FEEDING ECOLOGY OF COPEPODID STAGES OF *EUCALANUS BUNGII* IN THE CHUKCHI AND NORTHERN BERING SEAS IN OCTOBER 1988

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Abstract: Gut contents of the third to sixth copepodid stages of *Eucalanus bungii* (except for the sixth copepodid stage of male) from the Chukchi and northern Bering Seas in October 1988 were investigated with a light and a scanning electron microscopes. According to LM analysis all the copepodid stages of *E. bungii* fed on diatoms, dinoflagellates, tintinnids, crustaceans, and mineral particles. SEM examinations of gut contents of the fourth and fifth copepodid stages revealed that they ingested fecal pellets and discarded houses of oikopleurid larvaceans in addition to phytoplankton cells, suggesting that *E. bungii* showed coprophagy and saprophagy. The presence of an oil drop in the prosome and the reduced, thread-like gut of *E. bungii* indicated that *E. bungii* in the Chukchi and northern Bering Seas in October may supposedly have been originated from non-feeding diapausing stocks in deep-waters or prediapausing stages in the southern seas.

1. Introduction

Eucalanus bungii is a subarctic oceanic calanoid copepod and predominantly distributed in the central and western parts of the Bering Sea in early summer (Motoda and Minoda, 1974). Miller *et al.* (1984) investigated the life cycle of *E. bungii* in the northeastern Pacific in detail, and have come to a conclusion that *E. bungii* appears to be typically biennial and its third to sixth copepodid stages overwinter in deep waters. In the northeastern Pacific, *E. bungii* feeds, reproduces and develops in the mixed layer only in mid-April to mid-July, and descends to depths between 250 and 500 m by September (Miller *et al.*, 1984).

Eucalanus bungii has been regarded as a typical particle-feeder (Itoh, 1970; Cooney and Coyle, 1982; Miller *et al.*, 1984). Lately Turner (1984) examined with SEM the fecal pellet contents of a congeneric species, *E. pileatus*, from the Gulf of Mexico, and concluded it to be a primarily opportunistic herbivore.

The present paper studies gut contents of the copepodid stages of *Eucalanus bungii* collected from the Chukchi and northern Bering Seas in October 1988 with a light and

a scanning electron microscopes and the presence of an oil drop in their prosomes.　In *E. bungii* from the North Pacific the absence of contents in the gut and the presence of the oil drop are indicators of diapausing copepods (Miller *et al.*, 1984).　The life history of *E. bungii* in the Chukchi and northern Bering Seas is inferred from these observations and previous works.

2.　Materials and Methods

Plankton samples were collected with a NORPAC net (mesh size: 0.33 mm) towed vertically from the near-bottom to the surface in the Chukchi and northern Bering Seas from 3 to 18 October 1988 (Fig. 1).　The samples were fixed in 10% neutralized formalin/seawater immediately after capture.　For the gut content analysis of copepodid stages of *Eucalanus bungii*, we used intact specimens from Stns. 31, 69, 118, 119, 120, 121, and 123, where *E. bungii* was relatively abundant (Hattori *et al.*, 1991).　All
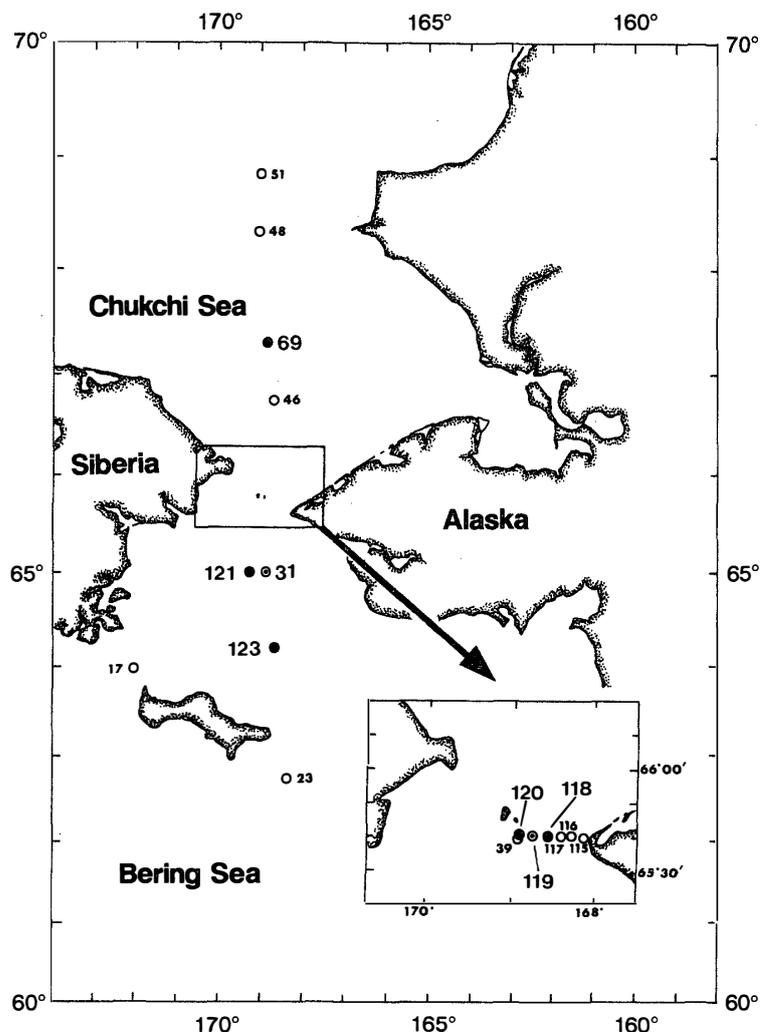
Fig. 1.　Location of sampling stations in the Chukchi and northern Bering Seas.　Closed circles: stations for gut content analysis with LM; Double circles: stations for gut content analysis with SEM; Open circles: stations not examined in the present study.

intact copepodids of *E. bungii* were picked up from the original or split samples, and identified based on JOHNSON's (1937) description of the developmental stages of *E. bungii*. Gut contents of 126 individuals of the second (CII) to sixth (CVI) copepodid stages from Stns. 69, 118, 120, 121 and 123 were examined with an interference differential microscope (Nikon Optiphot), and those of 15 individuals of CIV and CV from Stns. 31 and 119 with a scanning electron microscope (Jeol JSM-T20). The first copepodid stage (CI) was not included in the samples. The methods of gut content analysis with LM and SEM were described in our previous papers (OHTSUKA *et al.*, 1987; OHTSUKA and ONBÉ, 1989; OHTSUKA and KUBO, 1991).

The presence of a visible oil drop in the prosome of *Eucalanus bungii* which is an indicator of diapause (MILLER *et al.*, 1984) was examined under a binocular microscope before dissection for gut content analysis.

3. Results

Gut contents of *Eucalanus bungii* are depicted in Figs. 2–5. The frequency of occurrences of main items in the guts at each station is shown in Table 1. Centric and pennate diatom fragments (Figs. 2A–D, 3A–C, 4A–D) were most frequently detected in the guts of CIII to CVI at all the stations. Not only solitary diatoms such as *Coscinodiscus* and *Thalassiosira* (Figs. 2A, 3B, C) but chain-forming ones such as *Chaetoceros* and *Melosira* (Figs. 2C, 3C, 4D) were observed in the guts. Diatom resting spores (Fig. 4C) were also found in the guts of CIII to CV. A dinoflagellate, *Prorocentrum* sp. and tintinnids were rarely found in the guts of CIV and CV only from Stns. 121 and 123, and from Stns. 69, 121 and 123, respectively. Crustacean fragments (Fig. 3D) were also detected in the guts of CIII to CV at Stns. 31, 69 and 121 with low frequency. Unidentified remains and mineral particles of variable sizes were main items in almost all the guts of CIII to CVI irrespective of locality. All the copepodid stages except CII had some gut contents regardless of locality (Table 1). Diatoms were detected in all copepodid stages at all stations (average = 82.2%). Individuals with an empty gut were only 12.3% on an average.

Numerous fine fibers were observed in the gut contents, and pore structures composed of the fibers were observed at Stns. 31 and 119 (Fig. 5A, B, indicated by arrows). One of the pores with obvious lattice-like structure was 0.9 μm in width and 5.3 μm in length. The pharyngeal filter of *Oikopleura vanhoeffeni* is morphologically characterized by arrangement of fibers in a rectangular pattern, lack of nodes and appearance of overlapping of fibers (DEIBEL and POWELL, 1987a). The fibers found in the gut contents of *Eucalanus bungii* are likely to correspond to pharyngeal filters of oikopleurid larvaceans (Fig. 5C, D). The food-concentrating filters are distinguished from incurrent and pharyngeal filters by three types of fibers (microfibers, nodulated fibers, smooth fibers) and much smaller pore sizes (see DEIBEL and POWELL, 1987b). These three types of fibers were also observed in the gut contents of male CV (Fig. 5D). The pore widths found in the copepod gut contents ranged approximately from 0.1 to 0.2 μm, although the pore lengths could not be measured due to entangling fibers. No incurrent filters and house membranes of oikopluerids were included in the gut contents. Hence *E. bungii* may probably feed on discarded oikopleurid houses, which
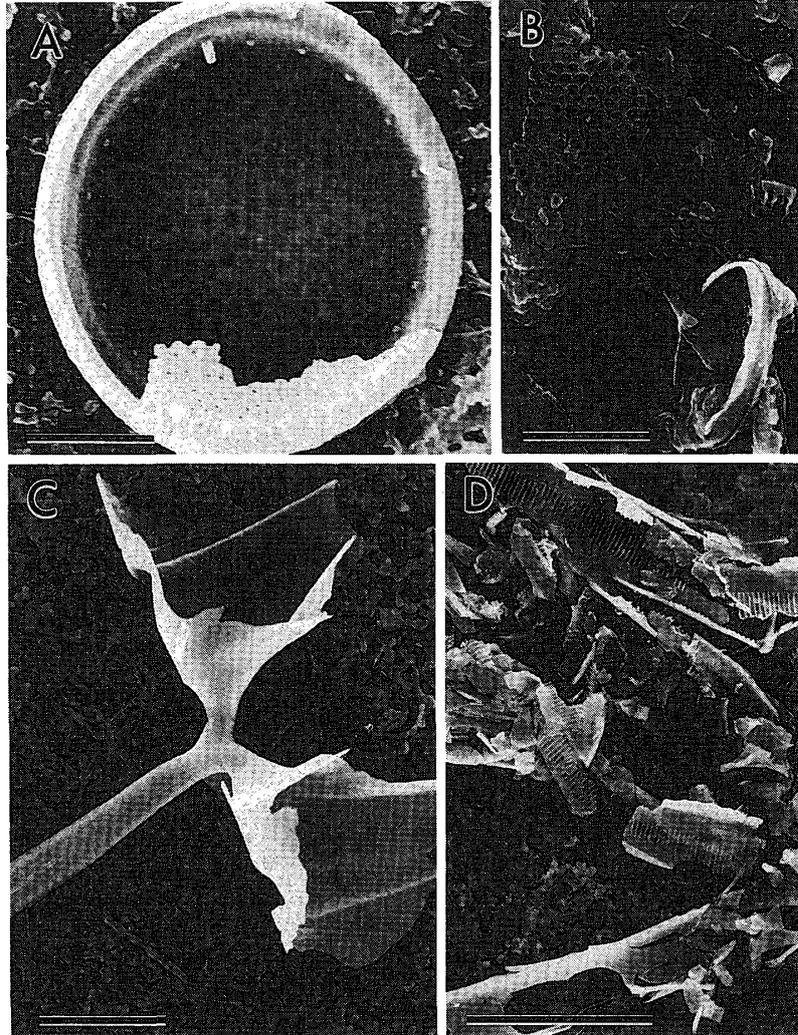
Fig. 2. Eucalanus bungii. *Gut contents of CV from Stn. 119 (A, B: female; C, D: male). A, B, Centric diatom fragments; C, Fragments of* Chaetoceros *sp.; D, Pennate diatom fragments. Scales = 5 μm (A–C); 10 μm (D).*

were nearly decomposed.

The number of copepods with an oil drop varied with stations, much more in late copepodid stages, CV and CVI (average = 91.3%) than in early copepodid stages, CII and CIII (average = 32.2%) (Table 1).

4. Discussion

Late copepodid stages of *Eucalanus bungii* in the northeastern Pacific feed in the upper 100 m for only three months from mid-April through mid-July, whereas CIII and CIV remain within the upper layer longer than the former stages for feeding (Miller *et al.*, 1984). The present study revealed that CIII to CVI of *E. bungii* (excluding male CVI) from the northern Bering and Chukchi Seas fed even in October 1988 when the

Table 1. *Frequency of occurrence of main items in the guts of second (CII) to sixth (CVI) copepodid stages of* Eucalanus *bungii, and frequency of occurrence of copepods with visible oil drop. Dia: diatoms; Din: dinoflagellates; Tin: tintinnids; Cru: crustacean fragments; Uni: unidentified remains; –: no occurrence.*

	Number of individuals examined (A: gut contents; B: oil drop)		Frequency of occurrence of main items in copepod guts (%)					Empty guts (%)	Frequency of occurrence of individuals with oil drop (%)
	A	B	Dia	Din	Tin	Cru	Uni		
Stn. 69									
CII	1	1	–	–	–	–	–	100.0	0.0
CIII	1	1	100.0	–	–	–	100.0	0.0	0.0
CIV(♀)	4	9	25.0	–	–	–	50.0	50.0	44.4
CIV(♂)	8	10	62.5	–	25.0	12.5	75.0	25.0	10.0
CV(♀)	2	5	100.0	–	–	–	100.0	0.0	80.0
CV(♂)	3	4	100.0	–	–	33.3	100.0	0.0	100.0
CVI(♀)	0	0							
Stn. 118									
CII	0	0							
CIII	7	10	85.7	–	–	–	85.7	14.3	20.0
CIV(♀)	7	7	85.7	–	–	–	85.7	14.3	28.6
CIV(♂)	5	7	80.0	–	–	–	80.0	20.0	28.6
CV(♀)	4	6	100.0	–	–	–	100.0	0.0	33.3
CV(♂)	1	1	100.0	–	–	–	100.0	0.0	100.0
CVI(♀)	1	1	100.0	–	–	–	100.0	0.0	100.0
Stn. 120									
CII	0	0							
CIII	1	2	100.0	–	–	–	100.0	0.0	100.0
CIV(♀)	1	1	100.0	–	–	–	100.0	0.0	100.0
CIV(♂)	2	2	100.0	–	–	–	100.0	0.0	100.0
CV(♀)	0	0							
CV(♂)	0	0							
CVI(♀)	0	0							
Stn. 121									
CII	0	0							
CIII	9	9	88.9	–	–	11.1	88.9	11.1	44.4
CIV(♀)	12	12	100.0	8.3	–	8.3	100.0	0.0	83.3
CIV(♂)	10	11	100.0	–	–	–	100.0	0.0	90.9
CV(♀)	11	14	72.7	–	–	–	72.7	27.3	100.0
CV(♂)	17	24	70.6	–	5.9	–	76.5	23.5	100.0
CVI(♀)	1	1	100.0	–	–	–	100.0	0.0	100.0
Stn. 123									
CII	0	0							
CIII	5	7	100.0	–	–	–	100.0	0.0	28.6
CIV(♀)	4	6	100.0	50.0	–	–	100.0	0.0	16.7
CIV(♂)	6	7	66.7	33.3	–	–	66.7	33.3	14.3
CV(♀)	2	2	100.0	50.0	50.0	–	100.0	0.0	100.0
CV(♂)	1	1	–	–	–	–	100.0	0.0	100.0
CVI(♀)	0	0							
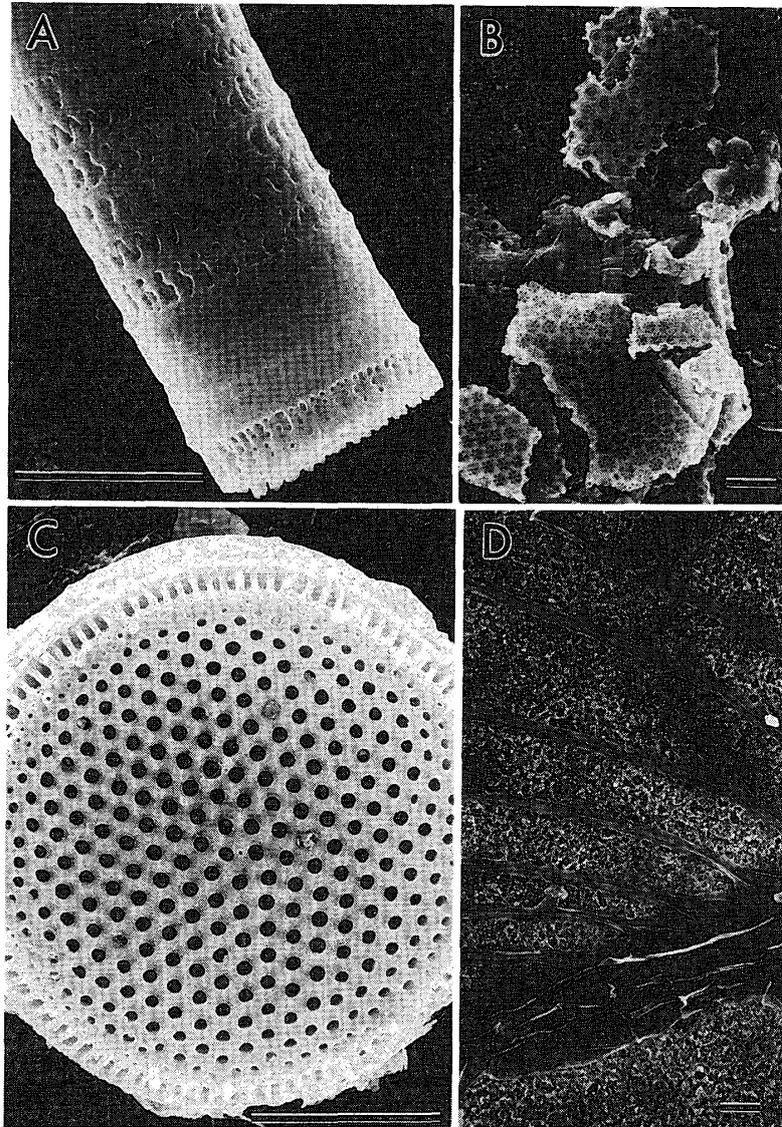
Fig. 3.   Eucalanus bungii.   *Gut contents of female CIV and CV from Stn. 31 (A: CV; B–D: CIV).*
A, Melosira *sp.;*   B, *Centric diatom fragments;*   C, Thalassiosira *sp.;*   D, *Crustacean*
appendage.   *Scales = 10 μm.*

diapausing stock (CIII to CVI) should have been established in the deep layer between
250 m and 500 m in the northeastern Pacific (Miller *et al.*, 1984).   Since all the sam-
pling stations in the present study are less than 60 m deep, it is likely that the life his-
tory of *E. bungii* in these two areas differs from each other.   Johnson (1963) and
Springer *et al.* (1989) suggested that *Acartia longiremis, Derjuginia tolli, E. bungii,*
Metridia pacifica, Mimocalanus distinctocephalus, Neocalanus cristatus, and *N. plum-*
churus in the Chukchi and northern Bering Seas were transported northward from the
southern Bering Sea by Anadyr Water.   Water temperature of the 250–500 m layer
where diapausing *E. bungii* resides is constantly *ca.* 4°C throughout the year at a station
in the northeastern Pacific (Miller *et al.*, 1984).   On the other hand, water temperature
in the Chukchi and northern Bering Seas in winter is much lower than in the northeast-
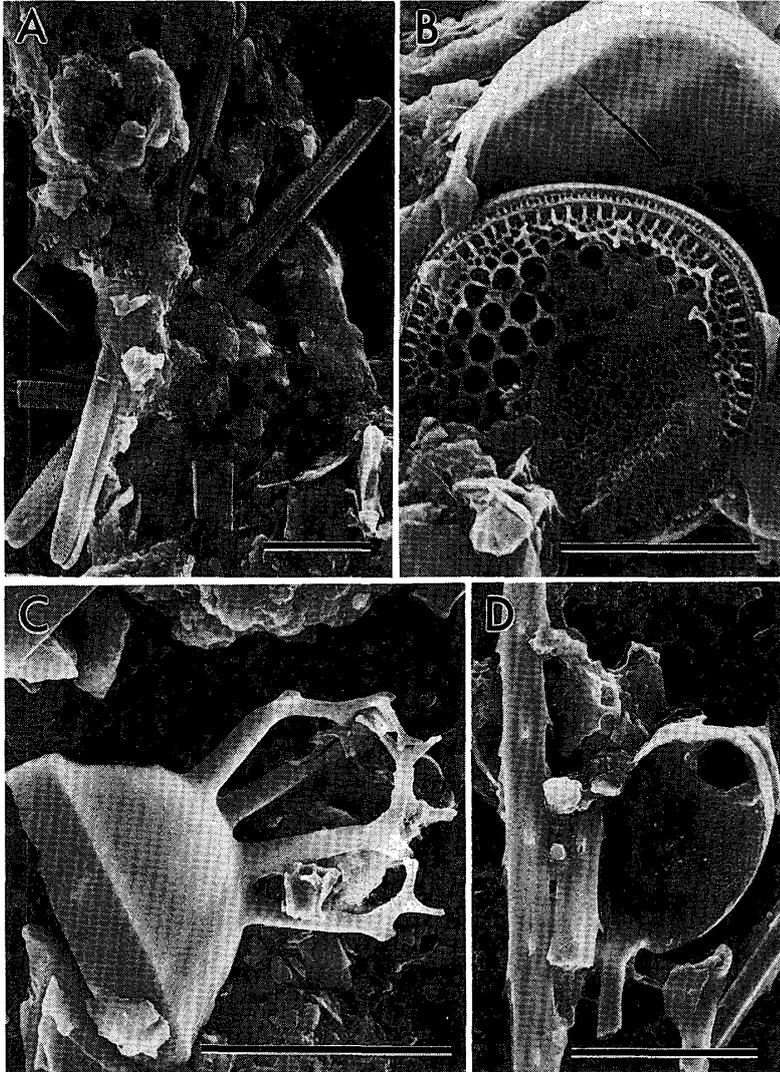
Fig. 4. Eucalanus bungii. *Gut contents of male CIV from Stn. 31. A, Intact pennate diatoms; B, Centric diatom fragments; C, Fragment of diatom resting spore; D, Fragments of* Chaetoceros *sp. Scales = 10 μm (A,C,D); 5 μm (B).*

ern Pacific, being below 0°C (*e.g.*, COACHMAN *et al.*, 1977). *E. bungii* is reported to be unable to overwinter in shallow waters off British Columbia (<200 m in depth), suggesting that the copepod appearing in late spring through July in the same region may have been originated from a population in upwelled oceanic water (KRAUSE and LEWIS, 1979). According to JOHNSON (1963), most of the expatriated *E. bungii* succumb before reaching about latitude 75 to 80°N, but some reproduction by *E. bungii* occurs in the Chukchi Sea. Considering these reports, *E. bungii* in the Chukchi Sea may survive during winter only in relatively warmer water of over 0°C at depths of 300 to 800 m in the high polar basin (see JOHNSON, 1963, Fig. 4).

Diapausing adult females below 100 m typically have an oil drop and a closed gut (MILLER *et al.*, 1984). Although MILLER *et al.* (1984) did not mention whether or not earlier copepodid stages in diapause have such a condition, it seems that the stages are
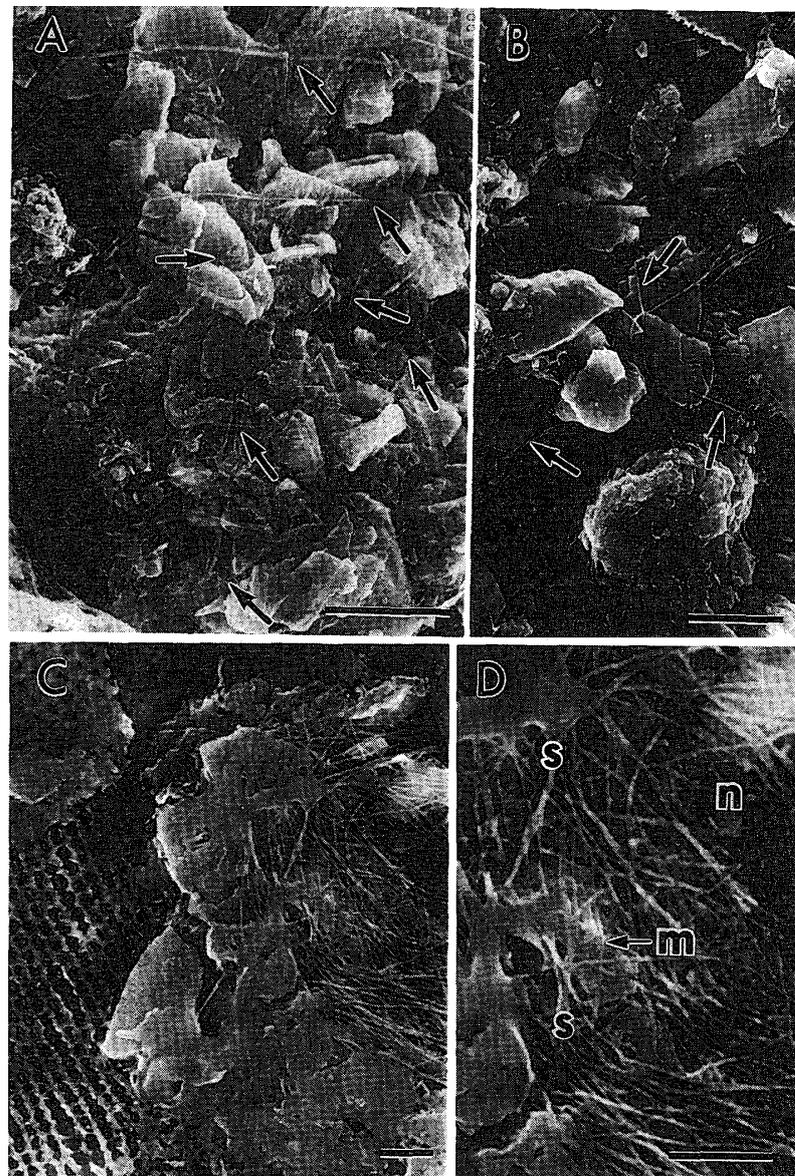
Fig. 5. Eucalanus bungii. *Gut contents of male CIV (A) and female CIV (B) from Stn. 31 and male CV (C, D) from Stn. 119. A, Larvacean pharyngeal filter indicated by arrows, note fibers arranged in rectangular pattern; B, Larvacean phargeal filter indicated by arrows; C, Larvacean food-concentrating filter attached onto diatom fragments; D, Enlargement of C, (s) smooth fiber, (n) nodulated fiber, (m) microfiber. Scales = 5 μm (A,B); 1 μm (C,D).*

in the same condition as in adult female because they may well depend on oil drops as the only energy source. Almost all the copepodids of *Eucalanus bungii* examined in the present study had a thread-like gut with or without a little ingested material. The presence of the oil drop in the prosome and the reduced, thread-like gut of *E. bungii* in this study suggest that *E. bungii* in the study area may have been originated from non-feeding diapausing stocks in deep waters or pre-diapausing stages. It may be that *E. bungii* which is expatriated into the study area resumes feeding and then either descends to deep waters in the high Polar Basin to overwinter again or succumbs in the

shallow, cold waters.

Gut content analysis showed that *Eucalanus bungii* is a particle feeder mainly ingesting phytoplankters, microzooplankters and mineral particles. These particles, particularly small ones, in the guts of *E. bungii* might have been directly captured and/or derived indirectly from fecal pellets of copepods and other zooplankters like larvaceans and discarded larvacean houses. The frequent detection of mineral particles in the guts of *E. bungii* suggests that the copepod is an opportunistic particle feeder like *E. pileatus* (TURNER, 1984). SEM examinations of the gut contents revealed that *E. bungii* fed on oikopleurid secretions such as pharyngeal and food-concentrating filters on which phytoplankton cells and microzooplankters remain (ALLDREDGE, 1972; DEIBEL and TURNER, 1985; OHTSUKA and KUBO, 1991). Most likely the pharyngeal filter detected in the guts of *E. bungii* has been derived from ingestion of larvacean fecal pellets in which the pharyngeal filter fibers are contained (see DEIBEL and TURNER, 1985; DEIBEL and POWELL, 1987a), because there was no evidence to show that *E. bungii* preyed on larvacean bodies. The pharyngeal filter found in the guts of *E. bungii* is similar in size to that of *Oikopleura vanhoeffeni* whose pores range from 0.90 to 6.00 µm in width and from 1.96 to 14.3 µm in length (DEIBEL and POWELL, 1987a). The pore sizes of food-concentrating filters of 5 species of the genus *Oikopleura* range from 0.10 to 0.22 µm in width and from 0.61 to 1.04 µm in length (DEIBEL and POWELL, 1987b). The pore widths of the food-concentrating filters found in the *E. bungii* guts fell within the range described by DEIBEL and POWELL (1987b).

Larvaceans were predominant zooplankters in the study areas, ranging from 1.2 to 91.7 individuals/m^3, and followed copepods (HATTORI, unpublished data). Since an opportunistic feeder *E. bungii* may probably have fed on larvacean fecal pellets and discarded houses, these detrital matters as food for copepods may have been relatively abundant at the stations. Coprophagy is widely known in pelagic suspension feeding copepods such as *Eucalanus pileatus*, *Temora turbinata* (PAFFENHÖFER and KNOWLES, 1979), *Metridia pacifica*, *Pleuromamma scutullata* (HATTORI, 1989), *Pseudocalanus elongatus* (NOJI et al., 1991), *Calanus sinicus* (OHTSUKA, unpublished data), and deep-sea hyperbenthic calanoid copepods (GOWING and WISHNER, 1986). These copepods appear to feed on pellets proper, peritrophic membranes of fecal pellets and/or bacteria attached onto fecal pellets (TURNER and FERRANTE, 1979; LAMPITT et al., 1990; NOJI et al., 1991). Coprophagy commonly occurs in both shallow- and deep-sea suspension feeders in arctic and also in antarctic to tropical waters. Saprophagy also has been lately found to occur commonly in pelagic copepods such as *Scolecithrix danae* and *Oncaea* spp. (OHTSUKA and KUBO, 1991). Suspended detrital matters such as fecal pellets, discarded larvacean houses, and exuviae and carcasses of zooplankters seem to play an important role as food for pelagic copepods in the world oceans.

Acknowledgments

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