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The Intrasponge Fauna of *Spheciospongia vesparia* (Porifera, Demospongiae) at Curaçao and Bonaire

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Abstract

The infauna of 35 individuals of *Spheciospongia vesparia* (Lamarck, 1814) of different volumes and from different sites and depths have been inventoried and compared. The number of sponge-inhabiting taxa is logarithmically related to sponge volume. Biomass and total number of the animals contained in the sponge are directly proportional to sponge volume. Numerical and taxonomic composition of infaunas from different sampling sites is fairly constant. Biomass and total number of sponge-inhabiting animals is not significantly different for any of the 4 sampling sites. Several taxa, however, are more abundant in sponges from one or more localities. The ratio of total biomass to total number of intrasponge fauna is found to be significantly smaller for sponges collected in deep water than in shallow water. Differences from and similarities with Pearse's results (1932, 1950) on the infauna of the same sponge species at Dry Tortugas and Bimini are discussed. The relation of the number of contained taxa and the volume of a sponge is compared with the relation of island size and number of taxa present according to MacArthur and Wilson's island-theory (MacArthur, 1972). Finally the erratic occurrence of some taxa as opposed to the highly regular occurrence of some other taxa is discussed. It is concluded that the composition of the sponge-infauna in specimens larger than 1 l is highly constant and that the sponge-inhabiting fauna constitutes an ecological community.

Introduction

Most sponges are inhabited by a wide diversity of animals the bulk of which consists of Crustacea, Polychaetes and fishes. The animals are often present in large numbers. One reason for this is the excellent shelter the sponge provides for these animals. Possibly the sponge also provides food by the constant flow of water containing plankton or organic particles not used by the sponge. The associates may also feed on the sponge tissue itself.

Some animals are obligatory sponge-dwellers and cannot live outside the sponge. They are strongly adapted physically to a life in the many canals of the sponge. This is especially apparent in a number of fishes (Böhlke and Robins, 1969; Tyler and Böhlke, 1972). Other animals in contrast may move in and out of the sponge freely, but are still so strongly allied with the sponge that they are not found elsewhere (e.g. some copepods). Finally a number of animals occur both elsewhere and inside sponges.

Not much concerning the community inside sponges has been published so far. Arndt (1933) reviewed what was known up to 1933 about crustaceans and their relationships with sponges. Băcescu (1971) reviewed all relations between sponges and their inhabitants. Pearse (1932, 1950) did some quantitative and comparative work on the relation between sponge-infauna, water depth and volume of the sponge. Long (1968) and Frith (1975) compared the infaunas of several species of sponges quantitatively and qualitatively. Fishelson (1966) gave a qualitative inventory of animals he found in sponges. Dauer (1973) studied the occurrence of several species of polychaetes in different sponges and the preference of some of the worms for certain species of sponges. Other publications dealt with the occurrence of several fish species in sponges (Gudger, 1950; Böhlke, 1969; Schwartz, 1971; Tyler and Böhlke, 1972; Greenfield, 1975).

The purpose of this study is to go beyond a qualitative inventory and to obtain a quantitative insight into the way the community within the sponge is structured, the relationship between the intrasponge fauna and the volume of the sponge individual, depth occurrence of the sponge individual and locality.

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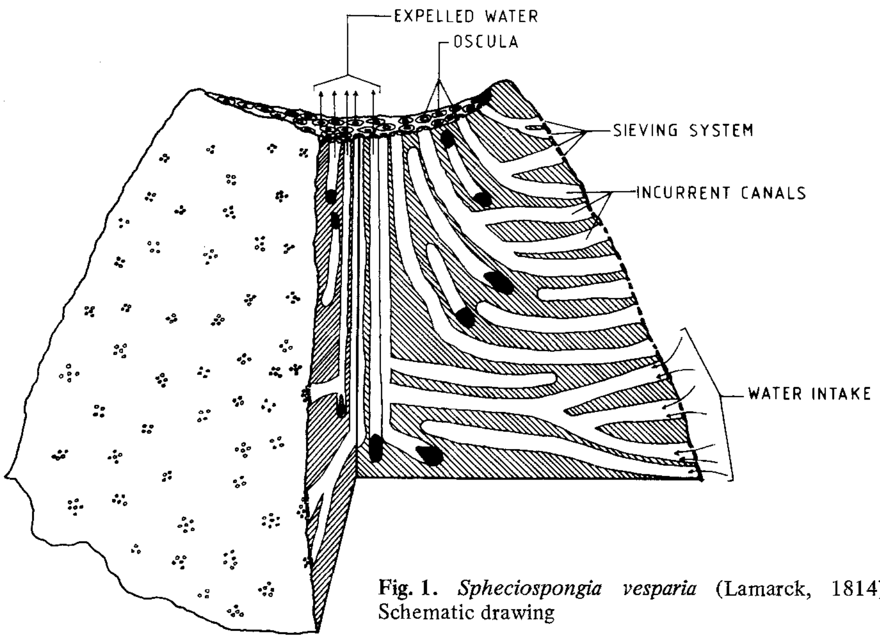

Fig. 1. *Spheciospongia vesparia* (Lamarck, 1814). Schematic drawing

Materials and Methods

A SCUBA-survey was made of the occurrence of the sponge *Spheciospongia vesparia* (Lamarck, 1814) along the leeward coast of Curacao and Bonaire, Netherlands Antilles. In shallow water no individuals were found save for a few rare exceptions. Starting at a depth of 20 to 30 m, the sponges were distributed more or less evenly down to a depth of at least 60 m. An outstanding exception was the St. Michiel's Bay, where many individuals occurred at a depth of only 3 m. Four sites were selected for sampling, *viz*. St. Michiel shallow (3 m), St. Michiel deep (40 to 60 m), Eastpoint (40 to 60 m) and Hato on the west coast of Bonaire (40 to 60 m).

Spheciospongia vesparia or Loggerhead sponge, is a solid hemispherical to barrel-shaped sponge which may reach a diameter of 1 m. The consistency is very firm and rubbery; its colour is dark purple to black. The interior of the sponge (Fig. 1) is riddled by a maze of canals, 0.5 to 1.0 cm in diameter (even in very small specimens). The canals start at the surface of the sponge where they are closed off by a "sieve" with holes of 1 to 2 mm in diameter. The oscula lie in a shallow depression at the top of the sponge; here the openings may be closed by an iris-type diaphragm. The base burrows deeply into the substrate, causing great difficulty in making a clear distinction between sponge and substrate.

Using SCUBA equipment, sponges were selected according to size and a normal growth form. The outer surface was brushed firmly to prevent the taking of non-sponge-dwelling animals. A plastic bag was then placed over the sponge and after removing it from the substrate as completely as possible, the plastic bag was immediately closed.

The volume of the sponges was measured by means of water displacement after draining the canals (error ± 5%). The specimens were then cut into slices of about 2 cm thickness and placed in a solution of 5% ethanol in seawater to remove most of the infauna from the canals. Finally the slices were washed off and examined for remaining animals. By sieving all water from the sponge tissue (mesh size about 0.1 mm^2), practically all animals larger than 0.5 mm were collected. The animals were sorted, identified and counted.

Animals possibly originating from outside the sponge were not taken into account. Wet weight was measured to the nearest mg for each taxon, after repeated draining on filterpaper, using a Sartorius balance. Relative error in weight was found to be about 10%.

During the period between December 1975 and January 1977 a total of 35 sponges was sampled at the 4 selected sites. Twenty-five of these were collected at St. Michiel shallow, 4 at St. Michiel deep, 2 at Eastpoint and 4 at Hato, Bonaire.

To compare the taxonomic composition of the intrasponge fauna of all sponge individuals, Czekanowsky's coefficient (C_z) was used:

$$C_z = \frac{2W}{A+B} \cdot 100\%$$

in which: W is the number of shared taxa in both sponge A and sponge B, A is the total number of taxa in sponge A only, and B is the total number of taxa in sponge B only. C_z may range between 0 and 100%. At 100%, the taxa-composition of sponges A and B is identical (Dauer and Simon, 1975).

To compare numerical composition of intrasponge faunas of different sponges, the number of individuals of each sponge-inhabiting taxon, expressed as percentage of the total number of individuals per sponge, is determined. Pairs of sponges are compared. For each instance of co-occurrence, the smaller percentage is recorded and summed. The sum thus acquired (C_n) is a measure of the

Table 1. Infaunal taxa of *Spheciospongia vesparia* (Lamarck, 1814), including literature references. The material is deposited in the collections of the Zoological Museum Amsterdam

Taxon	Habitat according to literature	Literature used for identification and habitat data
PISCES		
Evermannichtyhys metzelaeri Hubbs	*Spheciospongia vesparia*	Böhlke & Chaplin, 1970
Pariah scotius Böhlke	*S. vesparia*	Böhlke, 1969
Enneannectes sp.	-----	Böhlke & Chaplin, 1970
DECAPODA		
Pachycheles ackleianus A. Milne Edwards	Corals, sponges	Haig, 1956
Alpheus cylindricus Kingsley	*S. vesparia*, rocks	Crosnier & Forester, 1966; Chace, 1972
Synalpheus goodei Coutière	Corals, rocks, *S. vesparia*	Holthuis, pers.comm.; Chace, 1972
Synalpheus sanctithomae Coutière	-----	Holthuis, " " ; Chace, 1972
Synalpheus pectiniger Coutière	*S. vesparia*, turtle grass, mangrove roots	Holthuis, " " ; Chace, 1972; Pearse, 1950
Synalpheus brooksi Courtière	*S. vesparia*, other sponges, turtle grass, mangrove roots	Holthuis, " " ; Chace, 1972; Pearse, 1932
Discias serratirostris Lebour	-----	Chace, 1972
Typton tortugae McClendon	Corals, *S. vesparia* and other sponges	Chace, 1972; Pearse, 1932
Periclimenaeus sp.	-----	Chace, 1972
Axius inequalis Rathbun	Sand, mud	Rathbun, 1901
AMPHIPODA		
Leucothoe spinicarpa Abildgaard	Sponges, tunicates, sea anemones, pelecypods, sediment	Shoemaker, 1935; Ortiz, 1975
Other Gammaridea[a]	-----	-----
ISOPODA		
Bopyridae:		
Paraphrixus subcaudalis (Hay)	Abdominal parasite of Alpheids	Markham, pers.comm.
Hemiarthrus schmitti Pearse	" " " "	Markham, " "
Bopyrella lata Nierstrasz & Brender à Brandis	Branchial " " "	Markham, " "
cf. *Probopyrus pandalicola*	" " " "	Markham, " "
Species unkown to science	Parasite of *Pachycheles ackleianus*	Markham, " "
Other Isopoda[a]	-----	-----
POLYCHAETA		
Branchiosyllis oculata Ehlers[c]	Calcareous algae. *S. vesparia*	Long. pers.comm.; Ehlers, 1887
Branchiosyllis sp.	-----	Long. " "
Other Syllidae[a]	-----	Banse & Hobson, 1974
Polynoidae[b]	-----	Long. pers.comm.
Chrysoptalidae[a]	-----	Banse & Hobson, 1974
Nereidae[a]	-----	Banse & Hobson, 1974
Glyceridae[a]	-----	Banse & Hobson, 1974
SIPUNCULA	-----	-----
CIRRIPEDIA		
Balanus declivus Darwin	*S. vesparia*	Darwin, 1851; Arndt, 1933

[a] Probably several species included
[b] Very likely only one species
[c] 28 Specimens were deposited in the United States National Museum, no.55199

similarity of the numerical composition of the 2 infrasponge faunas (Glynn, 1965; McCloskey, 1970).

C_n was used instead of C_z because the sponges are of different volumes and the number of animals is directly proportional to the volume of the sponge (see Results). By using percentages in computing C_n, the influence of sponge volume is eliminated. C_n also ranges between 0 and 100%, where 100% signifies identical numerical composition of intrasponge faunas of a pair of sponges.

To study the spatial distribution of the infauna some individuals were submerged in liquid nitrogen immediately after having been taken from the water. The frozen sponges were sawn into slices using a diamond saw.

Results

All sponge individuals contained many animals of several classes (Table 1). To compare infaunas of different

Table 2. Numbers of specimens of infaunal taxa found in the studied individuals of *Spheciospongia vesparia*, arranged according to locality and increasing volume. Also shown in the ratio between total biomass of the infauna and total number of infaunal specimens of each sponge individual (bottom line)

Spheciospongia vesparia No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Volume in litres	0.025	0.04	0.05	0.08	0.3	0.3	0.35	0.35	0.4	0.5	0.5	0.6	0.9	1.0	1.6	2.2	2.25	2.4
Depth in metres	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Location	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Evermannichthys metzelaeri	–	–	–	–	–	–	–	–	–	–	–	1	4	1	1	7	2	2
Pariah scotius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Enneanectes sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pachycheles ackleianus	–	–	1	1	–	–	2	2	–	3	1	1	6	10	2	3	8	3
Alpheus cylindricus	–	–	2	2	21	12	20	14	20	22	46	26	37	57	90	41	128	95
Synalpheus goodei	–	–	1	1	–	3	1	8	2	–	3	9	12	23	25	35	22	25
Synalpheus sanctithomae	–	–	–	–	–	1	–	1	2	–	1	2	5	4	1	3	–	4
Synalpheus pectiniger	–	–	–	–	–	–	–	–	1	–	–	1	4	–	–	1	3	–
Synalpheus brooksi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Discias serratirostris	–	–	–	–	2	–	–	–	–	–	4	–	6	–	–	–	1	–
Typton tortugae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	2
Periclimenaeus sp.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	1
Axius inequalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucothoe spinicarpa	–	–	–	2	–	2	3	16	2	1	10	3	20	–	19	9	5	–
Other Gammaridea	2	–	–	3	–	–	2	–	2	–	–	1	2	1	2	1	–	2
Isopoda	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	+	–
Branchiosyllis oculata	–	–	–	1	12	7	8	7	11	11	26	16	19	20	36	50	45	49
Other Syllidae	1	–	–	–	1	–	–	–	3	–	1	–	1	1	3	16	1	1
Polynoidae	–	–	–	–	–	1	3	3	2	2	5	4	3	–	7	3	–	–
Chrysoptalidae	1	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–
Nereidae	–	–	1	–	2	–	–	–	3	–	2	–	–	1	–	–	–	–
Glyceridae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sipunculidae	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Balanus declivus	–	–	–	1	–	–	–	4	–	–	2	1	3	2	1	80	13	–
$\frac{\text{Biomass}}{\text{number of inhabitants}}$ mg	0.5	0	106.0	45.4	37.5	60.0	47.6	39.1	25.2	49.0	29.7	51.7	46.7	62.8	57.2	40.7	62.8	67.0

individuals, however, only those animals capable of moving freely within the sponge were considered. The barnacle *Balanus declivus* Darwin, 1851 was not considered as it is a sessile organism. The number of individuals of *B. declivus* varied enormously per sponge individual, probably because the settlement of the larvae, as with other balanids, depends strongly on the presence of already settled balanids (Arndt, 1933). Bopyrid isopods are parasites of the shrimps and crabs, so their occurrence depends on the occurrence of shrimps and crabs. Therefore they were not considered in comparisons of intrasponge faunas. Copepods were present in the sponges in large quantities. However, because they are ubiquitous and very difficult to identify, they were not considered either. Of the worms of the families Nereidae, Chrysophthalidae and Glyceridae and of those of the Class Sipuncula, it was not clear whether they inhabited the sponge or the substrate. Because of the burrowing of sponge-tissue into the substrate, pieces of substrate in the transition zone between sponge and substrate were also cut off when collecting a sponge. Nevertheless these worms were taken into consideration for the comparison of intrasponge faunas.

Intrasponge Fauna and Volume of Sponge Individuals

Table 2 shows the number of animals per taxon found in each sponge individual. The individuals are arranged according to sampling site and sponge volume. The occurrence of taxa was mostly consistent in all individuals, except for small sponges, in which certain taxa did not occur. The fish species *Evermanichthys metzelaeri* was only found in sponges larger than 0.6 l, the

Table 2. (continued)

Spheciospongia vesparia No.	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Volume in litres	5.0	8.5	8.75	9.5	13.5	14.0	57.0	2.75	3.9	7.5	7.8	7.2	10.4	1.0	2.5	2.5	4.0
Depth in metres	3	3	3	3	3	3	3	52	45	48	45	50	51	40	40	40	40
Location	S	S	S	S	S	S	S	S	S	S	S	0	0	B	B	B	B
Evermannichthys metzelaeri	–	8	–	4	4	37	4	4	21	31	51	3	6	1	12	10	8
Pariah scotius	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Enneannectes sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Pachycheles ackleianus	27	16	18	20	14	18	41	5	3	6	23	46	44	1	4	4	5
Alpheus cylindricus	200	450	300	315	1000	440	1650	83	226	363	300	185	282	50	87	210	127
Synalpheus goodei	96	82	63	166	75	419	270	78	120	142	97	88	51	9	43	29	58
Synalpheus sanctithomae	50	19	33	11	7	21	9	–	7	5	1	–	1	2	9	1	8
Synalpheus pectiniger	4	6	1	43	3	35	10	25	37	160	27	118	256	1	5	1	14
Synalpheus brooksi	2	3	–	–	–	5	–	1	1	–	1	40	58	–	–	1	–
Discias serratirostris	–	–	–	2	–	–	–	–	–	–	1	–	–	1	–	–	–
Typton tortugae	–	1	2	–	1	–	2	–	–	–	2	–	–	–	–	–	–
Periclimenaeus sp.	–	1	–	6	–	–	–	–	2	–	1	1	–	4	5	3	1
Axius inequalis	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	14	–
Leucothoe spinicarpa	11	40	9	35	44	24	60	68	20	92	152	16	11	22	35	32	48
Other Gammaridea	–	2	6	4	30	8	135	2	–	1	21	5	6	–	1	1	17
Isopoda	–	+	–	+	+	+	+	+	+	–	+	+	+	+	+	+	
Branchiosyllis oculata	90	137	90	183	281	260	800	86	100	371	210	100	190	33	74	131	113
Other Syllidae	2	–	2	1	–	2	2	–	–	1	12	7	9	8	9	2	–
Polynoidae	4	17	10	20	46	3	40	4	1	3	8	–	2	–	3	–	1
Chrysoptalidae	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Nereidae	–	–	1	1	10	1	8	–	–	1	23	6	10	12	11	1	3
Glyceridae	–	–	–	–	–	–	–	–	–	–	4	1	3	2	–	–	–
Sipunculidae	–	3	2	1	14	2	5	–	–	–	–	–	5	–	1	–	–
Balanus declivus	10	81	1	51	24	6	8	40	15	44	360	8	4	28	29	8	3
$\frac{\text{Biomass}}{\text{number of inhabitants}}$ mg	51.1	51.8	88.5	73.4	49.9	69.5	108.7	26.7	29.1	29.9	29.9	36.3	49.5	20.8	29.2	36.7	30.0

shrimp *Synalpheus pectiniger* in sponges larger than 0.4 l, *S. brooksi* in sponges larger than 2.5 l, the shrimp *Typton tortugae* in sponges larger than 2.2 l. Isopoda (excluding Bopyridae) were found in sponges larger than 0.6 l, shrimps of the genus *Periclimenaeus* sp. in sponges larger than 0.5 l, and Sipunculids in sponges larger than 2.5 l. Some taxa were only rarely found, *viz*. the fishes *Pariah scotius, Enneannectes* sp. and the shrimp *Axius inequalis*. The erratic occurrence of the shrimps *Discias serratirostris, Typton tortugae* and *Periclimenaeus* sp. is treated in the Discussion.

The number of taxa per sponge individual increases rapidly with increasing volume till the sponge volume reaches about 1 l. When the sponge volume increases still more, the rate of increase in the number of taxa slows down and finally the number stabilizes at a constant level of about 15 taxa, with some fluctuations (Fig. 2). Mathematically this relation can best be described as an exponential function (curve in Fig. 2):

$$a = 9.55.b^{0.22},$$

where a is the number of taxa, and b is the volume of the sponge. (correlation coefficient = 0.86, $P < 0.005$, n = 34). This function is valid only in the region of 0 to 14 l.

One individual containing no infauna had to be excluded from the regression.

The number of animals in an individual is directly proportional to its volume (Fig. 3):

$$a = 97.51.b + 25.36,$$

where a is the number of animals and b is the sponge volume. (correlation coefficient = 0.96, $P < 0.005$, $n = 34$).

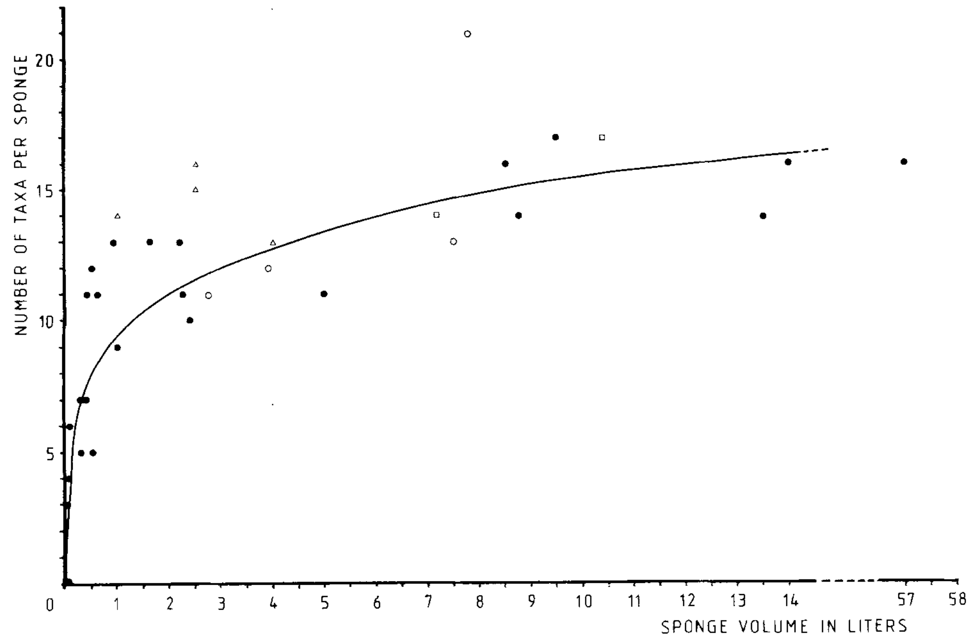

Fig. 2. The number of infaunal taxa plotted against sponge volume (l). The sponges were collected at St. Michiel, Curaçao, at depths of 3 m (filled circles, •), and 40 to 60 m (unfilled circles, ○), at Eastpoint, Curaçao, at a depth of 40 to 60 m (squares, □), and at Hato, Bonaire, at a depth of 40 to 60 m (triangles, △)

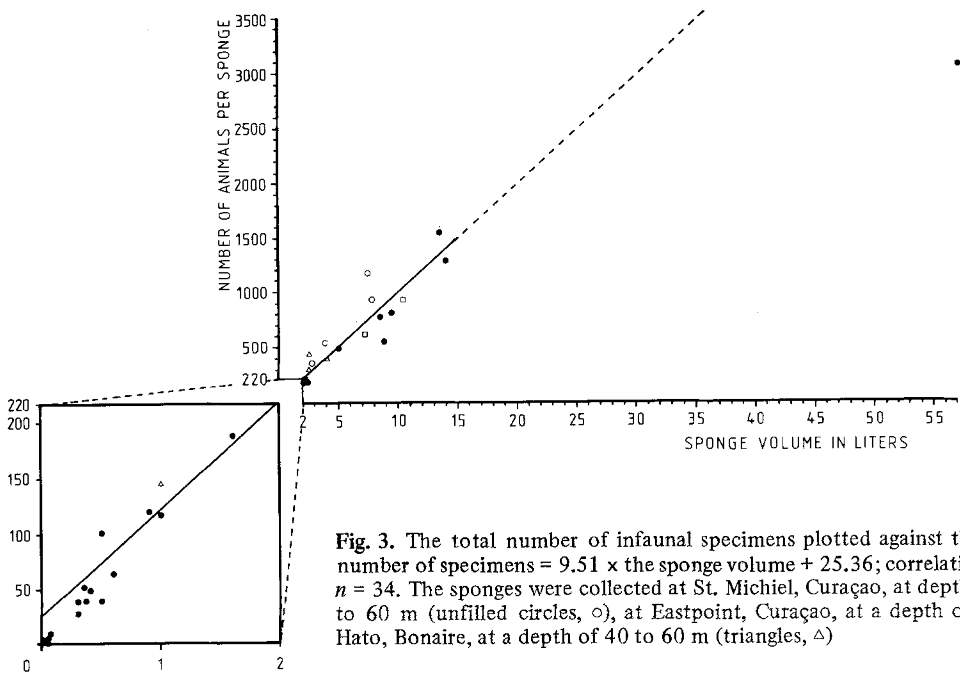

Fig. 3. The total number of infaunal specimens plotted against the volume of the sponge (l). The number of specimens = 9.51 x the sponge volume + 25.36; correlation coefficient = 0.96, $P < 0.0005$, $n = 34$. The sponges were collected at St. Michiel, Curaçao, at depths of 3 m (filled circles, •), and 40 to 60 m (unfilled circles, ○), at Eastpoint, Curaçao, at a depth of 40 to 60 m (squares, □), and at Hato, Bonaire, at a depth of 40 to 60 m (triangles, △)

The sponges from Bonaire and St. Michiel deep seem to have more animals per unit of volume than the sponges from Eastpoint and St. Michiel deep, but the difference is not statistically significant. One individual, with a volume of 57 l, scored widely beyond the range of the other sponges (see Fig. 3) and was therefore not considered in the regression. The dashed line in the Fig. 3 is an extrapolation of the regression line to show the relative position of the 57 l sponge. The number of animals per unit of volume may decrease with volumes increasing above 15 l; this cannot be confirmed, however, with data from one sponge only.

The biomass of the intrasponge fauna is directly proportional to the sponge volume (Fig. 4):

$$a = 5.78.b - 2.38,$$

where a is the biomass of all animals from a sponge and b is the sponge volume (correlation coefficient = 0.99, $P < 0.0005$, $n = 35$).

The biomass of infauna per unit of volume of sponges from deep water appears to be lower than that of sponges from shallow water, but these values fall within the variation of the regression line.

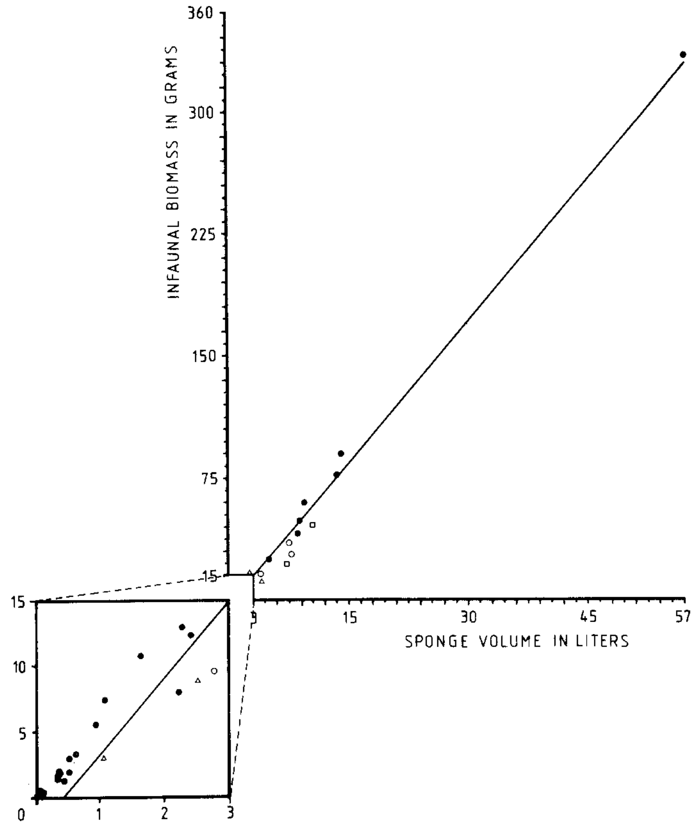

Fig. 4. The total biomass of infaunal specimens plotted against the volume of the sponge (l). Biomass = 5.78 × sponge volume − 2.38; correlation coefficient = 0.99, $P < 0.0005$, $n = 35$. The sponges were collected at St. Michiel, Curaçao, at depths of 3 m (filled circles, •), and 40 to 60 m (unfilled circles, ○), at Eastpoint, Curaçao, at a depth of 40 to 60 m (squares, □), and at Hato, Bonaire, at a depth of 40 to 60 m (triangles, △)

The biomass per litre (Fig. 5) of the infauna seemed to become stabilized with increasing volume of the host sponge, as was stated in an earlier paper (Hoetjes *et al.*, 1976). However, the variance of biomass per litre of the sponges smaller than 2 l proved to be not significantly greater than that of larger sponges. This means that the theory of stabilisation of biomass per litre with increasing sponge volume cannot be confirmed.

Intrasponge Fauna and Sampling Site

Regarding the occurrence of taxa in sponges from different localities (Table 2), *Axius inequalis, Synalpheus brooksi* and the Glyceridae seem to prefer deeper water, whereas *Typton tortugae* and the Sipunculids appear to prefer shallow water. All other taxa do not show any marked preference for either deep or shallow water sponges.

In Fig. 6 the abundance is shown of the taxa numerically most important. It is expressed for each sponge as number of animals per litre of sponge tissue. The individuals are arranged according to size and sampling site. Note that all represented taxa occur in approximately the same order of magnitude. However, the shrimp *Alpheus cylindricus*, the polychaete *Branchiosyllis oculata* and *Synalpheus goodei* are clearly most abundant. Using Wilcoxon's test ($\alpha = 0.05$) the intrasponge faunas of the different sampling sites were compared as to number of animals of each taxon present per litre of sponge tissue. *S. pectiniger* proved to be more abundant in sponge individuals from St. Michiel deep and Eastpoint, than in those from St. Michiel shallow and Bonaire ($W = 343$, $m = 6$, $n = 8$). *S. brooksi* was more

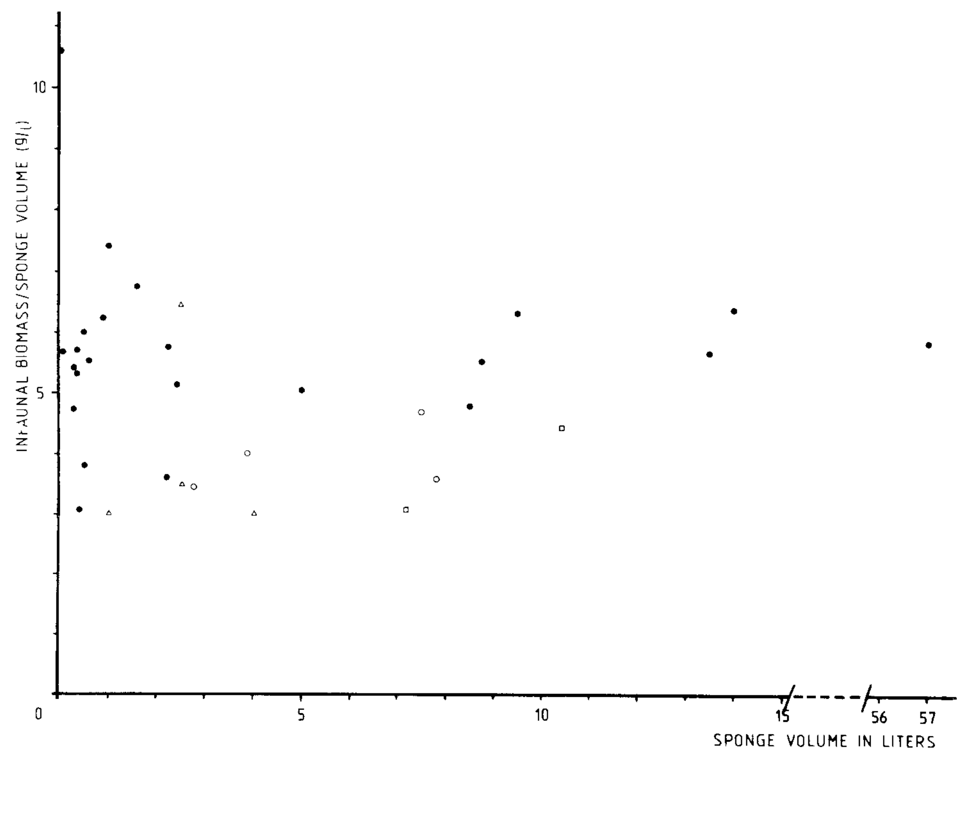

Fig. 5. The total biomass of infaunal specimens per litre sponge-tissue, plotted against sponge volume. The sponges were collected at St. Michiel, Curaçao, at depths of 3 m (filled circles, •), and 40 to 60 m (unfilled circles, ○), at Eastpoint, Curaçao, at a depth of 40 to 60 m (squares, □), and at Hato, Bonaire, at a depth of 40 to 60 m (triangles, △)

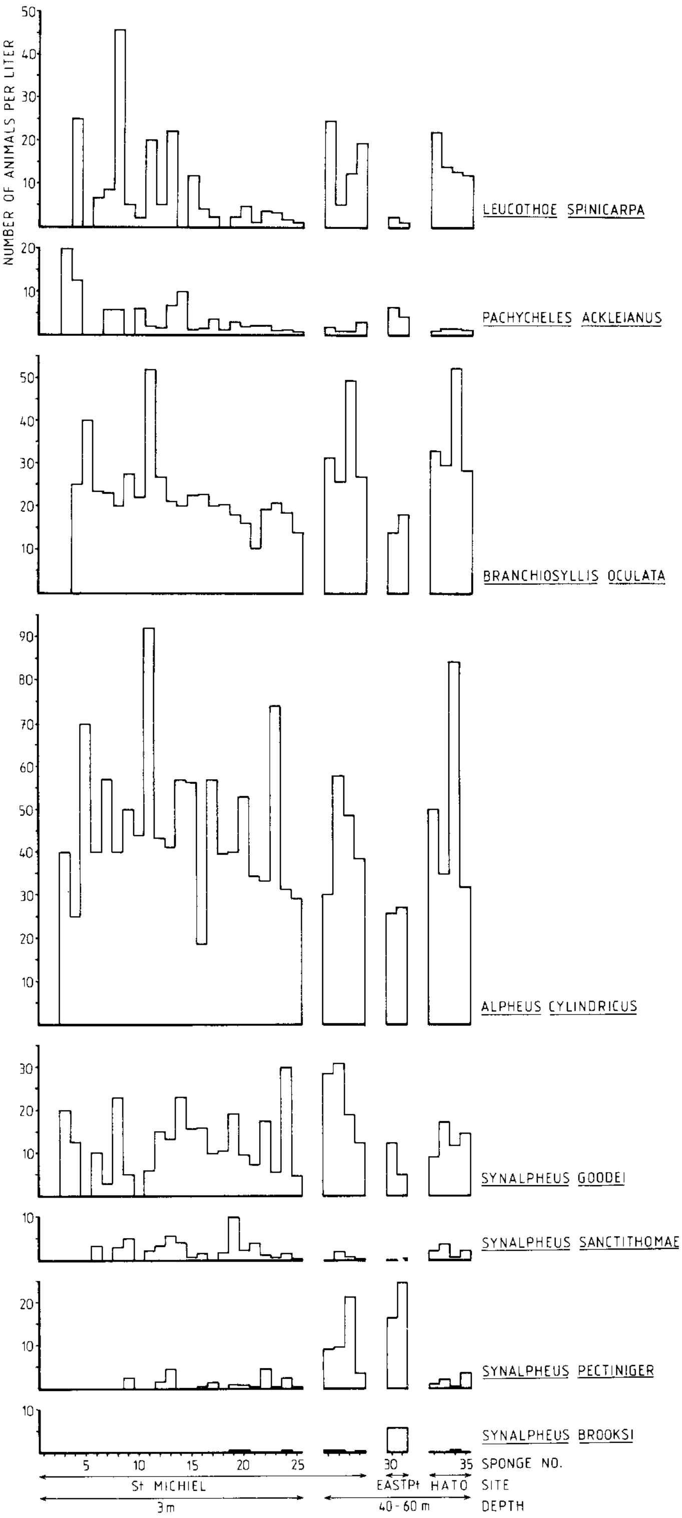

Fig. 6. The abundance of numerically important infaunal taxa, expressed as the number of animals per litre of sponge tissue. The sponge individuals are arranged according to size and locality (cf. Table 2)

numerous in sponges from Eastpoint than in those from other localities (W = 132, m = 2, n = 33). *S. sanctithomae* was more abundant at St. Michiel shallow and Bonaire (W = 72, m = 6, n = 29). The amphipod *Leucothoe spinicarpa* and *B. oculata* were more numerous at St. Michiel deep and Bonaire (W = 370, m = 8, n = 27 and W = 414, m = 8, n = 27, respectively). All these differences seem to contribute to a small distinction in total number of animals per litre between individuals from different localities. This disparity is, however, not statistically significant.

The ratio between total biomass and total number of animals found in a sponge individual (Table 2, bottom line) provides a means to distinguish the infaunas of deep water individuals from those of shallow water individuals. This ratio is significantly higher for infaunas from shallow water individuals than for infaunas from deep water individuals (Wilcoxon's test, W = 416, m = 25, n = 10, α = 0.005).

The ratio between total biomass and number of animals per taxon, or the mean weight per animal per taxon, is shown in Fig. 7. The sponges are arranged according to sampling site and sponge volumes. Using Wilcoxon's test (α = 0.05), the mean weights of animals of each taxon from deep and shallow water individuals are compared. Only those taxa that contribute significantly to the infaunal weight have been taken into account. *Alpheus cylindricus* (W = 428, m = 23, n = 10), *Synalpheus goodei* (W = 318, m = 21, n = 10), and the shrimp *Pachycheles ackleianus* (W = 146, m = 20, n = 10) appear to be lighter in deep water than in shallow water individuals. *Evermannichthys metzelaeri* (W = 153, m = 12, n = 10), *Branchiosyllis oculata* (W = 150, m = 22, n = 10), *S. sanctithomae* (W = 199, m = 17, n = 8), *S. pectiniger* (W = 97, m = 12, n = 10) and *S. brooksi* (W = 24, m = 3, n = 6) show no significant differences in mean weight between deep and shallow water. It looks as if *S. brooksi* is much heavier in individuals from Eastpoint than in those from the other localities (Fig. 7). This could not be proved statistically though, because *S. brooksi* occurred only in 9 sponges.

Alpheus cylindricus, Synalpheus goodei and *Pachycheles ackleianus* are the most important components of the total biomass of the infaunas and their mean weight is smaller in deep water than in shallow water individuals. This causes the total biomass of the infauna per unit of sponge volume to appear smaller in deep water than in shallow water individuals, as may be seen in Fig. 4 but the difference is not statistically significant.

The taxonomic and numerical composition of intrasponge faunas from the different sampling sites were compared using respectively the Czekanowsky-coefficient (C_z) and the numerical coefficient (C_n) [see Materials and Methods]. Only sponges of more or less equal size were used in the comparison. In Table 3 the taxonomic and numerical composition of intrasponge faunas from St. Michiel deep, St. Michiel shallow and Bonaire are compared. Each figure in the table expresses the degree of resemblance of the infaunas of 2 individuals: 100% indicates identical composition and 0% means that a pair

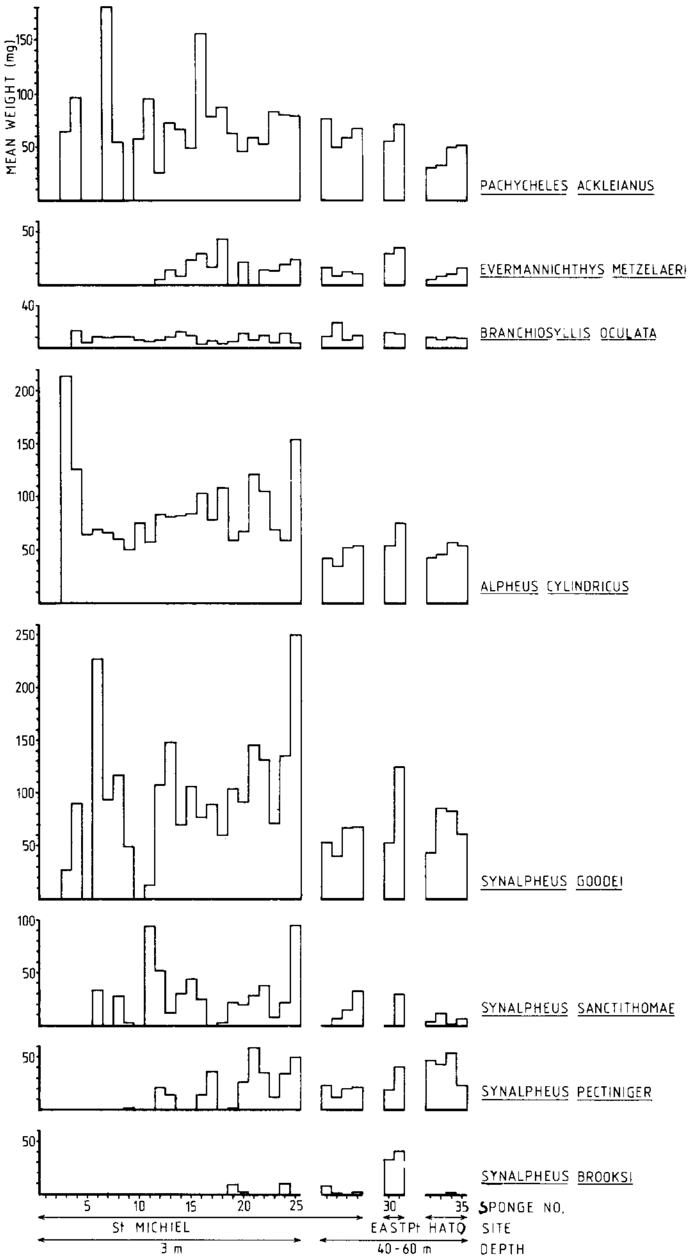

Fig. 7. The mean weight of specimens of infaunal taxa that contribute significantly to the infaunal weight. The sponge individuals are arranged according to size and locality (cf. Table 2)

of intrasponge faunas have nothing in common. With the exception of 2 cases (58.8 and 58.9%) all sponges resemble each other for more than 60% in taxonomic as well as in numerical composition. There are no differences between the sampling sites in taxonomic and/or numerical composition. The taxonomic and numerical composition of the intrasponge faunas from Eastpoint were compared with those from St. Michiel deep and St. Michiel shallow (Table 4). Again all infaunas resemble each other for more than 60% both in taxonomic and in numerical composition and again there are no differences between the sampling sites. The taxonomic and numerical composition of the intrasponge faunas of all sampling sites show great resemblance.

Spatial Distribution of Infaunal Components

With the exception of *Balanus declivus* none of the larger animals (crabs, fishes, shrimps and worms) appeared to have a preference for any special part of the sponge body; they were distributed evenly throughout the sponge. Small animals such as gammarids, copepods and isopods were hard to distinguish in the slices of frozen sponge tissue, and have therefore not been considered.

Balanus declivus is exclusively embedded in the outer surface of the sponge, sometimes encapsuled in a gall-like swelling of sponge tissue. The swelling is a defensive reaction of the sponge to the settlement of the barnacle; according to Arndt (1933) the sponge tries to overgrow the barnacles. Some species of cirripeds have developed a defense against overgrowing consisting of teeth on their outer shell, but *B. declivus*, however, does not possess this defense mechanism. *B. declivus* is not distributed evenly over the surface of the sponge but is more abundant in the lower part of the sponge.

Discussion

The infaunas of sponge individuals from different localities showed no significant taxonomic or numerical differences. The biomass and the number of animals per litre of sponge tissue showed only erratic differences for some taxa. Only the ratio between total biomass and total number of animals per sponge reveals a distinction between deep and shallow water individuals. We conclude that, although small differences are present between sampling sites, as a whole the intrasponge faunas of individuals of *Spheciospongia vesparia* are very similar.

The number of animals and the biomass of the sponge infauna are directly proportional to the sponge volume. This suggests that all available living space within the sponge is occupied.

The number of taxa of a sponge individual increases with increasing volume until a constant level is reached. Some taxa occur only in sponges larger than a certain volume, but from that size upwards are almost always present, *viz. Evermannichthys metzelaeri, Synalpheus pectiniger, S. brooksi, Typton tortugae*, Isopoda and Sipunculids. If the sponge is considered as a habitat-island in the sense of MacArthur (1972), comparison of different sizes (volumes) of the habitat-islands (sponges) would then show the number of taxa to increase with increasing size (volume) till a more or less constant level is reached (the species pool). This is in agreement with the island theory of MacArthur and Wilson (MacArthur, 1972). The relationship between the number of taxa and volume (Fig. 2) should not be viewed as a colonisation curve of one island, as was sup-

Table 3. Comparison of taxonomic and numerical composition of infauna of pairs of sponge individuals, using Czekanowski coefficient (C_z) and numerical coefficient (C_n). Sponge individuals listed here were collected at St. Michiel (shallow and deep water) and Hato (deep water). For further explanation see text

C_z / C_n		Volume (Liters)	St. Michiel Curaçao, Depth 3m 2.2	2.25	2.4	5.0	Depth 40 - 60 m 2.75	3.9	Hato Bonaire 1.0	2.5	2.5	4.0
St Michiel Curaçao	Depth 3 m	2.2		75.0	78.3	83.3	75.0	72.0	66.7	82.8	71.4	76.9
		2.25	58.5		66.7	63.6	72.7	69.6	80.0	66.7	69.2	66.7
		2.4	65.8	86.8		57.1	57.1	63.6	66.7	69.2	72.0	69.6
		5.0	65.6	75.9	76.5		72.7	78.3	64.0	74.1	69.2	66.7
	Depth 40 - 60 m	2.75	72.2	60.6	64.1	66.3		87.0	64.0	74.1	76.9	83.3
		3.9	67.4	75.9	77.6	83.4	76.4		76.9	78.6	81.5	88.0
Hato Bonaire		1.0	63.2	67.0	66.8	64.0	69.3	66.4		80.0	82.8	81.5
		2.5	76.7	66.4	72.6	70.9	78.6	73.3	80.9		83.9	89.7
		2.5	62.1	80.3	84.3	69.4	63.9	74.8	73.5	72.2		85.7
		4.0	71.4	68.6	77.3	70.4	80.2	75.9	76.6	88.7	77.3	

Table 4. Comparison of taxonomic and numerical composition of infauna of pairs of sponge individuals, using Czekanowski coefficient (C_z) and numerical coefficient (C_n). Sponge individuals listed here were collected at St. Michiel (shallow and deep water) and at Eastpoint (deep water). For further explanation see text

C_z / C_n		Volume (Liters)	St. Michiel, Depth 3 m 8.5	8.75	9.5	Depth 40 - 60 m 7.5	7.8	Eastpoint 7.2	10.4
St. Michiel	Depth 3 m	8.5		80.0	84.8	69.0	81.1	73.3	78.8
		8.75	90.7		83.9	81.5	74.3	64.3	77.4
		9.5	77.9	75.2		80.0	84.2	77.4	82.4
	Depth 40 - 60 m	7.5	66.9	62.2	76.7		70.6	74.1	80.0
		7.8	70.2	66.0	76.7	78.1		80.0	78.9
Eastpoint		7.2	63.3	64.2	72.1	75.7	68.3		83.9
		10.4	59.1	58.8	66.4	72.5	66.6	86.3	

posed in an earlier stage of this study (Hoetjes *et al.*, 1976).

Some taxa occur only now and then in some individuals and in small numbers, *viz. Typton tortugae, Discias serratirostris, Axius inequalis* and *Periclimenaeus* sp. Arndt (1933) ascribes the differences in frequency and abundance between these taxa and the more constant and abundant taxa to the difference in larval periods. *Synalpheus* spp. and *Alpheus* spp. produce fewer but larger eggs, causing the larval period to be very short. When the larvae metamorphose, they will not have moved far from the sponge. This greatly increases the chance of finding a host. According to Dobkin (1965) *S. brooksi* does not have a free-swimming larval period and he states that other species of *Synalpheus* and *Alpheus* have a similar development. Without a free-swimming larval period these species are not exposed to the risks of finding a host sponge. *Leucothoe spinicarpa* may also complete its life-cycle within its host (Ortiz, 1975). The other taxa mentioned above do not have this advantage, and that probably explains the sporadic and less numerous occurrence of these taxa in the sponges. This explanation, however, leaves the problem unsolved of how other sponges are colonized if the taxa have no free-swimming larval stages. We can only assume that adults or juveniles do sometimes venture out of their host-sponge. However, no pertinent data were collected on this subject.

When the results of this study are compared to the results of Pearse's work on *Spheciospongia vesparia* from the Dry Tortugas (Pearse, 1932), a number of differences can be noted. The first striking difference is the absence of *Alpheus cylindricus* and *Pachycheles ackleianus* from Pearse's sponges. In addition Pearse found only a few specimens of *Branchiosyllis oculata* (as, *B. lamellifera* Verrill), *viz*, only 0.8 to 3.0 specimens per litre of sponge tissue, while we found an average of 23.2 specimens. The majority of the animals (97%) found by Pearse consisted of *Synalpheus* spp.; however, they were the very species we did not encounter (*S. mcclendoni*) or only rarely found (*S. brooksi*). Finally Pearse found *Bopyro choprae* Pearse to be the most numerous parasite of the shrimp, whereas we did not encounter this species. However, Pearse notes that this species is a parasite of *S. brooksi*, a shrimp found only in small numbers and in few sponge individuals by us.

Similarity of infaunas of sponges collected by Pearse (1932) and during this study is observed in the occurrence of: *Evermannichthys metzelaeri, Leucothoe spini-*

carpa, Hemiarthrus schmitti, Balanus declivus, Typton tortugae, and *Branchiosyllis oculata* and *Synalpheus brooksi*, although in different numbers.

Pearse (1950) also examined 2 individuals of *Spheciospongia vesparia* from Bimini. In these sponges *Branchiosyllis oculata, Evermannichthys metzelaeri, Leucothoe spinicarpa* and *Balanus declivus* were absent. Again *Synalpheus brooksi* were found to be the most numerous of the snapping shrimps present. Other snapping shrimps encountered by Pearse were *S. longicarpus* (Herrick) and *S. rathbunae* Coutière, both absent from the sponges of this study, and *S. pectiniger*, which did occur in the sponges examined during this study. Strikingly the 2 individuals of *Spheciospongia vesparia* from Bimini also contained *Alpheus cylindricus* (as *Crangon cylindricus* Kingsley), *viz*. 10 individuals from the 2 sponges with volumes of 15.7 and 10.1 l, respectively. This snapping shrimp was found to be the most important in number as well as in weight in our sponges. Other similarities between individuals from Bimini and individuals from Curaçao and Bonaire are the occurrence of *Typton tortugae* and *Hemiarthrus schmitti*. The 2 individuals of *S. vesparia* from Bimini appear to have an infauna consisting of fewer species and fewer numbers than the sponges from both Dry Tortugas (Pearse, 1932) and from Curaçao and Bonaire.

The number of animals per volume of sponge for individuals collected in deep water seemed to be larger than that of sponges collected in shallow water, but was not significantly so. Pearse (1932) did notice a difference between deep and shallow water sponges, but this is probably due to the fact that only a few sponges were compared.

The results of our study indicate that the number of animals is directly proportional to the volume of the sponge, at least up to a volume of about 15 l. One individual of 57 l, however, showed a relatively smaller number of animals per unit of sponge volume. Pearse (1932) concludes that small sponges contain a relatively larger number of animals than large sponges. Pearse studied sponges in the size-range of 50 to 185 l. Thus it may be possible that the number of animals per volume decreases with increasing volume above 15 l.

Few data are available on the feeding behaviour of sponge-inhabiting animals; some notes are given below. According to Tyler and Böhlke (1972) *Evermannichthys metzelaeri* is an obligatory sponge dweller, feeding on invertebrates and/or their eggs or larvae found in the sponge. This was confirmed by the data collected in this study. The stomach contents of *E. metzelaeri* were investigated. Some copepods and crustacean eggs were found. Most copepods were cyclopoid copepods of the genus *Asterocheres* and a few harpacticoids. The Asterocheridae are semi-parasitic animals transformed but little by their mode of life, being able to move freely within their host and even leave it for a while (J. H. Stock, personal communication).

On the feeding behaviour of the snapping shrimps very little has been published. Hazlett (1962) found that an *Alpheus* species collected in Bermuda was omnivorous. Goldberg (1971) found the same for a *Synalpheus* sp. Arndt (1933) noted that *Typton tortugae* and a few *Synalpheus* spp. probably are predators of sponges and eat the sponge tissue.

Leucothoe spinicarpa is assumed to be parasitic on sponges by Ortiz (1975) and Arndt (1933).

Balanus declivus is a filter feeder, living on the outside of the sponge. It probably uses the sponge only as a substrate, but the waterflow created by the sponge probably aids it in obtaining its food.

For the other sponge-inhabiting species no feeding data are available. More knowledge of this kind would probably give a better understanding of the interrelations of infaunal components. The results of this study have shown the community within *Spheciospongia vesparia* to be highly constant. We suspect the presence of many interactions both between the host and its inhabitants and between the different sponge-inhabiting animals.

Conclusions

Summarizing we conclude with respect to the intrasponge-fauna of *Spheciospongia vesparia* that: (a) the composition is highly constant, although some small differences occur between different localities and depths; (b) the number of infaunal taxa increases logarithmically with the sponge volume; (c) the total number of animals present as well as their total biomass are directly proportional to sponge volume, which means that all available living space is occupied; (d) the mean weight of 3 infaunal species constituting roughly two-thirds of the total biomass of the infauna, is smaller in deep water than in shallow water; (e) it is indeed an ecological community, in which, however, interrelationships are not yet clear.

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