

Skeletal growth of the deep-sea hexactinellid sponge *Euplectella oweni*, and host selection by the symbiotic shrimp *Spongicola japonica* (Crustacea: Decapoda: Spongicolidae)

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Abstract

Aspects of the skeletal growth of the deep-sea hexactinellid sponge *Euplectella oweni* Herklots and Marshall, and host size and type selection by the symbiotic shrimp *Spongicola japonica* Kubo were investigated using field-collected material. Two phases, flexible and stiff, were observed in the framework of the sponges. In the flexible sponges, the circular, longitudinal and oblique systems of the skeletal beams that constitute the principal framework were not fused to each other, and the parietal ledges running circularly, or sometimes obliquely, on the wall were not developed. The skeletal wall was fragile in texture, readily torn by any external force. The wall was much sturdier in the stiff sponges, in which the systems of the skeletal beams were coarse, fused to each other to make the principal framework tough in texture, and parietal ledges developed so as to reinforce the sponge wall. The flexible phase is mainly seen in smaller and younger sponges, while the stiff phase was seen in the larger (or dead) ones. Almost all the solitary and young pairs of shrimps were collected from flexible sponges.

Key words: skeletal growth, host selection, *Spongicola*, *Euplectella*

INTRODUCTION

Deep-sea hexactinellid sponges belonging to the genus *Euplectella* (Hexactinellida: Hexasterophora: Lyssacina: Euplectellidae), often called 'Venus' flower baskets', are columnar or vase-like organisms standing upright on the bottom of the deep-sea floor. The appearance of the completely sealed mesh basket skeleton is so sophisticated that mediaeval Europeans mistook it for glass craftwork made in China. In Japan, a species of *Euplectella* has been called 'Kairou-Douketsu', which means 'together for eternity' and is treasured as bringing good fortune. This symbolism is apt because in many cases a mature pair of small shrimps of the family Spongicolidae live trapped inside the cavity of the host sponge, appearing to be locked in an eternally monogamous relationship as befits a virtuous man and wife. The Japanese compare this relationship to that of an ideal couple, and use this phrase in congratulation speeches at wedding ceremonies to wish the couple everlasting happiness. It was the spongicolids that were once called 'Kairou-Douketsu', but this phrase is nowadays used for the *Euplectella* species.

It is of interest to understand how the spongicolid shrimps reproduce and how pair formation occurs in

such a specialized environment. Recently, aspects of reproductive biology have been described for *Spongicola japonica* Kubo. The shrimps hatch directly as the first juvenile and live mainly in the cavity of a host sponge until they reach the size at which gonadal maturity starts. They then move from the cavity of the host sponges and mate (see Saito & Konishi, 1999; Saito & Koya, 2001; Saito, Uchida & Takeda, 2001; Saito, 2002). To understand the mating systems of the symbiotic shrimp in such a specialized habitat, it is necessary to clarify what size or type of hosts they select.

Most species of the Spongicolidae are reported to be associated with deep-sea hexactinellid sponges. Arndt (1933) reviewed the associations between host sponges and symbiotic crustaceans, but did not refer to their ecology in detail. In Japanese waters the associations between spongicolids and euplectellid sponges have been recognized as: *Spongicola venusta* with *Euplectella aspergillum*, *E. marshalli*, *E. oweni*, *E. curvistellata* and *Hyalonema sieboldi*; *S. japonica* with *E. marshalli* and *E. oweni*; and *S. levigata* probably with *E. oweni* (see Haan, 1833–50; Bate, 1888; Ijima, 1901; Kubo, 1942; Hayashi & Ogawa, 1987). Although Ijima (1901) described the morphology of four species of *Euplectella* from Japanese waters, he did not report in detail on the relationship between hosts and shrimps.

As for the hexactinellid sponges themselves, physiological studies such as the recognition of the syncytial

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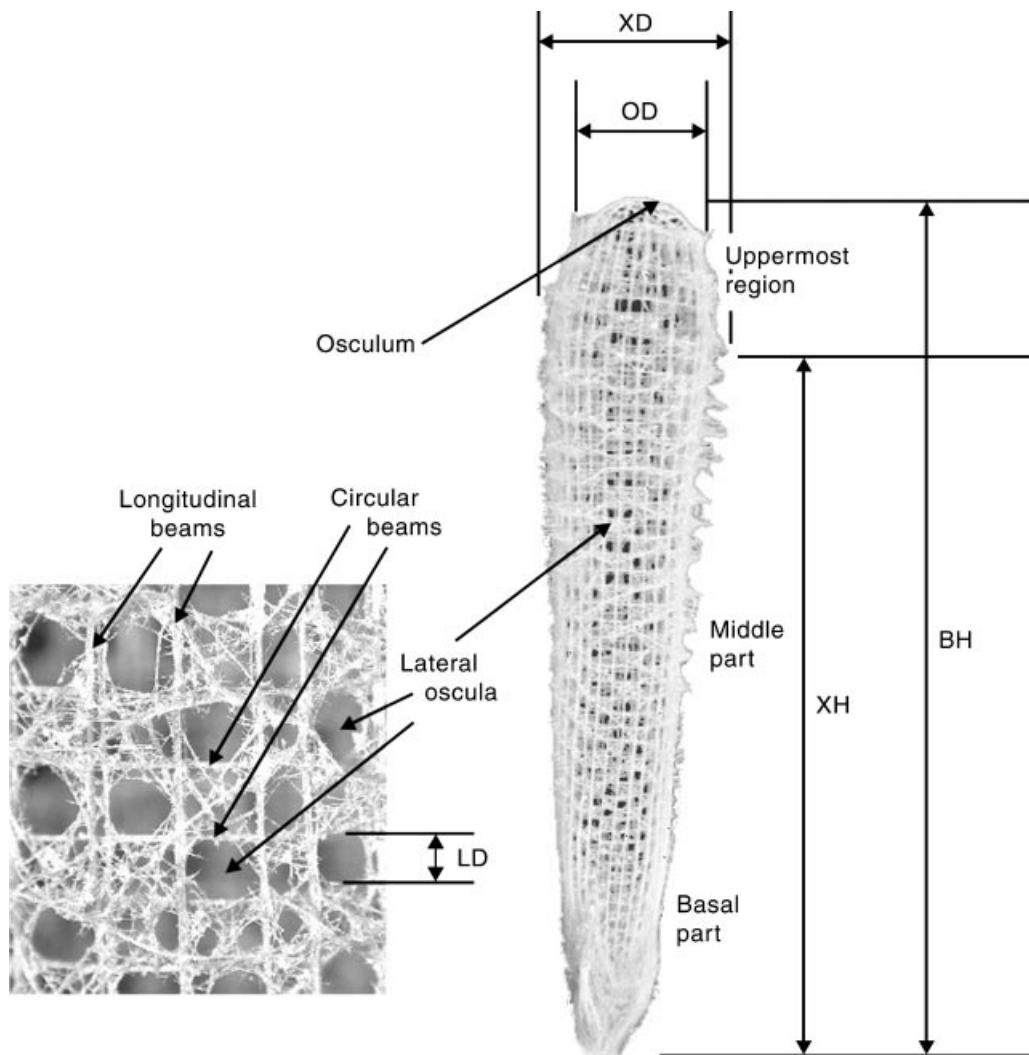


Fig. 1. Measurements made on individual specimens of *Euplectella oweni*. See text for abbreviations.

organization of tissue are available (Reiswig, 1979, 1991; Pavans de Ceccatty & Mackie, 1982; Mackie & Singla, 1983). However, basic knowledge about their growth or life history is poorly documented for deep-sea species. This paper presents aspects of skeletal growth of the host sponge *Euplectella oweni*, and host size and type selection by the symbiotic shrimp *Spongicola japonica*.

MATERIALS AND METHODS

Host sponges *Euplectella oweni* were collected during commercial shrimp trawling from a depth of 300 m off Makurazaki (130°E, 31°N), Kagoshima Prefecture, southern Japan, 2 or 3 times a year from 17 June 1996 to 4 December 1999, except for the closed fishing season from January to March. Only sponges that were perfectly flawless or, if damaged, only superficially damaged and retaining their original morphology, were used as material for this study. The temperature of the bottom water in the field had been kept at 9–10°C (T. Higashi & Y. Tokutome, pers. comm.). The sponges

were kept separately in cooled seawater at the same temperature as the bottom water in 1–31 containers according to the size of the sponges, and transported to the laboratory of the Port of Nagoya Public Aquarium within 10 h. Some of the materials were cultured for aquarium exhibition or for laboratory experiments, and were measured after any symbiotic shrimps had died. Sponges with flexible skeletal frameworks were categorized as flexible phase sponges, whereas perfectly stiff sponges, which were hard to break and could not be bent by a little manual pressure, were categorized as stiff phase sponges. The following parts of the sponges were measured with callipers (Fig. 1): body height (BH), maximum body diameter (XD), diameter of lateral oscula (LD), the height of the XD (XH), osculum diameter (OD), proportion of XH of BH ($PXH = XH/BH$); and counted numbers of: circular beams (CB), longitudinal beams on uppermost region (UB), longitudinal beams at the point of the XD (XB), longitudinal beams at the middle part of BH (MB), longitudinal beams at the basal part (BB). Shrimps were removed from the cavity of the hosts and fixed for examination in 5% buffered formalin. Measurement of

Table 1. Number and size of collected materials at each sampling date

Sampling date Collection method ^a	17 Jun 96 Random	25 Nov 96 Selected	15 Dec 97 Selected	12 Jun 97 Selected	4 Dec 97 Selected	21 May 98 Random	1 Dec 98 Selected	4 Jun 99 Selected	4 Dec 99 Selected	Total –
Host sponge										
Total (T)	49	11	35	24	24	25	41	37	45	291
Alive (A)	–	11	34	23	24	21	41	36	45	235
Dead	–	0	1	1	0	4	0	1	0	7
Stiff phase	–	3	16	4	4	16	17	17	19	96
Flexible phase	–	7	19	20	12	9	24	20	26	137
Flawless	20	1	4	7	10	6	10	9	6	73
Damaged	29	10	31	17	14	19	31	28	39	218
Symbiosis (S)	15	8	25	19	24	15	30	27	33	196
No symbiosis	34	3	10	5	0	10	11	10	12	95
Ratio of symbiosis (%): S/A*100	–	72.7	73.5	82.6	100.0	71.4	73.2	75.0	73.3	83.4
Range of BH (mm)	73.0–268.5	80.3–218.7	102.0–246.3	155.2–242.5	137.7–259.8	130.0–249.0	151.4–265.0	138.0–226.0	44.5–214.8	44.5–268.5
Mean ± SD of BH (mm)	181.2 ± 46.7	174.6 ± 41.8	183.7 ± 45.4	197.3 ± 23.0	212.4 ± 29.7	202.3 ± 33.8	208.3 ± 23.7	189.0 ± 22.6	167.7 ± 49.9	192.2 ± 38.3
Shrimp										
Total	24	23	63	37	56	45	55	46	93	442
Sex not determined	1	0	5	0	1	2	1	1	0	11
Male	14	7	30	19	30	17	32	21	46	216
Female	9	16	28	18	25	26	22	24	47	215

^a Random, sponges collected without sorting; selected, sorted collected sponges.

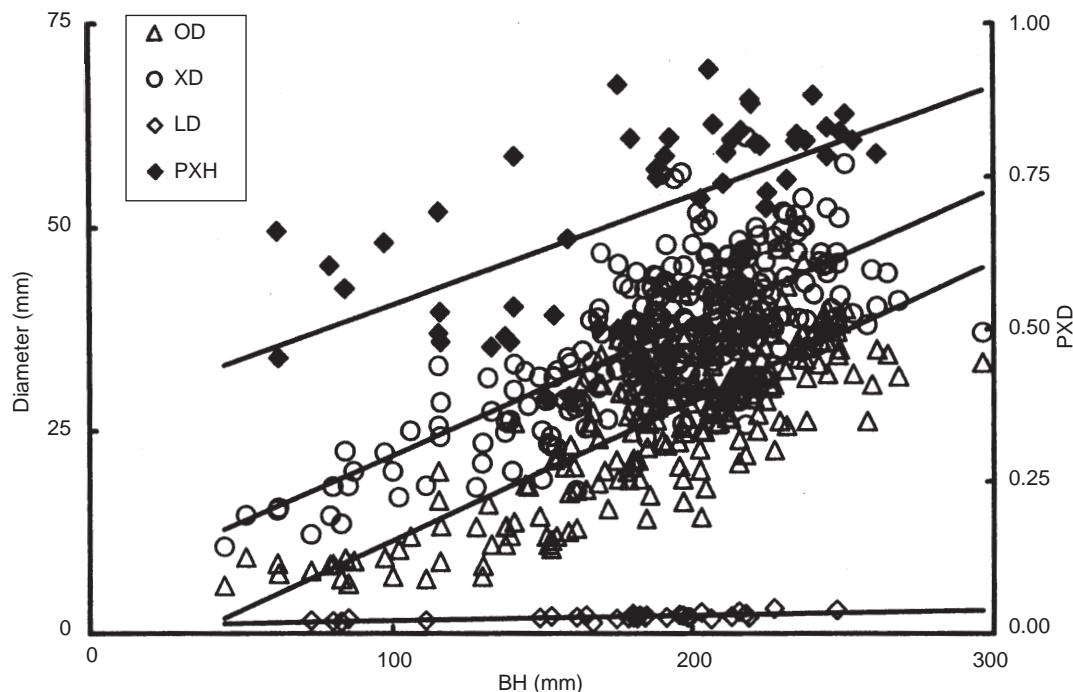


Fig. 2. Size relationships between BH and OD, XD, LD, PXH in *Euplectella oweni*. See text for abbreviations.

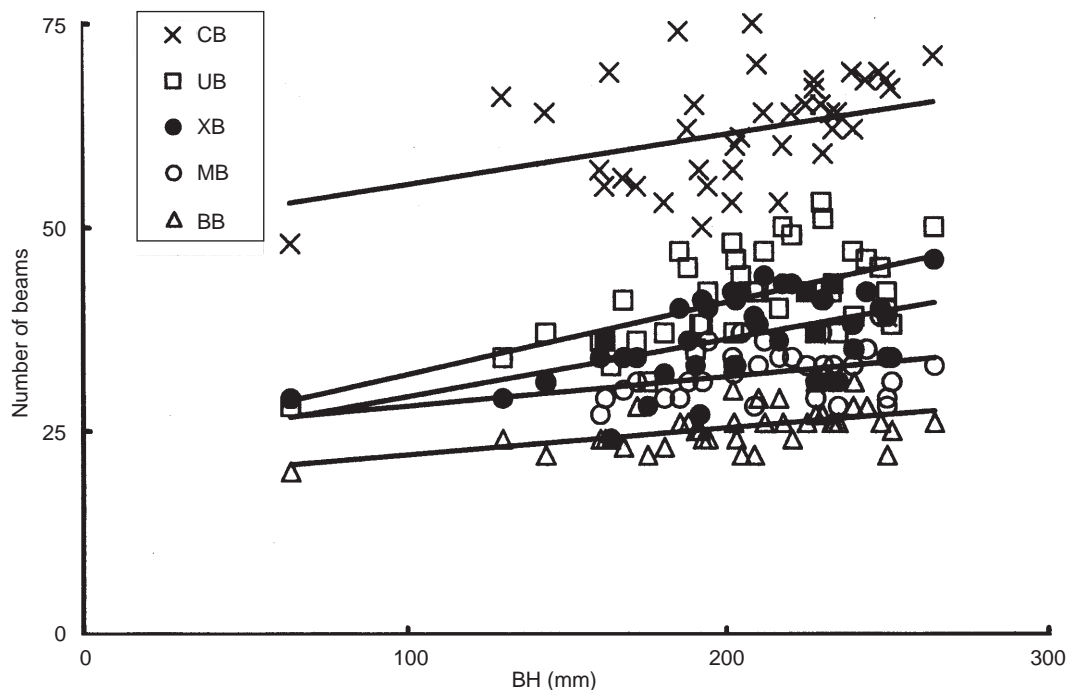


Fig. 3. Relationships between BH and numbers of principal skeletal beams, CB, UB, XB, MB, BB in *Euplectella oweni*. See text for abbreviations.

the dorsal postorbital carapace length (CL), and discrimination of the sex of shrimp by the presence of gonopores on pereopodal coxa were conducted under a stereomicroscope (Saito, 2002). Composition patterns of symbiotic shrimp in host sponges were divided into 3 categories by sex and number as:

- (a) *solitary*, only a solitary inhabitant;
- (b) *sexually paired*, a pair of male > 5.2 mm CL and female > 5.8 mm CL, which were the minimum

mature sizes of a pair found with an ovigerous female (Saito, 2002);

- (c) *grouped*, multiple inhabitants except for those designated as sexually paired.

For observation of the principal framework of the glass skeleton of a sponge, sponges were soaked in a bucket of seawater for about 2 weeks, to rot the soft tissues. Table 1 shows the numbers and size ranges of all material collected on each sampling date. The per-

Table 2. Regression coefficients represented by $Y = aX + b$ between BH and OD, XD, LD, PXH in Fig. 2, BH and CB, UB, XB, MB, BB in Fig. 3, and BH and CL in Fig. 7. r , Correlation coefficient; n , number of specimens; * $P < 0.05$; ** $P < 0.01$

X	Y	a	b	r	n	F
BH	OD	0.1715	-5.7494	0.6151	246	389.9**
BH	XD	0.1642	5.5177	0.5658	258	333.6**
BH	LD	0.0064	0.9420	0.5097	31	30.14**
BH	PXH	0.0018	0.3612	0.3918	53	32.9**
BH	CB	0.0616	49.0620	0.1040	41	4.5*
BH	UB	0.0881	23.1110	0.3539	42	21.9**
BH	XB	0.0700	22.2050	0.2594	42	14.0**
BH	MB	0.0358	24.4810	0.1459	42	6.8*
BH	BB	0.0330	18.7500	0.2168	42	11.1**
BH	CL (FPS) ^a	0.0169	2.2348	0.1313	86	5.9*
BH	CL (SPS) ^b	-0.074	6.5968	0.0059	57	0.3

^a FPS, flexible phase sponges.^b SPS, stiff phase sponges.

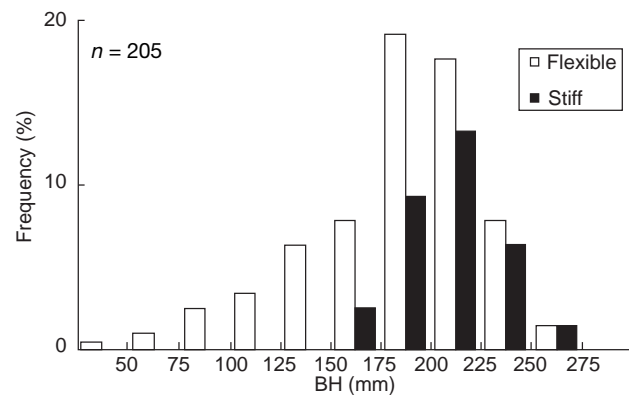
centage of live specimens in all sponges collected was calculated to be 84%, based only on the samples of 21 May 1998. Nearly 75% of collected sponges were broken off from the substrate, but 73 of 291 sponges were flawless. Sponges in 2 phases, 96 stiff and 137 flexible, were collected on all sampling dates except for 17 June 1996. CL frequency distributions by sex at 0.5 mm intervals were established for shrimps, and BH frequency distributions by sponge phase at 25 mm intervals were established for the sponges measured.

RESULTS

Skeletal growth of sponges

Figure 2 shows the relationships between BH and OD, XD, LD, PXH. Figure 3 shows the relationships between BH and CB, UB, XB, MB and BB. The relationships are modelled by the least squares regression line: $Y = aX + b$ (Table 2). XD and OD seemed to rise gradually and almost in parallel, and PXH rose to a value of 1.0 with the increase of BH, while LD did not change much (Fig. 2). The numbers of longitudinal beams were fewest in the basal part, and it increased gradually from basal to uppermost parts. In the body of flexible sponges, the borderline between the flexible and stiff parts was located adjacent to XH, where the number of longitudinal beams was increasing by splitting off, and the diameter of the body was increasing. The body shape of the sponges changes from vase-like to columnar, as they grow larger (see Fig. 9).

Figure 4 shows the frequency distribution of body height (BH) of the glass sponge. The means (\pm SD) of BH were 203.2 ± 22.1 and 189.4 ± 39.9 mm in the stiff and flexible sponges, respectively. Thus the size of the stiff phase hosts was larger than that of the flexible hosts. The main differences between stiff and flexible sponges were recognized as the preference of the parietal ledges and the set of the longitudinal, transverse and oblique principal beams. These served to reinforce the sponge walls. From observations of the structure of the

**Fig. 4.** Body height (BH) frequency distribution of *Euplectella oweni*.

principal skeletal framework of flexible sponges, the parietal ledge was not developed on the external surface, and skeletal beams were not linked to each other. The skeletal framework was fragile, easy to tear by hand in flexible phase sponges (Fig. 5b, b', d), whereas it was difficult to break off pieces of the skeleton of the stiff phase sponges; the principal skeletal beams were tough and conjoined, and the parietal ledge had developed on the external surface, reinforcing the latticework of the sponge skeleton (Fig. 5a, a', c, c'). When the latticework was damaged, the oblique beams grew flexibly and filled the hole (Fig. 5e). For example, such regenerated parts of the body were observed in 7 of the 16 stiff phase sponges collected on 21 May 1998.

Host size and type selection

The ratio of symbiosis, the percentage of the hosts with symbiotic shrimps in all live specimens, ranged from 71.4% to 100.0% with an average of 83.4% in each collection of sponges (Table 1). No symbiotic shrimps were collected from dead hosts, even in those that were flawless.

The body height of the flawless host sponges categorized according to shrimp composition pattern is shown

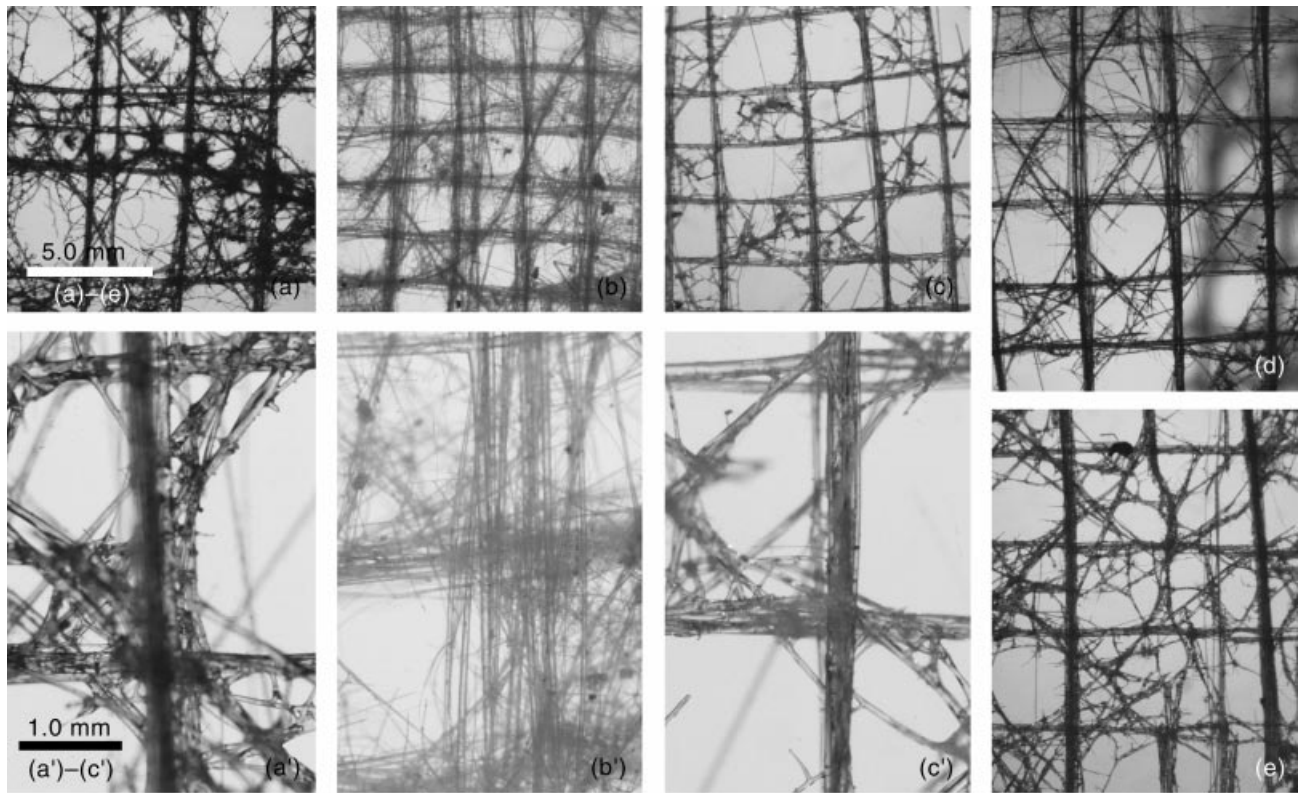


Fig. 5. *Euplectella oweni*. (a) Structure of principal skeletal beams in the upper part of a fully grown stiff sponge; (a') same as (a), spicules combined and difficult to dislocate; (b) structure of principal skeletal beams in the upper part of a flexible sponge; (b') same as (b), spicules not combined and easy to dislocate; (c) structure of principal skeletal beams in the basal part of a flexible sponge; (c') same as (c), spicules combined and difficult to dislocate; (d) structure of principal skeletal beams in the middle part of a flexible sponge; (e) regenerated part of framework in a stiff sponge.

Table 3. Composition pattern of shrimp *Spongiicola japonica* in complete host sponge *Euplectella oweni*

Composition pattern		Grouped (≥2)	Sexually paired (2)	Solitary (1)	Zero (0)	Total	Grouped ^a
Host sponge	Number	4	27	25	17	73	26
	Rate (%)	5.5	37.0	34.2	23.3	100.0	—
	Range of BH (mm)	177.1–213.0	159.4–248.5	80.3–259.8	51.6–242.1	51.6–259.8	169.6–248.2
	Mean ± SD of BH (mm)	192.6 ± 17.3	205.6 ± 23.2	173.6 ± 54.2	162.3 ± 52.6	184.1 ± 45.2	200.4 ± 21.5 ^b
	Stiff phase	191.3 ± 16.5	205.0 ± 18.9	208.0 ± 21.8	231.4 ± 15.2	203.2 ± 22.1 ^c	—
	Flexible phase	204.2 ± 29.8	195.0 ± 27.9	186.0 ± 46.7	153.1 ± 50.7	189.4 ± 39.9 ^c	—
Shrimp	Total number	27	54	25	—	106	152
Sex not determined	Number	—	—	1	—	1	6
Male	Number	13	27	14	—	54	60 (8 sexually paired)
Female	Number	14	27	10	—	51	86 (11 sexually paired)

^a Including shrimp from damaged sponges. ^b From 12 measurable sponges. ^c From 201 measurable sponges given in Fig. 4.

in Table 3. In the 73 flawless sponges, the shrimp composition consisted of 25 solitaires, 27 sexually paired, 4 grouped and 17 zero. The BH of the flawless host sponges varied in each composition pattern. The relationships between BH and the composition patterns of the symbiotic shrimp present are shown in Fig. 6a–d.

Mean body heights (±SD) (range) for sponges were 192.6 ± 17.3 (177.1–213.0) mm, 205.6 ± 23.2 (159.4–248.5) mm, 173 ± 54.2 (80.3–259.8) mm, and 162.3 ± 52.6 (51.6–242.1) mm in the grouped, sexually paired, solitary and zero categories, respectively. The BH frequency distributions of the sponges with solitary and

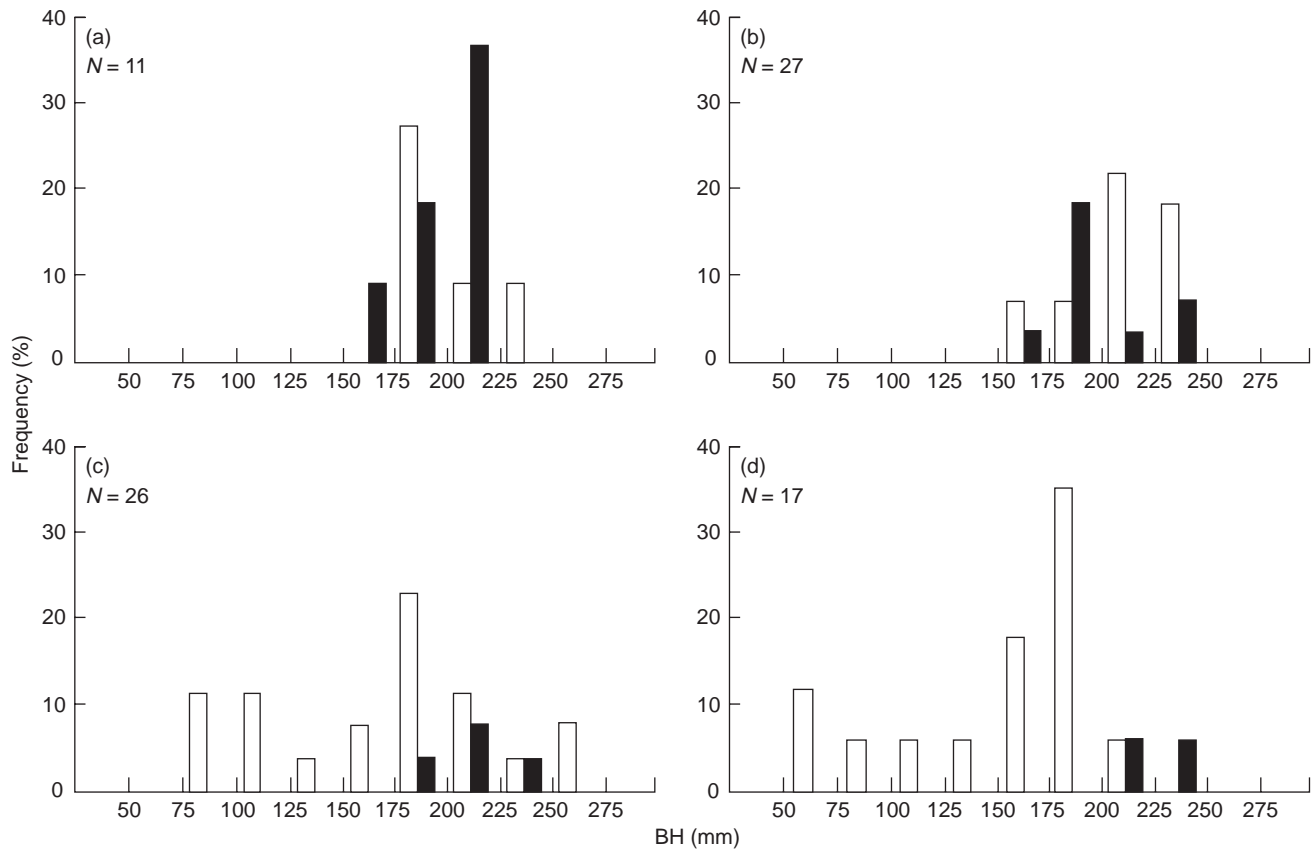


Fig. 6. Body height (BH) frequency distributions of *Euplectella oweni* categorized by the composition pattern of symbiotic shrimp. (a) Grouped shrimps in damaged and complete sponges; (b) sexually paired shrimps in complete sponges; (c) solitary shrimps in complete sponges; (d) no shrimps (zero) in complete sponges.

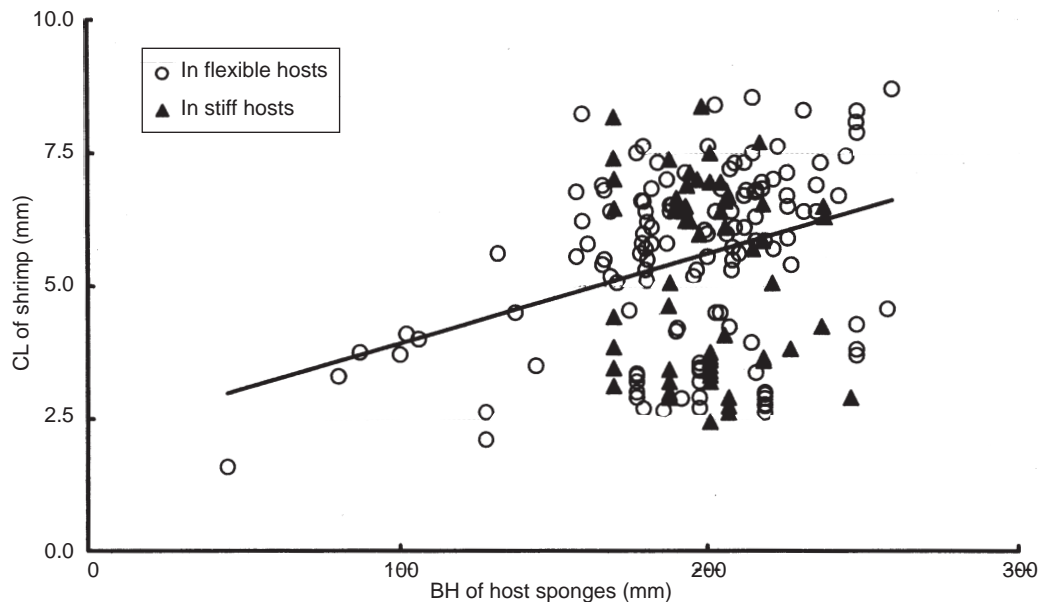


Fig. 7. Relationship between body height (BH) of *Euplectella oweni* and carapace length (CL) of *Spongicola japonica*.

zero categories in shrimp composition (Fig. 6c, d) appear clearly different from those of the sponges with grouped or sexually paired shrimp compositions.

The relationships between BH of host sponges and CL of its symbiotic shrimp by the host type are shown

in Fig. 7 and Table 2. Larger shrimps exclusively lived in the larger hosts, while small shrimps seemed to live in all sizes of hosts.

In Fig. 8, the carapace length (CL) frequency distributions of shrimp categorized by their composition pattern

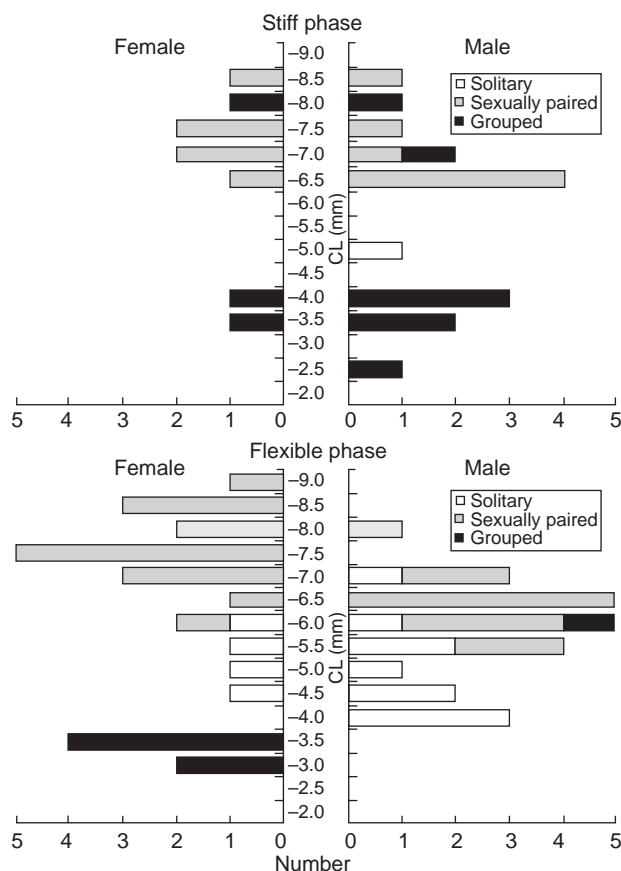


Fig. 8. Comparison of carapace length (CL) frequency distributions of *Spongiicola japonica* in the stiff and flexible phases of *Euplectella oweni*.

are compared in the two phases of perfectly flawless host sponges. In the stiff phase sponges, median \pm 95% CI of female and male CL (mm) were 7.0 ± 1.3 and 5.4 ± 1.0 mm, respectively, in comparison to 6.8 ± 0.8 and 5.8 ± 0.5 mm in the flexible sponges. Most of the solitary, newly mated sexually paired and grouped shrimps (4.0–6.0 mm CL) were observed in the flexible phase host sponges. The size of males and females differed significantly between the host phases (males: $Z = 2.54$, $P < 0.01$; females: $F = 7.00$, $P < 0.05$).

DISCUSSION

Schulze (1904) assumed that distinctive nodes increased the strength of the fused skeleton in lychnisc sponges (Hexactinellida: Lychniscosa). Reif & Robinson (1976) indicated that the so-called 'lychnisc' (lantern) nodes, the connection of each of the six rays of a spicule by bridges of solid silica, were unfused in younger specimens, but after maturity they were fused and increased the strength of the skeleton. Ijima (1901) observed a certain degree of flexibility and elasticity in the upper portion of the sponge wall of hexactinellid sponges, where the new formation of the circular and longitudinal beams splits and still continues to grow in the

young specimens of *Euplectella imperialis*. Stability resulted from the fusion of the principal skeletal elements in the lower portion where the body was almost destitute of living tissue and could be considered dead. Schulze (1895) observed the multiplication of beams by splitting at the upper region of the body of *E. simplex* and *E. oweni*, and Ijima (1901) recognized a similar situation in *E. marshalli*. The two-phase phenomenon of sponges is considered to relate to the growth process in most species of the family Euplectellidae. Figure 9 shows schematic drawings of the morphological changes of *E. oweni* during growth and development.

Saito *et al.* (2001) described the possible system of pair formation in *S. japonica*, showing that more than two periods of free-living were present. Saito & Konishi (1999) reported that juvenile shrimp leave the hosts through the mesh of the osculum or lateral oscula. However, during the second free-living period, the maturing shrimps (Saito & Koya, 2001; Saito *et al.*, 2001) are too large to move through the mesh size of the osculum or lateral oscula. The carapace length distributions of shrimp in the stiff phase sponges contrast with those in the flexible phase sponges. The flexible hosts mainly contain solitary and young sexually paired shrimp, all of which are lacking from stiff sponges. It is not known whether or not the wall of flexible hosts is easy for the shrimp to break into. These results show that solitary shrimps select flexible sponges. In the juvenile stage, the movements of symbiotic shrimps are associated with the mesh size of the osculum and lateral osculum of sponges. After the juvenile stage they are associated with the phase of the principal framework of sponges.

The selection of flexible sponges by solitary shrimps might have further significance. No symbionts were recognized in dead sponges. Solitary shrimps can be presumed to have two roles: (1) to search for a suitable mating partner; (2) to discover an unoccupied sponge habitat for a living space. In the latter role, they must select a sponge with an appropriate living space for a mate, and a probability of survival for at least as long as a shrimp's life span. Flexible sponges of a certain body height are suitable for a solitary shrimp preparing to mate.

Studies on the inhabitants of the loggerhead sponge *Spheciospongia vesparia* have shown that the biomass and population size of the inhabitant shrimp of the genus *Synalpheus* were directly proportional to the sponge volume (Westinga & Hoetjes, 1981; Erdman & Blake, 1987). In the present study, the number of individuals and size of the inhabitant shrimp have been divided into three categories, the presence of which changes in proportion to increasing sponge volume. Ijima (1901) reported that the ratios of symbiosis of undescribed shrimp of the superfamily Alpheoidea were high in the larger host sponge *E. imperialis*, but low in smaller ones. Thus, symbiotic shrimps were more numerous in older sponges than in younger ones. A similar tendency has been recognized in the present study. It is natural that older host sponges have a higher rate of being inhabited by symbiotic shrimps than

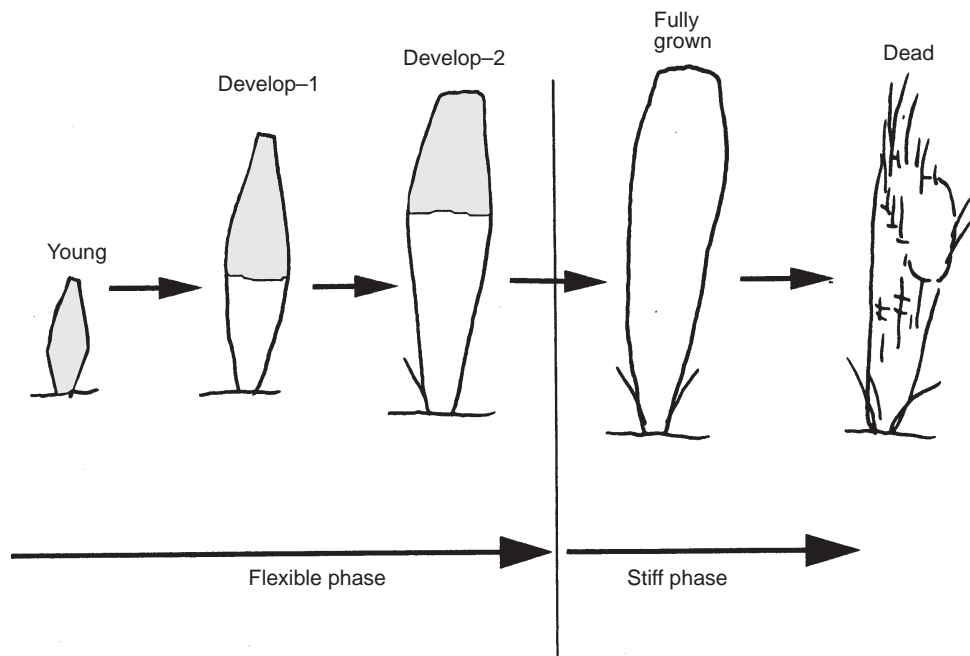


Fig. 9. Schematic drawing of body growth of *Euplectella oweni*. Grey areas indicate the flexible parts of sponges.

younger sponges, because their longevity offers many more chances to be associated with shrimps. This result also indicates that sexually paired shrimps never move from the host after it hardens. A change of the phase of host from flexible to stiff with the growth of the sponge effectively results in the imprisonment of the pair of shrimps and ensures their monogamous relationship.

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