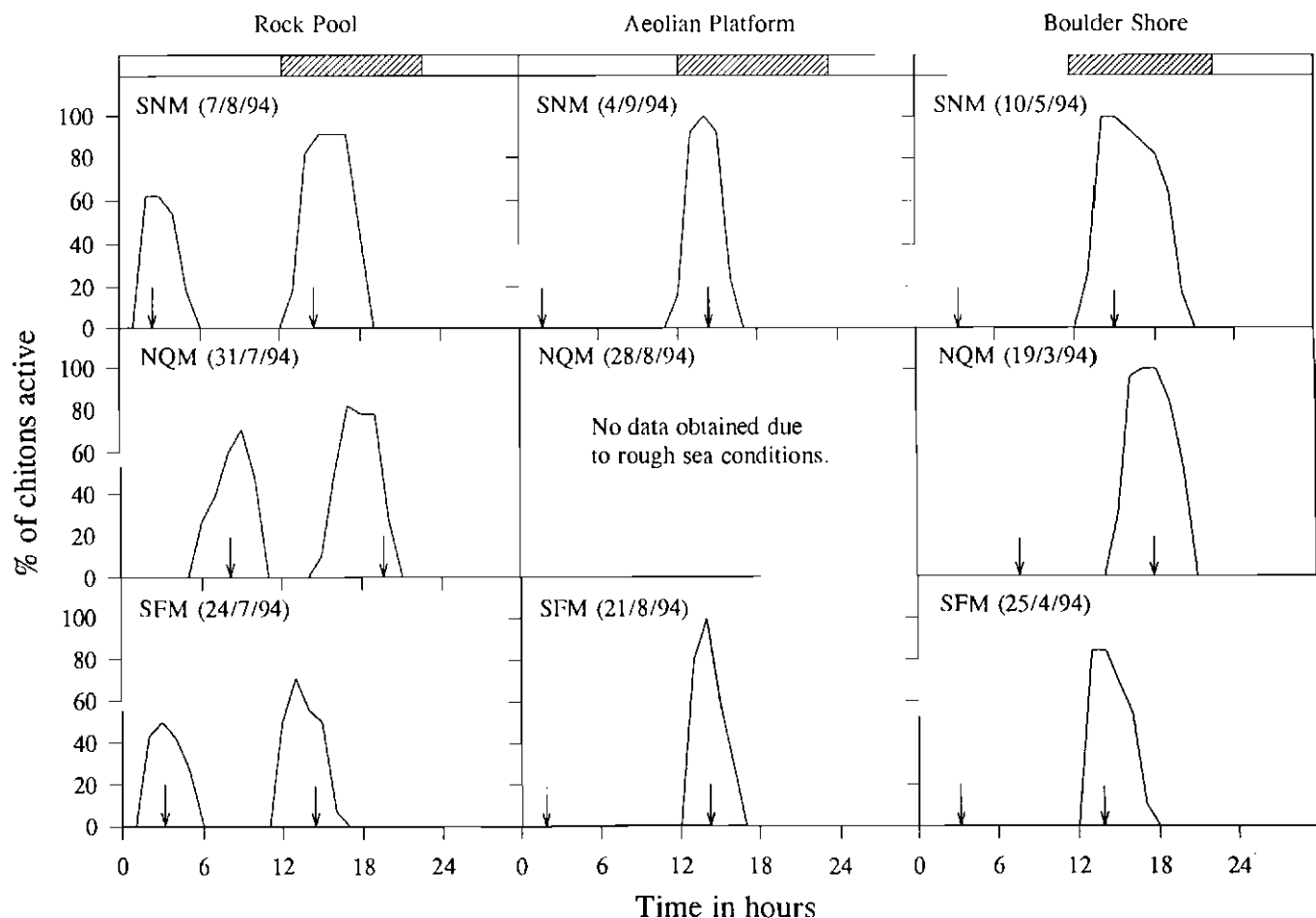


Figure 1 The percentage of *Acanthochitona garnoti* recorded as active every hour for 24 h during three tidal cycles in a high-shore rock pool (Kenton-on-sea), on an aeolian sandstone platform (Kenton-on-sea), and on a quartzitic sandstone boulder shore (Cannon Rocks). Note that in the rock pool the chitons were permanently submerged. Arrows indicate time of low tides; horizontal hatched bars, periods of darkness. SNM, spring new moon; SFM, spring full moon; NQM, neap quarter moon.

Table 1 Summary of activities of *Acanthochitona garnoti* over 24 h observation periods during spring and neap tides. ND = no data. Data given as $\bar{x} \pm S.D.$

Site	Total % homed	Total time spent active (min)			Total distance travelled (mm)		
		SNM	SFM	NQM	SNM	SFM	NQM
Platform	92	220±47	174±53	ND	195±122	86±54	ND
Rock Pool	90	382±148	253±149	333±131	200±100	154±122	246±123
Boulder	12	346±50	236±34	282±52	487±273	331±210	310±173

rock pools returned to a home depression or hole in the rock. By contrast, only 12% of the chitons marked on the boulder shore (Cannon Rocks) returned to their starting site (Table 1). Observations of those chitons which returned to a home site revealed that individuals never returned to the home site by their outward path.

At all sites, chitons spent a significantly greater ($p < 0.001$; multifactor analysis of variance) amount of time foraging during New Moon and the least time at Full Moon (Tables 1 & 2). The total time spent grazing at a particular phase of the moon varied significantly between sites ($p < 0.001$; multifactor analysis of variance). For example on a spring new moon, chitons inhabiting rock pools and the boulder shore spent about 340–380 min foraging, 1.7 times as long as animals on the horizontal platform (about 220 min) (Tables 1 & 3). During foraging excursions the total distances travelled by the chitons also varied with tidal regime and site (Table 1). Chitons travelled significantly greater distances ($p < 0.001$; MANOVA) on spring new moon relative to either neap quarter moon or spring full moon (Table 2). The distance moved on the boulder beach was significantly greater than on the aeolian sandstone ($p < 0.001$; MANOVA). The total distance travelled by chitons in the rock pool was also significantly greater than on the horizontal platform (Table 3), although there was no difference in the distance travelled between these habitats

Table 2 Results of Scheffe's multiple range tests to determine any significant differences between the time spent foraging and distances travelled by *A. garnoti* during different phases of the tide

Tidal phase	<i>n</i>	Time spent foraging		Distance travelled	
		LS mean	Homogeneous groups	LS mean	Homogeneous groups
Spring Full moon	42	3.99	X	18.18	X
Neap Quarter moon	42	4.61	X	21.12	X
Spring New moon	39	5.50	X	31.26	X

Table 3 Results of Scheffe's multiple range tests to determine any significant differences between time spent foraging and distances travelled by *A. garnoti* at the three different study sites

Study site	<i>n</i>	Time spent foraging		Distances travelled	
		LS mean	Homogeneous groups	LS mean	Homogeneous groups
Aeolian platform	22	3.21	X	10.46	X
Boulder shore	66	4.79	X	23.41	X
Rock pool	35	6.10	X	36.68	X

on a spring new moon (Table 1).

Estimates of speed of movement on the boulder shore revealed that chitons travelled away from their home site relatively rapidly ($\bar{x} = 0.7 \pm 0.3$ cm. min⁻¹) before slowing down ($\bar{x} = 0.2 \pm 0.1$ cm. min⁻¹). Prior to immersion by the rising tide, they moved rapidly ($\bar{x} = 0.6 \pm 0.2$ cm. min⁻¹) back to a resting site.

Discussion

On both exposed aeolian rock platforms and quartzitic sandstone boulder shores, *Acanthochitona garnoti* had a distinct period of activity which was confined to nocturnal low tides. A similar observation was made for crevice-dwelling individuals of this species from quartzitic rocky reefs at Port Elizabeth (Reddy 1993). By contrast, those chitons which inhabited upper-shore rock pools, and hence were permanently submerged, were active during both day and nighttime low tides. Branch & Cherry (1985) obtained a similar result for the pulmonate limpet *Siphonaria capensis*. Although the sum total of time spent foraging by *A. garnoti* in 24 h was greater in the rock pool than on the platform and boulder shore, the distances moved by the rock-pool chitons were significantly less.

The timing of activity in intertidal molluscan grazers has been linked to a number of factors, including avoidance of desiccation, predators and wave activity (Branch & Marsh 1978; Garrity & Levings 1983; Chelazzi, Focardi, Deneubourg & Innocenti 1983; Branch & Cherry 1985; Gray & Hodgson 1997). In the case of *A. garnoti* we suggest that all of these factors play a role in controlling the timing of foraging activity. By foraging at night *A. garnoti* is active when the humidity is higher (always > 70%) and temperatures lower, thus desiccation must be reduced. Where the risk of diurnal desiccation is reduced, e.g. in permanently filled rock pools or in the shade, the chitons can be active during every low tide. The importance of desiccation as a controlling factor in the timing of grazing activity has been shown for other molluscs (Branch & Cherry 1985; Gray & Hodgson 1997). Foraging at low tide and retreating to crevices or hollows during immersion probably enables these chitons to reduce the risk of predation, as has been suggested for *Acanthopleura gemmata* (Chelazzi, Focardi, Deneubourg & Innocenti 1983). Finally although not measured, the tenacity of *A. garnoti* appears to be relatively low, as is the case for high-shore limpets (Branch & Marsh 1978; Gray, 1997). By retreating beneath boulders and into crevices or, in the case of aeolian platforms by excavating holes, *A. garnoti* is able to avoid being swept away by wave action.

Many species of chiton have been shown to exhibit homing, whereas others do not return to their previous position

after a foraging excursion (see Chelazzi, Focardi & Deneubourg 1983 for review). *Acanthochitona garnoti* displays different degrees of homing in different habitats. On boulder shores (this study) and quartzitic rocky reefs (Reddy 1993), very few individuals return to their initial position, and in this respect these individuals display a ranging pattern of foraging (see Chelazzi *et al.* 1988). By contrast, on aeolian rock (both exposed platforms and pools) *A. garnoti* exhibits a degree of homing, returning to a home hollow. These individuals display central place foraging. Underwood (1979) has suggested that the homing behaviour of grazers could ensure that populations maintain an even pattern of dispersion, which will maximise the availability of food. Whether this applies to *A. garnoti* which inhabit aeolian sandstone is not known, but this species could be an ideal model with which to test relationships between homing, population density, dispersion and food abundance in intertidal grazers. The degree of home/hollow fidelity was not examined in this study and it would be interesting to see whether *A. garnoti* shows territoriality and aggression towards conspecifics as has been shown in *Acanthopleura gemmata* (Chelazzi & Parnagnoli 1987).

The mechanism by which *A. garnoti* returns to a crevice or home site was not investigated. Some chitons have been shown to use trail following (e.g. Deneubourg, Focardi & Chelazzi 1988; Chelazzi, Della Santina & Parnagnoli 1990). However, none of the chitons in this study returned to a refuge via their outward trail, although some trail crossing did occur and it is possible that encountering previous trails may provide the chitons with sufficient information for correct orientation. In some species of gastropod, trail information has been found to survive on intertidal rocks for one or two days (Cook 1969, 1971; Chelazzi, Della Santina & Vannini 1985).

Studies on South African limpets have shown that these animals travel further and are active for longer during spring low tides than during neap tides (Branch & Cherry 1985; Gray & Hodgson 1997). It has been suggested that siphonariid limpets are limited to foraging whilst exposed owing to their low tenacity; foraging excursions will then be shorter in duration and distance on neap tides, allowing the limpets to return home before being subjected to wave activity (Branch & Cherry 1985; Branch 1988). At all sites *A. garnoti* travelled further and was active for longer on new moon spring low tide than during other phases of the moon. Their foraging activity was least on a full moon spring tide. Thus it is very difficult to explain the distance travelled by *A. garnoti* during nocturnal foraging in terms of the time it is free from wave activity. It is possible that bright moonlight, which would be experienced during a full moon, suppresses the activity of the chitons.

The distance moved during foraging was significantly less in chitons inhabiting the aeolian sandstone platform. A possible reason for this could be the increased distance the boulder-beach chitons have to travel to find a suitable grazing patch since these animals appear to have to migrate from the bottom to the upper surface of boulders to graze. However, seasonal influences on grazing activity must also be considered. In a study of foraging activity of *Patella granularis* (Gray & Hodgson 1997), limpets were found to forage further in summer compared to winter. Whereas the observations on *A. garnoti* from the boulder beach were made at the beginning

of autumn, those on the aeolian platform were in spring. The effect of season on grazing activity clearly needs further investigation. A final factor which may have influenced the results is rock topography. Dr. G.A. Williams (pers. comm.), in measuring limpet activity, has found that when the three-dimensional nature of foraging is taken into account, actual distances travelled are increased three-fold. Whereas the boulders were very smooth, the aeolian platform had an uneven topography.

Finally, the foraging activity of *A. garnoti* on the boulder beach could be divided into three distinct phases; a relatively rapid outward phase travelling away from the resting site, a slower foraging phase and a rapid homeward phase. Such behaviour has been recorded for limpets (Hartnoll & Wright 1977; Little *et al.* 1988; Chelazzi *et al.* 1994; Gray & Hodgson 1997), grazing activity being most intense in the middle phase of the cycle (Little & Stirling 1985; Evans & Williams 1991). Whether or not *A. garnoti* feeds throughout activity bouts is not known.

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