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by V.S. Levin

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Composition of the food particles of Aspidochirote holothurians of the upper sublittoral zone of the Indo-West Pacific

/20

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The content of the gut of 32 species of holothurians (Aspidochirota), collected from various types of coral reefs, was investigated. The physical and genetic composition, the median diameter and the degree of sorting of macroparticles in most groups of holothurians varies considerably in different species and in individuals of the same species from different biotopes. On the basis of the mean size and range of sizes of the food particles, all of the studied species can be combined in groups characterized by a broad, average or narrow granulometric spectrum.

The study of the distinctive feeding features of massive species of holothurians has been very inadequate. Few works have been devoted to the study of individual species of tropical holothurians (Crozier, 1918; Yamanouchi, 1939, 1956; Glynn, 1965; Bakus, 1968, 1973).

We studied the composition of the food particles of the massive species of Aspidochirota in a number of regions of the tropical Indo-West Pacific on various types of coral reefs. We use the term "food particles" as do the authors from abroad (for example, Bakus, 1973) although the main portion of the content of the gut of Aspidochirota consists of inorganic matter.

Material and method

The contents of the guts of 32 species of Aspidochirota were studied - 1-8 individuals per species - from various regions. The gut of freshly caught

or fixed holothurians were opened, and methanol was poured over the contents. After settling the upper layer of the settled particles was collected with a pipet and was impregnated with acid and enclosed in polystyrene. The preparations were examined under a microscope and were photographed. The regions where the investigation had been carried out and the method of collection were described earlier (Levin, 1979).

After being dried in a thermostat, the greater part of the content of the gut was subjected to a granulometric sieve analysis. Because most of the studies on the mechanical composition of coral sediments have been conducted abroad, in order to facilitate comparison of the data we used the Uentvors (Wentworth ?) scale with a 1 mm base and a 2 modulus (Holme and McIntyre, 1971) rather than the decimal scale of fractions which is most commonly used in the USSR (Leont'ev, 1963).

The data of granulometric analysis were processed according to known methods used in analyzing sediments (Holme and McIntyre, 1971). For every sample a cumulative curve of mechanical composition was plotted from which the median diameter (Md) as well as the first and third quartile diameters were derived (M_1 and M_3) (Fig. 1). In order to determine the degree of sorting of the particles the coefficient of sorting S_0 was calculated.

$$S_0 = \sqrt{\frac{M_1}{M_3}}$$

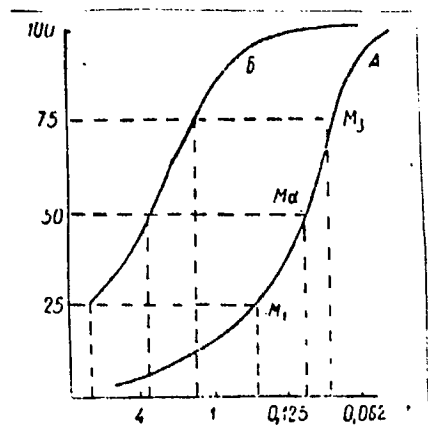


Fig. 1. Examples of cumulative curves of the mechanical composition of the food particles of (A) Holothuria edulis and (B) H. leucospilota.

Along the abscissa - median diameter, mm;
Along the ordinate - relative content, %

The mean (M) and the standard deviation of the mean (m) were calculated from the results of the individual measurements taken for each species. The mean values of parameters characteristic of the species and supraspecies taxa (subgenera and genera) were determined by the methods of combined sampling (Urbakh, 1964). If the parameter of any species and the mean of the corresponding supraspecies taxon fell into various groups during classification,

the mean parameters for the groups of "remaining" species were calculated.

Used in the analysis of the size composition of predominant fractions of food particles were triangular diagrams whose angles corresponded to the content of 100% of the particles > 2 mm, $2-0.125$ mm and < 0.125 mm in size (corresponding to gravel, sand and silt according to the Uentvors scale). Dots were placed on the diagrams to correspond with the mean percent ratio between the three indicated fractions and the standard deviations of the means. In plotting the field of the standard deviations, the lines that corresponded to the two maximum absolute values of the three were taken as its boundaries.

Results and discussion

The greatest relative mass of gut content was recorded for Labidodemas rugosum and Holothuria atra: 243% and 105% of the mass of the skin-muscular sac, respectively. In other species of holothurians this value was considerably smaller, from 10 to 80%. The greater part of the food particles of holothurians inhabiting the reefs consists of coral fragments, coral sand, segments of calcareous algae, the shells of gastropods, and fragments of the shells of sea urchins and their needles (Table I). Encountered less often are terrigenous particles, fragments of non-calcareous algae and other components. Spicules of sponges and holothurians, foraminifera and particles of detritus were found in most of the samples during a microscopic study of the fine fraction.

Our data show that the material composition and genesis of the macro-particles in most of the groups of holothurians vary considerably not only in various species but also in individuals of the same species from various habitats. Particularly varied is the gut content of holothurians that are collected in reef zones that are adjacent to the shore, primarily in the littoral part of the post-reef lagoon. Large terrigenous particles and various fragments of terrigenous origin are encountered among the food particles of Holothuria cinerascens, H. flavomaculata and H. leucospilota ^{that inhabit this zone}. Large fragments of green algae (12 x 2 mm) were found in the gut of M. erinaceus taken from the protected rocky beach of Efate Isl. (New Hebrides). /2

Very important parameters that objectively characterize the assemblage of particles contained in the gut of holothurians can be obtained as a result of a granulometric analysis of samples. The median diameter (Md) and the degree of sorting (S_o) of the particles vary within broad limits depending on the systematic position of holothurians (Table 1). In some samples the /24

Table 1

Characteristics of food particles in the guts of holothurians

Species	Number of investigated individuals	Parameters		Composition
		Md	S ₀	
<i>Actinopyga mauritiana</i>	8	0,3±0	2,1±0,2	K, П, Д, M, T, X
<i>A. lecanora</i>	2	0,4±0,1	2,0±0,1	П, X, P
<i>A. echinites</i>	2	0,6±0,3	1,5±0,1	M, Д, K, П
<i>A. plebeja</i>	1	1,5	0,5	K, P, П, T
<i>A. serratidens</i>	1	1,1	1,5	K, X, П
<i>Actinopyga</i> sp.	1	0,2	1,3	П, K, P
Род Actinopyga (genus)		0,5±0,1	1,9±0,1	
<i>Bohadschia graeffei</i>	2	0,2±0	1,6	Д
<i>B. tenuissima</i>	5	0,8±0,1	2,0±0,2	P, П, П, X, Kk
<i>B. vitiensis</i>	1	0,3	1,1	П
Род Bohadschia (genus)		0,7±0,1	2,0±0,3	
<i>Labidodemas semperianum</i>	1	0,3	1,1	П
<i>L. rugosum</i>	1	6,0	1,2	Kk, X
Род Labidodemas (genus)		3,2±2,5	1,3±0,1	
<i>Holothuria (Acantholtrapeza) pyxis</i>	2	1,1±0,8	1,6±0,2	X, П
<i>H. (Halodeima) edulis</i>	1	0,9±0,3	2,0±0,1	P, M, X, Km
<i>H. (H.) atra</i>	13	1,9±0,6	2,0±0,2	Kc, П, Kk, P, X, M
Подрод H. (Halodeima) (subgenus)		1,1±0,3	2,0±0,2	
<i>H. (Lessonothuria) pardalis</i>	3	0,3±0,1	2,0±0,1	П
<i>H. (Mertensiothuria) leucostriata</i>	1	1,4±0,6	1,8±0,3	Kk, П, Km, M, Д
<i>H. (M.) pervicax</i>	4	0,5±0,1	1,8±0,2	X, П, M
<i>H. (M.) fuscocinerea</i>	1	0,7	1,7	X, П
Подрод H. (Mertensiothuria) (subgenus)		0,9±0,2	1,8±0,2	
<i>H. (Microthete) nobilis</i>	2	0,7±0,1	1,8	X, П
<i>H. (Platyperona) difficilis</i>	2	0,1±0	1,7	M, Д
<i>H. (Selenkothuria) erinacens</i>	2	0,6±0,1	2,0	X, K, M, B _g
<i>H. (Semperothuria) cinerascens</i>	1	2,1±0,6	2,1±0,1	P, Kk, M, Tok, П, Bk
<i>H. (S.) flavomaculata</i>	1	0,2	1,3	M
Подрод H. (Semperothuria) (subgenus)		2,0±0,7	1,7±0,5	
<i>H. (Stanropora) sp.</i>	1	0,2	1,9	M
<i>H. (S.) discrepans</i>	1	0,8	2,5	X, M
Подрод H. (Stanropora) (subgenus)		0,5±0,3	2,2±0,3	
<i>H. (Thymiosycia) impatiens</i>	1	0,4	2,1	X, П
<i>H. (T.) strigosa</i>	2	0,6±0,1	1,9±0,1	P, П
<i>H. (T.) hilla</i>	10	1,1±0,2	1,8±0,1	P, M, T, K, X, П
Подрод H. (Thymiosycia) (subgenus)		0,7±0,1	1,9±0	
<i>Stichopus variegatus</i>	1	0,1	1,0	Д
<i>S. chloronotus</i>	2	0,4±0,1	2,0±0,3	П, K
<i>S. horrens</i>	1	0,1	1,0	Д
Род Stichopus (genus)		0,3±0,1	1,6±0,2	
<i>Thelenota ananas</i>	4	0,3±0,1	1,0	Д

Note. K - coral fragments (Km - largest size 2-4 mm; Kc - 4-8 mm; Kk - over 8 mm); П - sand; T - terrigenous particles; Д - detritus; M - unidentified particles; P - shells of mollusks; И - needles of sea urchins; B - non-calcareous algae (Bk - red, Bz - green); X - calcareous algae Xalimeda. The symbols are placed in order of decreasing relative content of the corresponding particles.

Table 2

Composition of the food particles of Holothuria hilla
in various size groups

Dry mass of body, g	Parameters				Content (%) of particles			Composition
	Md	M ₁	M ₃	S ₀	>2 mm	2-0.125 mm	<0.125 mm	
Upolu Isl., Western Samoa								
2.5	0.7	1.1	0.4	1.7	9.4	89.5	1.1	P, M, T
6.2	1.3	2.2	0.7	1.9	30.1	69.9	0	T, M
13.4	0.8	1.2	0.5	1.6	13.7	86.0	0.3	X, K
18.2	0.6	1.0	0.4	1.7	10.1	89.4	0.5	K, X, Π
18.9	0.9	1.2	0.6	1.4	5.8	94.2	0	K, Π
19.1	1.7	3.2	0.9	1.9	41.0	58.8	0.2	X, Π
Mean	1.0±0.1	1.7±0.4	0.6±0.1	1.7±0.1	18.0±5.1	81.3±5.8	0.3±0.1	
Southern Nilandu Isl., Maldive Isls.								
6.1	0.5	0.9	0.3	1.7	4.2	95.8	0	X, Π
7.5	1.4	2.7	0.7	2.1	39.6	60.4	0	>
10.9	1.7	2.6	0.8	1.8	39.7	60.3	0	>
26.1	1.1	2.0	0.6	2.0	26.5	73.1	0.4	>
Mean	1.2±0.2	2.1±0.4	0.6±0.1	1.9±0.1	28.0±7.6	72.4±7.5	0.1±0.1	

Note. Symbols are the same as in Table 1.

particles can reach very large sizes - the largest coral fragment from the gut of H. leucospilota was 1.52 g. At the same time only tiny particles were encountered in the gut of a number of species - Bohadschia graeffei, H. pardalis and H. difficilis.

A relatively high concentration of particles of similar origin are observed in individual size intervals of most samples during the sieve analysis. This phenomenon is associated with the general patterns of the "step-by-step" fragmentation of calcareous skeletons of organisms as a result of wave action on the reefs (Folk and Robles, 1964).

In order to determine the degree of constancy in the size characteristics and the composition of food particles in relation to the size of the holothurians an analysis was made of the gut contents of H. hilla (Table 2). The holothurians were collected in two regions with sharply differing conditions: in the littoral part of the post-reef lagoon of the fringing reef of Upolu Isl. (Western Samoa) with a high content of terrigenous particles in the bottom, and in the semi-protected inner lagoon of Southern Nilandu Atoll (Maldive Isls.) with frequent coral fragments. An increase in the size of the ^{used} food particles is seen in the early stages of growth of the holothurians, whereas the size of the food particles can even decrease with further growth of the animal (Table 2).

Yamanouchi (1939) investigated the composition of the food particles of two species of holothurians that differed in size. In order to compare the results obtained by this investigator with our data the former were reduced to the Uentvors scale. It was found that there was no distinct relationship between the size of the holothurians and the size of the particles of earth that they swallow. This confirms that there is very negligible selectivity during the feeding of mature Aspidochirota.

Table 3

Relationship between the parameters of food particles and the systematic position and size of holothurians and the nature of the surrounding bottom (based on data from Yamanouchi (1939))

Parameters	<u>Holothuria atra.</u> body length, cm		<u>Stichopus</u> <u>variegatus,</u> body length, cm		Ground
	5-10	20-25	5-10	20-25	
Md	0,8	0,9	0,4	0,9	0,5
S ₀	2,1	2,1	2,7	2,1	2,8

Data on the individual species were combined in order to obtain the generalized characteristics of the food particle spectrum (Table I). For purposes of clarification the values for the relative content of the main food-particle fractions are presented on triangular diagrams (Fig. 2). The range of variation of particle sizes used by the holothurians is characterized by the position and size of the area of the mechanical composition of the particles on the diagrams. The resulting data (Table 1, Fig. 2) indicate that food-particle sizes of various holothurian species differ both in absolute parameters and in the range of variation.

According to the characteristic median diameter Md of the used food particles all of the investigated species can be combined into the following groups¹:

1. Holothurians that use small food particles (Md < 0.25 mm, corresponds to fractions of fine sand and smaller: Actinopyga sp., Bohadschia graeffei, H. (Platyperona) difficilis, H. (Semperothuria) flavomaculata, H. (Stauropora) sp., Stichopus variegatus and S. horrens.

2. Holothurians that use average-sized food particles (Md 0.25-1 mm, corresponds to fractions of average and coarse sand): genera Actinopyga, Bohadschia (the majority of species) and Stichopus (except S. variegatus and S. horrens); subgenera of genus Holothuria - Mertensiothuria (except H. leucospilota) Stauropora (except Holothuria Sp.) and Thymiosycia (except H. hilla); species - Labidodemas semperianum, H. (Halodeima) edulis, H. (Lessonothuria) paradalis, H. (Microthele) nobilis, H. (Selenkothuria) erinaceus and Thelenota ananas.

3. Holothurians that use large food particles (Md > 1 mm, corresponds to fractions of coarse sand and larger): genus Labidodemas (except L. semperianum); subgenera of genus Holothuria - Halodeima (except H. edulis), and Semperothuria (except H. flavomaculata); species - Actinopyga plebeja, A. serratidens, H. (Acanthotrapeza) pyxis, H. (Mertensiothuria) leucospilota and H. (Thymiosycia) hilla.

We named the range of variation of the median diameter Md of the food particles of different individuals (for species) or of individual species (for subgenus or genus) the food granulometric spectrum. Taking this parameter into consideration, we can isolate the following groups from among the investigated species.

¹The mean values from species parameters for a given taxon were taken as criteria for assigning a subgenus or genus to a corresponding group; species whose characteristics differ considerably from the means were separated into groups that correspond to these characteristics.

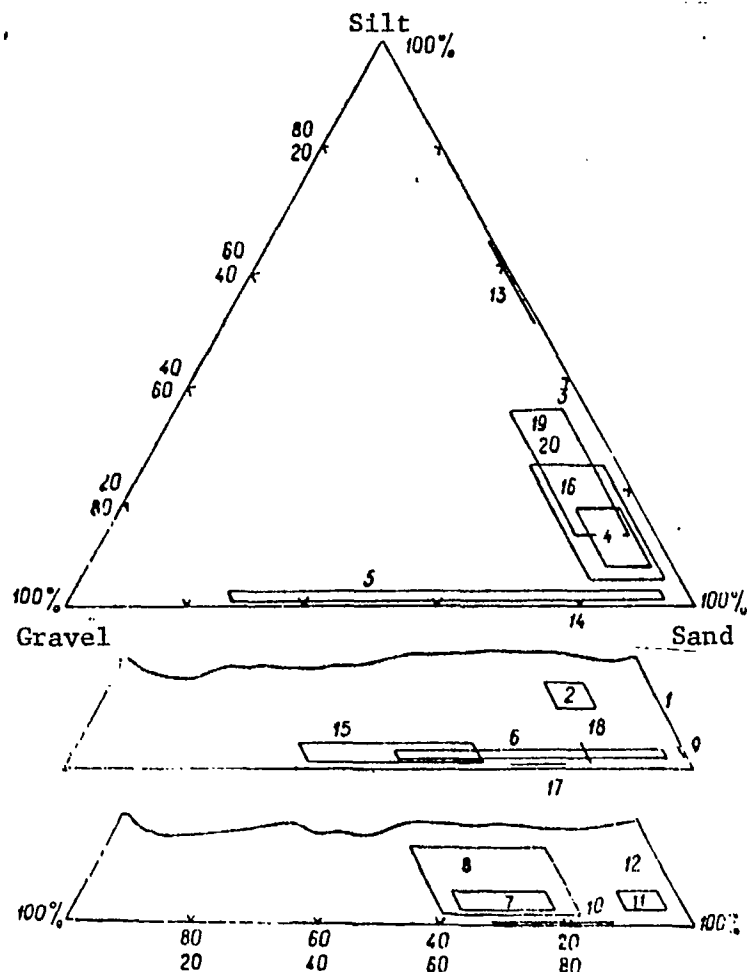


Fig. 2. Food granulometric spectra of holothurians.

Gravel - particles larger than 2 mm, sand - 2-0.125 mm, silt - smaller than 0.125 mm, 1 - *Actinopyga* sp., 2 - other species of genus *Actinopyga*, 3 - *Bohadschia graeffei*, 4 - other species of genus *Bohadschia*, 5 - genus *Labiiododemas*, 6 - *Holothuria* (*Acanthotracheza pyxis*, 7 - *H. (Halodeima) atra*, 8 - *H. (H.) edulis*, 9 - *H. (Lessonothuria) pardalis*, 10 - *H. (Mertensiothuria) leucospilota*, 11 - other species of subgenus *H. (Mertensiothuria)*, 12 - *H. (Microthele) nobilis*, 13 - *H. (Platyperona) difficilis*, 14 - *H. (Selenkothuria) erinaceus*, 15 - subgenus *H. (Semperothuria)*, 16 - subgenus *H. (Stauropora)*, 17 - *H. (Thymiosycia) hilla*, 18 - other species of subgenus *H. (Thymiosycia)*

1. Holothurians with a narrow food granulometric spectrum

(range of variation of Md < 0.2 mm): genera *Actinopyga* (except *A. echinites*), *Bohadadschia* and *Stichopus*: subgenus *Holothuria (Thymiosycia)* (except *H. hilla*); species - *H. (Lessonothuria) pardalis*, *H. (Mertensiothuria) pervicax*, *H. (Microthele) nobilis*, *H. (Platyperona) difficilis*, *H. (Selenkothuria) erinaceus* and *Thelenota ananas*.

2. Holothurians with a food granulometric spectrum of average width

(range of variation of Md 0,2-0.5 mm): subgenera of genus *Holothuria* - *Halodeima* (except *H. atra*), *Mertensiothuria* (except *H. leucospilota*)

and Stauropora; species - Actinopyga echinites and H. (Thymiosycia) hilla.

3. Holothurians with a broad granulometric spectrum (range of variation $Md > 0.5$ mm): genus Labidodemas, subgenus Holothuria (Semperothuria); species - H. (Acanthotrapeza) pyxis, H. (Halodeima) atra and H. (Mertensiothuria leucospilota).

A comparison of the width of the food granulometric spectrum and the characteristic median diameter of the food particles of individual species indicates a positive correlation between these parameters within the order Aspidochirota. From an analysis of the size, material-genetic composition of the food particles and the width of the food granulometric spectrum it can be concluded that in a number of systematic groups of holothurians most species have approximately the same feeding spectra, while in others there are species that differ considerably from closely related species in one or several of these characteristics - Actinopyga sp., Bohadschia graeffei, Holothuria (Holodeima) atra, H. (Mertensiothuria) leucospilota and H. (Thymiosycia) hilla.

Yamanouchi (1939) was the first to undertake the classification of Aspidochirote holothurians based on the size of the food particles used by them. On the basis of the type of feeding he assigned all of the species to earth eaters but divided them into two categories: sand eaters - Bohadschia bivittata, B. vitiensis, Holothuria atra, H. edulis, H. scabra, Stichopus chloronotus and Actinopyga sp., and silt eaters - Actinopyga lecanora, Actinopyga lecanora var. and H. flavomaculata.

When we compare our data with the results obtained by Yamanouchi, attention is drawn to the considerably smaller range of variation of food particle sizes in the samples obtained by this investigator (Table 3). This is possibly explained by the fact that all of the holothurians collected were from one reef zone with relatively constant conditions. At the same time, the comparative characteristics of the food spectra of individual species are quite similar.

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