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Abundance and *In-situ* Feeding Habits of *Neocalanus cristatus* (Copepoda: Calanoida) in the Central and Western North Pacific Ocean in Summer and Winter

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The abundance and *in-situ* feeding habits of copepodids of *Neocalanus cristatus* were investigated in the upper 150 m along south-to-north transects in the subarctic central and western North Pacific Ocean in June-July 1995 and January 1996. Stage IV and V copepodids (CIV and CV) were dominant in June-July, but Stage I to III copepodids (CI to CIII) exclusively occurred in January. The abundance of *N. cristatus* varied latitudinally, being the highest in the Transitional Domain and southern subarctic region in June-July and also in the northern Transitional Domain in January. The summer latitudinal variations in abundance were caused by a difference in regional abundance of CV individuals. There was a statistically significant negative relationship between abundance of *N. cristatus* (both all and CV individuals) and chlorophyll-*a* concentration in June-July. Copepodids of four stages (CII to CV) fed mainly on a wide variety of diatoms (e.g., *Thalassiosira* spp. and *Coscinodiscus* spp.) in both June-July and January. Tintinnids and silicoflagellates followed diatoms in June-July and January, respectively. Dinoflagellates and zooplantkers were much less frequently detected in the copepodid guts. Copepodids may also employ detritivory and feed on secretions and fecal pellets of zooplankton. It is likely that *N. cristatus* more actively feeds on phytoplankters and ciliates than previously suggested.

Key words: *Neocalanus cristatus*, seasonal and regional abundance, feeding habits, North Pacific Ocean

Introduction

Neocalanus cristatus is one of the most abundant calanoid copepods in the subarctic North Pacific (Mackas and Tsuda, 1999). Various studies have been conducted on the distribution, life cycle and feeding ecology of this species (e.g., Omori, 1970; Frost *et al.*, 1983; Miller *et al.*, 1984; Greene and Landry, 1988; Dagg, 1993a,b; Gifford, 1993; Mackas *et al.*, 1993). However, most of the previous studies were done for the populations in the eastern North Pacific, including the Gulf of Alaska, and there have been a few studies conducted in oceanic waters of the western and central North Pacific (Sekiguchi, 1975; Tsuda and Sugisaki, 1994; Shiga *et al.*, 1995; Kobari and Ikeda, 1999, 2000; Saito and Tsuda, 2000). In particular, information on the ecology and life history of *N. cristatus* occurring in the central Pacific is very limited, and much remains unknown about the feeding although the species has been suggested to feed on large sinking detrital particles (Daggs, 1993a,b). Knowledge on the feeding of *N. cristatus* is very important in order to understand its role in the subarctic Pacific ecosystem. The purpose of the present paper is to examine seasonal and latitudinal variations in abundance and *in-situ* feeding habits of *N. cristatus* in the western and central North Pacific in summer and winter.

Materials and Methods

Copepods were collected at 43 stations (Fig. 1) in the northern North Pacific, including the central Bering Sea, from June 18 to July 8, 1995 (R/V *Wakatake maru*: cruise I, 21 stations), from July 7 to 18, 1995 (R/V *Hokko maru*: cruise II, 11 stations), and from January 9 to 19, 1996 (R/V *Kaiyo maru*: cruise III, 11 stations), using a NORPAC net (mesh size 0.33 mm). During these cruises, sampling stations were set nearly every one latitude along south-to-north transects at 179°30'W (from 38°28' to 58°31'N, St. 1−21) in the central North Pacific and Bering Sea (cruise I), 165°00'E (from 41°00' to 51°00'N, St. 1−11) in the western North Pacific (cruise II), and 160°00'E (from 40°00' to 45°58'N, St. W1−W5) and 168°00'W (from 41°30' to 48°58'N, St. E1−E6) each in the western and central North Pacific (cruise III)(Nagasawa and Ishida, 1997a,b; Nagasawa, 2000). The net was vertically towed from 150 m to the surface at a speed of 1 m/sec. Filtered water volume was estimated with a flow meter (Rigosha Co. Ltd.,

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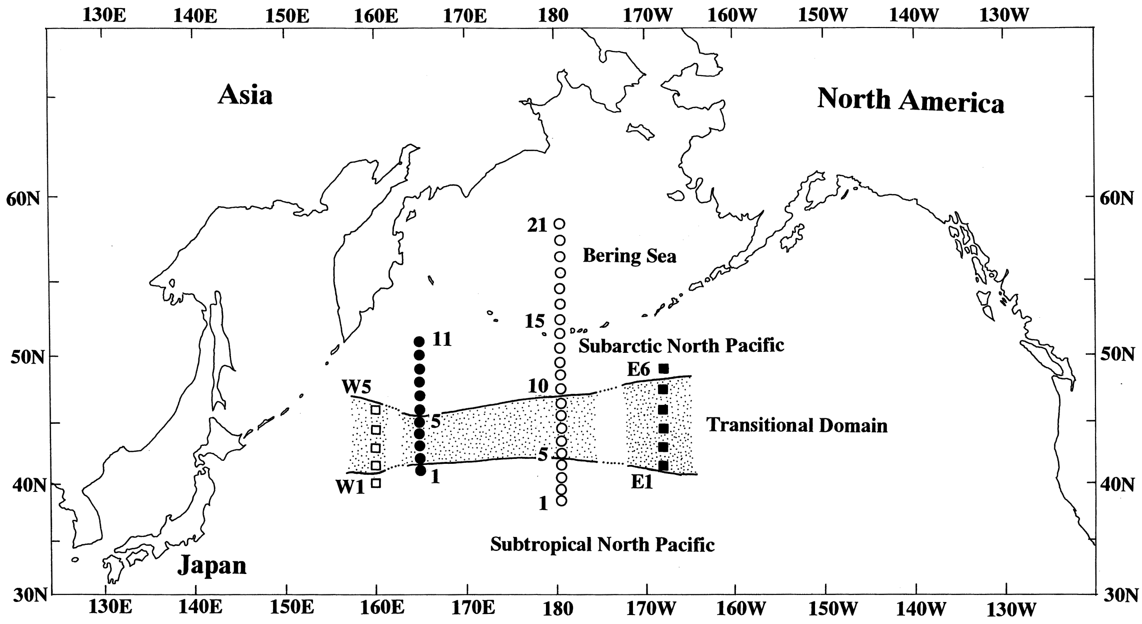

Fig. 1. Location of sampling stations in the western and central North Pacific Ocean and Bering Sea. Hatched area indicates the Transitional Domain. Cruise I (○, St. 1—21, June 18—July 8, 1995); cruise II (●, St. 1—11, July 7—18, 1995); cruise III (□ and ■, St. W1—W5 and St. E1—E6, January 9—19, 1996).

Tokyo) attached to the mouth of the net. Samples were fixed in 10% neutralized formalin/sea-water immediately after capture.

Water temperature and salinity were measured using a STD or CTD system to identify the oceanographic structure. Based on the definitions of Dodimead *et al.* (1963) and Favorite *et al.* (1976), the study region was divided into four regional groups: the subtropical North Pacific (STNP), Transitional Domain (TD), subarctic North Pacific (SNP), and Bering Sea (BS).

Chlorophyll-*a* (Chl-*a*) concentrations at the surface were measured at all of 32 stations in June-July 1995 (cruise I and II) and at six of 11 stations in January 1996 (cruise III). Seawater samples were collected using an acid-cleaned plastic bucket. A Whatman GF/F filter (ca. 0.7 μm pore size) was used to determine the Chl-*a* concentration. The filters were stored frozen at -20 ° C until analysis ashore. Chl-*a* was extracted in 90% acetone. Chl-*a* concentrations were measured with a Hitachi F-2000 fluorophotometer, according to the method of

Table 1. Occurrence and sizes of main gut content items of *Neocalanus cristatus*. The occurrence was classified into one of the following three ranks: ++, common; +, rare; and -, absent. The sizes of relatively non-broken plankton in the guts were measured in μm.

Cruise number	I						II		III						
Station number	6		11		21		9		W1	W4		E2		E6	
Copepodid stage	CII	CV	CIII	CV	CII	CV	CIII	CV	CII	CII	CIV	CII	CIV	CII	CIV
Number examined	2	18	5	19	3	7	11	20	7	17	8	15	16	13	14
Diatoms	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
centric (diameter)	18	15-147	13-19	7-47		16-128		52-94	15-23	14-36	10-51	8-59	20-46	14-61	14-61
pennate (length)	5-12		4-17	19-27	25	7-10		16		30-37	35	32	27-31	9-34	31-47
Dinoflagellates	-	-	-	-	-	++	-	-	+	-	-	-	+	+	+
largest dimesion						24-147			21				36	16	62-67
Silicoflagellates	-	-	+	-	-	-	-	+	+	++	+	++	+	+	+
largest dimension										31		41			
Tintinnids	++	+	++	++	-	+	-	+	++	-	-	+	+	-	+
lorica length	26-48	32-64	30-47	25-89				24-218	33			33	39-71		
Foraminifera	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-
largest dimension		74		43		93									
Radiolaria	-	-	+	-	-	-	-	+	-	-	-	-	+	-	+
largest dimension			19					21					56		64
Crustacean fragments	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-

Parsons *et al.* (1984). Calibration of the fluorophotometer was performed with a commercially prepared Chl-*a* standard from Wako Pure Chemical Industries, Ltd. (Tokyo).

All individuals of *N. cristatus* were sorted out from the original samples or split subsamples (1/16—1/2), identified and counted by copepodid stage [Stage I copepodid (CI) to Stage VI copepodid (=adult, CVI)].

Gut contents of intact individuals of early (CII and CIII) and late (CIV and CV) stages of *N. cristatus* were examined with a scanning electron microscope (SEM, Jeol JSM-T20). The number of individuals and stages of *N. cristatus* examined from selected stations is shown in Table 1. Up to 20 individuals of each stage with packed gut contents in the prosome were sorted out of the samples or subsamples and rinsed in distilled water for several hours to overnight. The guts were carefully removed from the prosomes with a pair of fine needles under a dissecting microscope and then rinsed in distilled water in order to avoid contamination. They were moved to a deep hole glass slide filled with distilled water and dissected using fine needles.

After all remains of the gut wall were picked up by a pair of tweezers, only all gut contents were picked up by a fine pipette and mounted on a small area (within the diameter of a stub) of a Millipore filter with the aid of a vacuum pump. The filer was dehydrated by alcohol series (70, 90, 99, and 100%) and deposited in a decicator overnight. The totally dried filter was trimmed and mounted on a stub, and then ion-sputterred. Gut contents from all individuals of the same copepodid stage taken at each station were mounted together on the stub. The occurrence of each of the gut contents was classified into one of three ranks: common (over 10 non-broken or broken cells/stub), rare (one or a few cells/stub), and absent. The sizes of relatively intact cells detected in the guts were taken from SEM microphotographs. In the present gut content analysis, the body condition types (Ikeda *et al.*, 1990) were not distinguished because we used only individuals with gut contents packed in the prosome.

Results

Regional Variations in Abundance of *N. cristatus*

Neocalanus cristatus was most abundant in the TD and the southern SNP in summer. In the central Pacific (along a transect at 179° 30'W), the highest abundance was recorded at St. 6 in the TD (2066

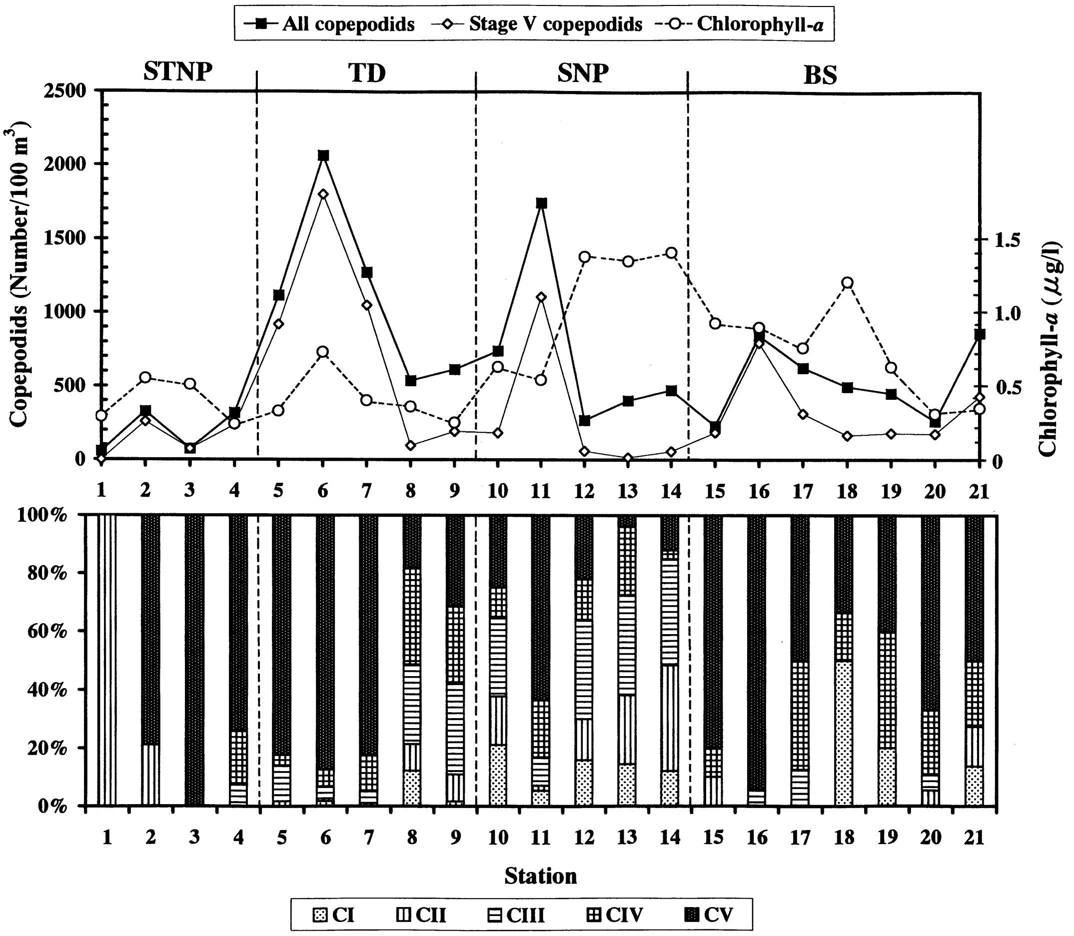

Fig. 2. Latitudinal changes in abundance of all and Stage V copepodids of *Neocalanus cristatus* and chlorophyll-*a* concentration (top) and copepodid stage composition (bottom) along a transect at 179° 30'W from 38° 28' to 58° 31'N in June-July 1995. STNP, subtropical North Pacific; TD, Transitional Domain; SNP, subarctic North Pacific; BS, Bering Sea.

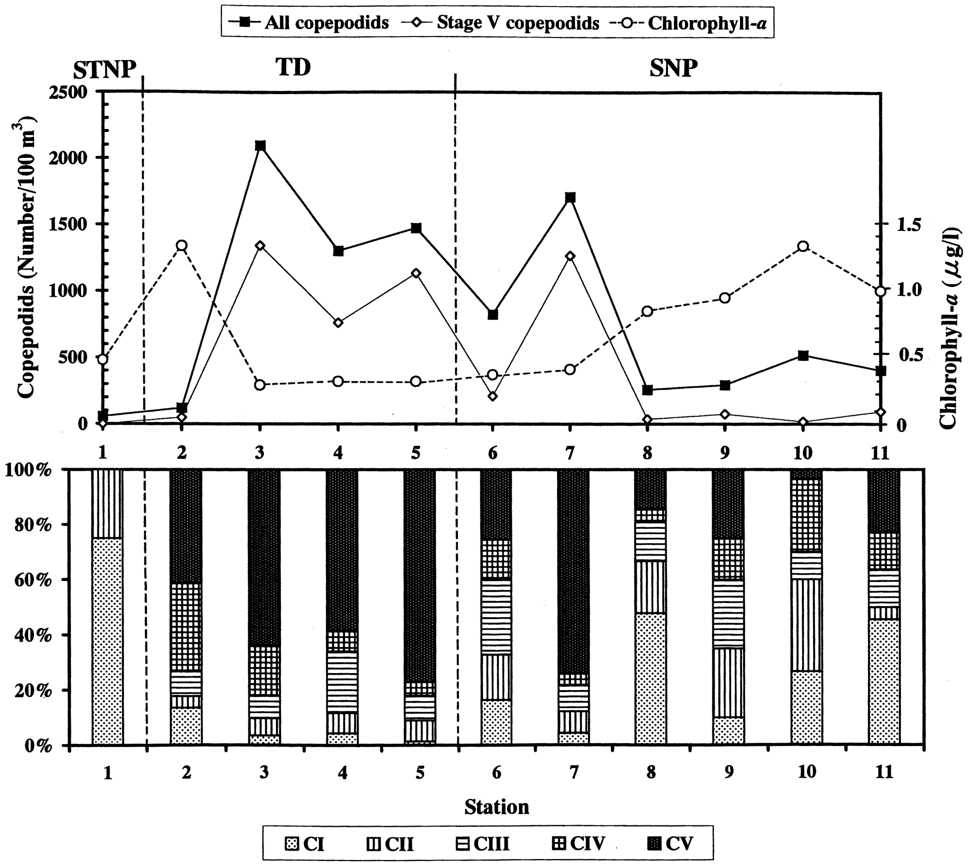

Fig. 3. Latitudinal changes in abundance of all and Stage V copepodids of *Neocalanus cristatus* and chlorophyll-*a* concentration (top) and copepodid stage composition (bottom) along a transect at 165° 00'E from 41° 00' to 51° 00'N in July 1995. STNP, subtropical North Pacific; TD, Transitional Domain; SNP, subarctic North Pacific.

ind./100 m³), followed by St. 11 in the southern SNP (1745 ind./100 m³)(Fig. 2). The species was a little abundant in the BS. The abundance was low in the northern SNP and the STNP. In the western Pacific (along a transect at 165° 00'E), the highest abundances (>1000 ind./100 m³) were recorded in the TD and the nearby southern SNP (Fig. 3). The species was much less abundant in the northern SNP. As in the central Pacific, a few individuals were collected in the STNP.

Because only one sampling was made each in the STNP and SNP and no collection was done in the BS during winter, no sufficient data on the regional abundance of *N. cristatus* were available in this season. The species was abundant in the northern TD of both the central and western North Pacific (along transects at 168° 00'W and 160° 00'E) (Fig. 4).

Regional Variations in Stage Composition of *N. cristatus*

Individuals of late stages (CIV and CV) were predominant in summer (49.7% and 67.6% on average, respectively, in the western and central Pacific), whereas those of early stages (CI and CIII) exclusively occurred in winter (92.2% and 89.5% in each of the same regions)(Figs. 2-4). No adults (CVI) were found.

The summer abundance of *N. cristatus* at each sampling station was highly affected by the abundance of CV individuals (Figs. 2-3). At the stations in the TD and southern SNP where the abundance of *N. cristatus* was very high, there was a tendency that the percentage of CV was also very high. In the BS, a comparatively high percentage was recorded for CV. In the northern SNP where the abundance of *N. cristatus* was not so high, CV individuals were rare, and early and late copepodid stages were mixed. In the STNP, late and early stages were predominant in cruise I and II, respectively.

The stage composition of *N. cristatus* was almost constant at stations in winter (Fig. 4). In the northern TD where the abundance was high, individuals of three early stages (CI to CIII) were almost equally mixed together with some CIV individuals. In the southernmost TD where *N. cristatus* was least abundant, both CI and CII individuals highly predominated.

Relationship between Copepod Abundance and Chlorophyll-*a* Concentration

Chl-*a* concentrations remained low (high) in summer at stations where the abundance of *N. cristatus* was high (low) in the central and western North Pacific Ocean (Figs. 2-3), although such a relation was not found at Sts. 8-10 during cruise I in the central North Pacific. There is a statistically

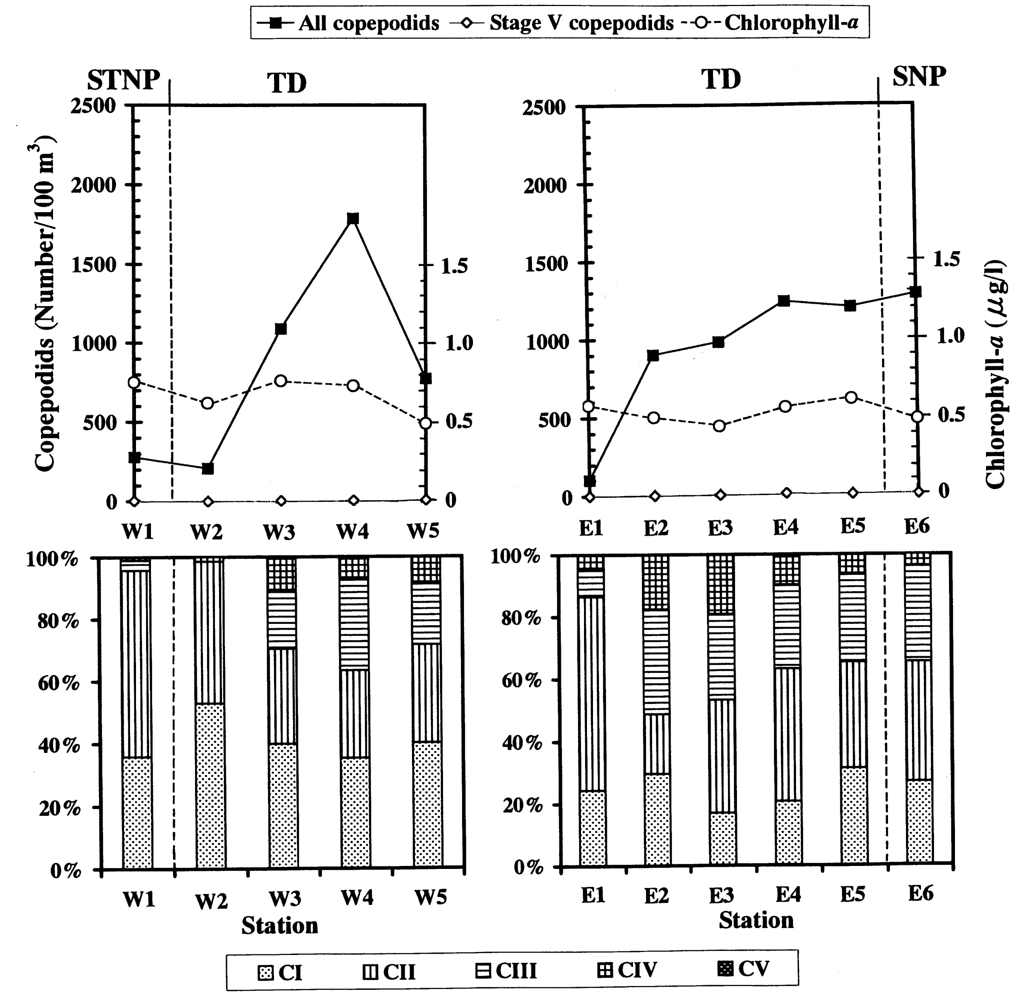

Fig. 4. Latitudinal changes in abundance of all and Stage V copepodids of *Neocalanus cristatus* and chlorophyll-*a* concentration (top) and copepodid stage composition (bottom) along two transects at 160° 00'E from 40° 00' to 45° 58'N (left) and at 168° 00'W from 41° 30' to 48° 58'N (right) in January 1996. STNP, subtropical North Pacific; TD, Transitional Domain; SNP, subarctic North Pacific.

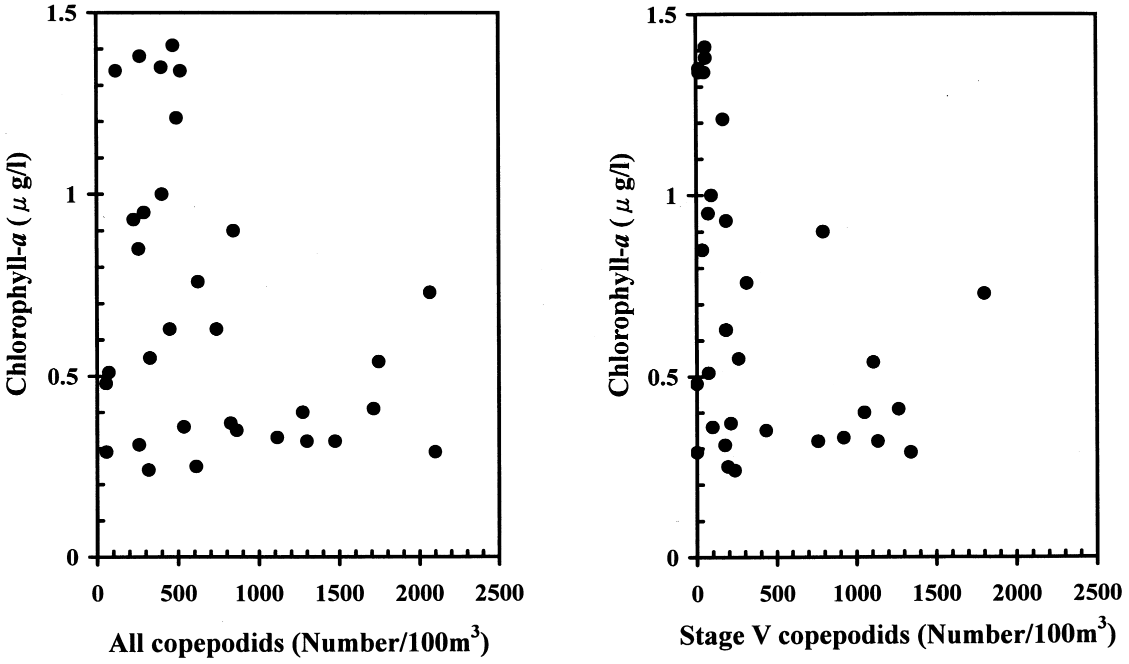

Fig. 5. Relationship between abundance of all (left) and Stage V (right) copepodids of *Neocalanus cristatus* and chlorophyll-*a* concentration in June-July 1995. Left, $r=-0.349$, $n=32$, $P=0.0499$; right, $r=-0.377$, $n=32$, $P=0.0328$.

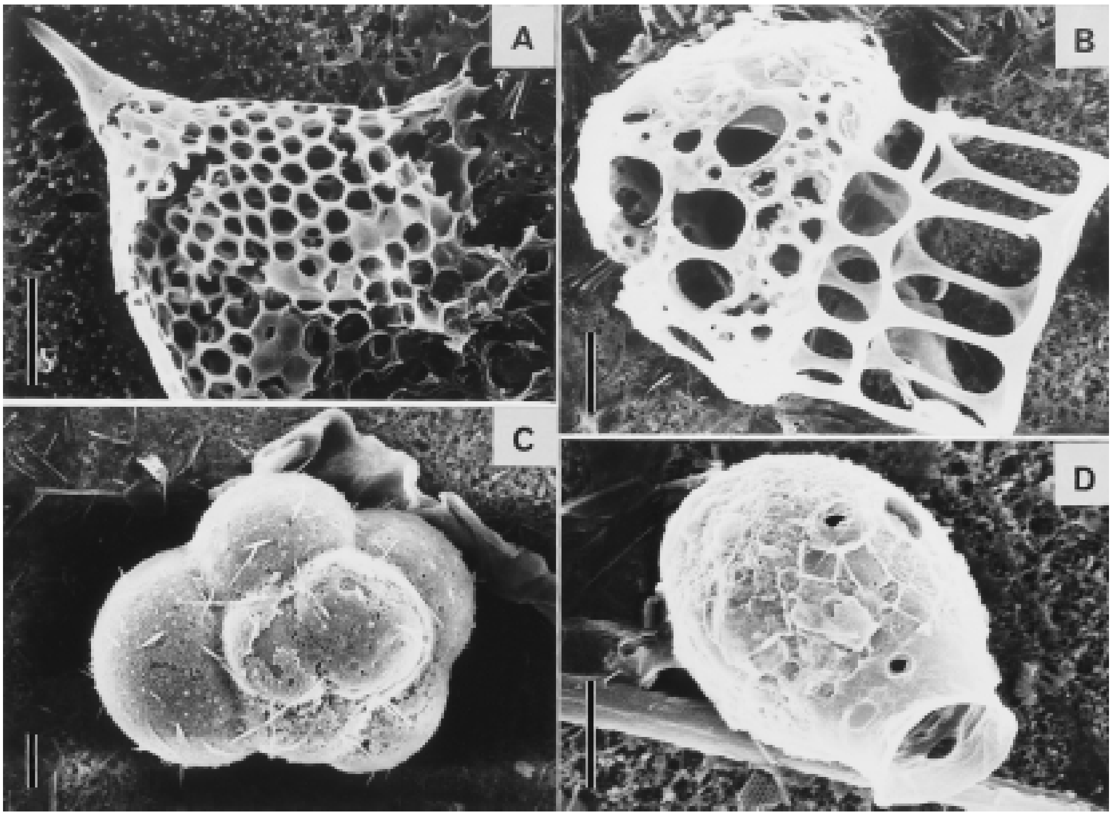

Fig. 6. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise I, St. 6). A, Lorica of *Parafavella* sp.; B, Lorica of *Dictyocysta elegans*; C, Pelagic foraminiferan *Globigerina* sp.; D, Lorica of *Codonellopsis pusilla*. Scales =10 μ m.

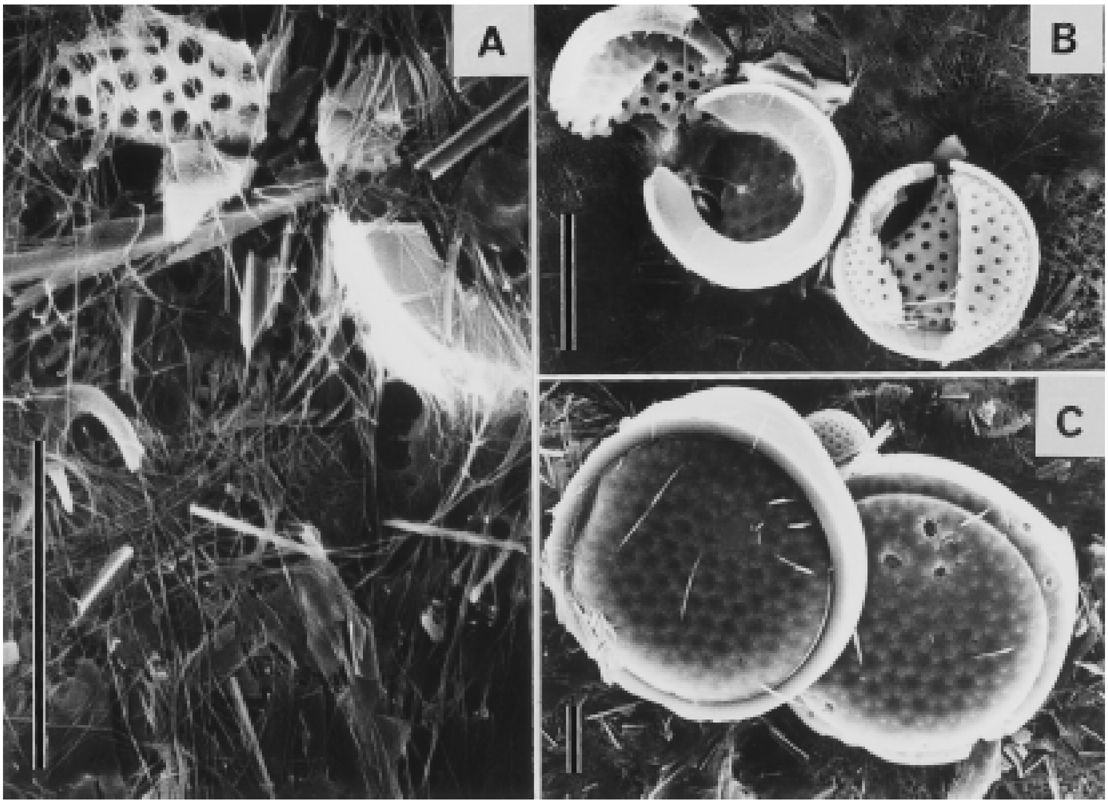

Fig. 7. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise I, St. 6). A, Entangled fibers and diatom fragments; B, Valves of *Thalassiosira* cf. *oestrupii*; C, Auxospores of centric diatoms. Scales = 10 μ m.

significant ($P<0.05$) negative relationship between abundance of *N. cristatus* (both all and CV individuals) and Chl-*a* concentration (Fig. 5). On the other hand, such a negative relationship was not observed in winter.

In-situ Feeding Habits of *N. cristatus*

Table 1 summarizes main gut contents and their size ranges found in copepodids of four stages (CII to CV). Diatoms were most commonly found in both summer and winter. Tintinnids and silicoflagellates followed diatoms in summer and winter, respectively. Dinoflagellates and zooplantkers such as foraminiferans (Fig. 6C), radioralians (Figs. 10C, 12B, 15E, 17E) and crustaceans (Fig. 10A) were infrequently detected. The gut contents were essentially consistent throughout the developmental stages, excluding the zooplankters that were found mainly in individuals of late stages (CIV and CV). Entangled fibers were also always detected in the guts.

A wide variety of diatoms were found. Centric diatoms such as *Thalassiosira* spp. (Figs. 7B, 11D, 13B, 15D, 16A-B, 17C) and *Coscinodiscus* spp. (Fig. 11C) and *Chaetoceros* spp. were most frequently detected in both summer and winter. Auxospores of centric diatoms (Figs. 7C, 12F) were often found in summer. Pennate diatoms such as *Nitzschia* spp. (Fig. 14C), *Fragilaria* (?) spp., and *Neodenticula seminae* (Fig. 17E) were a little more frequently found in winter than in summer. The size of centric diatoms found in the guts ranged from 10 to 147 μm in diameter, and that of pennate diatoms from 4 to 47 μm in length.

A diversity of tintinnids (e.g., Figs. 9B, 12E) also occurred in the guts: *Acanthostomella norvegica* (Figs. 8D, 10B, 12A), *Codonellopsis pusilla* (Figs. 6D, 8C, 9A, 13A, 15A, 16C, 17A), *Dictyocysta elegans* var. *speciosa* (Figs. 6B, 15C), *Parafavella* spp. (Figs. 6A, 8B, 14B) and *Ptychocylis obtusa* (Fig. 8A). These tintinnids, except for *A. norvegica* and *P. obtusa* (both only in winter), occurred in summer and winter. Tintinnids were more frequently detected in copepodids from the TD and its adjacent SNP in early summer (cruise I) than in mid-summer (cruise II) and winter (cruise III), but their winter occurrence was more regionally restricted. The lorica length ranged from 24 to 218 μm.

The occurrence of silicoflagellates such as *Distephanus speculum* (Figs. 12F, 16B) was almost restricted to winter. This tendency was invariable in both early (CII and CIII) and late (CIV and CV) stages. The size of *D. speculum* found in winter were ca. 30-40 μm in largest dimension.

Dinoflagellates (e.g., Figs. 11A-B, 17D) were less frequently found than diatoms and silicoflagellates. Armored dinoflagellates such as *Protoperidinium* spp. (Figs. 11E, 15B) and *Mesoporus* sp. (Fig. 13B) were not often detected, but the two dinoflagellates appeared in both summer and winter. The sizes of relatively intact dinoflagellates ranged from 16 to 147 μm.

Entangled fibers (Figs. 7A, 17B), which could have derived from appendicularian filters (Ohtsuka *et al.*, 1993), salp feeding filters (Silver and Bruland, 1981), pteropod mucous webs (Lalli and Gilmer, 1989) and/or diatom threads (Steinberg, 1995), were constantly found in the guts. Grid-like structures (> 10 μm in diameter) in the fiber mass were often observed (Fig. 7A), which could have been derived from appendicularian filters (cf. Alldredge, 1977; Deibel *et al.*, 1985; Deibel and Powell, 1987) and/or from salp feeding filters (Silver and Bruland, 1981).

Discussion

Regional Variations in Abundance and Stage Composition of *N. cristatus*

The present study shows that the summer abundance of *N. cristatus* was highest in the TD and southern SNP of the central and western North Pacific. This result is almost consistent with that of a previous study by Shiga *et al.* (1995) in the same area, especially in the western Pacific. However, they reported that, in the mid-summer (July) in the central Pacific, the abundance of *N. cristatus* was high in the southern SNP but very low in the TD. This difference between their and our results may be ascribed to different sampling seasons: their sampling was made in mid- and late-July, whereas our material was taken in late June. Since *N. cristatus* migrates from the surface to deep waters for diapause mainly from July to August (Miller *et al.*, 1984; Kobari and Ikeda, 1999, 2000), it may be plausible that most of the copepods might have moved downward when Shiga *et al.* (1995) made sampling in mid- and late-July in the TD.

A top-down control theory of biomass has been proposed by Shiomoto *et al.* (1997) for relationships between summer zooplankton (including copepods) biomass and pink salmon (*Oncorhynchus gorbuscha*) abundance in the northern SNP of the central Pacific. A similar suggestion has been made by Nagasawa *et al.* (1999). These authors found that both in years when and in areas where salmonids (especially pink salmon) were abundant, the zooplankton biomass was low. The present study shows that the abundance of *N. cristatus* was low in the northern SNP of the central and western North Pacific and in the BS (Figs. 2-3), and the abundance of salmonids was high when our sampling was made (Ishida and Ito, 1996). Therefore, it is likely that the observed low abundance of *N. cristatus* in the northern SNP and BS was caused by salmonid predation.

The dominance of copepodids of late and early stages, respectively, in summer and winter coincides with the life cycle proposed for the populations in the eastern and western North Pacific (Miller *et al.*, 1984; Kobari and Ikeda, 1999, 2000). The observed high dominance of early copepodid stages in January is thought to have resulted from upward migration of individuals of such early stages from deep waters where the spawning of *N. cristatus* occurs in autumn and winter.

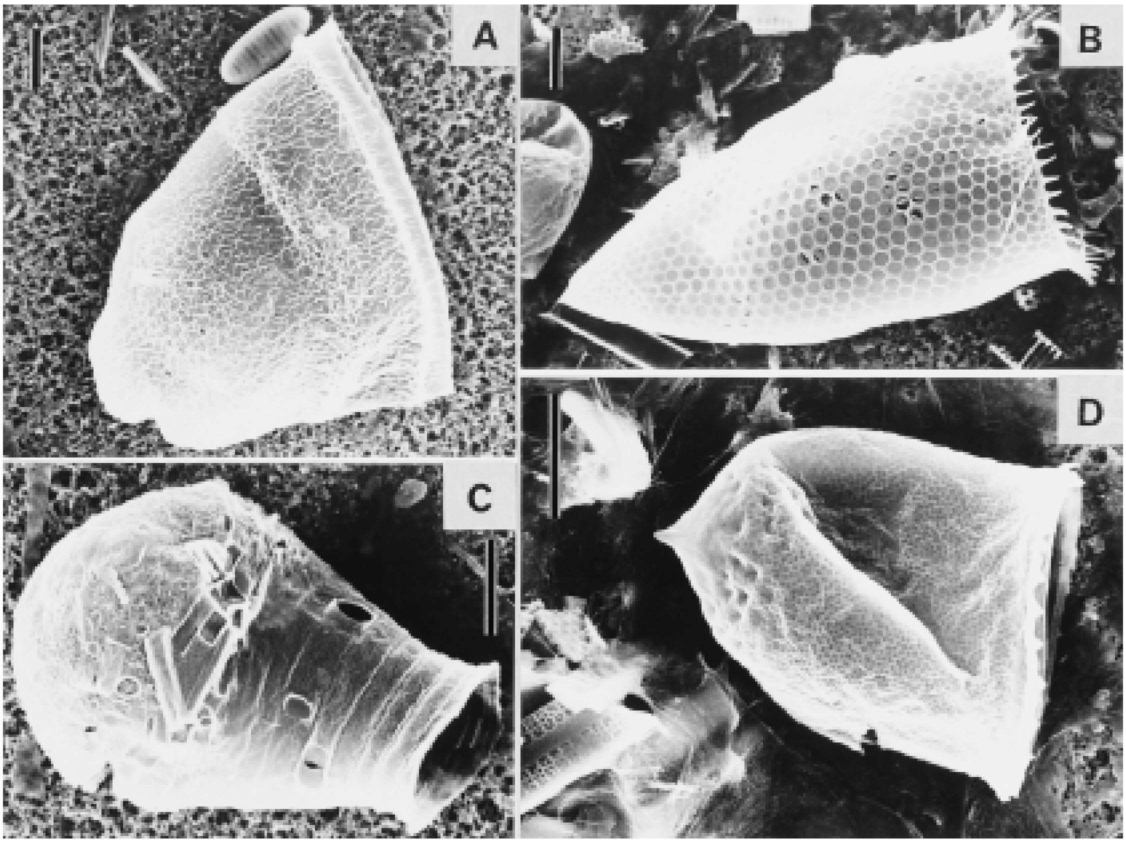

Fig. 8. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise I, St. 11). A, Lorica of *Ptychocylis obtusa*; B, Lorica of *Parafavella jorgenseni*; C, Lorica of *Codonellopsis pusilla*; D, Lorica of *Acanthostomella norvegica*. Scales = 10 μ m.

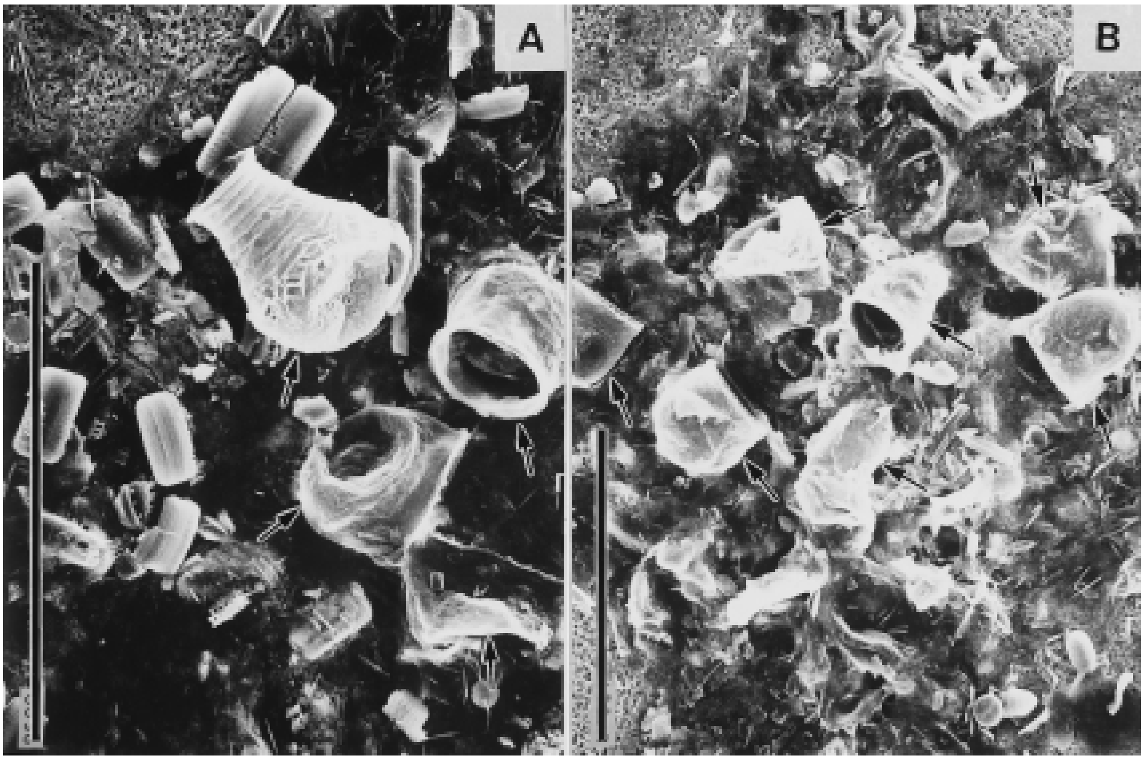

Fig. 9. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise I, St. 11). A-B, Loricae of tintinnids (arrowed) and diatom fragments. Scales = 10 μ m.

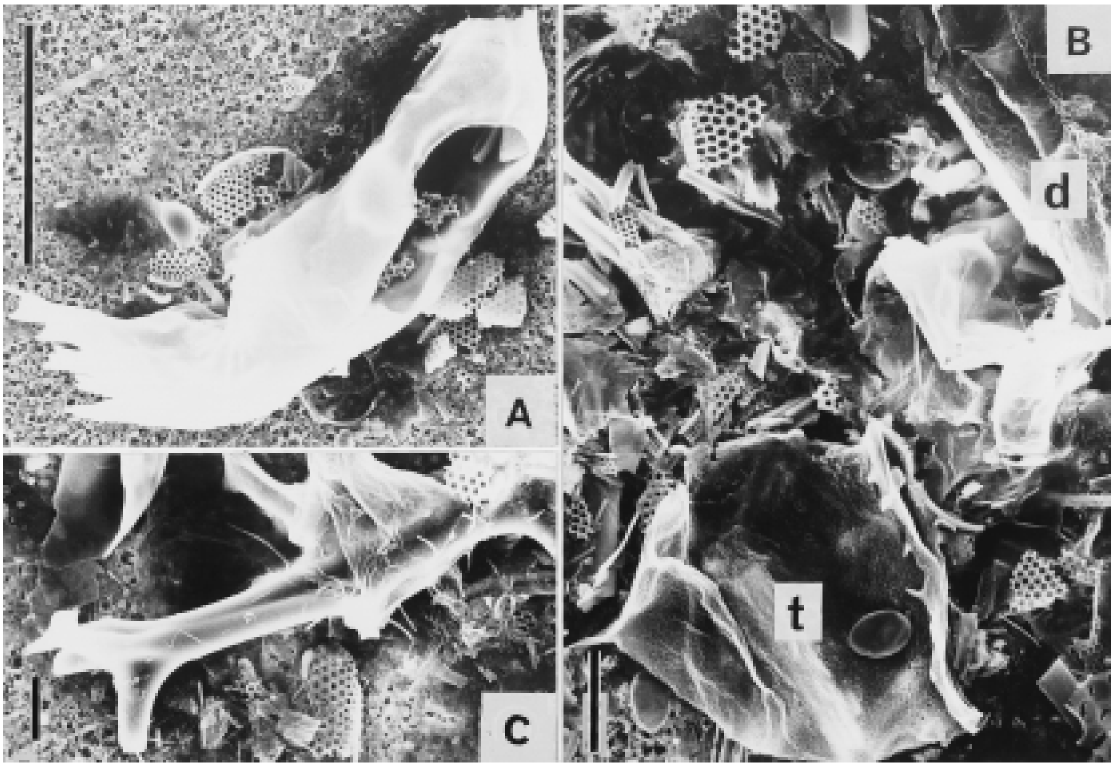

Fig. 10. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise I, St. 21). A, Copepod mandibular gnathobase; B, Unidentified dinoflagellate (d), tintinnid *Acathostomella norvegica* (t), and diatom fragments; C, Radiolarian spicule. Scales = 10 μ m.

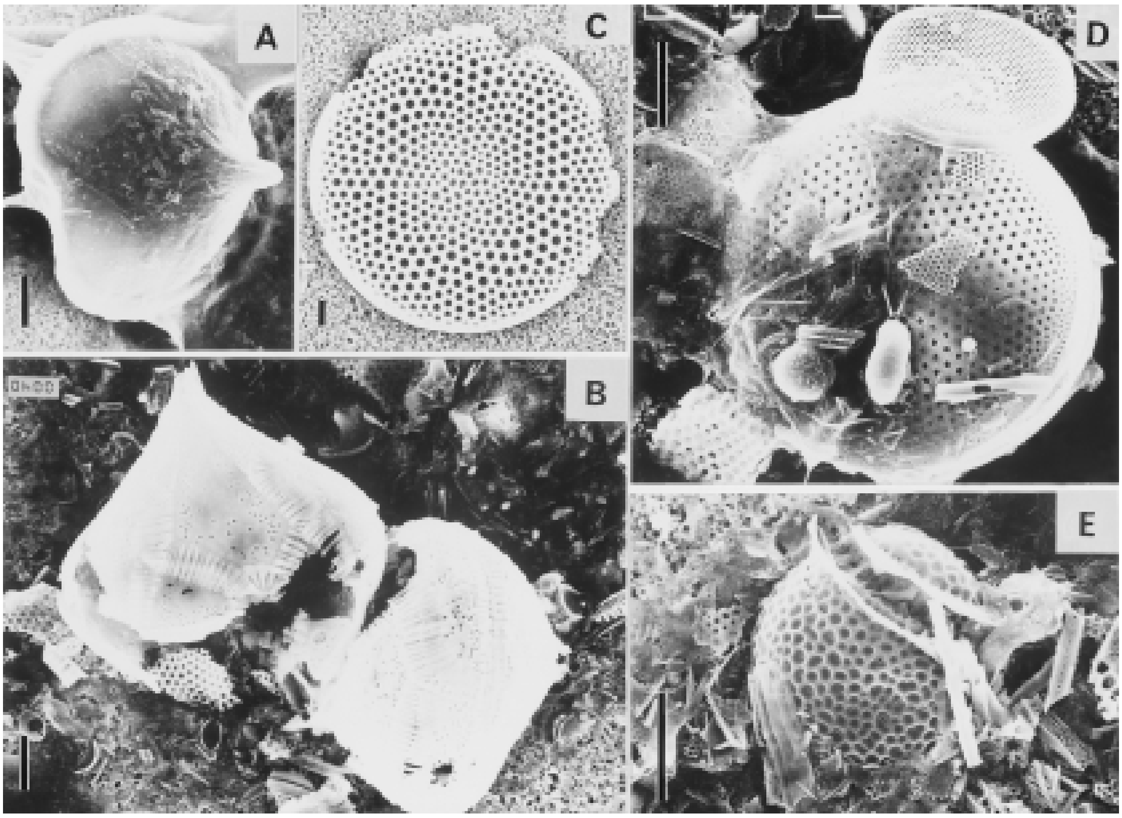

Fig. 11. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise I, St. 21). A-B, *Protoperidinium* spp.; C, Valve of *Coscinodiscus radiatus*; D, Valve of *Thalassiosira* cf. *leptopus* and other diatom fragments; E, Dinophysiaceae sp. Scales = 10 μ m.

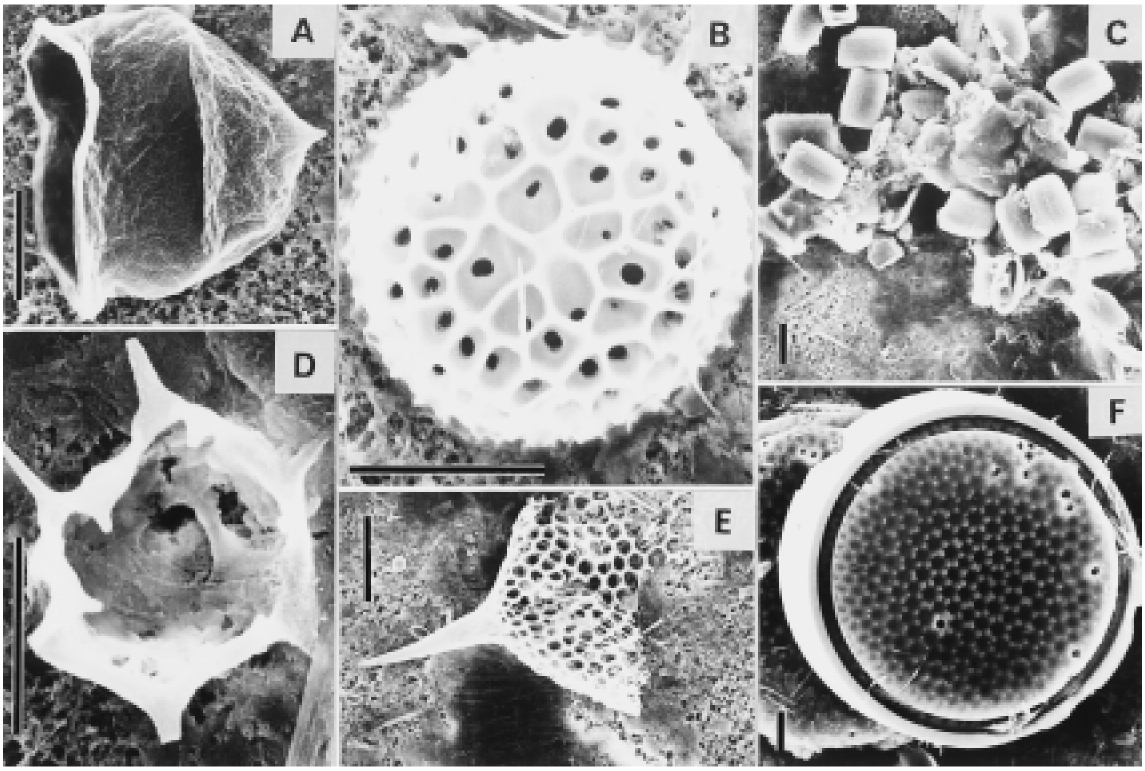

Fig. 12. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise II, St. 3). A, Tintinnid *Acathostomella norvegica*; B, Radiolarian; C, Small unidentified diatoms; D, *Distephanus speculum*; E, Fragmented lorica of tintinnid; F, Auxospore of centric diatom. Scales = 10 μm.

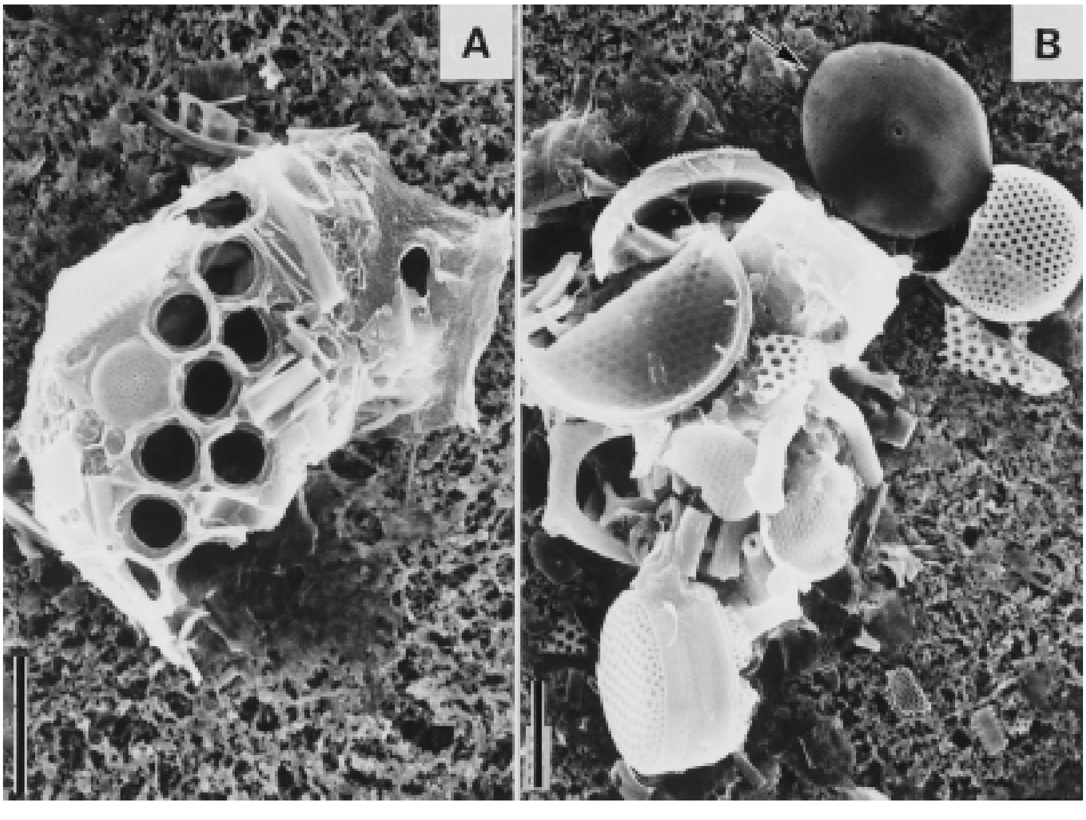

Fig. 13. Microphotographs of gut contents of *Neocalanus cristatus* CII (cruise III, St. W2). A, Lorica of *Codonellopsis pusilla*; B, Fragments of *Thalassiosira* spp. and dinoflagellate *Mesoporus* sp. (arrowed). Scales = 10 μm.

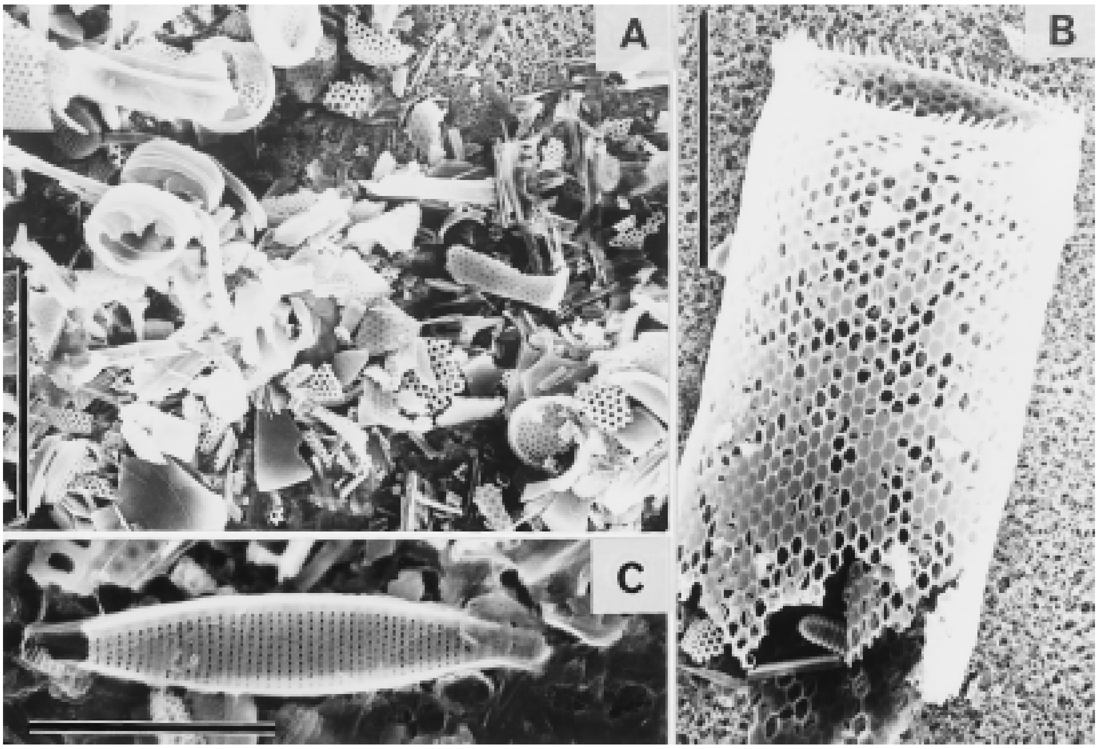

Fig. 14. Microphotographs of gut contents of *Neocalanus cristatus* CV (cruise III, St. W5). A, Fragments of centric diatom; B, Lorica of *Parafavella* sp.; C, *Nitzschia* sp. Scales = 10 μ m.

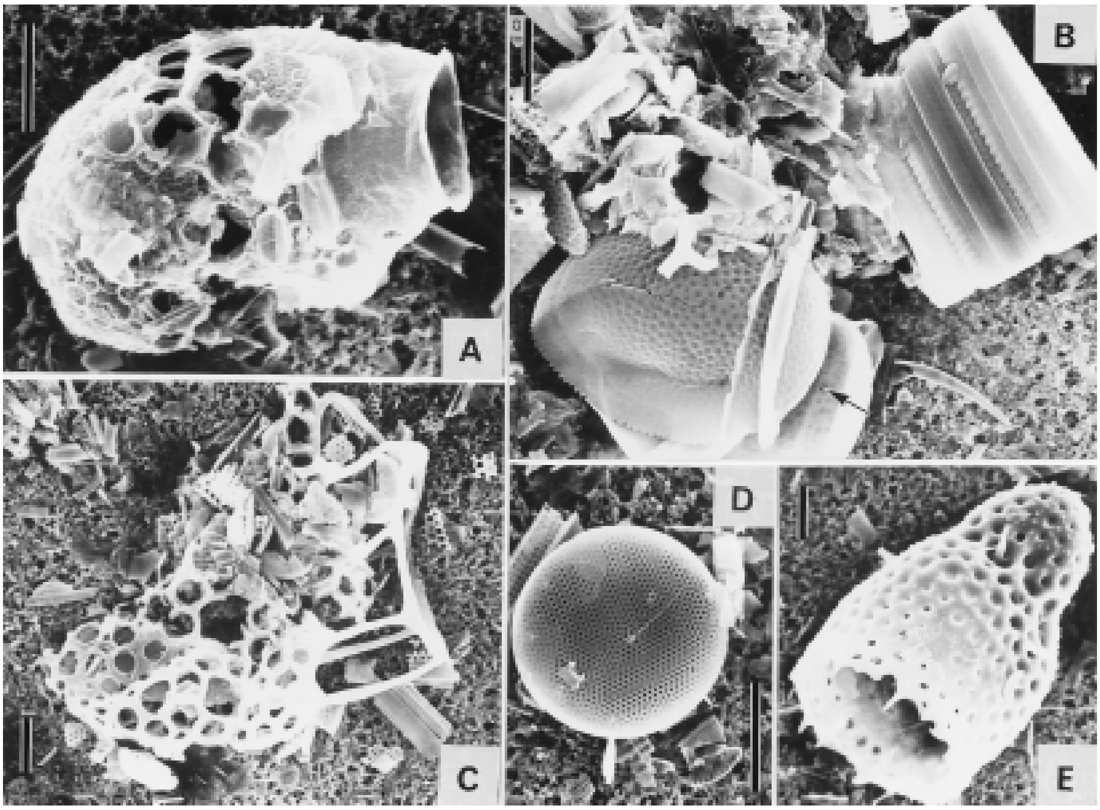

Fig. 15. Microphotographs of gut contents of *Neocalanus cristatus* CIV (cruise III, St. E2). A, Lorica of *Conodonellopsis pusilla*; B, *Dinophysis* sp. (arrowed) and diatom fragments; C, Lorica of *Dictyocysta elegans*; D, *Thalassiosira* sp.; E, Radiolarian. Scales = 10 μ m.

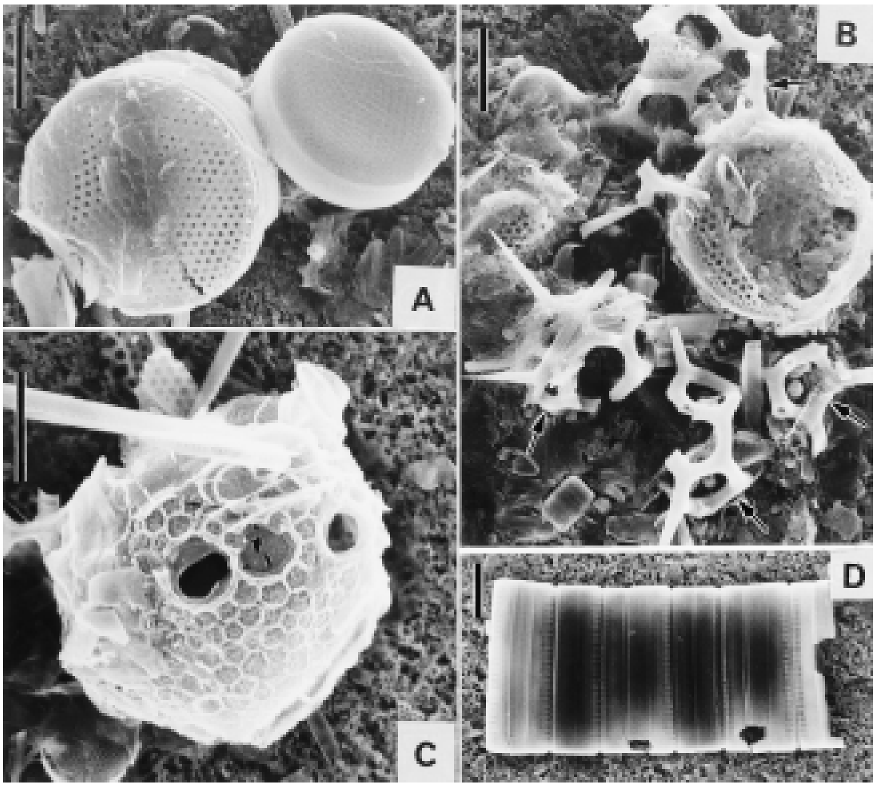

Fig. 16. Microphotographs of gut contents of *Neocalanus cristatus* CII (cruise III, St. E2). A, *Thalassiosirsa* spp.; B, *Thalassiosira* spp. and *Distephanus speculum* (arrowed); C, Lorica of *Codonellopsis pusilla*; D, Unidentified chain-forming diatom. Scales = 10 μm.

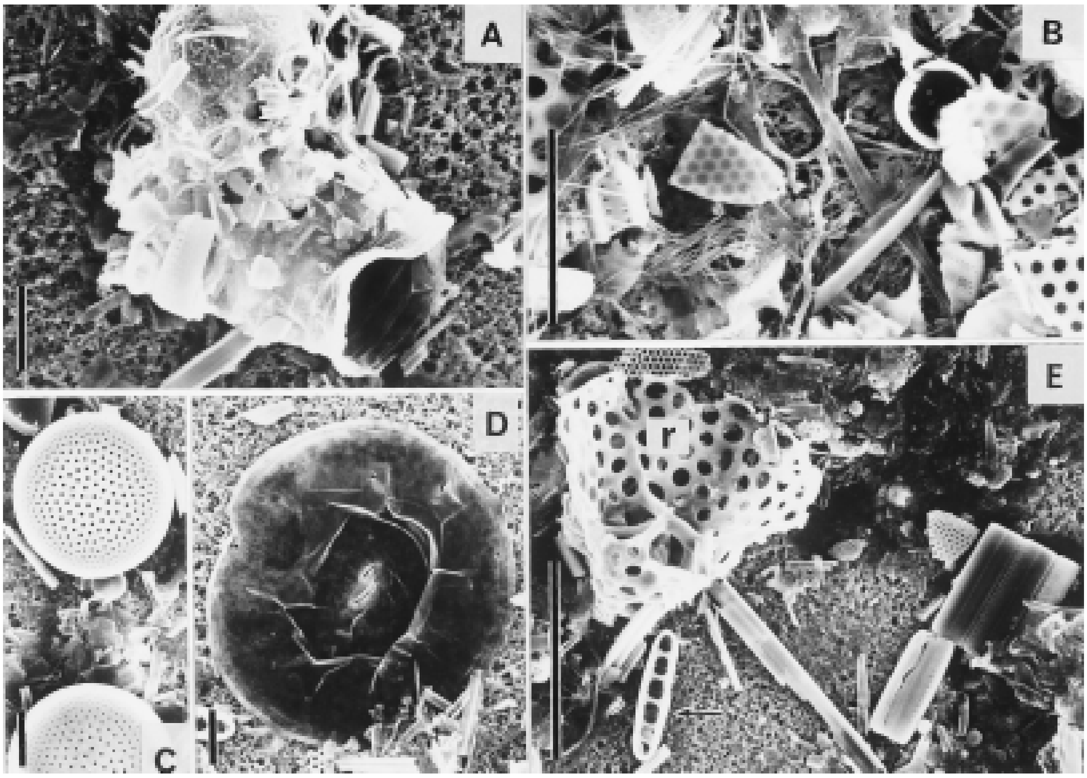

Fig. 17. Microphotographs of gut contents of *Neocalanus cristatus* CIV (cruise III, St. E6). A, Lorica of *Codonellopsis pusilla*; B, Diatom fragments and entangled fibers; C, *Thalassiosira* sp.; D, *Protoperidinium* sp.; E, Radiolarian (r), *Neodenticula seminae* (arrowed) and other diatom fragments. Scales = 10 μm.

Feeding Ecology

The present gut content analysis indicates that copepodids of both early and late stages feed mainly on dominant phytoplankters and protozoan microzooplankters, as has been reported for *Eucalanus bungii* (Ohtsuka *et al.*, 1993). Phytoplankters (*Thalassiosira* spp., *Coscinodiscus* spp. and *Nitzschia* spp.) and a silicoflagellate (*Distephanus speculum*), both of which were most frequently detected in the guts, are dominant species in the subarctic Pacific Ocean (Takahashi, 1987; Booth *et al.*, 1993). Tintinnids were also commonly found in the guts but usually comprise 1 % or less of the ciliate community, which consists mainly of aloricate choreotrich ciliates (Taniguchi, 1984; Strom *et al.*, 1993). Considering their size (10-20 μm wide and 10-40 μm long), aloricate ciliates can become potentially important prey for *N. cristatus*, but no evidence was obtained in the present study because our analysis is almost inapplicable to detection of readily digested food items such as naked protozoans. An exception is hypotrichid ciliates with cirri, which are readily detected in the copepod guts with light and scanning electron microscopy (cf. Ohtsuka and Hiromi, 1987).

Based on laboratory experiments, Dagg (1993a) suggested that sinking detrital matter is nutritionally more important food for *N. cristatus* than phytoplankton and microzooplankton. His results are partially supported by the fact that entangled fibers, parts of which were provisionally identified as derivatives of zooplankton, were always detected in the guts, irrespective of season, locality, and copepodid developmental stage. It is thus possible that *N. cristatus* consumed fecal pellets and secretions of appendicularians, salps and pteropods, although the biomass of these animals was low in the study area (Nagasawa and Ishida, 1997a,b; Nagasawa, 2000). There is another indirect evidence of the detritivory of *N. cristatus*. That is, the peritrophic membrane-like structure of a copepod or other zooplankter's fecal pellet was found in the gut of CII (Fig. 18), but partially torn by copepod maceration and/or during SEM preparation, in which diatom fragments were packed. Although the pellet must have been artificially modified during dehydration for SEM observation, its width (ca. 50 μm) seems to fall within the sizes of calanoid copepods (Hiromi *et al.*, 1988; Noji *et al.*, 1991). Since the peritrophic membrane of fecal pellets is easily broken by copepod grazing (Noji *et al.*, 1991), it is difficult to detect ingested fecal pellets in the guts.

Tsuda and Sugisaki (1994) supported Dagg's (1993a,b) results for *N. cristatus* CV and other particle-feeding calanoid copepods predominating in the subarctic western Pacific (45°N, 165°E) in spring and stated that the copepods are not important as primary consumers of phytoplankters. Gifford (1993) also suggested that protozoans, consisting mainly of aloricate ciliates, are insufficient to meet the basic metabolic needs for *N. cristatus* CV and

Fig. 18. Microphotograph of probable zooplankter's fecal pellet detected in the gut of *Neocalanus cristatus* CII (cruise III, St. E2). Scale = 10 μm.

supported Dagg's (1993a) hypothesis. However, the conditions of some ingested food items found in the present study indicate that *N. cristatus* feeds directly on phytoplankters and tintinnid ciliates. A number of tintinnid loricae and large-sized phytoplankters were actually found fairly undamaged in the guts, which suggests that these food items did not experience mutilple ingestion by macrozooplankters (especially copepods) but were taken by active direct feeding (without indirect ingestion through detrital particles such as zooplankton fecal pellets).

In the subarctic northeastern Pacific, feeding stages of four dominant calanoids (*N. cristatus*, *N. flemingeri*, *N. plumchrus* and *E. bungii*) partition both habitats and foods in the upper 150 m during spring (May and June)(Mackas *et al*., 1993): *N. flemingeri* and *N. plumchurus* occur in the surface mixed layer and feed on ciliates and phytoplankton, whereas *N. cristatus* and *E. bungii* dwell the layer immediately beneath the surface mixed layer and take mainly particulate materials (e.g., fecal pellets descending from the upper layer). However, it is also known that *N. cristatus* and *E. bungii* invade the surface layer with maximum ciliate biomass later in summer after *N. plumchrus* and *N. flemingeri* have completed their downward ontogenetic migration (Mackas *et al.,* 1993). *Neocalanus plumchrus* begins to move to deep waters mainly in July in the northeastern Pacific (Miller *et al*., 1984). Although our sampling was conducted mainly in mid-summer (July) and a little earlier than the invasion season of *N. cristatus* (around August, Mackas *et al*., 1993), it may be possible that *N. cristatus* invaded the surface layer and fed directly on phytoplankters and ciliates. For more detailed discussion from this viewpoint, we need information about the abundance of dominant calanoids other than *N. cristatus*.

Dagg's (1993a) hypothesis of detritivory of *N. cristatus* depends on an assumption of a growth rate of 2 % body C/day, and he did not examine the body condition of the specimens used for the experiments. Recently, the following three types of morphologically/physiologically different body conditions of *N. cristatus* CV (Ikeda *et al*., 1990) have been distinguished: solid type (with well-developed musculature and conspicuous lipids); transparent type (with poorly developed musculature and no lipids); and intermediate type (with characters between the two types). The occurrence of each of these types is known to greatly vary between seasons in the Oyashio region (Kobari and Ikeda, 1999): the solid-type increased from May to August (highest Chl-*a* concentration (>9 mg/m^3) was recorded in May), but both the transparent type and the intermediate type predominated from October to February. Considering the peculiar feeding strategy of *N. cristatus*, it may be necessary to take account of the body condition when the ingestion and growth rates are assessed.

Shiomoto *et al*. (1999) found a significant negative relationship between summer copepod biomass and Chl-*a* concentration in the surface layer of the TD in the central North Pacific and suggested that grazing by copepods heavily reduced the phytoplankton standing stock. The present study obtained a similar result for relationships between abundance of *N. cristatus* and Chl-*a* concentration (Fig. 5). These findings are inconsistent with the results based on the experimental works of Dagg (1993a,b) and Tsuda and Sugisaki (1994). However, since data on the abundance of copepods other than *N. cristatus* are lacking in this study, it is premature to say that this species is a primary consumer of phytoplankton. Nevertheless, we can say that *N. cristatus* more actively feeds on phytoplankters and ciliates than previously suggested.

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夏季と冬季の北太平洋中央部と西部における*Neocalanus cristatus*の南北分布および餌料

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摘　要

1995年6～7月と1996年1月に北太平洋中央部と西部における南北定線上の定点において表層（水深150 mから海表面）で採集されたカイアシ類*Neocalanus cristatus*の現存量と消化管内容物を調べた．6～7月にはコペドディド4期と5期が卓越したが，1月にはコペドディド1～3期が多くを占めた．本種の現存量は緯度によって変化し，6～7月には移行領域と亜寒帯域南部で最も高く，1月には移行領域北部で高かった．夏季における現存量の南北分布の地域差は，コペドディド5期の現存量に原因していた．6～7月には本種の現存量と表層のクロロフィル量との間に統計的に有意な負の相関が認められた．本種は夏季と冬季に様々な珪藻類を主に食べており，夏季には有鐘繊毛虫類，冬季には珪質鞭毛虫類が珪藻類に次いだ．消化管内に渦鞭毛藻類と動物プランクトンの出現は少なかった．また，本種はデトリタス食性も示し，動物プランクトンの分泌物や糞粒を食べていると考えられた．以上の結果から，本種は従来考えられていたよりも活発に植物プランクトンや繊毛虫類を食べると推定される．

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