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High incidence of copepod-bacteria associations in Tokyo Bay waters and Woods Hole waters*

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Abstract: SEM examination revealed that calanoid copepods *Acartia* spp. from Tokyo Bay waters and Woods Hole waters have a high incidence of bacterial colonization on their body. In some samples from Tokyo Bay one hundred percent of adult copepods were colonized by bacteria. Many of these bacteria produced slime. More than 80 % of copepods from Woods Hole were covered with bacteria and some of these copepods had slime. Small pores and slots which are scars of bacteria either vertically or horizontally attached to copepods were observed adjacent to dense colonies of bacteria. Bacteria were sometimes present in the internal part of body, suggesting that bacterial invasion occurred inside the body. These findings suggest that copepod-bacteria associations which are global phenomena cannot be commensalism but parasitism.

1. Introduction

Bacterial epibionts of copepods have been examined in coastal waters (SOCHARD *et al.*, 1979; COLWELL *et al.*, 1980; HUQ *et al.*, 1983; NAGASAWA *et al.*, 1985a; NAGASAWA and NEMOTO, 1986, in press; NAGASAWA, 1986) as well as lakes (HOLLAND and HERGENRADER, 1981) using scanning electron microscopy. One measure of this association, incidence of copepods with bacteria (ICWB), has been obtained from samples in coastal waters in different parts of the world (NAGASAWA, 1986; NAGASAWA and NEMOTO, in press). Values of ICWB ranged from 0 to 84 %. So far Woods Hole samples had the highest incidence, 84 %, but in general ICWB was less than 10 % (NAGASAWA, 1986). Seventy-five percent of the adult calanoid copepods *Diaptomus* spp. were colonized as compared to only 10.5 % of the copepodites at three lakes in Nebraska (HOLLAND and HERGENRADER, 1981). Bacteria capable of producing polysaccharides occurred on calanoid copepods *Acartia* spp. from Woods Hole, San Francisco Bay and Vera Cruz (NAGASAWA, 1986).

The present study provides information on variation of ICWB at two stations in Shinhamako (Tokyo Bay) where at times all adult copepods *Acartia* spp. are colonized by bacteria as well as with attached bacteria including production of polysaccharides. Discussion is focused on the ecological aspects of the frequent occurrence of copepods with bacteria, and of the mutual relation between copepods and bacteria.

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2. Materials and methods

Tokyo Bay and Woods Hole samples were used in this study; the former includes *Acartia omorii* and *A. plumosa* obtained from Shinhamako, a saline lake which is connected to Tokyo Bay (see NAGASAWA, 1984) and the latter includes *A. tonsa* from Woods Hole. Copepods known as *A. clausi* in Japanese coastal and inlet waters consist of two species, *A. omorii* and *A. hudsonica* (UEDA, 1986). He also mentions that samples from almost all areas are composed of *A. omorii*. Waters of Shinhamako cover an area of 300,000 square meters and hereafter are referred to as Tokyo Bay waters, since water from Tokyo Bay flows into and out of this lake through a sluice gate. The Tokyo Bay samples are composed of 25 collections taken from January 6 through November 4, 1976 at two stations separated by about 1,000 m. The Woods Hole sample consists of only one sample collected on September 1, 1984. Each sample was preserved in 5 % neutralized formalin seawater solution immediately after collection. The seasonal cycle of *Acartia* was described by FUROTA (1979) for Shinhamako where *A. omorii* was dominant from November through June and was replaced in dominance during summer by *A. plumosa*. Three samples taken in June and November include both species of copepods. The other 22 samples were composed of either *A. omorii* (11 samples) or *A. plumosa* (11 samples).

In most cases 100–200 *Acartia* adults were removed from preserved plankton samples, and examined in a JSM-35 scanning electron microscope following the preparation procedure described by NAGASAWA *et al.* (1985a). After critical-point drying some specimens collected on August 15, 1976 were cut transversely or exoskeletons of copepods were cut open so that internal tissue could be seen easily. These also were then coated with gold and examined in an SEM.

The density of bacteria is defined as number of bacteria per unit surface area: when several to several tens bacteria are dispersed, the density is low; when more than 100 to several hundreds bacteria are colonized, the density is high. The

Table 1. Data on copepod collections used in the present study, incidence of copepods with bacteria (O and P in parentheses represent *A. omorii* and *A. plumosa*, respectively) and characteristics of bacteria attached to copepods. ND indicates no data.

Station	Date (1976)	No. of copepods examined	Incidence of copepods with bacteria (%)	Characteristics of bacteria			
				1) Attachment	2) Density	3) Shape	4) Slime
Tokyo (Shinhamako) Bay							
1	Jan. 6	126	0 (O)	ND	ND	ND	ND
2	Jan. 6	127	0 (O)	ND	ND	ND	ND
1	Jan. 21	216	0.5 (O)	Head only	High	Slender rods	Absent
2	Jan. 21	113	0 (O)	ND	ND	ND	ND
1	Feb. 10	215	100.0 (O)	Everywhere	Low	Short or indented rods	Absent
2	Feb. 27	59	0 (O)	ND	ND	ND	ND
1	Mar. 31	113	100.0 (O)	Everywhere	Low, rarely high	Short or long rods, spiral	Present
2	Mar. 31	103	2.9 (O)	Selective	Low	Short or long rods	Absent
1	Apr. 16	158	92.4 (O)	Everywhere	Low, rarely high	Short or long rods, spiral	Present
2	Apr. 16	139	3.6 (O)	Selective	Low, rarely high	Short or long rods	Absent
1	May 7	127	100.0 (O)	Everywhere	High	Short or indented rods, spiral	Present
1	June 19	52	3.8 (O, P)	Selective	Low	Short or long rods	Absent
2	June 19	23	0 (O, P)	ND	ND	ND	ND
2	July 9	66	0 (P)	ND	ND	ND	ND
1	July 27	86	0 (P)	ND	ND	ND	ND
2	July 27	150	0 (P)	ND	ND	ND	ND
1	Aug. 15	130	43.1 (P)	Selective, dorsal	Low, on the back high	Short or long rods	Present
2	Aug. 15	208	54.3 (P)	Selective, dorsal	Low, rarely high	Short or long rods	Absent
1	Sept. 5	137	12.4 (P)	Selective	Low	Short or long rods	Present
2	Sept. 5	142	25.4 (P)	Selective	Low, rarely high	Short or long rods	Absent
1	Sept. 30	174	100.0 (P)	Everywhere	High	Short, long or indented rods	Present
2	Sept. 30	66	16.7 (P)	Selective	Low	Short or long rods	Absent
1	Oct. 17	190	100.0 (P)	Selective	Low	Short or long rods	Absent
2	Oct. 17	158	16.5 (P)	Selective	Low, rarely high	Short, long or indented rods	Absent
2	Nov. 4	125	47.2 (O, P)	Selective	Low, sometimes high	Short or long rods, beaded	Absent
Woods Hole							
1	Sept. 1, 1984	117	83.8	Selective, dorsal	High, rarely low	Short or long rods	Present

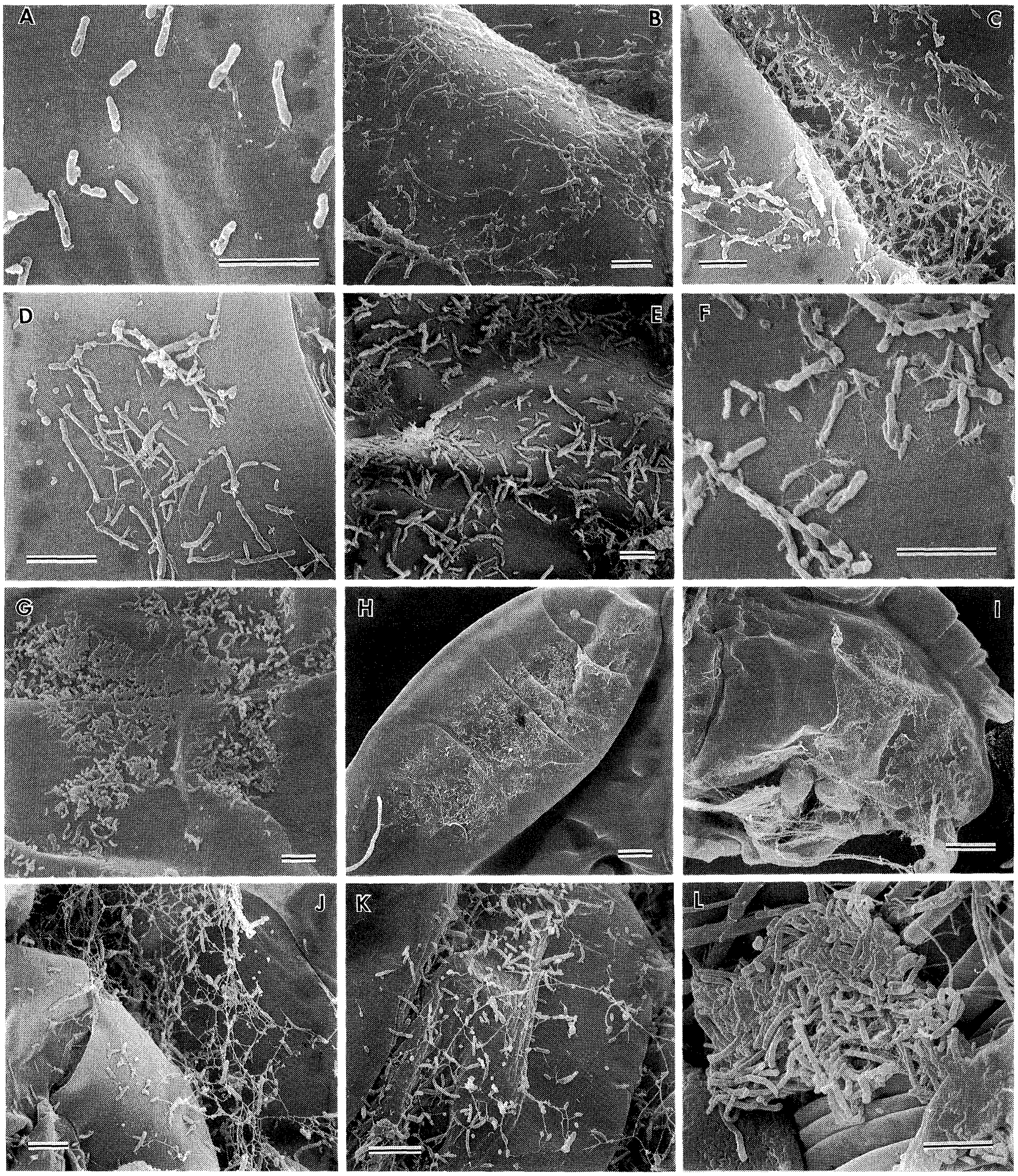

Fig. 1. Scanning electron micrographs of bacteria attached to copepods obtained from Tokyo Bay waters. Specimens were collected on February 10, 1976 (A), March 31, 1976 (B and C), April 16, 1976 (D), May 7, 1976 (E and F), August 15, 1976 (G) and September 30, 1976 (H-L). Twelve different specimens were used in the following 12 pictures. Scale bars indicate 5 (A-G and J-L) and 50 μm (H and I). (A) A small number of indented bacteria are attached to the head of copepod. No slime was found on other February specimens. (B) Long or short rods colonize the body surface together with slime. (C) A quantity of slime is present on the tail segment together with bacteria. (D) A small number of long or short rods with slime are found on the ventral side. (E) Most of bacteria which cover the dorsal side are indented, producing a slime layer. (F) Indented bacteria which slightly produce slime are present on the dorsal side. (G) Heavy colonization of bacteria occurs on the dorsal side. Slime covers part of colony. (H) A copepod showing heavy colonization of bacteria on most of the back. (I) Lateral view of head which is covered with bacteria and slime, looking filmy. (J) Slime is more marked than bacteria on the ventral side. (K) Bacteria and slime are striking on the ventral side. (L) A colony of bacteria is on the maxilla. A slime layer covers bacteria in small quantities.

definition of ICWB is the percentage of number of copepods with bacteria to number of those examined for each sample (NAGASAWA, 1986; NAGASAWA and NEMOTO, in press). Water temperature and salinity were measured for Tokyo Bay waters at a depth of 5 m.

3. Results

1) Characteristics of bacteria attached to copepods

Some features of bacteria attached to copepods are found in Table 1. In most cases attachment of bacteria to copepods was selective as reported by NAGASAWA *et al.* (1985a), NAGASAWA (1986), and NAGASAWA and NEMOTO (1986, in press). Bacteria were found more frequently on the ventro-lateral side than on the dorsal side. These examples are referred to as "selective" in Table 1. However, in some copepods bacteria were found everywhere on the ventral, lateral and dorsal sides of copepods; they are referred to as "everywhere" (Table 1). Attachment of bacteria to the back of copepods (Fig. 1G, H; Fig. 2D, E, F) occurred intensively only on samples obtained on August 15 and September 30, 1976 in Tokyo Bay and September 1, 1984 in Woods Hole.

The density of bacteria in Tokyo Bay was usually low, which suggests that bacteria were just beginning to attach. Woods Hole specimens usually had a large number of bacteria. Although accurate estimates of bacterial density on copepods were not obtained, counts based on the photographs indicate an order of at most 10^4–10^5 cells per copepod. Small pores were observed close to the dense colonies of bacteria for the first time (Fig. 2E, F), but on uninfested copepods there were no pores.

Most bacteria were rods of various shapes—short, long, indented (Fig. 1A, E, F) or slender. Occasionally spiral bacteria were found in Tokyo

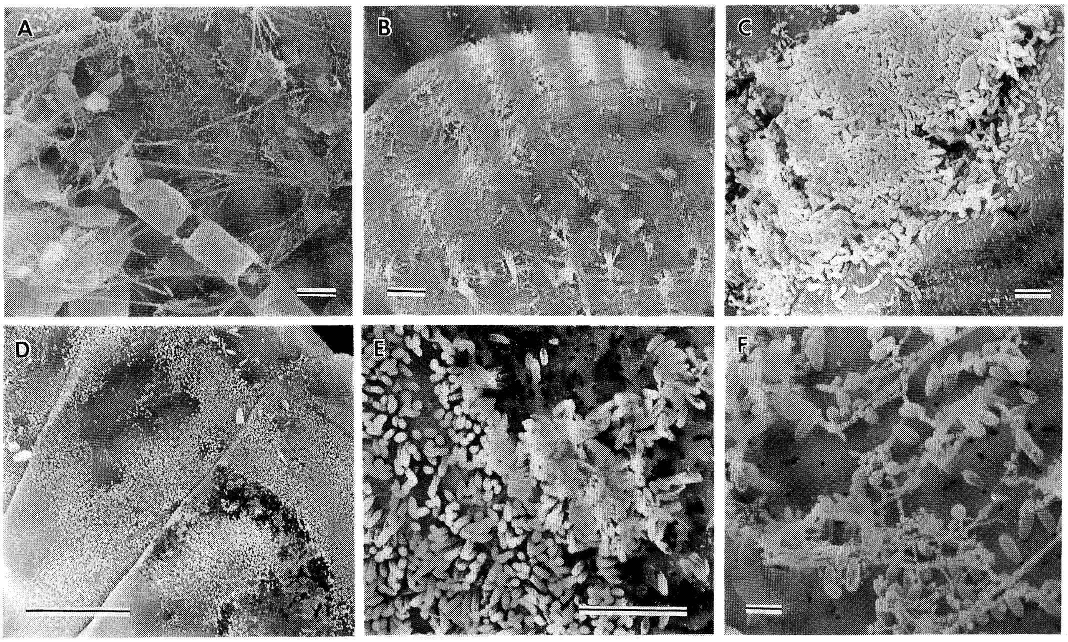

Fig. 2. Scanning electron micrographs of bacteria attached to copepods obtained from Woods Hole waters on September 1, 1984. Five different specimens were used in the following 6 pictures. Scale bars indicate 1 (F), 5 (A–C and E) and 50 μm (D). (A) Bacteria producing exopolymers are attached to the lateral side of copepod. Attachment of diatoms may be due to sticky exopolymers. (B) Organic polymers cover the labrum in large quantities. (C) Heavy colonization of bacteria occurs near the joints of segments. Organic polymers slightly cover a colony of bacteria. (D) Bacteria are present on the whole area of back. (E) Higher magnification of part of (D). Small pores are observed adjacent to bacteria. (F) Bacteria and slime are present on the dorsal side. Like the picture (E) small pores are found.

Bay samples. Beaded bacteria were observed rarely in Tokyo Bay samples, and were also seen in copepods from Vera Cruz (NAGASAWA, 1986).

Two types of bacterial attachment were observed on copepods: bacteria attached along the entire length of the cell and those attached to the exoskeleton at one end perpendicular to the skeletal surface. I refer to the former as horizontal and the latter as polar attachment. The horizontal attachment usually was more frequently than polar attachment. In the Tokyo Bay samples horizontal attachment was common as shown in Fig. 1, whereas in Woods Hole polar attachment occurred more frequently than in Tokyo Bay. The polar attachment was observed dorsally on prosome segments of copepods (Fig. 2). Copepods from other areas than Tokyo Bay and Woods Hole so far investigated were some-

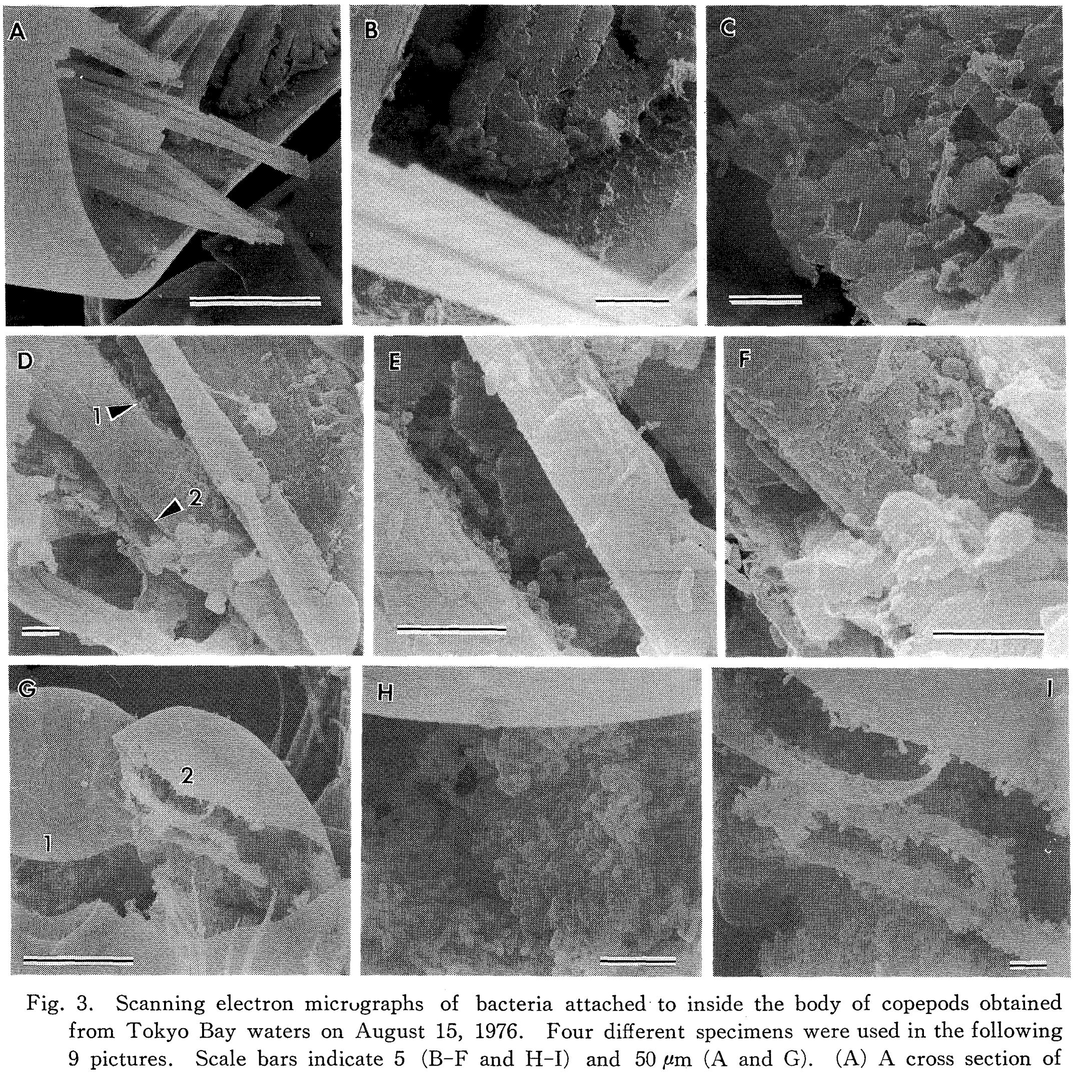

Fig. 3. Scanning electron micrographs of bacteria attached to inside the body of copepods obtained from Tokyo Bay waters on August 15, 1976. Four different specimens were used in the following 9 pictures. Scale bars indicate 5 (B–F and H–I) and 50 μm (A and G). (A) A cross section of copepod. (B) Enlargement of part in (A). A small number of bacteria are present. (C) Bacteria are dispersed in the inside of body where exoskeleton came off. (D) An internal part which came out after cutting open exoskeleton. Arrows with figures indicate the presence of bacteria. (E) Enlargement of the part marked "1" in (D). (F) Higher magnification of the part marked "2" in (D). (G) Exoskeleton cut roughly open and the inner part of copepod. (H) Enlarged view of the part marked "1" in (G). A large number of bacteria are colonized inside the copepod. (I) Higher magnification of the part marked "2" in (G). Bacteria densely colonize the inside of body.

times covered with bacteria which are attached polarly to the skeletal surface, but horizontal attachment usually predominated as was the case in three lakes reported by HOLLAND and HERGENRADER (1981). There is no information about mechanisms or causes of these different attachments.

Bacteria which produce exopolysaccharides (SUTHERLAND, 1977) occurred in some samples (Table 1); bacteria capable of producing slime were present on copepods obtained only from Stn. 1. Slime was found on the dorsal (Fig. 1B, C, E, F, G, H; Fig. 2D, E, F), ventral (Fig. 1D, J, L; Fig. 2B) and lateral (Fig. 1I; Fig. 2A) surfaces and appeared as filaments, interconnected fibers, or film.

2) Bacterial colonization of the inside of copepods

Evidence of the bacterial attachment to the inside of copepods is shown in Fig. 3. These bacteria appeared as a huge mass of cells (Fig. 3G, H, I). Specimens whose inside was attacked by bacteria also were colonized by bacteria on the body surface, although the number of bacteria attached externally to these specimens was not numerous. The incidence of copepods with interior bacteria was not determined due to observations on several specimens of copepods. NAGASAWA (1985) and NAGASAWA *et al.* (1985b) reported bacterial colonization of chaetognaths inside the body, among thin lateral bands of the body-wall musculature. As a result of such bacterial infection, the chaetognaths' shape changed and they looked abnormal. In contrast, copepods did not appear morphologically abnormal. Nevertheless, the marked growth of bacteria inside the body of copepod may be disadvantageous to swimming.

3) Incidence of copepods with bacteria

In January, June and July very few copepods with bacteria occurred in Tokyo Bay samples (Table 1), but in other months extremely high values of ICWB (92–100 %) were obtained at Stn. 1; copepods at Stn. 2 showed lower values of ICWB. In August the ICWB at both stations was similar, whereas in September (September 5) it was 2 times higher at Stn. 2 than at Stn. 1. Values of ICWB were also higher (17–54 %) at Stn. 2 between August and November than at that station in other months. At Stn. 1 both species (*A. omorii* and *A. plumosa*) having bacteria ranged from 0 to 100 %, whereas at Stn. 2 ICWB of *A. omorii* ranged from 0 to 3.6 % and that of *A. plumosa* from 0 to 54.3 % (Table 1). Such difference in ICWB may depend on the locality rather than species, since TAKAHASHI and FUROTA (1977) stated that chlorophyll *a* was higher at Stn. 1 than at Stn. 2 as well as dissolved oxygen.

Water temperatures and salinities at Stn. 1 were similar to those at Stn. 2 (Fig. 4). Most specimens of *A. omorii* with attached bacteria inhabited water with temperatures ranging from

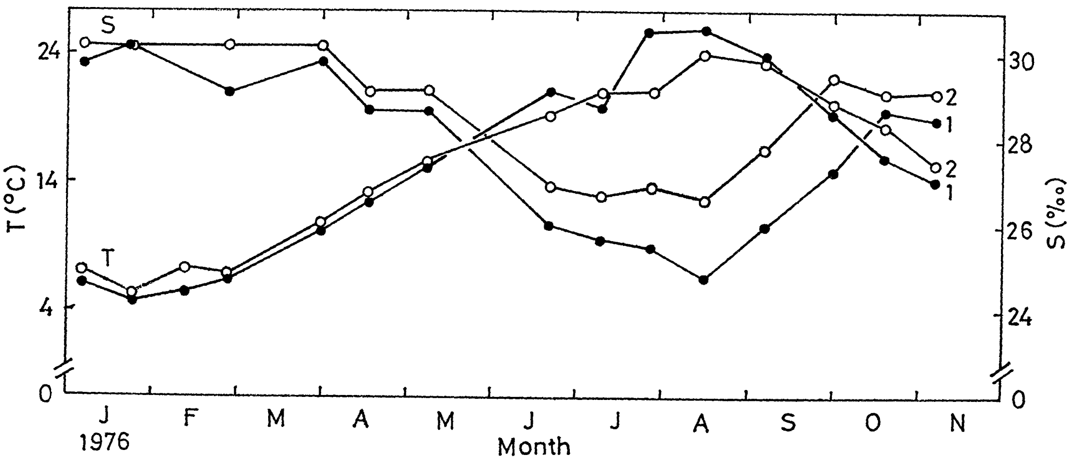

Fig. 4. Water temperature (T) and salinity (S) from January 6 through November 4, 1976 at a depth of 5 m. Salinity records were not available on February 10. Solid circle for Stn. 1 and open circle for Stn. 2.

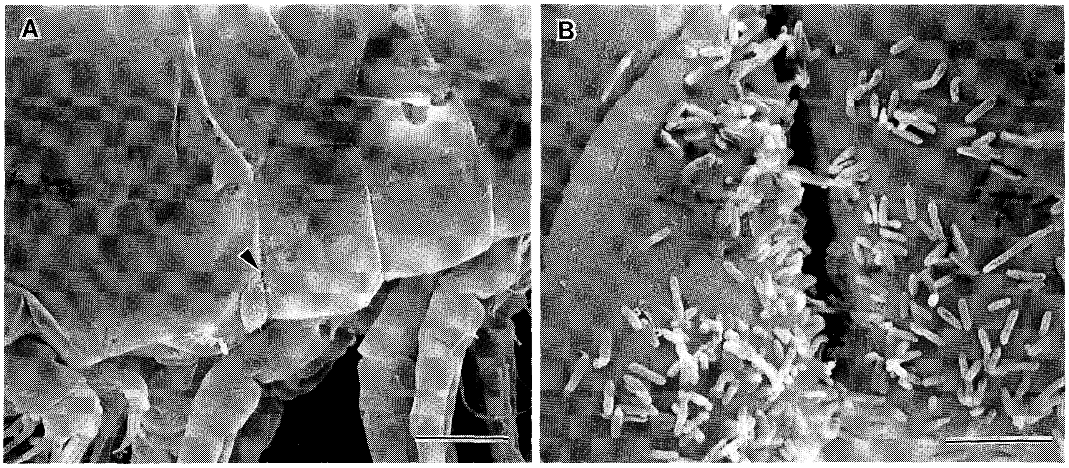

Fig. 5. Scanning electron micrographs of copepods collected at Stn. 7 in Tokyo Bay (see NAGASAWA and NEMOTO, in press) on June 10, 1984. Scale bars indicate 5 (B) and 50 μm (A). (A) Dark spots are present together with large numbers of tiny spots which are mass of either pores or slots on the lateral side of copepod. An arrow indicates the location of attachment of bacteria. (B) Enlargement of the part indicated by an arrow in (A). Two types of bacterial attachment, horizontal and polar attachments, are observed. Small pores and slots are found.

5.5 to 15.3°C and salinities from 28.7 to 30.2‰ S: most specimens of *A. plumosa* with bacteria were found at 16.0 to 26.1°C and from 24.8 to 29.5‰ S, respectively (Table 1, Fig. 4). UYE (1982) reported that ecological longevities of adult *A. clausi* s. l. vary from 9.8 to 1.4 days at temperatures ranging from 5.9 to 21.9°C. The ecological longevities of Tokyo Bay copepods may be similar to those estimate: the adults of each sample probably belong to different cohorts.

Woods Hole copepods had a high value of ICWB (83.8 %). The hydroids in Woods Hole harbor are reported to be particularly healthy and free from bacterial growths and debris in the early spring months, but in mid-summer contaminating organisms affect hydroids adversely (GRAVE, 1933). Woods Hole copepods may have a similar seasonal history of infection with bacteria.

4. Discussion

The presence of pores (Figs. 2 & 5) and slots (Fig. 5) on the skeleton adjacent to dense colonies of bacteria may represent sites of previous bacterial attachment. Sizes of these scars indicate either polar or horizontal attachment. Large numbers of scars, looking like dark spots, present a rough appearance. These scars suggest that bacterial attachment may damage copepod exoskeleton and may indicate that the relationship is not commensalism but parasitism. Another evidence supporting this hypothesis is bacterial invasion of the inner part of copepod (Fig. 3).

In Tokyo Bay waters during several months all adult copepods examined were colonized by bacteria. Similar results have been reported for adults of *Diaptomus nevadensis* in Goose Lake, Nebraska and those of *D. siciloides* in Branched Oak Lake, Nebraska (HOLLAND and HERGENRADER, 1981). High incidences of copepods with bacteria do not seem to be correlated with locality or season. This has serious implications for experimental studies of copepods. During experimental studies of physiological parameters of copepods (e.g. oxygen consumption) animals should be examined to determine the extent of bacterial attachment. The weight specific respiration rate or the Q_{O_2} of *Acartia clausi* s. l. and bacteria is 2–5 (IKEDA, 1974) and 1,000–3,000 μl O_2/mg dry weight/h (GALE, 1951), respectively. Adults of *A. clausi* are 1 mm in length and bacteria attached to this copepod are 1 μm long. Weight of bacteria is obtained from a length-weight relationship and corresponds to 10^{-9} of that of *Acartia*. In this study the highest density of bacteria is estimated as 10^4–10^5 per copepod. Therefore, the Q_{O_2} of bacteria with this density is calculated as 10^{-2}–10^{-1} μl O_2/mg dry weight/h which accounts for 1–10 % of the Q_{O_2} of copepod. The degree of infestation (>10^5 cells per copepod) may affect differences in respiratory rate for the same species which previously was interpreted as the result of different generations (GAULD and RAYMONT, 1953), size differences (MARSHALL and ORR, 1958), regional (CONOVER, 1959) and seasonal (MARSHALL and ORR, 1958; CONOVER, 1959; BERNER, 1962) variations. Antibiotics are sometimes added to prevent bacterial growth in water during experiments (see IKEDA, 1970). However, the effect of these antibiotics on bacteria previously established on the exoskeleton has not been determined. Substances which specifically suppress bacterial respiration may be more useful for future physiological studies.

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東京湾およびウッズホールにおける細菌付着のかいあし類の高い出現率

永　沢　祥　子

要旨: 走査電子顕微鏡による調査から，東京湾とウッズホールのカラヌス目かいあし類 *Acartia* spp. には細菌の付着が頻繁に起こっていることがわかった。東京湾のある試料では成体の 100 % に細菌が付着していた。これらの細菌の多くは粘質物を産生していた。ウッズホールからのかいあし類の 80 % 以上は細菌におおわれ，そのうちのいくつかには粘質物が存在した。かいあし類に垂直あるいは水平に付着した細菌の跡を示す小孔や細長い穴が細菌の濃密なコロニーの近くに観察された。細菌はかいあし類の体内にも存在することがあった。これは細菌の侵襲が体内に起こっていることを示すものである。これらのことから，地球的規模の現象であるかいあし類への細菌付着は片利共生ではなく寄生であろう。