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DIET AND FEEDING IN THE SEA STAR *ASTROPECTEN INDICUS* (DÖDERLEIN, 1888)

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ABSTRACT. **–** This study investigates the feeding ecology of *Astropecten indicus*, one of the most common sea stars in Singapore's waters. Examination of the regurgitated stomach contents of 69 specimens collected from four sites revealed that *A. indicus* is a generalist molluscan feeder; but the Asian date mussel, *Musculista senhousia*, was the dominant prey species (42.68%). *Astropecten indicus* preferred *M. senhousia* over the button snail, *Umbonium vestiarium*, when given a choice under laboratory conditions. This pattern was significant, and held for experiments regardless of whether prey were shelled or unshelled. *Astropecten indicus* also consumed more *M. senhousia* than *U. vestiarium* when fed these prey ad libitum. This is the first study of its kind on *A. indicus* and thus contributes to the small pool of knowledge regarding the ecology of this species.

KEYWORDS. **–** Singapore, choice experiment, stomach contents, ingestion.

INTRODUCTION

Sea stars (Echinodermata: Asteroidea) are ubiquitous marine predators with diverse diets (Sloan, 1980) that play functionally important roles in the benthos (Jangoux, 1982; Ganmanee et al., 2003). Experimental studies on asteroid predation since the mid 1960s (e.g. Paine, 1966) have shown that these animals often dominate upper trophic cascades (Jangoux, 1982). During his classic experimental removal of *Pisaster* asteroids, Paine (1969) witnessed a complete change in the intertidal community's composition. Subsequent studies further demonstrated that these keystone predators exert a disproportional influence on community structures (Paine, 1995).

The sand star *Astropecten indicus* (Döderlein, 1888), order Paxillosida, family Astropectinidae, is widely distributed in both intertidal and subtidal habitats throughout the world (Peres, 1982). This penta-symmetrical sea star is usually found in mud, sand, and shell habitats (Hopkins et al., 1994) where it ingests a large number of bottom-dwelling animals (Wells et al., 1961). The predation activities of *Astropecten* species in soft sediments are known to influence the densities of their infaunal prey (Christensen, 1970). *Astropecten* species are able to distinguish the quality of their prey using their chemoreceptive abilities (Sloan, 1980) and can therefore preferentially select those with greater nutrient and energy value (Beddington & McClintock, 1993).

The carnivorous diet of *Astropecten* sea stars involves intraoral digestion, in which live prey are swallowed whole (Hyman, 1955). Prey size is limited by the size of their stomach and oral disc, leading to a preference for small prey items (Lemmens et al., 1995) as compared to asteroid taxa that digest extraorally. Sea stars of the genus *Astropecten* are generalists, feeding on a wide variety of prey such as crustaceans, polychaetes, sipunculids, pennatulids, ascidians, fish, other echinoderms and even sediments (Sloan, 1980; Jangoux, 1982; Wells & Lalli, 2003). Their main diet, however, consists of shelled molluscs (gastropods and bivalves) (Ribi & Jost, 1978; Town, 1980; Beddington & McClintock, 1993; Ganmanee et al., 2003) that constitute approximately 90% of the diet in *Astropecten zebra* and about 75% of the diet in *Astropecten velitaris* (Lemmens et al., 1995). The shells remain after the soft body parts have been digested (Wells et al., 1961) and regurgitated prey items provide a good indication of *Astropecten* diets (Wells & Lalli, 2003).

The predator's diet reflects, and is fundamental to, its ecological niche (Sih & Christensen, 2001; Paine, 1966). Diet preferences are influenced by factors such as prey abundance and energy content (McClintock & Lawrence, 1985; Sloan, 1980). Emlen (1966) predicted that predators will consume prey that are abundant even if they are less preferred. Energy maximisation is also an important influence on feeding preference. In lobsters (*Homarus americanus*), for example, there exists strong prey preference for small crabs and molluscs instead of echinoderms, which tend to have lower calorific content (Ojeda & Dearborn, 1991). Prey selectivity is considered a significant part of optimal foraging models (Pulliam, 1974) reflecting the efficiency of diet utilisation (Beddington & McClintock, 1993). A review on the diet of most asteroids types showed that carnivorous species are usually generalists (Jangoux, 1982) with a certain level of prey selectivity. The feeding biology of asteroids is a key component of the ecology of benthic communities (Hatanaka & Kosaka, 1959; Gaymer et al., 2001) and the evaluation of their feeding behaviour can provide a better understanding of their impact as predators.

Astropecten indicus is one of the most common sea stars in Singapore waters, where it reaches a maximum arm length (centre to tip of 4th arm) of ~50 mm (pers. obs.). Despite its abundance, knowledge on the biology and ecology of this species is scarce (but one example is Riccio et al., 1987). The large populations of *A. indicus* along Singapore shores provide an excellent opportunity for more research on these tropical asteroids and here we focus on their diet and prey preference. First, the diet of *A. indicus* in its natural habitats was examined via field sampling and stomach contents analysis. Second, their feeding behaviour when presented with the Asian date mussel *Musculista senhousia* and the button snail *Umbonium vestiarium*n was determined in controlled experiments. Third, the number of prey ingested, and ejected, by *A. indicus* when fed *M. senhousia* and *U. vestiariumn* ad libitum was measured.

MATERIAL AND METHODS

Study areas. **–** Four sandy bottom habitats along the eastern Johor Strait of Singapore, where *A. indicus* is abundant, were selected as field study sites (Fig. 1). These were the intertidal flats at Changi; Site 1 (103°59'11"E, 1°23'34"N), Chek Jawa; Site 2 (103°59'E, 1°24'N) and two locations at Pasir Ris; Site 3 and Site 4 (103°57'17"E, 1°22'59"N and 103°56'21"E, 1°23'22"N respectively). The waters of Johor Strait are nutrient rich and turbid, due to both river and sewage discharge (Gin et al., 2006). River inputs from Singapore and Johor also causes lower salinities (19–33‰, mean ~28‰) compared to the Singapore Straits (28.7–32.2‰, mean ~30.6‰) (Gin et al., 2006). The tides in the eastern Johor Straits surrounding the study sites are semi-diurnal with a range of 0.6 to 2.9 m above chart datum (MPA, 2009).

Diet analysis. **–** During low spring tides between December 2008 and February 2009, the type of diet and prey size of *A. indicus* in their natural environment was investigated at all four sites. Sea stars (mean arm length of subsample = 24.60 mm ± S.E. 0.23, n = 40) were hand collected at the intertidal zone and placed in separate plastic containers (6.5 × 5.0 cm; diameter × height) with fresh ambient sea water for approximately 3 h; sufficient time for the sea stars to regurgitate their gut contents. Only hard prey items were surveyed. The sea stars were later returned to the location from which they were captured. Each regurgitated food item was identified to the lowest possible taxonomic level and its maximum dimension recorded.

Collecting and maintaining the sea stars for experimental work. **–** *Astropecten indicus* was collected at low tide at the intertidal zone by hand between Jul.2008 and Feb.2009 from Changi and Pasir Ris and transported to the marine aquaculture facility in the Tropical Marine Science Institute (TMSI) on St John's Island (103°50'60"E, 1°13'03"N), Singapore. In rectangular glass-fibre holding tanks (45 × 26 × 30 cm; length × width × height), sea stars were kept in aerated and sand-filtered sea water in a flow-through system. Based on temperature loggers (StowAway TidbiT) the mean ambient water temperature was 29.39 ± S.E. 0.31°C. The salinity range was 29 to 32‰ as measured by ABMTC handheld refractometer. These parameters were the same for all ensuing experiments. Each holding tank contained a 3-cm layer of fine sand as substrate for the sea stars to burrow in.

Prey choice experiment. **–** Prey choice was examined using two common prey species: button snails, *Umbonium vestiarium*, and Asian date mussels, *Musculista senhousia*. Before each experiment, sea stars were conditioned by starving them for a week. With-shell individuals of each prey type were offered to *A. indicus* to study its preference. In order to match the 'value' (dry flesh weight) of *U. vestiarium* to *M. senhousia*, the relationship between *U. vestiarium* maximum shell diameter and dry flesh weight was calculated using 30 specimens (dry weight of *U. vestiarium* [g] = 0.0021 × diameter [mm] – 0.01; R = 0.86) with a size range of 5.82 to 8.90 mm (mean 7.21 mm ± S.E. 0.84). For *M. senhousia*, the equation for the shell length to dry flesh weight regression was derived from Crooks (1996). Therefore, for both species, it was possible to predict (and thus match) the dry flesh weight of either species simply by measuring their shell length (*M. senhousia*) or diameter (*U. vestiarium*). This did, however, result in *M. senhousia* being consistently larger (longer) than *U. vestiarium* in these trials. The choice experiment was repeated, using the same two prey

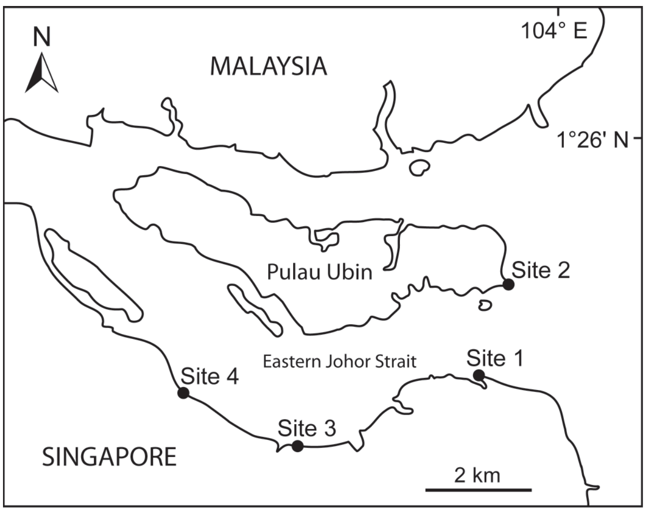

Fig. 1. Map of north-eastern Singapore showing the four study sites along the Eastern Johor Strait.

species, but with their shells removed (and the flesh matched for wet weight). For each of the prey choice experiments, 30 different sea stars were used. The two food items were placed equidistant (10 cm) from the sea star and 8 cm apart in a 2.2-L plastic tank (21 × 13 × 12 cm; length × width × height) filled with seawater to 10 cm height. Which species was to the left or right of the sea star was alternated between runs. Water was introduced into the tank 'upstream' so that it flowed past the prey items and towards the sea star. The first prey choice and the time taken (with S.E.) for the sea star to select (ingest) it was recorded. Significance of choice was examined using Chi-square tests.

Ingestion experiment. **–** The ingestion experiment was conducted by offering *A. indicus* (n=20) *U. vestiarium* (mean length of subsample = 6.74 mm ± S.E. 0.09, n = 40) and *M. senhousia* (mean length of subsample = 8.69 mm ± S.E. 0.15, n = 40) ad libitum. For each prey type, twenty 2.2-L replicate tanks (same dimensions as for the prey choice experiment) each containing one sea star and 40 prey were used. The number of prey ingested was recorded twice: after two hours, and again after 24 hours, by counting the number of remaining prey alive. A *t*-test was performed to evaluate the difference in the mean number of *M. senhousia* and *U. vestiarium* ingested after two hours, plus another *t*-test for the mean number ingested after 24 h. The relationship between the number of sea stars that ejected prey and the prey type (*M. senhousia* and *U. vestiarium*) was examined with a Chi-square test. Finally, the correlation between the number of prey items ingested after 24 h and sea star arm length was calculated.

RESULTS

Diet analysis. **–** The stomach contents of 69 *A. indicus* were examined from which 133 intact prey items were collected. These items comprised 27 species (Table 1, Fig. 2) and had a size range of 1.48 to 14.29 mm. Broken fragments were excluded from the analysis because the number of individuals could not be determined from these remains. Molluscs comprised 94.74% of all hard prey (n=133) while arthropods accounted for 3.76%. There were twice as many species of gastropods (16 species) than bivalves (8 species), but a slightly higher number of bivalve individuals were recorded (64 bivalves vs 62 gastropods). *Musculista senhousia* was the dominant prey (36.09%) among all regurgitated items; it was also the only prey type recorded at all four study sites. There were signs such as discoloration and worn broken edges on the dead shells of *Cerithium* species (Fig. 2) suggesting that these were consumed by *A. indicus* by accident, or for the living occupants of the shells, i.e. hermit crabs or barnacles (Wells et al., 1961).

Prey choice experiment. **–** Most of the sea stars did not immediately make a decision between the two prey choices, with mean time before consumption being 134 ± 14 s for without-shell prey and 163 ± 23 s for with-shell prey. For the experiment between with-shell *M. senhousia* and with-shell *U. vestiarium*, significantly more sea stars chose *M. senhousia* first (χ^2=4.80; *d.f.*=1, *P*<0.05) (Fig. 3a). Similar results were found for the experiment between without-shell *M. senhousia* and without-shell *U. vestiarium* (χ^2=6.53; *d.f.*=1, *P*<0.05) (Fig. 3a).

Ingestion experiment. **–** The number of *M. senhousia* and *U. vestiarium* ingested per sea star ranged from 6 to 25 and 2 to 17 respectively. Significantly more *M. senhousia* had been ingested compared to *U. vestiarium* after 2 h (*t*=-4.767, *d.f.*=19, *p*<0.001), and after 24 h (*t*= 7.647, *d.f.*=19, *p*<0.001) (Fig. 3b). By the 24 h mark, 12 sea stars had ejected *U. vestiarium* compared to only one that ejected *M. senhousia* (χ^2=13.79, *d.f.*=1, *P*<0.001). The stomach of *A. indicus* expanded dramatically after being fed ad libitum (Fig. 4). There were significant positive correlations (one-tailed tests) between the number of prey ingested at 24 h and *A. indicus* arm length, with a stronger correlation for *M. senhousia* (R=0.655, *p*<0.001) as compared to *U. vestiarium* (R=0.392; *p*<0.05) (Fig. 5).

DISCUSSION

Availability of food is one of the main factors determining the behaviour, distribution and abundance of species (Gaymer et al., 2001). Intraoral digestion in *Astropecten* sea stars facilitates the easy investigation of stomach contents and thus their feeding habits (Jangoux, 1982). Similar to other *Astropecten* diet analyses (Ribi & Jost, 1978; Wells & Lalli, 2003), the dominant (94.74%) phylum found in the stomach of *A. indicus* was Mollusca. A review by Christensen (1970) showed that almost all *Astropecten* species, with the possible exception of *A. johnstoni*, feed mainly on molluscs. Even though *A. indicus* consumed a total of 27 species, there was a very high percentage (36.09% of total prey items) of *M. senhousia*. From the Changi and Pasir Ris study areas, ≥10 *M. senhousia* were recovered from each site, whereas only one *M. senhousia* was regurgitated from Chek Jawa. There were, however, far fewer mussel beds at Chek Jawa compared to the other study sites (pers. obs).

The number of bivalves ingested was higher than that of gastropods, but the species diversity of the latter was greater. These included eulimid (family Eulimidae) and pyramidellid gastropods (family Pyramidellidae), potential parasites of *A. indicus*. Echinoderms are known to host ~800 ectoparasitic species from the family Eulimidae (Waren, 1984), but, even in large aggregations, these do not cause mortality (Jangoux, 1987). *Asterolamia hians*, a common eulimid gastropod, is known to feed on the aboral surface of *A. indicus* (Waren, 1980). Pyramidellidae are also often parasitic, but possess a certain degree of host specificity (Robertson & Mau-Lastovicka, 1979). Further work is required to determine whether any of the gastropods regurgitated by *A. indicus* are parasitic.

The prey choice experiment demonstrated that *A. indicus* selected *M. senhousia* over *U. vestiarium,* even though the *M. senhousia* were larger (maximum linear dimension). In addition, the ingestion experiment showed that *A. indicus*

Table 1. Species regurgitated by *A. indicus* collected at four sites (1=Changi, 2= Chek Jawa, 3= Pasir Ris Location 1, 4= Pasir Ris).

Taxon	Family	Site (No. sea stars that regurgitated) 1 (12)	2 (20)	3 (16)	4 (21)	Total	Percentage (%)	Rank
MOLLUSCA								
Bivalvia								
Musculista senhousia	Mytilidae	10	1	14	23	48	36.09	1
Anomalocardia squamosa	Veneridae		5			5	3.76	6
Venerid bivalve 1	Veneridae	1	1	2		4	3.01	7
Tellinid bivalve	Tellinidae	2		1		3	2.26	8
Dosinia sp.	Veneridae				1	1	0.75	9
Venerid bivalve 2	Veneridae				1	1	0.75	12
Anadara sp.	Arcidae			1		1	0.75	12
Mactrid bivalve	Mactridae			1		1	0.75	12
Total bivalves		13	7	19	25	64	48.12	
Gastropoda								
Rissoid gastropod	Rissoidae	2	1	15		18	13.53	2
Pyramidellid gastropod 1	Pyramidellidae		12			12	9.02	3
Trochoid gastropod	Trochidae	4	3			7	5.26	4
Umbonium vestiarum	Trochidae		6			6	4.51	5
Eulimid gastropod	Eulimidae		3		1	4	3.01	7
Stenothyra sp.	Stenothyridae		2		1	3	2.26	8
Batillaria sp.	Batillariidae			2		2	1.50	9
Cerithium sp.	Cerithiidae		1		1	2	1.50	9
Nassariid gastropod	Nassariidae				1	1	0.75	9
Pyramidellid gastropod 2	Pyramidellidae		1			1	0.75	10
Clithon oualaniensis	Neritidae		1			1	0.75	10
Costellariid gastropod	Costellariidae	1				1	0.75	10
Acteonid gastropod	Acteonidae		1			1	0.75	10
Iravadia sp.	Iravadiidae				1	1	0.75	10
Haminoea sp.	Haminoeidae			1		1	0.75	10
Pseudoliotia sp.	Vitrinellidae				1	1	0.75	10
Total gastropods		7	31	18	6	62	46.62	
ARTHROPODA								
Crustacea								
Balamus sp.	Balanidae				3	3	2.26	7
Crab cheliped	Unknown		1			1	0.75	9
Calappid crab cheliped	Calappidae	1				1	0.75	10
Portunid crab leg	Portunidae					0	0.00	10
Total crustaceans		1	1	0	3	5	3.76	
OTHERS								
Dead *Cerithium* sp. before ingestion					2	2	1.50	9
Total prey		21	39	37	36	133		

was able to consume more *M. senhousia* than *U. vestiarium* after two and 24 hours of prey introduction. Finally, *A. indicus* was observed to eject live *U. vestiarium* after consumption. All these findings suggest *A. indicus* prefers *M. senhousia* over *U. vestiarium*. Other sea stars, such as *Luidia clathrata*, have similar strong prey preference for one species (e.g. *L. clathrata* prefers the bivalve *Mulinia lateralis*) despite ingesting a wide range of organisms (McClintock & Lawrence, 1985).

The degree of diet specialisation usually depends on the stability of the environment. An unstable environment will often lead to a more generalised diet (Klopfer, 1959) while a stable environment (one where the preferred prey is more readily available across spatial and temporal scales) facilitates specialisation (Connell, 1970). The relative degree of diet specialisation will change according to the fluctuations in the abundance of the preferred prey (Emlen, 1966). *Musculista senhousia* populations are known to experience episodic high mortality (Crooks, 1996), therefore *A. indicus* probably requires the ability to switch feeding habits between the dominant preferred species and a wide range of other molluscan prey (Town, 1980; Wells & Lalli, 2003). *Astropecten scabra* also showed similar foraging strategies where feeding, growth and reproduction homeostasis was maintained even when their preferred prey species was less available (Town, 1980).

The flexibility of a sea star's stomach is important to determining the number of prey it can digest ad libitum. Due to its elastic dorsal body *Astropecten articulatus* can increase its stomach-capacity by up to 43% (Beddington & McClintock, 1993). An individual *A. articulatus* of arm length 35.4 mm was observed to ingest 10 bivalves ranging from 8.8 to 12.4 mm within 20 min (Christensen, 1970). In the present study, on average, *A. indicus* (mean arm length 26.4 mm, n=20) ingested 14 *M. senhousia* ranging from

Fig. 2. Examples of 16 prey types found in the stomachs of *Astropecten indicus* (n = 69) collected in Singapore. The white bar at the bottom right of each item = 1 mm. **Cerithium* sp. was dead before ingestion.

7.5 to 10.2 mm within two hours. Smaller sized prey are preferred by *A. articulatus* due to the stiff architecture of its oral frame (Beddington & McClintock, 1993). Conversely, *A. irregularis* can ingest large prey due to their highly flexible mouth (Christensen, 1970). The length of the mactrid bivalves (family Mactridae), the largest prey recorded in the diet of *A. indicus*, is approximately four times greater than the diameter of its oral orifice, suggesting that *A. indicus* is capable of extending its mouth opening. This should help *A. indicus* increase the breadth of its diet by including a larger range of prey sizes—potentially useful during low availability of smaller prey.

Due to the ease of handling and ingestion, sea stars with intraoral digestion prefer smaller prey compared to larger prey of similar dry weight (McClintock & Lawrence, 1985; Beddington & McClintock, 1993). Shorter handling time helps maximise food intake per unit time (Campbell, 1987). However, in the present study, the shell length of selected *M. senhousia* was consistently longer than *U. vestiarium* for the same dry weight of flesh. According to optimal diet theory, high calorific values are usually chosen as they can yield more energy per unit time (Sih & Christensen, 2001). But, *M. senhousia* has a slightly lower calorific content of 17.6 kJ g^{-1} (Oka et al., 1999) compared to *U. vestiarium*'s of 20.1 kJ g^{-1} (Berry, 1983). Thus, neither shell size nor calorific content explains *A. indicus* preference for *M. senhousia*. Calorific yield can, nonetheless, be of secondary importance to prey availability (Town, 1980). Prey availability is directly related to ingestion conditioning, i.e. the predator selecting for a particular prey because it has been feeding on it for some time (Christensen, 1970). Ingestion conditioning may account for the preference for *M. senhousia* in the choice experiment as it appears that *A. indicus* has been disproportionately exposed to this mussel species.

The prey preference for *M. senhousia* and the high number ingested by *A. indicus* may serve an important ecological role in the benthic community. *Musculista senhousia* is an opportunistic and gregarious mytilid native to the Indo-Pacific region (Crooks, 1996; Mistri, 2004). Although small as an individual, *M. senhousia* forms extensive mats which can predominate and alter benthic habitats (Creese et al., 1997; Yamamuro et al., 2000; Mistri, 2004). Furthermore, they have a high growth rate and often occur in huge numbers

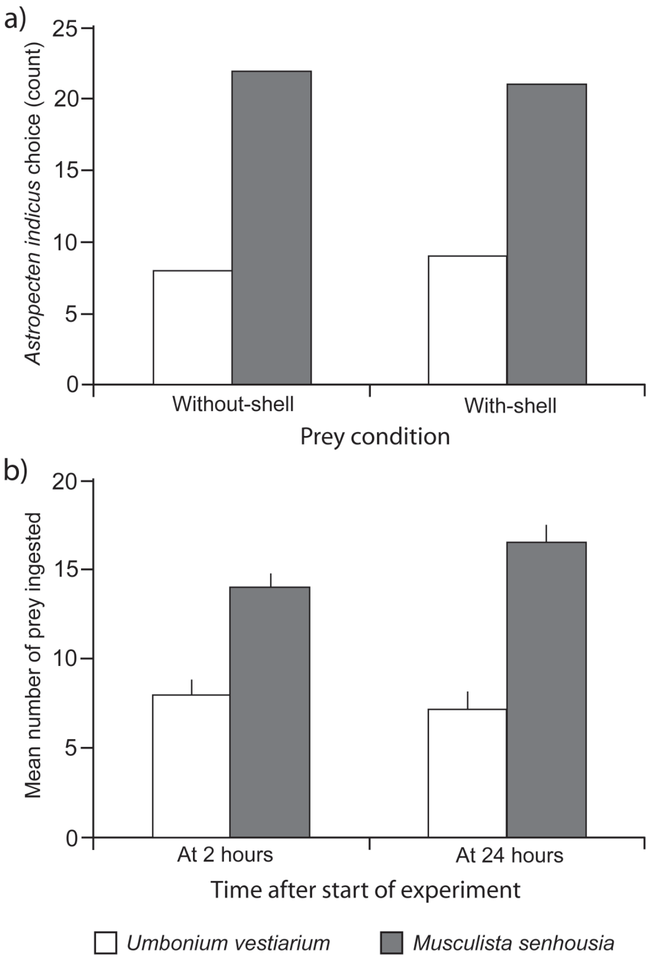

Fig. 3. a) Number of *Astropecten indicus* that chose with-shell and without-shell *Umbonium vestiarium* and *Musculista senhousia* prey (n=30). b) Mean number + S.E. of prey ingested at 2 h and at 24 h. Differences between light and dark bars are significant for both a) and b).

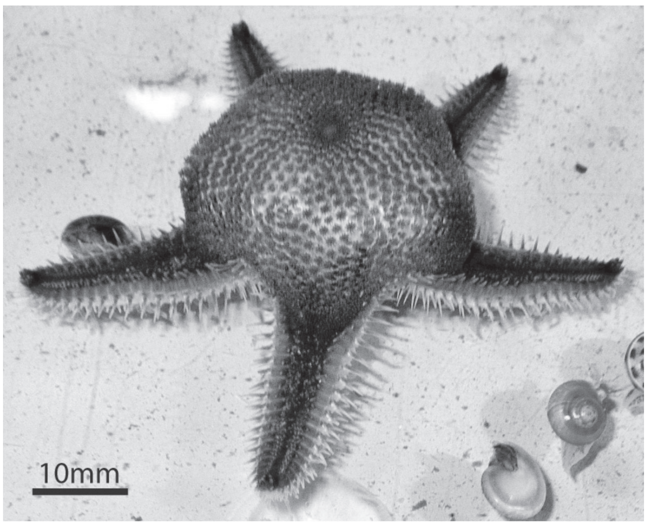

Fig. 4. Stomach packing of *A. indicus* after ingesting *Umbonium vestiarium* ad libitum.

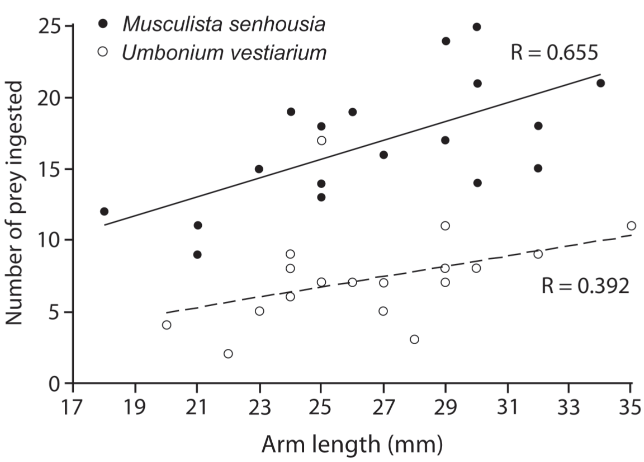

Fig. 5. Scatter plot showing the relationship between number of prey items ingested and *Astropecten indicus* (n=20) arm length after 24 h.

(Crooks, 1996). Sea star predation is an important factor in controlling populations of mussels (Yamamuro et al., 2000; Gaymer & Himmelman, 2002) and the feeding preference and high ingestion limit for *M. senhousia* by *A. indicus* should help promote habitat heterogeneity and higher species diversity by preventing mussel beds dominating intertidal soft sediments.

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