

Associations in the deep-sea benthopelagic zone: the amphipod crustacean *Caprella subtilis* (Amphipoda: Caprellidae) and the holothurian *Ellipinion kumai* (Elasipodida: Elpidiidae)

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SUMMARY: An association between the caprellid amphipod *Caprella subtilis* Mayer, 1903 and the elpidiid holothurian *Ellipinion kumai* (Mitsukuri, 1912) was confirmed through in situ submersible capture at 309 m depth in Sagami Bay, central Japan, and through shipboard observations. Information on this association, including behavioural and morphological data on both species, is presented. Information on the taxonomic standing of *C. subtilis* and related species is also introduced. Furthermore, we record swimming behaviour in the holothurian genus *Ellipinion* for the first time. We also introduce other biotic associations revealed during studies using submersible vehicles operated by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), including associations between benthopelagic holothurians and mysids, as well as hydrozoan polyps.

Keywords: *Caprella*, *Ellipinion*, holothurian, association, benthopelagic, submersible, Japan, Sagami Bay.

RESUMEN: ASOCIACIONES EN LA ZONA BENTOPELÁGICA: EL ANFÍPODO *CAPRELLA SUBTILIS* (AMPHIPODA: CAPRELLIDAE) Y LA HOLOTURIA *ELLIPINION KUMAI* (ELASIPODIDA: ELPIDIIDAE). – Este trabajo confirma la asociación entre el anfípodo caprelido *Caprella subtilis* Mayer, 1903 y la holoturia elasipodida *Ellipinion kumai* (Mitsukuri, 1912), a partir de la captura in situ, a 309 m de profundidad, con un submarino, y a través de observaciones a bordo, en la Bahía Sagami, zona central de Japón. Se presenta información de esta asociación, incluyendo datos de comportamiento y morfológicos para ambas especies. También se incluye información del estado taxonómico de *C. subtilis* y especies relacionadas. Además, registramos por primera vez el comportamiento natatorio del género de holoturia *Ellipinion*. Asimismo, presentamos información de otras asociaciones bióticas reveladas durante estudios en los que se han utilizados vehículos sumergibles dirigidos por la Japan Agency for Marine-Earth Science and Technology (JAMSTEC), incluyendo asociaciones entre holoturias bentoapélagicas y misidáceos, así como pólipos de hidrozooos.

Palabras clave: *Caprella*, *Ellipinion*, holoturias, asociación, bentoapélagico, submarino, Japón, Bahía Sagami.

INTRODUCTION

The benthopelagic zone has recently received renewed interest as the site of biogeochemical fluxes and transformations between the benthic and pelagic oceanic compartments (Marcus and Boero, 1998; Lindsay *et al.*, 1999; Miyake *et al.*, 2002; Raffaelli *et al.*, 2003; Miyake *et al.*, 2004). High fluxes and exten-

sive transformations of organic matter are expected in the benthopelagic zone at 300–500 m depth, where the vertically migrating midwater fauna comes into close contact with the sea floor during the daytime period of their diel migration cycle. These transition zones between two adjacent ecological communities, in this case the midwater and benthic communities, are termed ecotones. These areas usually have some

of the characteristics of each bordering community and often contain species not found in the overlapping communities. An ecotonal area often has a higher density of organisms and a larger number of species than in either of the two flanking communities. High densities of macroplankters have indeed been reported from the benthopelagic zone at these depths (Miyake *et al.*, 2002; Miyake *et al.*, 2004). No surveys comparing the species diversity of the benthopelagic zone at 300–500 m depth with the community within the benthic zone, or in similar depths in the mesopelagic zone, have currently been published. In the mesopelagic zone, the spatial and temporal complexity of gelatinous members of the macroplankton has increasingly been recognised as one of the factors that contributes to high species diversities (Harbison *et al.*, 1977; Kingsford, 1993; Lavaniegos and Ohman, 1999; Lindsay *et al.*, 2001; Lindsay and Hunt, 2005). In addition to the topological diversity offered by the sediment–water interface, the effect of interspecies interactions and associations can be expected to heighten biodiversity in the benthopelagic zone.

An association between the caprellid amphipod *Caprella subtilis* and the elpidiid holothurian *Ellipinion kumai* was recently confirmed through in situ submersible and shipboard observations. Members of the genus *Caprella* have often been reported in association with echinoderms (Guerra-Garcia, 2001) but records of associations with holothurians are rare (Wirtz, 1998; Guerra-Garcia, 2001). Information on this association, including behavioural, morphological and distributional data, is presented. To date, only three specimens of *C. subtilis* have been recorded in the literature with morphological descriptions, and figures have only been provided for the original holotype (Mayer, 1903). We present here a brief description of the specimens and record swimming in the holothurian genus *Ellipinion* for the first time. We also introduce other biotic associations with benthopelagic holothurians that have been revealed by studies using submersible vehicles.

MATERIALS AND METHODS

The elpidiid holothurian *Ellipinion kumai* was observed and sampled on ROV *Dolphin-3K* Dive 545 at 15:07:24 on 11 August 2001 in Sagami Bay, central Japan. The *Dolphin-3K* observational platform has previously been described elsewhere (Hunt and Lindsay, 1999). Video footage from the ROV

Dolphin-3K dive was recorded on BCT-D124L Digital Betacam tapes. Physico-chemical data were collected using a SeaBird SBE19 CTD with an SBE13 oxygen sensor. CTD and dissolved oxygen data were correlated with the presence of the animals by matching the time record on the CTD series to the time record on the video.

Specimens were collected using an 18-canister suction sampler with an internal hose diameter of 8 cm at the funnel, which was attached to the manipulator arm, and an internal diameter of 6 cm at the junction between the intake hose and sample canister proper. Sample canisters had thick acrylic walls to keep the water temperatures inside low. The sample was taken to the ship's deck approximately 40 minutes after being collected.

The holothurian with associated caprellids was transferred into a photography tank (2.7 l volume) using a small glass jar. Several photographs were taken in a darkroom on board ship using a Nikon D1^H digital camera with a macro lens (AF Micro Nikkor 105 mm 1:2.8 D) (F3.5, shutter speed 10/8000) and images were recorded in TIFF-RGB format at an image size of 2000×1312 pixels. Illumination was provided by National Ref Lamp colour-balanced flood bulbs (PRF-500WB), which lit the specimen, placed on a black felt backdrop, from the side. Photography lasted for approximately 5 minutes before the phototank was transferred to an incubator set to 9.5°C.

The live caprellids were also observed in the laboratory under a Nikon SMZ-U dissecting microscope (0.75–7.5×) outfitted with a video camera mounted on a C-0.45× Nikon TV lens, and recorded on miniDV tape. The horizontal field of view was 14 mm at 0.75× magnification. Clinging behaviour of the present species was categorized into 4 types, “moving”, “upright”, “bending” and “parallel” as defined by Takeuchi and Hirano (1995). The duration of each behaviour was determined by referring to the miniDV (digital video) tape record. The three caprellid specimens from ROV *Dolphin 3K* Dive 545 and the holothurian to which they were attached were fixed separately in a 70% ethanol solution.

RESULTS

Morphological observations

The species *Caprella subtilis* has hitherto been known only from the original description of a ma-

ture male by Mayer (1903) and from records by Utinomi (1973), McCain and Steinberg (1970), and Arimoto (1976). In view of the paucity of information on this species, we describe here the specimens from ROV *Dolphin-3K* Dive 545 with notes on other species of the genus *Caprella* with characters similar to *C. subtilis*.

***Caprella subtilis* Mayer, 1903**
(Fig. 1)

Caprella subtilis Mayer, 1903, 126, pl.5 fig. 32, pl.8 fig. 27. McCain and Steinberg, 1970, 42.

? *Caprella* aff. *subtilis* Utinomi, 1973, 36.

Caprella (Caprella) subtilis Arimoto, 1976, 80-82, figs. 39-40.

Materials examined. Male "a"; mature female "b", premature female "c"

Description. Male "a"; Body length 11.34 mm. Body somites slender. Head round and pereonites I to VII without projections. Pereonite V longest of body somites (i.e. head combined with pereonite I, pereonites II to VII). Antenna II 2/3 of body length with 13-segmented flagellum. Antenna II shorter than antenna I. Basis of gnathopod II half the pereonite II length. Propodus oblong with 1 palmar

and 2 subpalmar spines 1/3 from the proximal end. Gill length about 3 times width. Pereopod V elongated; basis lacking a distal projection, with a grasping spine near basal end of propodus. Pereopod VI ca. 1.3 times length of pereopod V and pereopod VII twice that of pereopod V. Features of pereopods VI and VII similar to pereopod V except for a very shallow projection on the proximal third and two pairs of projections used for grasping on the distal half of the propodus.

Mature female "b". Body length 11.18 mm with pereonite V longest followed by pereonite II. Antenna I longer than half of body length, with 12-segmented flagellum.

Type locality. Off Sado Island in the Sea of Japan (38°30'N, 128°35'E).

Other localities. Sagami Bay (Utinomi, 1973 and present study).

Remarks. In general, males of the genus *Caprella* grow to outsize mature females of the same species, which is confirmed by successful experiments

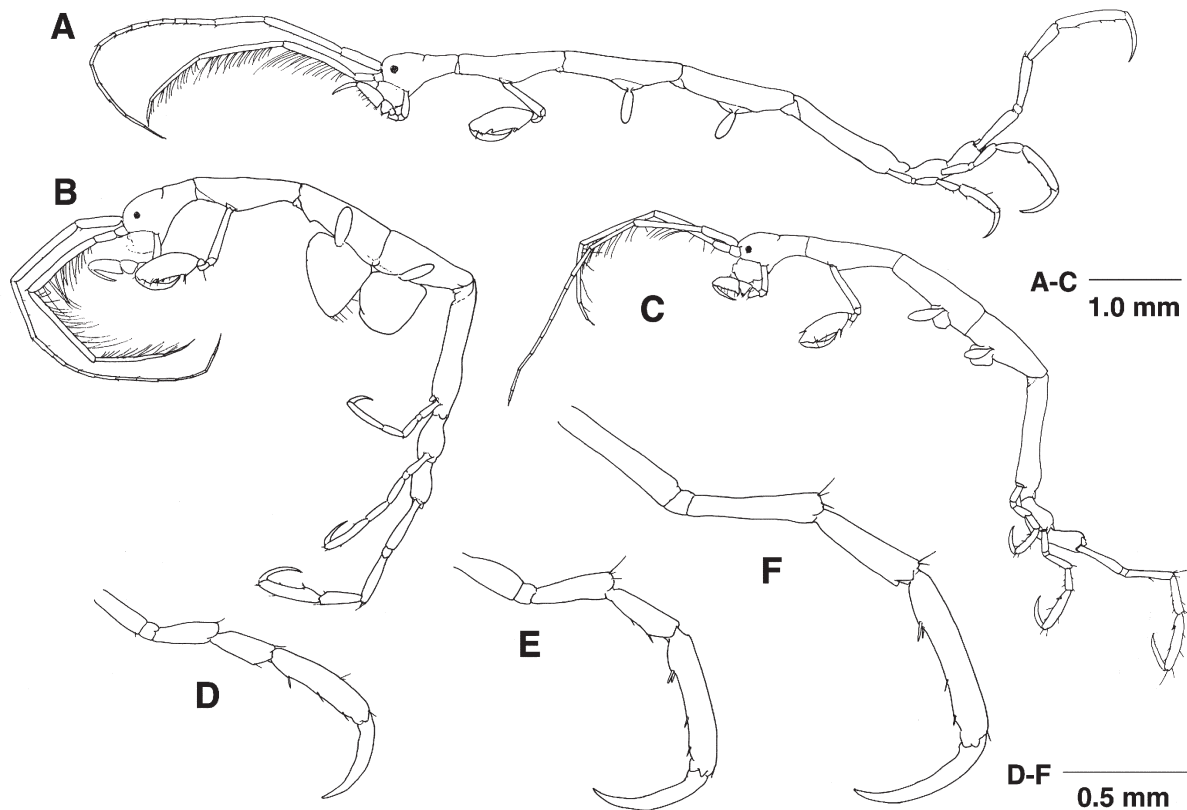


FIG. 1. – *Caprella subtilis* Mayer, 1903 from 309 m depth in Sagami Bay, Japan. A, male "a"; B, mature female "b"; C, premature female "c"; D, pereopod V of male "a"; E, pereopod VI of male "a"; F, pereopod VII of male "a".

on the life-history of *Caprella danilevskii* and *C. okadai* in the laboratory (see Takeuchi and Hirano, 1991, 1992). Furthermore, in several species of *Caprella* it has been reported that as they undergo development, the relative lengths of pereonites I and II increase disproportionately with respect to the lengths of the other pereonites (Arimoto, 1976). Moreover, the morphology of gnathopod II, especially the size and features of the propodus in males, is confirmed to change with every instar, even after maturation (Takeuchi, 1989; Takeuchi and Hirano, 1991). These general characteristics of the genus *Caprella*, combined with the near equal size of the male and mature female in the present study, indicate that the male had not yet reached the fully mature instar. It is only upon full maturation that the sexually dimorphic characteristics of males become apparent, although the ratios and features of each segment of gnathopod II are the basis for several species diagnoses in the genus *Caprella* (see Mayer, 1903; Arimoto, 1976).

The present species, *C. subtilis*, was originally recorded based on a single male specimen of 21 mm in body length collected from 80-100 fm (146-183 m) in the Sea of Japan (Mayer, 1903). Utinomi (1973) assigned two specimens of *Caprella* collected from 90 to 103 m in Sagami Bay to "*Caprella* aff. *subtilis*" without providing any figures or remarks. Although the difference in growth stage between the type specimen (21 mm in body length) and the present male (11 mm in body length) made making a clear identification difficult, the following features of the present specimens allowed us to assign them to *C. subtilis*; i.e., elongated body somites without any projections, longer pereonite V length, and antenna I longer than half the body length.

Prior to the description of *C. subtilis*, Mayer (1890) described *C. gracillima* based on 3 females collected from 109.8 to 182.9 m depth in the Sea of Japan and Tsugaru Strait. Although the mature female of *C. gracillima* in Mayer (1890) is 20 mm in body length, which is twice that of the mature female in the present study, the present mature female most closely resembles *C. gracillima*, i.e., elongated body somites without any projections, antenna I longer than half of the combined body segments. Mayer (1903) did not mention any diagnostic differences between *C. gracillima* and *C. subtilis* in his description of *C. gracillima* and his species key for the genus *Caprella* based on the characteristics of the males. According to the species key for *Caprella*

provided by Arimoto (1976), *C. gracillima* is listed in a group with the "basal segment of gnathopod 2 a little shorter than half of pereonite II in adult male", while *C. subtilis* is characterized as "basal segment of gnathopod 2 a little shorter than pereonite II in adult male". In addition to the difference in body lengths, the longest body somite differs between *C. gracillima* and the present specimens; *C. gracillima* (female) is 20 mm in body length with pereonite II longest, while the mature female in the present study is 11 mm in body length with pereonite V longest. However, the lack of a mature male specimen of *C. gracillima* makes it impossible to confirm any diagnostic differences between *C. subtilis* and *C. gracillima* based on comparisons with previous studies (Mayer, 1890, 1903; Arimoto, 1976).

Thus, although the present specimens from Sagami Bay are assigned tentatively as *C. subtilis* for the purposes of the present study, full descriptions of *Caprella subtilis* and *C. gracillima* based on various specimens of both sexes at different growth stages are required to clarify the species diagnoses and solve the affinity of *C. gracillima* to *C. subtilis*.

In situ and shipboard observations

Ellipinion kumai was swimming in an upright position above the muddy bottom at 309 m depth (Sagami Bay; 35°03.0'N 139°12.5'E) when first observed. Other inhabitants of the benthopelagic zone at this site included a large number of an argentinoid fish (?*Glossanodon semifasciatus*), several juvenile rattail fishes and some sepiolid squid that were sitting motionless on the bottom. Another yellowish lumpy holothurian species was common on the sediment as were anemones and a long-legged shrimp species resembling *Nematocarcinus*. Physico-chemical parameters of the water column habitat were as follows: temperature 9.70°C, salinity 34.32, dissolved oxygen 2.73 ml/L, sigma-t 26.47 kg/m³.

The "palmure" appendage of *E. kumai*, consisting of modified webbed podia on the anteroventral surface of the animal, was used in swimming and contributed the majority of lift to the swimming holothurian. The posterior brim and anterodorsal veil appeared to be used almost exclusively to propel the animal forward during swimming. The time required for a complete swimming cycle ranged from 1.9 to 3.2 seconds, for an average of 0.4-0.5 Hz. During the observation, the holothurian maintained an altitude of 1 to 3 metres above the muddy substrate.

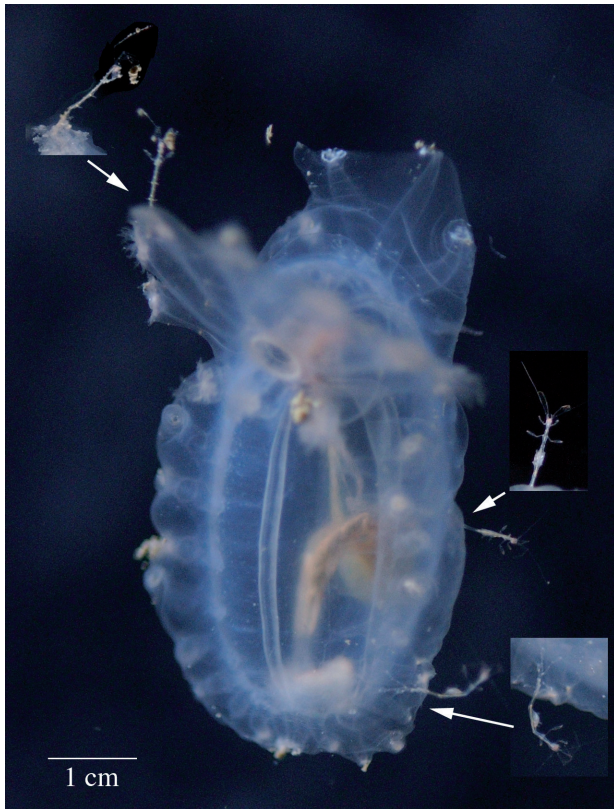


FIG. 2. – Photograph of *Ellipinion kumai* (Mitsukuri, 1912) in the aquarium showing the attachment sites of the three *Caprella subtilis* individuals. Insets show the individuals' respective macromorphologies.

Although the caprellids were not visible on the surface of the holothurian due to the low resolution of the video camera system, the animal was nevertheless sampled. When alive, the holothurian was approximately 4 cm in length and 2 cm in diameter. The three caprellid individuals were attached in the positions shown in Figure 2 when the sample was taken to the ship's deck approximately 40 minutes after collection. The holothurian remained completely immobile during transfer to the phototank and subsequent photography. As other gelatinous deep-sea organisms, such as the trachymedusa *Halicreas minimum* and the ctenophore *Thalassocalyce inconstans* (personal observations), have also been observed to stop moving when exposed to daylight spectra, the holothurian was placed in a dark incubator set to 9.5°C for 30 minutes to “recover.” After this recovery period the holothurian still did not move, but neither had the attachment positions of the caprellids on its dermis. The pereopods of the caprellids remained firmly attached to the holothurian's external surface until the organisms expired.

When viewed under the dissecting microscope, the body colour of all the caprellid individuals was transparent to very weakly brownish while eye pigment was orange. The “upright” position, as defined by Takeuchi and Hirano (1995), was observed for the entire recorded time; male “a” for 36 sec, mature female “b” for 61 sec and premature female “c” for two observations of length 40 and 55 sec respectively. In all digital photographs where the caprellids can be visualized, they are also in the “upright” position. Of the three individuals, mature female “b” was observed to grasp the substratum with only pereopods VI and VII, while male “a” and premature female “c” both used pereopods V to VII for grasping the substratum. Mature female “b” was observed to use pereopods V to clean her antennae.

DISCUSSION

In situ and shipboard observations

Two members of the holothurian family Elpidiidae have so far been reported to be capable of swimming and therefore to be benthopelagic in their ecology. They are both in the genus *Peniagone* and are specifically *Peniagone leander* Pawson and Foell, 1986 (Pawson and Foell, 1986), and *Peniagone diaphana* (Theel) (= *Scotoanassa translucida* Herouard) (Hansen, 1975). This is the first record of swimming in the holothurian genus *Ellipinion*, which also belongs to the family Elpidiidae. Field observations of *C. subtilis* suggest that the holothurian provides a platform for filter-feeding activity and a transport mode to areas where food patches occur. All three caprellids faced in the direction of the forward swimming motion of the holothurian, thereby increasing the rate of encounter with food particles while the holothurian was in motion.

In the present caprellid specimens, mature female “b” did not use pereopod V for grasping the substratum. This may be because in the relatively calm conditions of the deep sea, *Caprella* spp. does not need to use all pereopods (V to VII) for clinging to the substratum. This hypothesis was inferred from the small size of pereopod V compared with pereopods VI and VII (see Figure 1). It can also be inferred that the benthopelagic holothurian *E. kumai* is a relatively gentle swimmer, as evidenced by in situ observations.

Takeuchi and Hirano (1995) reviewed the clinging behaviour of 22 species of 8 genera of Caprellidea with 4 species of 3 genera of Podoceridae, which is thought to be the gammaridean group most closely related to the Caprellidea (e.g. Takeuchi, 1993), and concluded that the “upright” group inhabits environments with little wave action, while the “parallel” group attach to macroalgae that are exposed to strong wave action. The genus *Caprella*, which is considered one of the most apomorphic genera among the *Caprogammarus-Caprella* complex of Caprellidea (Takeuchi, 1993), contains both behavioural groups. In the “parallel” species of *Caprella*, the basis of gnathopod II is shorter than half the length of pereonite II, while in the “upright” species of *Caprella* the basis is longer than half the length of pereonite II. The characteristics of the present deep-sea species, *C. subtilis* (i.e., the basis of gnathopod II is equal to half the length of pereonite II, and the dominance of “upright” clinging behaviour) are in line with the hypothesis of Takeuchi and Hirano (1995) for environmental determinism of behaviour and morphology, which suggests that the “parallel” Caprellid group evolved from the “upright” group for survival in high wave-action areas.

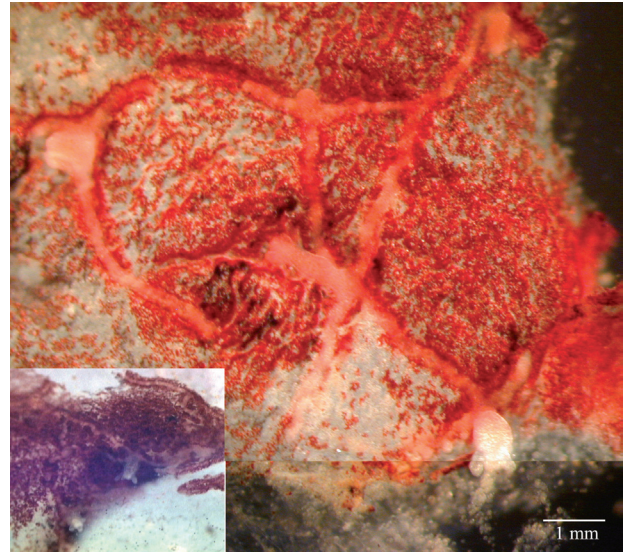


FIG. 3. – Photograph mosaic of athecate hydrozoan polyp colony on dermis of *Eynpniastes eximia*. Inset is miniDV video framegrab of separate fragment of dermis, also supporting polyps.

Small “benthic” animals associated with highly mobile members of the benthopelagic fauna were observed repeatedly during the course of our surveys of the benthopelagic zone. A second species of pelagic holothurian, *Eynpniastes eximia*, collected at 689 m depth in Suruga Bay (34°39.2’N 138°39.6’E) on 14 November 2001 by the crewed submersible *Shinkai*

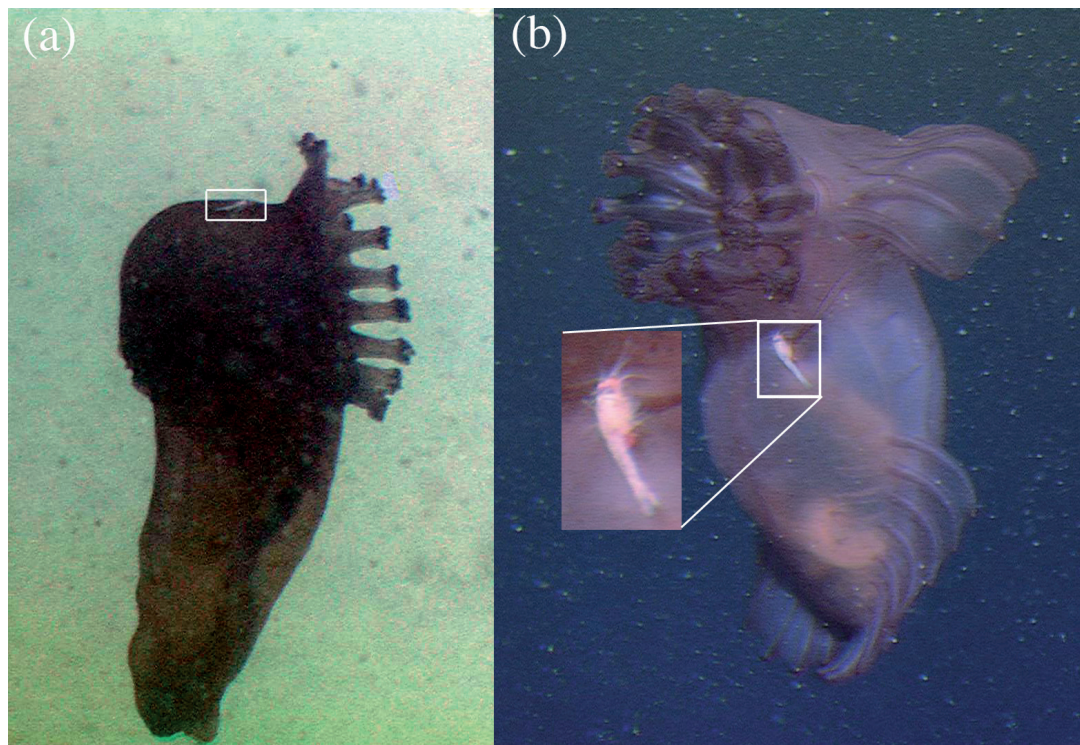


FIG. 4. – (a) In situ HDTV video framegrab of *Eynpniastes eximia* observed on 20 May 2000. Associated mysid located within a rectangle. (b) In situ HDTV video framegrab of *Eynpniastes eximia* observed on 4 February 2004. Inset is a portion of a separate zoomed-in video framegrab of the associated mysid.

2000 was also host to a “benthic” organism, in this case a colony of athecate hydrozoan with 4-tentacled polyps that formed a network over the scraps of holothurian epidermis that remained attached to the animal after collection (Fig. 3). These polyps had the following characteristics: hydranth without moniliform or capitata tentacles, only filiform tentacles and not divided into aboral and oral groups but concentrated at oral end, hydranth without trumpet-shaped hypostome, hydrocaulus not branched, colony stolonial and not polymorphic, gonophores and medusae unknown. These characters suggest that the polyps belong to either the family Cytaeidae or Pandeidae (Hirohito, 1988). Of the hydroids reported from Japanese waters it most resembles *Perarella parastichopae* Hirohito, 1988 within the Cytaeidae and with naked hydrorhizae, which was described from a colony growing around the mouth of the holothurian *Parastichopus nigripunctatus* (Hirohito, 1988).

The holothurian species *E. eximia* has also been observed in association with mysid shrimps on two occasions. During ROV *HyperDolphin* dive number 7 in Suruga Bay off Doi (34°54.7'N 138°39.4'E) on 20 May 2000, *E. eximia* was observed swimming at 1499 m depth just above the bottom with its long axis vertical. A mysid was positioned on the anteroventral surface of the holothurian on the immobile central axis of the anterodorsal veil, facing in the direction of the oral opening (Fig. 4a). The second observation was during ROV *HyperDolphin* dive number 271 in Suruga Bay off Heda (35°00.0'N 138°39.0'E) on 4 February 2004. The holothurian was observed floating with its long axis vertical at 1085 m depth over a bottom depth of 1403 m. Marine snow particles had gathered in the pits formed where the upward-pointing anterodorsal veil meets the anteroventral surface. A mysid was attached firmly to the ventral surface, slightly posterior to the oral tentacles, with its head facing towards the oral opening (Fig. 4b). No amount of agitation in the wash of the submersible caused the mysid to dissociate from its holothurian substrate, and the pleopods were observed to beat so that the mysid was not torn from its host.

Pelagic/benthopelagic holothurians may be a previously underrated substrate for smaller members of the benthic/benthopelagic fauna. The holothurians transport these organisms from one food-rich environment to another and increase the hitchhikers' food particle capture rate during forays into the water column.

ACKNOWLEDGEMENTS

We thank Dr. Hiroshi Miyake for his field support and S. Tanada for support in the video laboratory. We also greatly appreciate information pertaining to holothurian taxonomy provided by Drs. F. Solis-Marin and D. Billett. We sincerely thank the captain and crew of the R/V *Natsushima* as well as the commander Y. Yoda and the operations team of the ROV *Dolphin-3K* for their dedicated efforts. This manuscript was improved by the comments of two anonymous reviewers, to whom we are indebted.

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Scient ed.: M.P. Olivar.
 Received December 17, 2007. Accepted March 5, 2008.
 Published online July 7, 2008.