Periodic movement and sheltering behaviour of *Actinopyga mauritiana* (Holothuroidea: Aspidochirotidae) in Solomon Islands

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Abstract

Spatial patterns, movement, and sheltering behaviour of the holothurian Actinopyga mauritiana *were examined on an intertidal reef in Solomon Islands over several days between March and October 1998, and in May 1999. Adult animals were associated most commonly with solid reef rock and scattered tables of the coral* Acropora *sp. The holothurians were found in patches with densities ranging from 2.8 to 6.6 animals 100* m^{-2}*. Individuals were identified from the white markings on the tegument. Rates of movement ranged from a minimum of 0.04* $m\ h^{-1}$ *(± 0.01 SE) during high tide at night to a maximum of 0.21* $m\ h^{-1}$ *(± 0.02 SE) during low tide in the daytime. Analysis of movement patterns and sheltering behaviour over 24-hour periods from four tidal cycles revealed that* A. mauritiana *has activity rhythms related to the diel cycle and/or tides. The method used in the study offers a repeatable, accurate, and quantitative way of studying movement of holothurians inhabiting shallow water, provided individual animals can be identified.*

Introduction

Although much research has been devoted to reproduction and feeding of tropical holothurians, relatively little is known about other aspects of their behaviour and its effect on distribution. However, one of the main behaviour patterns to emerge across a range of species is a diel activity rhythm with nocturnal feeding (Crump 1965; Reese 1966; Hammond 1982; Conand 1991; Preston 1993; Wiedemeyer 1992, 1994; Mercier et al. 1999, but see Yamanouchi 1939 for conflicting evidence).

One of the species for which little information on diel activity exists is the surf redfish, *A. mauritiana*. This species is widespread in the Indo-Pacific and typically inhabits hard substrates on reef flats. These habitats are approximately 1–3 m deep and are subject to strong waves and currents (Baker 1929; Yamanouchi 1939; Bakus 1968, 1973; Conand and Chardy 1985; Zoutendyk 1989; Conand 1991, 1993; Hopper et al. 1998). These holothurians graze on epifaunal algal films that consist mainly of plant debris and on the brown and blue-green algae common on the hard substrates they inhabit (Conand 1990; Ramofafia et al. 1997).

The shallow, intertidal and sub-littoral habitat of *A. mauritiana*, and its relatively high commercial value, has led to overexploitation in many countries. Accordingly, the potential for using aquaculture to increase the productivity of *A. mauritiana* has been investigated by the International Center for Living Aquatic Resources Management (ICLARM) (Ramofafia et al. 1997). Our goal was to study the periodic behaviour of *A. mauritiana*, particularly time spent moving and sheltering, to complement work being done to assess the potential for farming this species. Other aspects of behaviour that were investigated included foraging range and homing.

Methods

Study location

Our study was carried out at ICLARM's Coastal Aquaculture Centre (CAC) at Aruligo (159°47'E, 9°18'S), 25 km west of Honiara, Guadalcanal Island, Solomon Islands (Fig. 1). A 400-m section of the foreshore at the CAC was declared as a marine reserve in 1986 and was among the few locations in Solomon Islands where individuals of *Actinopyga mauritiana* were not being harvested at the time of this study.

The foreshore reserve at the CAC consisted of a fringing coral reef, 20–40 m wide. At a depth of 5–10 m, the reef gave way to a rapidly shelving sandy substrate. The reef was exposed to moderate to high wave action, varying both on a daily and a seasonal basis.

The tidal regime in the vicinity of the CAC is mixed and during the study, high and low tide occurred at a similar time each day for many months, with a maximum tidal range of 1.1 m. From late March until late November 1998, high tide occurred at night and low tide during daylight hours (Solomon Islands Hydrographic Unit 1998). The tidal pattern changed only for the months of December 1998 through March 1999, when the cycle reversed and high tide occurred during the day and low tide occurred at night. A fixed reference point on the reef was used to measure water height at the start of each sampling. The average water depth over the reef at low tide was ~20 cm.

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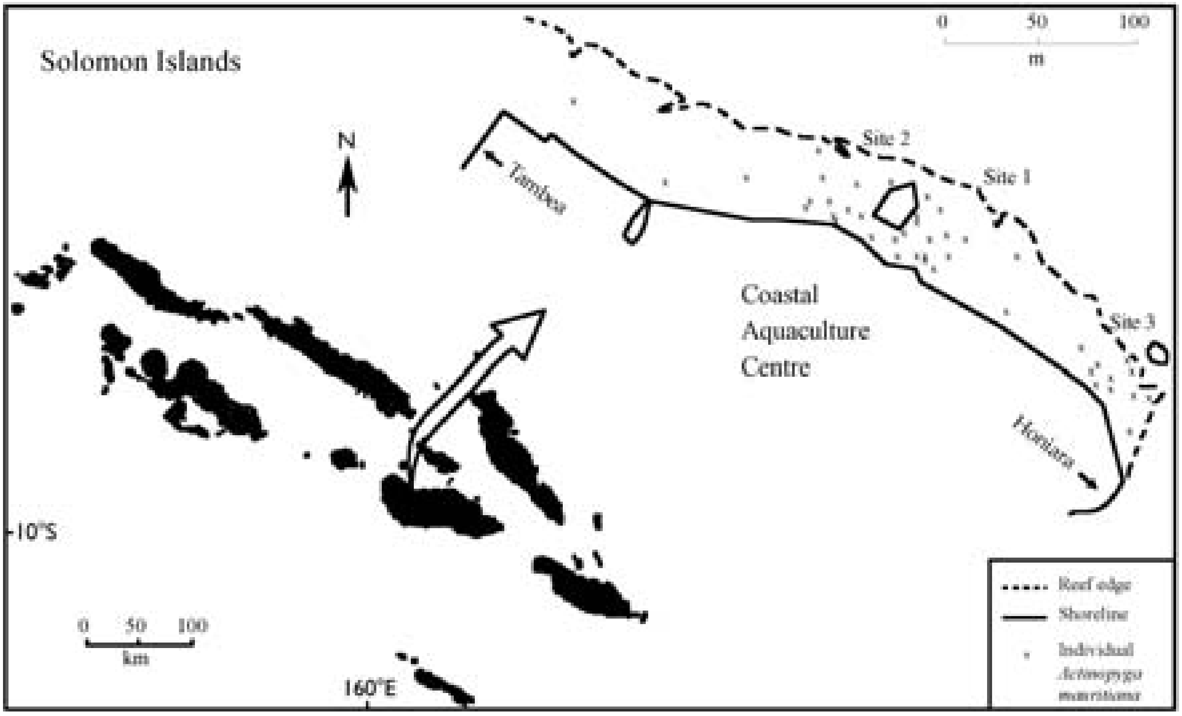

Figure 1. Location of study sites in Solomon Islands. Inset shows the size of the sites at Aruligo and the distribution of individuals at each site in March 1998.

Three sites were identified within the reserve, each selected to contain at least 10 specimens of A. mauritiana (Fig. 1). All sites were located on the reef flat close to the wave impact zone and consisted of solid reef rock with scattered boulders of dead coral. At each site, individual holothurians could be distinguished from one another by the size and pattern of white spots on their tegument (Fig. 2).

Measuring movement and sheltering behaviour

Movement and sheltering behaviour of *A. mauritiana* were studied at Site 1 on 18 and 19 March 1998. Observations were restricted to individuals >300 cm^3. Movement was assessed by measuring the position of each individual every 3 h, for a period of 24 h.

Figure 2. Individuals of *Actinopyga mauritiana* showing unique patterns of markings on the tegument.

To calculate distances, 2 steel posts were driven into the reef flat at the landward edge of an area ~240 m^2 containing 16 animals (Fig. 1). The distance from each post to the centre of the upper surface of each animal was measured to the nearest 0.01 m. By triangulation, we calculated the extent and direction of movement from one observation period to the next using the method of Underwood (1977). This technique calculates linear displacement over a sampling interval, not the total distance moved. The accuracy of measurements was calculated as ± 0.05 m and was determined by moving 20 animals to known distances of 0.1 m to 2.0 m and comparing the known distance with the calculated displacement. For all analyses, any movement <0.05 m was treated as zero.

An individual was considered to be "sheltered" if more than half its body was obscured from view. Sheltering animals were not seen to feed and so sheltering behaviour was used to estimate the proportion of non-feeding individuals. When an animal could not be found, its most recent position was located using the previous coordinates and the surrounding area was searched (without disturbing rocks and boulders) to a radius of 3 m. Animals that were not found within five minutes were considered sheltered. All animals that were not sheltering were considered to be "exposed."

Patterns of movement and sheltering behaviour over a 24-hour period

To determine if *A. mauritiana* had a pattern of movement and sheltering behaviour, the positions and behaviours of all individuals found within the three sites were recorded at 3 h intervals for 24 h, beginning at 1700 hours. The study was conducted on three non-consecutive days between 29 March and 5 April 1998 at Site 1 and on another three non-consecutive days between 8 and 27 April 1998 at Sites 2 and 3. Site 2 (240 m^2) contained 12 animals and Site 3 (390 m^2) contained 11 animals. Movements of individuals were plotted over 24 hours to determine if they returned to the same position when sheltering (homing), and to examine the extent of overlap in the foraging ranges. In addition, data from the first and last sampling intervals were used to calculate the net displacement and direction of movement over a 24-hour period.

Patterns of movement and sheltering behaviour at different tidal height

We tested the null hypothesis that there was no difference between the distances moved by these holothurians, or the proportion of individuals sheltering, during high and low tide. The positions and visibility of 35 individuals within the reserve were recorded at 1.5 h before and after high and low tide for two consecutive tidal cycles. To ensure independent estimates of movement and sheltering behaviour among sampling intervals, eight animals were chosen at random for each sampling interval. These animals were not used again in statistical analysis. The study was conducted from 15 to 17 June 1998 (low tide: 15 June 1448 hours, high tide: 16 June 0542 hours, low: 16 June 1521 hours, high: 17 June 0356 hours) and repeated from 17 to 19 March 1999 (low: 17 March 1328 hours, high: 18 March 0430 hours, low: 18 March 1405 hours, high: 19 March 0456 hours).

Data analysis

A 3-factor analysis of variance (ANOVA) was used to test for the effect of tidal height on the movement and sheltering behaviour of individuals. Years and tides were fixed factors and day was nested in tides (n = 8). Student-Neuman-Keuls (SNK) tests were used to separate those means that differed significantly at a = 0.05. Homogeneity of variance was evaluated using Cochran's test and data transformed using ArcSin when necessary. Pooling of factors to increase the power of tests was carried out only if p > 0.25 (Winer 1971; Underwood 1981).

Results

Density and distribution

The density of *Actinopyga mauritiana* was 6.6, 5.0, and 2.8 animals 100 m^{-2} at Sites 1, 2, and 3, respectively. However, the distribution of animals was patchy. They were encountered most frequently on solid reef rock where scattered tables of *Acropora* sp. provided shelter. *Actinopyga mauritiana* were absent from areas of the reef dominated by foliaceous corals. No specimens were found on sandy substrate.

Patterns of movement and sheltering behaviour over a 24-hour period

The average total distance moved by individuals over 24 hours at all three sites in 1998 was 3.02 m (SE ± 0.16, n = 72). The animals showed marked diel differences in activity and sheltering behaviour (Fig. 3). The pattern was one of increasing movement during the day, peaking in the evening, then declining through the night to a period of relative immobility between 0300 hours and 0630 hours (0.04 m h^{-1} ± 0.01 SE, n = 72). The most movement occurred during the 3 h period 2000–2300 hours (0.21 m h^{-1} ± 0.02 SE, n = 72). The periods of greatest and least movement corresponded to low and high tide, respectively (Fig. 3). Sheltering behaviour was closely related to movement, with the greatest proportion of animals exposed during the periods of most movement (Fig. 3).

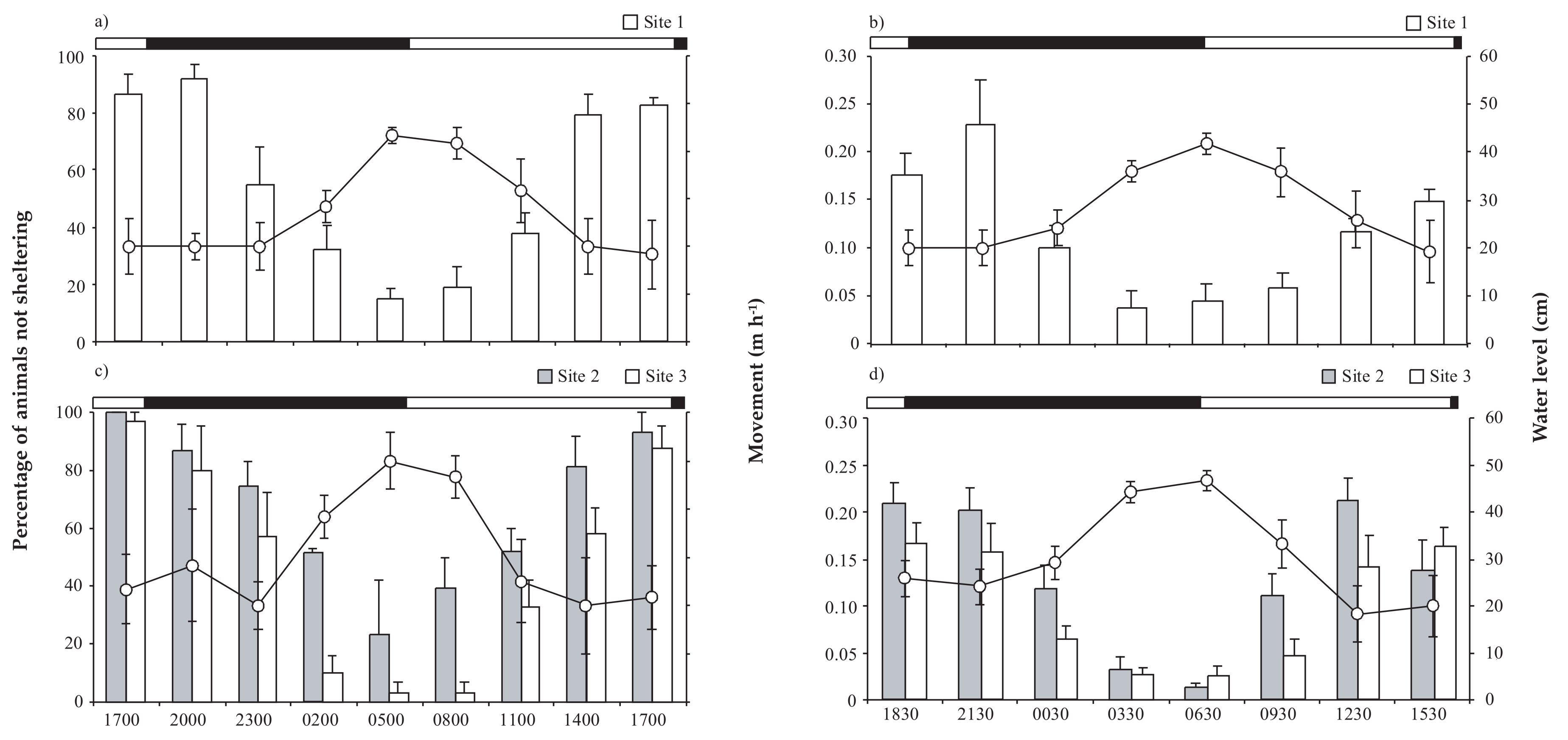

Figure 3. Mean (± SE) rates of movement (m h^{-1}), and percentage of animals exposed, at three sites at Aruligo.
Data were averaged over 3 sampling days, n = 9–17 for each sampling period.
Open circles represent water level above the reef measured from a fixed reference point (cm ± SE).
Horizontal bars give times of daylight (open bar) and darkness (closed bar).
a) and c) percentage of animals not sheltering at each observation period at Site 1 and Sites 2 and 3, respectively;
b) and d) rate of movement during each 3 h sampling interval at Site 1 and Sites 2 & 3, respectively.
Site 1 and Sites 2 and 3 are separated due to different sampling dates.

Homing behaviour, net displacement, and direction

We detected no evidence of homing behaviour or exclusive foraging ranges (Fig. 4). Although the movement of animals showed no strict directional pattern when averaged over all sites and times, there was a tendency for animals to move seaward within the NE to SE quadrant (Fig. 5). The average net displacement and direction of movement of individuals was calculated using coordinates at 0500 hours on Day 1 and 0500 hours on Day 2. The net displacement of individuals over a 24-hour period, pooled across all sites and sampling times, averaged 1.11 m (± 0.06 SE, n = 97); only 15% of individuals were found within 0.50 m of their original position.

Patterns of movement and sheltering behaviour at different tidal heights

Both movement and sheltering were associated with water height. During both years, the movement of animals at high vs low tide differed significantly, with animals moving more during low tide than high tide (Fig. 6, Table 1). The average rate of movement was 0.25 m h^{-1} (± 0.03 SE, n = 32) at low tide and 0.09 m h^{-1} (± 0.03 SE, n = 32) at high tide. Sheltering behaviour was again associated with periods of less movement, with a significantly greater percentage of animals sheltering during high tide than low tide (Table 1). Movement of individuals was significantly greater in 1999 than in 1998 (Table 1). However, there was no difference between the two consecutive days in 1998 or 1999 (Table 1).

Discussion

The method used in this study provides a repeatable and accurate way of analysing the movement patterns of at least some holothurians. The method was particularly suitable for *Actinopyga mauritiana* because individuals could be identified from one sampling interval to the next by patterns on the tegument. Raj (1998a, b) found that photography of individuals of *Stichopus mollis* prevented disturbance of animals but the angle of the photograph and the extent of body markings affected success in identifications. Both the physical examination of animals and photo-identification clearly have advantages over invasive tags, which can alter behaviour and require experimental controls (Chapman 1986; Conand 1989; Chapman and Underwood 1992), but they depend on the presence of distinctive markings.

The low and patchy density of *A. mauritiana* at the Aruligo reserve (2.8–6.6 individuals 100 m^{-2}) is comparable to the reports of 2.0 animals 100 m^{-2} in Vanuatu (Baker 1929) and 3.0 animals 100 m^{-2} in Papua New Guinea (Lokani 1991). All these densities are low among those recorded for tropical aspidochirotes, which range from 0.11 animals 100 m^{-2} for *Holothuria fuscogilva* to 20,000 individuals 100 m^{-2} for *H. difficilis* Semper (Bakus 1973; Preston 1993). However, density estimates for different species must be compared with caution because of the different

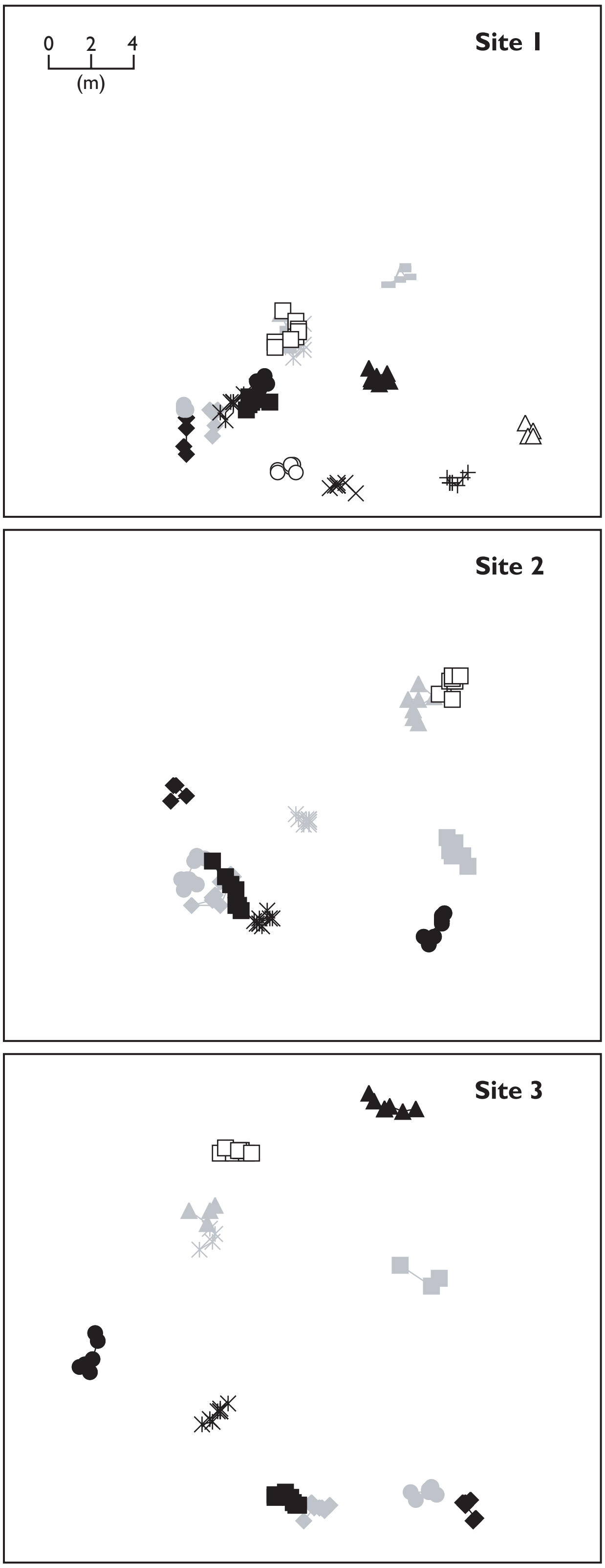

Figure 4. Plots of the movement of individual *Actinopyga mauritiana* at the 3 sites at Aruligo over a period of 24 hours.

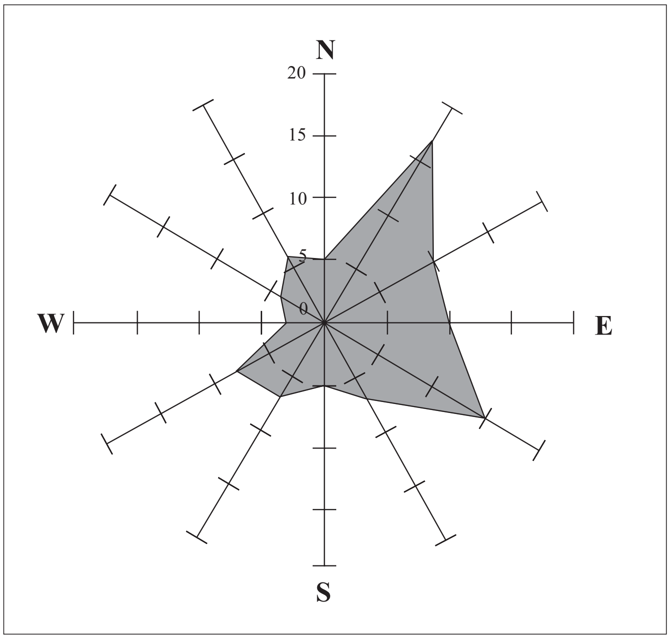

Figure 5. Graph of the net direction of movement of all individuals at the three sites at Aruligo on three days.

sizes of animals and variety of sampling techniques. Variation in levels of harvesting across species can also be expected to confound estimated densities. Moreover, this study shows that the cryptic behaviour of *A. mauritiana* may lead to underestimation if surveys are not carried out during periods of activity.

Yamanouchi (1956), Hammond (1982), DaSilva et al. (1986), and Wiedemeyer (1994) have investigated rates of movement of holothurians, although not of *A. mauritiana*. The rates of locomotion recorded in this study (0.04 to 0.21 m h^{-1}) were comparable to those found by Hammond (1982) for two other aspidochirotes, *H. mexicana* (Ludwig) (0.08 to 0.40 m h^{-1}) and *Isostichopus badionotus* (Selenka) (0.04 to 0.4 m h^{-1}), but far less than those found by Wiedemeyer (1994) for adult *A. echinites* (9 m h^{-1}). Yamanouchi (1956) found that *H. atra* and *H. scabra* moved between 0 and 52 m d^{-1} although, as noted by Wiedemeyer (1994), this study involved moving individuals to artificial habitat and is therefore not comparable. Mercier et al. (in press) found that movements of released, cultured juveniles of *H. scabra* ranged between 0.017 m h^{-1} and 0.033 m h^{-1} depending on the substrate type.

The difference between the cumulative displacement over 24 h (3.02 m d^{-1}) and net displacement (1.11 m d^{-1}), together with the plots of individual movements (Fig. 4), show that movements of *A. mauritiana* over 24 h were not

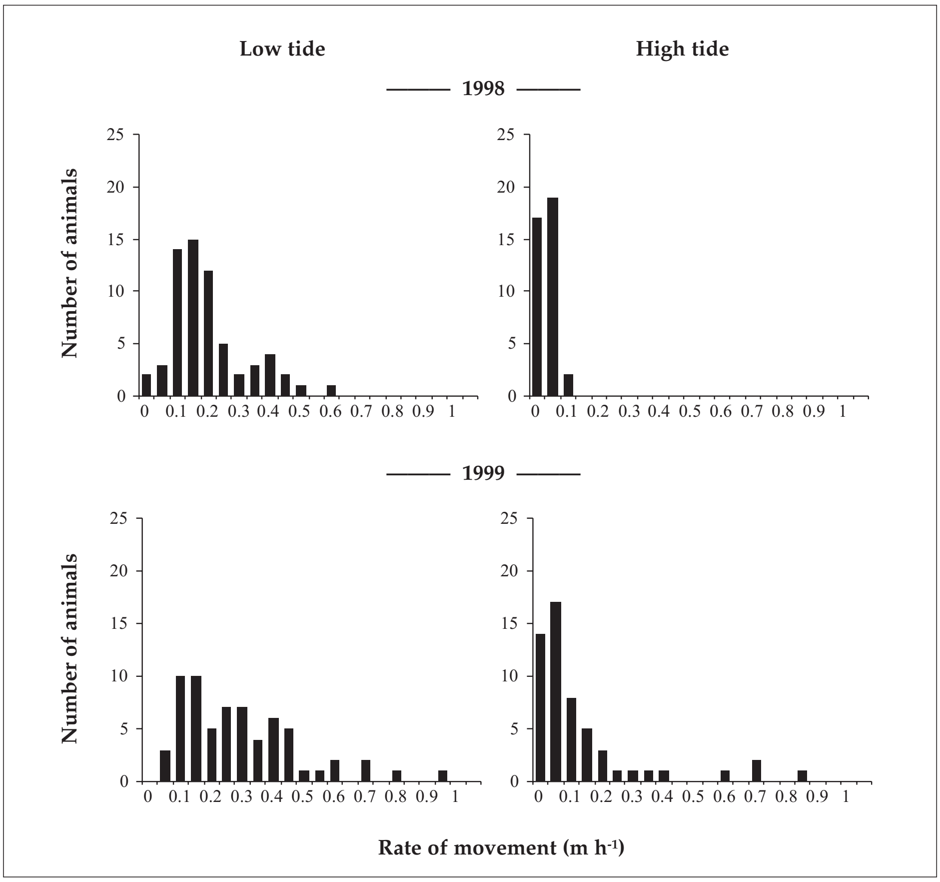

Figure 6. Frequency histograms for rates of movement by *Actinopyga mauritiana* during low and high tide for two days in 1998 and 1999.

Table 1. **ANOVA results for the effect of water level (high and low) on movement and exposure of *A. mauritiana* on two consecutive days in the field at Sites 1, 2 and 3 in 1998 and 1999 (n = 8). Year and tides were fixed factors and days were random and nested in tides. Movement data were transformed to ArcSin(%) to stabilise variances (C = Cochrans test). SNK test for differences in movement and sheltering between high and low tides. Numbers in brackets are standard errors. ns=p>0.05; *= p<0.05: **=p<0.01.**

	Movement (m)				Sheltering (%)			
	C = 0.3096, n.s.				C = 0.50, n.s.			
Source of variation	MS	df	*F*	*p*	MS	Df	*F*	*p*
Years	27.00	1	90.39	*	1.00	1	8	ns
Tides	47.39	1	89.85	*	16.00	1	128	**
Days (Tides)	0.53	2	0.91	ns	0.13	2	0.25	ns
Year* Tides	0.25	1	0.84	ns	0.25	1	2	ns
Year* Day (Tides)	0.29	2	0.51	ns	0.13	2	0.25	ns
Residual	0.58	56			0.50	8		
SNK	*1998 0.07 (0.02)<1999 0.27 (0.04)							
	*High 0.09 (0.03)<Low 0.25 (0.03)				*Low 3.87 (0.13) > High 1.88 (0.30)			

in a consistent direction. Reflected in the lack of directional movement is the finding that individuals did not return to the same shelter sites (Fig. 4). Rather, our data indicate that animals sheltered in the closest available cover after feeding, even though this often resulted in partial exposure. This finding is in contrast to that of Hammond (1982), who found that 68% of *H. tomasi* Pawson and Caycedo, and 72% of *A. agassizi* (Selenka), returned to the same hole to shelter, and who suggested that this was due to the limited number of crevices available for shelter. The abundance of suitable shelter on the reef at Aruligo, and the ability to attach firmly to the substrate for long periods without displacement, appears to explain why the animals in our study did not return to the same shelter sites.

In a study in New Caledonia, Conand (1991) found that *A. mauritiana* displayed some "preferential" (directional) movement towards the reef crest or surf zone to compensate for passive displacement towards the shore by the rising tide. We found a similar net direction of movement of individuals seaward towards the reef crest (Fig. 5), although we found no evidence for passive movement by tides. In contrast, we found that the scope for passive displacement of the animals was minimised by their small movements at high tide. Further investigation into the small-scale patterns of directional movements of *A. mauritiana* is required to determine whether long-term patterns of movements are due to short-term random feeding, or a series of directed movements in response to patchy distributions of food or shelter. However, the fact that the same individuals of *A. mauritiana* remained within a small area of reef for > 12 months, suggests that they did not need to migrate to find these resources.

Due to the mixed nature of the tides in Solomon Islands, we were unable to separate the relative influences of the diel and tidal cycles on the movement and sheltering behaviour of *A. mauritiana*: high tide occurred at night, and low tide in the day, during our study. Thus, the distinct pattern of activity peaking at dusk, and sheltering beginning at dawn, can be described equally well as activity at low tide and sheltering at high tide. Other studies of aspidochirote activity have proposed that nocturnal activity is the dominant behaviour and that periods of increased activity are associated with feeding (e.g. Hammond 1982). This is in line with anecdotal evidence from local harvesting patterns of *A. mauritiana* in Solomon Islands, which suggests that the highest catch per unit of effort occurs during dusk and early evening. Wiedemeyer (1992), however, found that *H. scabra* and *H. atra* deviated from the accepted pattern of nocturnal activity in that their feeding behaviour was not restricted to the period of darkness, and differed among seasons and habitats.

Separating the effects of photoperiod and tidal height on the behaviour of *A. mauritiana* will depend on repeating the research described here when the tidal pattern reverses so that high tide occurs during the day and low tide at night. We were unable to do this because of ethnic tension on the island of Guadalcanal in 1999, which prevented further research at Aruligo. We trust that others will have the opportunity to do this work at another location.

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