The feeding selectivity and ecological role of shallow water holothurians in the Red Sea

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Abstract

This study examined the feeding selectivity and ecological role of the most dominant holothurian species — *Holothuria atra*, *Holothuria hawaiiensis* and *Bohadschia vitiensis* — on the tidal flats and in the shallow waters in the Red Sea at Hurghada, Egypt. The three species exhibited a wide range of variations in their gut sediment contents, depending on their total weight. Medium-weight individuals, which require considerable food for growth and gonad development, were found to consume more gravel than light- and heavy-weight individuals. The selective behaviour of the holothurians illustrates that gravel and coarse sands are the main sediment components in the animals' guts during the different seasons. During the spawning period (early summer to autumn), the animals tended to assimilate fine sediments more than coarse sediments, perhaps due to their increasing need for organic matter.

Sediment reworking processes by the different species varied during the year and depended on individual numbers, food availability, individual sizes and local conditions. *H. atra* showed the highest sediment reworking in July (summer) and November (autumn), *H. hawaiiensis* in autumn/winter (September and December, and *B. vitiensis* mainly from summer (May to August. It was observed that the reworking lasted from late spring to the end of autumn. This period covers the two essential phases of holothurian reproduction: maturation and spawning.

Introduction

The deposit feeding holothurians are the dominant megafauna, in terms of both number and biomass, in many littoral ecosystems (Coulon and Jangoux 1993) and on sheltered marine shallow water substrates (Conde et al. 1991).

Variability in food supply is a major controlling factor in the population dynamics of benthic animals, in particular holothurians. Deposit feeders are among the most important consumers of detritus on the ocean floor, playing an important role in the removal, recycling and repackaging of nutrients, especially organic matter (Jumars and Self 1986). The way in which the various species feed on the top layer of sediments is highly variable, depending on their tentacles and gut morphology (Roberts et al. 2001). Holothurians feed by either ingesting material on the surface of the substrate or by swallowing nutrient-laden sediments. The sediments ingested by deposit feeding holothurians comprise mainly inorganic compounds (coral debris, shell remains, coralline algae, foraminiferal tests, inorganic benthos remains, and silicates), organic detritus (seagrass, algae, dead and decaying animals), microorganisms (bacteria, diatoms, protozoan and cyanophyceans), or the faecal pellets of other animals or their own faecal pellets (Massin 1982; Moriarity 1982).

The quantity and quality of organic matter varies from year to year depending on numerous factors, including underlying sediments, and possibly pollution levels (Dar 2004). The three holothurian species examined in this study — *Holothuria atra*, *Holothuria hawaiiensis* and *Bohadschia vitiensis* — are known to feed more rapidly during the day than at night and continuous feeding may be necessary to keep sediments moving through the gut (Hammond 1982).

The objectives of this study were to investigate:

1) holothurian feeding behaviour throughout the year,
2) feeding selectivity habits of holothurians,
3) the most effective periods of sediment reworking by holothurians, and
4) the relationship between reproductive seasons and the type of sediments consumed.

Materials and methods

Site morphology and field investigations

Three different sites on the shallow tidal flat at Hurghada, Egypt were chosen for sampling (Fig. 1). Each one had an abundance of three holothurians: *Holothuria atra*, *H. hawaiiensis* and *Bohadschia vitiensis*.

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Site I: 4 km north of the National Institute of Oceanography and Fisheries (NIOF). This site has a relatively heterogeneous thin sand bed mainly from the biogenic origin of coral debris and shell remains. This site shows healthy and widespread coral reef patches and seagrass beds with water depth varying between 0.5 m at low tide and 1.50 m at high tide.

Site II: an area sheltered from intense wave action and in deeper water than Site I. The area surrounding this site is considered a natural sedimentation basin due to its morphology. This site has a thin, lose sediment layer partially covered with seagrass and macroalgae.

Site III: 4 km to the south of NIOF. This site has a homogeneous thick sediment layer composed of a mixture of biogenic and terrestrial sands. This site has high turbidity, especially on windy days, and very few coral patches as compared with Sites I and II.

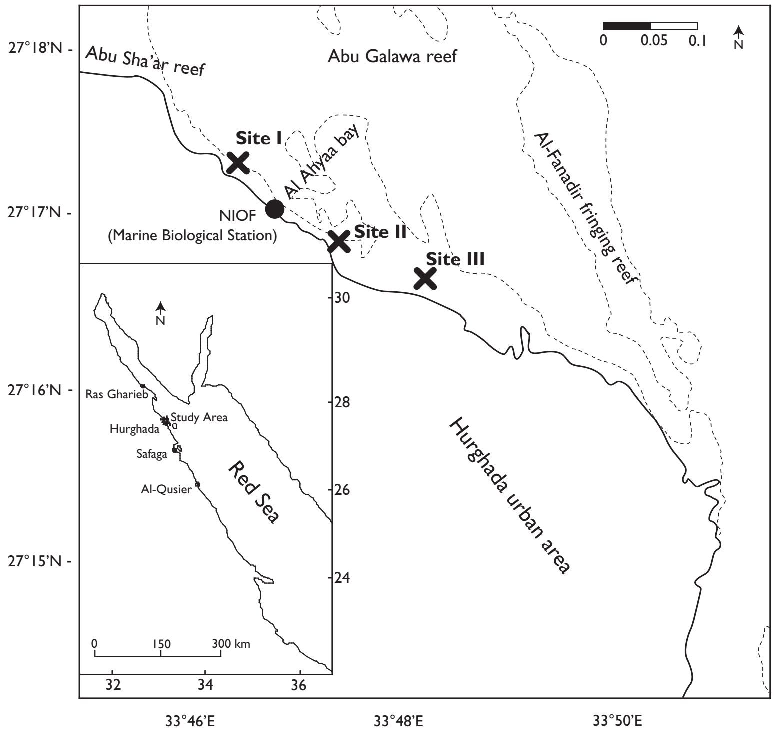

Figure 1. **The study area and the three selected sites.**

Between April 2003 and March 2004, at least 10 individuals of each holothurian species were collected monthly and randomly using quadrates (10 m x 10 m) from the selected sites. Also, five sediment samples were collected from each site to compare sediment types between the sites and the gut contents of the sea cucumbers at those sites.

Analyses

The collected individuals were weighed in order to estimate total weight under natural conditions. The gut contents of each individual were dried and weighed. Sieving and grain size analysis were applied to the gut contents to evaluate the different fractions of gut contents using a one-*phi* interval sieve set according to Folk (1974). Benthic sediment samples were dried and sieved in order to study the degree of divergence or coincidence between them and the gut contents of the animals. Seven fractions were obtained: gravel ($Ø_{-1}$), very coarse sand ($Ø_0$), coarse sand ($Ø_1$), medium sand ($Ø_2$), fine sand ($Ø_3$), very fine sand ($Ø_4$) and mud ($Ø_5$). Each fraction was weighed and expressed as a percentage of total weight.

The sediments and gut contents were grouped into three categories: coarse sediments ($Ø_{-1} + Ø_0 + Ø_1$), medium sediments ($Ø_2 + Ø_3$), and fine sediments ($Ø_4 + Ø_5$). This grouping is more efficient for determining sediment variations in the different sites and animal guts, and consequently, the grouping gives an indication of the actual behaviour of the animal feeding in these sites.

The total organic matter (TOM) content in the gut contents and sediments were determined as the ignition weight loss at 550°C (Yingst 1976; Brenner and Binford 1988), and expressed as (mg g^{-1}).

Results and discussion

The sediments at the investigated sites comprise biogenic gravel, sand and mud. At site I, the average percentage of gravel was 23.83%, sand 75.34%, and mud 0.82%. At site II, the average percentage of gravel was 18.53%, sand 80.05%, and mud 1.44%. And at site III, gravel averaged 23.03%, sand 76.12%, and mud 0.85%. The TOM content of sediments averaged 47 mg g^{-1} at site I, 41.6 mg g^{-1} at site II, and 45 mg g^{-1} at site III. At site I, an average of 55.17% of all sediment belonged to the coarse sediment group, 43.22% to the medium sediment group, and 1.77% to the fine sediment group. The averages for the different sediment groups at site II was 45.93% coarse, 46.80% medium and 7.29% fine;

and at site III it was 71.37% coarse, 24.21% medium and 4.42% fine (Table 1).

Holothuria atra and *H. hawaiiensis*

The body weights of *H. atra* individuals varied between 50 g and 590 g. The highest body weight was recorded in April at 590 g, while the lowest weight (50 g) was recorded in February. July showed the highest average weight of gut contents (58.26 g) accompanied with the highest average percentage of gut contents (33.72%) in relation to total weight, while the lowest average (13.28 g) was recorded in June with the lowest gut content percentage (2.10%) (Table 2).

Table 1. **Sediment fraction and group percentages and the total organic matter (TOM) contents of the sea floor sediments at the study sites.**

	Sample	Gravel (%)	Sand (%)	Mud (%)	($Ø_{-1}$+$Ø_0$+$Ø_1$) (%)	($Ø_2$+$Ø_3$) (%)	($Ø_4$+$Ø_5$) (%)	TOM (mg g^{-1})
Site I	1	24.22	73.26	2.52	48.93	45.64	5.43	55.00
	2	24.49	74.65	0.85	59.5	39.03	1.29	51.00
	3	26.93	72.81	0.26	74.55	25.90	0.55	43.00
	4	26.08	73.60	0.32	48.74	49.98	1.26	45.00
	5	17.45	82.40	0.15	44.11	55.53	0.34	41.00
	Average	23.83	75.34	0.82	55.17	43.22	1.77	47.00
	SD	3.74	4.00	0.99	12.22	11.41	2.09	5.83
Site II	1	15.45	83.92	0.72	47.60	44.65	7.75	55.00
	2	17.38	80.47	2.15	39.73	53.33	6.94	51.00
	3	11.19	87.98	0.83	28.46	61.29	10.25	34.00
	4	24.56	72.30	3.10	60.91	33.40	5.69	33.00
	5	24.07	75.56	0.38	52.97	41.32	5.71	35.00
	Average	18.53	80.05	1.44	45.93	46.80	7.27	41.60
	SD	5.74	6.29	1.15	12.45	10.80	1.88	10.53
Site III	1	27.39	71.81	0.80	75.91	21.63	2.46	64.00
	2	26.07	73.84	0.09	77.7	21.08	1.23	41.00
	3	22.85	76.15	1.00	66.93	28.95	4.14	32.00
	4	14.29	84.05	1.66	54.9	32.17	12.93	35.00
	5	24.55	74.76	0.69	81.43	17.24	1.33	53.00
	Average	23.03	76.12	0.85	71.374	24.214	4.418	45.00
	SD	5.17	4.70	0.57	10.64	6.14	4.90	13.32

Table 2. **Body weight, gut sediment percentages, reworking sediment load, and TOM content (mg g^{-1}) for *Holothuria atra*.**

		Body weight (g)	Sed. weight (g)	Sed. (%)	Re. load (kg y^{-1})	Gravel (%)	Sand (%)	Mud (%)	TOM (mg g^{-1})
Spring	Apr-03	315.88	22.98	7.99	18.28	19.89	78.86	1.25	65.00
	May-03	369.17	29.20	8.43	23.23	17.54	81.35	1.12	67.80
	Jun-03	209.00	13.28	6.32	10.56	27.21	70.34	2.45	63.00
	Average	298.01	21.82	7.58	17.36	21.55	76.85	1.61	65.27
	SD	66.60	6.55	0.91	5.21	4.12	4.71	0.60	1.97
Summer	Jul-03	178.00	58.26	33.72	46.36	3.15	95.18	1.67	70.30
	Aug-03	225.00	22.92	10.24	18.24	31.56	66.30	2.08	58.40
	Sep-03	277.50	17.52	6.75	13.94	16.13	80.73	3.15	51.50
	Average	226.83	32.90	16.91	26.18	16.95	80.74	2.30	60.07
	SD	40.64	18.07	11.97	14.38	11.61	11.79	0.62	7.77
Autumn	Oct-03	206.00	30.15	14.56	23.99	2.97	90.97	6.06	64.20
	Nov-03	121.00	19.16	16.15	15.25	31.75	65.69	2.56	51.40
	Dec-03	133.50	18.89	14.94	15.03	28.13	69.46	2.41	63.80
	Average	153.50	22.73	15.22	18.09	20.95	75.37	3.68	59.80
	SD	37.47	5.24	0.68	4.17	12.80	11.14	1.69	5.94
Winter	Jan-04	135.00	21.02	16.55	16.73	37.05	61.57	1.38	65.10
	Feb-04	115.50	18.15	18.72	14.44	18.58	76.91	4.51	60.60
	Mar-04	141.25	18.07	12.98	14.38	27.11	70.66	2.22	61.40
	Average	130.58	19.08	16.08	15.18	27.58	69.71	2.71	62.37
	SD	10.97	1.37	2.37	1.09	7.55	6.30	1.32	1.96

The highest average weight of *H. hawaiiensis* (745 g) was recorded in February and the lowest (323 g) in January. The highest average gut contents weight (68.97 g) was recorded in December, and the lowest (11.20 g) in July. December showed the highest average percentage (18.51%) of gut contents and July the lowest (1.50%). Individuals of *H. hawaiiensis* were much heavier than *H. atra* (Fig. 2), subsequently the amount of sediment they consumed was relatively higher (Table 3).

Medium-weight individuals of *H. atra* and *H. hawaiiensis* consume proportionally more sediments than light- and heavy-weight individuals. *H. atra* consume around one-third (and up to one-half) of their total weight; *H. hawaiiensis* around 22.74%. This could be due to growth and sex organ development (maturation), which require high amounts of energy. The highest average gravel percentage of *H. atra* (37.05%) was recorded in January, while the lowest percentages were recorded in November, December and February (less than 1%). Sand percentage showed the highest average 95.18% in July and the lowest 61.57% in January. Mud percentage varied between 0.19% in November and 25.88% in February, while the highest average (6.06%) was recorded in October. The average gravel percentage in *H. hawaiiensis* varied between 3.53% in October and 38.86% in December. The average sand percentage fluctuated between 60.12% in November and 98.13% in August, and mud between 0.36% in September and 7.59% in February.

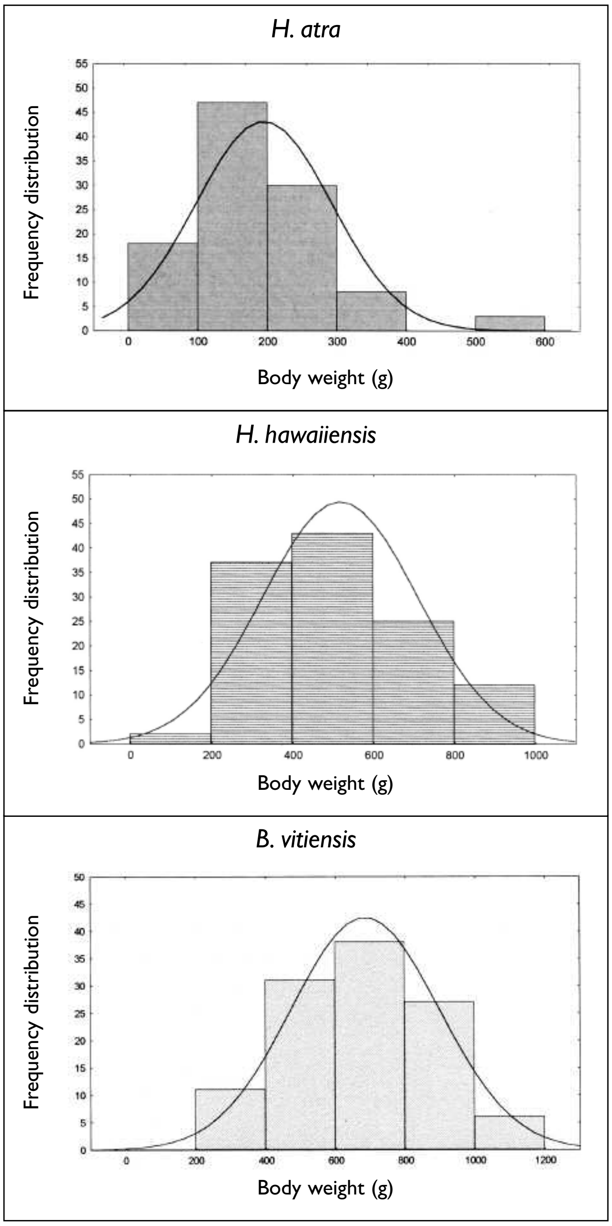

Figure 2. **Body weight frequency distribution of *H. atra, H. hawaiiensis* and *B. vitiensis.***

The gravel percentage in the gut contents of some individuals of *H. atra* and *H. hawaiiensis* reached about 75% of the total sediment content while in others it was less than 1%. The recorded gravel percentage of the animal guts reached about three times that of the benthic sediments. The sand content in the guts varied relative to the gravel percentage, while the mud percentage was highly variable: in most months, the mud percentage in the gut contents was slightly higher than in the benthic sediments; but in October and November, it increased abruptly to about 11 and 9 times more, respectively, than in the sediments; and in February, it was about 25 times more than in the sediments. This value is also found in light-weight individuals.

Light-weight individuals may not be able to consume the larger particles due to their thin tiny tentacles, or they may prefer sediment quality to quantity, and subsequently consume the finest organic-rich particles rather than coarse particles. This finding is supported by the TOM contents in *H. atra*, which may reach two times those of the benthic sediments.

TOM contents in *H. atra* recorded the highest value (99 mg g^{-1}) with the highest mud content (25.88%) in February. TOM in *H. hawaiiensis* guts showed the highest average (95.72 mg g^{-1}) in April and the lowest (42.90 mg g^{-1}) in August (Tables 2 and 3).

Two observations were made with TOM contents in guts: the first is that the highest TOM content corresponded to the highest mud contents; the second is that the highest TOM averages were recorded in light- and heavy-weight individuals, rather than in medium-weight individuals. This means that the light- and heavy-weight individuals tended to consume the organic-rich sediments more than the other sediment types, while the

Table 3. **Body weight, gut sediment percentages, reworking sediment load, and TOM content (mg g^{-1}) for *Holothuria hawaiiensis.***

		Body weight (g)	Sed. weight (g)	Sed. (%)	Re. load (kg y^{-1})	Gravel (%)	Sand (%)	Mud (%)	TOM (mg g^{-1})
Spring	Apr-003	573.50	21.24	3.58	16.90	15.34	82.11	2.55	95.72
	May-003	455.56	16.03	4.64	12.76	7.90	57.36	21.42	85.50
	June-003	510.00	43.67	8.68	34.75	21.37	77.43	1.20	51.55
	Average	513.02	26.98	5.63	21.47	14.87	72.30	8.39	77.59
	SD	48.20	11.99	2.20	9.54	5.51	10.73	9.23	18.88
Summer	July-003	739.00	11.20	1.50	8.92	5.92	91.80	2.27	51.95
	Aug.-003	508.00	56.95	11.11	45.32	24.98	74.42	0.60	42.90
	Sep.-003	480.00	67.78	14.03	53.93	24.57	75.06	0.36	52.25
	Average	575.67	45.31	8.88	36.05	18.49	80.43	1.08	49.03
	SD	116.06	24.52	5.35	19.51	8.89	8.05	0.85	4.34
Autumn	Oct.-003	720.50	65.10	9.02	51.80	3.53	89.73	6.74	85.30
	Nov.-003	406.50	59.49	14.86	47.34	32.76	65.63	1.67	52.80
	Dec.-003	379.50	68.97	18.51	54.88	38.86	60.12	1.01	78.90
	Average	502.17	64.52	14.13	51.34	25.05	71.83	3.14	72.33
	SD	154.78	3.89	3.91	3.09	15.42	12.86	2.56	14.06
Winter	Jan.-004	323.00	47.42	14.94	37.73	26.78	72.19	1.02	63.00
	Feb.-004	745.00	39.14	5.33	31.15	17.12	75.29	7.59	52.60
	Mar.-004	346.50	50.01	14.91	39.79	14.66	78.53	6.82	50.60
	Average	471.50	45.52	11.72	36.22	19.52	75.34	5.14	55.40
	SD	193.63	4.63	4.52	3.69	5.23	2.59	2.93	5.44

medium-weight individuals may have consumed all particles to make up for their increased biogenic activities. Also, the higher TOM contents in the animals' guts, rather than in the benthic sediments, show that *H. atra* and *H. hawaiiensis* may absorb the rich biogenic film on top of the sea floor (the upper 5 mm of the sediment surface).

During the study period, some individuals were left in water basins at the Marine Biological Station at Hurghada. These basins were connected to the sea and held sediments significantly covered with a bio-film of organic matter. With time, holothurian individuals seemed accustomed to the organic film and the seawater appeared to be clearer than in basins that did not contain holothurians. This observation indicates that holothurians may be able to feed on organic sources other than sediments. But, sediments, and especially coarse particles, may be required for other functions.

In the gut contents of *H. atra*, the coarse sediments group is the predominant category in the animals' guts in all seasons. In summer, the fine sediments group represented 26.60% and 20.39% in autumn, while it only represented 7.10% in winter and 9.23% in spring. The coarse sediments group is the predominant category in *H. hawaiiensis* guts while the fine sediments group recorded equal percentages in all seasons. Autumn recorded the highest average weight of the gut sediments (64.52 g), sediment and gravel percentages; 14.13% and 25.05%, respectively.

Bohadschia vitiensis

B. vitiensis recorded the highest average body weight (863 g) among the studied species. It was recorded in June while the lowest average (372.50 g) was recorded in March (Table 4). The weight of the gut contents varied between 25.50 g in March and 56.22 g in August. Gut contents percentage, in relation to total weight, varied between 3.33% in June and 7.23% in March. Gravel recorded the highest average (23.83%) in April and the lowest (1.61%) in November. Mud percentage varied between 0.09% in May and 43.06% in February. Recorded gut content weights in *B. vitiensis* were higher than in *H. atra* and nearly subequal to the gut contents of *H. hawaiiensis.* Gut sediment percentages gradually increased as body weight decreased, indicating that the relatively light-weight individuals ingested proportionally much more sediment than did heavy-weight individuals. Gravel represented the main component of the sediments inside the animals' guts, especially for light-weight individuals. This means that the medium- and heavy-weight individuals ingested smaller organic-rich particles, rather than coarse ones. This finding is supported by the mud percentages and TOM contents. High TOM contents corresponded to the highest mud contents, which were generally observed inside the heavy-weight individuals' guts.

The highest average body weight (772.15 g) and the highest gut sediments average weight (45.93 g) were recorded in summer. The highest gut sedi-

Table 4. **Body weight, gut sediment percentages, reworking sediment load, and TOM content (mg g^{-1}) for *Bohadschia vitiensis.***

		Body weight (g)	Sed. weight (g)	Sed. (%)	Re. load (kg y^{-1})	Gravel (%)	Sand (%)	Mud (%)	TOM (mg g^{-1})
Spring	Apr-003	496.90	25.49	5.29	20.28	23.83	75.54	0.63	72.60
	May-003	672.00	42.55	6.19	33.86	16.57	82.17	1.27	58.15
	June-003	863.00	29.25	3.33	23.27	5.69	91.14	3.17	73.20
	Average	677.30	32.43	4.94	25.80	15.36	82.95	1.69	67.98
	SD	149.51	7.32	1.20	5.83	7.45	6.39	1.08	6.96
Summer	July-003	782.50	37.90	4.97	30.15	4.81	83.82	11.37	58.31
	Aug.-003	854.44	56.22	6.64	44.73	14.41	83.22	2.37	67.61
	Sep.-003	679.50	43.66	6.53	34.74	6.06	86.47	7.48	42.85
	Average	772.15	45.93	6.05	36.54	8.42	84.51	7.07	56.26
	SD	71.79	7.65	0.77	6.09	4.26	1.41	3.69	10.21
Autumn	Oct.-003	691.88	42.28	6.78	33.64	2.12	87.71	10.17	68.94
	Nov.-003	742.00	38.69	5.25	30.79	1.61	84.91	13.47	53.60
	Dec.-003	704.00	43.73	6.30	34.80	5.04	81.47	13.50	57.30
	Average	712.63	41.57	6.11	33.07	2.92	84.70	12.38	59.95
	SD	21.35	2.12	0.64	1.68	1.51	2.55	1.56	6.54
Winter	Jan.-004	697.00	38.49	5.53	30.62	5.66	81.04	13.30	58.00
	Feb.-004	628.50	39.14	6.13	31.15	5.32	68.57	26.10	49.00
	Mar.-004	372.50	25.50	7.23	20.29	11.47	75.32	13.21	55.13
	Average	566.00	34.38	6.30	27.35	7.48	74.98	17.54	54.04
	SD	139.65	6.28	0.70	5.00	2.82	5.10	6.06	3.75

ments average percentage (6.30%) and the highest mud average percentage (17.54%) were recorded in winter (Table 4).

Feeding behaviour

The three holothurians consumed large amounts of benthic sediments but did not depend on them completely as their main food source. The measured TOM in the animals' guts and surrounding sediments illustrate that the TOM contents in the guts are much higher than those in the surrounding environment, and that the holothurians absorbed particulate materials from the water column and by sweeping the organic biofilm off the top 5 mm of sediment (as indicated by Moriarty 1982).

The highest average weight and the lowest sediment percentage average of *H. atra* were recorded in spring. During this season, the animals are mostly in the pre-maturation stage and are preparing for the spawning period in June and July. The highest sediment average weights were recorded in summer when the animals need sediments to help contraction and gamete expulsion. In autumn, *H. hawaiiensis* consume the highest amounts of sediments in order to to help the sex organs to grow and spawn. The lowest average weights in winter indicate that the animals suffered from food shortage and/or were in their first stages of growth (see Fig. 5).

The seasonal variation in the body weights of *B. vitiensis* was relatively small. The spawning season began in May and extended through to June, July and August. Late spring and early summer are the periods of maturation, spawning and post-spawning. The highest recorded TOM average content in spring corresponded to the increasing energy needs for maturation and spawning.

Feeding selectivity of the deposit feeder holothurians

Particle selectivity is the selection of certain grain sizes or particles with higher organic content within a given sediment patch or microhabitat. In contrast, patch selectivity describes the choice of a mobile organism to feed on preferred sediment patches in a heterogeneous environment (Uthicke and Karez 1999). According to Trefz (1958), holothurians are able to choose the richest organic sediments. Diversity in tentacle structure and mode of feeding may allow a degree of selectivity, but studies of deepsea holothurians have shown no correlation between tentacle structure and gut contents (Wigham et al. 2003).

Yingst (1976) recorded that selection of grain size by holothurians is generally low. Uthicke and Karez (1999) concluded that *H. atra* and *H. edulis* exhibited no preference for any food type, but that *S. chloronotus* significantly selected sediments with the highest contents of microalgae. Miller et al. (2000) reported that the surface deposit feeders fed very selectively on particles settled on the sea floor. *Stichopus tremolus* feeds mainly on coarse particles

(Haukson 1979), and *H. scabra* tends to assimilate the coarsest particles more than the finest fractions (Basker 1994). *S. japonicus* may ingest select sediments and their faeces contain higher organic contents than benthic sediments (Michio et al. 2003). Dar (2004) recorded that there is a strong selective behaviour in the feeding habits of some holothurians in the Red Sea: *H. atra, B. marmorata* and *H. leucospilota* scavenge through coarse sediments much more than through medium or fine ones.

The medium-weight individuals were the most efficacious animals in selective operations. They mostly represented the pre-maturation stage while the medium–heavy- and heavy-weight animals represented adult stages. The adult animals tended to ingest the finer sediments that provide the essential needs for growth, gamete maturation and spawning, while in the pre-maturation stage, the animals tended to consume coarser sediments.

The authors think that the presence of coarse particles in gut contents may help in many essential operations such as: 1) the contraction process for moving downward and upward from one depth to another, in addition to horizontal motion (in many places, the animals' faecal pellets were observed as long rows along their motion path) from locations with little food availability to locations with rich organic matter, and from high temperature areas to lower temperature areas; 2) the digestion process; 3) *B. vitiensis* cuvierian tubule expulsion (when it is threatened); and, most importantly, 4) the expulsion of gametes during spawning.

The selective feeding of holothurians throughout the seasons has been observed during this study (Fig. 3). The animals alternatively select between the coarse and fine sediment groups in the different seasons according to their biogenic needs and food availability. The relatively high fine and particulate sediment contents inside the animal guts during the summer demonstrates that the animal requires enough amounts of sediments that help in biological activities (Fig. 3). *H. hawaiiensis* is considered one of the coarse sediment consumers.

There are definite variations in the feeding mechanism of holothurians throughout the different seasons corresponding with the animals' life stages (immature, pre-maturation and maturation stages).

The ecological role of holothurians in sediment reworking

Holothurians are very important members of benthic communities as they can cause significant changes in the sea floor sediment composition. On tidal flats and sheltered coastal areas, dead algae and the organic remains of other benthos often cause anaerobic conditions, as, over time, sediments become rich in organic matter that decompose and cause dissolved oxygen depletion (Michio et al. 2003). Holothurians are active sediment "reworkers" that alter the bottom stability (Rhoads and Young 1971) by reducing volatile sulfide concentrations and increasing oxidation-reduction potential. Holothurians are also important recyclers of inorganic nutrients and are thus a part of the closed nutrient cycling (Uthicke and Karez 1999). *H. mexicana* and *Isostichopus dadionotus* faecal pellets influence the nutrient cycle: the organic matter from decaying faecal pellets can be re-suspended by waves, currents and biota and help in relocating the particulate materials, rather than the dis-

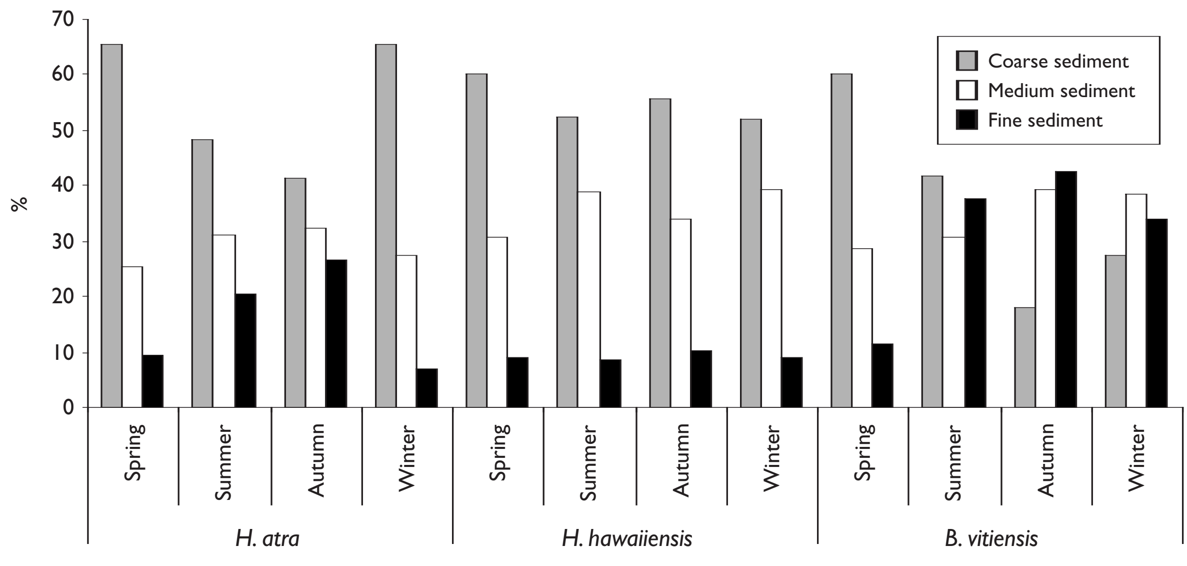

Figure 3. **Percentage of three different sediment sizes in *H. atra*, *H. hawaiiensis* and *B. vitiensis* gut contents.**

solved nutrients (Conde et al. 1991). High densities of *H. arenicola* in shallow lagoons may significantly rework the top 3 cm of sediment in less than a month (Powell 1977). Populations of *H. atra* and *Stichopus chlorontus* can be dense enough to turn over the upper 5 mm sediments of the reef flat at least once a year (Uthicke 1999). Pawson (1966) recorded that in a small (1.7 km^2) enclosed bay of Bermuda, *Stichopus* species passed between 500 and 1000 t of substrate through their intestines annually. Coulon and Jangoux (1993) reported that *H. tubulosa* only ingests the upper few millimetres of sediments. Kaufmann and Smith (1997) estimated that seven species of holothurian in the northeastern Pacific Ocean move over 100% of the sediment surface in about 400 days.

H. atra may ingest as much as 40 g of sediments containing 80–216 mg of organic matter per day and the sediments take about 11 h to pass through a 25-cm-long specimen (Trefz 1958). Klinger et al. (1993) recorded that the total sediment consumption by *H. atra* and *H. leucospilota* in the lagoon and reef flat of Horn Island was 3.93 and 12.76 g m^2 day^{-1} respectively. Uthicke (1999) demonstrated that the average-sized individual of *H. atra* (125–129 g) consumed about 67 g day^{-1} of sediment (dry weight). Rhoads and Young (1971) reported that *Molpadia oolitica* feeds selectively on the fine particle sediments and produces vertical sediment sorting, high sediment–water contact and topographical relief of the sea floor. Dar (2004) indicated that holothurians consume large amounts of the surface sediments throughout each feeding period: the annual reworked sediments by each individual of *B. marmorata, H. atra* and *H. leucospilota* were estimated at 45.78 kg yr^{-1}, 28.72 kg yr^{-1} and 21.23 kg yr^{-1} respectively.

Month and season of highest recorded sediment-reworking effectiveness were July (46.36 kg yr^{-1} $ind.^{-1}$) and summer (27.77 kg yr^{-1} $ind.^{-1}$) for *H. atra*; December (54.88 kg yr^{-1} $ind.^{-1}$) and autumn (51.34 kg yr^{-1} $ind.^{-1}$) for *H. hawaiiensis*; and August (44.73 kg yr^{-1} $ind.^{-1}$) and summer (36.71 kg yr^{-1} $ind.^{-1}$) for *B. vitiensis*. It was observed that the most active reworking operations take place from late spring to the end of autumn (Fig. 4). This period covers the three essential stages of the holothurian reproduction: maturation, spawning and post-spawning. It shows that the effective sediment reworking operations are increasing during the maturation and reproduction periods, as shown in Figures 5, 6 and 7, and as mentioned by Wiedemeyer (1992), who reported that the dry weight of daily reworked sediment was 46.5% and 45.2% of the drained body weight of *H. atra* individuals during spawning and post-spawning seasons.

Conclusion

Holothuria atra, *Holothuria hawaiiensis* and *Bohadschia vitiensis* are found in the shallow water and tidal habitats of the Red Sea. Feeding selectivity is a distinctive behaviour of these species. Sediments inside the animals' guts vary widely throughout the different seasons depending on the animal's weight, local conditions and the maturity status of the species. Proportionally, the medium-weight individuals are more able to swallow larger amounts of sediments than light- and heavy-weight individuals.

The light- and heavy-weight individuals tended to consume the rich organic sediments more than the other sediment types, while the medium-weight individuals consumed all sized particles in order to find the elements necessary for their biogenic activities. The coarse sediments may be required for some essential operations and not just as a food source: the contraction/motion process, which regulates the dynamics of deposit feeders, helps in the digestion process, and facilitates spawning.

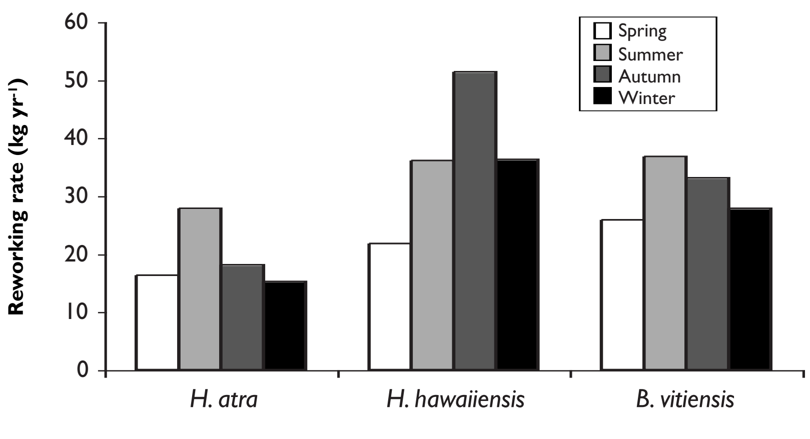

Figure 4. Sediment reworking rate of the three species in relation to seasons.

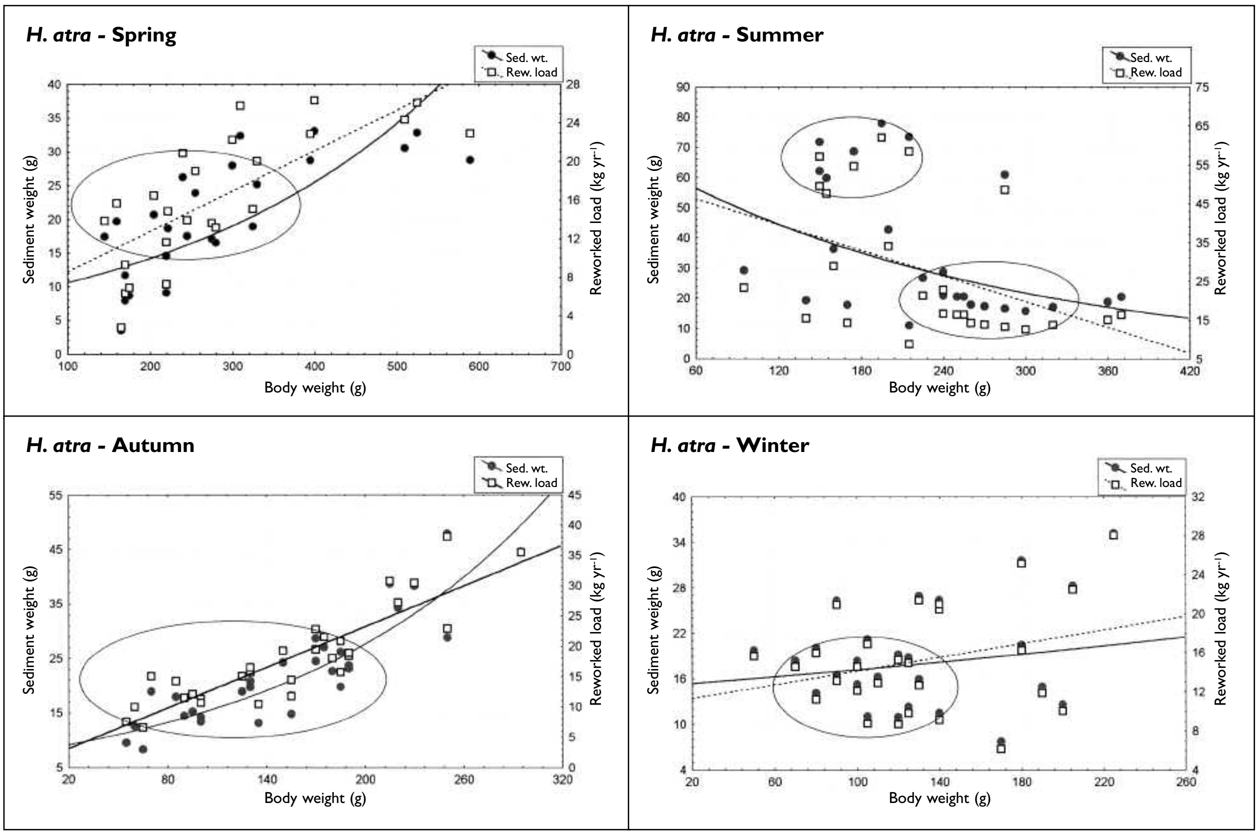

Figure 5. **Relationship between body weight, sediment weight, and reworked loads in *H. atra* for the different seasons.**

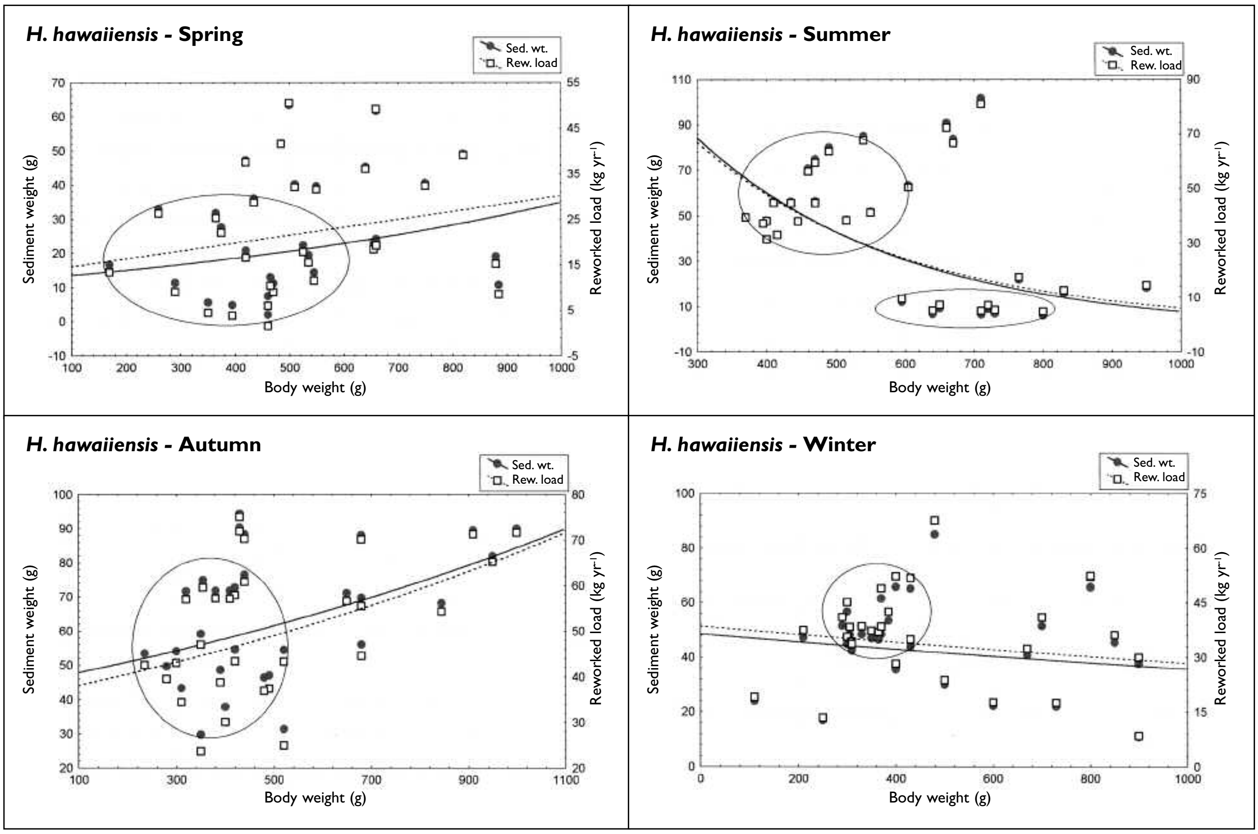

Figure 6. **Relationship between body weight, sediment weight, and reworked loads in *H. hawaiiensis* for the different seasons.**

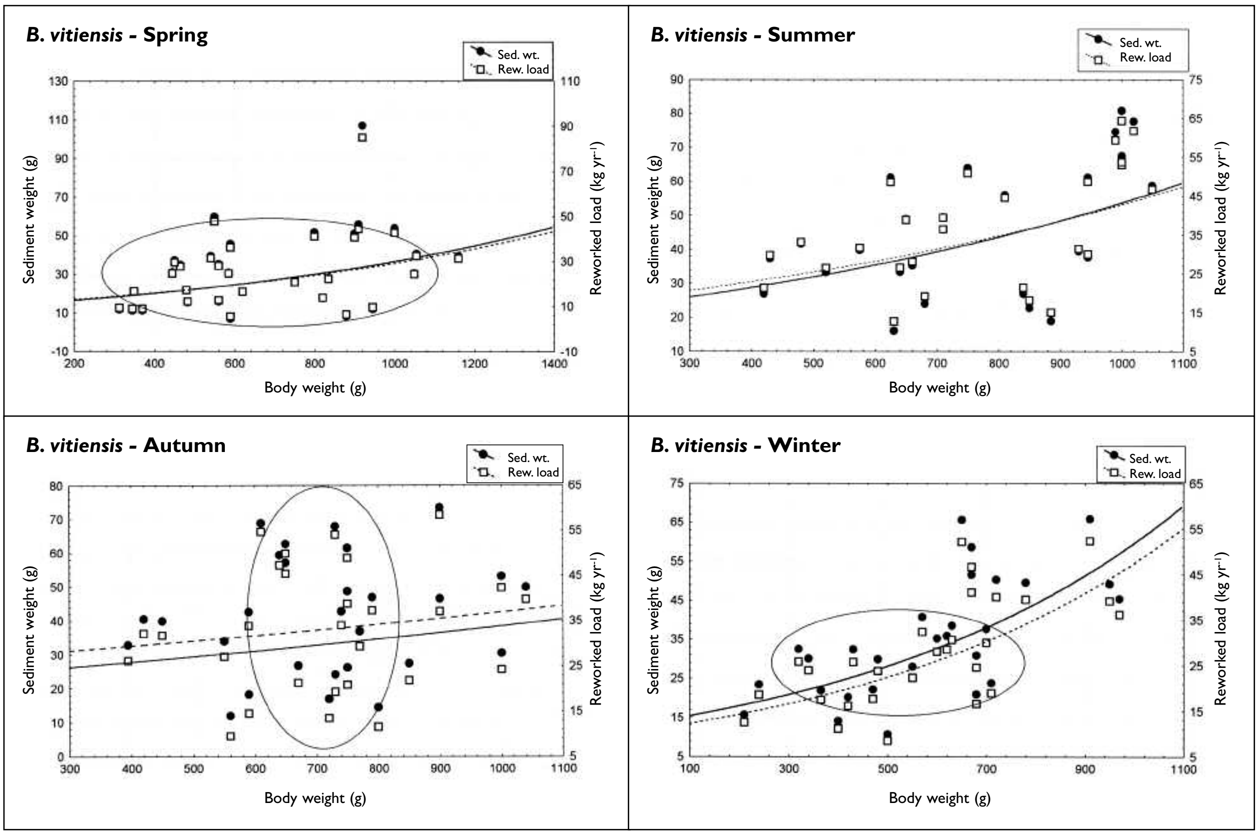

Figure 7. **Relationship between body weight, sediment weight, and reworked loads in *B. vitiensis* for the different seasons.**

The feeding selectivity of the holothurians throughout the different seasons illustrated that the coarse sediments were the main component in the animals' guts during the different seasons, but there was a differential occurrence present between the coarse sediments and the fine sediments. The animals alternatively selected between the two categories in the different seasons according to their biogenic needs and food availability. The feeding behaviour and mechanism in the different seasons were related to the animals' sexual maturity stages.

The sediment reworking process increases as the amount of sediment consumed by the holothurian individuals increased. The volume of reworked sediment amounts was controlled by the number, size and the sexual maturity stage of the sea cucumbers and food availability as well as local conditions. The intensive sediment reworking by *H. atra*, *H. hawaiiensis* and *B. vitiensis* began in late spring and lasted until the end of autumn.

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