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Distribution and Feeding of the Sea Cucumber *Isostichopus badionotus* in Relation to Shelter and Sediment Criteria of the Bermuda Platform*

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ABSTRACT: The distribution (habitat preference) of the holothurian *Isostichopus badionotus* (Selenka) on the Bermuda platform is related primarily to shelter from wave action. Within sheltered habitats *I. badionotus* occupies stable rocky, sandy or muddy substrates with epibenthic biota. *I. badionotus* of similar size are unselective feeders with regard to particle size of muddy or sandy sediments. *I. badionotus* can ingest its own feces, which may provide a potentially enriched food resource that is unlikely to persist in areas of turbulent water conditions. The first summary of knowledge on stichopodid feeding is provided. It is suggested that the absence of deposit-feeding holothurians co-occuring with *I. badionotus* may allow the latter to occupy so many different sheltered habitats, because in more tropical reef flat habitats coexisting holothurian species have better defined habitat and sediment-food requirements.

INTRODUCTION

Holothurians (Echinodermata: Holothuroidea) can occur in great numbers on sheltered shallow-water sediments in the tropics. In these habitats they are important reworkers of sediments (Bakus, 1973; Webb et al., 1977). From sediments they assimilate microorganisms associated with both organic and inorganic material (Yingst, 1976). Despite their ecological importance, holothurians have received little attention from ecologists; hence our understanding of their feeding biology and of the ecological effects of deposit feeding by tropical holothurians (Bakus, 1973) is incomplete.

We are reporting here on distribution (habitat preferences) and gut contents of *Isostichopus badionotus* (Selenka), still often referred to as *Stichopus moebii* Semper, on the Bermuda platform. *I. badionotus* is a common, large (up to 30 cm long), epibenthic species widely distributed on shallow muddy, sandy and sea grass beds from Central America to West Africa and from Ascension to Bermuda (Pawson, 1976, 1978). The abundance of *I. badionotus* around Bermuda was studied in relation to exposure to water turbulence and sediment grain sizes. Within a sheltered habitat the abundance, biomass and sediment-feeding of *I. badionotus* as related to sediment porosity, grain sizes, total organic material and total phosphorus is discussed. Grain sizes of gut contents are compared with those of ambient sediments to estimate feeding selectivity.

The holothurian fauna in semi-tropical Bermuda, like its marine fauna generally, is depauperate (W. E. Sterrer, personal communication). *Isostichopus badionotus* is the only common, conspicuous epibenthic holothurian species wheras in other, albeit warmer, shallow-water habitats, complexes of large epibenthic (Yamanouti, 1939; Yanamouchi, 1956; Trefz, 1958 in Bakus, 1973; Rowe and Doty, 1977; Roberts, 1979; Lawrence, 1980) or smaller cryptic (Sloan, 1979) holothurian species usually co-occur. Since the co-occuring species may use a combination of reef flat zonation, substrate type, feeding and behavioural differences to partition resources, it is of interest to analyze some of these factors for the solitary *I. badionotus* from Bermuda.

MATERIALS AND METHODS

Areas were sampled around the Bermuda platform as well as in sheltered inshore waters like Harrington Sound (Fig. 1). Divers collected surface sediments and

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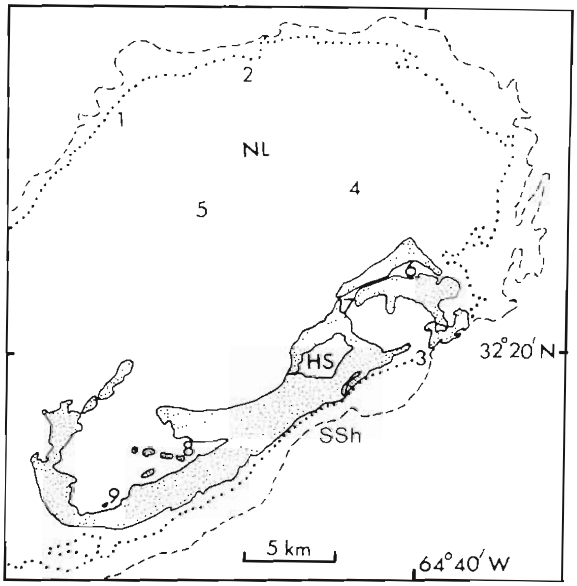

Fig. 1. Bermuda Islands and their surrounding platform (after Morris et al., 1977). Dotted line: outer reef edge; dashed line: 20 m isobath. Numbers correspond to the 9 sampling sites listed in Table 1. NL: North Lagoon; HS: Harrington Sound; SSh: South Shore

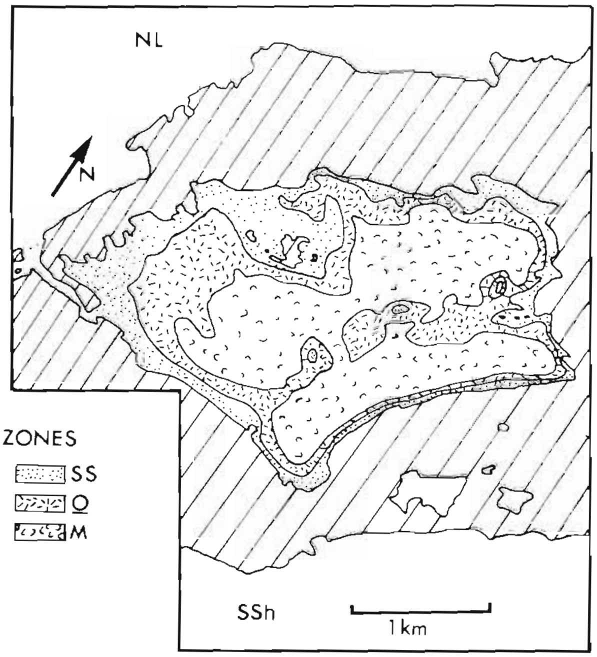

Fig. 2. Ecological zones of Harrington Sound. (After Neumann, 1965.) SS: Shallow Sandy Zone; *O: Oculina*; M: Muddy; NL: North Lagoon; SSh: South Shore

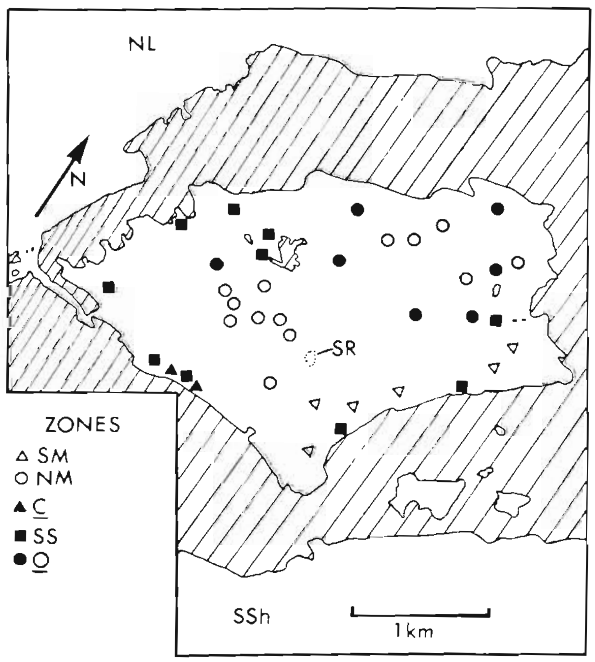

Fig. 3. Sampling site distribution in Harrington Sound. (After Barnes and von Bodungen, 1978.) SM: South Muddy Zone; NM: North Muddy; C: *Cladorphora*; SS: Shallow Sandy; *O: Oculina*. SR: shallow, isolated ridge; NL: North Lagoon; SSh: South Shore

made holothurian counts on three 20 m long × 2 m wide transects at each site, except Harrington Sound. Since *Isostichopus badionotus* is a surface sediment feeder, samples within the first 2.5 cm only were taken except in Harrington Sound. To determine grain size classes, the sediments were wet-sieved to remove the majority of fine particles (< 140 μm); the remaining coarser material was rinsed with fresh water, dried at 70 °C and then sieved.

Within the different zones in Harrington Sound (Fig. 2), a total of 38 stations were sampled (Fig. 3). At each station the depth was recorded, a 23.74 cm^2 core of 5 cm depth was taken and a 20 m long × 1 m wide transect sampled. Each core was divided into 0–2.5 cm and 2.5–5.0 cm strata; the sediments were examined for porosity and total organic material. Porosity was calculated according to the method of Berner (1971, p. 92). Total organic material (TOM) of sediments was estimated by the loss of weight on ignition at 500 °C of a dried sample.

The zones in Harrington Sound are the 'Shallow Sandy Zone' which includes a '*Cladophora* Zone' formed by the recent invasion of mats of *Cladophora prolifera* (Roth), the '*Oculina* Zone' characterized by the sediment-dwelling coral *Oculina valenciennesi* Edwards and Haime and the deep 'North and South Muddy Zones' which are identical to Neumann's (1965) 'Subthermocline Zone'.

A shallow, isolated ridge, indicated in Figure 3, was investigated in order to compare holothurian gut contents with ambient sediments from the Shallow Sandy and *Oculina* Zones. Entire guts were excised from holothurians and the contents, similarly to ambient sediments, examined for grain size classes as mentioned above. Since *Isostichopus badionotus* was observed ingesting fecal casts in this area, feces and ambient sediments in front of animals were examined for TOM and total phosphorus (TP) in order to compare their content in potential nutrients. TP was estimated after ignition at 500 °C for 2 h of a preweighed sample, which was then boiled in 3 % HCl for 0.5 h; the remaining liquid was filled up to 100 ml with deionized water and the phosphates determined according to Strickland and Parsons (1972). Five 20 m long × 1 m wide transects were sampled in each Zone for an estimation of holothurian abundance, and 100 individuals from each Zone were measured *in situ* and undisturbed for body length estimation. A subsample of 20 of these were eviscerated to remove the sediment-filled gut, and the blotted body walls were weighed for an estimation of biomass. Five body walls were examined for TOM as a percentage of live weight.

RESULTS

Habitat Preferences on the Bermuda Platform

Table 1 lists holothurian abundance and sediment grain sizes from the sites around Bermuda. At the high-energy reef edges of North Lagon and South Shore (Fig. 1, Sites 1–3), the sediment patches were rippled and devoid of epibiota. The sediments contain mostly coarse material, the fines being readily resuspended and deposited elsewhere. The patch reefs in North Lagoon (Sites 4 and 5) are more sheltered with more fine material in their surrounding sediments and established communities of epibenthos which were described in deatil by Garrett et al. (1971), Jordan (1973) and Scoffin and Garrett (1974). In the sheltered inshore areas holothurians occur on sandy sea-grass beds (Site 7), with their relatively rich fauna (Orth, 1971), but not on high-sedimentation areas with sparse epibenthos like the shipping channels of Hamilton and St. George's Harbours (Sites 6 and 8a). Dense stands of sea grass in Ferry Reach contain fewer individuals than mixed, patchy stands. *Isostichopus badionotus* is common on sandy or rock ledge substrates with well established epibenthos around the islands of Hamilton Harbour and Little Sound (Sites 8b and 9). The rock ledge has a thin layer of relatively fine sediment.

Distribution in Harrington Sound

Table 2 contains data on holothurian abundance and various sediment criteria from stations within the different ecological Zones of Harrington Sound, a sheltered inshore area.

Isostichopus badionotus is restricted to the Shallow

Table 1. Holothurian abundance and sediment grain size classes from different sites on Bermuda platform (sediment depth: 0–2.5 cm)

Sites*	Water depth (m)	Holothurians 120 m^{-2}	Grain size (μm) classes as dry weight (%) > 2,000	2,000–700	700–515	515–250	250–140	< 140
Offshore waters								
(1) Reef edge of North Lagoon	10	0	78.60	20.70	0.42	0.14	0.07	0.07
(2) Reef edge near North Rock	6	0	70.25	22.45	4.10	3.20	0.00	0.00
(3) South Shore off Castle Harbour	8	0	10.83	63.50	2.10	18.87	4.36	0.35
(4) Patch reef in North Lagoon	11	14 (0.12 m^{-2})	5.90	32.00	6.80	9.60	7.30	38.40
(5) Patch reef in North Lagoon	10	27 (0.22 m^{-2})	3.10	23.80	10.40	22.70	10.00	30.00
Inshore waters								
(6) St. George's Harbour, shipping channel	12	0	2.90	5.90	2.50	12.00	12.60	64.10
(7) Ferry Reach, sea grass beds (a)**	2	2 (0.92 m^{-2})	3.68	38.17	12.37	25.35	14.35	6.08
(b)***	1.5	20 (0.16 m^{-2})	9.20	23.40	11.83	37.33	11.08	7.60
(8) Hamilton Harbour								
(a) shipping channel	15	0	9.73	16.60	12.58	24.16	13.92	23.01
(b) west side of Marshal Island	5	26 (0.22 m^{-2})	24.04	28.23	9.35	22.71	11.24	4.43
(9) Little Sound, Five Star Is.								
(a) wide rock ledge	2.5	17**** (0.42 m^{-2})	6.40	18.68	7.88	20.20	13.79	32.05
(b) level bottom at ledge base	6	92 (0.76 m^{-2})	17.88	30.83	9.48	27.24	11.73	2.84

* See Figure 1 for localities.
** Dense stand of 'Manatee grass' *Syringodium filiforme* Kützing.
*** Patchy,mixed stand of *S. filiforme* and *Thalassia testudinum* Koenig & Sims.
**** 40 m^{-2}.

Table 2. Holothurian abundance and sediment characteristics in different zones of Harrington Sound

	No. of stations*	Total holothurians and area sampled	Water depth (m) $\bar{x}$ ± SD	Sediment strata (cm)	Total** organic material $\bar{x}$ ± SD	Porosity (Φ) $\bar{x}$ ± SD	Grain size (µm) classes as dry weight (%); from 2 stations only: > 2,000	2,000–700	700–515	515–250	250–140	< 140
South Muddy	6	0/120 m²	20.5 ± 0.8	0–2.5	4.22 ± 1.13	0.88 ± 0.07	2.5	17.5	3.2	8.0	7.3	61.5
				2.5–5.0	3.72 ± 1.13	0.82 ± 0.05						
North Muddy	13	0/220 m²	19.1 ± 1.8	0–2.5	3.91 ± 1.26	0.79 ± 0.10	3.1	15.3	2.6	8.2	6.4	64.6
				2.5–5.0	3.79 ± 0.97	0.74 ± 0.07						
Cladophora	2	0/40 m²	5.0 ± 1.4	0–2.5	5.77 ± 0.53	0.82 ± 0.13	12.4	13.3	8.1	30.1	22.3	13.8
				2.5–5.0	2.54 ± 1.30	0.73 ± 0.13						
Shallow Sandy	10	56/200 m² (0.28 m⁻²)	6.1 ± 3.0	0–2.5	3.20 ± 2.25	0.67 ± 0.12	10.2	16.6	7.2	28.4	25.3	12.3
				2.5–5.0	2.66 ± 1.27	0.61 ± 0.11						
Oculina	7	23/140 m² (0.16 m⁻²)	14.3 ± 2.11	0–2.5	4.36 ± 2.00	0.78 ± 0.12	5.2	9.7	3.5	8.3	5.5	67.8
				2.5–5.0	3.13 ± 0.47	0.69 ± 0.15						

* See Figures 2 and 3 for zone distribution and station localities.
** Measured as ‰ organic material per g dry weight.

Sandy and *Oculina* Zones. The latter is made topographically more complex by the presence of *Oculina* heads and their associated biota. It also has much more fine and porous sediments on the patches between the heads, to which the holothurians are restricted. The organic material content of the *Oculina* Zone top sediment is greater, although fewer holothurians are present than in the Shallow Sandy Zone.

Feeding, Population Density and Sediment Criteria in Harrington Sound

Table 3 shows that holothurian numbers and biomasses are greater in the Shallow Sandy Zone. The length and weight structure of the populations from both Zones is similar. Holothurians from these 2 Zones are unselective in regard to the sediments they ingest (Table 4). Holothurian guts and ambient sediments contain similar relative amounts of the particle size classes examined. There is a slight tendency for the holothurians in the *Oculina* Zone to ingest the finest and coarsest particles available.

Among the many observations of actively feeding *Isostichopus badionotus,* individuals were twice observed ingesting fecal casts which, in both cases, were well consolidated. Casts remain intact for at least 2 d. Preliminary results in Table 5 show that both total organic material and total phosphorus are greater in the holothurian feces from the Shallow Sandy and *Oculina* Zones than in the ambient sediments.

DISCUSSION

The distribution, i.e. habitat preference, of *Isostichopus badionotus* around Bermuda is related to shelter from turbulent areas, not to depth (Table 1). Shelter from wave action is the key factor influencing the distribution of most holothurians on tropical reef flats (Bakus, 1973). Within sheltered areas *I. badionotus* occurs on rocky, sandy and muddy substrates with an epibenthic community. Sheltered sandy areas around small inshore islands, patch reefs or associated with sea-grass beds are preferred habitats. If the epiflora is too dense (*Caldophora* mats or thick stands of sea grass) and thus prevents access to the sediments, holothurians are rare. Unstable muddy areas with little or no epibiota like the shipping channels in Hamilton or St. George's Harbours or the deeps of Harrington Sound have no holothurians. In these areas sediments are perhaps more readily moved or resuspended, thus inundating sluggish holothurians, than in the relatively more stable *Oculina* Zone of Harrington Sound or the rock ledge around Five Star Island with their esta-

Table 3. *Isostichopus badionotus*. Abundance and size of individuals from *Oculina* and Shallow Sandy Zones on the isolated ridge in Harrington Sound

Zones	Holothurian numbers 40 m^{-2} $\bar{x}$ SD	100 m^{-2}	Length (cm) of 100 holothurians $\bar{x}$ SD	Biomass* (g) of 20 holothurians $\bar{x}$ SD	Approximation of total holothurian biomass* (g m^{-2})	Approximation** of the TOM of the holothurians (g m^{-2})
Oculina	9.2 ± 2.6	23	20.9 ± 4.1	288.6 ± 59.1	66.4	2.14
Shallow Sandy	15.8 ± 2.7	39	21.3 ± 3.6	293.4 ± 56.2	114.4	3.69

* Biomass of eviscerated and blotted body walls (n = 20).
** Based on mean TOM of 3.23 ± 0.56 % of living body wall (n = 5).

Table 4. Grain sizes of holothurian gut contents and ambient sediments from the *Oculina* and Shallow Sandy Zones on the isolated ridge in Harrington Sound (n = 5 in all cases)

Zone sediments and holothurian gut contents	Mean and standard deviation of grain size (μm) classes as dry weight (%) > 2,000 $\bar{x}$ SD	2,000–700 $\bar{x}$ SD	700–515 $\bar{x}$ SD	515–250 $\bar{x}$ SD	250–140 $\bar{x}$ SD	< 140 $\bar{x}$ SD
Oculina sediments	4.48 ± 1.37	9.80 ± 4.46	2.40 ± 1.18	7.87 ± 0.62	6.10 ± 0.24	69.35 ± 3.80
Oculina holothurians	1.73 ± 1.94	12.22 ± 6.77	4.83 ± 3.24	12.23 ± 4.32	9.90 ± 5.33	59.09 ± 9.80
Shallow Sandy sediments	6.69 ± 3.00	17.47 ± 2.09	9.23 ± 0.32	33.57 ± 2.54	24.88 ± 3.23	8.16 ± 0.15
Shallow Sandy holothurians	6.45 ± 3.94	18.75 ± 7.24	11.63 ± 7.38	30.61 ± 3.01	23.50 ± 6.06	9.06 ± 1.66

Table 5. Holothurian feces, total organic material and total phosphorus of ambient sediments from two Zones of the isolated ridge in Harrington Sound

Zone	Sample type	Total organic material* (%) $\bar{x}$ SD	Total phosphourus** (%)
Shallow Sandy	sediments	2.97 ± 1.80	0.24
	holothurian feces	3.76 ± 1.61	0.27
Oculina	sediments	5.16 ± 1.82	0.59
	holothurian feces	6.48 ± 2.31	0.62

* % organic material g dry weight; n = 6 in all cases.
** % of the ash weight of one sample.

blished, dense epibenthic communities. The large *I. badionotus* may find locomotion more difficult on soft featureless muddy substrates. Around Bermuda, large *I. badionotus* are relatively unselective of the sediments they occupy, provided the sediments are sheltered and rendered more stable by the presence of an epibenthic community.

Within Harrington Sound, sediment porosity or total organic material cannot be correlated with holothurian abundance. Indeed, the preferred substrate of the Shallow Sandy Zone has the lowest amount of organic material in its surface sediments (Table 2). Within each zone surface sediments have the greater amount of total organic material and thus potential nutrients for these sediment-surface feeders. *I. badionotus* (approximate mean dry weight 19.0 g) from fine *Oculina* Zone sediments selects weakly against the coarsest and finest fractions of ambient sediments and is not selective when occupying the coarser Shallow Sandy Zone Sediments (Table 4). By contrast, *Stichopus tremulus* (Gunnerus) (mean dry weight 2.17 g), living on muddy substrates, selects strongly for coarser material from ambient sediments (Hauksson, 1979).

Coprophagy is well known among deposit-feeders, including holothurians (Bakus, 1973; Hauksson, 1979). Although not often observed, *Isostichopus badionotus* may profitably exploit its own feces because the casts have greater amounts of potential nutrients than ambient sediments (Table 5). *Stichopus tremulus* selectively feeds on 'faecal pellets' and 'sediment aggregates' rich in organic material, but Hauksson (1979) did not specify whether the 'pellets' were those

Table 6. Feeding selectivity of stichopodid holothurians

Species	Reference	Locality and habitat	Remarks
Astichopus multifidus (Sluiter)	Glynn (1965)	Western Puerto Rico; bare sandy and sea-grass substrates	Individuals found on a wide variety of sediments although feeding was considered more efficient on fine sediment
Parastichopus parvimensis (H. L. Clark)	Yingst (1976)	Southern California (USA); sediment-covered rocky and level substrates	Laboratory experiments; individuals utilized decomposed animal matter and micro-organisms associated with plant detritus but the detritus itself was not utilized until decomposed; avoided ingesting sediments containing blue green algae
Stichopus chloronotus Brandt	Yamanouti (1939), Yamonouchi (1956)	Palao (Western Caroline Islands); rubble and sand reef flats	Select finer particles from sediments, fast for about 8 h before dawn
	Townsley and Townsley (1973)	Fanning Island (Line Islands of Central South Pacific); seaward reef flats and lagoon passes, flats and patch reefs	Associated with finer sediments from which they reject coarsest particles (> 1 mm ∅) in favor of particles around 0.25 mm ∅; dissolution of calcareous sediments occurs; small individuals browse fine material of surface of brown algae (*Turbinaria* sp.)
Stichopus japonicus Selenka	Tanaka (1958)	Usu Bay, Hokkaido (Japan); no habitat data	Selective ingestion of sediments proposed as sediment in gut contains 4 × total nitrogen in ambient sediments; feeding periods last 1.5-5 h; capable of seasonal fasting (Mitsukuri, 1903)
	Choe (1963) (cited from Bakus, 1973)	Pusan (South Korea); no habitat data available	Juveniles ingest 'microalgae and detritus', adults are 'nonselective deposit feeders'
Stichopus moebii Semper [= *Isostichopus badionotus* (Selenka)]	Crozier (1918)	Bermuda; sheltered inshore sandy areas	No suggestion of selective feeding; gut filled twice a day but feeding discontinuous
Stichopus tremulus (Gunnerus)	Jespersen and Lutzen (1971)	Oslofjord (Norway); muddy and boulder strewn substrates at 60–200 m	Continuous, unselective feeder; may aggregate near 'favorable food conditions', i. e. sediments enriched by dead *Fucus* fronds
	Hauksson (1979)	Raunefjord (Norway); muddy substrates at 250 m	Selectively ingests coarser material (200-300 µm) from ambient sediments and qualitatively selects 'faecal pellets and other sediment particles, which are richer in organic material' during laboratory and *in situ* experiments in shallow water; results differ from those of Jespersen & Lutzen (1971)
Strichopus variegatus Semper	Yamanouti (1939) Yamanouchi (1956)	Palao (Western Caroline Islands); rubble and sand reef flats	Ingests less coarse sands than co-existing *Holothuria (Halodeima) atra* Jaeger, finer material when small, and coarser material when larger; usually fasts for 8 h before dawn
	Roberts (1979)	Jakarta Bay (Indonesia); seaward half of wide reef flats on sand or coral rubble	Selective of sediment grain size compared to the 3 other species that share its habitat; selectivity related to differing tentacular surface texture for each species
Thelenota anax H. L. Clark	Lamberson (1978)	Enewetak Atoll (Marshall Islands); lagoonal flats, patch reefs and channels	A large-sized species which ingests coarse sediments, shell and *Halimeda* sp. fragments, algal fronds and small molluscs

of *S. tremulus*. If *I. badionotus* does exploit its own feces, then areas of turbulent water conditions, where fecal casts are likely to be dispersed would not have this advantageous food resource.

We confirm Crozier's (1918) finding that local populations if *Isostichopus badionotus* are usually composed of individuals of similar body size. Small *I. badionotus* were not found; body size-related selectivity, well known in some holothurians and other deposit feeders (Sloan, 1979), could not be examined. Stichopodid feeding biology reviewed in Table 6 reveals how incomplete our knowledge is on these holothurians and the confusing nature of varying reports on their feeding selectivity. Sitchopodids can be generally selective of sediment grain size (e.g., *Astichopus multifidus, Stichopus chloronotus, S. variegatus, Thelonota anax*), qualitatively selective, according to nutrients in sediments *(Parastichopus parvimensis, S. japonicus)*, or both *(S. tremulus)* (Table 6).

Isostichopus badionotus has no large, epibenthic co-occurring deposit-feeding holothurian species in Bermuda to compete with. On the reef flats of Hawaii, Indonesia and Enewetak (Trefz, 1958; in Bakus, 1973; Webb et al., 1977; Roberts, 1979; Lawrence, 1980) co-occuring deposit-feeding holothurians partition resources by occupying particular areas and substrates and ingesting different grain-size classes of sediments. Perhaps in the absence of co-occuring species, *I. badionotus* has spread out into a variety of habitats and is able to exploit a range of differing food sources as do geographically isolated, and therefore 'released' from interspecific competition, predatory gastropod *(Conus)* species (Kohn, 1978).

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