RELATIONSHIPS BETWEEN MOUTHPART STRUCTURES AND *IN SITU* FEEDING HABITS OF FIVE NERITIC CALANOID COPEPODS IN THE CHUKCHI AND NORTHERN BERING SEAS IN OCTOBER 1988

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Abstract: The mouthpart structures and gut contents of the following five neritic calanoid copepods collected from the Chukchi and northern Bering Seas during the daytime in October 1988 were examined with scanning electron and light microscopes: *Acartia longiremis; Centropages abdominalis; Epilabidocera longipedata; Eurytemora herdmani; Tortanus discaudatus.* The sharpness of the mandibular ventralmost tooth and the fine structures of maxillary setae are evidently indicative of feeding habits. The mouthpart of *E. herdmani* with the lowest ventralmost tooth and regularly spinulose setae on all maxillary endites and endopod mainly suits suspension-feeding, whereas that of *T. discaudatus* with the sharpest ventralmost tooth and hooked, serrate setae only on the basal endite and endopod is specialized for raptorial feeding. Gut content analyses revealed that *A. longiremis, C. abdominalis, E. herdmani* and *E. longipedata* fed on various phytoplankter particles while *E. longipedata* and *T. discaudatus* preyed on zooplankters such as copepodids, appendicularians and polychaetes. Although *A. longiremis, C. abdominalis* and *E. longipedata* possibly employ both feeding modes, there were some differences in the mouthpart structures and food items. The feeding ecology of the five families containing these five species is briefly reviewed.

1. Introduction

The relationships between mouthpart structures and feeding habits of calanoid copepods have long been studied to clarify their niches in marine food webs (*e.g.* Esterly, 1916; Anraku and Omori, 1963; Turner, 1978; Ohtsuka and Onbé,1989, 1991). In particular, mandibular cutting edges and maxillae have been suggested to be strongly relevant to their feeding habits (Anraku and Omori, 1963; Arashkevich,1969; Itoh, 1970; Tranter and Abraham, 1971; Turner, 1978; Ohtsuka and Onbé,1989, 1991). Recent cinematographic studies on the feeding mode of calanoid copepods revealed that maxillae play the most important roles in suspension-feeding (previously reported as filter-feeding) (*e.g.* Koehl and Strickler, 1981; Paffenhöfer *et al.*, 1982;

PRICE and PAFFENHÖFER, 1986).

Our recent investigations on the in-situ feeding habits of calanoids have shown that carnivory, saphrophagy and coprophagy have been commonly found in these copepods. Suspension-feeding calanoids frequently prey on microzooplankters such as ciliates and copepod nauplii (OHTSUKA and HIROMI, 1987; OHTUSKA, 1991). Selective predation on appendicularians has been found in the family Candaciidae (OHTSUKA and ONBÉ,1989; OHTSUKA and KUBO, 1991). The genera *Labidocera* and *Pontellopsis* belonging to the family Pontellidae show completely different in-situ feeding habits, the former feeding mainly on both copepod nauplii and particles and the latter preying on various copepodids (OHTSUKA and ONBÉ, 1991). The family Scolecitrichidae frequently utilizes detrital matter such as discarded appendicularian houses and copepod carcasses and/or exuviae (ALLDREDGE, 1972; NISHIDA et al., 1991; OHTSUKA, 1991; OHTSUKA and KUBO, 1991; FERRARI and STEINBERG, 1993). Coprophagy is also widely known in suspension-feeding calanoids (HATTORI, 1989; NOJI et al., 1991; OHTSUKA et al., 1993). Thus feeding habits in calanoid copepods have been revealed to be much more complex than previously expected.

The present paper deals with the relationships between the mouthpart structures and in-situ feeding habits of five species of neritic calanoids, *Acartia longiremis, Centropages abdominalis, Epilabidocera longipedata, Eurytemora herdmani* and *Tortanus discaudatus,* collected from the Chukchi and northern Bering Seas in October 1988, and briefly reviews the feeding ecology of the families containing these five species.

2. Materials and Methods

Plankton samples were collected at five stations in the Chukchi and northern Bering Seas during the daytime from 5 to 17 October 1988, where the five neritic calanoid species were relatively abundant: Stns. 23 (5 Oct.) and 121 (17 Oct.) in the Bering Sea, Stn. 115 in the Bering Strait (17 Oct.), Stns. 46 and 48 in the Chukchi Sea (9 Oct.) (Fig. 1). Water temperature and salinity at each station were briefly reported in HATTORI et al. (1991). The vertical distribution of chlorophyll a at each station except for Stn. 48 was measrured with a Turner Designs Fluorometer (McROY, 1988). The sampling methods and gear used were described in our previous papers (HATTORI et al., 1991; OHTSUKA et al., 1993). Intact adult females of the above five species and males of *Epilabidocera longipedata* and *Tortanus discaudatus* were picked up from the original or split samples for observation of the mouthpart structures and gut contents. The body lengths of the five species and the numbers of individuals examined are presented in Table 1. Before dissection the gut fullness was examined for *A. longiremis* and *E. herdmani*: the relative length of gut containing some contents in whole prosome against the prosomal gut length. We were unable to determine the gut fullness of female *C. abdominalis* owing to their blackish developed ovaries.

The mandibular cutting edges and maxillae of all species and the gut contents of *Acartia longiremis, Centropages abdominalis* and *Eurytemora herdmani* were observed with a scanning electron microscope (JEOL JSM-T20), and the gut contents of *Epilabidocera longipedata* and *Tortanus discaudatus* were observed with a differential interference contrast microscope (Nikon Optiphot). The grouping of mandibular teeth
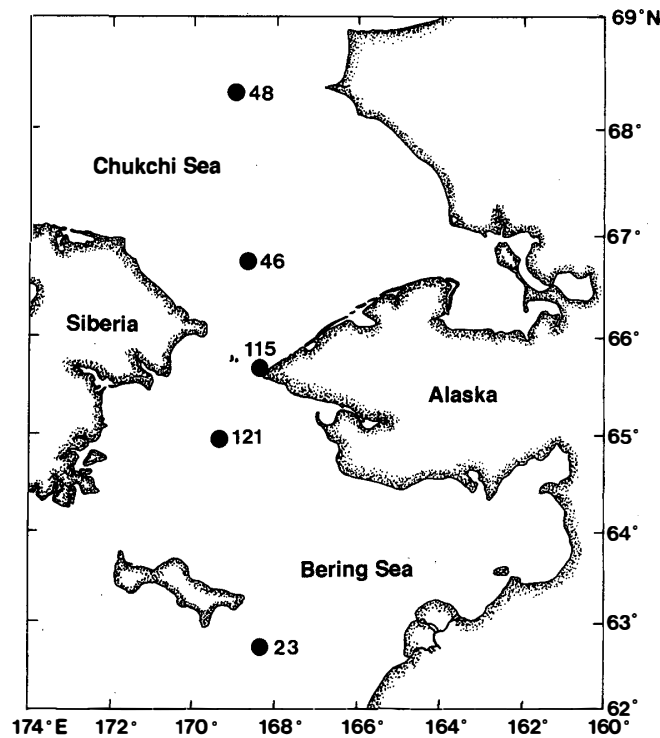
Fig. 1. Locations of sampling stations in the Chukchi and
         northern Bering Seas on 5–17 October 1988.

Table 1. Body lengths and numbers of individuals of five species. (n): number of individuals examined.

Species	Sex	Body length (mm)		Number of individuals examined for gut content analysis at each station
		Range	Mean±s.d.	
Acartia longiremis	♀	0.96–1.35	1.07±0.07 (38)	Stn. 23 (4), Stn. 46 (24), Stn. 48 (21), Stn. 115 (10)
Centropages abdominalis	♀	1.48–2.10	1.80±0.18 (25)	Stn. 46 (7), Stn. 48 (4) Stn. 115 (2), Stn. 121 (7)
Epilabidocera longipedata	♀	3.68–3.93	(2)	Stn. 46 (2)
	♂	2.78–3.28	3.01±0.20 (5)	Stn. 46 (4)
Eurytemora herdmani	♀	0.73–1.39	1.19±0.15 (19)	Stn. 46 (8), Stn. 115 (6)
Tortanus discaudatus	♀	1.95–2.33	2.17±0.13 (7)	Stn. 46 (8), Stn. 48 (1)
	♂[1]	1.36–2.00[2]		

[1]Used only for observation of mouthparts. [2]From BRODSKY (1950).

was based on BEKLEMISHEV (1959), SULLIVAN et al. (1975) and TURNER (1978) although
the central and dorsal teeth are not distinguished here.

3. Results

3.1. Environmental data

Surface and bottom water temperature and salinity at each station were described
by HATTORI et al. (1991). At Stn. 48 in the Chukchi Sea and Stn. 23 in the Bering Sea
weak thermocline and halocline were observed at depths of about 40 and 20 m,
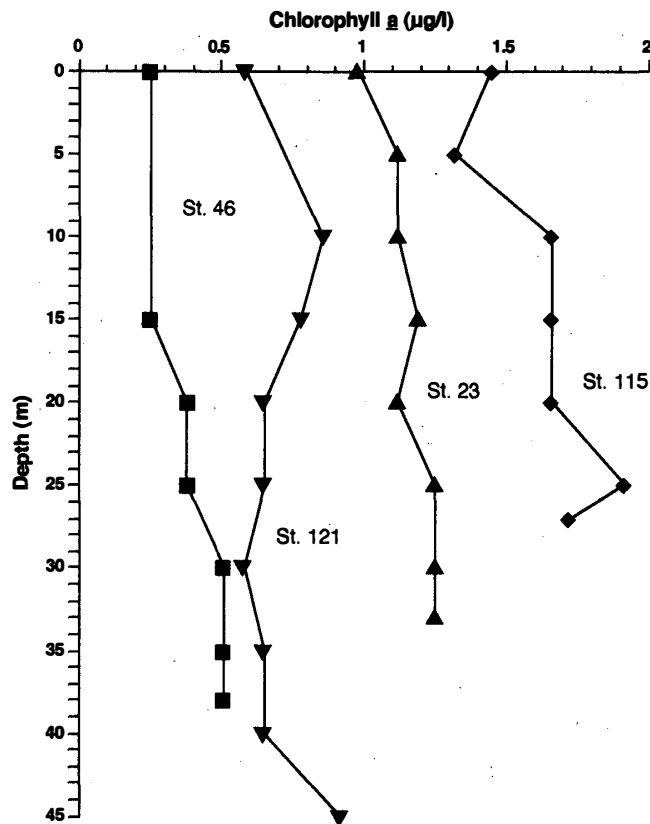respectively (see McROY, 1988). The vertical profile of chlorophyll a concentration is

*Fig. 2. Vertical profile of chlorophyll a at Stns. 23, 46, 115
and 121.*

shown in Fig. 2 on the basis of the data compiled by McRoy (1988). Chlorophyll *a* concentration was relatively low at all stations, ranging from 0.25 (Stn. 46) to 1.92 (Stn. 115) $\mu g/l$, but was slightly higher in the Bering Sea and the Bering Strait than in the Chukchi Sea. No marked vertical gradient of chlorophyll *a* was observed at any station.

3.2. Mandibular cutting edge

The mandibular cutting edges of the five species are shown in Figs. 3A, B, 4 and 7A. The ventralmost tooth (V1) is monocusped in all species, but their sharpness is very different between the species.   The second ventral tooth (V2) is monocusped in *Epilabidocera longipedata* (Fig. 4B) and *Tortanus discaudatus* (Fig. 7A), and bicusped in *Acartia longiremis* (Fig. 3A), *Centropages abdominalis* (Fig. 4A) and *Eurytemora herdmani* (Fig. 4D).   The ventralmost teeth of *E. longipedata* (Fig. 4B) and *T. discaudatus* (Fig. 7A) are sharper than those of any other species, whereas that of *E. herdmani* (Fig. 4C, D) bluntest. The number and shape of the central and dorsal teeth are different in the five species: seven relatively sharp mono- or bicusped teeth in *A. longiremis* (Fig. 3A, B); six blunt, mono- or polycusped teeth in *E. herdmani* (Fig. 4C, D) and *C. abdominalis* (Fig. 4A); three pointed, mono- or bicusped teeth in *E. longipedata* (Fig. 4B) and *T. discaudatus* (Fig. 7A).

The dagger-like spinules near the base of the central and dorsal teeth differ in length and number in the five species. The spinules are most developed in *E. longipedata* (Fig. 4B) and *T. discaudatus* (Fig. 7A) and least in *A. longiremis* (Fig. 3A) and *E. herdmani*
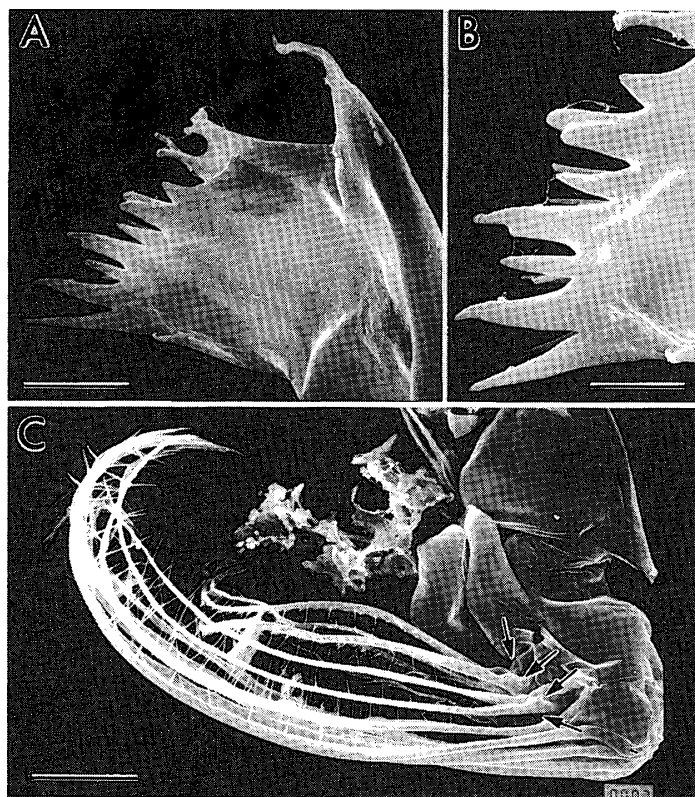
Fig. 3. Acartia longiremis, *female. A. Mandibular cutting edge;*
B. Dorsal teeth of mandibular cutting edge; C. Maxilla,
praecoxal and coxal endites (arrowed). Scale = 10 μm
(A,C); 5 μm (B).

(Fig. 4C, D).

3.3. Maxilla

The maxillae of the five species are depicted in Figs. 3C, 5, 6 and 7B–D. Except for *Tortanus discaudatus* (Fig. 7B), developed setae on the praecoxal, coxal and basal endites and endopod are furnished with rows of fine setules almost perpendicular to the seta along the inner margin (Fig. 6). The distance between two contiguous setules greatly changes in these species and on different setae of a species. The distance between two contiguous setules ranges from less than 5 μm in *Eurytemora herdmani* to about 40 –50 μm in *Epilabidocera longipedata* in the middle part of the endopodal setae. In *Acartia longiremis* (Fig. 3C), *Centropages abdominalis* (Fig. 5A) and *E. longipedata* (Fig. 5B) setae on the basis and endopod are more developed than those on the praecoxa and coxa, while in *E. herdmani* (Fig. 5D), those on both the praecoxa and coxa, and the basis and endopod, are equally developed. These setal tips are finely serrated along the inner margin in these four species (see Fig. 5C).

Tortanus discaudatus has quite different maxillae from the other species (Fig. 7B–D). The development of the endopodal setae and the reduction of the praecoxal and coxal setae are characteristic of this species. These endopodal setae are entirely serrate along the inner margin with a hook on the tip (Fig. 7C, D).
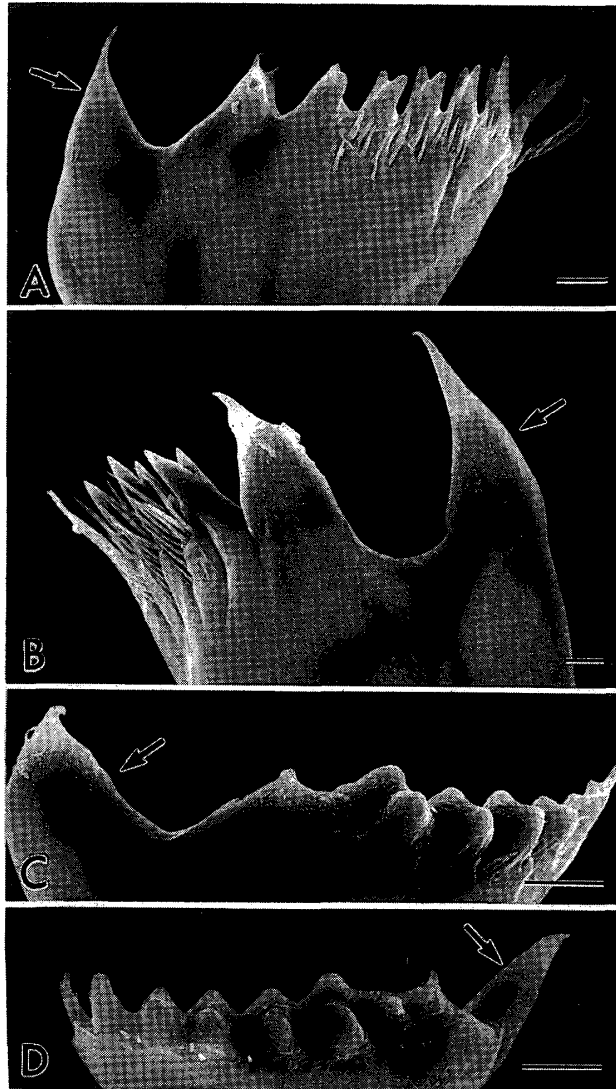
Fig. 4. Mandibular cutting edges, ventralmost tooth
(arrowed). *A.* Centropages abdominalis,
female; B. Epilabidocera longipedata, *female;*
C, D. Eurytemora herdmani, *female. Scale=10*
μm (A-D).

3.4. Gut contents

Individuals of *Acartia longiremis* with an empty gut ranged from 8.3% (Stn. 115) to 44.4% (Stn. 23), but the gut fullness was very low at all stations; 95.8–100.0% of individuals contained only a small amount of gut contents ($<1/4$). In contrast, no individuals of *Eurytemora herdmani* had an empty gut, and 66.6% (Stn. 46)–66.7% (Stn. 115) of individuals had a relatively large quantity of gut contents ($>1/4$). Although the gut fullness was not determined in *Centropages abdominalis*, a large amount of contents was frequently found in the guts. Individuals of *Tortanus dis-caudatus* with an empty gut numbered 11.1% (Stns. 46 and 48).

In the guts of *A. longiremis* (Fig. 8), *C. abdominalis* (Fig. 9) and *E. herdmani* (Fig. 10), various diatoms and dinoflagellates were detected. However, in *A. longiremis*, only
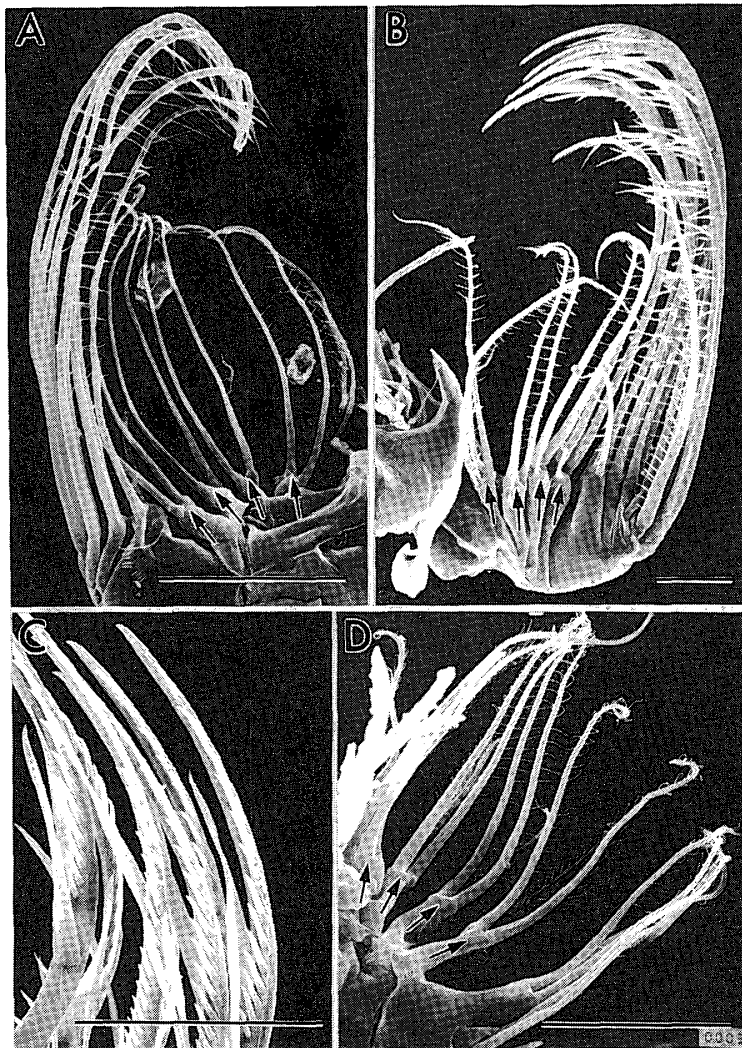
Fig. 5. Maxillae, praecoxal and coxal endites (arrowed). A. Centropages abdominalis, female; B. Epilabidocera longipedata, female; C. Tips of termial maxillary setae of Epilabidocera longipedata, female; D. Eurytemora herdmani, female. Scale = 100 μm (A–C); 50 μm (D).

minute diatom fragments were found in small quantity, whereas in C. abdominalis and E. herdmani, slightly damaged (perhaps due to maceration by mandibles), large diatoms and dinoflagellates were frequently detected. In the guts of C. abdominalis, relatively large, almost intact frustules and plates of phytoplankters such as Protoperidinium sp. (Fig. 9A: ca. 54 μm in largest dimension), Coscinodiscus sp. (Fig. 9C; about 51 μm in diameter) and Stephanopyxis sp. (Fig. 9B) were found.   Protoperidinium sp. was found solely in the guts of C. abdominalis. Also in the guts of E. herdmani a variety of diatoms such as Navicula sp. (Fig. 10A; over 65 μm long), Thalassiosira spp.(Fig. 10B, C) and unidentified species (Fig. 10D; ca. 27 μm long) were observed.

In the guts of females of Epilabidocera longipedata (Stn. 46) an incompletely digested polychaete (Fig. 11A) and copepod fragments (Fig. 11B) were detected together with diatom fragments and unidentified remains. Copepod and some crustacean fragments, diatom fragments (Fig. 11C) and unidentified remains were found in
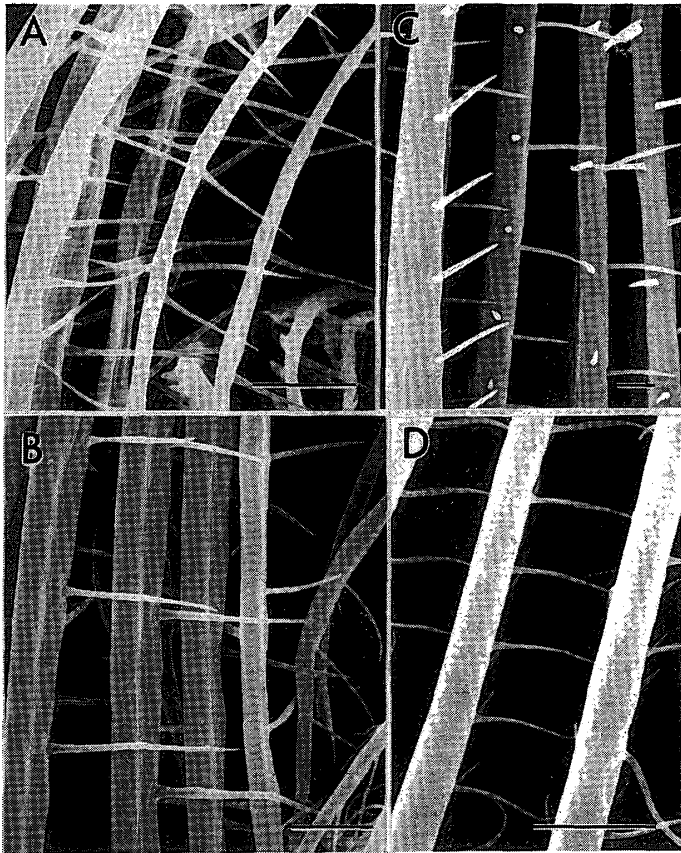
Fig. 6. Maxillary setae. A. Acartia longiremis, female, basal and endopodal setae; B. Centropages abdominalis, female, basal and endopodal setae; C. Epilabidocera longipedata, female, endopodal setae; D. Eurytemora herdmani, female, syncoxal setae. Scale = 10 μm (A–C); 5 μm (D).
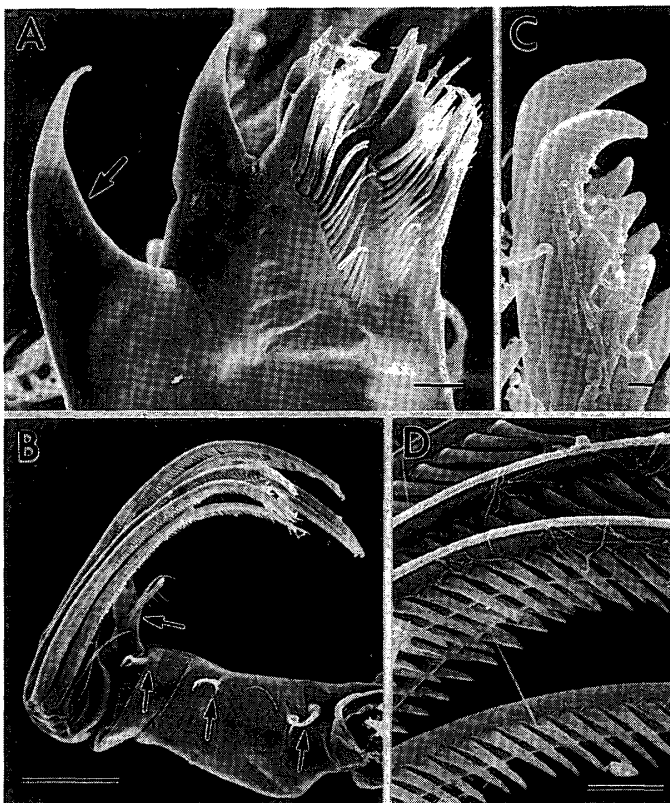

Fig. 7. Tortanus discaudatus, male. A. Mandibular cutting edge, ventralmost tooth arrowed; B. Maxilla, praecoxal and coxal endites (arrowed); C. Tips of endopodal setae of maxilla; D. Middle part of terminal setae of maxilla. Scale = 10 μm (A,D); 100 μm (B); 1 μm (C).

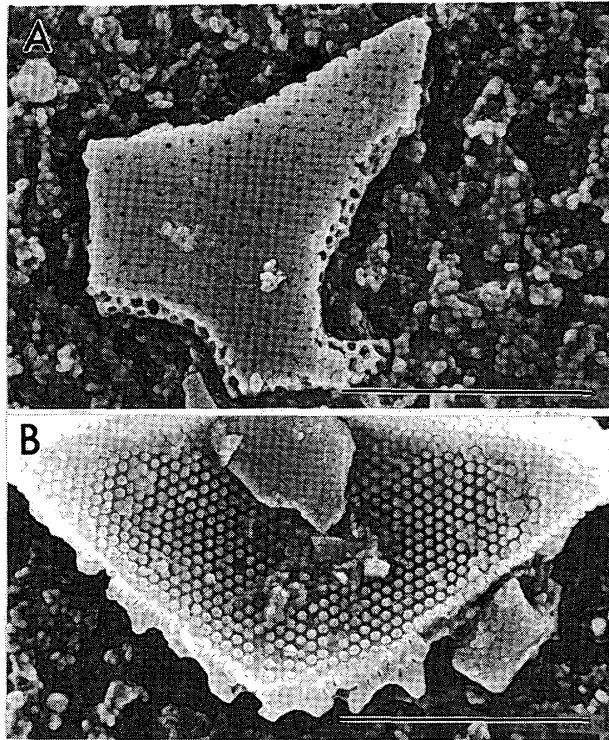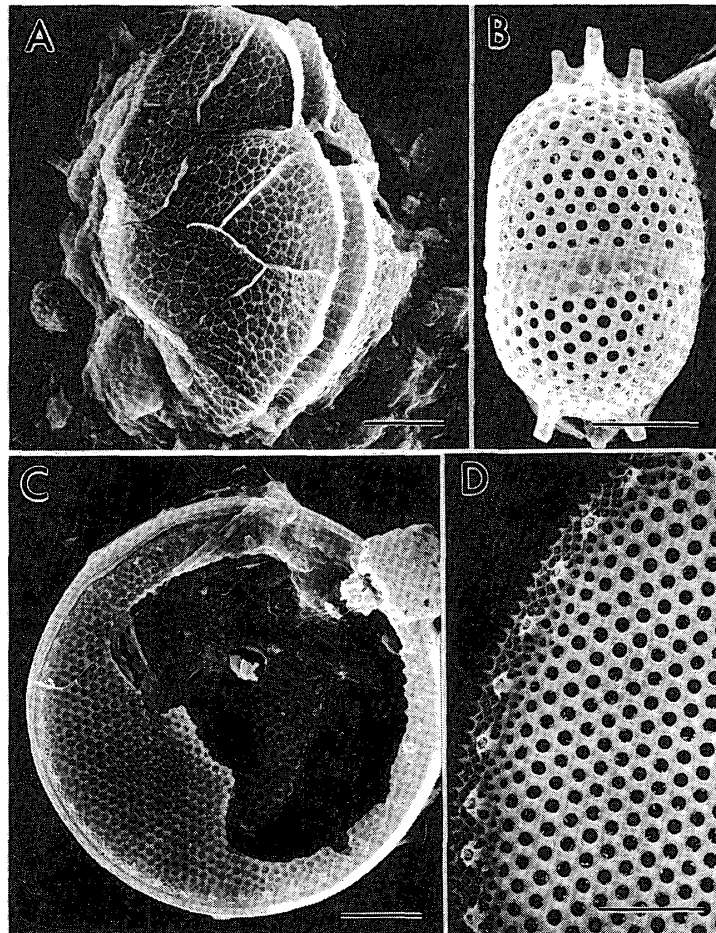*Fig. 8. Gut contents of* Acartia longiremis, *female, Stn. 48. A, B. Fragments of centric diatoms. Scale = 10 μm.*

Fig. 9. Gut contents of Centropages abdominalis, *female, Stn. 121 (A–C), Stn. 46 (D). A.* Protoperidinium *sp.; B.* Stephanopyxis *cf.* nipponica; *C. Unidentified centric diatom; D.* Thalassiosira *sp. Scale = 10 μm (A–C); 5 μm (D).*
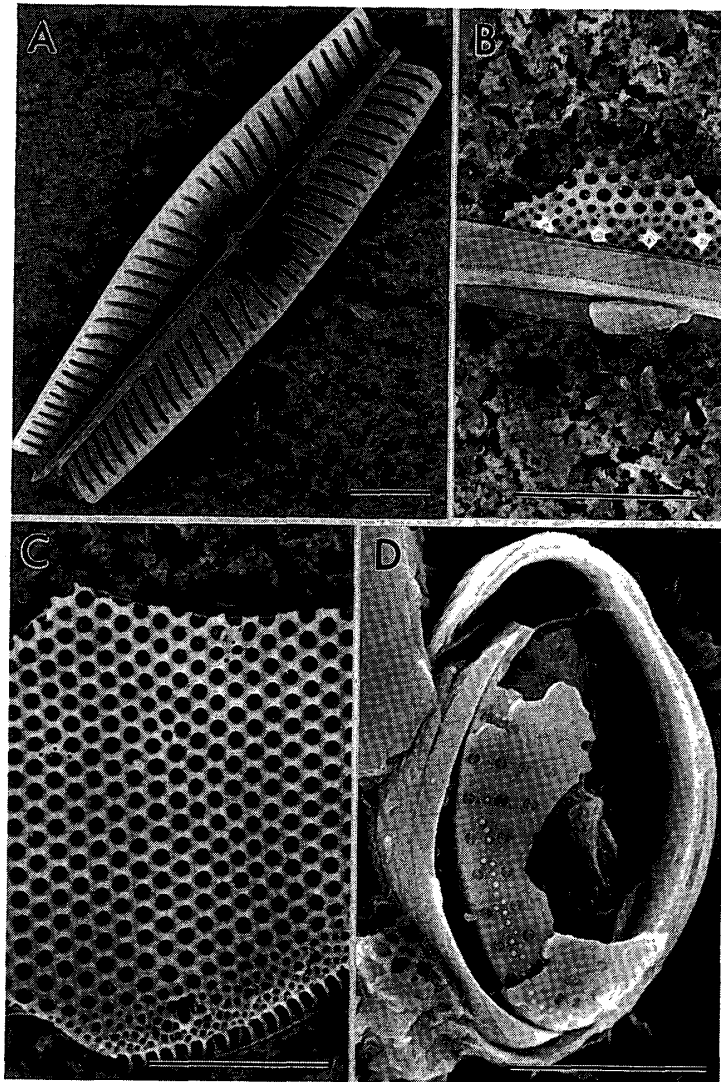
Fig. 10. *Gut contents of* Eurytemora herdmani, *female, Stn. 46. A.
Navicula cf. yarrensis; B–D. Unidentified diatom fragments.
Scale=10 μm (A–C); 5 μm (D).*

the guts of two of the three males (Stn. 46).

Copepod fragments (Fig. 12A), polychaete spines (Fig. 12B) and probably appendicularian fecal pellets (Fig. 12C) were observed in the guts of female *Tortanus discaudatus* at Stns. 46 and 48. The length of polychaete spines was over 0.3 mm. Contents other than these prey zooplankters were unidentified crustacean fragments, minute particles such as diatom fragments, and unidentified remains. The particles found in the guts may have been derived from prey zooplankters.

4. Discussion

Mandibular gnathobases are a good indicator of feeding habits of calanoids (Anraku and Omori, 1963; Arashkevich, 1969; Itoh, 1970; Ohtsuka, 1991). Generally the ventral teeth become sharper in raptorial predators than in suspension feeders
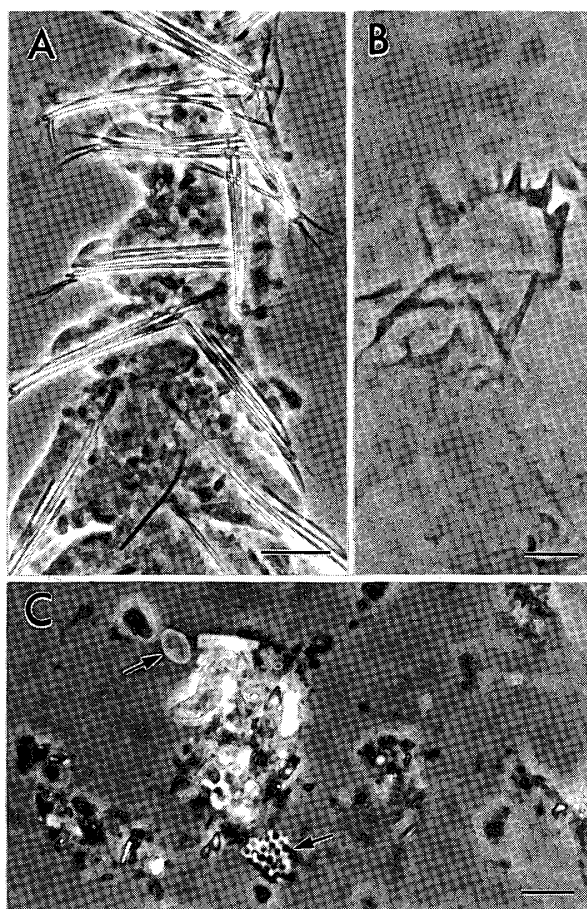
Fig. 11. Gut contents of Epilabidocera longipedata, female (A), male (B, C), Stn. 46. A. Polychaete; B. Copepod mandible; C. Unidentified remains and diatom fragments (arrowed). Scale=50 μm (A); 10 μm (B, C).

(OHTSUKA, 1991). The fewer number of teeth also indicates the strength of carnivory (ITOH, 1970; OHTSUKA, 1991). Tortanus discaudatus, with the sharpest ventralmost tooth of the five species and only five teeth in total, undoubtedly exhibits strong carnivory, whereas Eurytemora herdmani with the bluntest ventralmost tooth and eight teeth, the least carnivory (Fig. 4C, D). Dagger-like spinules on the mandibular gnathobase tend to be more developed in Epilabidocera longipedata (Fig. 4B) and Tortanus discaudatus (Fig. 7A), and less in Acartia longiremis (Fig. 3B), Centropages abdominalis (Fig. 4A) and Eurytemora herdmani (Fig. 4C, D). In the Pontellidae and Tortanidae containing the former two species, which exhibit strong carnivory, these spinules may be so developed as to groom the cutting edges (OHTSUKA, 1991).

Maxillae are diversified in calanoids, in particular, deep-sea species (cf., ARASHKE-VICH, 1969). Some evident correlations between their structures and feeding habits have been found (ANRAKU and OMORI, 1963; ARASHKEVICH, 1969; ITOH, 1970; TURNER, 1978; SCHNACK, 1982, 1989; OHTSUKA, 1991). Among these the following characteristics are most important to study their feeding habits: (1) the development of basal and/or endopodal setae compared with praecoxal and coxal ones; (2) the development of setules or spinules along the inner margin of setae; (3) the presence of stout setae or spines on
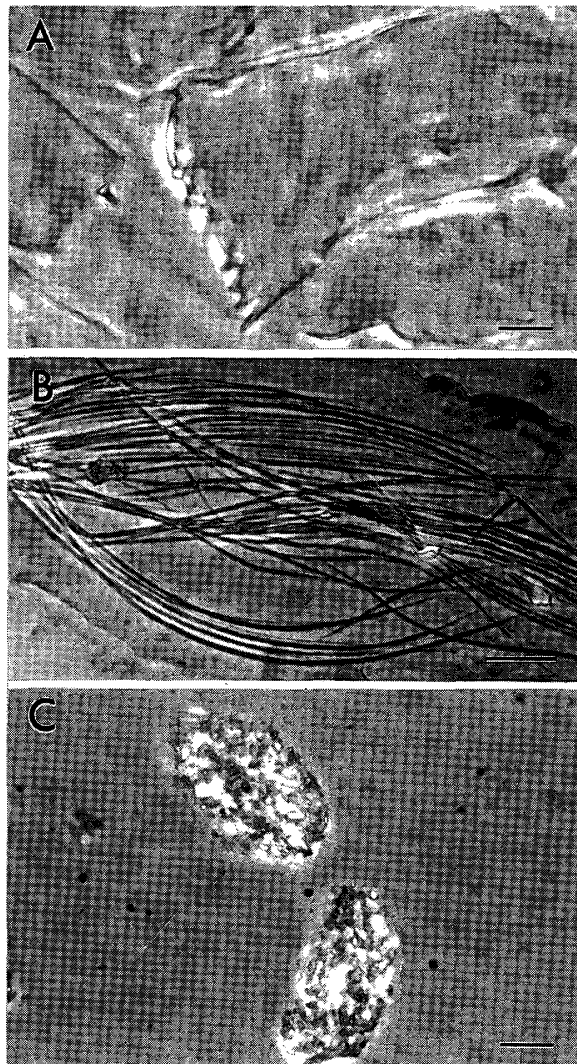
Fig. 12.   Gut contents of Tortanus discaudatus, female,
           Stn. 48 (A, B), Stn. 46 (C). A. Copepod
           mandible; B. Parapodium setae of polychaete;
           C. Appendicularian fecal pellets. Scale=10
           μm (A, C); 50 μm (B).

the basis and/or endopod. Calanoids with rows of fine setules along the inner margin of
a developed seta and perpendicular to it (Fig. 6) obviously employ suspension-feeding.
This is because suspension-feeding calanoids such as Eucalanus (Koehl and Strickler,
1981; Paffenhöfer et al., 1982), Acartia (Rosenberg, 1980) and Centropages (Cowles
and Strickler, 1983) all have such setae on the maxillae (Ohtsuka, 1991). Therefore,
A. longiremis, C. abdominalis, E. longipedata and E. herdmani most likely use them for
suspension-feeding.   Among these four species the basal and endopodal setae are
relatively developed compared with the praecoxal and coxal ones in A. longiremis (Fig.
3C), C. abdominalis (Fig. 5A) and E. longipedata (Fig. 5B), whereas setae on all the
endites and the endopod are equally developed in E. herdmani (Fig. 5D). This suggests
that the chopstick raptorial mode is relatively stronger in the former than in the latter.
Probably T. discaudatus employs only raptorial feeding because serrate setae on the

second coxal and the basal endites and the endopod suit grasping large food. The reduction of setae on the praecoxal and the coxal endites (Fig. 7B) and the formation of the hook on the setal tip (Fig. 7C) are more conspicuous in *T. discaudatus* than in *A. longiremis, C. abdominalis* and *E. longipedata,* suggesting that its maxillae exclusively function as "chopsticks" for capture of large prey zooplankters (OHTSUKA, 1991).

Maxillules are remarkably modified only in *Tortanus* (OHTSUKA *et al.,* 1987; present study): the terminal three setae on the elongate coxal endite are serrated as in the maxillae; the basis, endopod and exopod are completely reduced. This modification seems to play a supplementary role in grasping prey zooplankters with the maxillae.

The relationships between the mouthpart structures, the main food items and the possible feeding modes of the five species are summarized in Table 2 based on the present and previous data. The ventralmost teeth of the mandible and the development and characteristics of setae on the endites and the endopod of maxilla clearly reflect their main food items. *A. longiremis* (Family Acartiidae), *C. abdominalis* (Family Centropagidae), *E. herdmani* (Family Temoridae) and *E. longipedata* (Family Pontellidae) probably employ suspension-feeding for small particles. Raptorial feeding for relatively large particles and zooplankters is employed by all five species. However, raptorial feeding seems to be most intense in *E. longipedata* and least in *E. herdmani* of these four species. On the other hand *T. discaudatus* (Family Tortanidae) appears to be a typical raptorial feeder.

The families Acartiidae and Temoridae have been believed to be particle feeders with suspension-feeding (ITOH, 1970; TURNER, 1983, 1984, 1991; OHTSUKA, 1991), as confirmed also in the present study. However, some species are reported to exhibit carnivory (DAVIS, 1977; TURNER, 1983, 1991; OHTSUKA, 1991). DAVIS (1977) suggested that *A. longiremis* occurring in high latitudes employs a special feeding strategy, *viz.,* switching from particle feeding to carnivory in the dark winter period when phytoplankters completely disappear in the water column. No zooplankter remains were, however, detected in the guts of *A. longiremis* collected in October just before the dark winter

Table 2. *Summary of relationships between mouthpart structures, main food items and possible feeding modes of five species. V1: ventralmost tooth; V2: second ventralmost tooth; No.: number of teeth; L: lowest; S: sharpest; I: intermediate; B: bicusped tip; M: monocusped tip. PC: praecoxal and coxal endites; BE: basis and endopod; P: well developed, regularly spinulose setae; E: well developed, serrate setae; =: setae on all endites and endopod well developed; <: basal and endopod setae more developed than praecoxal and coxal ones. ●: main feeding mode; ◎: feeding mode frequently employed; ○: feeding mode rarely employed; —: impossible feeding mode.*

Species	Mouthpart structures					Main food items	Possible feeding modes	
	Mandible			Maxilla			Suspension feeding	Raptorial feeding
	V1	V2	No.	PC	BE			
Eurytemora herdmani	L	B	8	P=P		Phytoplankters	●	○
Acaria longiremis	I	B	9	P<P		Phytoplankters, Micro- & Macrozooplankters	●	◎
Centropages abdominalis	I	B	8	P<P		Phytoplankters, Microzooplankters	●	◎
Epilabidocera longipedata	S	M	5	P<P		Phytoplankters, Micro- & Macrozooplankters	○	●
Tortanus discaudatus	S	M	5	P, E<E		Micro- & Macrozooplankters	—	●

period in the present study. Seasonal switching in feeding has also been suggested in other calanoid copepods in Greenland (DIGBY, 1954). *E. herdmani* can be cultured by feeding only flagellates and diatoms in the laboratory (GRICE, 1971), which supports the conclusion that *E. herdmani* hardly depends on carnivory.

The feeding habits of the Centropagidae and Pontellidae are more complex than those of the former two families. In the Seto Inland Sea and its environs, western Japan, two oceanic species of the Centropagidae, *Centropages calaninus* and *C. gracilis* voraciously preyed on copepodids and copepod nauplii, whereas two neritic species, *C. abdominalis* and *C. tenuiremis*, mainly fed on phytoplankton particles with some microzooplankters such as tintinnids and copepod nauplii (OHTSUKA, 1991). *C. abdominalis* in the present study exclusively fed on phytoplankton particles. The particle size spectrum in the guts of the species was *ca.* 10–60 μm in the Bering and Chukchi Seas, which falls within that of the same species occurring in the Seto Inland Sea (OHTSUKA, 1991). The genera of the Pontellidae were classified into two groups based on the mouthpart structures and feeding modes (OHTSUKA and ONBÉ, 1991); *Epilabidocera* belongs to "Type I" which employs both suspension and raptorial feeding modes, feeding on both various zooplankters and particles. PARK (1966) observed that *E. longipedata* (as *E. amphitrites*) is omnivorous but prefers animal diets to diatoms. The present observation of *E. longipedata* supports PARK's (1966) observation.

The family Tortanidae is undoubtedly a true carnivore. Many species of the family have been reported to prey on a variety of zooplankters such as copepodids, copepod nauplii, cladocerans, polychaetes and tintinnids in fields and laboratories (JOHNSON, 1934; AMBLER and FROST, 1974; MULLIN, 1979; ROBERTSON, 1983; OHTSUKA et al., 1987; OHTSUKA, 1991). Although *T. discaudatus* in the present study preyed on a variety of zooplankters, MULLIN (1979) found in the laboratory that *T. discaudatus* prefers larger copepodids to smaller copepod nauplii. LANDRY (1981) mentioned as a personal communication from P. Donaghay that *T. discaudatus* had been observed with its gut full of phytoplankters during blooming in Puget Sound. However, OHTSUKA (1991) examined gut contents of 150 individuals of adults of *T. gracilis* and of 83 of *T. forcipatus* collected from different regions in the Seto Inland Sea during September–December, but had never encountered such a case. Therefore this seems to have been caused by cod-end feeding.

Acknowledgments

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