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Spatial and temporal distribution of feeding of Aspidochirotida (Holothuroidea) on Heron Island, Great Barrier Reef

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ABSTRACT: Aspidochirotida are distributed throughout the reef flat of Heron Island, contributing 34-44 g wet biomass · m^{-2}. On the reef flat, feeding by *Holothuria edulis* and *Stichopus chloronotus* is concentrated on sediments 2-5 cm from coral outcroppings, while *Holothuria atra* and *Holothuria leucospilota* feed at 5-16 cm from coral outcroppings. Reef flat sediments actively fed upon by Aspidochirotida do not differ significantly ($p>0.05$) in total organic, chlorophyll a, or phaeophytin from sediments not fed upon. Spatial variation in the apparent food quality of sediment is low and probably does not contribute to the distribution of Aspidochirotida on the reef flat. In the lagoon, Aspidochirotida are highly aggregated around the bases of coral patch reefs, where their biomass is 214 g wet weight · m^{-2}. Biomass of Aspidochirotida approaches zero beyond 15 m from coral patch reefs. Sediments at the bases of coral patch reefs in the lagoon do not differ in total organic, chlorophyll a, or phaeophytin from sediments at 20 m distant. However, sediments at the bases of coral patch reefs contain significantly more protein and are significantly skewed toward the coarser grain sizes (phi -1.5 to 1.0). This suggests either that Aspidochirotida in the lagoon aggregate in areas of higher quality sediment, or that intense feeding by Aspidochirotida alters the composition of sediment near coral patch reefs. Most Aspidochirotida feed continuously. *Holothuria atra, H. edulis, H. leucospilota* and *Stichopus variegatus* do not exhibit any diel rhythm in feeding or the passage of sediment through the gut, whereas *S. chloronotus* demonstrates a clear diel rhythm, extending oral tentacles more frequently and passing more sediment late in the day. The aggregated spatial distribution of Aspidochirotida, and the spatial separation of some species, is not driven by resource availability and niche partitioning, but rather by some other factor, such as the availability of shelter.

1. INTRODUCTION

Numerous species of Aspidochirotida coexist on reef flats and in lagoons of coral reefs. Distributions of deposit-feeding holothuroid species on coral reefs are not uniform (Uthicke 1994; Klinger et al. 1994; Massin and Doumen 1986). Physical factors such as water movement influence spatial distribution between localities on reefs (Uthicke 1994; Kerr et al. 1993). However, fine-scale separation of holothuroid species has not been examined. Kohn (1971) contended that partitioning of activities, like feeding, is important where deposit feeders coexist. Spatial separation of some Aspidochirotid species occurs (Klinger et al. 1994). However, coexistence of species occurs in most areas. The purpose of this study was to document small-scale spatial distributions of *Holothuria atra* Jaeger, *Holothuria edulis* Lesson, *Holothuria leucospilota* (Brandt), *Stichopus chloronotus* Brandt, and *Stichopus variegatus* Semper on the reef flat and in the lagoon of Heron Island Reef, to relate these distributions to estimates of potential nutrients available from sediment, and to examine the potential for temporal separation of feeding activities between species.

2. METHODS

Densities of Aspidochirotida on the reef flat were estimated using ribbon transects (rectangular plots) run perpendicular to the shore and spanning the inner and middle reef. In the lagoon, measured circular sweeps were conducted around coral patch reefs and all Aspidochirotida were censused. Biomass estimates were calculated from measured lengths and

Table 1. Densities and biomass of Aspidochirotida on the inner and middle reef flat of Heron Island. Means±1 SEM. n=137 1 m x 5 m rectangular plots. Means with the same letter are not significantly different.

SPECIES	DENSITY ($ind \cdot m^{-2}$)	BIOMASS ($g \cdot m^{-2}$)
H. atra	0.21±0.03 a	16.1±2.6 a
H. leucospilota	0.09±0.02 b	17.5±3.3 a
H. edulis	0.02±0.01 c	1.3±0.6 b
S. chloronotus	0.06±0.01 c	4.1±0.9 b
ALL ASPIDO-CHIROTIDA	0.37±0.04	39.1±4.9

Table 2. Segregation of feeding of Aspidochirotida on the inner and middle reef flat of Heron Island. Distance from anterior ends of individuals to nearest coral outcropping. Means±1 SEM. n given in parentheses. Means with the same letter are not significantly different.

SPECIES	DISTANCE (cm)
H. atra	13.6±2.2 a (146)
H. leucospilota	6.1±1.5 ab (58)
H. edulis	3.5±1.1 b (13)
S. chloronotus	3.5±1.4 b (38)

widths of all censused holothuroids. The weights of twenty measured individuals of each species were used to estimate the relationship between length, width, and wet weight. Spatial separation of feeding activities of Aspidochirotida on the reef flat was examined by measuring the distance from the anterior ends of feeding individuals to the nearest coral outcropping. Displacements of feeding activities from coral outcroppings for each species were compared using an analysis of variance. To determine whether differences existed in characteristics of sediments actively fed upon and those not actively being consumed, the top 5 mm of sediment was collected from immediately in front of the oral tentacles of holothuroids and from 30 cm distant. Total organic, chlorophyll a, and phaeophytin contents of the sediments were measured and compared using paired Student's *t*-tests. To determine if sediment characteristics varied with distance from coral patch reefs in the lagoon, the top 5 mm of sediment was collected from sites 1, 5, and 20 m from coral patch reefs. Total organic contents and granulometry were estimated with samples dried at 60°C. Samples for granulometric analysis were washed in 5% hypochloric acid before drying. Dried samples were separated into component fractions by dry sieving. Organic contents were estimated by loss-on-ignition at 500°C. Protein and pigment contents were estimated from drained sediment samples. Protein was estimated using the method of Bradford (1976). Pigment contents were estimated using the method of Nusch (1980). Total organic, protein, chlorophyll a, and phaeophytin contents, and sediment granulometry were compared using analyses of variance. Temporal separation of feeding activities was investigated in aquaria by recording the number of individuals raking sediment with their oral tentacles and numbers of fecal pellets produced during haphazard times during the morning (3:00-9:00), day (9:00-15:00), evening (15:00-21:00), and night (21:00-3:00). Each aquarium was supplied with fresh sediment from the point of collection of the individuals and flow-through seawater from the reef flat, and was under natural lighting. Fecal pellet production was also monitored for individuals on the reef flat surrounded *in situ* by circular, open-top, nytex cages (1 cm mesh) enclosing *ca.* 3 m^2.

3. RESULTS

Aspidochirotida are numerous and contribute significant biomass to the inner and middle reef flat of Heron Island Reef (Table 1). Small-scale separation of feeding activities occurs on the reef flat (Table 2). *Holothuria edulis* and *S. chloronotus* feed on sediments near coral outcroppings while *H. atra* and *H. leucospilota* feed in the open areas between coral outcroppings. Holothuroids are concentrated near the bases of coral patch reefs in the lagoon where the majority of the biomass of Aspidochirotida is concentrated within 5 meters of coral patch reefs (Table 3). On the reef flat, sediments higher in potential nutrients are not selected for feeding. Sediments which are fed upon do not differ significantly ($p>0.05$) from sediments located distant from feeding holothuroids (Table 4). The nutritional quality of sediment on the reef flat varies little. In

Table 3. Density (individuals · m^{-2}) and biomass (g · m^{-2}) of Aspidochirotida surrounding coral patch reefs in the lagoon of Heron Island. Means of complete censuses of 2 patch reefs at intervals of 1 m distance.

DIST. (m)	*H. atra*		*H. leucospilota*		*H. edulis*		*S. chloronotus*		*S. variegatus*	
	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
1	0.06	5.5	0.04	7.5	0.16	21.3	0.02	1.9	0.10	178.0
2	0.03	4.3	0.00	0.0	0.03	2.4	0.00	0.0	0.02	27.7
3	0.03	3.4	0.00	0.0	0.01	0.4	0.02	0.8	0.02	32.3
4	0.01	1.1	0.00	0.0	0.00	0.0	0.01	1.2	0.01	20.6
5	0.02	1.8	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.00
6	0.02	2.0	0.00	0.0	0.00	0.0	0.00	0.0	0.01	12.3
7	0.02	2.6	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
8	0.01	0.8	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
9	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.01	5.1
10	0.01	0.7	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
11	0.00	0.0	0.01	1.7	0.00	0.0	0.00	0.0	0.00	0.0
12	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
13	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
14	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.01	4.3
15	0.01	0.5	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0

contrast, sediment at the bases of coral patch reefs in the lagoon are richer in protein and are comprised of larger grain sizes than sediment distant from coral patch reefs (Table 5). However, total organic and photosynthetic pigment contents of sediment does not vary with distance from coral patch reefs in the lagoon.

Stichopus chloronotus exhibits a clear, significant diel rhythm to feeding and passage of sediment through the gut in aquaria (Fig. 1). Oral tentacles are extended more frequently, and defecation is higher in the afternoon and evening than in the morning. However, *H. atra*, *H. edulis*, and *H. leucospilota* feed continuously and defecated at a constant rate. Similarly, fecal production by *S. variegatus* varies little with time of day.

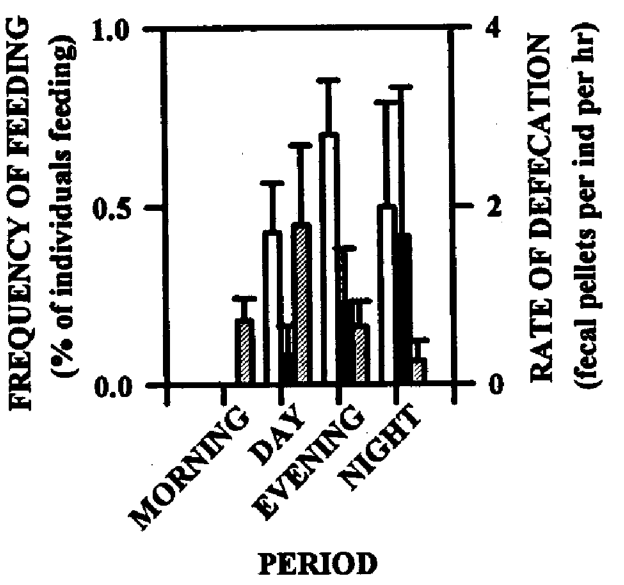

Figure 1. Frequencies of feeding (% of individuals with tentacles extended and raking the substratum; open bars) and rates of defecation (fecal pellets · hr^{-1}; black bars) of *S. chloronotus* maintained in aquaria with flow-through seawater and natural lighting (n=4-16 observations of 4 individuals) during 6-hour diel periods. Rates of defecation (fecal pellets · hr^{-1}; shaded bars) of *S. chloronotus* maintained in cages on the reef flat (n=4 individuals observed over 8 time periods).

4. DISCUSSION

Aspidochirotida contribute significant numbers and biomass to the composition of the reef flat and lagoon communities of Heron Island Reef. Feeding activities of the most prevalent of the Aspidochirotida have a high potential for impact upon the biological communities in which these holothuroids reside. Some spatial separation between areas on reefs occurs

Table 4. Organic and pigment contents of sediment collected at the anterior feeding tentacles of Aspidochirotida and of sediment not actively being fed upon (30 cm distant from holothuroid). Means±1 SEM. n=3, n=1 for *H. edulis*.

	H. atra	*H. leucospilota*	*H. edulis*	*S. chloronotus*
Total Organic Matter (%)				
Actively Fed Upon	3.2±0.1	3.0±0.0	2.6	3.3±0.1
At A Distance	3.4±0.0	3.3±0.0	3.5	3.2±0.1
Total Pigments (μg/g sediment)				
Actively Fed Upon	1.05±0.33	1.25±0.48	0.62	1.17±0.34
At A Distance	0.72±0.41	1.31±0.46	1.45	1.66±0.53
Chlorophyll a (μg/g sediment)				
Actively Fed Upon	0.06±0.05	0.06±0.02	0.15	0.04±0.03
At A Distance	0.02±0.04	0.05±0.04	0.03	0.04±0.01
Phaeophytin (μg/g sediment)				
Actively Fed Upon	1.00±0.29	1.19±0.47	0.48	1.13±0.36
At A Distance	0.70±0.39	1.26±0.49	1.43	1.62±0.53

among Aspidochirotid species on the Great Barrier Reef (Uthicke 1994; Klinger et al. 1994). The present study suggests that small-scale separation of feeding activities also occurs where species coexist. Comparisons of characteristics between sediments which are actively fed upon and which are not fed upon, and between sediments from location to location, suggests that the reef flat is a very fine-grained feeding environment with little variation in the nutritive characteristics. It is unlikely that Aspidochirotids are segregating based upon the characteristics of food resources on the reef flat. Uthicke (1994) found no relationship between the distribution of *H. atra* and *S. chloronotus* despite significant differences in protein and photosynthetic pigment contents of sediments collected at different locations on Lizard Island Reef. In contrast, marked differences in sediment characteristics exist between areas where Aspidochirotida are common and areas where they are absent in the lagoon. Aspidochirotida are most common at the bases of coral patch reefs where protein content is highest and where sediments are most coarse. Whether selection of high quality sediments by Aspidochirotida, disturbance through intense feeding activities altering sediment characteristics, or some unrelated factor is the basis of this co-occurrence is not known. Selection of habitat based on grain size of sediment seems unlikely. Contrary to the distribution observed in the present study, selection of finer sediments has been proposed where selection of sediment by grain size has been suggested (Klinger et al. 1994; Franklin 1980). As suggested by Uthicke (1994), it is likely that Aspidochirotida are non-selective of grain size and that grain sizes consumed simply reflects availability. The aggregated small-scale spatial distribution of Aspidochirotida, and the spatial separation of some species, is probably not driven by resource availability and niche partitioning, but rather by some other factor, such as the availability of shelter.

Continuous defecation by *H. atra*, and diurnal defecation by *S. chloronotus* has previously been noted (Uthicke 1994; Franklin 1980; Yamanuchi 1956). Frequencies of individuals making feeding motions of the oral tentacles mirrored defecation. It is likely that defecation is driven by feeding and that times of fecal production closely track periods of feeding. *Holothuria edulis*, *H. leucospilota*, and *S. variegatus* also feed and defecate continuously without any apparent diel periodicity. Times of intense feeding activity overlap for all species. Therefore, temporal segregation of feeding to reduce overlap of utilization of resources is unlikely.

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Table 5. Organic, protein, and pigment contents and granulometry of sediments surrounding coral patch reefs in the lagoon of Heron Island Reef. Sediment grain size fractions presented in ϕ units. Mean±1 SEM. n=6. Where significant ($p \leq 0.05$) differences exist, means with the same letter do not differ.

SEDIMENT CHARACTERISTIC		DISTANCE FROM CORAL PATCH REEF		
		1 m	5 m	20 m
Total Organic Matter (%)		4.1±0.3	4.2±0.2	4.2±0.6
Protein (μg/g sediment)		93.8±3.8 a	79.1±7.2 ab	56.6±12.6 b
Total Pigments (μg/g sediment)		0.54±0.03	0.60±0.07	0.45±0.04
Chlorophyll a (μg/g sediment)		0.16±0.03	0.29±0.07	0.09±0.03
Phaeophytin (μg/g sediment)		0.37±0.03	0.31±0.01	0.36±0.06
Sediment Grain Size Fractions (%)				
	≤-1.5	5.6±1.3 a	1.5±0.5 b	0.4±0.3 b
	-1.0	3.7±0.9 a	1.3±0.4 b	0.3±0.2 b
	-0.5	5.4±1.1 a	2.4±0.6 b	1.2±0.4 b
ϕ	0.0	5.4±1.0 a	3.2±0.4 b	1.6±0.4 b
	0.5	6.5±0.8 a	5.1±0.3 a	2.3±0.5 b
	1.0	8.7±1.0 a	8.1±0.6 a	4.2±0.9 b
	>1.5	No significant difference in fractions		

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