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Gonadal Maturation and Embryonic Development in the Deep-Sea Sponge-Associated Shrimp, *Spongicola japonica* Kubo (Crustacea: Decapoda: Spongicolidae)

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ABSTRACT—Development of the gonads and embryo in the deep-sea sponge-associated shrimp, *Spongicola japonica* Kubo, was observed based on field samples collected from July 1993 to June 2000. Histological observation of gonads revealed that the gonadal maturities were divided into 4 and 5 stages in males and females, respectively. In females the smallest mature size was 5.5–6.0 mm in carapace length (CL), and the beginning of oocyte development was related to body size. The beginning of spermatogenesis was not related to body size. Grouped males started spermatogenesis at more than 3.0 mm CL, but the immature testis was recognized at 4.0–4.5 mm CL in solitary males. Embryonic development was classified into 12 stages based on the morphology of embryonic appendages. Ovarian maturity was almost always synchronized with embryonic stages in ovigerous females, and the females with fully developed embryos had fully ripened ovaries. The ovigerous females molted after hatching juveniles, and laid new eggs. Reproductive seasonality was not recognized in *S. japonica*. The induction of reproduction in this species may be controlled not by any physical environmental factors, but by other factors such as body size.

INTRODUCTION

Japanese fauna of the family Spongicolidae include the following 5 species belonging to 2 genera: *Microprosthema validum* Stimpson, *M. scabricaudatum* (Richters), *Spongicola venusta* de Haan, *S. levigata* Hayashi and Ogawa, and *S. japonica* Kubo (Miyake, 1982; Hayashi and Ogawa, 1987; Hayashi, 1995). In particular, the deep-sea members of the family are known to live entrapped by a pair of shrimp in the atrium of hexactinellid sponges, and are attracting much attention from biologists. However, the life histories of the group members have long been poorly documented due to the difficulty of collecting a large series of samples from the deep-sea.

Recently, Saito (in press) described the development of external sexual characters and sexual pair sizes in *S. japonica*. However, this is insufficient to determine the minimum size at which they first participate in reproduction. This paper represents the first attempt to classify the developmental stages of gonads of both sexes of *S. japonica* to further our knowledge of its reproductive biology and the factors inducing reproduction.

According to previous studies of embryonic development in deep-sea shrimp, the incubation period is a long one; e.g., the eggs of *Oplophorus spinosus* are estimated to take about 145 days to develop at 12°C, and those of *Systellaspis debilis* a similar period (Herring, 1974). *S. japonica* is described as having a direct larval development (Saito and Konishi, 1999), and the incubation period would take as much time as those abbreviated larval development species. Therefore, it can be estimated from the developmental stages of embryos whether the reproductive seasonality of *S. japonica* is present or not. In this paper, that embryonic development is described and compared on each sampling day to clarify reproductive seasonality.

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MATERIALS AND METHODS

Spongicola japonica Kubo, associated with the deep-sea hexactinellid sponge *Euplectella oweni* Herklots and Marshall, were collected at a depth of 300 m off Makurazaki (130°E, 31°N), East China Sea, as a by-product of commercial shrimp trawling from July 1993 to June 2000 except during the closed fishing season from January to March. Gathered sponges were placed separately into 1-liter vials with cooled seawater at 10.0–12.0°C on the deck of a trawler and transported within 10 hr to the Port of Nagoya Public Aquarium (PNPA). In the laboratory the sponges were dissected, and the shrimp in the atrium were counted, their dorsal postorbital carapace length (CL) measured, and then sexed by the presence of gonophores. The composition pattern of shrimp in a flawless sponge host is divided into 3 types by sex and numbers, i. e., solitary, sexually paired, and grouped. Solitary denotes a shrimp found alone in a perfectly flaw-

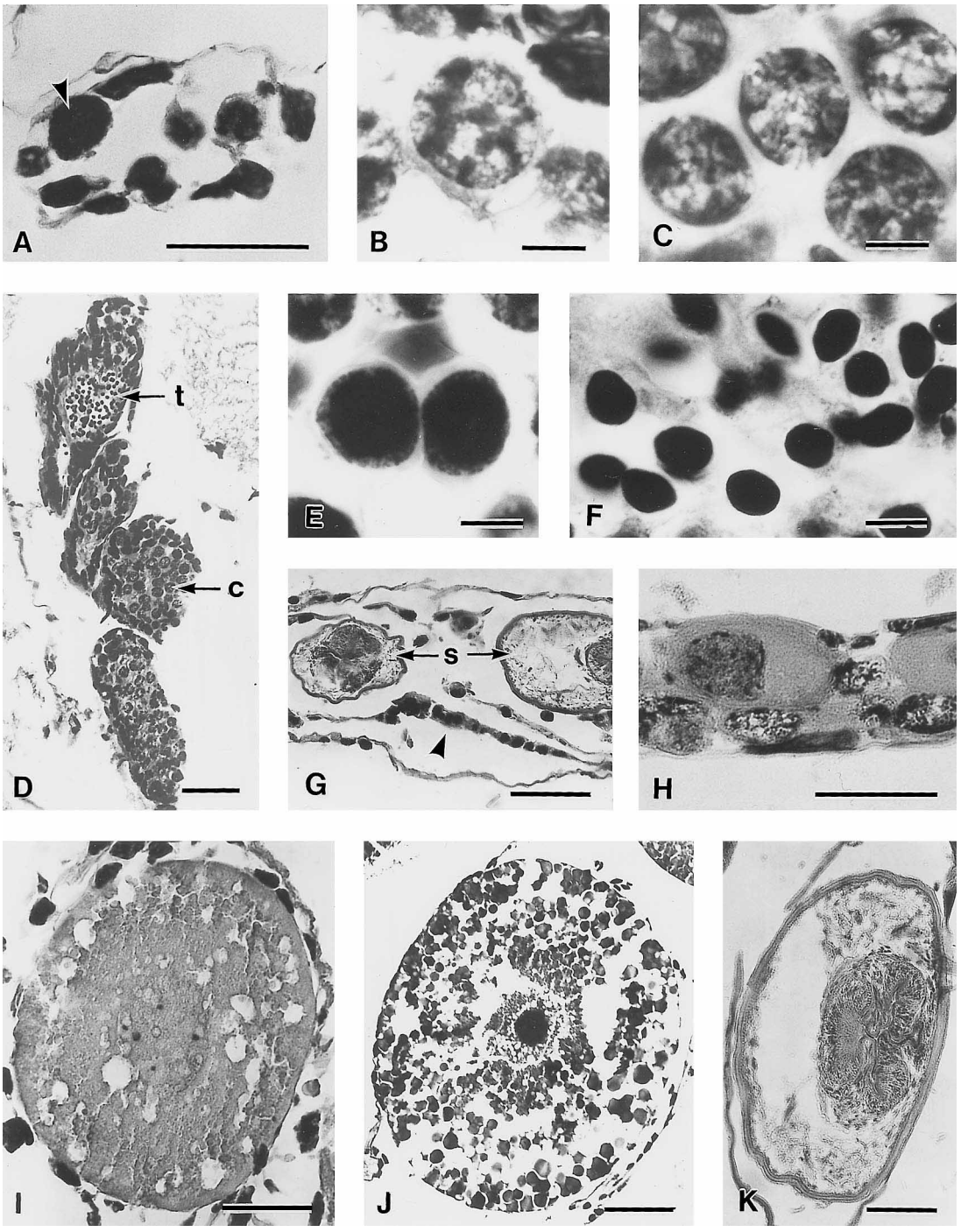

Fig. 1. Gonads of *Spongicola japonica* Kubo. A: Immature testis composed of epithelial cells and a few spermatogonia (arrowhead). B: Spermatogonia observed in the testis of early spermatogenesis stage. C: Primary spermatocytes. D: Bent testis at the late spermatogenesis stage mainly composed of spermatocytes (c) and spermatids (t). E: Secondary spermatocytes. F: Spermatids. G: Spermatophores (s) formed in the vas deferens. Note thick epithelia (arrowhead) lining the vas deferens. H: Young-stage oocytes. I: Pre-vitellogenic oocyte with small vacuoles in the cytoplasm. J: Small vitellogenic oocyte. K: Spermatophore observed in female genital tract. Scale bars: B, C, E and F=10 μm; A, H, I and K=50 μm; D, G and J=100 μm.

less host sponge. Sexually paired indicates a male above 5.2 mm CL and a female above 5.8 mm CL, which is the minimum size of a pair to be found in an ovigerous female (Saito, in press). The grouped type covers cases of multiple individuals except for those sexually paired. Specimens used in the gonadal, embryonic and captive studies are shown in Appendix 1, Tables 3 and 4, respectively. For observation of the growth-reproductive pattern, 8 sexual pairs of shrimp were kept separately in cubic cages with 10-cm sides, mesh size of 0.5 mm and suspended in a dimly lit tank holding 500 liters of aerated sea water with a filtration system using 1.2 m^3 of crushed coral and silica sand under the following conditions: 0–10 lux in illumination intensity, 12.0±1.0°C water temperature, pH 7.8–8.1 and 34.0–36.0

ppt in salinity. Minced fish was given as food every day using a fine-tipped pipette. Dissection and measurement of shrimp and eggs were conducted using a stereomicroscope, and drawings were made with the aid of an attached drawing tube after fixation in 5% buffered formalin. In particular, ovary and embryo photographs were taken just before fixation. For histological observation, the whole animal was fixed in Bouin's solution for at least 48 hr. After fixation, samples were dehydrated in a graded ethanol series, cleared with xylene, and embedded in paraffin. Sections were cut at 6 μm, and stained with Delafield's hematoxylin and eosin.

RESULTS

Testis

Testicular maturity was divided into the following 4 stages based on histological observations.

Stage I (immature): the gonadal anlage of the male is still small and composed of epithelial cells and a few spermatogonia (arrowhead) (Fig. 1A).

Stage II (early spermatogenesis): spermatogenesis begins in the lobules where spermatogonia (Fig. 1B) and primary spermatocytes (Fig. 1C) are located. Spent testis corresponds to this stage.

Stage III (late spermatogenesis): testis has complex bends (Fig. 1D). Various stages of germ cells including primary spermatocytes (c), secondary spermatocytes (Fig. 1E) and spermatids (t) (Fig. 1F) are observed throughout the testis (Fig. 1D).

Stage IV (mature): spermatids are released into the vas deferens, where epithelia (arrowhead) become thick and spermatophores (s) are formed (Fig. 1G).

Table 1 shows the maturity stages of testes in relation to CL of shrimp. All the males below the 2.5- mm CL class had stage I testes. Most shrimp above the 3.0- mm CL class started spermatogenesis, though stage I testis was recognized in a 4.5- mm CL male which was collected as a solitary (see Appendix 1).

Ovary

Ovarian maturity was divided into the following 5 stages based on the condition of oogenesis and the diameter of the most abundant ova in the ovary.

Stage I (immature): the most abundant oocytes in the ovary are at an early stage (–50 μm; Fig. 1H).

Stage II (pre-vitellogenic): oocytes (50–200 μm; Fig. 1I) with centrally located large nuclei and small vacuoles are found in the cytoplasm.

Stage III (early vitellogenesis): small vitellogenic oocytes (200–700 μm; Fig. 1J, 4A', B') with yolk globules are observed. Spent ovaries, which are flaccid and transparent (Fig. 4A'), correspond to this stage. They are largely empty and contain only a few remnant ova.

Stage IV (mid vitellogenesis): medium-size vitellogenic oocytes (700–1200 μm; Fig. 4C', D') with large vacuoles and yolk globules are observed in the cytoplasm.

Stage V (late vitellogenesis): large vitellogenic oocytes (1200 μm- ; Fig. 4E') are observed.

Table 1 shows the maturity stage of the ovary in relation to CL of shrimp. All females below the 3.5- mm CL class had stage I ovaries, and females in 3.5–5.5 mm CL range had stage II ovaries. Females in the 5.5–6.0 mm CL range had stage II or V ovaries. Females above the 6.0 mm CL class had stage III–V ovaries. Spermatophores were found in the genital tract of 4 of 10 ovigerous females having stage IV or V ovaries (Fig. 1K) among which the stages of embryos varied (Table 5).

Embryonic development

The eggs were globular in shape during the early stages, becoming gradually oval as their size increased. The yolk was cobalt blue in color in contrast to the translucent embryo. The diameter of *S. japonica* eggs increased from 1.78±0.16 mm (mean±SD) to 2.32±0.12 mm in the course of embryonic development, which was divided into 12 stages based on morphological characters, appendages and ratio of yolk area to total egg area in lateral view (Fig. 2, 3, 4; Table 2). All egg measurements indicate the long axis of mean±SD.

Stage I (Fig. 2A, 4A): Fully grown oocytes. Beginning of embryonic development. Yolk area about 100% in lateral view. The eggs are globular in shape with a diameter of 1.78±0.16 mm (n=27).

Stage II (Fig. 2B, B', 4B): Egg nauplius. Optic lobes distinct. Antennules, antennae and mandibular buds rudimentary.

Table 1. Components of gonadal maturity in each class of CL in *Spongicola japonica* Kubo

CL class (mm)		–2.0	–2.5	–3.0	–3.5	–4.0	–4.5	–5.0	–5.5	–6.0	–6.5	–7.0	–7.5	–8.0
Number of examined males		1	2	0	1	1	4	1	3	1	1	4		
Testicular stage	I	1	2				1							
	II						1					1		
	III				1		1							
	IV					1	1	1	3	1	1	3		
Number of examined females		1	2	1	2	1	2	0	1	4	2	5	8	7
Ovarian stage	I	1	2	1	2									
	II					1	2		1	3				
	III										2	1	2	1
	IV											3	4	2
	V									1		1	2	4

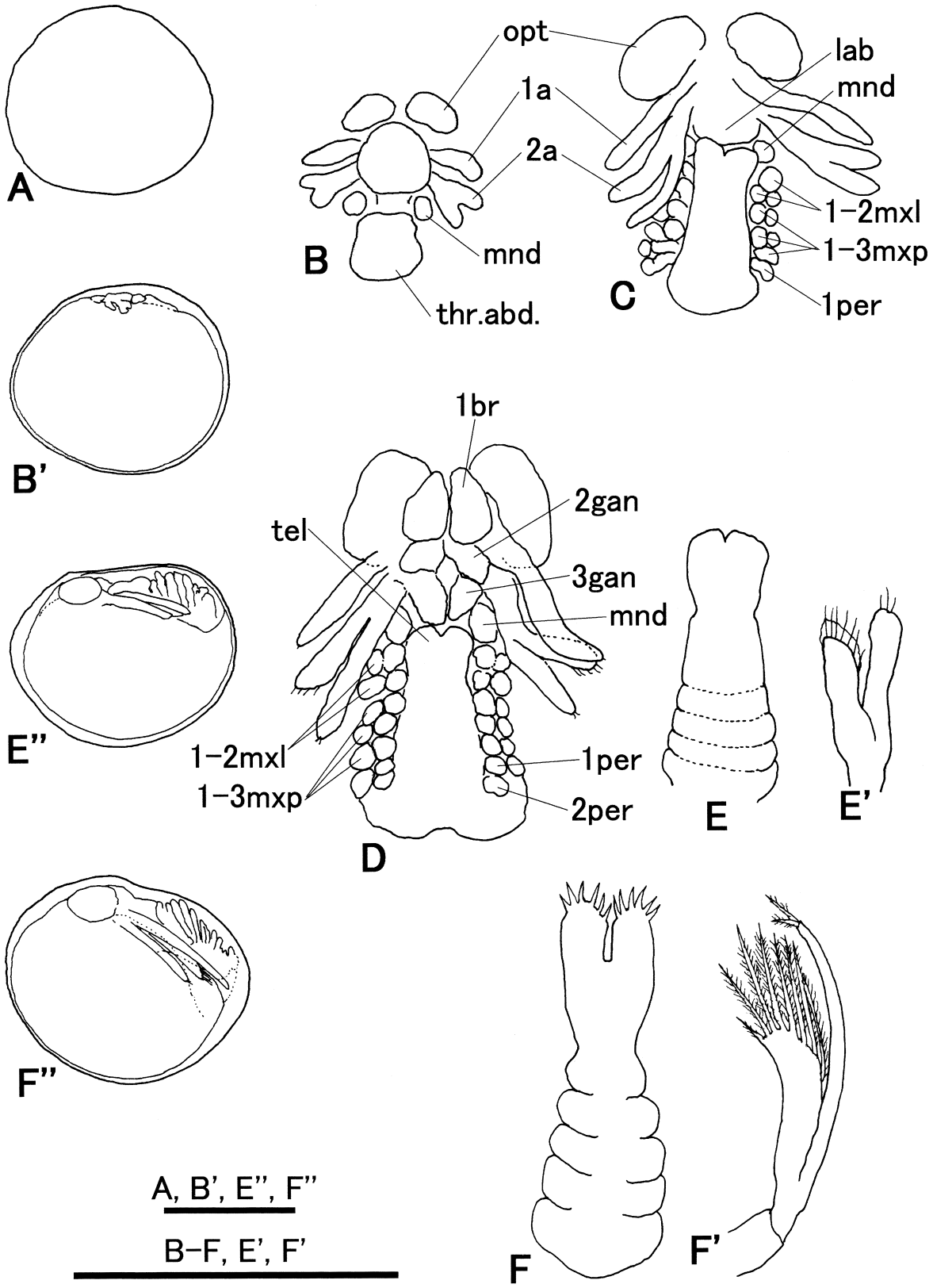

Fig. 2. Embryonic developmental stages I–VI in *Spongicola japonica* Kubo. A–F: stage I–VI; A, B', E" and F": stage I, II, V and VI egg in lateral view; B, C and D: embryo in ventral view; E, F: telson of stage V, VI embryo; E', F': antenna of stage V, VI embryo. lab: labrum; mnd: mandible; opt: optic lobe; tel: telson; thr. abd.: thoracic abdominal plate; 1–2a: antennule, antenna; 1 br: forebrain; 2–3gan: 2^{nd}–3^{rd} ganglia, 1–2 mxl: maxillule, maxilla; 1–3 mxp: 1^{st}–3^{rd} maxillipeds; 1–2 per: 1^{st}–2^{nd} pereopods. Scale bars = 1.0 mm.

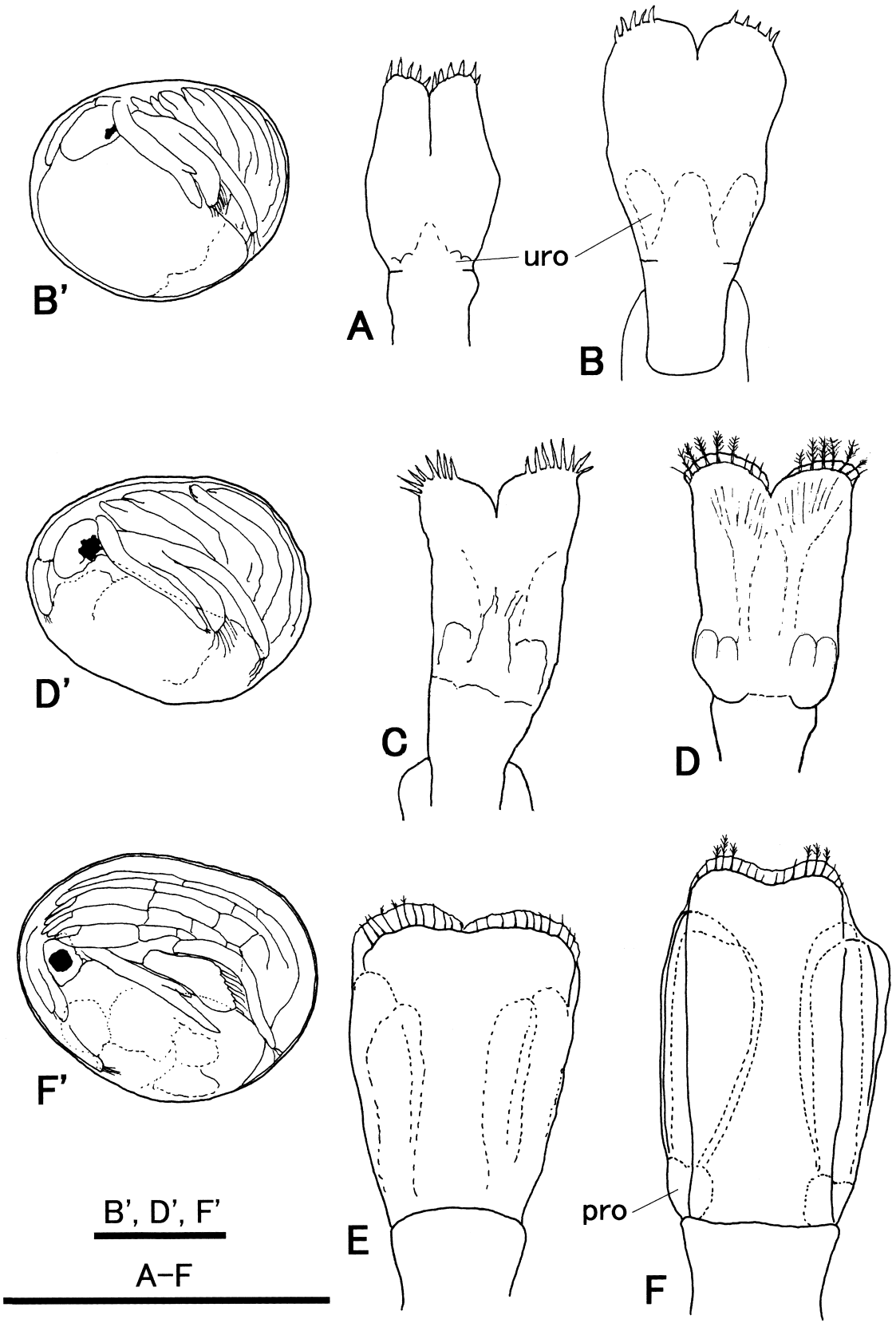

Fig. 3. Embryonic developmental stages VII–XII in *Spongicola japonica* Kubo. B', D', F': stage VIII, X and XII egg in lateral view; A–F: telson of stage VII-XII embryo. pro: uropodal protopod; uro: uropod. Scale bars = 1.0 mm.

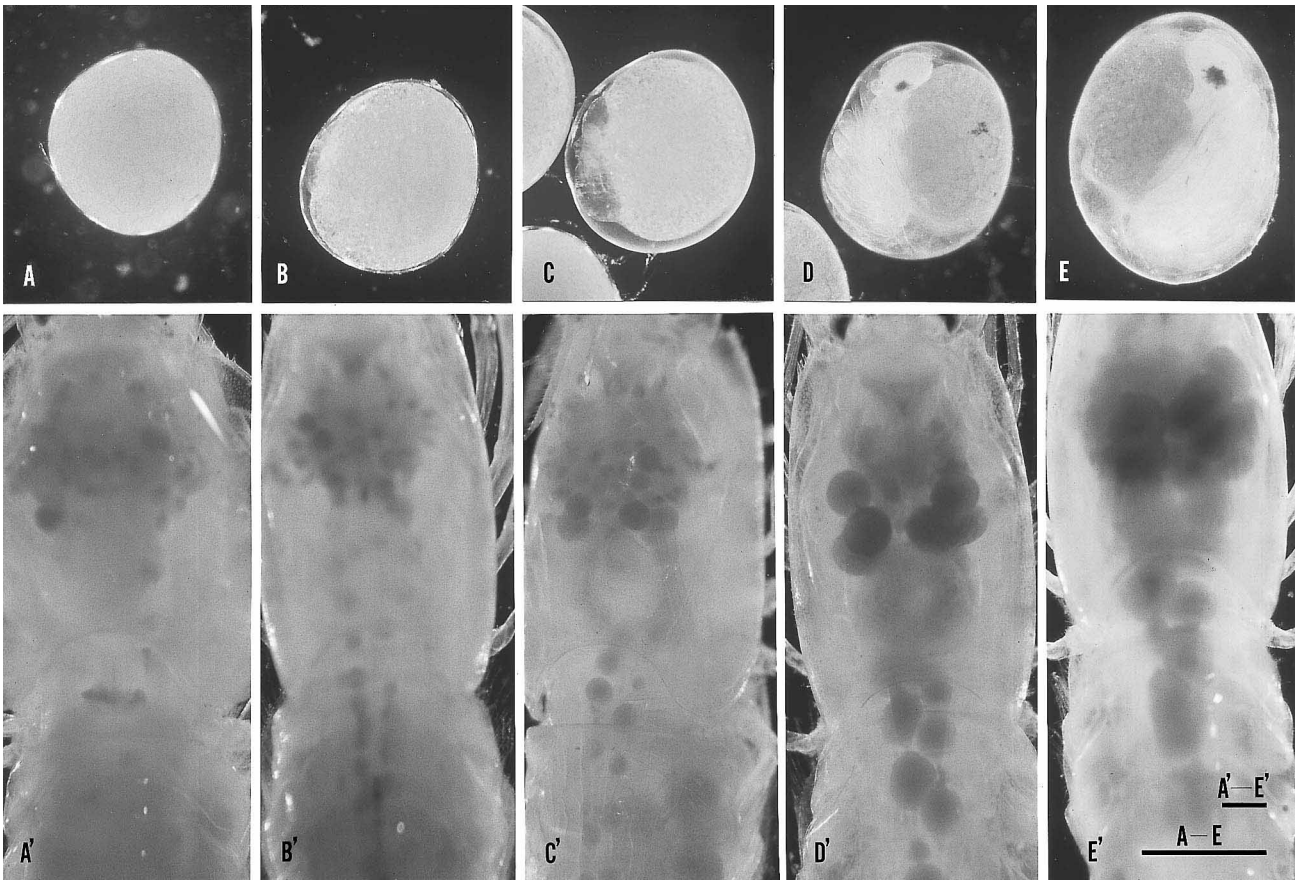

Fig. 4. Embryonic developmental stage and the next clutch of oocytes in ovary of female *Spongicola japonica* Kubo. A–E: stage I, II, IV, IX and XII embryo; A'–E': ovaries of female corresponding to each embryonic stage; A': stage III ovary; B': stage III ovary; C', D': stage IV ovary; E': stage V ovary. Scale bars=1.0 mm.

Rod-shaped antennules and bifurcated antennae bear no terminal process. Thoracic-abdominal plate visible. Embryo thin, and rate of yolk area 78% in lateral view. Egg diameter=1.69±0.12 mm (n=10).

Stage III (Fig. 2C): Embryo thicker than in previous stage. Telson slightly bifid. Maxillules, maxillae, maxillipeds 1–3 and pereopod 1 appeared. Yolk area about 70% in lateral view. Egg diameter=1.73±0.11 mm (n=21).

Stage IV (Fig. 2D, 4C): Maxillules, maxillae, maxillipeds 1-3 and pereopods 1–2 developed. Forebrain, ganglia 2–3 are observed. Terminal process on each lobe of antenna and antennules. Telson bilobed. Yolk area about 65% in lateral view. Egg diameter=1.85±0.08 mm (n=24).

Stage V (Fig. 2E, E', E''): Telsonal segmentation. Yolk area about 60% in lateral view. Egg diameter=1.86±0.14 mm (n=20).

Stage VI (Fig. 2F, F', F''): Telson deeply cleft with six spines on each lobe. Two terminal and 8 plumose setae are observed on exopod and endopod of antenna, respectively. Yolk area about 57% in lateral view. Egg diameter=1.98±0.11 mm (n=63).

Stage VII (Fig. 3A): Eye pigmented. Telsonal lobes united featuring 5-6 spines on each lobe. Uropodal buds rudimentary and slightly notched from 6th abdominal somite. Yolk area about 47% in lateral view. Egg diameter=2.03±0.15 mm (n=12).

Stage VIII (Fig. 3B, B'): Telson enlarged with 5–6 spines on each lobe. Uropodal buds more developed than at previous stage. Yolk area about 42% in lateral view. Egg diameter=1.86±0.11 mm (n=6).

Stage IX (Fig. 3C, 4D): Each telsonal lobe bears 8 spines. Heartbeat, yolk and limb pigment recognized. Yolk area about 35% in lateral view. Egg diameter=2.19±0.06 mm (n=20).

Stage X (Fig. 3D, D'): Each telsonal lobe bears 7–9 plumose setae. Bifid uropodal buds rudimentary. Yolk area about 30% in lateral view. Egg diameter=1.97±0.07 mm (n=45).

Stage XI (Fig. 3E): Eye stalked but not separated from carapace. Uropod developed to 3/4 of telson length. Distal shaft of telsonal setae, which are not covered with thin membrane, are plumose. Yolk area about 20% in lateral view. Egg diameter=2.21±0.13 mm (n=94).

Stage XII (Fig. 3F, F', 4E): Just before hatching. Eye stalked and separated from carapace. Uropodal protopod recognized. Yolk area about 17% in lateral view. Egg diameter=2.32±0.12 mm (n=12).

Table 2. Egg diameter and embryonic development of *Spongicola japonica* Kubo

Stage	Number of samples		Egg diameter	Main characteristics			
	Ovigerous females	Eggs	Long axis mean ±SD (mm)	Rate (%) of yolk area	Eye	Telson	Others
I	3	27	1.78±0.16	100	–	–	Initiation of embryonic development
II	3	10	1.69±0.12	78	Naupliar eye	–	Egg nauplius, antenna 1–2 and mandible rudimentary
III	4	21	1.73±0.11	70		Slightly bifid	
IV	2	24	1.85±0.08	65		Bilobed	Terminal process on antenna 1–2
V	2	20	1.86±0.14	60		Telsonal segmentation	
VI	6	63	1.98±0.11	57	Not pigmented	6 spines on each lobe, deep median cleft	8 plumose setae on antennal scale
VII	2	12	2.03±0.15	47	Pigmented	Lobes united, uropod rudimentary	Slight notch from 6th abdominal somite
VIII	2	6	1.86±0.11	42		Each lobe enlarged with 5–6 spines	Not heart beat
IX	2	20	2.19±0.06	35		8 spines on each lobe	Heart beat, limb and yolk chromatophore
X	4	45	1.97±0.07	30		7–9 plumose setae, bilobed uropod rudimentary	
XI	8	94	2.21±0.13	20	Stalked and unseparated from carapace	Uropod developed as 3/4 of telsonal length	
XII	4	12	2.32±0.12	17	Stalked and separated from carapace	Uropodal protopod recognized	Just before hatching

Table 3. Number of ovigerous females of *Spongicola japonica* Kubo categorized by embryonic developmental stages at each sampling day

Date	Females above 5.8 mm CL	Ovigerous females	Examined ovigerous females	Embrynic stage											
				I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
11-Jul-93	2	2	2		1					1					
12-Apr-94	1	1	1										1		
5-Aug-94	5	4	3	1		1							1		
15-Jun-96	4	4	4			1	1							1	1
25-Nov-96	8	7	6						1	1			1	1	2
15-Dec-96	9	9	7		1			1	2			1		1	1
12-Jun-97	12	12	8	2	1	2		1	1					1	
4-Dec-97	14	13	9					1			1			2	5
4-Dec-99	17	13	9	1	1		1		1	1	1		2		1
2-Jun-00	7	6	6				1		1	1		1		2	

Table 4. Records of reproductive process in captive ovigerous females of *Spongicola japonica* Kubo

Collection date	CL(mm)	Days after collection			
		Hatching	Molting	Laying eggs	Death
4-Dec-97	8.7	105	–	–	125
4-Dec-97	8.0	366	374	378	683
21-May-98	6.7	44	–	–	57
1-Dec-98	6.8	35	71	–	418
1-Dec-98	6.6	9	19	–	24
1-Dec-98	7.5	126	129	131	227
1-Dec-98	8.5	15	56	58	75
4-Dec-99	7.9	40	56	–	63

Table 5. Concept of development of gonads and embryo in pairs of *Spongicola japonica* Kubo

		Embryonic stage													
		–	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	–
Gonadal stage	II											▲			
	III	○	○	○	○										
	IV			▲	▲	○▲		○▲	○▲		○		▲	▲	
	V											○	○	○	○
Spermatophore						×		×					×		×

○: observed in female, ▲: observed in male, ×: observed in female genital tract

Reproductive seasonality and reproductive process

The number of ovigerous females categorized by embryonic developmental stage in each sampling day is given in Table 3. Most females above 5.8 mm CL were ovigerous, and the embryonic stages were synchronized within each egg mass, but varied among each female of the same sampling date. Reproductive seasonality was not recognized in *S. japonica*.

Table 4 gives records of the reproductive process in captive ovigerous females of *S. japonica.* Hatchings were seen in all 8 ovigerous females. Overall the time intervals between the start of the culture and hatching varied from 9 to 366 days. Most ovigerous females with fully developed embryos had fully ripe ovaries of stage V. Molting was observed from 3 to 41 days after hatching juveniles, and successive spawning 2 to 4 days after molting. No copulation was recognized. However, the females fell out the newly laid eggs from the brooding chamber within about a week, and their ovaries were not developed after spawning under laboratory conditions. Spent ovaries were found on the ovigerous females with newly spawned eggs. The developmental stages of the embryo and the maturity of the ovary of each ovigerous female were almost synchronized (Fig. 4, Table 5, Appendix 1).

DISCUSSION

Ovarian stages III–V were observed over the 5.5–6.0 mm CL range, which corresponded to the formative period of the brooding chamber and the minimum size of ovigerous females (Saito, in press). The present study demonstrated that the beginning of gonadal maturation was related to body growth in the female, while it was not always so in the male *S. japonica*. Solitary males of the 4.5 mm CL had the testes of maturity stages I–III. However, the grouped males of 3.0–4.5 mm CL, which were smaller than the minimum size of 5.2 mm CL for sexually paired males, had the testes of more developed stages III or IV. These small mature males were cohabiting with a sexually mature male and female. The induction of spermatogenesis may be associated with the presence of mature adults in the same host. In the Norway lobster *Nephrops norvegicus,* Farmer (1974) found fully developed spermatozoa in males that were smaller than those of normal mature size.

Farmer (1974) showed that spermatogenesis occurred throughout the year, and spermatophores were found in the vas deferens at all times in male *N. norvegicus.* In *S. japonica*, the testicular maturity of sexually paired males seems not always to be synchronous with the ovarian maturity of their paired females, but spermatophores were stored in the vas deferens of 8 of 9 sexually paired males. This fact indicates that paired males of *S. japonica* are capable of copulating with paired females at any time. The orders of the reproductive process of the coral banded shrimp *Stenopus hispidus*, a species related to *S. japonica,* and *N. norvegicus* were typically reported as: hatching larvae, followed by molting, copulation and spawning (Farmer, 1974; Zhang *et al.*, 1998). However, it remains unclear when they became able to copulate in the reproductive process.

Spermatophores were seen to be stored in the genital tract of 4 of 10 ovigerous females. Waddy and Aiken (1991) showed that a single insemination was enough to fertilize 2 successive clutches of eggs in the over 120 mm CL of the American lobster *Homarus americanus*. They also observed inter-molt insemination in 20% of the individuals of that size that stored an insufficient amount of sperm. In *S. japonica*, the presence of spermatophores in the female genital tract suggests that females may be capable of holding sperm from a single copulation over successive spawnings, or that hatching juveniles or molting may not influence copulation.

The developmental stages of the embryo and maturity of the ovaries of each ovigerous female were almost synchronous. This synchronous type of ovary containing mostly single-stage oocytes enabled a single clutch during a spawning season to be continuous. Although the number of pre-puberty instars was not identifiable, the puberty molt was obvious from the full development of the brooding chamber. Only a single brood can be carried in a mature instar like the pelagic mysid shrimp *Metamysidopsis elongata*, which carries up to 14 series of broods in successive instars (Clutter and Theilacker, 1971).

It is well known that large volumes of yolk are associated with longer durations of embryonic development (Rabalais and Gore, 1985). Herring (1974) studied embryonic development in the deep-sea carideans, *Acanthephyra purpurea* and *Systellaspis debilis*, that lay large lecithotropic eggs that hatch as post-larva (Gurney and Lebour, 1941). The estimated incubation periods at 12°C were 62 days in *A. purpurea* and 145 days in *S. debilis*. In both species, the nauplius eye pigment stage occurs midway into the estimated incubation period and the first chromatophore stage one-third of the way. The incu-

bation period of *S. japonica*, whose eggs contain much yolk and show direct larval development (Saito and Konishi, 1999), is not known precisely, but we can estimate from the captivity data that it took more than a year.

Orton (1920) predicted that deep-sea organisms would reproduce throughout the year, because the physical conditions at that depth had long been considered more static than that of shallow water. Rokop (1974, 1977) periodically monitored the reproductive condition of a variety of benthic invertebrates such as the brittle star *Ophiophthalmus normani*, the Scaphopoda, *Cadulus californicus,* and the paracarid crustaceans *Eurycope californiensis,* etc., and proved that year-round reproduction was common in deep-sea benthic animals. Since those studies, the reproductive seasonality of deep-sea decapod crustaceans has only been documented in few species. Wenner (1978) found year-round reproduction in the deep-sea polychelid lobsters *Stereomastis nana* and *S. sulpta*. Sadakata (2000) confirmed reproductive seasonality in the northern shrimp *Pandalus eous* from the Japan Sea. Reproductive seasonality is recognized in the golden crab *Chaceon fenneri* (as *Geryon fenneri*), but not in *C. maritae* (as *G. maritae*) (Melville-Smith, 1987; Hinsch, 1988). Ohtomi and Matsuoka (1998) observed reproductive seasonality in the Jack-knife shrimp *Haliporoides sibogae,* the target species of the trawlers, not far from our study station where the bottom water temperature is constant at 9–10°C. Ohtomi (1997) and Ohtomi *et al*. (1998) reported that reproduction was induced by photoperiod in the deep-water shrimp *Solenocera melantho* and *Plesionika semilaevis* from Kagoshima Bay, where the bottom water temperature tended to be constant throughout the year at 15.8±0.5°C (Noro *et al*., 1991). In *S. japonica*, however, no reproductive seasonality is noted. Reproduction in this species may be controlled not by any environmental factors, but by other factors such as body size.

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Appendix 1. Reproductive parameters of each specimen of *Spongicola japonica* Kubo used in the gonadal study

Shrimp ID	Sampling date	CL (mm)	Host sponge ID	Composition pattern	ID of partner	Embryonic stage	Gonadal stage	Gonadal stage of partner	Spermatophore
MALE									
611	17–Jun–96	1.9	632	S			I		
853	15–Dec–96	2.1	827	G			I		
851	15–Dec–96	2.2	827	G			I		
621	17–Jun–96	3.1	647	G			III		
618	17–Jun–96	3.8	647	G			IV		
620	17–Jun–96	4.1	647	G			IV		
815	15–Dec–96	4.5	815	S			I		
1006	4–Dec–97	4.5	1004	S			II		
1039	4–Dec–97	4.5	1020	S			III		
1133	21–May–98	4.8	1118	G			IV		
619	17–Jun–96	5.2	647	G	616		IV		
709	25–Nov–96	5.5	703	P	710		IV		
613	17–Jun–96	5.5	644	P	614		IV		
1027	4–Dec–97	5.8	1011	S			IV		
1049	4–Dec–97	6.1	1022	P	1050		IV		
104	11–Jul–93	6.7	102	P	103		IV		
847	15–Dec–96	7.0	824	P	846		IV		
202	12–Apr–94	7.0	201	P	201		II		
102	11–Jul–93	7.0	101	P	101		IV		
FEMALE									
852	15–Dec–96	2.0	827	G		–	I		
854	15–Dec–96	2.2	827	G		–	I		
850	15–Dec–96	2.4	827	G		–	I		
1048	4–Dec–97	2.7	?	?		–	I		
617	17–Jun–96	3.1	647	G		–	I		
607	17–Jun–96	3.3	624	S		–	I		
612	17–Jun–96	3.9	643	S		–	II		
855	15–Dec–96	4.1	827	G		–	II		
849	15–Dec–96	4.4	827	G		–	II		
608	17–Jun–96	4.8	628	S		–			
811	15–Dec–96	5.1	814	S		–	II		
928	12–Jun–97	5.6	918	?		–	II		
1204	1–Dec–98	5.6	1207	S		–	II		
507	9–Dec–95	5.7	505	?		–	II		
1303	4–Jun–99	5.8	1302	G		–	V		+
1304	4–Jun–99	6.1	?	?		–	III		
101	11–Jun–93	7.6	101	P	102	II	III	IV	
614	17–Jun–96	6.5	644	P	613	III	III	IV	
616	17–Jun–97	6.9	647	G	619	IV	IV	IV	+
710	25–Nov–96	6.9	703	P	709	VI	IV	III	+
103	11–Jun–93	7.2	102	P	104	VII	IV	IV	
201	12–Apr–94	7.3	201	P	202	X	V	II	
1050	4–Dec–97	7.3	1022	P	1049	XI	V	IV	+
846	15–Dec–96	7.9	824	P	847	XII	V	IV	
*FEMALE									
1471	4–Dec–99	7.4	1429	P		I	III		
1419	4–Dec–99	7.1	1409	P		II	III		
1501	2–Jun–00	7.3	1501	P		IV	IV		
1467	4–Dec–99	6.8	1426	P		IV	IV		
1524	2–Jun–00	7.7	?	?		VI	IV		
1448	4–Dec–99	7.3	?	?		VI	IV		
1417	4–Dec–99	7.5	1407	P		VII	IV		
1455	4–Dec–99	6.8	?	?		VIII	III		
1503	2–Jun–00	7.6	1502	P		IX	IV		
1436	4–Dec–99	7.9	?	?		X	V		
1470	4–Dec–99	6.7	1428	P		X	V		
1507	2–Jun–00	7.6	1504	P		XI	V		
1464	4–Dec–99	7.9	1425	P		XII	V		

S: solitary, P: sexually paired, G: grouped, –: ova not observed, +: spermatophore observed in the female genital tract, ?: host sponges were broken and composition pattern couldn't be decided, *: ovaries were staged through the carapace under stereoscopic microscope. Broken line indicate the minimum size of sexually paired.