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Taxonomy and Life History of the Scale Worm *Hesperonoe hwanghaiensis* (Polychaeta: Polynoidae), newly Recorded in Japan, with Special Reference to Commensalism to a Burrowing Shrimp, *Upogebia major*

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ABSTRACT—A unique scale worm *Hesperonoe hwanghaiensis* Uschakov and Wu, 1959 (Polychaeta: Polynoidae) was collected from tidal flats in Japan and is described here taxonomically as the second record of this species since its original description from Chinese specimens. Some morphological features of our specimens differed slightly from the original description of this species. Marked differences in growth pattern, morphology of elytra and microhabitat were demonstrated between juveniles (1.8 mm or less in body width) and adults (1.9 mm or more).

We estimated the outline of the life history of the scale worm by sampling it in various seasons. The scale worm was commensal with the burrowing shrimp *Upogebia major*. Juveniles of the scale worm were commonly attached to the ventral or lateral surface of the thorax or abdomen of the host throughout May to September in Isahaya Bay in the Ariake Sea, Kyushu. In July 1998, 89% of the host shrimps were infested by the scale worm. Several juveniles (maximum: 7) of the scale worm often aggregated on a host body, with no adults found on the hosts. The adults were collected from sediment samples. These results suggest that the juveniles mainly live on the surface of the host body and that they later detach themselves from the host body and live freely on the inner surface of the burrow of the host.

INTRODUCTION

The burrowing shrimps *Upogebia* spp. (Crustacea: Decapoda: Upogebiidae) occur commonly in some Japanese muddy tidal flats (Sakai, 1968; Mukai and Koike, 1984; Sakai and Mukai, 1991; Sakai and Takeda, 1995; Kato and Itani, 1995). An adult of *U. major* (de Haan, 1841) can make a Y-shaped burrow with a depth of more than 50 cm (Kato and Itani, 1995), in some cases more than 2 m (Hamano, 1990; Kenji Kojima, personal communication). By beating its pleopods within a burrow, an *Upogebia* shrimp creates water currents that assist its filter-feeding (Mukai and Koike, 1984; Kato and Itani, 1995).

Various commensal organisms including an isopod, a shrimp, pinnotherid crabs, a bivalve and a polychaete have been found from the burrows of the genus *Upogebia* in California, North America (MacGinitie, 1935). In Japan, two bivalve species, *Peregrinamor ohshimai* Shoji, 1938 and *P. gastrochaenans* Kato and Itani, 2000 are known as commensal organisms in association with the larger *Upogebia* species, i.e., *U. major*, *U. natutensis* Sakai, 1986, *U. yokoyai* Makarov, 1938 and *U. issaeffi* (Balss, 1913), and the smaller *Upogebia* species, i.e., *U. carinicauda* (Stimpson, 1860), respectively (Shoji, 1938; Sakai, 1968; Sakai *et al.*, 1995; Kato

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and Itani, 1995, 2000). However, no polychaete was known to be commensal with *Upogebia* spp. in Japan.

Recently we collected many specimens of a scale worm belonging to the genus *Hesperonoe* Chamberlin, 1919, which was new to Japanese fauna, from the burrows of *U. major* in tidal flats in Japan, and we tentatively reported this species as *Hesperonoe* sp. with its new Japanese name, Anajako-urokomushi (Sato, 2000). To date, five species of the genus *Hesperonoe* have been described worldwide (Hartman, 1961; Uschakov and Wu, 1965; Averincev, 1990). In the present study, we examine the morphology of the Japanese *Hesperonoe* specimens, identified as *H. hwanghaiensis* Uschakov and Wu, 1959. We also estimated the outline of the life history of this species in relation to the host species, *U. major*, by sampling it in various seasons.

MATERIALS AND METHODS

Collection of specimens

At tidal flats in Isahaya Bay in the Ariake Sea, western Kyushu, Japan (Figs. 1, 2), traditional fishing for the burrowing shrimp *Upogebia major* has been maintained by local people during April to September every year (Sato, 2000). In ebb tides, they insert a writing brush into a burrow of the shrimp, and after a while, pull slowly the writing brush up near to an opening of the burrow. Then, a shrimp which comes up to push out the writing brush is caught by hand with a small spatula. By this method, many intact shrimps can be caught with the least disturbance to their habitat. The specimens of the scale worm were collected from the surface of the body of the shrimp specimens just after they were caught by local fisherwomen during the April to September fishing season in 1995 to 1998. The shrimp specimens caught here were 25–38 mm in carapace length including the rostrum (Table 1).

Additional specimens were collected from sediment samples in tidal flats of four localities in the Seto Inland Sea and one location in Tokyo Bay (Fig. 1), where *U. major* was common. At the study sites

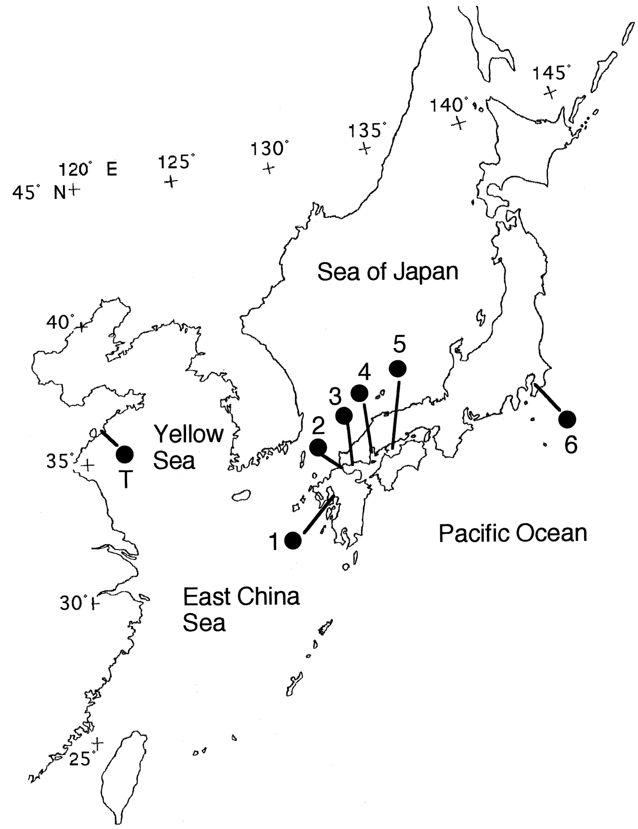

Fig. 1. Location of the type locality of *Hesperonoe hwanghaiensis* (T) and collection sites of this species in Japan in the present study (1-6). 1: Isahaya Bay in the Ariake Sea (see Fig. 2 in detail), 2: Sone-higata, Kitakyushu-shi, 3: Yamaguchi Bay, Yamaguchi-shi, 4: Miyajima Island, off Hiroshima-shi, 5: Iwashijima Island, off Onomichi-shi, 6: mouth of the Obitsugawa River in Tokyo Bay.

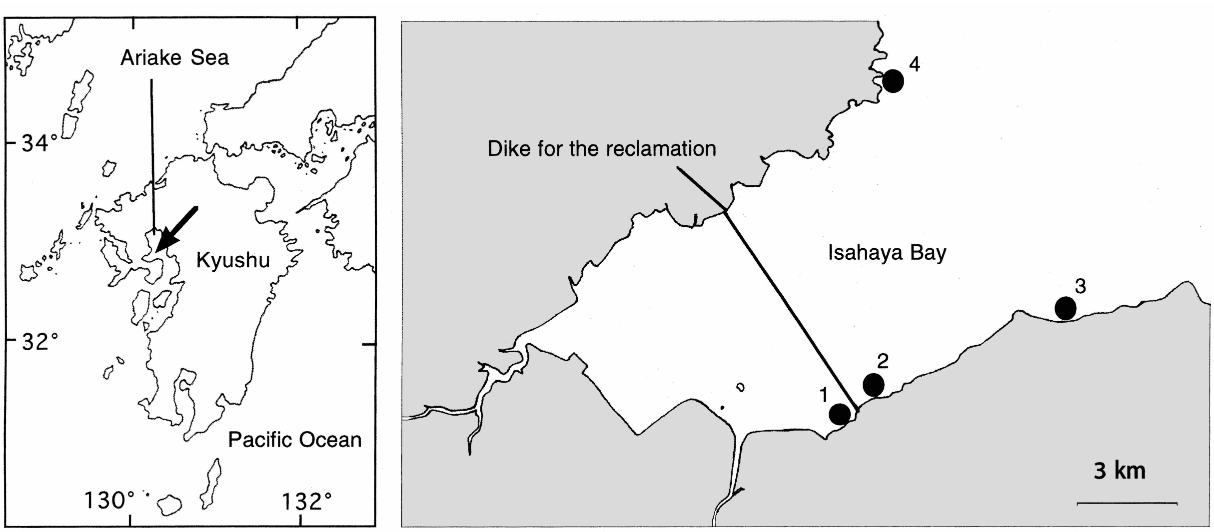

Fig. 2. Collection sites of *Hesperonoe hwanghaiensis* in Isahaya Bay in the Ariake Sea, Kyushu (Nagasaki Prefecture). 1: Around the mouth of the Yamadagawa River, Azuma-cho, 2: Motomura, Azuma-cho and Kobe, Mizuho-cho, 3: Kojiro-Nagahama, Kunimi-cho, 4: Isaki, Konagai-cho. The population around the mouth of the Yamadagawa River was lost upon completion of the dike that cut off the inner part of Isahaya Bay in April 1997.

Table 1. Prevalences of infectations by the commensal bivalve *Peregrinamor ohshimai* and the commensal scale worm *Hesperonoe hwanghaiensis* on the surface of the body of the burrowing shrimp *Upogebia major* in Isahaya Bay in the Ariake Sea

Date	Total no. of *Upogebia* examined	Carapace length of *Upogebi* (mm)	No. of *Upogebia* with *Peregrinamor* (% of total)	No. of *Upogebia* with *Hesperonoe* (% of total)	No. of *Hesperonoe* collected from all *Upogebia* (Average no. per an *Upogebia*)
28 May 1997	6	30–36	0 (0%)	no data	4 (0.7)
24 July 1998	27 *	25–38	2 (7%)	24 (88.9%)	60 (2.2)
20 Sep. 1998	27 *	27–35	2 (7%)	14 (51.9%)	19 (0.7)

*) All of them were examined individually.

we carefully dug the sediment with spades to about 40 cm deep and checked for the presence or absence of the scale worm on the *Upogebia* body or burrow wall.

A total of 242 specimens of the scale worm were examined. Specimens were fixed in 10% formalin or 80% ethanol and transferred to 80% ethanol. For the fixed specimens, body length (BL) and body width at midlength (without parapodia and chaetae) (BW) were measured under a stereomicroscope. We obtained a small amount of the body cavity contents of the larger specimens (more than 1.5 mm in BW) of the scale worm on a glass slide by injuring their bodies with a forceps, and examined the contents under a microscope in order to determine the presence or absence of oocytes or spermatozoa. Because the minimum size of specimens in which gametes were found was 1.9 mm in BW, specimens of 1.9 mm or more in BW were regarded as adults, while those of 1.8 mm or less were regarded as juveniles.

Specimens are deposited in the National Science Museum, Tokyo (NSMT-Pol. 107025), the Smithsonian Institution, Washington, D. C. (USNM 1000048, 1000049), Kagoshima University, and the Sabiura Marine Park Research Station.

Scanning electron microscopy

Specimens preserved in 80% ethanol were dehydrated through an ethanol series and then air-dried. They were coated with palladium and platinum and then examined with a scanning electron microscope (Hitachi S-800).

RESULTS

1. Taxonomy

Family Polynoidae

Subfamily Harmothoinae

Genus *Hesperonoe* Chamberlin, 1919

Hesperonoe hwanghaiensis Uschakov and Wu, 1959

Hesperonoe hwanghaiensis Uschakov and Wu, 1959: 35–36, Plate IX, A–H.

Hesperonoe hwanghaiensis: Uschakov and Wu, 1965: 170–172, figs. 30–32 (trans. 1979: 30–32, fig. 10).

Hesperonoe hwanghaiensis: Wu *et al*., 1997: 196–197, fig. 125.

Hesperonoe sp.: Sato, 2000: 192–195, fig. 8-6d.

Material examined. Specimens attached to the body surface of *Upogebia major* in tidal flats in Isahaya Bay (Nagasaki Prefecture) (Fig. 2): Around the mouth of the Yamadagawa River, Azuma-cho, 24 April 1995, coll. H. Yamashita, 10 specimens (BL: 5–15 mm, BW: 0.8–1.6 mm). Motomura, Azuma-cho, 14 June 1997, coll. M. Sato, 59 specimens (BL: 5–16 mm, BW: 0.6–1.8 mm). Kobe, Mizuho-cho, 28 May 1997, coll. T. Sakai, 4 specimens (BW: 0.8–1.3 mm); 24 July 1998, coll. M. Sato, 88 specimens (BL: 4–10.5 mm, BW: 0.6–1.3 mm, USNM 1000049); 20 September 1998, coll. M. Sato, 32 specimens (BW: 0.65–1.25 mm). Kojiro-Nagahama, Kunimi-cho, 23 July 1994, coll. H. Yamashita, 6 specimens (BL: 7–10 mm). Isaki, Konagai-cho, 12 August 1995, coll. H. Yamashita, 1 specimen (BW: 1.7 mm).

Specimens not attached to *U. major*: A tidal flat in the mouth of the Obitsugawa River, Kisarazu, Chiba Prefecture, 11 June 1996, coll. G. Itani, 2 specimens (BL: 15–24 mm, BW: 1.8–3.2 mm). A tidal flat in Iwashijima Island, Hiroshima Prefecture, 26 May 1998, coll. G. Itani, 1 specimen (BW: 2.8 mm). A tidal flat near the botanical field station of Hiroshima University on Miyajima Island, Hiroshima Prefecture, 23 November 1998, coll. K. Kinoshita, 1 specimen (BL: 23 mm, BW: 2.5 mm). A tidal flat in Yamaguchi Bay, Yamaguchi Prefecture, 15–16 November 1997, coll. G. Itani, 18 specimens (BL: 17–30 mm, BW: 1.7–3.7 mm, NSMT-Pol. 107025); 23 June 1998, coll. G. Itani, 4 specimens (BW: 0.7–1.4 mm); 4 November 1998, coll. G. Itani, 3 specimens (BW: 1.7–1.9 mm); 16 May 1999, coll. G. Itani, 4 specimens (BL: 7–32 mm, BW: 0.8–3.5 mm, USNM 1000048). A tidal flat (Sone-higata), Kitakyushu-shi, Fukuoka Prefecture, 10 December 1996, coll. M. Harato, 1 specimen (BL: 25.5 mm, BW: 3.0 mm); 17 to 18 April 1999, coll. G. Itani, 8 specimens (BW: 0.9–3.1 mm).

Description. Body flattened, bright red color in life (Figs. 3, 4), and pale in preserved specimens in ethanol. Body length to 32 mm for 41 segments.

Bilobed prostomium about as long as it is wide, produced anteriorly into cephalic peaks (Figs. 5a, b). Two pairs of eyes present; anterior pair located near the widest point of the prostomium; posterior pair smaller, closer together. Ceratophore of median antenna large, extending to cephalic peaks; style of the median antenna long, about three times prostomium length. Lateral antennae short, about one-fifth as long as median antenna, inserted beneath cephalic peaks. Both median and lateral antennae tapering to filiform tips, with scattered papillae. Palps 2–2.5 times prostomium length, tapering to filiform tips, with minute papillae.

Basal lobes of tentacular cirri, with a small digitiform process containing an aciculum at the antero-distal position, and with several notosetae behind the process. Tentacular cirri tapering, with relatively large papillae; dorsal pair longer than ventral pair, beyond end of palps.

Pharynx extended, with 9 dorsal and 9 ventral terminal papillae, two pairs of jaws visible in the center (Fig. 5c).

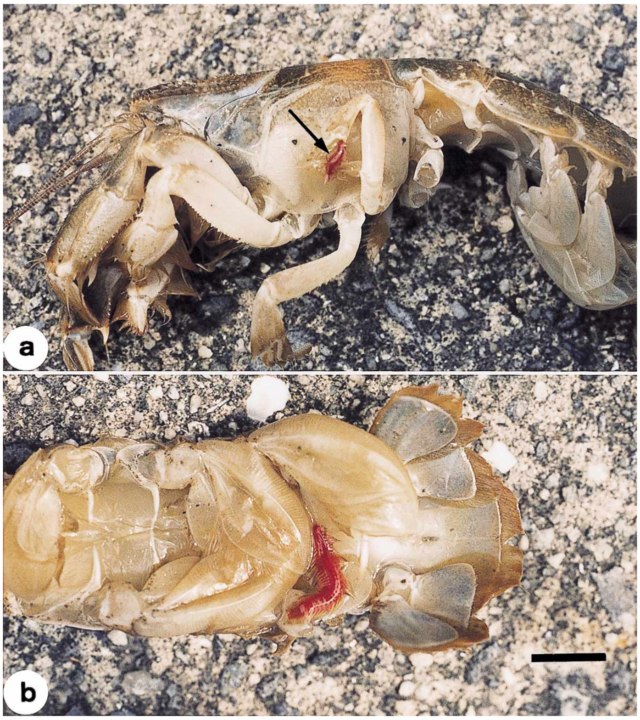

Fig. 3. Living juveniles of *Hesperonoe hwanghaiensis* attached to the lateral surface of the thorax (the arrow in a) and to the ventral surface of the abdomen (b) of the burrowing shrimp *Upogebia major* just after collection in Motomura, Azuma-cho in Isahaya Bay on 14 June 1997. Scale 1 cm.

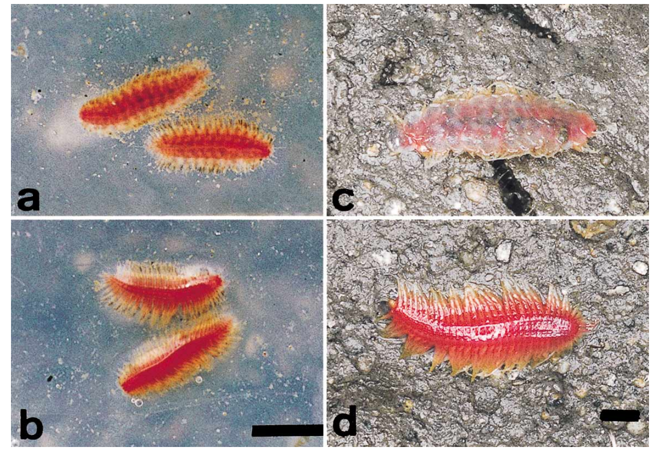

Fig. 4. Living specimens of *Hesperonoe hwanghaiensis*. a: Dorsal view of juveniles collected from Kobe, Mizuho-cho, in Isahaya Bay on 20 September 1998. b: Ventral view of the same individuals as in a. Scale 5 mm for a and b. c: Dorsal view of an adult collected from Sone-higata in the Seto Inland Sea on 10 December 1996. d: Ventral view of the same individual as in c. Scale 5 mm for c and d.

Elytra, 15 pairs in adults, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29 and 32, covering the dorsum completely; each elytron subquadrate, thin and semitransparent, with pigmentation over most of the posterior half (anterior half is covered with the foregoing elytron); marginal fringe of

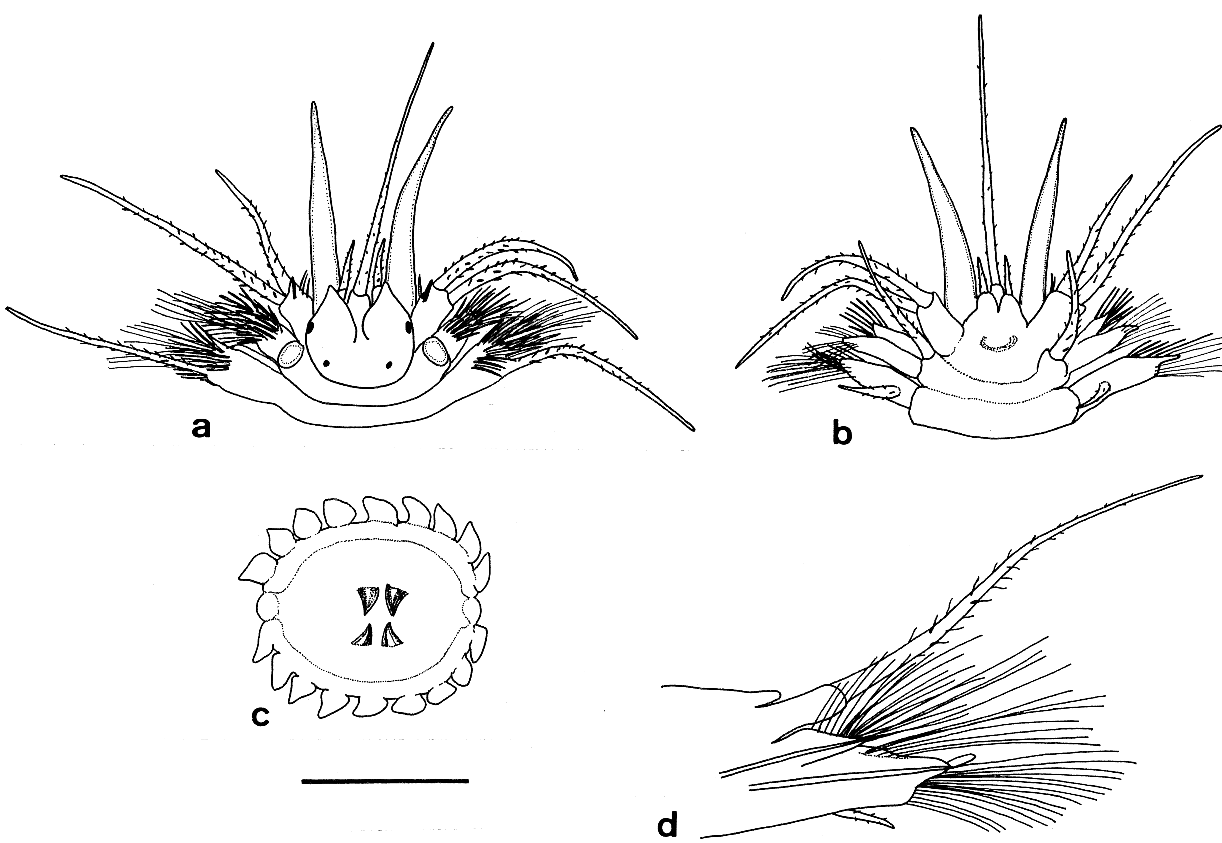

Fig. 5. *Hesperonoe hwanghaiensis*, specimens collected from Motomura, Azuma-cho, in Isahaya Bay on 14 June 1997. a: Anterior end, dorsal view. b: Ventral view. b: Anterior end, ventral view. c: Extended pharynx, anterior view. d: Median cirrigerous parapodium, anterior view. Scale 1 mm.

piliform papillae present on posterior and outer-lateral edges; numerous small conical microtubercles present over most of the upper surface except for a circular area anterior to an elytrophoral scar (Figs. 6, 7). A row of several conical macrotubercles present consistently along the posterior edge of the upper surface of most elytra in the larger adults (3.0 mm or more in BW) (Fig. 7). The macrotubercles rare in adults with BW of 1.9 to 2.7 mm, and not found in juveniles (1.8 mm or less in BW).

Parapodia biramous (Fig. 5d). Notopodia small, tapering to a digitate lobe with an emergent aciculum. Neuropodia larger, with a small digitate lobe above a protruding aciculum.

Dorsal cirri extending beyond setae, with a long cirrophore, and a style with scattered large papillae. Dorsal tubercles well developed at the base of dorsal cirri. Ventral cirri short, tapering to filiform tip, with occasional small papillae. Cirrophores of ventral buccal cirri inserted at base of segment 2; styles long, tapering, similar to ventral tentacular cirri, with scattered papillae.

Two kinds of notosetae present (Figs. 8, 9); superior and median notosetae relatively thick, tapering to blunt tip; inferior notosetae thinner, longer, capillary; all notosetae serrated markedly. Two kinds of neurosetae present; upper neurosetae

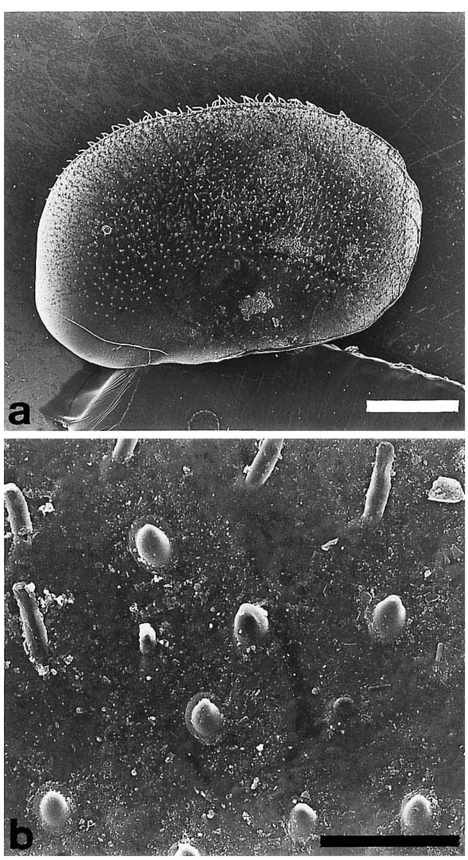

Fig. 6. Scanning electron micrographs of the outer surface of an elytron in a juvenile of *Hesperonoe hwanghaiensis* collected from the mouth of the Yamadagawa River in Isahaya Bay on 24 April 1995. Many microtubercles and marginal cirri are visible. Scale 0.5 mm for a, 50 μm for b.

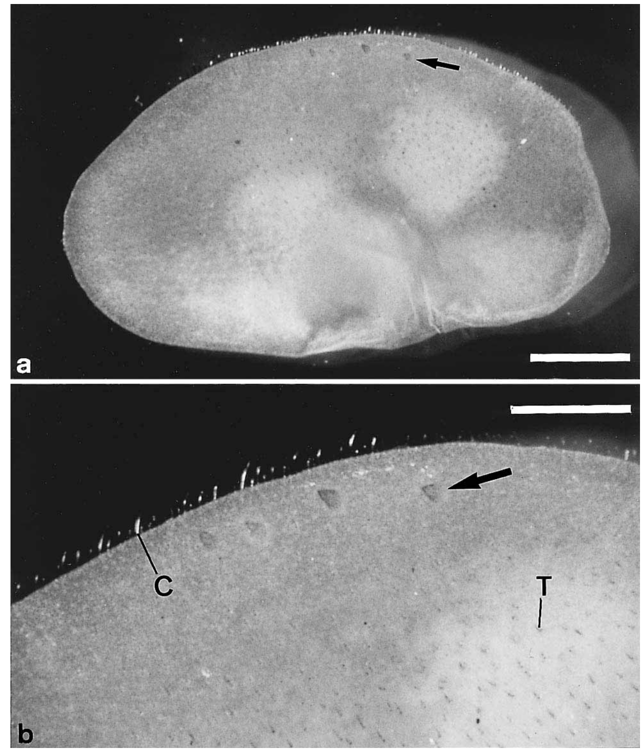

Fig. 7. Stereoscopic micrographs of the outer surface of an elytron in an adult of *Hesperonoe hwanghaiensis* collected from Yamaguchi Bay in the Seto Inland Sea on 16 November 1997. A row of 4 conical macrotubercles (arrows) is present along the posterior edge. T: microtubercles. C: marginal cirri. Scale 1 mm for a, 0.5 mm for b.

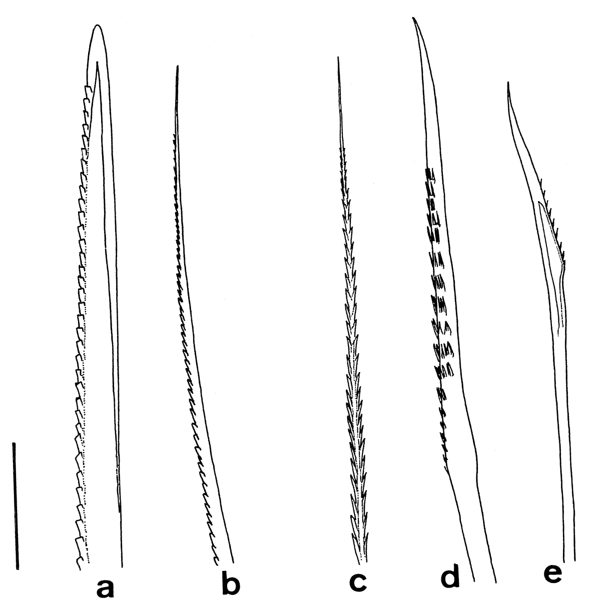

Fig. 8. Distal portion of setae of *Hesperonoe hwanghaiensis* collected from Motomura, Azuma-cho, in Isahaya Bay on 14 June 1997. a: Superior notoseta. b: Inferior notoseta. c: Superior neuroseta. d: Median neuroseta. e: Inferior neuroseta. Scale 0.1 mm.

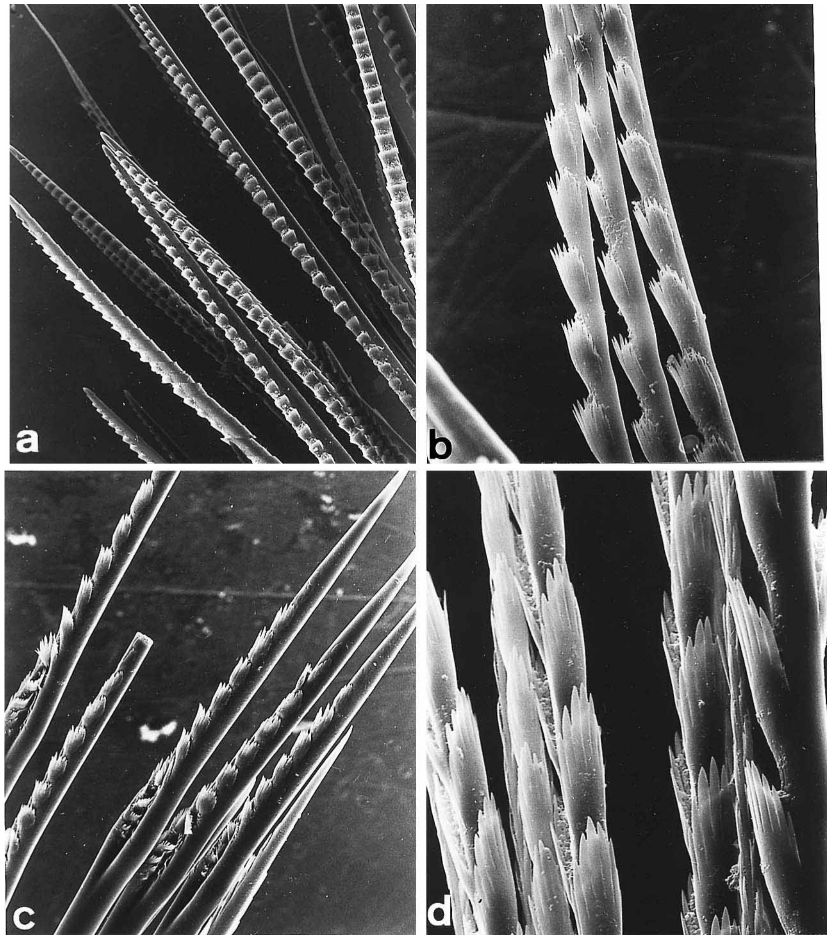

Fig. 9. Scanning electron micrographs of setae in *Hesperonoe hwanghaiensis* collected from the mouth of the Yamadagawa River in Isahaya Bay on 24 April 1995. a: Superior notosetae. × 180. b: Inferior notosetae. × 1200. c: Inferior neurosetae. × 360. d: Superior neurosetae. × 1500.

slender, with long spinous region tapering to fine tip; neurosetae in median and lower portions of fascile thicker, with expanded subdistal shorter spinous region, and smooth, sharp, slightly hooked tip.

Geographical distribution. Along the Chinese coast in the Yellow Sea, Japan (Fig. 1).

Remarks. Our specimens were identified as *Hesperonoe hwanghaiensis* because of the presence of not only microtubercles over most of the surface of the elytra but also a row of several conical macrotubercles on the posterior surface of the elytra, which is a unique characteristic of this species (Uschakov and Wu, 1959, 1965). The North American species *H. complanata* is most similar to this species in such characteristics as the body color in life and the presence of microtubercles over most of the surface of the elytra, but different from it in the absence of macrotubercles on the elytra in *H. complanata* (Table 2). In the present study, however, we demonstrated that the macrotubercles in *H. hwanghaiensis* appear only in larger (i.e., adult) individuals (1.9 mm or more in BW). Therefore, it seems to be rather difficult to distinguish *H. hwanghaiensis* from *H. complanata* in juvenile specimens.

There has been no record of *H. hwanghaiensis* since the original description (Uschakov and Wu, 1959) from specimens collected in Qingdao, China. According to Uschakov and Wu (1959, 1965), all prostomial appendages and dorsal cirri are smooth, the shape of macrotubercles is tear drop-like and notosetae are faintly serrated in Chinese specimens of *H. hwanghaiensis*. In our speciments, however, the prostomial appendages and dorsal cirri are not smooth but have papillae, the macrotubercles are conical and the notosetae are markedly serrated. In the present study, these differences were regarded as a geographic variation within *H. hwanghaiensis*.

2. Ecology and life history of the scale worm *Hesperonoe hwanghaiensis*

Growth pattern

We measured the body length and width and counted the number of segments in all undamaged specimens of the scale worm (Fig. 10). The body length (BL) was well correlated with the body width (BW) according to the following regression formula: BL=9.1 BW-1.2 (r^2=0.96, n=71).

Segment number (SN) was correlated with BW according to the following regression formula with a high gradient in juveniles (1.8 mm or less in BW): SN=9.8 BW+20.9 (r^2=0.73, n=53), and a low gradient in adults (1.9 mm or more in BW): SN=1.6 BW+34.4 (r^2=0.51, n=17).

Table 2. Comparison of five species of *Hesperonoe* in the Pacific regious.

species	*H. adventor*	*H. laevis*	*H. complanata*	*H.* sp.	*H. hwanghaiensis*
Distribution	west coast of North America	west coast of North America	west coast of North America	west coast of North America	east Asia
Host	*Urechis caupo* (Echiuroid)	*Listriolobus pelodes* (Echiuroid)	*Callianassa californiensis** (Decapod)	*Upogebia pugettensis* (Decapod)	*Upogebia major* (Decapod)
Colour of body in life	gray-green (as cross bands)	pale	yellowish orange or salmon red	?	pink or red
Elytra	smooth, except for some tubercles along edge	smooth, except for microtubercles in anterior part	microtubercles over most of surface	?	microtubercles over most of surface, macrotubercles along posterior edge in adults
Marginal cirri of elytra	absent	occasionally present	present or absent	?	present
Papillae on tentacular cirri and dorsal cirri	present	present	present	?	present (Japan) absent (China)
Serration on thicker notosetae	short fine spines	fine striation	minutely serrated	?	marked (Japan) faint (China)
References	Skogsberg, 1928 Hartman, 1961 Hartman, 1968	Hartman, 1961 Hartman, 1968 Ruff, 1995	Johnson, 1901 Berkeley & Berkeley, 1948 Hartman, 1961 Hartman, 1968	MacGinitie, 1935	Uschakov & Wu, 1959 Uschakov & Wu, 1965 Present study

*) *Callianassa californiensis* was classified as *Neotrypaea californiensis* by Manning and Felder (1991).

Microhabitat

Juveniles (0.6 to 1.8 mm in BW) were attached to the ventral or lateral surface of the thorax or abdomen of the burrowing shrimp *Upogebia major* and could move actively there in April to September in Isahaya Bay (Figs. 3, 11). Juveniles attached to the bodies of *Upogebia* were also observed in Yamaguchi Bay (no data shown in Fig. 11). Several juveniles free from the bodies of *Upogebia* were collected from sediment samples in the habitats of *U. major* in the Seto Inland Sea and Tokyo Bay during April to June.

Adults (1.9 to 3.7 mm in BW) were not found on the bodies of *Upogebia* but were collected from sediment samples in the habitats of *U. major* in April to June and November to December. In many cases, the burrows of *U. major* collapsed just after digging the sediment, making it difficult to determine whether adults of the scale worm were attached on the burrow wall or buried in the sediment. Fortunately, one of the authors (GI) found that several adults were attached to the inner surface of the burrow of *U. major* in tidal flats in the Seto Inland Sea and Tokyo Bay.

Sexual reproduction

Oocytes (Fig. 12a) of relatively homogeneous size (100–120 μm in maximum diameter) were found in the body cavity of 8 females (1.9 to 3.0 mm in BW), specifically, 7 females collected from Yamaguchi Bay on 15-16 November 1997, and a female collected from Sone-higata on 18 April 1999. Spermatozoa (Fig. 12b) of a “primitive type” (Franzén, 1956), which consisted of a rounded head (2.7 μm long, 2.3 μm wide) with a small acrosome at its top, a short middle piece (0.5 μm long) and a tail (about 55 μm long), were found in the body cavity of a male (3.5 mm in BW) collected from Yamaguchi Bay on 16 May 1997. All of these specimens containing larger oocytes or spermatozoa bore macrotubercles on their elytra, which was characteristic of adults.

Smaller oocytes (60 μm maximum diameter) were found in a specimen (1.9 mm in BW) collected from Yamaguchi Bay on 4 November 1998, but this specimen had no macrotubercles on its elytra.

Commensalism to *Upogebia major*

The burrowing shrimp *Upogebia major* was a dominant species in tidal flats of sandy mud in Isahaya Bay. In a tidal flat in Mizuho-cho, Nagasaki Prefecture, on 20 September 1998, the maximum density of the holes of the burrows of *U. major* was 4 in an area of 20×20 cm. Because a living individual of *U. major* makes a Y-shaped burrow, producing two holes on the sediment surface (Hamano, 1990; Kyoko Kinoshita, personal communication), the maximum density of *U. major* was estimated to be 50 individuals/m^2 (half of the density of the holes). Since an average wet weight of the *U. major* collected at that time was 18.6 g (range: 13.3 to 23.0 g, n=13), the maximum biomass was estimated as 930 g /m^2.

The infestation by juveniles of the scale worm on the body surface of *U. major* was observed throughout a period from April to September in the tidal flats of Isahaya Bay (Fig. 11,

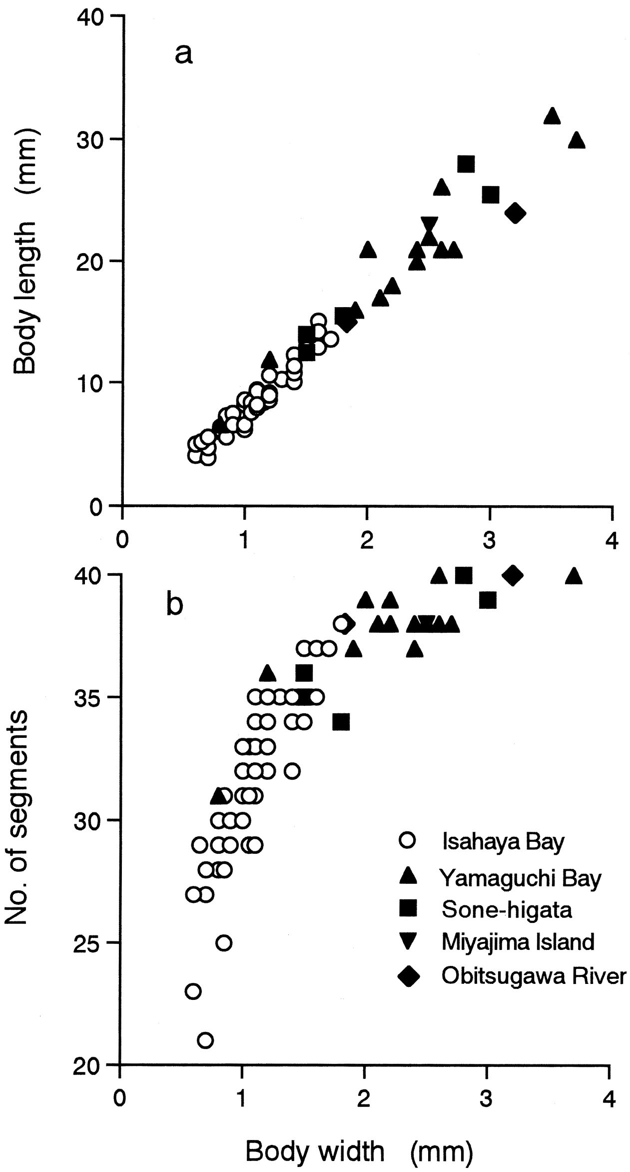

Fig. 10. Relationships between body width and body length (a) and between body width and segment number (b) in all undamaged specimens of *Hesperonoe hwanghaiensis* collected in the present study. Open circles: specimens attached to the body surface of *Upogebia major* in Isahaya Bay. Closed symbols: specimens not attached to the body surface of *U. major* found in 4 localities (Yamaguchi Bay, Sone-higata, Miyajima Island, Obitsugawa River).

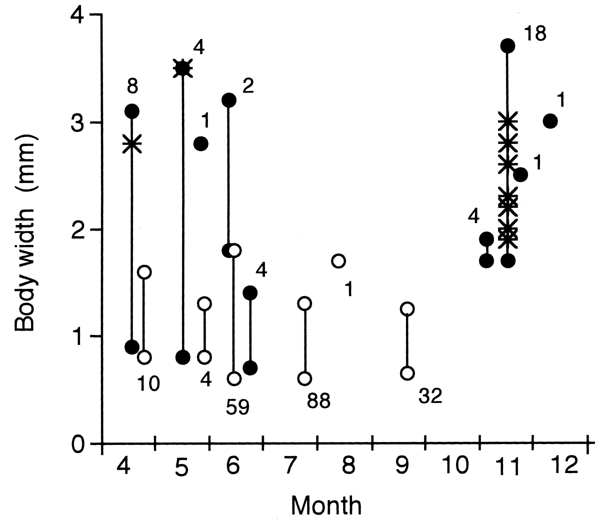

Fig. 11. Range of body width of *Hesperonoe hwanghaiensis* collected in different months. Data of different years (1994 to 1999) were pooled. Open circles: specimens attached to the body surface of *Upogebia major* in Isahaya Bay. Closed circles: specimens not attached to the body surface of *U. major* found in 4 localities (Yamaguchi Bay, Sone-higata, Miyajima Island, Obitsugawa River). Asterisks (∗) indicate adults with larger oocytes (more than 100 µm in diameter) or spermatozoa. The number on each datum indicates the sample size.

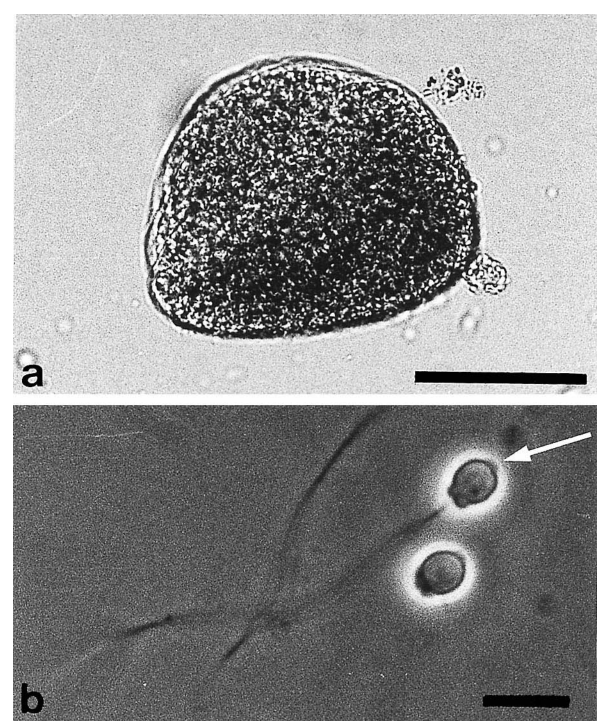

Fig. 12. Gametes of *Hesperonoe hwanghaiensis* collected from Yamaguchi Bay. a: An oocyte obtained from a female (1.9 mm in BW) collected on 15 November 1997. Scale 50 µm. b: A phase contrast micrograph of spermatozoa obtained from a male (3.5 mm in BW) collected on 16 May 1999. Scale 5 µm.

Table 1). The prevalence of infestation by the scale worm was significantly higher in July (89%) than in September (52%) (Fisher's exact probability test: p=0.0083). These values were much higher than the prevalence of infestation by a commensal bivalve, *Peregrinamor ohshimai* (7%). Several juveniles (maximum: 7) of the scale worm often aggregated on a host body (Fig. 13). The average number of juveniles attached to a host was higher in July (2.2) than in May and September (0.7).

Size-frequency distributions of the juveniles attached to the host bodies were similar to one another among 5 different sampling times during April to September, showing a dominance of sizes around 1 mm in BW (Fig. 14).

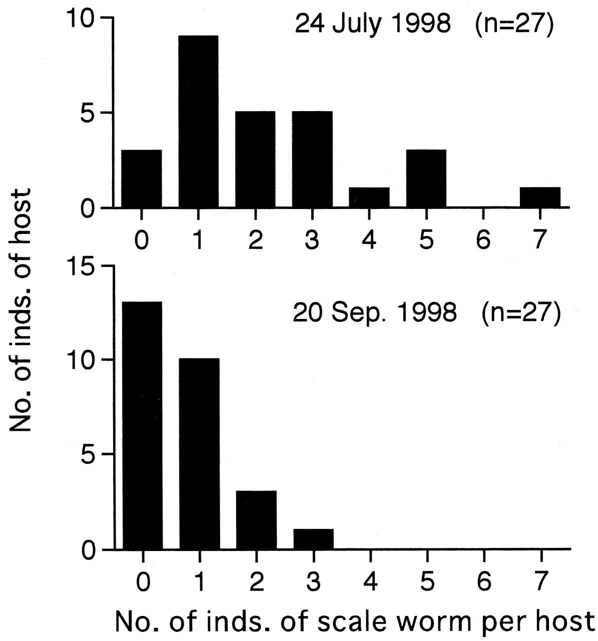

Fig. 13. Frequency of number of juveniles of *Hesperonoe hwanghaiensis* attached to an individual of the host (*Upogebia major*). Data from two collection dates (July and September 1998) in the same locality (Kobe in Isahaya Bay) are shown. The number of juveniles of the commensal scale worm was significantly higher in July than in September (Mann-Whitney *U*-test: $p < 0.001$).

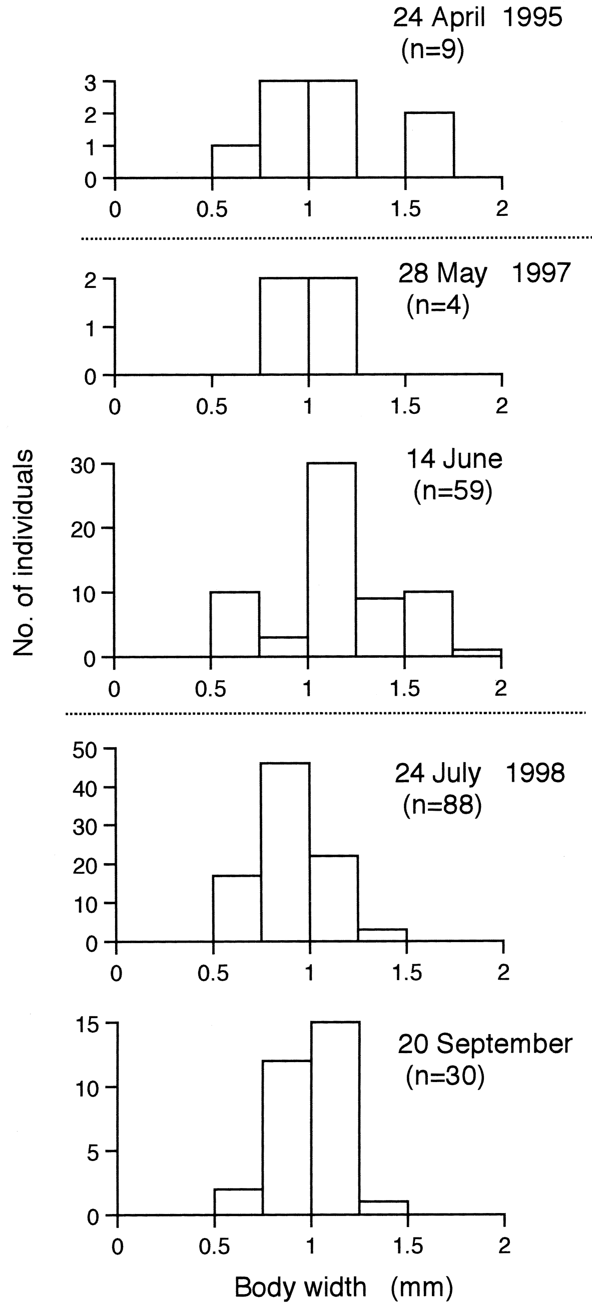

Fig. 14. Size-frequency histograms of *Hesperonoe hwanghaiensis* attached to the body of *Upogebia major* collected from Isahaya Bay. Data from five collection dates in 1995 to 1998 are shown.

DISCUSSION

Life history and commensalism to *Upogebia major*

According to Uschakov and Wu (1965), the area inhabited by the scale worm *H. hwanghaiensis* in Qingdao, China, was also inhabited by *Upogebia* and *Callianassa* shrimps, and they inferred that the scale worm may be commensal with the shrimps. Our result shows that the scale worm is commensal with the burrowing shrimp *Upogebia major.*

Marked differences in growth pattern, morphology of elytra and microhabitat were found between juveniles (1.8 mm or less in BW) and adults (1.9 mm or more) of the scale worm. Body length growth was correlated with the increase of segment number in juveniles up to a stage with 38 segments, after which only a few segments were added in spite of the continuous growth of the body length in adults (Fig. 10). Growth in the adult body seems to depend mainly on the increasing size of each segment.

The existence of macrotubercles along the posterior edge of the elytra is a diagnostic characteristic of *H. hwanghaiensis* (Uschakov and Wu, 1965). Our result shows that this characteristic appears only in adults.

Juveniles of the scale worm were commonly attached to the surface of the host body, though some juveniles free from the host body were collected from sediment samples. On the other hand, all adults were collected from sediment samples; none was attached to a host body. This suggests that the juveniles mainly live on the surface of the host body until they reach a size of 1.8 mm in BW, at which time they detach themselves from the host body and live freely on the inner surface of the burrow of the host. A similar change in the microhabitat between juveniles and adults is known in the closely related species *H. complanata*, which is commensal to the ghost shrimp *Callianassa californiensis* (= *Neotrypaea californiensis*) (MacGinitie, 1935; MacGinitie and MacGinitie, 1965). The adults of *H. adventor* commensal to the echiuroid *Urechis caupo* also live on the inner surface of the burrow of the host, though the habitat of juveniles is unknown (MacGinitie and MacGinitie, 1965).

Spawning of the scale worm seems to occur non-simultaneously over a long period during late November to May, with larger oocytes and spermatozoa found in this period, and smaller juveniles occurring over a long period (April to September). However, the most abundant juveniles occurred in summer around July. Processes of fertilization, early development and settlement of larvae on the host are unknown.

Upogebia major is the only known host species infested by *H. hwanghaiensis*. No specimens of *H. hwanghaiensis* were found in the body of other burrowing shrimps (*U. yokoyai*, *U. narutensis* and *U. issaeffi*) or in ghost shrimps (Callianassidae spp.) or their burrows in spite of our sampling efforts in Japanese tidal flats.

The host (*U. major*) can make a very deep burrow (Hamano, 1990; Kenji Kojima, personal communication) and produce water currents within the burrow to enable filter-feeding (Kato and Itani, 1995). The presence and activity of the host in tidal flats evidently supplies the scale worm not only with a microhabitat safe from larger carnivorous animals but also with food. The food of the *Hesperonoe* scale worm seems to consist of small animals or organic particles that come into the burrow with the water currents, as suggested in *H. adventor* (MacGinitie and MacGinitie, 1965). Particles entrapped in the filtering basket formed by the pereiopodal setae of the host and too large for the host to swallow may be important food for *H. hwanghaiensis*.

It is unknown whether the host (*U. major*) also benefits from the presence of the scale worm (*H. hwanghaiensis*). A likely benefit conferred upon the host is the cleaning activity of the scale worm, as suggested in other commensal polychates (Martin and Britayev, 1998).

Comparison with other *Hesperonoe* species

To date, five species of the genus *Hesperonoe* have been described worldwide (Hartman, 1961; Uschakov and Wu, 1965; Averincev, 1990; present study), including 3 species (*H. complanata*, *H. adventor*, *H. laevis*) from the west coast of North America, 1 species (*H. hwanghaiensis*) from Asia and 1 species (*H. andriashevi*) from the Arctic Sea. *H. andriashevi* may be unsuitable as a member of the genus *Hesperonoe*, because it has only one type of neurosetae and 13 pairs of elytra (Averincev, 1990) in contrast to two types of neurosetae and 15 pairs of elytra in all other *Hesperonoe* species. Based on specimens collected in the Arctic Sea, Averincev (1990) also described another species that were tentatively identified as *H. laevis* but slightly different from the species as it was originally described. An undescribed species (*H*. sp.) has been found in Monterey Bay in California on the west coast of North America (MacGinitie, 1935).

All *Hesperonoe* species are probably commensal to decapods or echiuroids. The host species and morphology of five known species in the Pacific region are compared in Table 2. Their flattened body and delicate and transparent elytra seem to be commensal features in relation to their life within burrows, but no other morphological specialization, such as those known in setae or other body parts in other genera of the commensal scale worms (Uchida, 1983; Britayev, 1998), has been found. Though the body color of many commensal scale worms resembles that of their hosts (Uchida, 1983), the red color of *H. hwanghaiensis* contrasts with the whitish body of its host. This color contrast seems to be ecologically meaningless because of their life within dark burrows.

H. hwanghaiensis seems to be the most closely related to *H. complanata* or *H*. sp., judging from the similarity in their morphology and host species. Their distributions are separated into the east coast of Asia and the west coast of North America (Table 2). The similar amphipacific distributions of closely related species is known in other genera in polychaetes (Uschakov, 1971) and other phyla (e.g., Sakai, 1940).

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