Marine Biology (2004) 145: 931–941
DOI 10.1007/s00227-004-1392-9

RESEARCH ARTICLE

Y. Nishibe · T. Ikeda

Vertical distribution, abundance and community structure of oncaeid copepods in the Oyashio region, western subarctic Pacific

Received: 15 March 2004 / Accepted: 21 April 2004 / Published online: 8 June 2004

Abstract The vertical distribution, abundance and community structure of oncaeid copepods were investigated in the Oyashio region, western subarctic Pacific. Samples were collected with a 0.10 mm mesh closing type net from five discrete layers down to a maximum depth of 2,000 m in September and December 1996 and in April and October 1997. The copepods were widely distributed from epipelagic to bathypelagic zones, and showed prominent peaks of abundance above the thermocline and/or between 250 and 1,000 m depth. Standing stocks of total oncaeid copepods ranged from 1.5 to 2.5×10^5 inds m^{-2} at 0–2,000 m in the water column, which are the same order of magnitudes as those reported in tropical, subtropical and polar regions by previous workers. A total of 38 species and two forms belonging to the genera *Oncaea*, *Triconia*, *Spinoncaea*, *Conaea* and *Epicalymma*, and two provisionally classified species of the family Oncaeidae were identified in this study. Of these, 14 species have already been recorded from the eastern subarctic Pacific. Several warm-water species were also found in December 1996 and/or October 1997, when the effect of warm-core rings originating from the Kuroshio Current was evident in the epipelagic zone. Dominant species throughout the whole water column were *T. borealis*, *T. canadensis*, *O. grossa*, *O. parila*, *O. rimula*, *O. lacinia*, *Epicalymma* spp. and *Oncaea* sp. A, and these eight species together always made up about half of the total oncaeid numbers. Community analysis revealed that species composition in epipelagic and upper mesopelagic zones varied temporally due to the changes of hydrographic conditions, whereas those in lower mesopelagic and bathypelagic zones were relatively stable, reflecting the constancy of deep environments.

Communicated by O. Kinne, Oldendorf/Luhe

Y. Nishibe (✉) · T. Ikeda
Graduate School of Fisheries Sciences, Hokkaido University,
3-1-1 Minato-cho, Hakodate 041-8611, Japan
E-mail: nishibe@fish.hokudai.ac.jp
Tel.: +81-138-405543
Fax: +81-138-405542

Introduction

The family Oncaeidae is a diversified group of marine poecilostomatoid copepods, consisting of 7 genera and >100 species. Oncaeid copepods have been shown to be distributed from epipelagic to bathypelagic zones of several oceanic regions (Furuhashi 1966; Boxshall 1977; Deevey and Brooks 1977; Scotto di Carlo et al. 1984). While oncaeid copepods are thus considered to occur widespread in the world oceans (cf. review of Malt 1983), their numerical importance has largely been overlooked in earlier zooplankton studies, because their body sizes are too small to be collected with standard zooplankton nets of 0.20–0.33 mm mesh sizes. In recent years, several studies using fine nets of 0.10 mm mesh size or less have revealed that these copepods are one of the most numerous groups in marine pelagic copepod communities (Böttger 1987; Cowles et al. 1987; Böttger-Schnack 1994; Webber and Roff 1995; Kršinić 1998). It is noteworthy that oncaeid copepods accounted for more than half of the total copepod numbers in mesopelagic and bathypelagic zones of the various oceanic areas (Böttger-Schnack 1995, 1996, 1997; Kršinić 1998; Yamaguchi et al. 2002). This implies that oncaeid copepods may be playing important trophic roles in marine pelagic food webs, particularly in deep oceanic systems.

In spite of the global distribution of oncaeid copepods, information about their species composition and vertical changes in community structure has been limited to a few areas in the North Atlantic (Boxshall 1977; Malt 1983), the Mediterranean Sea (Malt et al. 1989; Böttger-Schnack 1997; Kršinić 1998), the western Indian Ocean, including the Red Sea (Böttger-Schnack 1988, 1990a, 1990b, 1995, 1996; Böttger-Schnack et al. 2001), and the Southern Ocean (Metz 1995, 1996). In the subarctic Paci“c, corresponding information is currently available only on a few large-sized oncaeids (e.g. Furuhashi 1966; Minoda 1971; Marlowe and Miller 1975). In addition, many sibling oncaeid species, which were not treated as single species previously, have been separated and described as distinct species during the past two decades (Heron 1977; Heron and Bradford-Grieve 1995; Böttger-Schnack 1999, 2001, 2002, 2003). Heron and Frost (2000) provided detailed taxonomical accounts of oncaeid copepods in the eastern subarctic Paci“c.

In the present study, we investigated the abundance and community structure of oncaeid copepods from the surface layer to a maximum depth of 2,000 m in the Oyashio region, western subarctic Paci“c. We compare the present results with those reported from other oceans, and also discuss spatial/temporal di erences in species composition in relation to hydrographic conditions.

Materials and methods

Zooplankton samples were collected on four occasions, 4 September and 8 December 1996 and 11 April and 5 October 1997, in the Oyashio region in a rectangle de“ned by 41°30′ to 42°30′N and 145°00′ to 146°00′E, o southeastern Hokkaido (hereafter referred to as Site H, Fig. 1). At each sampling date, a closing type net (60 cm mouth diameter, 0.10 mm mesh size, Kawamura 1989) was hauled vertically at a speed of 1.0 m s^{-1} from “ve discrete layers between 0 and 2,000 m in the water column (Table 1). The volume of water “ltered was estimated by the reading of a ”ow meter (Rhigosha) mounted inside the mouth of the net. The depths the net reached were read by using a RMD depth meter (Rhigosha), which was attached to the suspension cable of the net. After collection, samples were preserved immediately on board ship in a 2% formaldehyde…seawater solution bu ered with borax. Vertical pro“les of temperature and salinity were determined simultaneously by using a CTD system (Neil Brown Mark III, General Oceanics) at each zooplankton sampling date.

The oncaeid copepods were sorted out from the entire sample or aliquots were taken by using a box type splitter (Motoda 1959). More than 1,000 individuals per sample were enumerated and identi“ed under a dissecting microscope. Taxonomical identi“cation of oncaeid copepods was made only for adult specimens (CVI); immature copepodite stages (CI…CV) of all oncaeid species were pooled and counted as *Oncaea* spp. juveniles. The adult females and males were always counted separately. Because of the 0.10 mm mesh size of the net used (diagonal dimension: 0.14 mm), possible underestimation of the abundance cannot be ruled out for smaller oncaeid species in the present study. Carcasses of oncaeid copepods were di erentiated from living specimens following the criteria established by Haury et al. (1995), and were not included in the abundance data.

For identi“cation, diagnostic features described by Olson (1949), Shmeleva (1969), Heron (1977), Heron

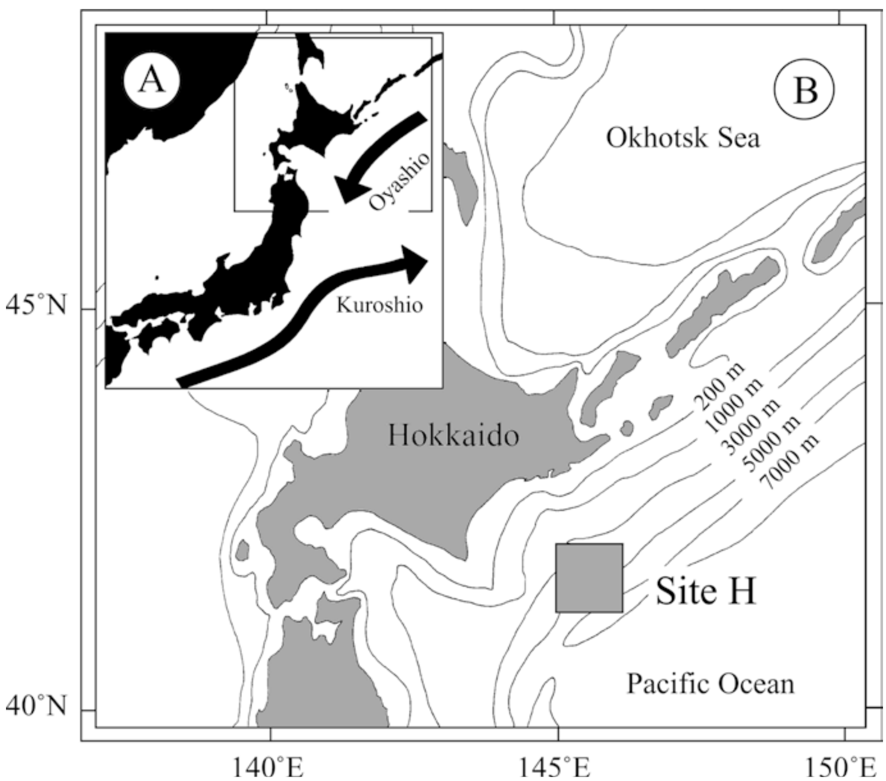

Fig. 1 A The Oyashio region in the western North Paci“c and B the sampling site (Site H; *shaded rectangle*). Bathymetric counters (200, 1,000, 3,000, 5,000 and 7,000 m) are also shown in panel B

Table 1 Summary of zooplankton sampling data at Site H (*DT* daytime; *NT* nighttime; *Os* T.S. "Oshoro Maru"; *Hs* R.V. "Hokushin Maru"; *Ho* T.S. "Hokusei Maru"). In each sampling series, the first sampling stratum denotes from the bottom of the thermocline (150 m in April 1997 is an exception) to the surface

Sampling date	Position	Time	Ship	Depth (m)	Sampling depth (m)
4 Sep 1996	42°00′N; 145°00′E	DT	Os	3,050	0–30, 30–250, 250–500, 500–1,000, 1,000–1,800
8 Dec 1996	41°30′N; 146°00′E	NT	Hs	6,280	0–80, 80–250, 250–500, 500–1,000, 1,000–1,700
11 Apr 1997	41°30′N; 145°47′E	NT	Ho	6,670	0–150, 150–250, 250–500, 500–1,000, 1,000–1,500
5 Oct 1997	41°30′N; 145°47′E	NT	Ho	6,670	0–75, 75–250, 250–500, 500–1,000, 1,000–2,000

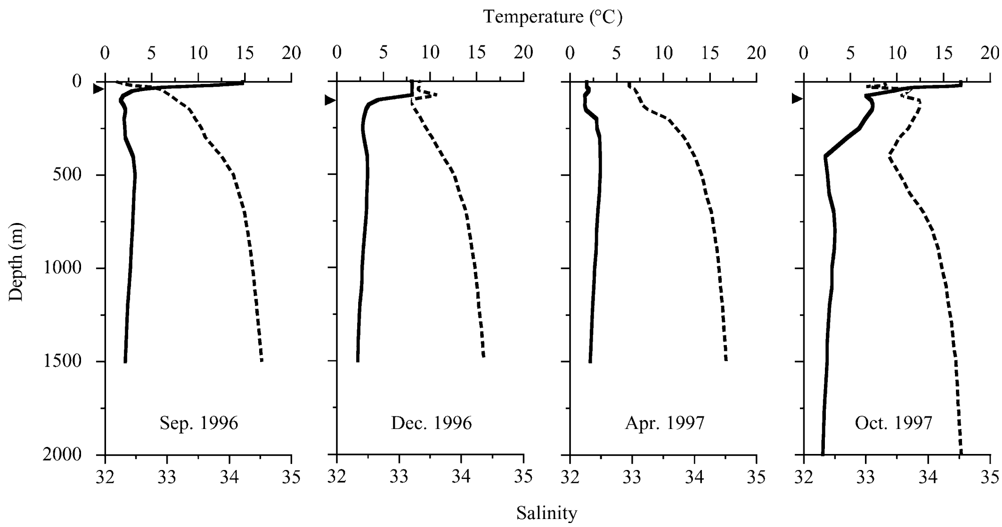

Fig. 2 Vertical profiles of temperature (*solid line*) and salinity (*broken line*) at Site H in September and December 1996 and April and October 1997. *Closed triangles* on the *Y*-axis indicate the depth of the bottom of the thermocline at each sampling date

et al. (1984), Kršinić and Malt (1985), Böttger-Schnack and Boxshall (1990), Heron and Bradford-Grieve (1995), Böttger-Schnack (1999, 2001, 2002, 2003), Heron and Frost (2000) and Böttger-Schnack and Huys (2004) were consulted. Recently, Heron and Frost (2000) described *O. canadensis* and *O. thoresoni* as new species of the genus *Oncaea* from the eastern subarctic Pacific. However, the two species have a conical process on the distal margins of the endopods of swimming legs 2–4, which is the most important character for generic definition of the genus *Triconia* proposed by Böttger-Schnack (1999). Also, the mandible and labral structure of them agrees well with those of *Triconia* species (R. Böttger-Schnack, personal communication). Hence, we treated the two species as *T. canadensis* and *T. thoresoni*, respectively, hereafter in this study. Some small specimens (body length <0.5 mm) could not be identified to species, but most of them could be identified to genera (*Spinoncaea* spp. and *Epicalymma* spp.), or were grouped into the provisionally classified species (*Oncaea* sp. A and *Oncaea* spp. "*tregoubovi*") based on their morphological characteristics. Thus, each of these four species was treated here as a single species and was included in the latter analysis of community structure.

To analyze spatial and temporal differences in the community structure of oncaeid copepods, we conducted cluster analysis and non-metric multidimensional scaling (NMDS) ordination. Abundance data (inds m^{-3}) of each species were transformed to square-root values prior to analysis, in order to reduce the bias of very abundant species. Similarities between samples were examined by the Bray–Curtis index (Bray and Curtis 1957) according to the differences in species composition. For grouping the samples, the similarity indices were coupled with hierarchical agglomerative clustering with a complete linkage method. The NMDS ordination was carried out to delineate the sample groups on the two-dimensional map. All of these analyses were carried out using BIOΣTAT II software (Sigma Soft).

Results

Surface temperatures on 4 September and 8 December 1996 and 11 April and 5 October 1997 were 14.8, 8.0, 1.8 and 16.8°C, respectively (Fig. 2). In April 1997, the Oyashio water, characterized by a temperature of <3°C and a salinity of 33.0–33.3 (Ohtani 1971), was observed in the top 150 m (Fig. 2), and the water column above that depth seemed to be vertically well mixed. Very high salinities (>33.5) were seen in the subsurface waters, both in December 1996 and October 1997 (Fig. 2). It is noted that the water characterized by high-salinity and warm temperature extended down to ca. 300 m depth in October 1997 (Fig. 2). This high-salinity/warm water may reflect the influences of warm-core rings originating from the warm Kuroshio Current. As evidenced in the images from TOPEX/Poseidon and ERS-2 satellite

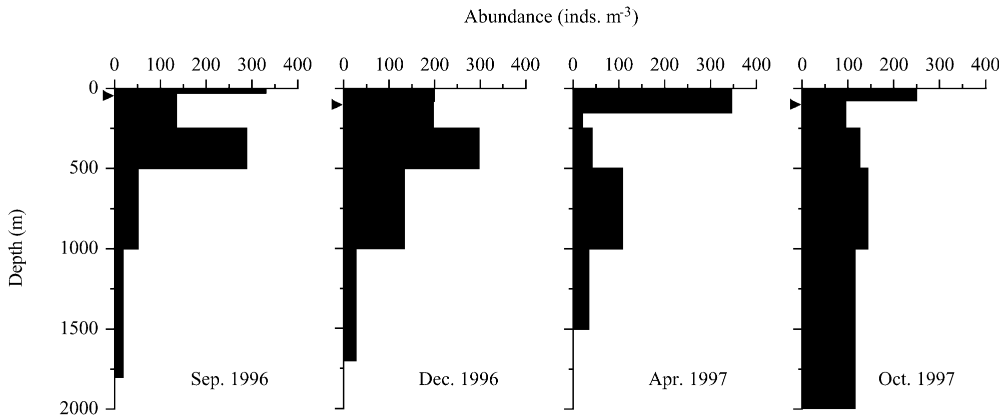

Fig. 3 Oncaeid copepods. Vertical distributions in abundance (inds m^{-3}) at Site H in September (daytime) and December 1996 (nighttime) and April (nighttime) and October 1997 (nighttime). *Closed triangles* on the *Y*-axis as in Fig. 2

altimetry, warm-core rings were located on the margin of Site H on both sampling dates. Below 500 m depth, the temperatures and salinities were almost constant at 2…3°C and 33.5…34.5, respectively, throughout the study period.

Oncaeid copepods were distributed throughout the water column, from the surface to around 2,000 m depth (Fig. 3). Except for December 1996, maximum abundances were found within the uppermost layer, above the thermocline, ranging between 198 and 346 inds m^{-3}. The mesopelagic peaks of abundance were observed between 250 and 500 m in September and December 1996, while they occurred deeper, between 500 and 1,000 m, in April and October 1997. Below 1,000 m depth, the copepod abundances were very low at all sampling dates, except for October 1997, when comparably high abundance values were found. In the water column from 0 to 2,000 m depth, standing stocks of total oncaeid copepods ranged from 1.5 to 2.5$\times$10^5 inds m^{-2} during this study (Table 2), with a mean of 1.9$\times$10^5 inds m^{-2}. *Oncaea* spp. juveniles accounted for 23…48% of the total standing stock (Table 2).

We found a total of 38 species and two forms belonging to the five genera *Triconia*, *Oncaea*, *Spinoncaea*, *Conaea* and *Epicalymma*, and two provisionally classified species *Oncaea* sp. A and *Oncaea* spp. '*tregoubovi*' (Table 2). *Oncaea* sp. A could be distinguished as a single species in this study, but is not yet described. *Oncaea* sp. A resembles species of *Spinoncaea* in general habitus and in leg armature, but differs from this genus by the lack of a strong spineform element on the posterolateral margin of caudal rami, by the absence of an undulating hyaline frill on the margins of urosomites, as well as by the proportional length of urosomites. *Oncaea* spp. '*tregoubovi*' included at least *O. tregoubovi* Shmeleva as an identifiable species, but there are also some types of very similar species. Thus, we counted them together as a single species group. Of a total of 40 species, 19 were consistently found throughout the four sampling dates (Table 2). The number of species found in the whole water column was distinctly higher in December 1996 (37 species) and October 1997 (31) than in September 1996 (21) and April 1997 (24) (Table 3). Seasonal differences in the number of oncaeid species were most pronounced in the upper 500 m, in particular from the surface to the thermocline, whereas the species numbers remained fairly constant below that depth between the four sampling dates (Table 3). The maxima of species numbers were always found in the deepest layer sampled, at 1,000…2,000 m.

Taxonomic composition of oncaeid copepods in the water column from 0 to 2,000 m depth is summarized in Table 2. Although the contributions of dominant species to total oncaeid numbers changed from one sampling date to the next, *T. borealis*, *T. canadensis*, *O. grossa*, *O. parila*, *O. rimula*, *O. lacinia*, *Epicalymma* spp. and *Oncaea* sp. A were always dominant, contributing about 1…30% of the total standing stocks. *O. scottodicarloi*, *O. media*, *O. zernovi* and *Spinoncaea* spp. were abundant only in December 1996 and/or October 1997. *Spinoncaea* spp. was especially abundant in December 1996, accounting for >10% of the total numbers. By contrast, *T. thoresoni*, *T. similis*, *O. damkaeri*, *O. olsoni*, *O. macilenta*, *O. brodskii*, *O. englishi* and *C. rapax* were consistently found, but their contribution to total numbers was low.

The dominant oncaeid species varied conspicuously with depth and season (Table 4). In Table 4, only the number of adult specimens was taken into account. In September 1996 and April 1997, *T. borealis* predominated in the upper epipelagic zone between 0 m and the thermocline (Th), accounting for >95% of the total numbers. In contrast, *O. scottodicarloi*, *O. media* and *O. zernovi* were abundant together with *T. borealis* in this zone in December 1996 and October 1997. In the lower epipelagic zone (Th…250 m), the most dominant species were similar to those in the upper epipelagic zone, excepting for the sampling date in December 1996. In the upper mesopelagic zone (250…500 m), *O. lacinia*, *T. borealis* and *O. grossa* were always numerous. In October 1997, however, *O. scottodicarloi*, *O. mediterranea*, *O. media* and *O. zernovi* were found down to this mesopelagic layer, though their contribution to the total number was very low (data not shown). This may be due to the fact that high-salinity/warm water reached this

Table 2 Oncaeid copepods. Species and standing stocks (inds m^{-2}) in the 0–2,000 m water column at Site H. The proportion (%) of the total standing stock of each species is also shown. *Asterisks* indicate that the species were found across all four sampling dates (*F* adult female; *M* adult male)

Taxa	Sexes/Stages	Sep 1996 (Day)		Dec 1996 (Night)		Apr 1997 (Night)		Oct 1997 (Night)	
		n	%	*n*	%	*n*	%	*n*	%
Triconia (= *conifera*/*similis* group)									
*T. borealis**	F, M	49,400	32	10,900	5.0	6,500	4.2	15,000	5.9
*T. canadensis**	F, M	2,640	1.7	2,310	1.1	1,610	1.1	3,140	1.2
*T. thoresoni**	F, M	803	0.5	333	0.2	572	0.4	59	<0.1
T. redacta	F, M			23	<0.1			228	0.1
T. conifera	F, M			47	<0.1			54	<0.1
*T. similis**	F, M	116	0.1	45	<0.1	66	<0.1	399	0.2
T. parasimilis	F			34	<0.1				
T. minuta	F			9	<0.1				
T. umerus	F, M			34	<0.1				
T. giesbrechti	F, M							36	<0.1
T. dentipes	F			9	<0.1				
Oncaea s. str. (= *venusta* group)									
O. venusta large form	F, M			200	0.1				
O. venusta medium form	F, M			17	<0.1			306	0.1
O. mediterranea	F, M			179	0.1			220	0.1
O. media	F, M			3,820	1.8			2,370	0.9
O. scottodicarloi	F, M	10	<0.1	3,990	1.8			3,710	1.5
O. clevei	F			9	<0.1				
Oncaea									
*O. grossa**	F, M	12,800	8.3	13,600	6.3	5,910	3.9	22,400	8.9
*O. parila**	F, M	14,600	9.4	12,000	5.6	15,700	10	21,600	8.5
*O. damkaeri**	F, M	171	0.1	249	0.1	713	0.5	604	0.2
O. walleni	F			18	<0.1				
O. insolita	F, M	80	0.1			33	<0.1	59	<0.1
O. rotata	F			23	<0.1				
O. convexa	F					49	<0.1		
O. compacta	F, M			53	<0.1			59	<0.1
*O. olsoni**	F, M	969	0.6	666	0.3	1,080	0.7	530	0.2
*O. macilenta**	F, M	308	0.2	205	0.1	372	0.2	770	0.3
*O. brodskii**	F, M	1,030	0.7	1,270	0.6	1,890	1.2	1,330	0.5
*O. englishi**	F, M	122	0.1	260	0.1	33	<0.1	221	0.1
*O. rimula**	F, M	1,530	1.0	2,730	1.3	5,160	3.4	9,760	3.9
*O. lacinia**	F, M	26,900	17	59,200	27	23,700	16	66,300	26
O. glabra	F, M			87	<0.1	68	<0.1	298	0.1
O. ovalis	F					31	<0.1	266	0.1
*O. zernovi**	F, M	120	0.1	473	0.2	255	0.2	16,200	6.4
O. longipes	F, M			88	<0.1	143	0.1	133	0.1
Other genera									
Spinoncaea spp.*	F, M	1,110	0.7	26,400	12.2	286	0.2	3,440	1.4
*Conaea rapax**	F, M	27	<0.1	70	<0.1	16	<0.1	59	<0.1
C. succurva	F			18	<0.1				
Epicalymma spp.*	F, M	4,020	2.6	4,700	2.2	9,600	6.3	11,900	4.7
Provisionally classified species and others									
Oncaea sp. A*	F, M	1,260	0.8	12,300	5.7	4,300	2.8	6,360	2.5
Oncaea spp. '*tregoubovi*'*	F, M	1,270	0.8	2,340	1.1	558	0.4	3,900	1.5
Oncaea spp. unidentified specimens	F, M			394	0.2	19	<0.1	100	<0.1
Oncaea spp. juveniles	<C5	36,100	23	56,900	26	74,100	48	61,500	24
Total		155,000	100	216,000	100	153,000	100	253,000	100

depth zone on that date. Species compositions in the lower mesopelagic (500–1,000 m) and bathypelagic zones (1,000–2,000 m) seemed to be temporally constant, and several species were found to be common in both zones. In the lower mesopelagic zone, the dominant species were *O. lacinia*, *O. parila*, *O. grossa*, *T. canadensis*, *Epicalymma* spp., *O. rimula* and *Oncaea* sp. A. In addition to these species, *O. olsoni*, *O. brodskii*, *Oncaea* spp. '*tregoubovi*' and *T. thoresoni* were also abundant in the bathypelagic zone.

Our 20 samples could be separated into two major groups by cluster analysis (Fig. 4A). The first major group (group 1) comprised all epipelagic samples (0 m–Th, Th–250 m) with one exception from the upper mesopelagic zone (250–500 m) in October 1997. This group was further divided into two subgroups, 1a and 1b, at a similarity level of 30%, according to the dates of sampling (Fig. 4A). The second major group (group 2) consisted of mesopelagic and bathypelagic samples (250–500 m, 500–1,000 m, 1,000–2,000 m), but also

Table 3 Oncaeid copepods. The numbers of species that occurred in each sampling layer at Site H (those of warm-water species are *in parentheses*). The total numbers of species found in the 0…2,000 m water column are also shown. Forma and provisionally classi“ed species are treated as single species. See the ••Discussion•• section for discriminating warm-water species from cold-water species

	Sep 1996	Dec 1996	Apr 1997	Oct 1997
0 m…thermocline	5	17 (10)	3	11 (5)
Thermocline…250 m	11	14 (3)	12	14 (2)
250…500 m	9	14	11	19 (2)
500…1,000 m	15	14	16	16
1,000…2,000 m	17	20	21	22
Total	21	37 (10)	24	31 (5)

included one sample from the lower epipelagic zone (Th…250 m), and could be split into two subgroups, 2a and 2b, at a similarity level of 46% (Fig. 4A). Subgroup 2a included three upper mesopelagic samples and the lower epipelagic sample on April 1997. Subgroup 2b showed high similarity at a level of >60% and contained all lower mesopelagic and bathypelagic samples. These four subgroups were clearly distinguished on the NMDS plot (Fig. 4B), thereby re-con“rming the results of cluster analysis. Accordingly, the lower mesopelagic and bathypelagic samples were clearly separated from the epipelagic and upper mesopelagic samples. Furthermore, epipelagic and upper mesopelagic samples, which were collected from the same depth layer but on di erent dates, overlapped into two or three subgroups (Fig. 4A), but all lower mesopelagic and bathypelagic

Table 4 Oncaeid copepods. Abundance (*n*, inds m^{-3}) and its contribution (%) to the total number in each designated depth stratum at Site H (adult specimes only). Species contributing <2% of the total number are not shown

Sep 1996			Dec 1996			Apr 1997			Oct 1997		
Species	*n*	%	Species	*n*	%	Species	*n*	%	Species	*n*	%
0 m…thermocline											
Triconia borealis	299.3	99	*Oncaea scottodicarloi*	48.8	34	*Triconia borealis*	33.5	95	*Oncaea zernovi*	91.1	43
			Triconia borealis	45.3	32				*Oncaea scottodicarloi*	47.2	23
			Oncaea media	36.6	25				*Triconia borealis*	31.9	15
			Oncaea zernovi	5.1	3.6				*Oncaea media*	30.9	15
Thermocline…250 m											
Triconia borealis	99.0	93	*Spinoncaea* spp.	128.4	85	*Triconia borealis*	6.8	74	*Oncaea zernovi*	53.1	68
Spinoncaea spp.	3.7	3.7	*Triconia borealis*	14.8	9.7	*Oncaea lacinia*	0.64	6.9	*Triconia borealis*	9.4	12
Oncaea lacinia	2.1	2.0	*Oncaea media*	5.5	3.6	*Oncaea zernovi*	0.42	4.6	*Spinoncaea* spp.	2.9	3.5
						Oncaea parila	0.35	3.8	*Oncaea lacinia*	2.2	2.8
						Oncaea sp. A	0.24	2.6	*Oncaea* sp. A	1.8	2.4
						Epicalymma spp.	0.19	2.1			
250…500 m											
Oncaea lacinia	83.2	41	*Oncaea lacinia*	120.3	66	*Oncaea grossa*	9.8	67	*Oncaea lacinia*	39.6	47
Triconia borealis	67.9	33	*Oncaea grossa*	21.0	12	*Triconia borealis*	2.0	13.5	*Triconia borealis*	19.9	24
Oncaea grossa	39.0	19	*Spinoncaea* spp.	17.1	9.4	*Oncaea lacinia*	1.6	10.6	*Oncaea grossa*	9.5	11
Oncaea parila	9.2	4.5	*Triconia borealis*	16.9	9.3	*Triconia canadensis*	0.75	5.1	*Spinoncaea* spp.	2.9	3.5
									Oncaea sp. A	2.4	2.9
500…1,000 m											
Oncaea parila	16.2	38	*Oncaea lacinia*	49.4	43	*Oncaea lacinia*	34.9	42	*Oncaea lacinia*	44.1	45
Oncaea lacinia	8.4	20	*Oncaea* sp. A	18.1	16	*Oncaea parila*	20.0	24	*Oncaea grossa*	22.6	23
Oncaea grossa	5.3	12	*Oncaea parila*	16.8	14	*Oncaea* sp. A	7.2	8.6	*Triconia borealis*	9.7	9.9
Triconia canadensis	3.5	8.3	*Oncaea grossa*	16.0	14	*Oncaea grossa*	6.8	8.1	*Oncaea parila*	7.7	7.9
Triconia borealis	2.7	6.4	*Triconia canadensis*	3.8	3.3	*Epicalymma* spp.	5.4	6.5	*Epicalymma* spp.	4.2	4.3
Epicalymma spp.	1.7	4.1	*Epicalymma* spp.	3.2	2.8	*Oncaea rimula*	4.1	4.9	*Oncaea* spp. ••*tregoubovi*••	2.2	2.3
Oncaea rimula	1.6	3.6	*Oncaea rimula*	3.1	2.7	*Triconia canadensis*	2.1	2.5	*Oncaea* sp. A	1.9	2.0
Oncaea sp. A	1.4	3.3									
1,000…2,000 m											
Oncaea parila	3.7	26	*Oncaea lacinia*	4.3	23	*Epicalymma* spp.	6.9	26	*Oncaea lacinia*	33.8	37
Epicalymma spp.	2.6	18	*Oncaea parila*	3.3	18	*Oncaea lacinia*	5.8	22	*Oncaeaparila*	17.7	19
Oncaea lacinia	1.4	9.7	*Epicalymma* spp.	3.0	16	*Oncaea parila*	5.6	21	*Epicalymma* spp.	9.5	10
Oncaea rimula	1.2	8.2	*Oncaea* sp. A	2.4	13	*Oncaea rimula*	3.1	12	*Oncaea grossa*	8.7	9.4
Oncaea spp. ••*tregoubovi*••	1.0	7.1	*Oncaea* spp. ••*tregoubovi*••	1.4	7.5	*Oncaea brodskii*	1.2	4.5	*Oncaea rimula*	8.5	9.2
Oncaea olsoni	0.90	6.3	*Oncaea rimula*	1.2	6.2	*Oncaea olsoni*	1.1	4.0	*Oncaea* sp. A	4.5	4.8
Triconia thoresoni	0.77	5.4	*Oncaea olsoni*	0.67	3.5	*Oncaea* sp. A	0.66	2.4	*Triconia canadensis*	2.4	2.6
Triconia canadensis	0.58	4.1	*Oncaea brodskii*	0.56	3.0	*Oncaea* spp. ••*tregoubovi*••	0.56	2.1	*Oncaea* spp. ••*tregoubovi*••	2.2	2.4
Oncaea brodskii	0.56	3.9				*Oncaea damkaeri*	0.56	2.1			
Oncaea sp. A	0.53	3.7				*Triconia thoresoni*	0.54	2.0			
Oncaea grossa	0.40	2.8									
Triconia borealis	0.29	2.1									

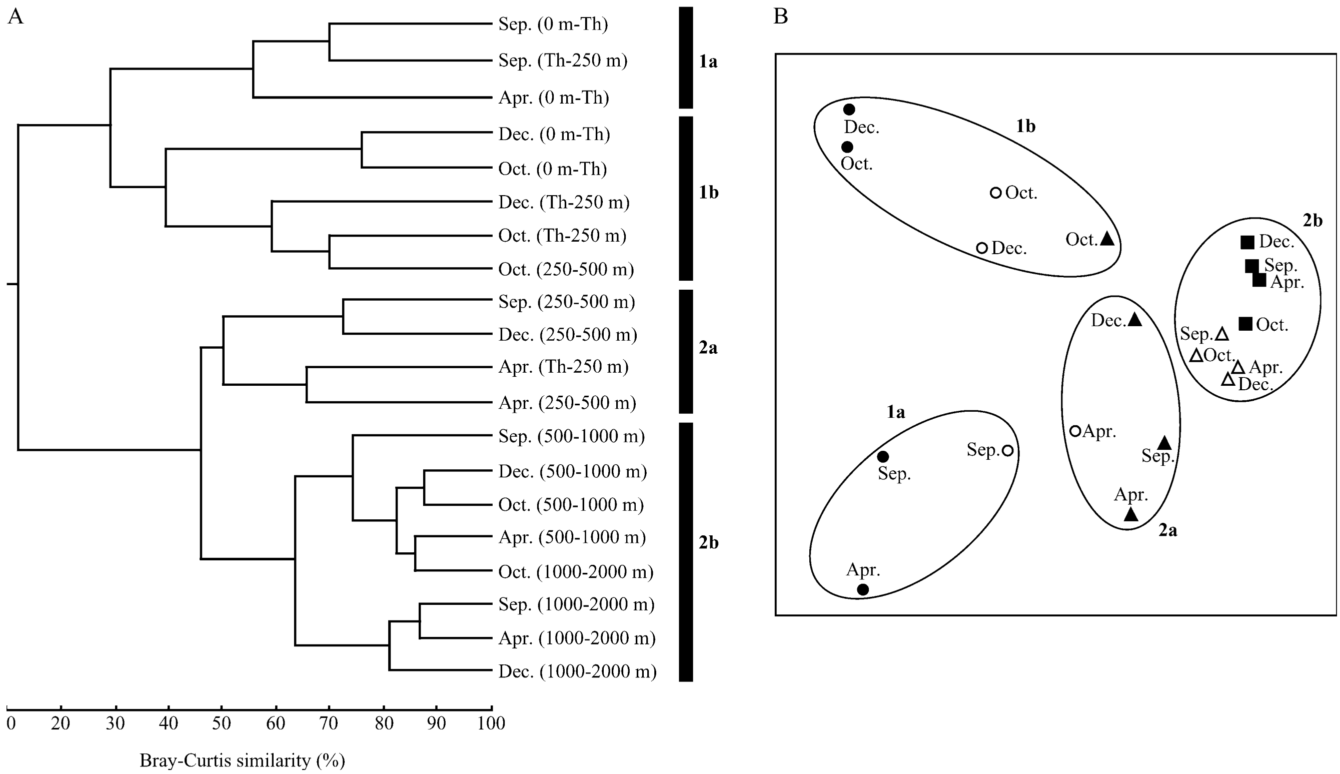

Fig. 4 Oncaeid copepods. A Dendrogram of cluster analysis comparing species composition in each sample. Cluster groups are also shown as 1a, 1b, 2a and 2b. B Non-metric multidimensional scaling ordination of samples. Cluster groups determined in panel A are superimposed. Axis scales are relative in NMDS; stress value=0.081. Depth strata of samples are shown as follows: 0 m–thermocline (*closed circle*), thermocline–250 m (*open circle*), 250–500 m (*closed triangle*), 500–1,000 m (*open triangle*) and 1,000–2,000 m (*closed square*)

samples were grouped together in a single subgroup. These results indicate that the temporal changes in species composition of oncaeid copepods occurred within the epipelagic and upper mesopelagic zones, while the community structure was stable within the lower mesopelagic and bathypelagic zones across all sampling dates of this study.

Discussion

In the present study, we used three nighttime and one daytime series to evaluate the temporal variation in vertical structures of abundance and species composition of oncaeid copepods at Site H in the Oyashio region (Table 1), without examining the day–night differences in distribution patterns caused by possible diurnal vertical migration. However, diurnal differences in the vertical distribution patterns may be assumed to be small, since previous studies have demonstrated the vertical migration of oncaeid copepods to be usually <100 m (Tsalkina 1977; Sameoto 1986; Böttger-Schnack 1990a). In addition, the amplitudes of the diurnal migration, if any, are smaller than the vertical resolution of most of our sampling intervals (Table 1). Thus, it may be assumed that the diurnal migration is of minor importance to interpret the general vertical distributional patterns of oncaeid species observed in this study.

The vertical distribution of the family Oncaeidae down to greater depths has been studied in the Mediterranean Sea (Böttger-Schnack 1994, 1997; Kršinić 1998), the western Indian Ocean (Böttger-Schnack 1994, 1995, 1996), the Arctic Ocean (Richter 1994) and the Southern Ocean (Metz 1995, 1996). According to these studies, oncaeid copepods are distributed over broad vertical ranges, from epipelagic to bathypelagic zones in these oceanic regions, as was observed in the Oyashio region in the present study (Fig. 3). On the other hand, the abundance of oncaeid copepods in the Oyashio region showed characteristic patterns of vertical distribution, having prominent peaks above the thermocline and in the mesopelagic zone, or only in the mesopelagic zone (Fig. 3). The pronounced peaks of oncaeid abundance in the mesopelagic zone, as found in the present study, have only been previously reported for the Arctic Ocean (Richter 1994).

There is still limited information on the vertical distribution pattern of species numbers of oncaeid copepods. Böttger-Schnack (1994) reported that the numbers of oncaeid species in the Red and eastern Mediterranean Seas are almost constant between 100 and 800 m, and then decrease gradually below 800 m depth, with minimum values at 1,250–1,850 m (Böttger-Schnack 1994). Also, Kršinić (1998) reported that the numbers of oncaeid species are constant below 100 m depth in the

Table 5 Oncaeid copepods. Common species between the western subarctic (Oyashio region) and the eastern subarctic Pacific (Heron and Frost 2000) and Kuroshio waters (H. Itoh, personal communication). *Asterisks* indicate the species occurred only in December 1996 and/or October 1997 in this study. See "Discussion" for details

Oyashio region vs. eastern subarctic Pacific	Oyashio region vs. Kuroshio water
Triconia borealis	*Triconia conifera**
Triconia canadensis	*Triconia minuta**
Triconia thoresoni	*Triconia umerus**
Triconia similis	*Triconia dentipes**
Oncaea grossa	*Triconia giesbrechti**
Oncaea parila	*Oncaea venusta* large form*
Oncaea damkaeri	*Oncaea venusta* medium form*
Oncaea insolita	*Oncaea mediterranea**
Oncaea rotata	*Oncaea media**
Oncaea olsoni	*Oncaea scottodicarloi*
Oncaea rimula	*Oncaea clevei**
Oncaea macilenta	*Oncaea ovalis*
Oncaea englishi	*Oncaea zernovi*
Epicalymma spp.	*Spinoncaea* spp.

Adriatic Sea, though his samplings were restricted to above 1,000 m depth. In contrast, the numbers of oncaeid species in the Arabian Sea increase below 800 m, reaching maximum values at depths of 1,050–1,850 m (Böttger-Schnack 1994, 1996). In the Oyashio region, the vertical distribution patterns of oncaeid species numbers seemed to differ between the periods when the surface layer was occupied by cold and/or less saline water (September 1996 and April 1997) and then by warm water from the Kuroshio Current (December 1996 and October 1997) (Table 3). If only the number of cold oncaeid species (except for the 11 species of warm-water immigrants; see below in "Discussion") were taken into account, however, it appeared that the vertical distribution patterns of oncaeid species numbers were very similar throughout the four sampling dates, tending to increase gradually from epipelagic to bathypelagic zones (cf. Table 3). These regional variations in the vertical distribution of species diversities and in the abundance of oncaeid copepods may be the reflections of the differences in abiotic (temperature and oxygen concentration) and biotic factors (magnitude of particulate organic matter flux into the deep sea) of one habitat to the next (Böttger-Schnack 1994).

We found a total of 40 species of oncaeid copepods in the Oyashio region, including the two provisionally classified species (Table 2). Heron and Frost (2000) have reported 17 species of oncaeid copepods in the upper 3000 m of the water column at ocean weather station P (50°N; 145°W) in the eastern subarctic Pacific, using a net with 0.22 mm mesh size. Among 38 oncaeid species identified in the present study (except for *Oncaea* sp. A and *Oncaea* spp. "*tregoubovi*"), 14 species are commonly distributed in the eastern subarctic Pacific (Table 5), suggesting that these species occur widespread in the subarctic Pacific. Some of these common species have been reported from the Arctic and from the Southern Ocean as well (Heron 1977; Heron et al. 1984). It is well known that similar zooplankton taxa occur between the western and eastern subarctic Pacific (cf. Miller et al. 1984; Mackas and Tsuda 1999).

On the other hand, 14 out of the 38 oncaeid species identified in this study have also been recorded from the epipelagic zone of Kuroshio waters (Table 5, H. Itoh, personal communication). In particular, ten of these species were found only at the upper 250 m depth in December 1996 and/or October 1997, when the epipelagic layer was influenced by high-salinity/warm water (cf. Fig. 2). Thus, these species are considered to be immigrants, originating from the warm Kuroshio Current. *Triconia parasimilis*, which was found only in the epipelagic zone in December 1996 in this study (cf. Table 2), was originally described from the tropical Red Sea (Böttger-Schnack 1999), but has not been recorded in Kuroshio waters as yet (H. Itoh, personal communication). From these results, seasonal differences in the total number of oncaeid species could be explained by the immigration of these warm-water species into the epipelagic zone of Site H on both sampling dates (cf. Table 3). Apart from oncaeid copepods, the occurrence of warm-water species in both December 1996 and October 1997 at Site H has also been noted for chaetognaths (Nishiuchi 1999) and appendicularians (Y. Shichinohe, unpublished data) from the same samples analyzed in this study.

Interpretation of earlier results on the distribution of oncaeid copepods in the western subarctic Pacific requires caution, because great numbers of sibling species in this family have been found during the past two decades (e.g. Heron 1977; Heron and Bradford-Grieve 1995; Böttger-Schnack 1999). For instance, Furuhashi (1966) and Minoda (1971) reported that *T. conifera* (as *O. conifera*) was abundant in the mesopelagic and bathypelagic zones of the western subarctic Pacific. However, sibling species of *T. conifera* were separated into eight species in the later taxonomic studies (Heron 1977; Heron and Bradford-Grieve 1995; Heron and Frost 2000). At present, *T. conifera* (Giesbrecht) is recognized as a tropical/subtropical species, being distributed in epipelagic and upper mesopelagic zones (Heron and Bradford-Grieve 1995; Böttger-Schnack 1999). Judging from the pattern of vertical distributions attributed to *T. conifera* by Furuhashi (1966) and Minoda (1971), it is probable that the specimens they identified were actually *T. canadensis* or *T. thoresoni*. Also, these authors reported *O. notopus* and *O. ornata* in their sample, but we could find only their sibling species, *O. grossa*, *O. parila*, *O. damkaeri* and *O. walleni*, and *O. englishi* in our samples from the Oyashio region.

Of the eight dominant species in the whole water column found at Site H in the Oyashio region (see "Results"), numerical information from other oceans is only available for *T. borealis*, *O. parila* and *O. lacinia*. *T. borealis* is considered to be an arctic/subarctic species (Malt 1983; Richter 1994; Kosobokova and Hirche 2000), while *O. parila* and *O. lacinia* have been reported to occur in high-latitude seas of both hemispheres (Heron et al. 1984; Heron and Bradford-Grieve 1995; Heron and Frost 2000). According to Auel and Hagen (2002), mean standing stock of *T. borealis* (as *O. borealis*) in the water stratum above 1,500 m in the central Arctic Ocean is about 6,000 inds m^{-2}, using a 0.20 mm mesh net. Unfortunately, it is difficult to directly compare our abundance data of *T. borealis* with those in Auel and Hagen (2002), because it is unclear whether their data included the abundance of immature copepodite stages of *T. borealis*. For *O. parila*, Metz (1996) noted that the abundance of total copepodite stages of this oncaeid species at 0–1,000 m in the water column in the Bellingshausen Sea, Southern Ocean, ranged from 14,200 to 27,100 inds m^{-2}, using a 0.055 mm mesh net. Since Metz (1996) also recorded the contributions of adults of *O. parila* to be about 30–65% of the abundance of total copepodite stages, it could be considered that the abundance of adults of *O. parila* obtained in this study is comparable to those in the Southern Ocean (cf. Table 2). A numerical dominance of *O. lacinia* was reported for the mesopelagic oncaeid community of the Arctic Ocean, when a net with 0.11 mm mesh was employed (Heron et al. 1984), as was recorded in the Oyashio region in this study (Table 3), though the data in Heron et al. (1984) were given as numbers of individuals per sample.

As noted above (cf. "Materials and methods" section), abundance of some oncaeid species with body lengths of <0.5 mm might be underestimated in the present study, because their greatest body width is less than the diagonal dimension (0.14 mm) of the 0.10 mm mesh net used in the present study. Despite the fact that *O. lacinia*, *Oncaea* sp. A and *Epicalymma* spp. are such small oncaeids, they predominated in the oncaeid community throughout the Oyashio region (Table 2). Numerical predominance of smaller species (body length <0.4 mm) has also been reported for the Red Sea (Böttger-Schnack 1988). To fill in the lack of quantitative information on these small oncaeid species in the Oyashio region, we have already begun collecting seasonal samples with a finer mesh net (0.060 mm mesh size) at Site H. Detailed analysis of these samples is currently in progress.

The community structure of oncaeid copepods in the Oyashio region could be differentiated into four subgroups (1a, 1b, 2a and 2b, cf. Fig. 4). Subgroup 1a is a typical shallow-water community, occurring during the period when the effect of warm Kuroshio Current is at its minimum, and it is characterized by a marked predominance (>90%) of the arctic/subarctic species *T. borealis*. In contrast, subgroup 1b was found in epipelagic and upper mesopelagic zones, when the effect of warm Kuroshio waters is evident, comprising mainly *O. media*, *O. scottodicarloi*, *O. zernovi* and *Spinoncaea* spp. Subgroup 2a is represented by *T. borealis* and the mesopelagic species *O. grossa* and *O. lacinia*, and is therefore considered a mid-water community. Subgroup 2b was restricted to lower mesopelagic or bathypelagic zones, including mesopelagic and bathypelagic species such as *O. lacinia*, *O. parila*, *O. grossa*, *T. canadensis*, *Oncaea* sp. A, *Oncaea* spp. "*tregoubovi*", *Epicalymma* spp., *O. rimula* and *O. brodskii*. High species richness and less predominance of single species also characterize this subgroup (cf. Tables 3, 4).

Standing stocks of oncaeid copepods from greater depth by using fine mesh nets (0.10 mm mesh size or less) have been reported from the western Indian Ocean (Böttger-Schnack 1995, 1996), the Mediterranean Sea (Böttger-Schnack 1997; Kršinić 1998) and the Southern Ocean (Hopkins and Torres 1988; Metz 1995, 1996). To compare the present results with these previous reports, we calculated the standing stocks of oncaeid copepods integrated over the top 1,000 m or 2,000 m of the water column in these oceanic areas. As a result, standing stocks of oncaeid copepods reported in these previous studies fall within the order of 10^5 inds m^{-2} in both water strata. In this study, standing stocks of oncaeid copepods ranged from 1.4 to 2.0×10^5 inds m^{-2} in the top 1,000 m, or from 1.5 to 2.5×10^5 inds m^{-2} in the top 2,000 m of the water column (cf. Table 2). Thus, it becomes obvious that the standing stock of oncaeid copepods in the Oyashio region is of the same order of magnitude as those of other oceans.

In addition to number, information about biomass of a particular zooplankton taxon is a basis for estimating its trophic functions in pelagic ecosystems. As a first step toward this goal, we established the relationship between dry mass (DM; µg) and total body length (TL; µm) for oncaeid copepods at Site H as: $\log_{10}DM = 2.902 \times \log_{10}TL - 8.008$ ($r=0.993$, $n=65$, $P<0.0001$; Y. Nishibe and T. Ikeda, unpublished data). From the relationship, combined with the size composition of oncaeid communities (data not shown), the biomass was calculated as 103–215 mg DM m^{-2} (grand mean: 160 mg DM m^{-2}) in the upper 2,000 m of the water column at Site H in the Oyashio region. The oncaeid biomass estimates in this study were markedly lower than those reported by Metz (1996) as 1,081 mg DM m^{-2} in the top 1,000 m of the water column in the Bellingshausen Sea, Southern Ocean. At Site H, our estimates of oncaeid copepod biomass is similar to those of the mesopelagic calanoid copepods *Pleuromamma scutullata* (66–255 mg DM m^{-2}, Yamaguchi and Ikeda 2000a), *Heterorhabdus tanneri* (71–169 mg DM m^{-2}, Yamaguchi and Ikeda 2000a) and *Gaidius variabilis* (155–351 mg DM m^{-2}, Yamaguchi and Ikeda 2000b), but is much less than those of the large calanoid copepods *Neocalanus* spp. (7,677–14,123 mg DM m^{-2}, Kobari and Ikeda 2000), *Eucalanus bungii* (1,854–3,471 mg DM m^{-2}, S. Shoden and T. Ikeda, unpublished data) and *Paraeuchaeta* spp. (393–987 mg DM m^{-2}, Yamaguchi and Ikeda 2001). In other words, the contribution of oncaeid copepod biomass to total copepod biomass is quite low in the Oyashio region, though the former outnumbers the latter. From the viewpoint that specific growth/metabolic rates increase with the decrease in body mass in copepods (Hirst and Lampitt 1998; Hopcroft et al. 1998; Ikeda et al. 2001), the possible importance of oncaeid copepods of <1 mm in body size in the energy flow/matter cycling of the pelagic ecosystem cannot be overlooked.

Acknowledgements We are grateful to Dr. R. Böttger-Schnack for her continuous support of our study and for reviewing an earlier draft; her constructive comments significantly improved the manuscript. We appreciate Dr. H. Itoh who kindly provided taxonomical information and unpublished data on oncaeid copepods around Japan. We thank Drs. A. Yamaguchi and T. Kobari who collected samples for this study, and Mr. M. Okegawa for providing the information about satellite altimetry at Site H. This work was supported partly by JSPS KAKENHI 14209001.

References

Auel H, Hagen W (2002) Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. Mar Biol 140:1013…1021

Böttger R (1987) The vertical distribution of micro- and small mesozooplankton in the central Red Sea. Biol Oceanogr 4:383…402

Böttger-Schnack R (1988) Observation on the taxonomic composition and vertical distribution of cyclopoid copepods in the central Red Sea. Hydrobiologia 167/168:311…318

Böttger-Schnack R (1990a) Community structure and vertical distribution of cyclopoid copepods in the Red Sea. I. Central Red Sea, autumn 1980. Mar Biol 106:473…485

Böttger-Schnack R (1990b) Community structure and vertical distribution of cyclopoid copepods in the Red Sea. II. Aspects of seasonal and regional differences. Mar Biol 106:487…501

Böttger-Schnack R (1994) The microcopepod fauna in the eastern Mediterranean and Arabian Seas: a comparison with the Red Sea fauna. Hydrobiologia 292/293:271…282

Böttger-Schnack R (1995) Summer distribution of micro- and small mesozooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoid copepods. Mar Ecol Prog Ser 118:81…102

Böttger-Schnack R (1996) Vertical structure of small metazoan plankton, especially non-calanoid copepods. I. Deep Arabian Sea. J Plankton Res 18:1073…1101

Böttger-Schnack R (1997) Vertical structure of small metazoan plankton, especially non-calanoid copepods. II. Deep eastern Mediterranean (Levantine Sea). Oceanol Acta 20:399…419

Böttger-Schnack R (1999) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. I. 11 species of *Triconia* gen. nov. and a redescription of *T. similis* (Sars) from Norwegian waters. Mitt Hamb Zool Mus Inst 96:37…128

Böttger-Schnack R (2001) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s. str. Bull Br Mus (Nat Hist) Zool 67:25…84

Böttger-Schnack R (2002) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. VI. Morphology and zoogeography of *Oncaea bispinosa* sp. nov., a sister taxon of *O. zernovi* Shmeleva. J Plankton Res 24:1107…1129

Böttger-Schnack R (2003) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. V. Three species of *Spinoncaea* gen. nov. (*ivlevi*-group), with notes on zoogeographical distribution. Zool J Linn Soc 137:187…226

Böttger-Schnack R, Boxshall GA (1990) Two new *Oncaea* species (Copepoda: Poecilostomatoida) from the Red Sea. J Plankton Res 12:861…871

Böttger-Schnack R, Huys R (2004) Size polymorphism in *Oncaea venusta* Philippi, 1843 and the validity of *O. frosti* Heron, 2002: a commentary. Hydrobiologia 513:1…5

Böttger-Schnack R, Hagen W, Schnack-Schiel SB (2001) The microcopepod fauna in the Gulf of Aqaba, northern Red Sea: species diversity and distribution of Oncaeidae (Poecilostomatoida). J Plankton Res 23:1029…1035

Boxshall GA (1977) The depth distributions and community organization of the planktonic cyclopoids (Crustacea: Copepoda) of the Cape Verde Islands region. J Mar Biol Assoc UK 57:543…568

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Mongr 27:325…349

Cowles TJ, Roman MR, Gauzens AL, Copley NJ (1987) Short-term changes in the biology of a warm-core ring: zooplankton biomass and grazing. Limnol Oceanogr 32:653…664

Deevey GB, Brooks AL (1977) Copepods of the Sargasso Sea off Bermuda: species composition, and vertical and seasonal distribution between the surface and 2,000 m. Bull Mar Sci 27:256…291

Furuhashi K (1966) Studies on the vertical distribution of copepods in the Oyashio region east of Japan and in the Kuroshio region south of Japan. Publ Seto Mar Biol Lab Spec Publ Ser 14:295…322

Haury L, Fey C, Gal G, Hobday A, Genin A (1995) Copepod carcasses in the ocean. I. Over seamounts. Mar Ecol Prog Ser 123:57…63

Heron GA (1977) Twenty-six species of Oncaeidae (Copepoda: Cyclopoida) from the southwest Pacific Antarctic area. In: Pawson DL (ed) Biology of the Antarctic seas. VI. Antarct Res Ser 26:37…96

Heron GA, Bradford-Grieve JM (1995) The marine fauna of New Zealand: pelagic Copepoda: Poecilostomatoida: Oncaeidae. NZ Oceanogr Inst Mem 104:1…57

Heron GA, Frost BW (2000) Copepods of the family Oncaeidae (Crustacea: Poecilostomatoida) in the northeast Pacific Ocean and inland coastal waters of Washington State. Proc Biol Soc Wash 113:1015…1063

Heron GA, English TS, Damkaer DM (1984) Arctic Ocean Copepoda of the genera *Lubbockia*, *Oncaea*, and *Epicalymma* (Poecilostomatoida: Oncaeidae), with remarks on distributions. J Crustac Biol 4:448…490

Hirst AG, Lampitt RS (1998) Towards a global model of in situ weight-specific growth in marine planktonic copepods. Mar Biol 132:247…257

Hopcroft RR, Roff JC, Webber MK, Witt JDS (1998) Zooplankton growth rates: influence of size and resources in tropical marine copepodites. Mar Biol 132:67…77

Hopkins TL, Torres JJ (1988) The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. Polar Biol 9:79…87

Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. Mar Biol 139:587…596

Kawamura A (1989) Fast sinking mouth ring for closing Norpac net. Nippon Suisan Gakkaishi 55:1121

Kobari T, Ikeda T (2000) Life cycle of *Neocalanus* species in the Oyashio region (in Japanese with English abstract). Bull Plankton Soc Jpn 47:129…135

Kosobokova K, Hirche HJ (2000) Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. Deep-Sea Res I 47:2029…2060

Krsinić F (1998) Vertical distribution of protozoan and microcopepod communities in the South Adriatic Pit. J Plankton Res 20:1033…1060

Krsinić F, Malt SJ (1985) Little known species of small Oncaeidae (Cyclopoida) from the South Adriatic. J Plankton Res 7:189…199

Mackas DL, Tsuda A (1999) Mesozooplankton in the eastern and western subarctic Pacific: community structure, seasonal life histories, and interannual variability. Prog Oceanogr 43:335…363

Malt SJ (1983) Studies on the taxonomy and ecology of the marine copepod genus *Oncaea* Philippi. PhD thesis, University of London, London

Malt SJ, Lakkis S, Ziedane R (1989) The copepod genus *Oncaea* (Poecilostomatoida) from Lebanon: taxonomic and ecological observations. J Plankton Res 11:949…969

Marlowe CJ, Miller CB (1975) Patterns of vertical distribution and migration of zooplankton at ocean station ••P••. Limnol Oceanogr 20:824…844

Metz C (1995) Seasonal variation in the distribution and abundance of *Oithona* and *Oncaea* species (Copepoda, Crustacea) in the southeastern Weddell Sea, Antarctica. Polar Biol 15:187…194

Metz C (1996) Life strategies of dominant Antarctic Oithonidae (Cyclopoida, Copepoda) and Oncaeidae (Poecilostomatoida, Copepoda) in the Bellingshausen Sea (in German with English abstract). Ber Polarforsch 207:1…123

Miller CB, Frost BW, Batchelder HP, Clemons MJ, Conway RE (1984) Life histories of large grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Paci“c. Prog Oceanogr 13:201…243

Minoda T (1971) Pelagic copepoda in the Bering Sea and the northwestern North Paci“c with special reference to their vertical distribution. Mem Fac Fish Hokkaido Univ 18:1…74

Motoda S (1959) Devices of simple plankton apparatus. Mem Fac Fish Hokkaido Univ 7:73…94

Nishiuchi K (1999) Studies on life cycle and interannual variability of chaetognaths (carnivorous zooplankton) in the northern North Paci“c (in Japanese). PhD thesis, Hokkaido University, Hakodate

Ohtani K (1971) Studies on the changes of the hydrographic conditions in the Funka Bay. II. Characteristics of the waters occupying the Funka Bay. Bull Fac Fish Hokkaido Univ 22:58…66

Olson JB [MS] (1949) The pelagic cyclopoid copepods of the coastal waters of Oregon, California and Lower California. PhD thesis, University of California, Berkeley

Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Ber Polarforsch 154:1…90

Sameoto DD (1986) In”uence of the biological and physical environment on the vertical distribution of mesozooplankton and micronekton in the eastern tropical Paci“c. Mar Biol 93:263…279

Scotto di Carlo B, Ianora A, Fresi A, Hure J (1984) Vertical zonation patterns for Mediterranean copepods from the surface to 3000 m at a “xed station in the Tyrrhenian Sea. J Plankton Res 6:1031…1056

Shmeleva AA (1969) Espèces nouvelles du genre *Oncaea* (Copepoda, Cyclopoida) de la mer Adriatique. Bull Inst Oceanogr (Monaco) 68:1…28

Tsalkina AV (1977) Vertical distribution and diurnal migrations of Cyclopoida (Copepoda) in the waters of the North Trade Winds Current and the Sulu Sea. Pol Arch Hydrobiol 24[Suppl]:337…362

Webber MK, Ro JC (1995) Annual structure of the copepod community and its associated pelagic environment o Discovery Bay, Jamaica. Mar Biol 123:467…479

Yamaguchi A, Ikeda T (2000a) Vertical distribution, life cycle and body allometry of two oceanic calanoid copepods (*Pleuromamma scutullata* and *Heterorhabdus tanneri*) in the Oyashio region, western North Paci“c Ocean. J Plankton Res 22:29…46

Yamaguchi A, Ikeda T (2000b) Vertical distribution, life cycle, and developmental characteristics of the mesopelagic calanoid copepod *Gaidius variabilis* (Aetideidae) in the Oyashio region, western North Paci“c Ocean. Mar Biol 137:99…109

Yamaguchi A, Ikeda T (2001) Abundance and population structure of three mesopelagic *Paraeuchaeta* species (Copepoda: Calanoida) in the Oyashio region, western subarctic Paci“c Ocean with notes on their carcasses and epizoic ciliates. Plankton Biol Ecol 48:104…113

Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, et al (2002) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Paci“c (WEST-COSMIC). Deep-Sea Res I 49:1007…1025