Contributions of heterotrophic and autotrophic prey to the diet of euphausiid, *Euphausia pacifica* in the coastal waters off northeastern Japan

Yoshizumi Nakagawa[1]*, Yoshinari Endo[1] and Kenji Taki[2]

[1] *Graduate School of Agricultural Science, Tohoku University, Sendai 981-8555*
[2] *Tohoku National Fisheries Research Institute, Shiogama 985-0001*

Abstract: The contributions of heterotrophic and autotrophic prey to the diet of *Euphausia pacifica* were examined in coastal waters off northeastern Japan in May and October 1999. The autotrophic contribution was estimated from gut pigment contents, and the heterotrophic contribution from the volume of each taxonomic group in the stomach. Our observations suggest that heterotrophic prey, especially copepods, were more important than autotrophic prey in both seasons. The contributions of heterotrophic prey items in adult *E. pacifica* ranged from 57–79% in May and from 27–93% of the total ingested carbon in October. The contribution of copepods was largest, ranging from 54–77% in May and from 27–93% in October. We discuss the contribution of athecate ciliates, another possible heterotrophic prey of importance, to the diet of *E. pacifica*.

key words: *Euphausia pacifica*, diet, copepods, naked ciliates, northeastern Japan

Introduction

Euphausia pacifica is the dominant euphausiid species in the subarctic northwestern North Pacific (Mauchline and Fisher, 1969). It plays an important role in transferring energy from lower to higher trophic levels in the sea because many endemic and migrant predators, including pelagic and demersal fish, marine mammals, seabirds and benthic organisms, depend on this species for food (Nemoto, 1962; Odate, 1991; Nicol and Endo, 1997; Yamamura *et al.*, 1998). Detritus, diatoms, dinoflagellates, silicoflagellates, tintinnids, foraminiferans, chaetognaths, echinoderm larvae, copepods, amphipods, other crustaceans and euphausiid ommatidia were found in the stomachs of this species (Ponomareva, 1963; Mauchline and Fisher, 1969; Endo, 1981; Nakagawa *et al.*, 2001).

Mauchline (1967) pointed out three food types utilized by euphausiids: (1) material such as diatoms, dinoflagellates, and tintinnids filtered by the mouthparts from the water, (2) zooplankton, and (3) detrital material obtained from bottom sediments. Previous studies suggested that heterotrophic prey items contributed to the diet of *E. lucens* (Stuart and Pillar, 1990; Gibbons *et al.*, 1991), *E. superba* (Price *et al.*, 1988; Nishino and Kawamura, 1994; Atkinson and Snÿder, 1997; Atkinson *et al.*, 1999; Perissinotto *et al.*, 2000), *E. pacifica* (Nakagawa *et al.*, 2001) and *Meganyctiphanes norvegica* (Båmstedt

---

and Karlson, 1998; Lass *et al.*, 2001). These studies proposed that copepods contributed to the diet of euphausiids.

Perissinotto *et al.* (2000) estimated autotrophic carbon from gut pigment contents and heterotrophic carbon from dry weight of stomach contents of *E. superba*, and they suggested that the heterotrophic component of the diet of *E. superba* was substantial and often much larger than the autotrophic component when chlorophyll-*a* concentrations were low. Nakagawa *et al.* (2001) suggested that copepods were the most important prey items of *E. pacifica* in terms of carbon throughout the year in Sanriku waters, northwestern North Pacific, based on calculated carbon contents of prey items in the stomach. However, ingestion of phytoplankton by *E. pacifica* is underestimated by this method because phytoplankton cells are broken by mastication and only a small fraction remains intact in the stomach (Nakagawa *et al.*, 2001). On the other hand, Ohman (1984) suggested that diatoms were optimal food items and copepods were suboptimal ones of *E. pacifica* from results of laboratory experiments.

The present study aimed at investigating the *in situ* contributions of heterotrophic and autotrophic prey items to the diet of *E. pacifica* in the coastal waters off northeastern Japan using conversion of volume to carbon for the former and gut pigment analysis for the latter.

Materials and methods

Euphausiid surveys were carried out at 3 stations during 12–19 May and at 5 stations each along transects at 40°N and 38°20′N during 11–21 October 1999 in the subarctic northwestern North Pacific (Fig. 1). The vertical profiles of temperature and salinity were determined using STD. Simultaneously with STD casts, a 100-ml water sample was collected from each of 6 depths (0, 10, 20, 30, 50, 75 and 100 m), filtered through a Whatman GF/F glass filter, and analyzed by the Turner Designs fluorometer for chlorophyll-*a*. Chlorophyll-*a* was represented as mean integrated value over the surface 100 m. A 10-100-ml subsample was taken from this sample depending on microplankton abundance, allowed to settle for 24 h, and then the numbers of different groups of ambient microplankton were enumerated with a modified Utermöhl method (Taniguchi, 1977).

E. pacifica was collected by using a ring net, with a mouth diameter of 130 cm and mesh aperture of 0.45 mm (Watanabe, 1992). Tows were made obliquely from 500 m to the surface, while tows at stations shallower than 500 m were made from near the bottom to the surface. The towing duration ranged from 8 to 33 min.

A total of 88 adults and 66 juveniles were sorted randomly from the collections for gut pigment analysis, and then were frozen and kept at −80°C. The remainder were preserved in 5% buffered formalin. Not all collections supplied enough *E. pacifica* in suitable condition for gut pigment analysis (*e.g.* Stns 5 and 30 in October). The procedure for chlorophyll-*a* and phaeopigment determination used was a modification of the method of Holm-Hansen *et al.* (1965). Samples were extracted in 6 ml 90% acetone for 24 hours at −25°C and the fluorescence was determined before and after acidification on a Turner Designs fluorometer. A large percentage of the chlorophyll pigments are resolved into phaeophorbides in the guts of copepods, with the conversion efficiency of
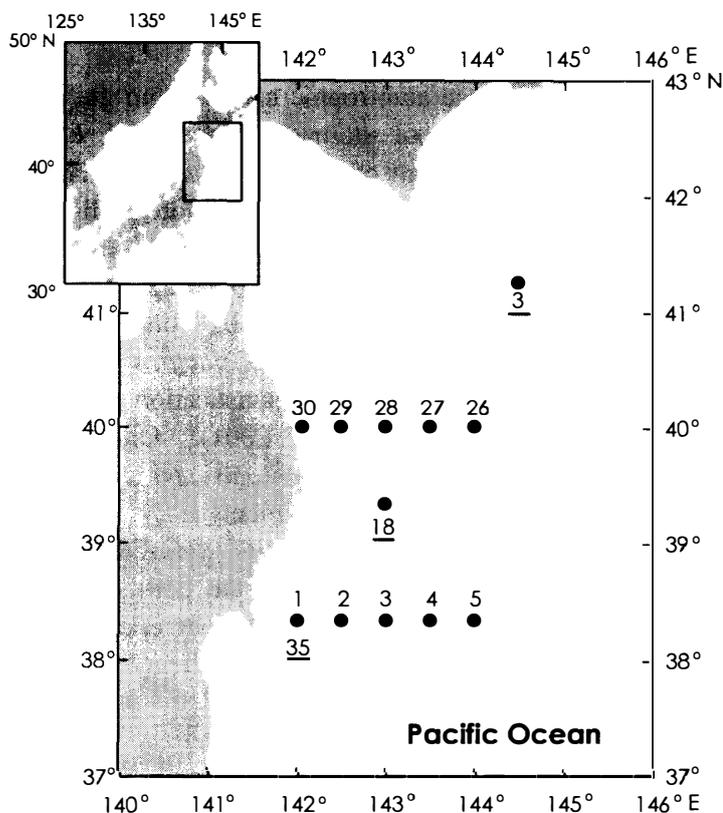
Fig. 1.   Locations of sampling stations in this study in May and October, 1999.
Underlined numbers show sampling stations in May.

100% on a molar basis (Shuman and Lorenzen, 1975).   Thus a conversion factor of 1.51 was applied to phaeopigment values because the molecular weight of phaeophorbide is 66.3% that of chlorophyll (Dagg and Wyman, 1983).   The amount of plant materials consumed by euphausiids can be expressed as the total gut pigment (chlorophyll-a + 1.51 × phaeopigmets), and the unit was ng chlorophyll-a equiv. indiv.$^{-1}$.

After analyses for gut pigment contents, their total length, from the anterior tip of the rostrum to the distal end of the telson, was measured, and stomachs were dissected out and the contents spread on glass slides.   Prey organisms were identified under a dissecting microscope, enumerated and the size was measured to calculate relative contributions of various prey types in carbon weight.

The carbon content of autotrophic prey consumed by $E.$ $pacifica$ was estimated from gut pigment contents with the carbon: chlorophyll-a ratio of 30 (Strickland, 1960; Geider, 1987).   The carbon content of heterotrophic prey was estimated according to Nakagawa et $al.$ (2001) as follows.   Tintinnid carbon was estimated from lorica volume according to Verity and Langdon (1984).   Foraminifera carbon was estimated from cell volume with a conversion factor of 89 fg C μm^{-3} (Michaels et $al.$, 1995).   Invertebrate eggs found in the stomachs were thought to be copepod eggs and the carbon content was estimated from egg size with a conversion factor of 0.14 pg C μm^{-3} (Kiørboe et $al.$, 1985).   Total length of copepods was measured when intact ones were found in the

stomach. Only 6 individuals of intact copepods were found and measured from 91 individuals of krill examined. In addition, when copepod mandibles occurred, the number of pairs of a size was taken as the number of individuals. In most cases, a pair or pairs of mandibles with the same size were found in the stomachs, when only a single mandible was present it was nevertheless counted as one copepod. The carbon content of copepods was obtained by estimating the prosome length from width of the mandible blade (Karlson and Bamstedt, 1994), then dry mass was calculated from the prosome length and it was assumed that carbon weight is 46% of the dry mass (Vidal, 1980). The carbon content of intact copepods was calculated from total length with the equation of Hirota (1986). Daily rations of *E. pacifica* were calculated according to Nakagawa *et al.* (2001), assuming a gut passage time of 1.08 h and a 12-h feeding period per day (Willason and Cox, 1987).

Results

Vertical profiles of temperature and salinity at each station in May are shown in Fig. 2. Surface water temperatures in May ranged from 7–12.8°C. Stns 3 and 35 were located in the Transition area (Kawai, 1955), with temperature at 100 m-depth more than 5°C (Fig. 2). However, water mass at Stn 3 was affected greatly by cold Oyashio water compared with the other stations because the temperature at 100 m-depth was as low as 6.6°C (Fig. 2). Stn 18 was located at the edge of a warm-core ring, where a thermostad temperature of 8–9°C existed at 40–160 m-depth (Fig. 2). In October, surface water temperatures ranged from 19.5–23.1°C along 38°20'N and 17.2–18.8 along 40°N (Fig. 3). All stations in October were located in the Transition area. The thermoclines were at 20–40 m-depth at Stns 2 and 3, and 40–50 m-depth at Stns 28 and 29 (Fig. 3).

Mean concentration of chlorophyll-*a* and abundance of diatoms in May were higher than those in October (Figs. 4 and 5). Diatoms in May were abundant at Stn 3 where considerable influence of Oyashio water was recognized (Fig. 4). Higher abundances of
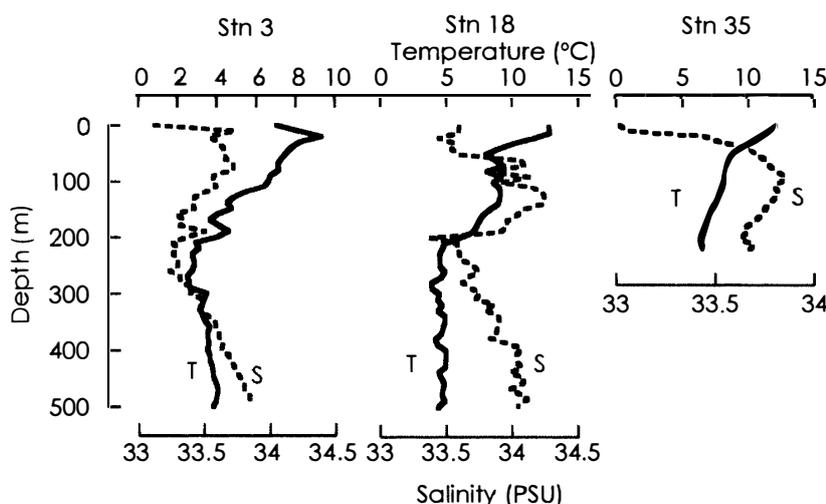

Fig. 2. Vertical profiles of temperature (solid line) and salinity (dotted line) at each station in May 1999.
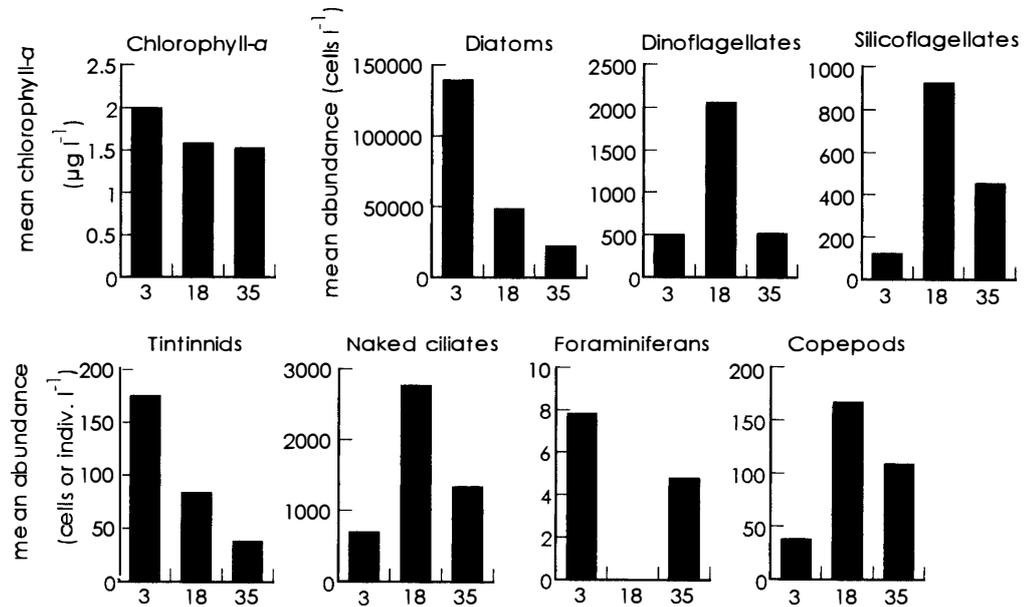
Fig. 3.   Vertical profiles of temperature along 40°N (upper) and 38°20'N (lower) in
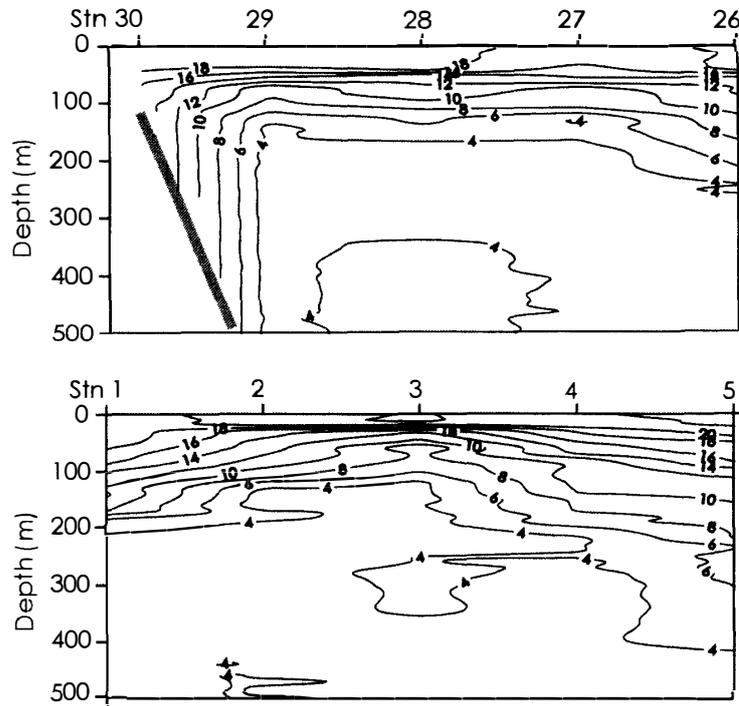   October 1999.

Fig. 4.   Mean concentration of chlorophyll-a and abundance of microplankton in the
          upper 100 m in May 1999.

diatoms, tintinnids and foraminiferans in May were found at Stn 3, while higher values of
dinoflagellates, silicoflagellates, naked ciliates and copepods were found at Stn 18 which
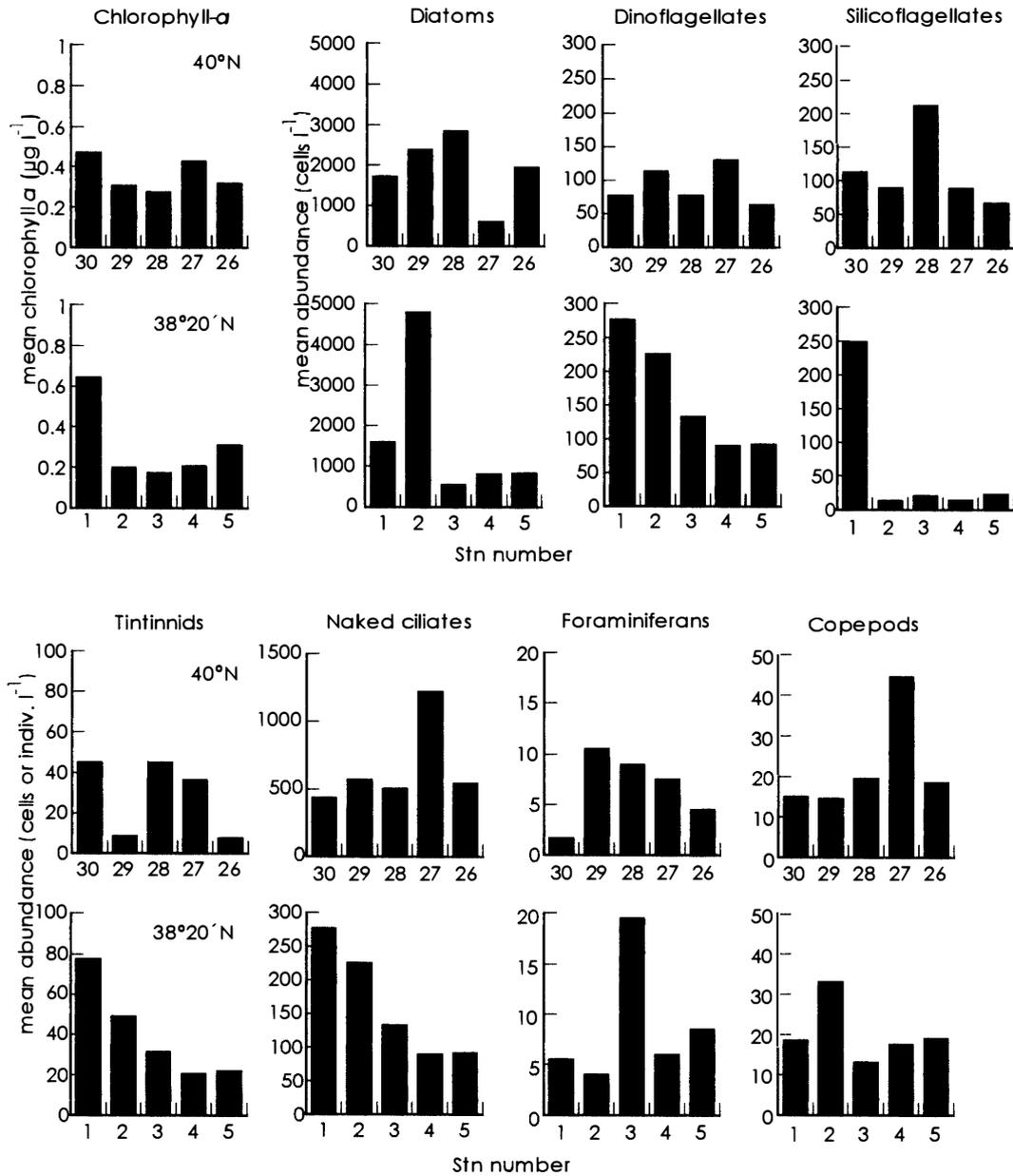
Fig. 5.   Mean concentration of chlorophyll-*a* and abundance of microplankton in the upper 100 m in October 1999.

was located at the edge of the warm-core ring.   In October, the mean concentration of chlorophyll-*a*, and abundances of dinoflagellates, silicoflagellates, tintinnids and naked ciliates along 38°20′N were highest at Stn 1.   The mean abundances of dinoflagellates, tintinnids and naked ciliates decreased toward Stn 5, namely from inshore to offshore (Fig. 5).   The highest values of diatoms and copepods were found at Stn 2, and that of foraminiferans at Stn 3. The higher values of chlorophyll-*a* along 40°N in October were found at Stns 30 and 27 (Fig. 5).   Mean abundances of diatoms and silicoflagellates were higher at Stn 28. Dinoflagellates, tintinnids and naked ciliates were highest at Stn 27, and
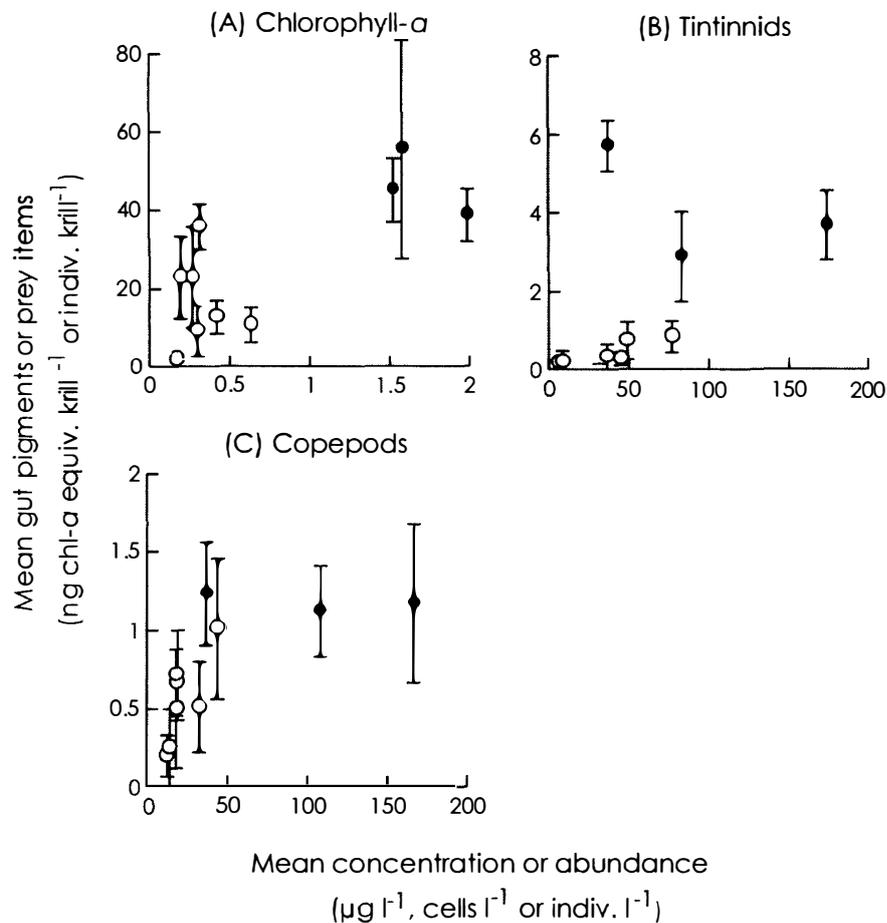
(A) Chlorophyll-a

(B) Tintinnids

(C) Copepods

Mean gut pigments or prey items
(ng chl-a equiv. krill^{-1} or indiv. krill^{-1})

Mean concentration or abundance
(μg l^{-1}, cells l^{-1} or indiv. l^{-1})

Fig. 6.   Chlorophyll-a concentration (A), and numbers of tintinnids (B) and copepods (C) in the stomach of one *Euphausia pacifica* individual as functions of their concentrations or abundances in the water column in May ($\bigcirc$) and October ($\bullet$). Vertical and horizontal bars represent $\pm$ 1 SE.

foraminiferans were highest at Stn 29.

Identifiable prey items found in the stomach contents of *E. pacifica* were classified into 7 taxonomic groups (diatoms, dinoflagellates, silicoflagellates, tintinnids, foraminiferans, copepods and invertebrate eggs). Gut pigment contents as a measure of consumed phytoplankton ranged from 39–55 and from 9–35 ng chl-a equiv. krill^{-1} in May and October respectively, with higher values in May (Fig. 6A). Gut pigment contents increased with the increase of pigment concentration in the water column. Higher numbers of tintinnids, 3–6 cells krill^{-1}, were found in the stomachs in May, while the numbers were low, 0.2–0.9 cells krill^{-1}, in October (Fig. 6B). Tintinnids in the stomachs also increased with their increasing mean abundance in the water column, except for Stn 35 in May. The mean number of copepods in the stomachs ranged from 1.1–1.2 and from 0.2–1.0 indiv. krill^{-1} in May and October respectively (Fig. 6C). The numbers of copepods in the stomachs increased with their ambient abundance up to 50 indiv. l^{-1}, and then saturated at more than that value. The mean numbers of invertebrate eggs in the stomachs ranged from 0.1–0.9 and less than 0.5 indiv. krill^{-1} in May and October
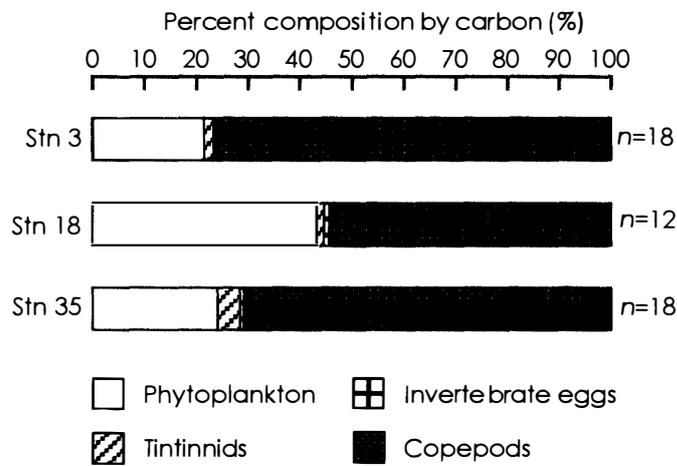
Percent composition by carbon (%)

0   10 20 30 40 50 60 70 80 90 100

Stn 3   n=18

Stn 18   n=12

Stn 35   n=18

☐ Phytoplankton   ⊞ Invertebrate eggs

▨ Tintinnids   ■ Copepods

Fig. 7.   Percentage in contribution of each prey item by carbon at each station in May.

Percent composition by carbon in adults (%)

0   10 20 30 40 50 60 70 80 90 100

Stn 30   No Data

Stn 29   n=4

Stn 28   n=7

Stn 27   n=6

Stn 26   n=6

Stn 1   n=8

Stn 2   n=4

Stn 3   n=5

Stn 4   No Data

Stn 5   No Data

Percent composition by carbon in juveniles (%)

0   10 20 30 40 50 60 70 80 90 100

Stn 30   No Data

Stn 29   n=12

Stn 28   n=7

Stn 27   n=10

Stn 26   n=8

Stn 1   n=6

Stn 2   n=9

Stn 3   n=10

Stn 4   n=4

Stn 5   No Data

☐ Phytoplankton   ⊞ Invertebrate eggs
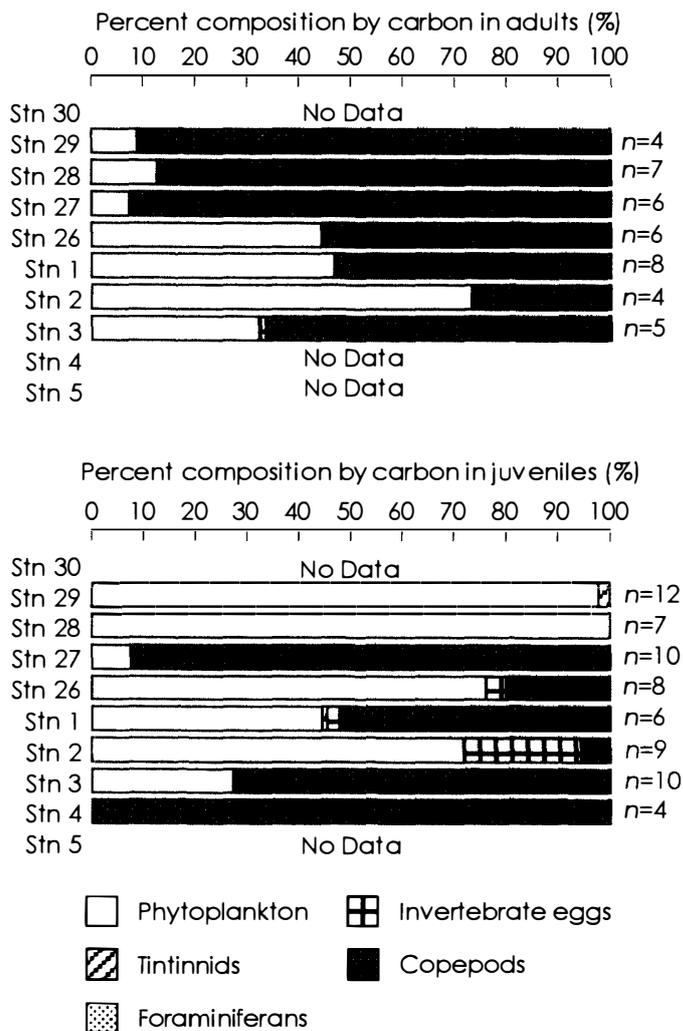
▨ Tintinnids   ■ Copepods

▦ Foraminiferans

Fig. 8.   Percentage in contribution of each prey item by carbon for adult (upper) and juvenile *Euphausia pacifica* (lower) at each station in October.

respectively. Foraminiferans were only found in the stomachs at Stn 27 in October, 0.16 indiv. krill^{-1}.

Percent composition of intact identifiable prey items by carbon was calculated. In May, the contribution of heterotrophic prey items was higher than that of autotrophic prey items at all three stations, with the former comprising from 57–79% of the total ingested carbon, and copepods proved to be most important prey item, comprising from 54–77% (Fig. 7). The daily ration of E. pacifica in May ranged from 42.8–62.3 μg C krill^{-1} day^{-1}, which corresponds to 1.8–2.7% body carbon. It was lowest at Stn 18, which was located at the edge of the warm-core ring. Daily rations at Stn 3, 2.4% body carbon, and at Stn 35, 2.7%, were higher than at Stn 18, 1.8%. The contribution of heterotrophic prey items of adult E. pacifica along 38°20′N and 40°N in October ranged from 53–93% of the total ingested carbon, except for Stn 2 where an exceptionally low value, 26.8% was obtained (Fig. 8). The daily ration of adult E. pacifica in October ranged from 7.5–59.2 μg C krill^{-1} day^{-1} along 38°20′N and 40°N, comprising from 0.4–3.0% body carbon. Daily rations along 40°N, 1.4–3.0% body carbon, were higher than those along 38°20′N, 0.4–0.9% body carbon. For juvenile E. pacifica, the contribution of heterotrophic prey items ranged from 0–99.6% of total ingested carbon along 38°20′N and 40°N lines, and the contribution of autotrophic prey items of juvenile E. pacifica was higher than that of adults, except for Stn 4 at which adult E. pacifica was not sampled, and Stns 2 and 3 (Fig. 8). Daily ration of juveniles ranged from 0.3–59.2 μg C krill^{-1} day^{-1} along 38°20′N and 40°N, comprising from 0.1–13.8% body carbon.

Discussion

Euphausiids masticate foods with their mandibles (Ponomareva, 1963; Mauchline, 1967; Nemoto, 1967) and their foregut is known to have functions to masticate and store foods (Suh and Nemoto, 1988; Suh and Toda, 1992; Suh et al., 1994). Food organisms in the stomach of euphausiids were broken to various degrees according to their body structure. For analyzing the diet and feeding of E. pacifica, examination of gut contents and faecal materials has been conducted by using a light microscope (Ponomareva, 1963; Endo, 1981), which provided qualitative, not quantitative information. Previous studies have reported that copepods were consumed by euphausiids (e.g. Mauchline and Fisher, 1969), but the ingested mass of copepods was not examined quantitatively. The copepod mandibles, which are composed of silica and chitin (Sullivan et al., 1975), are highly resistant to mastication and digestion (Karlson and Båmstedt, 1994). By measuring a specific size character of the identified copepod mandible and converting the size to mass, total copepod mass eaten by euphausiids can be obtained (Karlson and Bamstedt, 1994). Enumeration of such mandibles in the stomach contents of euphausiids has been used to quantify predation on copepods by euphausiids (Stuart and Pillar, 1990; Gibbons et al., 1991; Båmstedt and Karlson, 1998; Nakagawa et al., 2001).

Copepod is one of the prey items of E. pacifica in Japanese waters including the Sea of Japan (Ponomareva, 1963; Endo, 1981). Endo (1981) reported that tintinnids and copepods were the main prey items in the fall, based on the frequency of occurrence of food organisms. Nakagawa et al. (2001) suggested that copepods were by far the most important prey item by carbon calculated from their mandibles throughout the year.

They estimated the carbon weight of prey items other than copepods from their biovolumes in the stomachs of *E. pacifica*. The highest daily ration of phytoplankton was 0.04% body carbon in their study, which is at least one order of magnitude lower than that of previous studies, 0.8–6.3% (Ohman, 1984; Willason and Cox, 1987). Therefore, phytoplankton carbon was underestimated. In the present study, the gut pigment contents were analyzed to estimate phytoplankton contribution. Then the highest daily ration of phytoplankton was 0.8% body carbon in May, which was in the lower range of the previous studies.

The contributions of heterotrophic prey items of adult *E. pacifica* ranged from 57–79% of the total ingested carbon in May and from 27–93% in October, while the contribution of copepods ranged from 54–77% in May and from 27–93% in October. In April, the contribution of heterotrophic prey in the Oyashio water was 66% with copepods being the most important (unpublished data). Our observation suggests, therefore, that the heterotrophic prey, especially copepods, was more important than autotrophic prey throughout the year.

In the present study, the mean number of identifiable prey items in the stomachs increased with their increasing mean abundance in the water column except for copepods at densities more than 50 indiv. l^{-1} (see Fig. 6). Mean gut pigment contents (GP) and mean number of copepods (C) in the stomachs showed a significant correlation, while their regression equation was $GP = -2.12 + 37.41 \times C$ ($n=10$, $r=0.80$, $p<0.01$). This means that when *E. pacifica* is feeding actively, it feeds on both phytoplankton and copepods. However, the relative contribution of heterotrophic prey, especially copepods, at Stns 27, 28 and 29 in October was higher than that at any station in May. The daily rations of phytoplankton in October were lower than in May (3.0–7.5 and 12.8–18.5 μg C krill^{-1} day^{-1} in October and May, respectively), and those of copepods were not different between these two months (30.2–50.3 and 23.3–45.8 μg C krill^{-1} day^{-1} at those stations in October and May) in spite of the smaller number of copepods in the stomachs in October. Therefore, higher contributions of copepods in October might be caused partly by decreased ingestion of phytoplankton and partly by ingesting larger copepods. Gibbons *et al.* (1991) suggested that *E. lucnes* may be a preferentially herbivorous omnivore, and capture small and slow-moving copepods on an incidental encounter basis. However, in the present study, *E. pacifica* consumed larger copepods at Stns 28 and 29 in October, whose prosome length ranged from 0.77–1.0 mm. Begon *et al.* (1990) indicated that predators should choose the prey that gives the optimum ratio of energy gain per energy expenditure. This implies that prey as large as possible should be advantageous. Therefore, our results suggested that *E. pacifica* chose larger copepods in October when chlorophyll-*a* concentration and copepod abundance were low.

In October, a lower contribution of heterotrophic prey, 26.8%, was obtained at Stn 2. The mean abundance of autotrophic preys (diatoms and dinoflagellates) in the water column was high at Stn 2. Stuart and Pillar (1990) suggested that *E. lucens* only eats copepods when the ambient concentration of chlorophyll-*a* falls below a threshold value. Nakagawa *et al.* (2001) suggested that *E. pacifica* suspension-feed on phytoplankton when phytoplankton are abundant, and shift their food preference to copepods when phytoplankton decrease below the threshold density. Perissinotto *et al.* (2000) suggested that the heterotrophic component of the diet of *E. superba* is substantial and often much

larger than the autotrophic component at low chlorophyll-*a* concentrations. In the present study, therefore, *E. pacifica* might have shifted its main prey item from heterotrophic prey to autotrophic prey at Stn 2 in October.

Stuart and Pillar (1990) reported that gut passage time was 38.5 min for phytoplankton and 76.9 min for copepod mandibles. *E. lucens* fed on copepods with a mean prosome length of 0.86 mm. In the present study, the mean prosome length of copepods consumed by *E. pacifica* was 0.39 mm, which is much shorter than that given for *E. lucens*. The total length of adult *E. lucens* ranges from 10−18 mm (Mauchline and Fisher, 1969), and individuals examined by Stuart and Pillar (1990) are about the same size as adult *E. pacifica* or a little smaller than in the present study, 9−20 mm. Although there is a size difference in copepods, it might be better to apply the result of Stuart and Pillar (1990) that gut passage time was about 2 times longer for copepods than for phytoplankton to *E. pacifica* in the present study. Therefore, we recalculated the contributions of autotrophic and heterotrophic prey using 1.08 h for autotrophic prey and 2.16 h for copepods. Then the contributions of heterotrophic preys ranged from 41−65% and 16−86% of total ingested carbon in May and October respectively, and those of copepods ranged from 37−62% and 15−86% respectively. These values still support the hypothesis that the heterotrophic prey items, especially copepods, were the most important prey items except at Stn 18 in May and Stns 1 and 2 in October where autotrophic prey (dinoflagellates and silicoflagellates at Stn 18 in May and Stn 1 in October, diatoms and dinoflagellates at Stn 2 in October) were abundant in the water column.

Nakagawa *et al.* (2001) suggested that the nauplii and early stage of copepodites were consumed by *E. pacifica* because the small mandibles of copepods were abundant in the stomachs. Ohman (1984) suggested that copepods were not entirely consumed by *E. pacifica* because of the escape responses of adult *Pseudocalanus* and/or the difficulty *E. pacifica* has in handling and macerating the copepod exoskeleton. Therefore, large mandibles in the stomachs may be overestimated in calculating ingested carbon because *E. pacifica* may not ingest whole bodies of large copepods. To understand the more detailed contribution of heterotrophic prey items, it is necessary to investigate the gut passage time of copepods, and whether *E. pacifica* feed on whole copepods.

In the present study, we could not identify and quantify the detrital contents such as athecate protozoans, marine snow and other digested organisms in the stomach. Athecate protozoans were a major dietary item of *E. superba* in incubation experiments using natural and enriched seawater (Atkinson and Snÿder, 1997). Our unpublished experiments also suggested that *E. pacifica* ingest naked ciliates actively. The contribution of naked ciliates cannot be neglected because of their appreciable abundance in the water column. In the present study, the preservation method we used, 5% formalin, could lead to severe losses of athecate protozoans (Leakey *et al.*, 1994; Stoecker *et al.*, 1994). Kato (1995) reported that the biomass ratio of naked ciliates/ tintinnids ranged from 3 to 123 with a median of 8.7 in the sea area off northeastern Japan. We calculated the carbon content of naked ciliates that might be ingested by *E. pacifica* by multiplying the carbon content of tintinnids found in the stomachs by 8.7, assuming that naked ciliates and tintinnids were equally ingested in proportion to their numbers, and a gut passage time of 1.08 h and a 12-h feeding period per day. The contribution of naked ciliates for adult *E. pacifica* then ranged from 11−28% in May and

was less than 4% in October. These results suggest that naked ciliates can be one of the major prey items, at least in May. Therefore, the importance of naked ciliates as a prey of *E. pacifica* needs to be quantified by experimental studies in the field and laboratory. On the other hand, although marine snow can be an important prey item for *E. pacifica* (Dilling *et al.*, 1998; Dilling and Alldredge, 2000), we could not calculate the carbon contribution of marine snow because we do not have data on its natural abundance.

In conclusion, we could improve our understanding of contribution of prey organisms to the diet of *E. pacifica* by converting volume to carbon weight for heterotrophic prey and by gut pigment analysis for autotrophic prey.

Acknowledgments

References

Atkinson, A. and Snÿder, R. (1997): Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba*. Mar. Ecol. Prog. Ser., **160**, 63–76.

Atkinson, A., Ward, P., Hill, A., Brierly, A.S. and Cripps, G.C. (1999): Krill-copepod interactions at South Georgia, Antarctica, II. *Euphausia superba* as a major control on copepod abundance. Mar. Ecol. Prog. Ser., **176**, 63–79.

Bämstedt, U. and Karlson, K. (1998): Euphausiid predation on copepods in coastal waters of the Northeast Atlantic. Mar. Ecol. Prog. Ser., **172**, 149–168.

Begon, M., Harper, J.L. and Townsend, C.R. (1990): Ecology. Blackwell, Boston, 945 p.

Dagg, M.J. and Wyman K.D. (1983): Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus* calculated from gut contents. Mar. Ecol. Prog. Ser., **13**, 37–46.

Dilling, L. and Alldredge, A.L. (2000): Fragmentation of marine snow by swimming macrozooplankton: A new process impacting carbon cycling in the sea. Deep-Sea Res. I, **47**, 1227–1245.

Dilling, L., Wilson, J., Steingerg, D. and Alldredge, A.L. (1998): Feeding by the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow. Mar. Ecol. Prog. Ser., **170**, 189–201.

Endo, Y. (1981): Ecological studies on the euphausiids occurring in the Sanriku waters with special reference to their life history and aggregated distribution. Ph. D. Thesis, Tohoku University, Sendai, Japan, 1–166 (in Japanese with English abstract).

Geider, R.J. (1987): Light and temperature dependence of the carbon to chlorophyll *a* ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. New Phytol., **106**, 1–34.

Gibbons, M.J., Pillar, S.C. and Stuart, V. (1991): Selective carnivory by *Euphausia lucens*. Cont. Shelf Res., **11**, 625–640.

Hirota, R. (1986): Netplankton. Manual for Coastal Marine Environmental Research, ed. by The Oceanographical Society of Japan, Tokyo, Koseisha-Koseikaku, 178–191 (in Japanese).

Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W. and Strickland, J.D.H. (1965): Fluorometric determination of chlorophyll. J. Cons. Perm. Int. Explor. Mer., **30**, 3–15.

Karlson, K. and Bämstedt, U. (1994): Planktivorous predation on copepods. Evalution of mandible remains in predator guts as a quantitative estimate of predation. Mar. Ecol. Prog. Ser., **108**, 79–89.

Kato, S. (1995): Standing crops and productivities of planktonic ciliates in the sea area east of Japan, and tropical and subtropical Pacific Ocean. Ph. D. Tohoku University, Sendai, Japan, 1–282 (in Japanese with English abstract).

Kawai, H. (1955): On the polar frontal zone and its fluctuation in the waters to the northeast of Japan. (I).

Bull. Tohoku Reg. Fish. Res. Lab., **4**, 1–46 (in Japanese with English abstract).

Kiørbe, T., Mohlenberg, F. and Hamburger, K. (1985): Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. Mar. Ecol. Prog. Ser., **26**, 85–97.

Lass, S., Tarling, G.A., Virtue, P., Matthews, J.B.L., Mayzaud, P. and Buchholz, F. (2001): On the food of northern krill *Meganyctiphanes norvegica* in relation to its vertical distribution. Mar. Ecol. Prog. Ser., **214**, 177–200.

Leakey, R.J.G., Burkill, P.H. and Sleigh, M.A. (1994): A comparison of fixatives for the estimation of abundance and biovolume of marine planktonic ciliate populations. J. Plankton Res., **16**, 375–389.

Mauchline, J. (1967): Feeding appendages of the Euphausiacea (Crustacea). J. Zool., **153**, 1–43.

Mauchline, J. and Fisher, L.R. (1969): The biology of euphausiids. Adv. Mar. Biol., **7**, 1–454.

Michaels, A.F., Caron, D.A., Swanberg, N.R., Howse, F.A. and Michaels, C.M. (1995): Planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda: abundance, biomass and vertical flux. J. Plankton. Res., **17**, 131–163.

Nakagawa, Y., Endo, Y. and Taki, K. (2001): Diet of *Euphausia pacifica* Hansen in Sanriku waters off northeastern Japan. Plankton Biol. Ecol., **48**, 68–77.

Nemoto, T. (1962): Distribution of five main euphausiids in the Bering and the northern part of the North Pacific. J. Oceanogr. Soc. Jpn. **20 th Anniv. Vol.**, 615–627 (in Japanese with English abstract).

Nemoto, T. (1967): Feeding pattern of euphausiids and differenciations in their body characters. Information Bulletin on Planktology in Japan. Comm. No. of Dr. Y. Matsue 60th Birth, 157–171.

Nicol, S. and Endo, Y. (1997): Krill fisheries of the world. FAO Fish. Tech. Paper, **367**, 1–100.

Nishino, Y. and Kawamura, A. (1994): Winter gut contents of Antarctic krill (*Euphausia superba* Dana) collected in the South Georgia area. Proc. NIPR Symp. Polar Biol., **7**, 82–90.

Odate, K. (1991): Fishery biology of the krill, *Euphausia pacifica*, in the northeastern coast of Japan. Suisan Kenkyu Sosho, **40**, 1–100 (in Japanese with English abstract).

Ohman, M.D. (1984): Omnivory by *Euphausia pacifica*: the role of copepod prey. Mar. Ecol. Prog. Ser., **19**, 125–131.

Perissinotto, R., Gurney, L. and Pakhomov, E.A. (2000): Contribution of heterotrophic material to diet and energy budget of Antarctic krill, *Euphausia superba*. Mar. Biol., **136**, 129–135.

Ponomareva, L A. (1963): The Euphausiids of the North Pacific, Their Distribution and Ecology. Dokal. Akad. Nauk. SSSR, Moscow, 1–154 (English translation, I. P. S. T., Jerusalem, 1966).

Price, H.J., Boyd, K.R. and Boyd, C.M. (1988): Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. Mar. Biol., **97**, 67–77.

Shuman, F.R. and Lorenzen, C.J. (1975): Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr., **20**, 580–586.

Stoecker, D.K., Gifford, D.J. and Putt, M. (1994): Preservation of marine planktonic ciliates: losses and cell shrinkage during fixation. Mar. Ecol. Prog. Ser., **110**, 293–299.

Strickland, J.D.H. (1960): Measuring the production of marine phytoplankton. Fish. Res. Board Can. Bull., **122**, 1–172.

Stuart, V. and Pillar, S.C. (1990): Diel grazing patterns of all ontogenetic stages of *Euphausia lucens* and *in situ* predation rates on copepods in the southern Benguela upwelling region. Mar. Ecol. Prog. Ser., **64**, 227–241.

Suh, H.-L. and Nemoto, T. (1988): Morphology of the gastric mill in ten species of euphausiids. Mar. Biol., **97**, 79–85.

Suh, H.-L. and Toda, T. (1992): Morphology of the gastric mill of the genus *Euphausia* (Crustacea, Euphausiacea). Bull. Plankton Soc. Jpn., **39**, 17–24.

Suh, H.-L., Toda, T. and Hong, S.-Y. (1994): Ontogeny of foregut morphology in the euphausiid *Euphausia pacifica*. J. Crust. Biol., **14**, 47–53.

Sullivan, B.K., Miller, C.B., Peterson, W.T. and Soeldner, A.H. (1975): A scanning electron microscope study of the mandibular morphology of boreal copepods. Mar. Biol., **30**, 175–182.

Taniguchi, A. (1977): Distribution of microzooplankton in the Philippine Sea and the Celebes Sea in summer, 1972. J. Oceanogr. Soc. Jpn., **33**, 82–89.

Verity, P.G. and Langdon, C. (1984): Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. J. Plankton Res., **6**, 859–868.

Vidal, J. (1980): Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol., **56**, 111–134.

Watanabe, Y. (1992): Specifications of a new surface ring net and catch data processing method. Manual for Pelagic Fish Egg and Larval Survey, ed. by Natl. Fish. Res. Inst. Fish. Sci., 15–22 (in Japanese).

Willason, S.W. and Cox, J.L. (1987): Diel feeding, laminarinase activity, and phytoplankton consumption by euphausiids. Biol. Oceanogr., **4**, 1–24.

Yamamura, O., Inada, T. and Shimazaki, K. (1998): Predation on *Euphausia pacifica* by demersal fishes: predation impact and influence of physical variability. Mar. Biol., **132**, 195–208.