Diet of *Euphausia pacifica* Hansen in Sanriku waters off northeastern Japan

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Abstract: Stomach contents of *Euphausia pacifica* in Sanriku waters off northeastern Japan were examined bimonthly from April 1997 to February 1998 and compared to ambient microplankton abundance. Copepods were consumed by *E. pacifica* in proportion to their abundance in the water column in all sampling periods except April. Few copepods were consumed by *E. pacifica* in April despite their high abundance in the water column. Instead, in April the stomachs contained large numbers of diatoms. Copepods proved to be the most important food item, in terms of carbon, for most of the year in Sanriku waters. A tentative calculation of the impact of predation by *E. pacifica* on copepods in Sanriku waters showed that the daily impact accounted for 0.1–2.2% of copepod biomass. Since *E. pacifica* can suspension-feed on diatoms, dinoflagellates, tintinnids and invertebrate eggs, as well as raptorial-feed on small and slow-moving copepods, it appears to be capable of feeding on a wide variety of organisms by switching the feeding behavior according to ambient food conditions.

key words: *Euphausia pacifica*, diet, copepods, Sanriku waters

Introduction

Euphausia pacifica Hansen is the dominant euphausiid species in the northern North Pacific (Mauchline & Fisher 1969). It also occurs across the southern part of the Bering Sea, the Sea of Okhotsk and the Sea of Japan (Brinton 1962; Ponomareva 1963). *E. pacifica* is considered a key species in Sanriku waters off northeastern Japan 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 & Endo 1997; Yamamura et al. 1998).

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. Many species of euphausiids are omnivorous and exhibit multiple feeding behaviors, being able to filter-feed using 'compression filtration' and to feed raptorially on zooplankton (Hamner 1988). Seasonal shifts in diet composition have been observed for the euphausiids *Meganyctiphanes norvegica* and *Thysanoessa inermis*

(Mauchline & Fisher 1969). Diatoms were abundant in the diet in spring and autumn, and crustacean remains were frequent in summer and autumn. Switching from phytoplankton to zooplankton prey was also reported for the copepod *Calanus pacificus*, when phytoplankton levels declined (Landry 1981).

Studies on the feeding activities of *E. pacifica* have great importance for understanding the structure of marine ecosystems off Sanriku. However, since little is known about the food habits of *E. pacifica* in Sanriku waters (e.g. Endo 1981), or the relationship between diet and growth, the flow of energy from lower to higher trophic levels in food webs containing *E. pacifica* is not clear. In Sanriku waters, this species is known to be distributed both in the cold and productive Oyashio area and the warmer and less productive Transition area (e.g. Taki et al. 1996). However, it is not known which area is superior from the viewpoint of food quality and quantity on a yearly basis.

In this study, the stomach contents of *E. pacifica* in Sanriku waters were examined bimonthly throughout the year. Stomach contents were compared to ambient microplankton abundance to determine if the species exhibits food selectivity. Stomach contents analysis underestimates soft bodied organisms and maceration of food makes identification of food items difficult. In order to compensate for the

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underestimation, we made several calculations to obtain reasonable daily rations for *E. pacifica* and discussed which food items were greatly underestimated.

Materials and Methods

Samples were collected bimonthly from April 1997 to February 1998 at 4 stations along a transect at 40°N and at 5 stations along a transect at 38°20'N in Sanriku waters off northeastern Japan (Fig. 1). The number and locations of sampling stations in April were different from those in the other months. The profiles of temperature and salinity were determined using a CTD or STD. Water masses were determined for each sampling station based on the Temperature–Salinity (T–S) diagram and the classification scheme of Hanawa & Mitsudera (1987) (Table 1).

A ring net, with a mouth diameter of 130 cm and mesh aperture of 0.45 mm (Watanabe 1992), was towed obliquely from 15 m above the bottom to the surface at stations shallower than 300 m, and from 150-m depth to the surface at stations deeper than 300 m. Net sampling was confined to nighttime when the species occurs in the upper 150 m. The towing duration ranged from 5 to 31 min with a mean of 12.2 min. Collected euphausiid specimens were preserved in 5% formalin.

A 100-ml water sample was collected from each of 6 depths (0, 10, 20, 30, 50, 75 m), filtered through a Whatman GF/F glass fiber filter, and analyzed by the method of Yentsch & Menzel (1963) with a Hitachi 139 spectrofluorometer for chlorophyll *a*. Chlorophyll *a* was integrated over the upper 75 m, and then averaged for each cruise. A 100-ml water sample from 20-m depth was preserved in 5% formalin, assuming that *Euphausia pacifica* feeds in the surface layer as the percentage of full stomachs in *E. pacifica* is reported to be highest at 0–50-m depth at night for the Sea of Japan (Ponomareva 1963). 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).

Ten adult *E. pacifica* were sorted randomly form each station, and their total length, from the anterior tip of the rostrum to the distal end of the telson, was measured. A total of 435 stomachs were dissected out and the contents spread on glass slides. Stomachs were examined under a dissecting microscope, and scored into 5 classes based on their fullness: empty stomachs, class 0; less than 25% full, class 1; 25–50% full, class 2; 50–75% full, class 3; more than 75% full, class 4. Food organisms were identified, enumerated and dimensions measured to allow calculation of both total carbon content of the stomach contents and the relative contribution of the various prey types. The carbon contents of diatoms and dinoflagellates were estimated from cell volumes according to Strathmann (1967). Tintinnid carbon was estimated from lorica volume according to Ver-
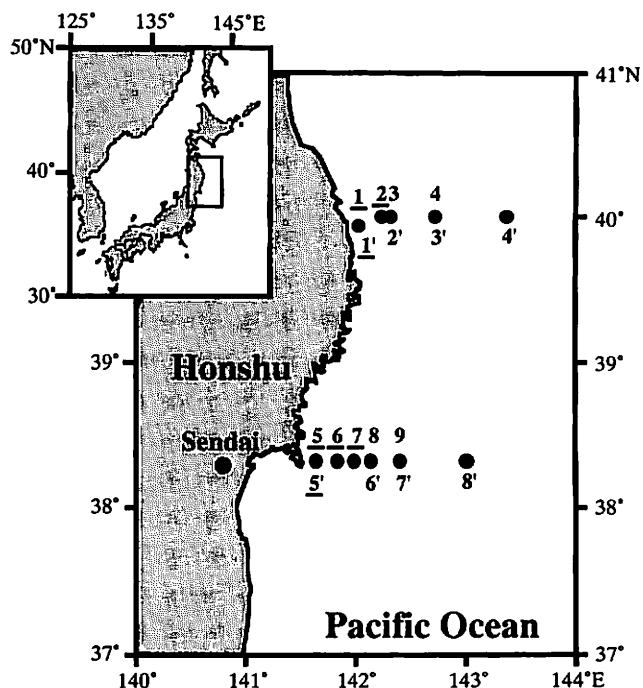

Fig. 1. Locations of sampling stations in this study from April 1997 to February 1998. Those in April were different from the other months and are marked by an apostrophe numbers. Underlined stations were shallower than 300 m.

Table 1. Water masses defined by Hanawa & Mitsudera (1987) which dominated at each sampling station in this study from April 1997 to February 1998. TW, the Tsugaru Warm Current water system; OW, the Oyashio water system; KW, the Kuroshio water system; SW, the surface-layer water system. The number of sampling stations in April was different from the other months.

	April	June	August	October	December	February
Stn 1/1'	OW	SW	TW	TW	TW	OW
Stn 2/2'	TW	TW	TW	SW	TW	TW
Stn 3/3'	TW	TW	OW	OW	TW	TW
Stn 4/4'	OW	TW	OW	OW	SW	OW
Stn 5/5'	TW	SW	TW	SW	TW	OW
Stn 6/6'	TW	TW	TW	SW	TW	OW
Stn 7/7'	OW	SW	TW	KW	TW	OW
Stn 8/8'	OW	OW	TW	KW	TW	OW
Stn 9		OW	TW	KW	SW	OW

ity & Langdon (1984). Invertebrate eggs found in the stomachs were thought to be copepod eggs and carbon content was estimated from egg size with a conversion factor of 0.14 pg C μm^{-3} (Kiørboe et al. 1985). Copepods in the stomachs were identified by their mandibles, and their number was determined from the number of pairs of mandible blades of a given size. Total length of copepods was measured when found intact in the stomach. The carbon content of copepods was obtained by estimating the prosome length from the width of the mandible blades using the equation of
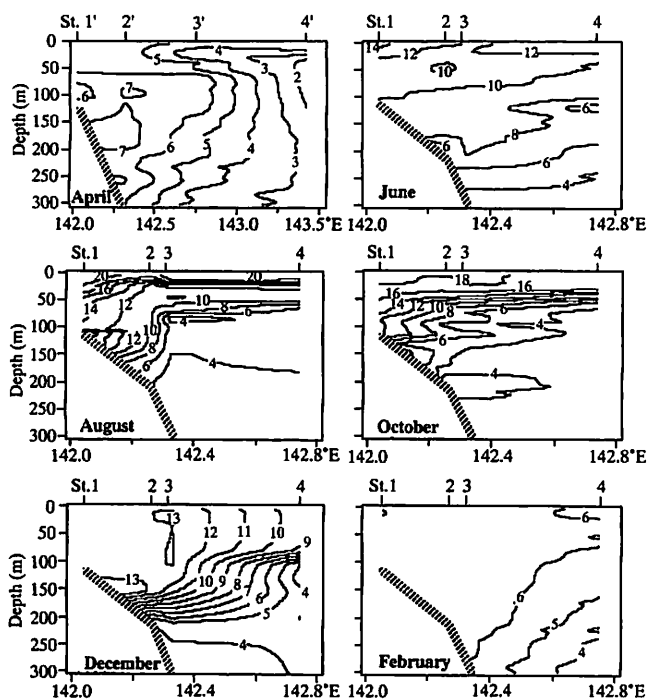
Fig. 2. Vertical profiles of temperature along the 40°N line from April 1997 to February 1998.

Fig. 3. Vertical profiles of temperature along the 38°20'N line from April 1997 to February 1998.

Karlson & Båmstedt (1994), then calculating dry mass from the prosome length of the copepod and assuming that 46% of the dry mass was carbon (Vidal 1980). The carbon contents of intact copepods in the stomach were calculated from total length with the equation of Hirota (1986).

A chi-square test of independence (Sokal & Rohlf 1969) was used to check for seasonal differences in stomach fullness. A single classification analysis of variance (ANOVA) and Fisher's PLSD were used to examine differences in the mean calculated carbon contents of total food items in the stomach between different water systems.

Results

Vertical profiles of temperature along 40°N and 38°20'N lines from April 1997 to February 1998 are shown in Figs 2 and 3. Data on the southern limit of the first (coastal) Oyashio Intrusion is reported by the Tohoku National Fisheries Research Institute (1998). Temperatures ranged from 2–8°C in April, and were higher in the coastal area than offshore. The second (offshore) Oyashio Intrusion occupied the offshore area in both transect lines in April (Tohoku National Fisheries Research Institute 1998). Oyashio water, of temperature <5°C at 100-m depth, was located east of 143°E along the 40°N line, and east of 142.75°E along the 38°20'N line. Surface water temperatures increased in June due to seasonal warming. A thermocline at 20–50-m depth in the offshore area in August and October was also the result of seasonal warming. In August and October only the offshore stations (Stns 3 and 4) along the 40°N line were influenced by the second Oyashio Intrusion; coastal areas
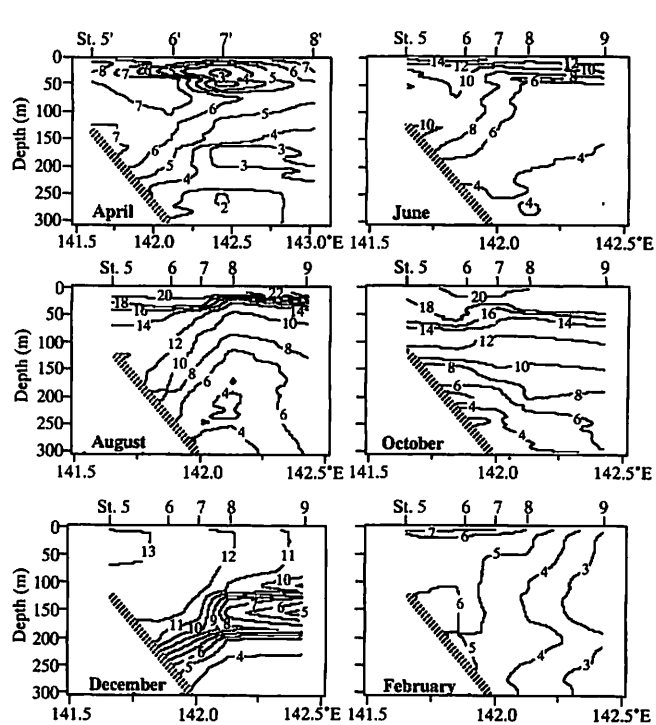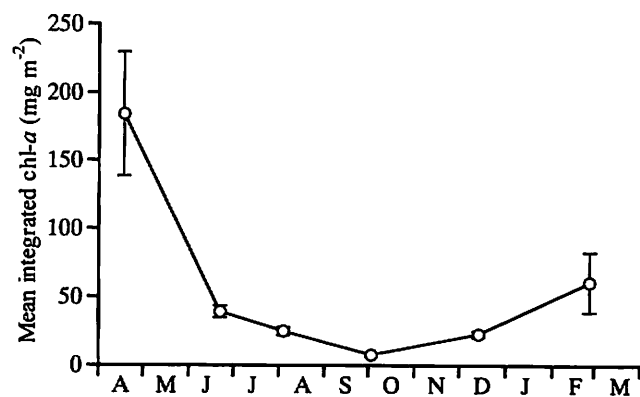

Fig. 4. Seasonal change in the mean integrated chlorophyll a in the upper 75 m from April 1997 to February 1998. Bars represent ± 1 SE.

(Stns 1 and 2) on both lines were influenced by the Tsugaru Warm Current. With surface cooling, the thermocline deepened to 100–200 m in December. The thermocline had disappeared by February, when water temperatures ranged from 3–7°C. Offshore stations (Stn 4 in Fig. 2 and Stns 7, 8 and 9 in Fig. 3) along both lines in February showed evidence of the first Oyashio Intrusion.

The integrated chlorophyll-a concentration in the upper 75 m was highest in April (184 mg m^{-2}) and lowest in October (7.7 mg m^{-2}) (Fig. 4). The high chlorophyll-a concentrations in April were the result of the spring bloom, also seen in Ocean Color and Temperature Scanner (OCTS) images (Inagake & Saitoh 1998). Chlorophyll-a concentra-
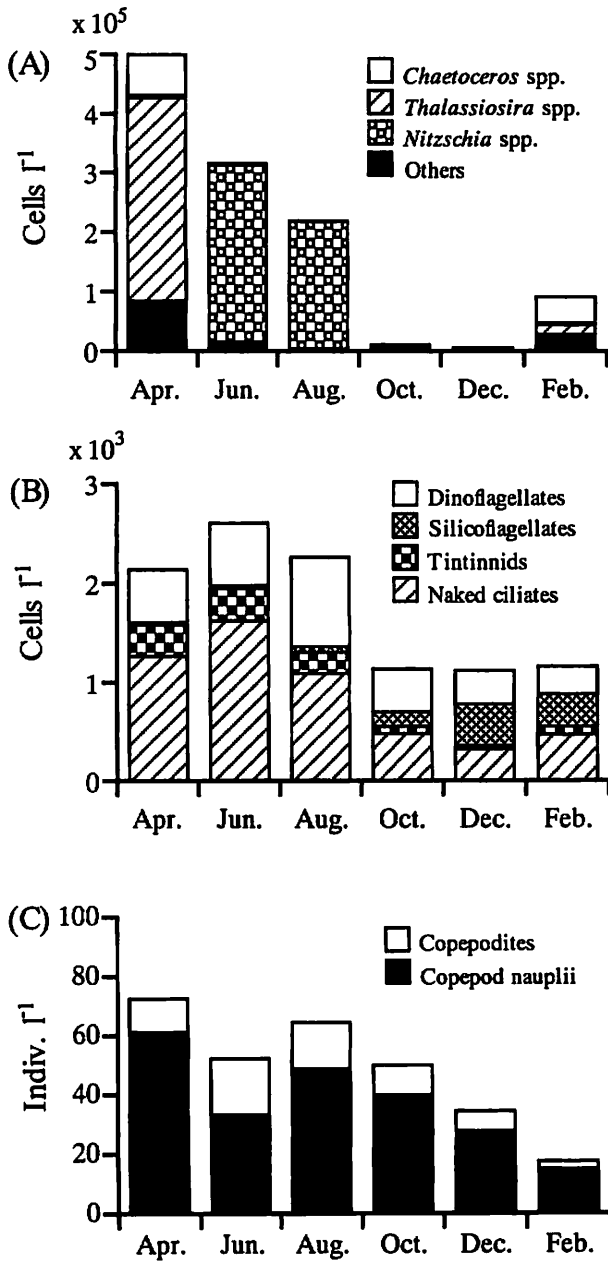
(A)

x 10^5

Cells l^{-1}

☐ *Chaetoceros* spp.
▨ *Thalassiosira* spp.
▩ *Nitzschia* spp.
■ Others

Apr. Jun. Aug. Oct. Dec. Feb.

(B)

x 10^3

Cells l^{-1}

☐ Dinoflagellates
▦ Silicoflagellates
▨ Tintinnids
▨ Naked ciliates

Apr. Jun. Aug. Oct. Dec. Feb.

(C)

100

Indiv. l^{-1}

☐ Copepodites
■ Copepod nauplii

Apr. Jun. Aug. Oct. Dec. Feb.

Fig. 5. Seasonal change in abundance of (A) diatoms, (B) other phytoplankton and ciliates and (C) copepods at 20-m depth from April 1997 to February 1998.

tions tended to be highest at 20–50-m depth throughout the year.

Diatoms were the most numerous microplankton at 20-m depth at each station throughout the survey period (Fig. 5). The abundance of diatoms was higher in April, June and August than the other months, with *Thalassiosira* spp. dominating in April, and *Nitzschia* spp. in June and August. The abundances of other phytoplankton (dinoflagellates and silicoflagellates), tintinnids and naked ciliates were also higher in April, June and August than in the other months (Fig. 5). Copepods (nauplii and copepodites) were most abundant in April, decreasing in number gradually towards
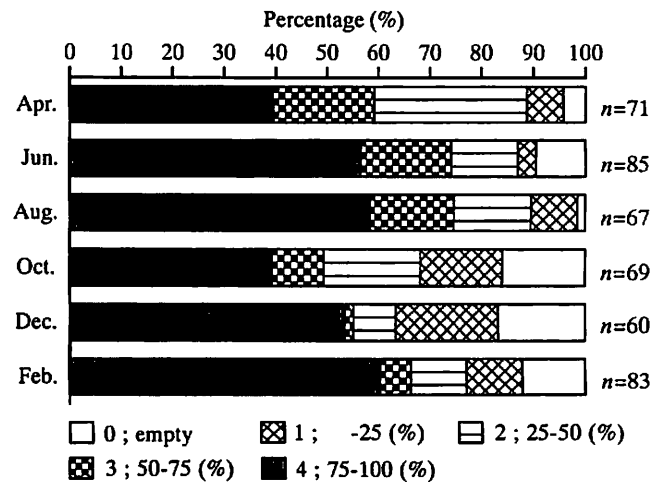
Percentage (%)

Apr. *n*=71
Jun. *n*=85
Aug. *n*=67
Oct. *n*=69
Dec. *n*=60
Feb. *n*=83

☐ 0 ; empty   ▨ 1 ;   -25 (%)   ▤ 2 ; 25-50 (%)
▦ 3 ; 50-75 (%)   ■ 4 ; 75-100 (%)

Fig. 6. Seasonal change in the stomach fullness index of *Euphausia pacifica* that were collected from April 1997 to February 1998.

Percent composition by number (%)

Apr. *n*=71
Jun. *n*=85
Aug. *n*=67
Oct. *n*=69
Dec. *n*=60
Feb. *n*=83

▤ Diatoms   ▨ Dinoflagellates   ▦ Tintinnids
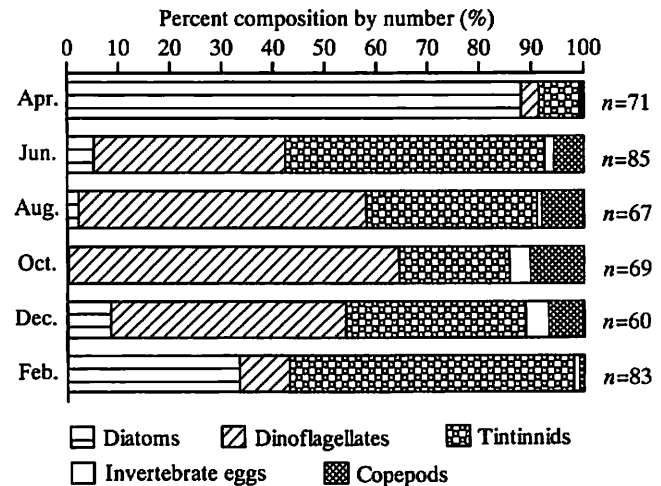☐ Invertebrate eggs   ▦ Copepods

Fig. 7. Seasonal change in percent composition by number of identifiable food items in the stomach contents of *Euphausia pacifica*. The average percent composition was calculated by dividing the total number of each of the food items in all euphausiids analyzed at each time of the year by the overall number of all food items at that time.

February with a slight anomaly in June (Fig. 5).

Seasonal changes were found in the stomach fullness of *Euphausia pacifica* ($p<0.001$, chi-square test for independence). The percentage of *E. pacifica* with empty stomachs (class 0) ranged from 1.5 to 16.7% (Fig. 6) over the year. Individuals with some food in their stomachs comprised more than 83% of the population of euphausiids throughout the survey period. The percentage of *E. pacifica* with stomachs half full or more (classes 3 and 4), was highest in June and August and lowest in October.

Identifiable food items found in the stomach contents of *E. pacifica* were classified into 5 groups (diatoms, dinoflagellates, tintinnids, invertebrate eggs and copepods), and their percent composition by number calculated throughout
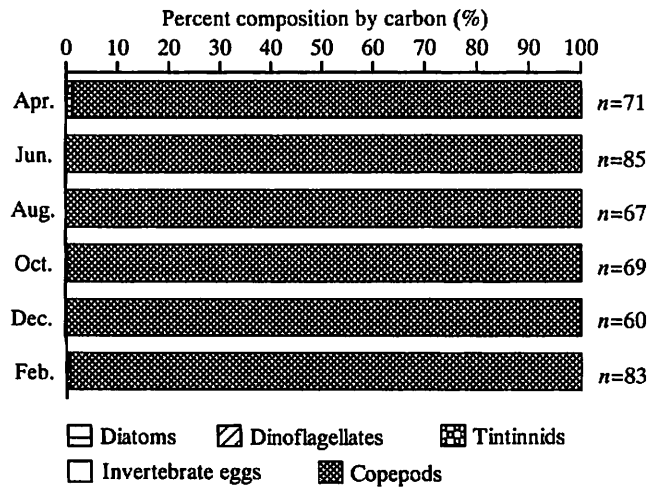
Percent composition by carbon (%)

Fig. 8. Seasonal change in percent carbon composition of identifiable food items in the stomach contents of *Euphausia pacifica*. The average percent composition was calculated by dividing the total carbon content of each of the food items in all euphausiids analyzed at each time of the year by the overall carbon content of all food items at that time.

Fig. 9. The relationship between the ambient abundance at 20-m depth and the mean number in the stomachs of *Euphausia pacifica* individuals for (A) diatoms, (B) dinoflagellates and tintinnids and (C) copepods. Vertical and horizontal bars represent ± 1 SE.

the year (Fig. 7). In April, the two most abundant groups in the diet were diatoms (88.0%), and tintinnids (7.9%). By June, the percentage of diatoms had decreased markedly (5.2%), whereas increases were seen in the percentages of tintinnids (50.1%) and dinoflagellates (37.2%). Dinoflagellates continued to increase over the summer to a high of 64.2% in October. The contribution of diatoms and tintinnids decreased from June to October to 0.2% and 21.3%, respectively. Between October and February the dinoflagellate contribution decreased to 9.8%, and the contribution of diatoms and tintinnids increased to 33.4% and 54.8%, respectively. Invertebrate eggs comprised a small percentage of the diet, 0.5% to 4.4%. Copepods comprised from 0.2 to 10.2% of the number of prey items identified during the survey period. The dominant identifiable prey groups, by number, were diatoms in April, tintinnids in June and February, and dinoflagellates in the other months.

The seasonal pattern in percent composition of identifiable food items by carbon was very different (Fig. 8). Copepods proved to be the most important food item throughout the survey period, comprising more than 98.5% of the total carbon in stomach contents. Total percentage contribution of all other food items was 1.5% in April, and was only 0.1% in June and August when high stomach fullness was observed.

The highest number of diatoms in the stomach, more than 100 intact cells per euphausiid, was found in April, when diatoms were most abundant in the water column (Fig. 9A). Diatoms were not consumed by *E. pacifica* in proportion to their ambient abundance in June and August when diatoms were still abundant in the water column, nor in October when concentrations were greater than in December. Only 0.5–2.0 intact diatom cells were found per
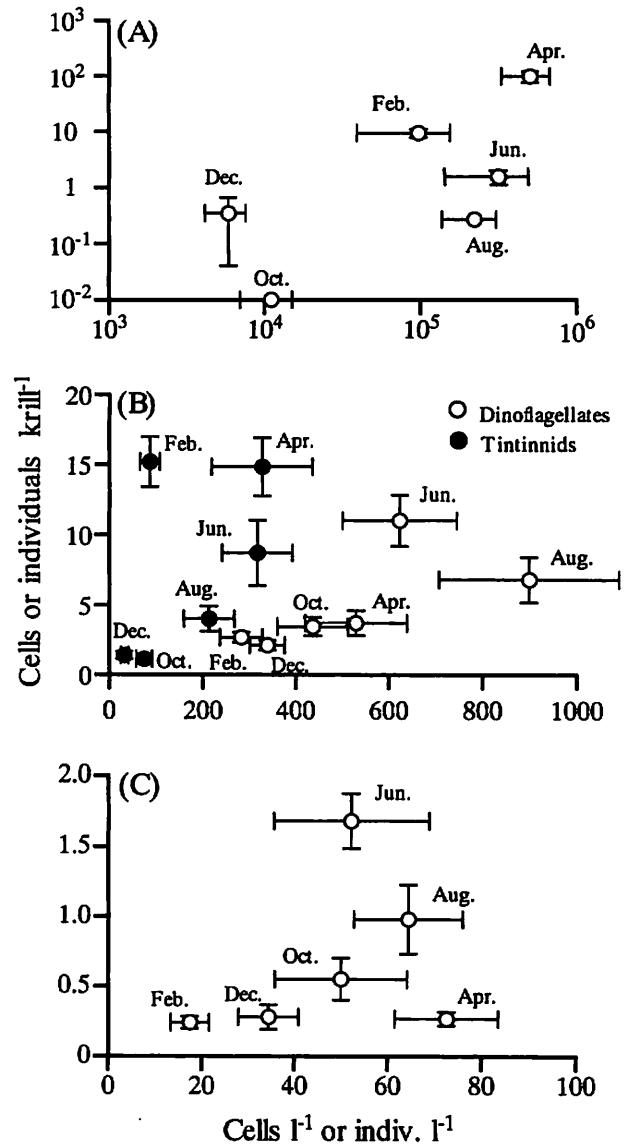
stomach in June, August and in December, despite the fact that diatom abundance was about 2 orders of magnitude less in December than in June or August (Fig. 9A). In June and August pointed and chain-forming *Nitzschia* spp., made up more than 94% of the ambient diatom community at 20-m depth.

Higher numbers of dinoflagellates, 7–11 cells per euphausiid, were found in stomachs in June and August, when dinoflagellates were abundant (600–900 cells l⁻¹) in the water column (Fig. 9B). However, the numbers of dinoflagellates were not proportional in June; there were more in stomachs than was predicted. Few dinoflagellates were found in stomachs in December and February, when they were at a concentration of only about 300 cells l⁻¹ in the water column. Cell numbers of dinoflagellates and tintin-

nids consumed by *E. pacifica* increased with their increasing abundance in the water column, except for February for tintinnids, when the tintinnid genera found in stomachs differed from those found at 20-m depth. For example, *Undella* spp. was found in the stomachs but not in the water column.

The abundance of copepods in stomachs also increased with their increasing abundance in the water column, except in April and June (Fig. 9C). The highest number of copepods in stomachs was 1.7 indiv. per euphausiid and was found in June. In October, when concentrations of copepods (about 50 indiv. l^{-1} of copepods at 20-m depth) were about the same as in June, the number of copepods per stomach was much less, only 0.6. The number per stomach in April, when diatoms dominated, was much less than would be predicted from numbers in the water column.

E. pacifica were larger in April and June than in the other months. The mean total length of *E. pacifica* analyzed for stomach contents in April and June was more than 17.8 mm, and less than 14.8 mm in the other months. The range of prosome lengths of the copepods in the stomachs was largest in June, 178–2059 μm, and smallest in April, 184–676μm. April seems exceptional because although the size

of *E. pacifica* was larger, fewer and smaller copepods were consumed despite the fact that copepods were abundant in the water column. In April diatoms appeared in the stomachs in greater numbers and copepods in fewer numbers than would be predicted from their abundances in the water column.

The width of copepod mandible blades in the stomachs ranged from 12 to 180 μm, which corresponds to the estimated prosome lengths of 178–2059 μm (Fig. 10). 76% of copepod mandible pairs found in the stomachs were less than 50 μm in width (estimated prosome length was less than 603 μm). Mandibles ranging in width from 20–30μm (estimated prosome length was 267–379 μm) were especially numerous in the stomachs. The minimum width of copepod mandible blades found in the stomachs ranged from 12 to 16 μm, regardless of the total length of *E. pacifica*. The maximum width, however, increased with the total length of *E. pacifica*, and increased abruptly when the total length of *E. pacifica* exceeded 16 mm (Fig. 10).

There was no significant difference in the total carbon content of food items in the stomachs of *E. pacifica* among the water masses of Hanawa & Mitsudera (1987) for any month (Table 2) when the variations were tested with ANOVA and the multiple comparisons were conducted using Fisher's PLSD (DF=3,431, F=2.2, p>0.3). The total carbon content tended to be higher in June than in other months.

Discussion

Endo (1981) reported that stomach contents of *Euphausia pacifica* changed seasonally in Sanriku waters. Based on the frequency of occurrence of each food item, diatoms and detritus dominated in spring, dinoflagellates, tintinnids and copepods in summer, and detritus, tintinnids and copepods in fall. In this study, the stomach contents of *E. pacifica* also changed seasonally in terms of the relative number of prey items. Diatoms dominated in April, tintinnids in June and February, and dinoflagellates in the other months.

The highest number of diatoms per stomach was found in April, when both integrated chlorophyll a and diatom cell numbers (dominated by *Thalassiosira* spp.) in the water column were the highest of the survey period. Diatom num-
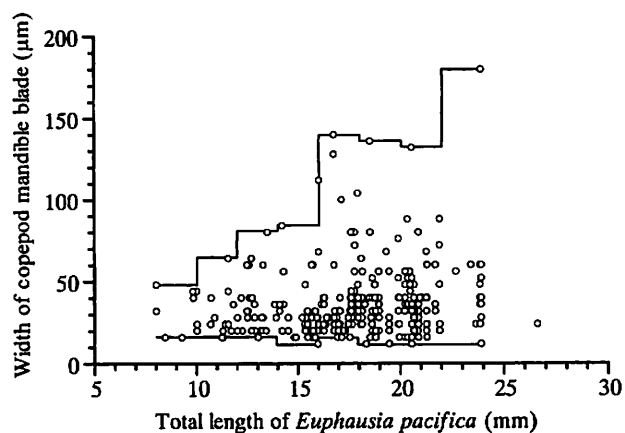

Fig. 10. The relationship between the total length of *Euphausia pacifica* and the width of copepod mandible blades found in the stomachs of *E. pacifica*. Upper and lower lines delineate the maximum and minimum width of mandible blades, respectively for each size class of *E. pacifica* separated at 2 mm intervals.

Table 2. Mean calculated carbon contents (μg C krill^{-1}) of total food items in the stomachs of *Euphausia pacifica* for different water masses as defined by Hanawa & Mitsudera (1987).

	Oyashio water system	Tsugaru Warm Current water system	Surface-layer water system	Kuroshio water system
April	0.50	1.69		
June	13.3	7.46	7.59	
Aug.	2.78	3.30		
Oct.	1.65		1.34	1.07
Dec.		1.41	1.25	
Feb.	0.76	0.29		
Average	3.80	2.83	3.39	1.07

Table 3. Ingestion by *Euphausia pacifica* of copepods from April 1997 to February 1998. Ingestion of copepods was calculated by assuming a gut passage time of 1.08 h (Willason & Cox 1987) and a 12-h feeding period per day. Copepod biomass in Sanriku waters is for 1993 and was taken from Kotani et al. (1996).

	μg C krill^{-1} d^{-1}	Ingested copepods μg C m^{-3} d^{-1}	% Body C d^{-1}	Copepod biomass mg C m^{-3}	% Copepod biomass
April	11.1	15.2	0.4	11.2	0.1
June	99.5	30.3	3.1	3.43	0.9
Aug.	34.9	19.4	2.5	1.33	1.5
Oct.	14.6	7.1	1.2	1.38	0.5
Dec.	15.2	2.4	1.7	0.54	0.4
Feb.	18.5	31.6	1.1	1.44	2.2

bers were also high in the water column in June and August, but were dominated by the pointed, chain-forming diatom *Nitzschia* spp. Since *Nitzschia* spp. were not found in stomachs during this study, they were probably not consumed by *E. pacifica*. Copepods were consumed by *E. pacifica* in proportion to their abundance in the water column except during April. Few copepods were consumed by *E. pacifica* in April despite their high abundance in the water column. Stuart & Pillar (1990) suggested that *Euphausia lucens* only eats copepods when the ambient concentration of chlorophyll *a* falls below a threshold value. The tendency for predatory behavior to increase when alternative food sources are limited has also been found in other organisms, e.g. omnivorous copepods (Landry 1981; Daan et al. 1988). Turner (1984) observed that crustacean remains were present in the fecal pellets of the copepod *Eucalanus pileatus* when phytoplankton abundance was low. In this study, judging from the relative proportions of prey items by number, *E. pacifica* might have shifted its food preference to abundant diatoms in April, rather than feed on copepods whose escape behavior likely costs the euphausiids additional energy to catch and ingest.

Gibbons et al. (1991) suggested that *E. lucens* may be a preferentially herbivorous omnivore, and capture small and slow-moving copepods on an incidental encounter basis. In this study, the range of prosome lengths of copepods consumed frequently by *E. pacifica* was 267–379 μm. This size range corresponds to stages N6–C2 of *Paracalanus parvus* (Davis 1984), the most dominant copepod species in Sanriku waters (Odate 1994). *E. pacifica* may be easily ingesting these slow moving nauplii and early copepodites.

Since *E. pacifica* can suspension-feed on diatoms, dinoflagellates, tintinnids and invertebrate eggs, as well as feed raptorially on small copepods, a wide variety of organisms can be ingested by switching feeding behavior according to ambient food conditions.

Copepods proved to be the most important food item in terms of carbon throughout the year in Sanriku waters, comprising more than 98.5% of total calculated stomach contents. There is contradicting evidence as to whether euphausiids consume the entire body of a copepod. In experiments with different prey types, including the diatom

Thalassiosira angstii and adults of the copepod *Pseudocalanus* sp., Ohman (1984) suggested that copepods were not entirely consumed by *E. pacifica*, and were judged to be suboptimal prey items. He ascribed this to the escape responses of adult *Pseudocalanus* and/or to the difficulty *E. pacifica* has in handling and macerating the copepod exoskeleton. His *E. pacifica* exhibited a daily carbon ration of only 0.45% based on copepods, compared to 8.8% on diatoms. On the other hand, the euphausiid *Meganyctiphanes norvegica* preying on *Calanus finmarchicus* had similar predation rates in both laboratory and field studies, giving 12.7% of the daily ration (Båmstedt & Karlson 1998). They showed that copepods were entirely consumed in about 80% of the predation occasions. In this study, most of the copepods ingested by *E. pacifica* seemed to be stages N6–C2 of *Paracalanus parvus*. Copepods of these stages may not be as difficult for *E. pacifica* to capture and macerate as adults are. We assumed that *E. pacifica* consumed copepods entirely, following Stuart & Pillar (1990) and Båmstedt & Karlson (1998).

A tentative calculation of the predation impact of *E. pacifica* on copepods in Sanriku waters shows that the daily impact accounts for 0.1–2.2% of copepod biomass (3.9–65.6% copepod biomass per month) (Table 3). The calculations were based on a gut passage time of 1.08 h (Willason & Cox 1987) and a 12-h feeding period per day. Copepod biomass in Sanriku waters was taken from Table 1 of Kotani et al. (1996). Since the prosome length of copepods consumed frequently by *E. pacifica* (267–379 μm) is smaller than the mesh size of the net used (450 μm), cod end feeding is unlikely to have occurred in this study. Atkinson et al. (1999) suggested that *E. superba* could potentially remove up to 40% of the copepod population per month in South Georgia.

In this study, the frequencies of diatoms, dinoflagellates, tintinnids and invertebrate eggs in the diet are underestimated because only intact cells or individuals in the stomach of *E. pacifica* were enumerated. The debris from mastication by *E. pacifica* and caused by dissection of the stomach were not quantified. To compensate for this unknown degree of underestimation, we multiplied the carbon contents of identifiable food items other than copepods by 100,

Table 4. Daily ration of *Euphausia pacifica* that were collected from April 1997 to February 1998. Body carbon of *E. pacifica* was estimated from total length using the equation of Heath (1977). Daily ration was calculated by assuming a gut passage time of 1.08 h (Willason & Cox 1987) and a 12-h feeding period per day.

	Average body C mg C	Stomach contents C μg C krill^{-1}	Daily ration μg C krill^{-1} d^{-1}	Daily ration % Body C d^{-1}
April	3.14	1.0	11.3	0.4
June	3.16	9.0	99.7	3.2
Aug.	1.40	3.1	34.9	2.5
Oct.	1.18	1.3	14.6	1.2
Dec.	0.90	1.4	15.2	1.7
Feb.	1.74	1.7	18.7	1.1

i.e. assuming that only 1% of the non-copepod prey items were whole and identified. This assumption was based on the fact that the highest ration calculated for phytoplankton prey was 0.04% in this study compared with several % or more reported previously (Ohman 1984; Willason & Cox 1987). In doing so, the percentage of carbon in the stomach contents due to copepods ranged from 37 to 90%, with the lowest value in April, and the value greater than 55% in the other months. Therefore, the dominance of copepods in terms of carbon content in the diet remains unchanged except for April.

According to Lasker (1966), 5% of the body carbon of *E. pacifica* is needed per day to maintain their growth, respiration, and molting rates. Ohman (1984) reported a maximum daily ration of 8.8% for *Thalassiosira angstii*. Ross (1982) found a carbon-specific ration of ca. 13% at 8°C and ca. 20% at 12°C for *Thalassiosira fluviatilis* and *T. angstii*. Daily rations calculated in this study were lower than these values, ranging from 0.4 to 3.2% of body carbon, with the lowest value in April (Table 4). However, *E. pacifica* exhibited rapid growth from April to June in this year (Taki, unpublished data) as well as in other years in Sanriku waters (Odate 1991; Taki & Ogishima 1997). The contribution of diatoms to the total carbon in the stomach was highest in April and *E. pacifica* are reported to have higher rations and are thus presumed to grow faster on diatoms than on animal prey (Ross 1982; Ohman 1984). Even if the carbon contents of food items other than copepods were multiplied by 100, the daily carbon ration of *E. pacifica* due to these food items increased only to 1.0% in April. Such a value does not seem to be sufficient to sustain their rapid growth in spring. The low carbon ration implies that we are still underestimating the carbon ingested as food items other than copepods. If we multiply carbon contents of food items other than copepods by 1000, instead of 100, the carbon ration goes up to 6.4–9.9%, which is similar to the values reported by Ross (1982) and Ohman (1984) and seems reasonable to support *E. pacifica* growth. In this case, the copepod contribution ranges from 6% in April to 47% in August.

In this study, unidentifiable detrital contents were frequently found in the stomachs of *E. pacifica*. They may be

organisms without shells such as naked flagellates and ciliates, marine snow, or other digested organisms. Athecate protozoans were a major dietary item of *E. superba* in incubation experiments at ambient food concentrations (Atkinson & Snyder 1997). We could not identify naked ciliates in the stomachs, but their contribution as a food source of *E. pacifica* cannot be neglected, since they occurred in the water samples from 20-m depth in appreciable numbers (Fig. 5). Because the preservation method we used (5% formalin) could lead to severe losses of athecate protozoans (Leakey et al. 1994; Stoecker et al. 1994), we used the biomass ratio of naked ciliates/tintinnids in Sanriku waters reported by Kato (1995) to calculate the carbon contribution of naked ciliates which might be ingested by *E. pacifica*. The ratio ranged from 3 to 123 with a median of 8.7. We calculated the carbon content of ingested naked ciliates 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 by the euphausiid. The ration then ranged from 2.7% (October) to 7.2% (February) when we multiplied the carbon content of food items other than copepods by 100. The contribution of naked ciliates was high in February and April, 67–73%, but the contribution of copepods, 46–68%, exceeded that of other food items in the other months. Therefore, naked ciliates could be one of the major prey items for *E. pacifica*. Marine snow can be an important food source for larger zooplankton (Alldredge & Silver 1988). *E. pacifica* assimilates natural marine snow with relatively high efficiency, similar to the values observed when feeding on diatoms (Dilling et al. 1998). Marine snow, therefore, can be one of the factors we missed in the calculation of the carbon content of food items.

For analyzing the diet of *E. pacifica*, examination of stomach contents with a dissecting microscope can yield important qualitative information. Ingestion by *E. pacifica*, however, is underestimated by this method. Phytoplankton cells are broken by mastication and only a small fraction remain intact in the stomach. Gut pigment analysis could help estimate the amount of phytoplankton ingested. We assumed that the gut passage time for all food items was the same. However, the gut passage times for major food items

have to be determined experimentally, since different values have been reported for phytoplankton and copepods (Stuart & Pillar 1990). Detrital material in the stomachs of *E. pacifica* needs to be quantified and identified to better understand the structure of marine ecosystems off Sanriku.

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