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Community and trophic structures of pelagic copepods down to the greater depths in the western subarctic Pacific (WEST-COSMIC)

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Abstract: As part of the research program "WEST-COSMIC (Western Pacific Environment Study on CO_2 Ocean Sequestration for Mitigation of Climate Change)", vertical distribution and community structure of copepods were studied at Station Knot (44˚N, 155˚E) down to 4000 m depth in the western subarctic Pacific. Vertical carbon flux mediated by copepod communities was also estimated. Both abundance and biomass of copepods were greatest in the near surface layer and decreased with increasing depth. Decrease of abundance with depth was best fitted to power regression model, while that of biomass was best described by an exponential regression model. Copepod carcasses occurred throughout the layer, and carcasses/living specimens ratios were greatest in the deepest layer (the ratio was 9.3 at 3000-4000 m depth). A total of 98 calanoid copepod species belonging to 38 genera and 15 families occurred in the 0-4000 m water column (Cyclopoida, Harpacticoida and Poecilostomatoida were not identified to species). The number of genera and species showed bimodal vertical distributions with peaks at 500-1000, and at 2000-3000 m both during day and night. Based on the species similarity indices, copepod community could be classified into epipelagic, mesopelagic and bathypelagic communities. Based on the feeding pattern, copepods were divided into four types: suspension feeders, suspension feeders in diapause, detritivores and carnivores. In terms of abundance, the most dominant group was suspension feeders (mainly the cyclopoid genus Oithona) in the epipelagic zone, while detritivores (mainly Poecilostomatoida genus Oncaea) were dominant in the meso- and bathypelagic zones. In terms of biomass, suspension feeders in diapause (calanoid genera Neocalanus and Eucalanus) were the major component (ca. 70%), especially at 200-2000 m depth. Comparison of vertical flux of particulate carbon with estimated copepod ingestion/egestion rates suggests that the suspension feeding copepods receive sufficient food. For detritivorous copepods, copepod carcasses, a possible food source, are not abundant enough, so other food sources need to be considered. As a food source for carnivorous copepods, the abundance of suspension feeding and detritivorous copepods appears to be high enough to meet their demand. Our calculation showed that an average of 32% of the particulate carbon flux is consumed by copepods in the 0-4000 m water column.

Key words: copepods, community structure, species diversity, carbon cycle, carbon flux
Regional terms: Japan, Station Knot, western subarctic Pacific Ocean

Introduction

Copepoda is one of the important zooplankton taxa, contributing 60-80% of net zooplankton biomass in the world ocean (Longhurst, 1985). From the viewpoint of the global carbon cycle, copepods feed on organic carbon produced by tiny primary producers in the epipelagic zone, and egest large fecal pellets which sink faster than those of protists (microzooplankton), thus accelerating the biological pump (Longhurst and Harrison, 1989). Seasonal vertical migrations of large grazing copepods in the high latitude seas are regarded as an other mechanism which accelerates organic matter transfer to the deep-sea (Bradford-Grieve et al., 2001). Vinogradov (1962) hypothesized that prey-predator linkages and vertical migrations of zooplankton living at various depths in the ocean are mechanisms of rapid transportation of organic matter from the surface to deeper layers. However, this hypothesis, called the "ladder of migration", has not been evaluated quantitatively yet.

While numerous studies have been made on copepod community structure in the neritic or epipelagic zone, information about copepod communities in the oceanic meso- and bathypelagic zone is extremely limited. As one of few exceptions, Roe (1972) studied copepod community structure down to mesopelagic zone in the North Atlantic, and revealed that the number of copepods decreases exponentially with increasing depth, whereas the number of genera and species of copepods increases with increasing depth, forming a peak in the mesopelagic zone. In the North Pacific, there are no studies comparable to that of Roe.

Deep-sea studies in the western subarctic Pacific by Russian scientists have been limited to vertical distribution of zooplankton biomass (Vinogradov, 1968, 1997), features of interzonal migrating copepods in mesopelagic zones (Vinogradov and Arashkevich, 1969) and the species diversity of certain mesopelagic copepod families (Markhaseva and Razzhivin, 1992). Detailed information about entire copepod communities and its characteristics over the great depths in the North Pacific has been lacking.

Japanese scientists have studied vertical distribution patterns of copepods in the western subarctic Pacific (Furuhashi, 1966; Minoda, 1971; Morioka, 1972; Hattori, 1989, 1991), providing the list of species and abundance of each species (no biomass data were given for each species). While the occurrence of large grazing copepods Neocalanus (Calanus) cristatus which undergo an extensive ontogenetic vertical migration had been well documented in the past (Kitou, 1965; Omori, 1967; Omori and Tanaka, 1967; Sekiguchi, 1975), the life cycles of N. cristatus and other Neocalanus spp. in this region were published recently (Kobari and Ikeda, 1999, 2001a, 2001b; Tsuda et al., 1999, 2001). Also the life cycles of some mesopelagic copepods such as Paraeuchaeta elongata (Ozaki and Ikeda, 1999), Pleuromamma scutullata and Heterorhabdus tanneri (Yamaguchi and Ikeda, 2000a) and Gaidius variabilis (Yamaguchi and Ikeda, 2000b) have been evaluated successfully in the western subarctic Pacific. Despite accumulation of this new information about copepods in the western subarctic Pacific, the data needed for a quantitative evaluation of the role of copepods in the cycling of energy and matter through the entire water column are still lacking.

We aim in the present study to evaluate vertical community structures of copepods living down to 4000 m depth at Station Knot in the western subarctic Pacific, based on day and night samples collected in August 1998. Copepods were identified to species (calanoids only) and classified into four groups depending upon feeding characteristics, i.e. suspension feeders, suspension feeders in diapause, detritivores and carnivores. By measuring the body length of each copepod, their numbers were converted to carbon biomass. Ingestion and egestion (fecal pellet production) rates of individual copepods were calculated from their metabolic rates (oxygen consumption) using Ikeda and Motoda's (1978) approach, and the rates of the four feeding groups at various depth layers were combined with particulate carbon flux data at the same site to evaluate the interference by copepod ingestion/egestion with sinking particulate carbon through the 0-4000 m water column.

Materials and Methods

Field sampling and enumeration

As part of the research program "WEST-COSMIC" ("Western Pacific Environment Assessment Study on CO_2 Ocean Sequestration for Mitigation of Climate Change" cf. Harada, 1999; Ishizaka, 1999), a set of day and night deep samplings were made at Station Knot (44˚N, 155˚E; ca. 5340 m depth) located in the western subarctic Pacific from 19 to 21 August 1998 (Fig. 1). Zooplankton was collected at discrete depth intervals with closing-NORPAC nets (mesh size 90 μm, mouth opening 0.16 m^2, cf. Motoda, 1957) from 0-100 and 100-200 m, and with VMPS (Vertical Multiple Plankton Sampler, mesh size 90 μm, mouth opening 1.0 m^2, Tsurumi Seiki, Co. Ltd., cf. Terazaki and Tomatsu, 1997) from 200-500, 500-1000, 1000-1500, 1500-2000, 2000-3000 and 3000-4000 m. A flowmeter (Rigosha, Co. Ltd.) was mounted in the mouth of the net to register the volume of water passed through the net. Daytime samplings were made during 09:07-13:28 (local time) and night samplings during 22:06-05:02. Zooplankton samples were split on board and 1/2 aliquots preserved immediately in 5% borax-buffered formalin-seawater after the collection. Remaining 1/2 aliquots were filtered with 50 μm mesh and stored at -80˚C for determination of total zooplankton biomass and chemical contents.

Water temperature and salinity were measured by using a CTD system (Seabird SBE-9). Dissolved oxygen was determined by the Winkler titration method on water samples from 12-l Niskin bottles (General Oceanics) rosette-mounted on the CTD system. For measuring primary production, seawater samples were collected from 6 depths between 0-100 m depth during 03:00-05:00 using 12-l Niskin bottles (General Oceanics). The water samples were dispensed into four 1-l polycarbonate bottles (one for initial and three for subsequent incubation), enriched with $NaH^{13}CO_3$ to about 10% of the total inorganic carbon, and incubated one full day in a deck incubator, through which the surface water circulated. The initial and incubated samples were filtered through precombusted Whatman GF/F filters, and the filters were frozen at -80˚C. In the land laboratory, the isotopic ratios of ^{13}C to ^{12}C were determined following the method of Hama et al. (1983).

In the land laboratory, copepods in the zooplankton samples were identified and counted under a dissecting microscope. The samples were split with a plankton splitting device (Motoda, 1959), and ≥2000 copepod specimens were enumerated in aliquots. Cyclopoida, Harpacticoida and Poecilostomatoida were identified at the order level. For Calanoida, identification was done at the species level and developmental stages whenever possible. The number of unidentified copepods was very small (<1% of the total copepod community), and they were ignored in the following calculations. The total length (=prosome length+urosome length) of copepods were measured to the nearest 0.2 mm under a dissecting microscope with an eye-piece micrometer. Copepod carcasses (exoskeletons with some body tissue inside) were also identified and measured for total length.

Biomass

Dry mass biomass of each copepod was estimated from its length using the allometric equation: $Log_{10}DM = 2.546 \cdot Log_{10}TL - 6.697$, where DM is μg dry mass per individual and TL is total length in μm (Mizdalski, 1988). Then, dry mass biomass was converted to carbon biomass, assuming the carbon content of copepods to be 44.7% of dry mass (Båmstedt, 1986). The calculated carbon biomass data are with a factor of 0.7-1.2 nearly equal to directly determined data from the literature (Omori, 1969; Ikeda et al., 1990; Ikeda and Hirakawa, 1998). Information about the biomass of carcasses is currently limited (Wheeler, 1967; Terazaki and

Wada, 1988). According to Terazaki and Wada (1988), dried carcasses accounted to 20% of that of living specimens for Neocalanus cristatus. Using this ratio (carcasses contain 20% DM of living specimen), dry mass of carcasses was estimated in the present study. Terazaki and Wada (1988) also reported that carbon content of N. cristatus carcasses was 51% that of dry mass, which does not differ appreciably from that (44.7%) assumed for living specimens. Because of this, the same conversion factor (44.7%) was used for the calculation of carbon biomass from dried biomass for both living specimens and carcasses of copepods.

Depth where population resided

To make a quantitative comparison possible, the depth above and below which 50% of the population resided ($D_{50\%}$) was calculated for each copepod species (cf. Pennak, 1943). Additional calculations were made of depths above which 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population occurred. Note that these calculations dealt with the whole populations of a given copepod species including all developmental stages.

Community structure

For calanoid copepod populations, a species diversity index (H') (Shannon and Weaver, 1949) was calculated as $H'=-\sum pi \ln pi$, where pi is the fraction of the ith ranked species in the calanoid copepod populations. Values of pi were calculated by using either the number or biomass of copepods in each sampling layer. Species similarity between samples was quantified by Mountford's (1962) similarity index (I), i.e. $I=2c/[2a \cdot b-(a+b) \cdot c]$, where a and b are the number of species in each paired samples and c is the number of species which occurred commonly in both samples. A matrix of similarity index between samples was generated for the subsequent cluster analysis by Mountford's method.

Carbon flux and copepod ingestion/egestion

Vertical flux of particulate carbon was estimated from the primary production data measured at the station (581 mg C m^{-2} day^{-1}), combined with the flux-primary production relationship established by Suess (1980); $C_{flux}=C_{prod}/(0.0238 \cdot z+0.212)$, where C_{prod} is primary production (581 mg C m^{-2} day^{-1}), and C_{flux} is carbon flux (mg C m^{-2} day^{-1}) at a given depth (z, m). The calculated particulate carbon flux in deep layer corresponds well with the values of particulate organic carbon collected by sediment traps in the same layer (e.g. Takahashi et al., 2000).

The feeding patterns of copepods (includes all orders) were classified into four types based on literature data (Arashkevich, 1969; Ohtsuka and Nishida, 1997): suspension feeders, suspension feeders in diapause, detritivores and carnivores. Detritivores in this study includes five calanoid families Diaixidae, Parkiidae, Phaennidae, Scolecitrichidae and Tharybidae and the poecilostomatoid Oncaea, all of which are considered to be adapted for feeding on detrital matter such as appendicularian houses (Ohtsuka and Nishida, 1997). Suspension feeders in diapause includes three Neocalanus species (N. cristatus, N. plumchrus, N. flemingeri) and Eucalanus bungii, which all undergo diapause at depth in the period (August) of this study (cf. Miller et al., 1984; Miller and Clemons, 1988). Since the diapause copepods cease feeding or egestion (Hallberg and Hirche, 1980; Hirche, 1989), they were omitted from the calculation of ingestion and egestion rates.

Metabolic rates (oxygen consumption, ammonia and phosphate excretion) of marine zooplankton have been expressed as a function of body mass and temperature (Ikeda, 1974). In this study, oxygen consumption rates of copepods were calculated from the observed in situ temperature and carbon biomass of each copepod using Ikeda et al's (2001) new formula for epipelagic copepods under the premise that their depth distribution does not affect the rates (cf.

Thuesen et al., 1998), i.e., ln R=0.124+0.780·ln B+0.073·T, where R is the oxygen consumption rate (µl O_2 individual^{-1} h^{-1}), B is the biomass of a copepod (mg C individual^{-1}) and T is temperature (˚C). T was represented by the integrated mean temperature of each sampling stratum. R was converted to carbon units assuming a respiratory quotient ($[CO_2]/[O_2]$) of 0.97 (protein metabolism, cf. Gnaiger, 1983). Carbon budgets of living copepods may be expressed as: Ingestion (I)= Metabolism (M)+ Growth (G)+ Egestion (E). Assuming assimilation efficiency ([M+G]/I, or [I-E]/I) and gross growth efficiency (G/I) to be 70% and 30%, respectively (for detail accounts, see Ikeda and Motoda, 1978), ingestion rates (I: µg C individual^{-1} h^{-1}) and egestion rates (E: µg C individual^{-1} h^{-1}) can be calculated as I=M/(0.7-0.3), and E=(1-0.7)·I, respectively. I and E of each copepod were computed, expressed on daily basis (x 24 hours), and summed for all individuals in each depth range (mg C m^{-2} day^{-1}).

To quantify the role of ingestion and egestion of copepods in vertical carbon flux, a "box model" which is similar to that used by Sasaki et al. (1988) was used. Basic assumptions associated with the model were: (1) part of the particulate carbon falling through a certain depth range is intercepted and consumed by copepods inhabiting that depth range, (2) assimilation efficiency of copepods remains unchanged throughout the water column (70%), and (3) the feces produced within a certain depth range contribute to the particulate carbon flux in the underlying layer. Our box model is different from the model by Sasaki et al. (1988) in the following points. Firstly, the depth dealt with was much greater (surface-4000 m vs. surface-1000 m). Secondly, the primary production rate was determined and the flux was estimated in this study, while primary production was assumed and flux was determined by Sasaki et al. (1988). Thirdly, four feeding patterns of copepods were taken into account in this study, whereas Sasaki et al. (1988) considered only dominant suspension feeders.

Results

Hydrography

The surface temperature at the sampling station was 13.5˚C (Fig. 2). Water temperature decreased with increasing depth, and a sub-minimum of 1.9˚C at 150 m and a sub-maximum of 3.3˚C at 500 m were observed. The decrease of temperature with depth became less below 500 m and showed a minimum of 1.5˚C at 4000 m depth. Integrated mean temperatures for each zooplankton sampling layer were: 5.1 (0-100 m), 2.3 (100-200 m), 3.2 (200-500 m), 2.9 (500-1000 m), 2.3 (1000-1500 m), 2.0 (1500-2000 m), 1.7 (2000-3000 m) and 1.5˚C (3000-4000 m). These values were used for the calculations of ingestion and egestion rates of copepods (see "Results-Carbon budgets of copepod communities").

Salinities ranged from 32.7 to 34.7 and increased with depth, which is a common feature throughout the subarctic Pacific (Dodimead et al., 1963). General hydrographical features were similar to those of the Oyashio region (Kono, 1991): i.e. presence of subsurface minimum and maximum temperatures at depths of about 100 m and 300 m, respectively, and the halocline at 200-300 m depth in summer.

Dissolved oxygen content was highest in the subsurface layer (maximum: 8.2 ml l^{-1} at 30 m), decreasing rapidly with increasing depth and reaching a minimum (0.46 ml l^{-1}) at 600-800 m. Dissolved oxygen lower than 2 ml l^{-1} extended to 300-2000 m depth. The integrated mean dissolved oxygen concentration in each zooplankton sampling layer was: 7.47 (0-100 m), 5.22 (100-200 m), 1.36 (200-500 m), 0.51 (500-1000 m), 1.18 (1000-1500 m), 1.25 (1500-2000 m), 2.47 (2000-3000 m) and 3.29 ml l^{-1} (3000-4000 m).

Numerical abundance and biomass

Both day and night, copepods were most numerous at 0-100 m depth (3509-5082 individuals m^{-3}), declined consistently downward 3000-4000 m depth (0.8-4.7 individuals m^{-3}) (Fig. 3a). Copepod carcasses were found throughout the whole water column. Carcasses were also abundant in the surface layer (75-189 carcasses m^{-3} at 0-100 m depth), but their decrease pattern with increasing depth was less marked than that of living specimens. The minimum abundance of carcasses was 7.6-13.6 carcasses m^{-3} at 2000-3000 m (day) or 3000-4000 m (night). The ratio of carcasses to living specimens increased with increasing depth. Below 1500 m depth, carcasses outnumbered the living specimens, increasing to a factor of 9.3 between 3000 and 4000 m depth at night.

Like as its numbers, copepod carbon biomass was also greatest in the shallower layer (maximum: 20.2 mg C m^{-3} at 0-100 m depth at night, 7.6 mg C m^{-3} at 200-500 m depth during daytime) and decreased downward (Fig. 3b). However, the pattern of decrease with depth was different from that of numerical abundance; the pattern of $\log_{10}$(carbon biomass) was linear with depth, which was not the case for $\log_{10}$(abundance). The minimum biomass (0.016-0.050 mg C m^{-3}) was at 3000-4000 m depth. In terms of carbon biomass, carcasses/living copepod ratios increased gradually toward 2000-3000 m depth, then increased markedly (1.1-1.2) at 3000-4000 m depth during day and night.

The relative composition of Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida varied greatly with depth (Fig. 4a). In terms of numerical abundance, Cyclopoida dominated in the upper 100 m (88-91% of the total). Harpacticoida occurred between 100-500 m both day and night, but their fraction was small (<20%). Below 200 m depth, the proportions of the copepod orders were stable, and Calanoida (30.4±4.7%: mean±1sd for 200-4000 m depth) and Poecilostomatoida (67.1±6.5%) were the dominant taxa.

The composition the orders expressed by carbon biomass was different from that expressed by numerical abundance (Fig. 4b). This is largely because carbon biomass per individual is greatest for Calanoida. In the surface layer, Cyclopoida dominated (49.1% at night and 70.9% during daytime of the total copepods). Their lower proportion at night was due to the ascent of large Calanoida from deeper layer. Below 200 m depth, the composition became stable both day and night. Calanoida (88.6±6.0%: mean±1sd for 200-4000 m depth) and Poecilostomatoida (11.0±6.1%) were the two dominant copepod taxa contributing biomass in the meso- and bathypelagic zone of the subarctic Pacific (>99% of the total copepod biomass).

A total of 98 calanoid species belonging to 38 genera and 15 families were identified from the 0-4000 m water column (Table 1). Suspension feeders included 53 species (Note: Table 1 shows 59 species, including 4 suspension feeders in diapause and 2 non-calanoid orders). Suspension feeders in diapause were composed of four large grazing calanoids: Neocalanus cristatus, N. plumchrus, N. flemingeri and Eucalanus bungii (cf. Miller et al., 1984; Miller and Clemons, 1988). Detritivores occurred 17 species and one non-calanoid order (Poecilostomatoida), and carnivores consisted of 24 species.

The most numerous calanoid copepods were Microcalanus pygmaeus, Metridia pacifica and Paracalanus parvus, all of them were suspension feeders. In terms of carbon biomass, the most dominant species was Eucalanus bungii followed by Neocalanus cristatus and N. flemingeri. Thus the numerical dominants were not necessarily the biomass dominants. Species numerically dominant but of smaller biomass were: Microcalanus, Paracalanus and Pseudocalanus, and those numerically less dominant but larger biomass were: Eucalanus and Neocalanus. Smaller biomass of numerically dominant forms resulted from either smaller adult size or predominance of earlier copepodid stages.

Vertical distribution

Vertical distributions of all suspension feeding species (including those in diapause) were arranged in the order from shallow to deep (Fig. 5). For suspension feeders, the depth where most of the population resided ($D_{50\%}$) did not vary greatly between day and night times. It is noted that suspension feeders in diapause had broader vertical distribution ranges than those of the other suspension feeders.

$D_{50\%}$ values of some detritivores varied between day and night (Fig. 6a). Some detritivorous species (Species no. 63 and 65: Scaphocalanus subbrevicornis and Scolecithricella globulosa) showed a shallower occurrence at night, while some other species (Species no. 62, 64, 66, 68 and 74: Racovitzanus antarcticus, Scolecithricella ovata, Scaphocalanus magnus, Amallothrix inornata and Scaphocalanus affinis) showed an opposite pattern. Both day and night changes in vertical distribution were significant for each copepod (Kolmogorov-Smirnov two-sample test: $p<0.05$). Carnivorous species tended to exhibit a stable vertical distribution pattern throughout day and night (Fig. 6b), as was seen for suspension feeders mentioned above (Fig. 5).

Community structure

The vertical distributions of the number of calanoid copepod genera and species showed bimodal peaks during day and night (Fig. 7). The shallower peak was at 500-1000 m (20 genera and 34-38 species), and the deeper peak was at 2000-3000 m (20 genera and 28-32 species). Species diversity index (H') based on abundance or biomass showed also the same bimodal distribution pattern. The shallower peak (500-1000 m) of the number of genera/species coincided well with that of H' based on abundance, and the deeper peak (2000-3000 m) with that of H' based on biomass.

Species similarity indices calculated for calanoid copepod populations in each sampling layer showed that: (1) the populations at near-surface layers (0-500 m) exhibited higher similarities, (2) below 500 m depth, the number of species decreased, resulting in lower similarities, and (3) copepod communities in the 0-4000 m depth could be classified into three groups; epipelagic (0-200 or 500 m), mesopelagic (500-1500 or 2000 m) and bathypelagic communities (>2000 m), and the boundaries between the three groups lay at 200-500 m and 1500-2000 m depths, respectively (Fig. 7). Day/night differences in similarity indices were observed at 0-500 m depth; higher similarities at night than daytime, were attributed by the nocturnal ascent of mesopelagic species to near-surface layers.

Carbon budgets of copepod communities

Numerically, suspension feeders dominated in the upper 200 m with 94-97% at 0-100 m and 72-73% at 100-200 m of the total copepods (Fig. 8a). Below the 200 m, the composition stabilized and detritivores (70±6%: mean±1sd between 200-4000 m) and suspension feeders (24±5%) became dominant groups. Throughout the whole water column, carnivores formed a small fraction (1.3±0.8%) and suspension feeders in diapause occurred in 200-4000 m depth, were also a small component (6.5±4.2%, 200-2000 m depth).

In terms of biomass, the composition of four feeding groups differed from that expressed by numerical abundance (Fig. 8b). Suspension feeders were abundant almost exclusively in the upper 200 m (of total copepods 95-98% at 0-100 m and 81-91% at 100-200 m). Below 200 m, detritivores (14.9±6.9%: mean±1sd in the 200-4000 m) and carnivores (9.9±5.5%) increased. Suspension feeders in diapause formed a large fraction at 200-2000 m (62.8±10.3%), while their relative importance decreased below 2000 m. The contribution of other suspension feeders increased in 2000-4000 m depth (42-44% at 2000-3000 m and 52-65% at 3000-4000 m).

Our calculations of ingestion/egestion rates of copepod suspension feeders, and the

balance of particulate carbon flux (units: mg C m^{-2} day^{-1}) over the entire 0-4000 m water column are summarized in Fig. 9. Ingestion rates were taken into account for suspension feeders only, and egestion rates were included for all feeding groups except suspension feeders in diapause. In our preliminary calculation, ingestion rates were calculated for both suspension feeders and detritivores. Resulting total ingestion rates of the two feeding types exceeded the carbon flux below 1000 m depth. Considering possible utilization of particulate carbon flux by non-copepod zooplankton, copepod detritivores were omitted from our calculation of ingestion rates (food requirements of detritivores and carnivores are discussed in "Trophic structure" in Discussion section). Our results in Fig. 9 indicated that copepod suspension feeders consume 37% of carbon flux below 500 m depth. Throughout the entire 0-4000 m water column, the mean ingestion/flux ratio was 32±13% (grand mean±1sd).

Discussion

Vertical distribution of standing stock

Saito et al. (1998) have reported on seasonal changes in nutrients, chlorophyll a and net zooplankton biomass in the epipelagic zone of the Oyashio region over four years. Copepoda is the most dominant taxon among net zooplankton in this region. Seasonally, net zooplankton biomass has a maximum in spring (means of four years; 37-342 mg C m^{-3}), and a minimum in summer (8-17 mg C m^{-3}) (Saito et al., 1998). Taking into account the present study season (August), the copepod biomass estimated in this study (7.4-20.2 mg C m^{-3} at 0-100 m) is close to Saito et al.'s data. Abundance of copepods in the epipelagic zone in the present study (3509-5082 individuals m^{-3} at 0-100 m) is close or beyond the upper range of 8-3560 individuals m^{-3} reported by previous workers (Minoda, 1972; Hirakawa, 1981; Hattori, 1989, 1991). This can partly be explained by the smaller mesh size used in the present study (90 μm) compared to that used by the previous workers (330 μm). Little information is presently available for standing stocks of zooplankton in meso- and bathypelagic zones in the western subarctic Pacific.

Numerical abundance and biomass of copepods decreased rapidly with increasing depth, but their reduction patterns were different each other (Fig. 3). Two models have been proposed to express decreasing patterns of zooplankton abundance/biomass (Y) with increasing depth (X). One is an exponential model ($Log_{10}Y=a+b\cdot X$, where a and b are fitted constants) by Vinogradov (1968), and the other is a power model ($Log_{10}Y=a'+b'\cdot Log_{10}X$, where a' and b' are fitted constants) by Koppelmann and Weikert (1992). Koppelmann and Weikert (1992) reported that the bathypelagic zooplankton biomass data fit the power model better than the exponential model. In the present study, we found that the numerical abundance data of copepods in the whole water column fit the power model and that their biomass data fit the exponential model (Table 2). With increasing depth, more pronounced reduction in the numerical abundance than in the biomass may be explained by the fact that the biomass per individual changes with depth.

Copepod carcasses

The occurrence of copepod carcasses from meso- and bathypelagic zones has been reported in the world ocean: e.g. North Atlantic (Wheeler, 1967; Roe, 1988), Indian Ocean (Geptner et al., 1990), North Pacific (Haury et al., 1995; Yamaguchi and Ikeda, 2001), Arabian Sea (Böttger-Schnack, 1996; Koppelmann et al., 2000) and Japan Sea (Terazaki and Wada, 1988). Wheeler (1967) mentioned that the species composition of the carcasses was not different from that of living specimens at the same depth, and considered that the origin of copepod carcasses is a fate of residents (they are not transported from the overlaying layer). In the present study,

we also observed that the composition of the taxonomic order of species which produced carcasses (Fig. 10) was similar to that of living specimens in the same sampling layers (Fig. 4) (note that no Harpacticoida carcasses were found, however). In the subarctic Pacific, the large grazing copepods Neocalanus cristatus, N. plumchrus and N. flemingeri, classified as suspension feeders in diapause in this study (cf. Fig. 8), end their life cycles in the meso- and bathypelagic zones. Harding (1973) observed bacterial decomposition of organic contents of copepod carcasses, and noted that its inner tissue decomposition took 11 days in the Scotian shelf water (4˚C) and 3 days in the Sargasso Sea water (22˚C). Seki (1965) studied chitin (the major component of copepod's exoskeleton) decomposition in seawater, and noted that chitin may be mineralized in 370 days at 5˚C and 500 days at 2˚C. Considering the habitat temperature of zooplankton in the Oyashio region (<5˚C below the 40 m depth, cf. Fig. 2), we speculate that complete decomposition of copepod carcasses may require >1 year. This slow decomposition may be a cause for the abundance of carcasses in the Oyashio region.

Added to low temperature, higher abundance of copepod carcasses than of living specimens in deeper layers (Fig. 3) may possibly reflect feeding by micronektonic crustaceans and fishes which are numerous in epi- and mesopelagic zones in the Oyashio region (Nishikawa et al., 2001). In addition to these taxa, recent observations using submersibles have revealed the occurrence of potential predators on copepods such as cnidarians and ctenophores from the meso- and bathypelagic zones of the western North Pacific (Hunt and Lindsay, 1999). Copepod carcasses contain some organic matter (ca. 20% as compared with living specimens, cf. Terazaki and Wada, 1988). Indeed, copepods have been noted as the major diet component of some dominant myctophid fishes such as Diaphus theta, Stenobrachius leucopsarus and S. nannochir (Moku et al., 2000), although the separation of its carcasses from living specimens from the stomach of these fishes has not been attempted. Not only as a potential food source, copepod carcasses may also be important as a site of bacterial growth to form deep-sea detritus (Harding, 1973).

Community structure

Our analysis of copepod communities in the 0-4000 m water column of the subarctic Pacific revealed that (1) both genus and species exhibited bimodal vertical distributions, at 500-1000 m and 2000-3000 m depth, and the number of genera and species composed of the shallow peak were slightly greater than those of the deep peak (Fig. 7), (2) species diversity indices indicated that the community structures of the peaks were different; biomass-dominant species formed the shallow peak while numerical-dominant species constituted the deep peak, and (3) similarity indices showed that the copepod communities could be divided into epipelagic, mesopelagic and bathypelagic communities, and their boundaries were at 200-500 m and 1500-2000 m depth, respectively. These vertical features of copepod communities at Station Knot are comparable to those being reported from the North Atlantic (Roe, 1972; Deevey and Brooks, 1977), Red Sea (Weikert, 1982), Arabian Sea (Böttger-Schnack, 1996), Mediterranean Sea (Weikert and Trinkaus, 1990) and Greenland Sea (Richter, 1994). Among these studies, Böttger-Schnack (1996) noted that Poecilostomatoida (mainly Oncaea) contributed 60-80% of total copepods in the meso- and bathypelagic zone of the Arabian Sea. Poecilostomatoida also dominated in abundance of the total copepods in the meso- and bathypelagic zone of Station Knot (ca. 70%, cf. Fig. 4a), thereby consistent with the finding of Böttger-Schnack (1996), despite the fact that hydrographic conditions (temperature, salinity and dissolved oxygen) between Station Knot (44˚N in the subarctic Pacific) and Böttger-Schnack's (1996) study site (15-20˚N in the Arabian Sea) are very different. While predominance of Poecilostomatoida in the meso- and bathypelagic zones has not been noted in the results of other studies mentioned above, it is probable that Poecilostomatoida (body length; <1.0 mm) could not be collected effectively in their samplings with larger mesh nets (>200 μm). The

mesh sizes of nets used by Böttger-Schnack (1996) and us were 55 and 90 μm, respectively.

Vertical structures of copepod species diversity have been studied in the North Atlantic (Roe, 1972, 1984), Sargasso Sea (Deevey and Brooks, 1977), Mediterranean Sea (Scotto di Carlo et al., 1984), Greenland Sea (Richter, 1994) and Arctic Ocean (Kosobokova and Hirche, 2000). As a common feature of these studies, the number of genera and species increased with increasing depth, as was seen in the present study. However, the depth where the peak of the number of species occurred is different, ranging from 50-200 m in Mediterranean Sea (Scotto di Carlo et al., 1984) to 1000-1500 m in the Greenland Sea (Richter, 1994). Bimodal peaks of the number of genera and species found in the present study has not been reported previously. The bimodal distribution pattern was observed both day and night (Fig. 7). Considering the depth range studied by previous workers (maximum: 600-3000 m), as compared with 4000 m in our study, possible overlooking of the bimodal pattern by previous workers cannot be ruled out.

Information about the similarities of community structures of copepods living in the 0-4000 m water column is extremely limited. Richter (1994) conducted year-round observations on copepod communities down to 3000 m in the Greenland Sea and noted that the epipelagic (0-300 m) and mesopelagic communities (300-1000 m) were very similar, while the bathypelagic community (1000-3000 m) was different and exhibited extremely low similarities to the epi-/mesopelagic communities, as was observed at Station Knot in the subarctic Pacific in the present study (Fig. 7). The boundary between epi-/mesopelagic communities and bathypelagic community is at 1000 m depth in the Greenland Sea (Richter, 1994), and at 1500-2000 m depth in the subarctic Pacific (Fig. 7).

Trophic structure

Our calculations of ingestion and egestion rates of copepods living at various depth strata based on oxygen consumption data given by Ikeda et al. (2001), may be underestimates because Ikeda et al.'s experiments were on specimens incubated in filtered seawater (no food). As an other source of possible error, assimilation efficiency of copepods, assumed as 70% in our calculation, could vary depending on food types (Conover, 1966), but there are no available data on deep-living copepods feeding on natural food particles. Feeding patterns of copepods were divided into four types, and the sinking particulate carbon was assumed to be utilized by suspension feeders only. It is concluded that suspension feeders could satisfy their food requirements by using sinking particulate carbon (Fig. 9), which agrees with Sasaki et al.'s (1988) conclusion.

As a source of detritus, copepod carcasses were quantified in the present study. However, the comparison between ingestion rates of detritivores and copepod carcasses showed that carcasses are used up by detritivores within 1.0-62.0 days (9.4±15.3 days, mean±1sd of water column) (Table 3). While there are no data on the production rates of copepod carcasses available, our calculation suggest that the carcasses may not be sufficient as a food source of detritivores and other food sources such as appendicularian houses need to be considered. Appendicularian houses are known to be an important source of detritus (Alldredge, 1976). However, because of their large size and the low density of appendicularian houses, it is difficult to quantify them by water samplings. By net sampling, appendicularian houses may be caught, but they will break down during the net towing process because of its fragile nature. Based on direct observations and sampling by using submersibles in the mesopelagic zone of Monterey Bay, Steinberg et al. (1994) reported that the density of zooplankton associated with detritus (giant larvacean houses) was one order of magnitude greater than that in the nearby water column. According to Steinberg et al. (1994), most (96%) of the zooplankton associated with detritus are detritivorous copepods (Scolecitrichidae and Oncaeidae). Detritivorous copepods utilize floating detritus not only

for feeding but also as a living habitat during juvenile stages (Ferrari and Steinberg, 1993), implying that pelagic detritus has a function of semi-enclosed microcosm in the water column. In the present study, most copepods have species-specific vertical distribution ranges, while only detritivorous species showed substantial day and night differences in their vertical distribution patterns (Table 4). The broader and uneven vertical distribution patterns of detritivores may be caused by their association with detritus, which is distributed unevenly in the water column (Alldredge, 1976).

As food for carnivorous copepods, suspension feeding and detritivorous copepods are assumed. Suspension feeders in diapause (Neocalanus spp. and Eucalanus bungii) are considered too large to eaten by carnivorous copepods. Suspension feeders in diapause in deep layer are known to be utilized by mesopelagic micronektonic fishes (Stenobrachius nannochir) in the western subarctic Pacific (Moku et al., 2000). Comparing carnivores' ingestion rates with the total abundance of suspension feeders (excepting those in diapause) and detritivores, our calculation indicated that carnivores feed up them in 49-688 days (179±211 days, mean±1sd of water column) (Table 5). While no production data for these non-carnivorous copepods are presently available, this calculation implies that carnivorous copepods in each depth layer may be satisfying their food demand by eating the non-carnivorous copepods.

Particulate carbon fluxes are utilized by meso- and bathypelagic copepods as "falling rain" (Vinogradov, 1968). The important suspension feeders in the mesopelagic zone of the subarctic Pacific are Gaidius variabilis, Pleuromamma scutullata and Gaetanus simplex (Species no. 13, 14 and 15 in Table 1, vertical distributions are 250-1000 m, cf. Fig. 5). They are considered to feed mainly on particulate carbon fluxes such as dead phytoplankton cells and fecal pellets falling from the upper layers. These species are known to reproduce throughout the year, adjusting their main reproduction events to phytoplankton bloom season (Yamaguchi and Ikeda, 2000a, b). In other words, the magnitude of particulate carbon flux is a main factor controlling their reproductive success. In the present calculation, suspension feeders consume 32% on average of the particles throughout 0-4000 m depth stratum (Fig. 9), which is close to 38% reported for copepod populations off Sanriku in the western subarctic Pacific by Sasaki et al. (1988) although Sasaki et al.'s calculations dealt with 0-1000 m depth only.

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Figure Captions

Fig. 1. Location of Station Knot (44˚N, 155˚E) in the western subarctic Pacific Ocean. For comparison, locations of Station Papa (cf. Miller et al., 1984) in the eastern subarctic Pacific and Site H (cf. Kobari and Ikeda, 1999) in the western subarctic Pacific are superimposed.

Fig. 2. Vertical distributions of temperature (˚C), salinity and dissolved oxygen (ml l^{-1}) at Station Knot in the western subarctic Pacific Ocean, 19-21 August 1998.

Fig. 3. Vertical distributions, on log scales, of abundance **(a)** and biomass **(b)** of copepods at Station Knot in the western subarctic Pacific Ocean. Squares denote ratio of carcasses to living specimens, and 1.0 values (carcasses equal to living specimens) are shown (dotted vertical lines).

Fig. 4. Vertical changes in the composition of four orders (Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida) of copepods at Station Knot in the western subarctic Pacific Ocean in terms of abundance **(a)** and biomass **(b)**.

Fig. 5. Vertical distribution of suspension feeding copepods at Station Knot in the western subarctic Pacific Ocean. Of each species, open and solid symbols indicate 50% distribution depth ($D_{50\%}$) at day and night, respectively. Vertical bars indicate depth ranges where 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population was distributed. For species number see Table 1. The four species with solid circles (no. 9, 5, 12, 10) indicate suspension feeders in diapause in the deep layer (cf. Miller et al., 1984; Miller and Clemons, 1988). Note that the vertical (depth) scales are not the same among panels.

Fig. 6. Vertical distribution of detritivorous **(a)** and carnivorous **(b)** copepods at Station Knot in the western subarctic Pacific Ocean. Symbols indicate 50% distribution depth ($D_{50\%}$), and vertical bars indicate depth ranges where 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population was distributed. For species number see Table 1. Note that the vertical (depth) scales are not the same among panels.

Fig. 7. Vertical distribution of the number of genera and species of calanoid copepods at Station Knot in the western subarctic Pacific Ocean **(left)**, species diversity indices (H') based on their abundance and biomass data **(middle)**, and similarity indices clustered by Mountford's method **(right)**.

Fig. 8. Percentage composition of four feeding types of copepods in terms of their abundance **(a)** and biomass **(b)** at Station Knot in the western subarctic Pacific Ocean.

Fig. 9. Schematic diagram showing particulate carbon flux (mg C m^{-2} day^{-1}) in the 0-4000 m water column via eight depth strata in the western subarctic Pacific Ocean. Copepod ingestion and egestion rates were shown as mean values of day and night, and estimated from the formulas of Ikeda and Motoda (1978) and Ikeda et al. (2001). Primary production (PP) was measured directly, and downward flux was estimated by the formula of Suess (1980).

Fig. 10. Percentage composition of copepod carcasses separated into the three orders (Calanoida, Cyclopoida and Poecilostomatoida) and expressed by abundance **(a)** and biomass **(b)** at Station Knot in the western subarctic Pacific Ocean. Note that carcasses of Harpacticoida did not occur.

Table 1
List of species of calanoid copepods at Station Knot in the western subarctic Pacific

No.	Species	inds m^{-2}	mg C m^{-2}
Suspension feeders			
1	Cyclopoida	391727	1569.7
2	*Microcalanus pygmaeus*	13351	39.6
3	*Metridia pacifica*	11452	334.5
4	*Paracalanus parvus*	11267	90.2
5	*Eucalanus bungii*[a]	7566	2302.4
6	Harpacticoida	5556	58.2
7	*Pseudocalanus minutus*	3648	15.8
8	*Calanus pacificus*	3353	62.1
9	*Neocalanus cristatus*[a]	3082	1296.4
10	*Neocalanus flemingeri*[a]	2896	679.3
11	*Metridia Okhotensis*	2233	313.4
12	*Neocalanus plumchrus*[a]	2220	390.3
13	*Gaidius variabilis*	2093	45.1
14	*Pleuromamma scutullata*	1275	51.1
15	*Gaetanus simplex*	1270	29.2
16	*Metrida asymmetrica*	1245	109.1
17	*Spinocalanus spinipes*	1057	31.8
18	*Pseudocalanus newmani*	1003	4.1
19	*Lucicutia flavicornis*	783	13.4
20	*Lucicutia ovaliformis*	716	11.3
21	*Metridia curticauda*	195	14.2
22	*Spinocalanus similis*	185	2.1
23	*Lucicutia ellipsoidalis*	156	6.7
24	*Lucicutia frigida*	118	2.0
25	*Acartia longiremis*	116	0.5
26	*Metridia gurjanovae*	84	8.1
27	*Gaidius brevispinus*	84	10.7
28	*Aetideus pacificus*	68	1.7
29	*Gaidius brevirostris*	48	6.3
30	*Gaidius tenuispinus*	36	5.2
31	*Gaetanus brevicornis*	34	5.7
32	*Pseudochirella polyspina*	30	10.2
33	*Mesocalanus tenuicornis*	29	0.2
34	*Pseudochirella pacifica*	25	2.4
35	*Rhincalanus nasutus*	25	6.6
36	*Euchirella sp.*	25	0.2
37	*Metridia similis*	23	0.9
38	*Metridia ornata*	21	16.3
39	*Spinocalanus magnus*	21	1.0
40	*Euchirella rostrata*	19	1.3
41	*Metridia brevicauda*	17	0.5
41	*Undeuchaeta sp.*	17	2.5
43	*Spinocalanus stellatus*	15	1.0
44	*Lucicutia pacifica*	11	1.8
45	*Metridia princeps*	11	7.8
46	*Aetideopsis rostrata*	8	1.3
47	*Pseudochirella spectabilis*	8	6.9
48	*Gaetanus paracurvicornis*	4	0.8
49	*Lucicutia gracilis*	4	3.3
50	*Lucicutia longifurca*	4	1.6
51	*Pseudochirella sp.*	4	0.9
52	*Pseudochirella spinifera*	4	1.0
53	*Gaetanus secundus*	2	0.3
54	*Lucicutia grandis*	2	1.7
55	*Lucicutia orientalis*	2	0.2
56	*Undeuchaeta major*	2	0.5
57	*Undinopsis pacificus*	2	0.3
58	*Lucicutia profunda*	1	0.1
59	*Lucicutia oblonga*	1	0.1
Detritivores			
60	Poecilostomatoida	123063	542.4
61	*Scolecithricella mintor*	1039	11.9
62	*Racovitzanus antarcticus*	985	33.8
63	*Scaphocalantus subbrevicornis*	729	19.7
64	*Scolecithricella ovata*	335	9.6
65	*Scolecithricella globulosa*	131	2.4
66	*Scaphocalanus magnus*	126	26.5
67	*Scaphocalanus medius*	76	5.5
68	*Amallothrix inornata*	55	9.2
69	*Amallothrix sp.*	42	1.8
70	*Amallothrix valida*	40	5.7
71	*Amallothrix paravalida*	38	1.6
72	*Xanthocalanus kurilensis*	27	2.6
73	*Scaphocalanus insignis*	25	0.7
74	*Scaphocalanus affinis*	13	3.2
75	*Lophothrix frontalis*	8	3.3
76	*Onchocalanus magnus*	4	1.1
77	*Scottocalanus securifrons*	4	1.0
Carnivores			
78	*Heterorhabdus tanneri*	864	67.3
79	*Paraeuchaeta birostrata*	821	141.0
80	*Paraeuchaeta elongata*	653	90.8
81	*Paraeuchaeta rubra*	303	85.0
82	*Heterostylites major*	204	28.6
83	*Haloptilus pseudooxycephalus*	84	14.2
84	*Heterorhabdus robustoides*	57	11.2
85	*Heterorhabdus pacificus*	36	3.5
86	*Candacia bipinnata*	31	0.9
87	*Paraeuchaeta pseudotumidula*	28	5.0
88	*Candacia columbiae*	25	3.8
89	*Heterorhabdus compactus*	21	1.9
90	*Euaugaptilus similis*	11	3.0
91	*Euaugaptilus pseudaffinis*	8	1.3
92	*Halptilus longicirrus*	8	1.4
93	*Pachyptilus pacificus*	8	1.8
94	*Augaptilus cornutus*	6	1.7
95	*Paraeuchaeta barbata*	6	4.3
96	*Euaugaptilus graciloides*	5	1.4
97	*Euaugaptilus parabullifer*	4	1.7
98	*Paraeuchaeta abyssalis*	4	4.6
99	*Paraeuchaeta brevirostris*	4	0.8
100	*Neoaugaptilus distinctus*	2	1.2
101	*Paraeuchaeta orientallis*	1	0.5

Abundance (individuals m^{-2}: 0–4000 m) and biomass (mg C m^{-2}: 0–4000 m) of each species and that of cyclopoida, Harpacticoida and Poecilostomatoida are also shown (values were mean of day and night). Based on the feeding pattern, copepods divided into four types: suspension feeders, suspension feeders in diapause, detritivores and carnivores.

[a] Indicate suspension feeders in diapause (cf. Miller et al., 1984; Miller and Clemons, 1988).

Table 2
Regression statistics of abundance/biomass of copepods on depth

Exponential model	a	b	r^2	p
Abundance (day)	5.81	-7.27×10^{-4}	0.81	0.0024
Abundance (night)	5.65	-7.49×10^{-4}	0.77	0.0040
Biomass (day)	3.99	-7.27×10^{-4}	0.99	<0.0001
Biomass (night)	4.13	-7.79×10^{-4}	0.89	0.0003
Power model	a'	b'	r^2	p
Abundance (day)	9.17	−1.52	0.96	<0.0001
Abundance (night)	8.65	−1.41	0.74	0.0064
Biomass (day)	6.22	−1.10	0.72	0.0081
Biomass (night)	6.81	−1.32	0.64	0.0167

Regression models are exponential ($\mathrm{Log}_{10}\ Y = a + bX$) and power ($\mathrm{Log}_{10}\ Y = a' + b'\ \mathrm{Log}_{10}\ X$) ones, where Y is abundance (individuals $1000\,\mathrm{m}^{-3}$) or biomass ($\mu\mathrm{g\,C\,m}^{-3}$), X is depth in m, and a, b, a' and b' are fixed constants.

Table 3
Ingestion rates ($\mathrm{mg\,C\,m}^{-2}\,\mathrm{day}^{-1}$) of detritivorous copepods as compared with biomass of copepod carcasses ($\mathrm{mg\,C\,m}^{-2}$) at each depth stratum in the western subarctic Pacific

Depth stratum (m)	Day			Night		
	Ingestion rates, A ($\mathrm{mg\,C\,m}^{-2}\,\mathrm{day}^{-1}$)	Carcass biomass, B ($\mathrm{mg\,C\,m}^{-2}$)	B/A	Ingestion rates, A ($\mathrm{mg\,C\,m}^{-2}\,\mathrm{day}^{-1}$)	Carcass biomass, B ($\mathrm{mg\,C\,m}^{-2}$)	B/A
0–100	2.7	23.2	8.6	11.5	18.4	1.6
100–200	9.7	24.2	2.5	1.3	6.7	5.3
200–500	28.9	53.2	1.8	24.0	37.7	1.6
500–1000	23.5	56.6	2.4	21.7	21.9	1.0
1000–1500	11.5	40.4	3.5	13.1	56.5	4.3
1500–2000	4.4	24.9	5.6	8.0	43.2	5.4
2000–3000	3.0	24.0	7.9	3.7	43.2	11.5
3000–4000	2.1	53.0	25.6	0.3	19.0	62.0

Table 4
Comparison of vertical distribution pattern of copepods with their feeding patterns

	Feeding pattern		
	Suspension feeders (31)	Detritivores (11)	Carnivores (13)
Diel difference (m)	47	241	110
(sd)	46	307	158

"Diel difference" indicates diel variation in $D_{50\%}$. Number in the parentheses is the number of species observed. (sd): standard deviation.

Table 5
Ingestion rates of carnivorous copepods (mg C m^{-2} day^{-1}) as compared with potential prey biomass (mg C m^{-2}) at each depth stratum in the western subarctic Pacific

Depth stratum (m)	Day			Night		
	Ingestion rates, A (mg C m^{-2} day^{-1})	Prey biomass, B (mg C m^{-2})	B/A	Ingestion rates, A (mg C m^{-2} day^{-1})	Prey biomass, B (mg C m^{-2})	B/A
0–100	0	740	—	3.49	1984	568
100–200	2.11	582	277	0.47	199	420
200–500	9.64	581	60	10.86	579	53
500–1000	9.50	469	49	8.55	478	56
1000–1500	2.86	190	66	4.14	267	64
1500–2000	0.93	85	92	2.98	148	50
2000–3000	1.46	96	65	2.15	118	55
3000–4000	0.07	49	688	0.09	11	118

As potential prey, suspension feeding (excepting suspension feeders in diapause) and detritivorous copepods were assumed.

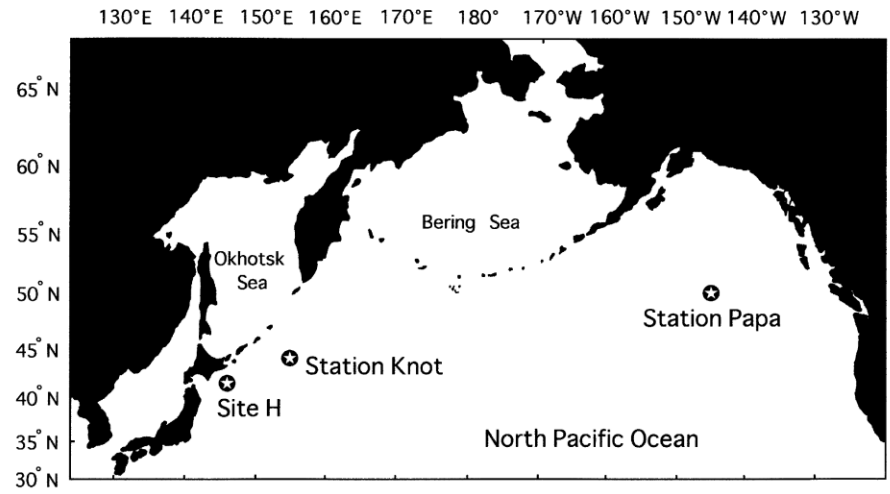


Fig. 1. Location of Station Knot (44°N, 155°E) in the western subarctic Pacific Ocean. For comparison, locations of Station Papa (cf. Miller et al., 1984) in the eastern subarctic Pacific and Site H (cf. Kobari and Ikeda, 1999) in the western subarctic Pacific are superimposed.

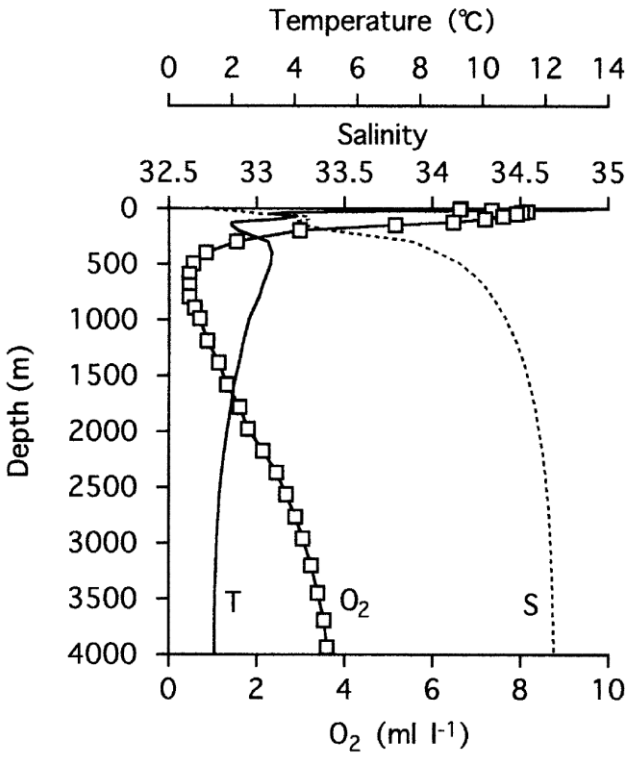


Fig. 2. Vertical distributions of temperature (°C), salinity and dissolved oxygen ($ml\,l^{-1}$) at Station Knot in the western subarctic Pacific Ocean, 19–21 August 1998.

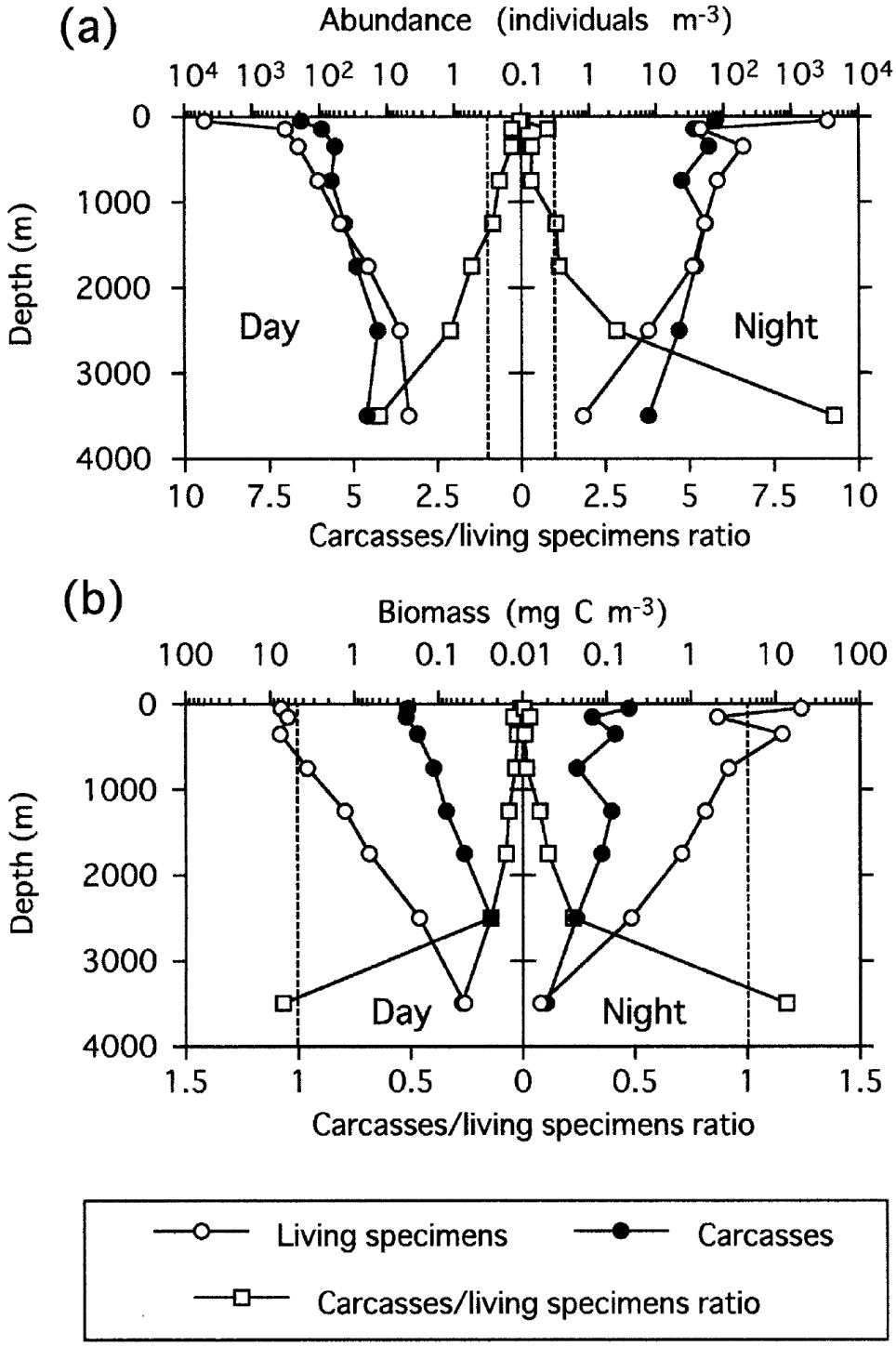


Fig. 3. Vertical distributions, on log scales, of abundance (a) and biomass (b) of copepods at Station Knot in the western subarctic Pacific Ocean. Squares denote ratio of carcasses to living specimens, and 1.0 values (carcasses equal to living specimens) are shown (dotted vertical lines).

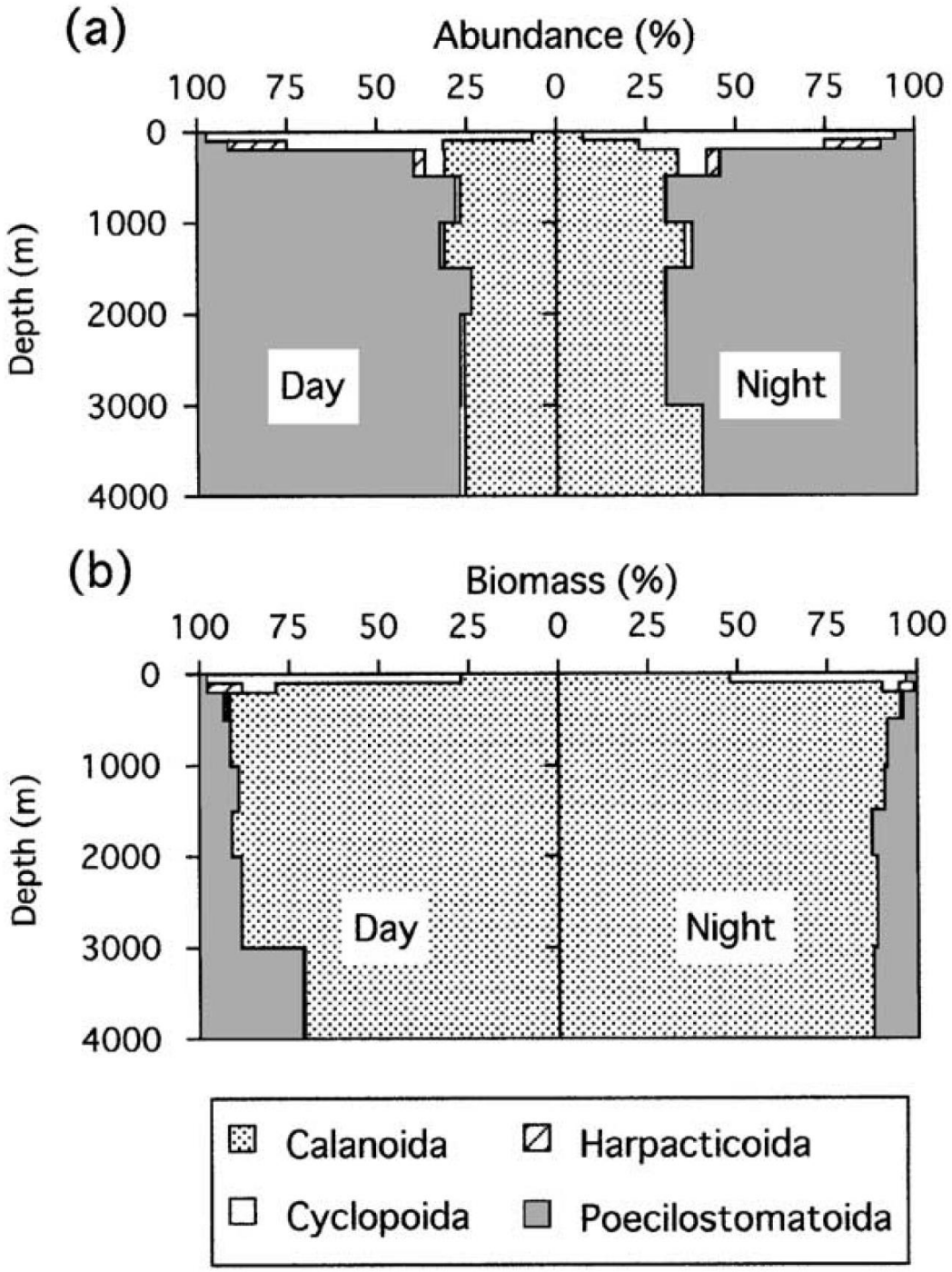


Fig. 4. Vertical changes in the composition of four orders (Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida) of copepods at Station Knot in the western subarctic Pacific Ocean in terms of abundance (a) and biomass (b).

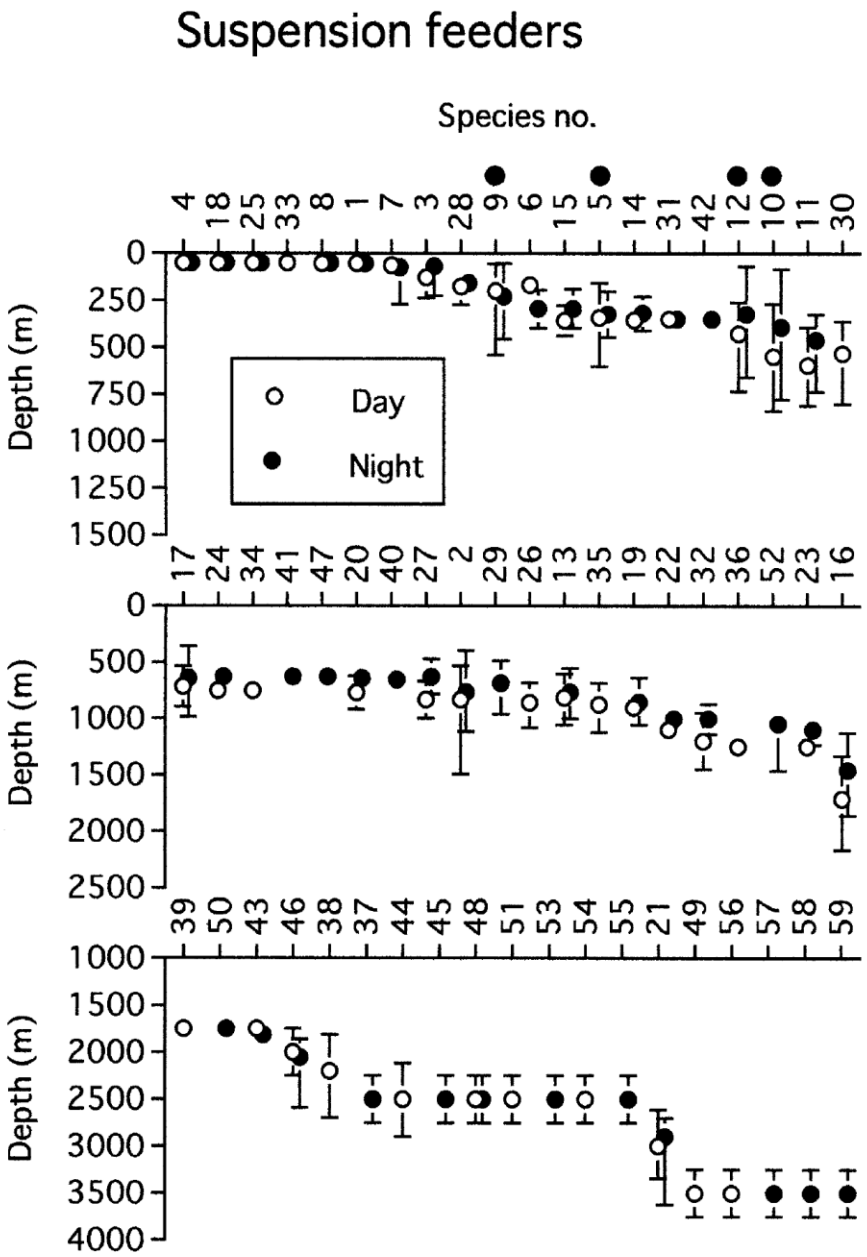
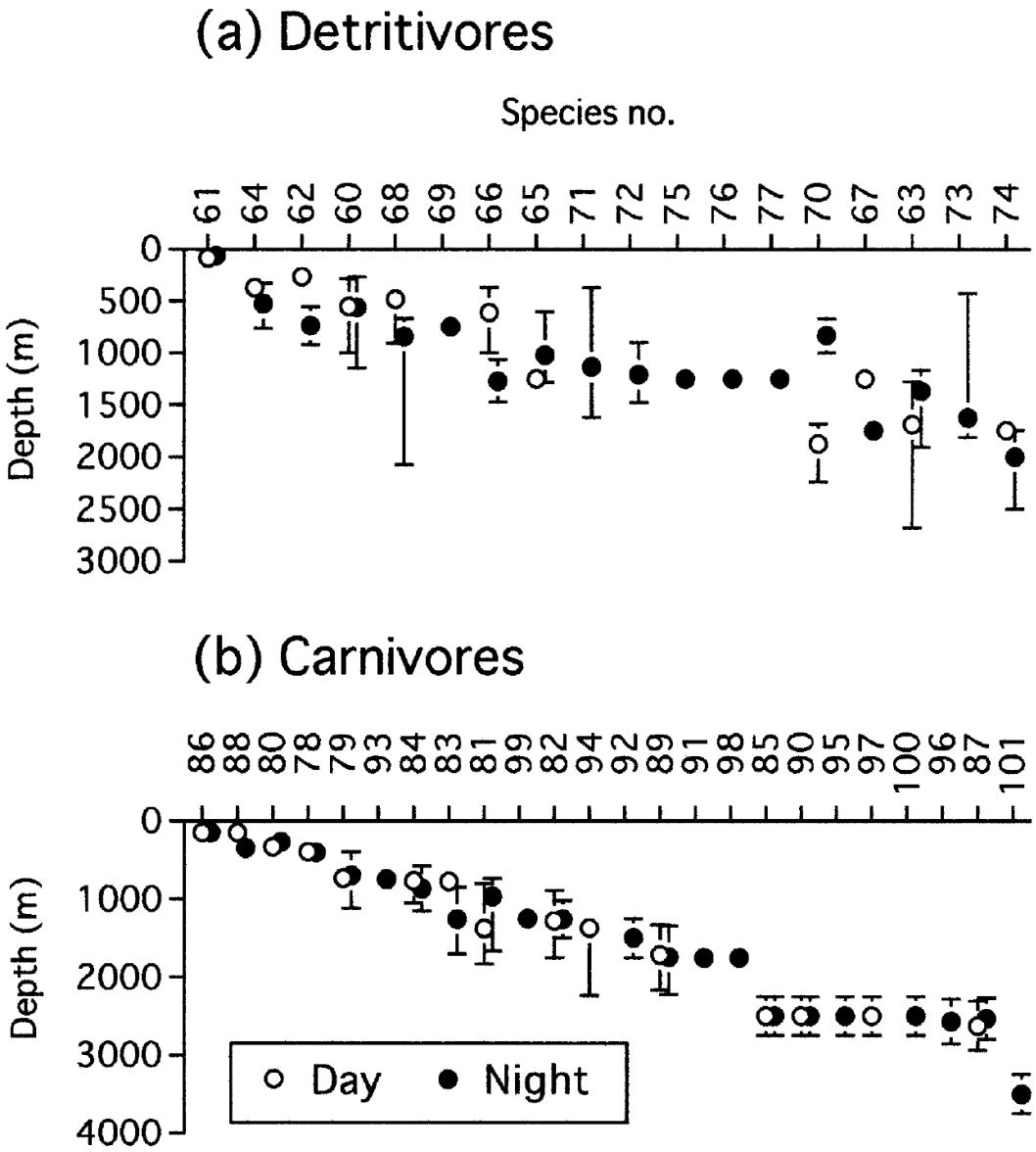


Fig. 5. Vertical distribution of suspension feeding copepods at Station Knot in the western subarctic Pacific Ocean. Of each species, open and solid symbols indicate 50% distribution depth ($D_{50\%}$) at day and night, respectively. Vertical bars indicate depth ranges where 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population was distributed. For species number see Table 1. The four species with solid circles (no. 9, 5, 12, 10) indicate suspension feeders in diapause in the deep layer (cf. Miller et al., 1984; Miller and Clemons, 1988). Note that the vertical (depth) scales are not the same among panels.



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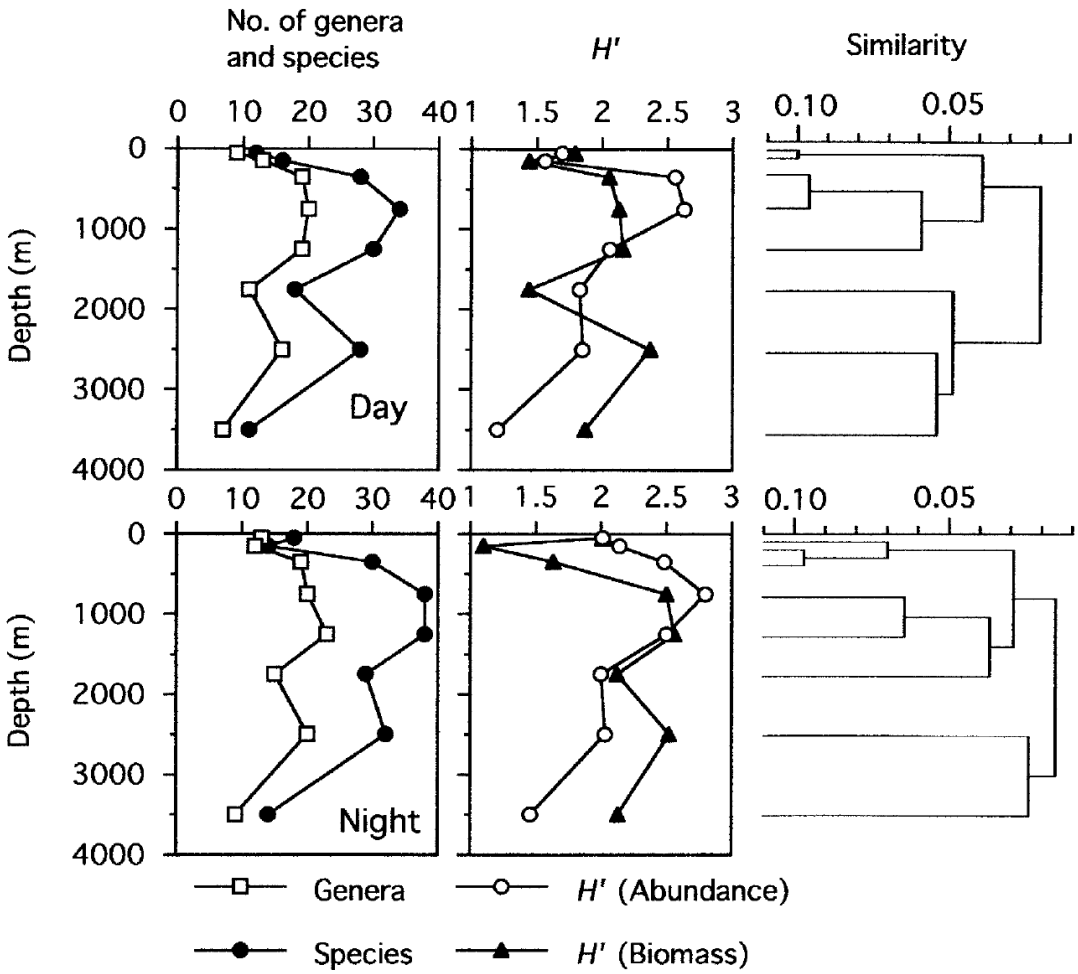

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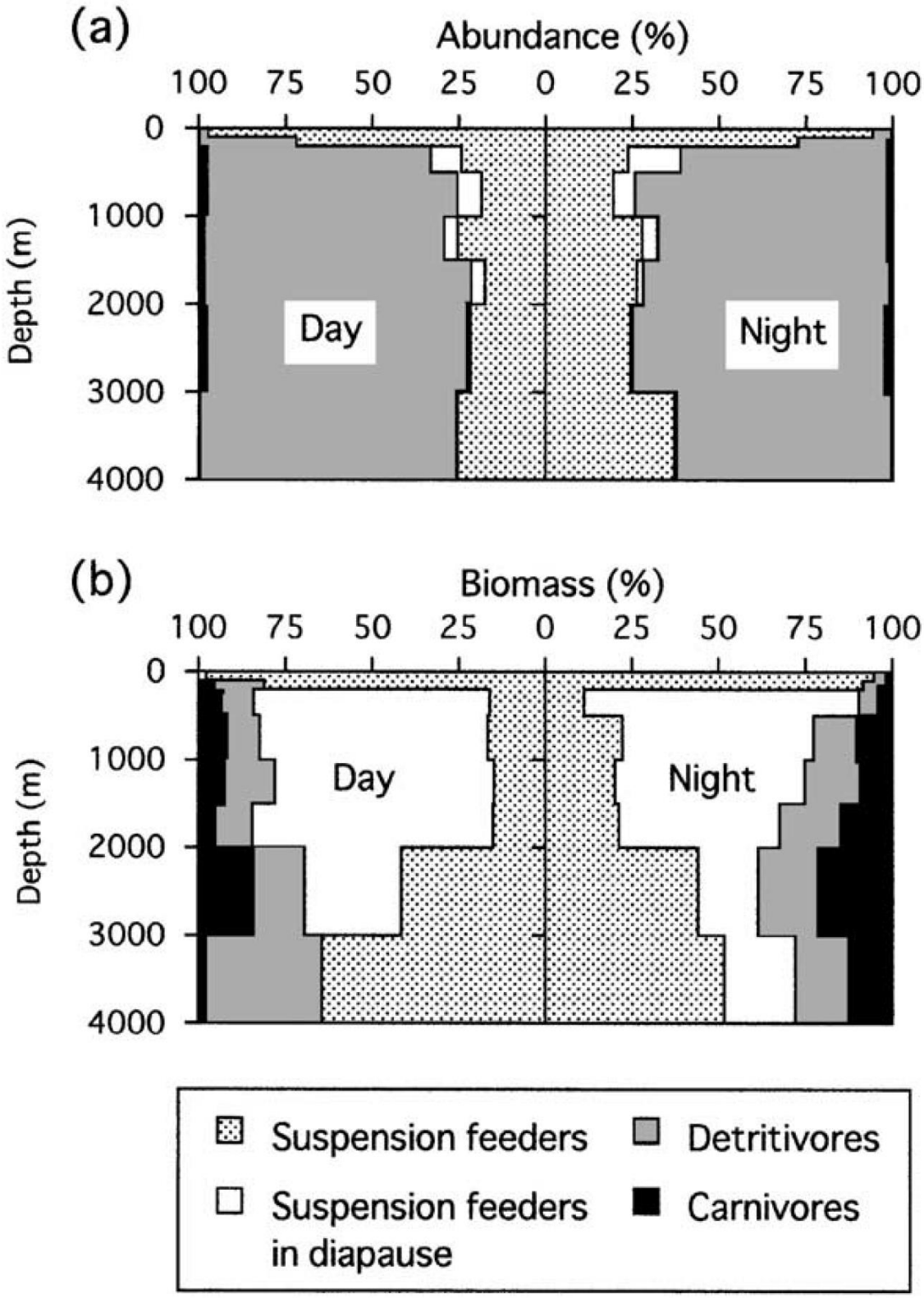

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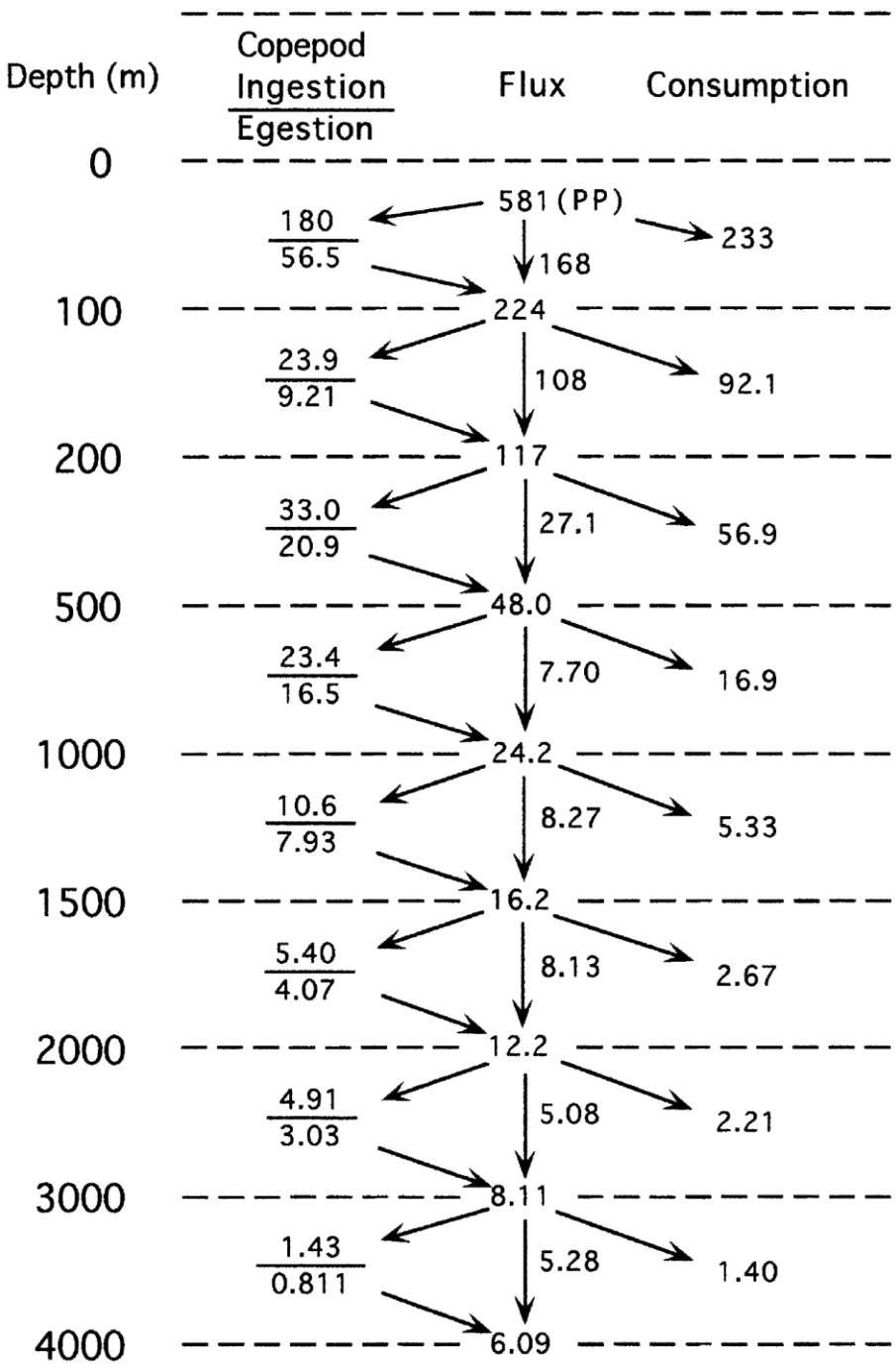

Fig. 9. Schematic diagram showing particulate carbon flux (mg $C\,m^{-2}\,day^{-1}$) in the 0–4000 m water column via eight depth strata in the western subarctic Pacific Ocean. Copepod ingestion and egestion rates were shown as mean values of day and night, and estimated from the formulas of Ikeda and Motoda (1978) and Ikeda et al. (2001). Primary production (PP) was measured directly, and downward flux was estimated by the formula of Suess (1980).

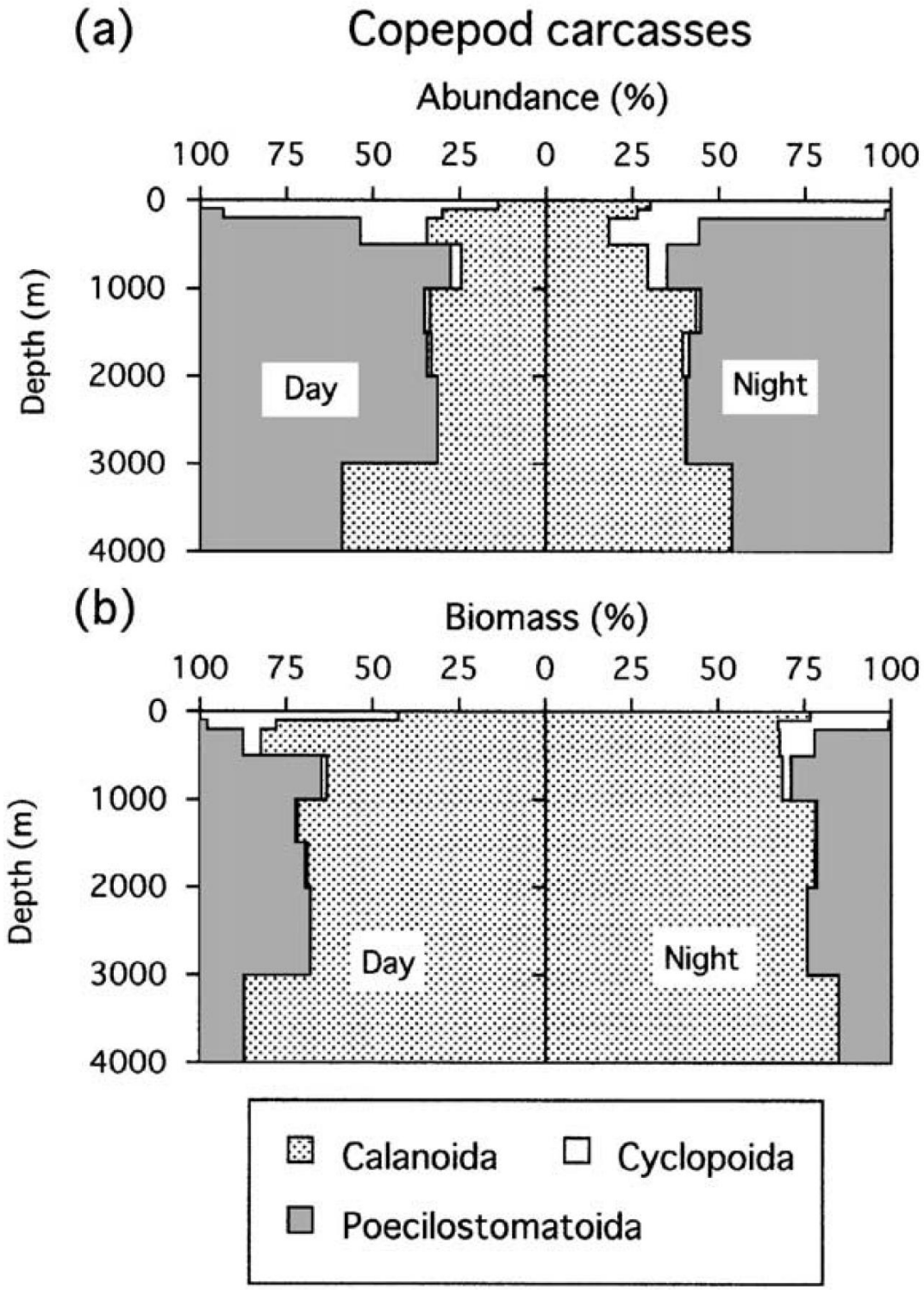

Fig. 10. Percentage composition of copepod carcasses separated into the three orders (Calanoida, Cyclopoida and Poecilostomatoida) and expressed by abundance (a) and biomass (b) at Station Knot in the western subarctic Pacific Ocean. Note that carcasses of Harpacticoida did not occur.