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Latitudinal Differences in the Planktonic Biomass and Community Structure Down to the Greater Depths in the Western North Pacific

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As part of the research program WEST-COSMIC Phase I (1997–2001), vertical profiles down to the greater depths (0–2000 m or 5800 m) of the plankton community structure composed of heterotrophic bacteria, phytoplankton, protozooplankton and metazooplankton were studied at one station in each subarctic (44°N) and in transitional region (39°N), and two stations in subtropical region (30°N and 25°N); all in 137–155°E in the western North Pacific Ocean. The biomass of all four taxonomic groups decreased rapidly with increasing depths at all stations, although the magnitude of depth-related decrease differed among the groups. As plankton community structure, metazooplankton biomass and bacterial biomass occupied >50% of the total in 0–2000 and 2000–4000 or 5000 m strata, respectively, at subarctic and transitional stations, while bacterial biomass contributed to >50% of the total consistently from 0 through 4800 or 5800 m at subtropical stations. Metazooplankton biomass integrated over the greater depths exhibited a clear latitudinal pattern (high north and low south), but this was not the case for those of the other taxonomic groups. As a component of metazooplankton, an appreciable contribution of diapausing copepods to the metazooplankton was noted at subarctic and transitional stations, but they were few or nil at subtropical stations. As protozooplankton assemblages, heterotrophic microflagellates (HMF) and dinoflagellates were two major components at subarctic and transitional stations, but were only HMF predominated at subtropical stations. From biomass ratios between heterotrophic bacteria, HMF and dinoflagellates, "sinking POC-DOC-heterotrophic bacteria-HMF-heterotrophic dinoflagellates" link was proposed as a microbial food chain operative in the deep layer of the western North Pacific. All results are discussed in the light of latitudinal differences in the structure and functioning of plankton community contributing to the 'biological pump' in the western North Pacific Ocean.

Keywords:
· Plankton,
· community structure,
· vertical distribution,
· mesopelagic,
· bethypelagic,
· abyssopelagic,
· biological pump,
· biogeochemical cycle.

1. Introduction

In the oceanic system, CO_2 in seawater is converted to organic matter by photosynthetic activity of phytoplankton, and enters pelagic food webs via ingestion by a wide variety of heterotrophic organisms. The transport of organic matter to the depth of the ocean is mediated by biological processes called the 'biological pump'. In the oceanic areas where the biological pump is working actively, sea surface CO_2 decreases and promotes

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the dissolution of CO_2 from the atmosphere (ocean is a sink of CO_2). The situation may be reversed when the biological pump is weak (ocean a source of CO_2) (Longhurst and Harrison, 1989). The function of the biological pump could vary from one oceanic region to another, depending on the structure of the plankton communities and abundance of the component organisms which determine the pathway of carbon through planktonic food webs, as was demonstrated in the eastern North Pacific Ocean (Booth *et al*., 1993; Boyd *et al*., 1995), western North Pacific Ocean (Shinada *et al*., 2001), equatorial Pacific Ocean (Ishizaka *et al*., 1997), subtropical Pacific Ocean (Bradford-Grieve *et al*., 1999), off Bermuda (Roman *et al*., 1995), North Sea (Nielsen *et al*., 1993), and Baltic Sea (Uitto *et al*., 1997). However, all these previous studies are concerned with plankton communities in the epipelagic zone, and comparable information about the plankton community structure in the mesopelagic and bathypelagic zones is extremely limited (cf. Yamaguchi *et al*., 2002a). From the viewpoint of global carbon cycle, the remineralization in the mid- to deep-ocean waters is a key process which governs the feedback to the biogeochemical carbon cycle. Since a significant portion (ca. 50%) of planktonic respiration occurs in the mesopelagic layer (Biddanda and Benner, 1997), information about plankton community structure at deep ocean is important to evaluate carbon cycle in the ocean.

As part of the research program "WEST-COSMIC" (Western Pacific Environment Assessment Study on CO_2 Ocean Sequestration for Mitigation of Climate Change, cf. Ishizaka, 1999) Phase 1 (1997–2001), the data gained during 1997–1999 have already been reported with special emphasis on vertical profiles down to the greater depth of plankton biomass and its taxonomic/size compositions at three stations in the western North Pacific (Yamaguchi *et al*., 2002a). These data and those obtained by subsequent cruises in 1999–2001 at a total of four stations were combined together in this study to extend our discussion to the spatial (latitudinal) variations in the vertical profiles of the plankton biomass of each taxonomic group, to taxonomic group-specific vertical profiles as a possible reflect of nutritional modes, then to the implication for 'biological pump' in the western North Pacific.

2. Methods

2.1 Sampling

Deep plankton samplings were conducted at four stations in the western North Pacific Ocean during the period of November 1997 through August 2001 (Fig. 1). The two out of the four stations (39°N, 147°E and 30°N, 147°E) were visited twice at different years (1997 and 2001 for 39°N, and 1999 and 2000 for 30°N, respectively) (Table 1).

Water samples were taken from 17 to 22 discrete depths using 12 l rosette-mounted Niskin bottles (General Oceanics) on a CTD system (Seabird SBE-9). Net zooplankton was collected from discrete depths with a modified NORPAC net (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, cf. Terazaki and Tomatsu, 1997) from deeper than 200 m depths, total number of discrete sampling depths were 6 to 10 between 0–2000 m and 0–5800 m (Table 1).

At each station, water samplings were made only once disregarding the time of the day, but net samplings were made both day and nighttime excepting for only night sampling at 39°N in 1997. Water samples for chlorophyll *a* were filtered through Whatman GF/F filters, and measured fluorometrically after the extraction with dimethyl-formamide (Suzuki and Ishimaru, 1990). Nitrate (plus nitrite) in seawater was determined using a Bran and Luebbe Auto Analyzer II, immediately after the collection.

2.2 Enumerication

Several different methods were used to enumerate and determine the size of plankton over a size-range of four orders of magnitude (0.2–2000 μm) (cf. Kiyosawa *et al*., 1995). Pico- and nanoplankton (0.2–20 μm) were

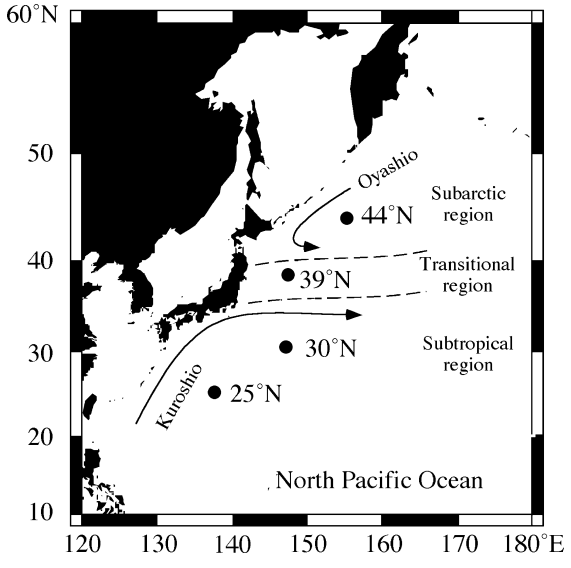

Fig. 1. Plankton sampling stations in the western North Pacific during the Phase 1 (1997–2001) of the research program "WEST-COSMIC". Current systems (arrows) and approximate positions of front and boundary (dashed lines) are also shown.

analyzed by fluorescent microscopy; water samples were filtered through 0.2 and 3 μm Nuclepore filters, preserved with glutaraldehyde or neutralized formalin and stained with DAPI and FITC (Ishizaka *et al*., 1994). Neutralized formaldehyde (final concentration: 2%) was used to preserve microplankton and mesoplankton samples. Microplankton (20–200 μm) were counted and sized under a microscope after settling 1 l water samples, or by filtering 5 l water samples through 10 μm mesh netting. Considering the water sample size (1 or 5 l) of this study, most protists were considered as 'free-living', not those associated with aggregate particles which were sparsely distributed in the oceanic water column (Ploug *et al*., 1999). While we handled water samples as gently as possible, a rapid change in hydrostatic pressure in the course of water collection from depth and preservation may have caused an underestimation of our counts of protists (cf. Patterson *et al*., 1993). For mesoplankton (>200 μm), specimens in net plankton samples were counted and sized. In the course of enumeration and sizing of each size/category of plankton, systematic characteristics of individuals were also recorded.

The size data for individual organisms were converted to biovolumes (μm^3) then carbon mass assuming appropriate geometric body shapes. The carbon mass of heterotrophic bacteria was estimated to be 0.02 pg C per cell assuming a cell diameter of 0.4 μm (Lee and Fuhrman, 1987). The biovolume-carbon factor for *Prochlorococcus* (cell diameter of 0.6 μm, assumed) and *Synechococcus* (0.9 μm, measured) was 0.47 pg C μm^{-3} (Verity *et al*., 1992). Non-diatom phytoplankton carbon was calculated from the biovolume-carbon equation defined by Verity *et al*. (1992), and the diatom carbon from the equation of Strathmann (1967). The Verity *et al*.'s (1992) equation for non-diatom phytoplankton was also used for estimating protozoan carbon. For metazooplankton, the biovolume-carbon conversion factors were 0.06 pg C μm^{-3} for non-gelatinous zooplankton, and 0.003 pg C μm^{-3} for gelatinous zooplankton (cnidarians, ctenophores and tunicates) (Parsons *et al*., 1984). In addition to size-based categories, the plankton community was divided into four large taxonomic groups (heterotrophic bacteria, phytoplankton, protozooplankton and metazooplankton) and their carbon biomass was expressed as mg C m^{-3} or mg C m^{-2} in this study. Note that *Prochlorococcus* and *Synechococcus* were categorized into phytoplankton as prochlorophytes and Cyanobacteria, respectively (cf. table 1 of Yamaguchi *et al*., 2002a).

The carbon conversion factor per cell or volume is known to vary with literature, especially for microbes. For instance, a 9-fold range of carbon conversion factors exists for the per cell of heterotrophic bacteria in the literature (cf. Carlson *et al*., 1999). Recent calculations tend to use lighter conversion factors such as 11, 35 and 100 fg C $cell^{-1}$, respectively, for heterotrophic bacteria, *Prochlorococcus* and *Synechococcus* (Landry and Kirchman, 2002). However, we used "old" conversion factors (20, 53 and 179 fg C $cell^{-1}$, respectively, for heterotrophic bacteria, *Prochlorococcus* and *Synechococcus*) to make inter-comparison with our previous results (Yamaguchi *et al*., 2002a) possible.

Table 1. Plankton sampling data in the western North Pacific during the "WEST-COSMIC" project Phase 1. The number of discrete sampling depths is shown in parentheses aside sampling layer for CTD/RMS.

Date	Day/Night	Location	Sampling layer (m)	
			CTD/RMS	Plankton net
21 Nov. 1997*	Night	39°00′ N, 147°00′ E	0–2000 (17)	0–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000
19–21 Aug. 1998*	Day/Night	44°00′ N, 155°00′ E	0–5367 (22)	0–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000, 2000–3000, 3000–4000
20–21 Sep. 1999*	Day/Night	25°00′ N, 137°00′ E	0–5011 (22)	0–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000, 2000–3000, 3000–4000, 4000–4800
4–6 Oct. 1999	Day/Night	30°00′ N, 147°00′ E	0–5800 (21)	0–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000, 2000–3000, 3000–4000, 4000–5000, 5000–5800
13–15 Oct. 2000	Day/Night	30°00′ N, 147°00′ E	0–5800 (21)	0–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000, 2000–3000, 3000–4000, 4000–5000, 5000–5800
15–18 Aug. 2001	Day/Night	39°00′ N, 147°00′ E	0–5439 (21)	0–100, 100–200, 200–300, 300–500, 500–1000, 1000–2000, 2000–3000, 3000–4000, 4000–5000

*Reported by Yamaguchi *et al*. (2002a).

3. Results

3.1 Hydrography

Across the four sampling stations, the surface temperature ranged from 13.5°C (44°N) to 29.5°C (25°N) (Fig. 2(a)). Stations were designated to those in subarctic (44°N), transitional (39°N) and subtropical (30°N and 25°N) regions. Water temperature decreased with increasing depth, and a subsurface minimum (1.9°C) was observed at 150 m at the subarctic station. Water temperature at 1000 m depth did not differ appreciably between stations (range: 2.4–3.6°C) and was almost the same below 2000 m depth (range: 1.4–2.0°C).

The vertical profile of nitrate concentrations at each station corresponded well to those of water temperature of respective stations; high nitrate was associated with low temperature (or weak thermocline) at the subarctic station (44°N), while low nitrate was seen at high temperature (or strong thermocline) at the subtropical station (30°N and 25°N; Fig. 2(b)). The transitional station (39°N) exhibited intermediate values of temperature and nitrate. Within the same station, nitrate concentration at 30°N was higher in October 2000 than that in October 1999. At 39°N station, nitrate concentration below 75 m was higher in November 1997 than that in August 2001.

Vertical profiles of chlorophyll *a* concentration could be divided into two types: one showing a near surface peak (0.71–0.76 mg m^{-3} at 30–50 m) at subarctic and transitional stations, and another showing a subsurface peak (0.24–0.31 mg m^{-3} at 90–125 m) at subtropical stations (Fig. 2(c)). At the same 39°N, the profile in November 1997 classified to the former type, and that in August 2001 to the latter type. Such marked between-year differences were not observed in the profiles in 1999 and 2000 at 30°N. Integrated mean chlorophyll *a* concentrations over the upper 200 m were 0.22 mg m^{-3} at subarctic, 0.18–0.22 mg m^{-3} at transitional and 0.10–0.12 mg m^{-3} at subtropical stations.

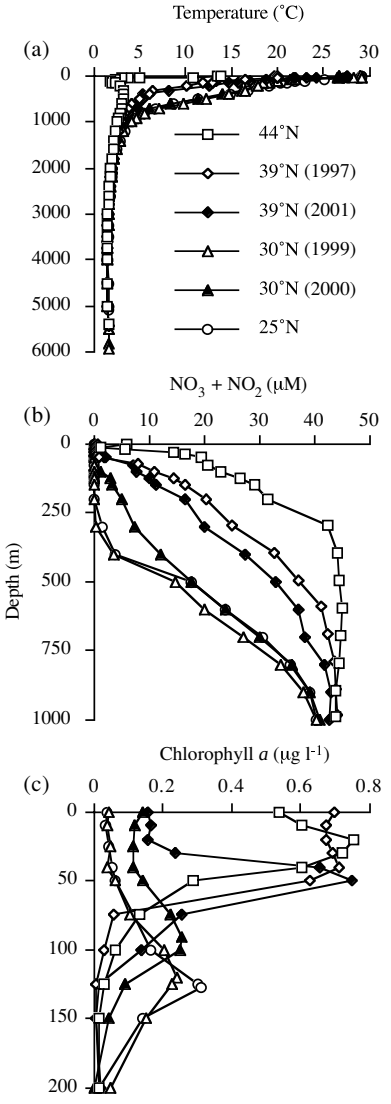

Fig. 2. Vertical profiles of temperature (a), nutrients (NO_3 + NO_2) (b), and chlorophyll *a* (c) at four stations in the western North Pacific Ocean.

3.2 Plankton biomass vs. depth

At all four stations, biomass of heterotrophic bacteria in the upper 100 m fell into a narrow range (6–20 mg C m^{-3}), and decreased exponentially with increasing depth from 100 to 1000 m (note that Fig. 3 are $\log_{10}$–$\log_{10}$ plots). Differences in biomass of heterotrophic bacteria in the 0–1000 m water column were not appreciable between stations (Fig. 3(a)). Below 1000 m depth, biomass of heterotrophic bacteria differed between stations, being highest at the subarctic station (1.2–1.8 mg C m^{-3}) and lowest at the subtropical stations (0.2–0.3 mg C m^{-3}), with intermediate at the transitional station (0.4–1.7 mg C m^{-3}).

Phytoplankton biomass in the upper 100 m depth varied greatly between stations; it was highest at the subarctic station (surface phytoplankton biomass: 114 mg C m^{-3}), followed by the transitional station (5–17 mg C m^{-3}) then the subtropical stations (1.3–4.7 mg C m^{-3}) (Fig. 3(b)). Vertical profiles of phytoplankton biomass closely paralleled those of chlorophyll *a* at each station (cf. Fig. 2(c)). The subsurface maximum of phytoplankton biomass at 90–125 m of subtropical stations corresponded well with that of chlorophyll *a*. Below 300 m, the phytoplankton biomass was <0.1 mg C m^{-3}, and decreased with increasing depth.

Protozooplankton biomass in the upper 100 m was highest at the subarctic station (maximum concentration; 63 mg C m^{-3}), followed by 39°N in 2001 (9.8 mg C m^{-3})

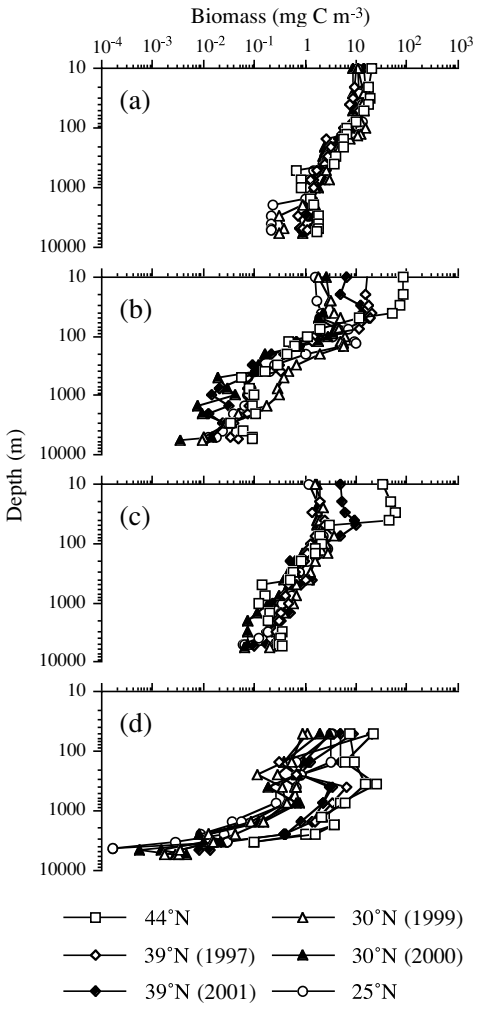

Fig. 3. Vertical distribution of plankton biomass at four stations in the western North Pacific Ocean. (a): heterotrophic bacteria, (b): phytoplankton, (c): protozooplankton, (d): metazooplankton.

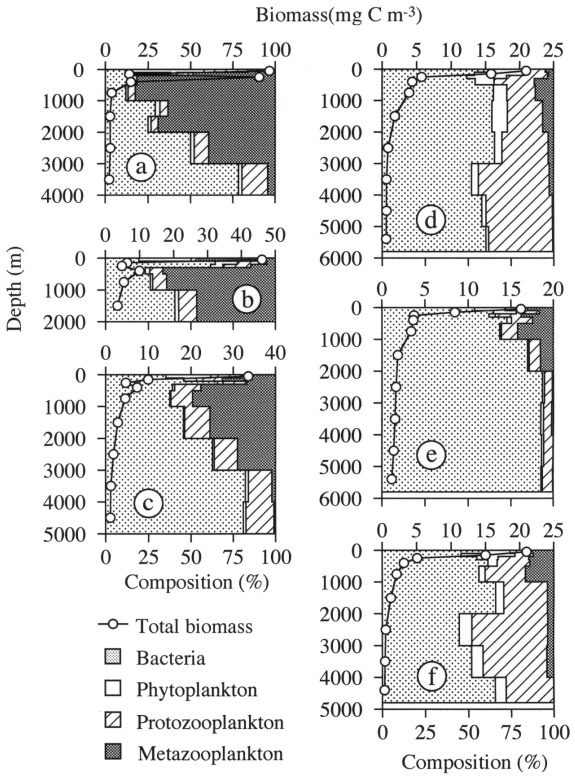

Fig. 4. Vertical distribution of total plankton biomass and its major taxonomic composition at four stations in the western North Pacific Ocean. (a): 44°N, (b): 39°N (1997), (c): 39°N (2001), (d): 30°N (1999), (e): 30°N (2000), (f): 25°N.

then the other stations (2.3–3.6 mg C m^{-3}) (Fig. 3(c)). Between 100 and 5000 m, protozooplankton biomass decreased with increasing depth. The protozooplankton biomass at the subarctic station was nearly the same to those in the 100–400 m depth range of the other stations, but showed a much lower value between 500 and 2000 m or a much higher value between 3000 and 5367 m.

Metazooplankton biomass varied greatly with location: highest at subarctic station and lowest at subtropical station, with intermediate at transitional station (Fig. 3(d)). Regional differences in biomass were marked for metazooplankton but not for the other taxonomic groups. At all stations, differences in the vertical distribution patterns of metazooplankton biomass between day and night were not significant (Kolmogorov-Smirnov two-sample test: $p > 0.05$). Vertical distribution patterns of metazooplankton biomass at subarctic and subtropical stations never overlapped. Vertical profiles of metazooplankton biomass at the transitional station (39°N) were similar to those at subtropical stations between 0 and 300 m depth, while the profiles were similar to those at the subarctic station below 500 m depths. Interestingly, vertical profiles of metazooplankton exhibited a marked sub-minimum at 100–200 m or 200–300 m at most of the stations, irrespective of day or night. The between-year variations in biomass profiles of the four taxonomic groups of metazooplankton at 30°N (sampled in October of 1999 and 2000) and at 39°N (November 1997 and August 2001) fell well within the range of between-station variations (Fig. 3).

For the comparison of the biomass (B) pattern declining with depth (Z), the biomass data for heterotrophic bacteria, phytoplankton, protozooplankton and metazooplankton at the four stations were pooled for each group and fitted to the regression model: $B = B_{100}[Z/100]^b$, where B_{100} was the biomass at 100 m depth, and b is constant (cf. Yamaguchi *et al.*, 2002a) (Table 2). As judged by correlation coefficients, the better fit to the regression

Table 2. Summary of biomass decreasing rate (b) with depth for planktonic taxa. Regression statistics: $B = B_{100}[Z/100]^b$, where B, B_{100} and Z are biomass in mg C m^{-3}, biomass at 100 m and depth in m. In this calculation, B shallower than 100 m depth was omitted. All the regressions are highly significant ($p < 0.0001$).

Taxa	N	Slope (b)	95% CI	r^2
Heterotrophic Bacteria	88	–0.627	(–0.712~–0.541)	0.71
Phytoplankton	88	–1.204	(–1.363~–1.044)	0.72
Protozooplankton	88	–0.651	(–0.731~–0.570)	0.75
Metazooplankton	87	–1.613	(–1.950~–1.275)	0.51

Table 3. Comparison of planktonic standing stocks integrated over the water column. Bacteria: heterotrophic bacteria, Phyto: phytoplankton, Proto: protozooplankton, Meta: metazooplankton.

Location	Date	Depth (m)	Standing stocks (mg C m^{-2})				
			Bacteria	Phyto	Proto	Meta	Total
44°N, 155°E	19–21 Aug. 1998	0–4000	8,084	4,136	3,635	13,917 (D)	29,772 (D)
		0–4000				16,965 (N)	
39°N, 147°E	21 Nov. 1997	0–2000	4,182†	1,701†	1,142†	6,849† (N)	13,873† (N)
	15–18 Aug. 2001	0–5000	7,661	1,089	2,374	4,661 (D)	15,785 (D)
		0–5000				4,063 (N)	
30°N, 147°E	4–6 Oct. 1999	0–5800	7,026	1,513	2,496	745 (D)	11,780 (D)
		0–5800				549 (N)	
	13–15 Oct. 2000	0–5800	9,867	526	1,022	816 (D)	12,231 (D)
		0–5800				1,144 (N)	
25°N, 137°E	20–21 Sep. 1999	0–4800	4,702	1,117	1,622	1,192 (D)	8,633 (D)
		0–4800				738 (N)	
Grand $\overline{X}$			7,468	1,676	2,230	4,479	15,640
SD			1,872	1,419	987	5,999	8,297
N			5	5	5	10	5
CV (= SD / $\overline{X}$, %)			25.1	84.7	44.3	133.9	53.0
Correlation coefficients for [$\log_{10}$ Standing stock] vs. [Latitude]			0.494^{NS}	0.656^{NS}	0.712^{NS}	0.930**	0.961**

(D): day, (N): night.
†Omitted from the calculations, NS: not significant, **: $p < 0.01$.

model was seen for the biomass data of heterotrophic bacteria, phytoplankton and protozooplankton ($r^2 > 0.71$) as compared with those of metazooplankton ($r^2 = 0.51$). Comparison of the slopes (b) of the regression lines revealed that the decrease in biomass with increasing depth was most rapid for metazooplankton, slowest for heterotrophic bacteria and protozooplankton, with phytoplankton being intermediate (Table 2, Fig. 3).

3.3 Plankton community structure vs. depth

The vertical profile of the entire plankton community structure as viewed from the composition of the four major taxonomic groups was markedly different between subarctic-transitional stations (Figs. 4(a)–(c)) and subtropical stations (Figs. 4(d)–(f)). At 39°N station in the transitional region, samplings were made in November 1997 (Fig. 4(b)) and August 2001 (Fig. 4(c)), but no appreciable differences in the community composition in the top 2000 m of the water column were observed. At these subarctic and transitional stations, heterotrophic bacteria and metazooplankton were the most dominant groups. The contribution of metazooplankton to the total plankton biomass was greatest in the 200–1000 m depth range (ca. 80%), and decreased with increasing depth. On the other hand, the contribution of heterotrophic bacteria to total plankton biomass increased with increasing depth, reaching its maximum in the deepest layer (3000–4000 m, ca. 80%) (Figs. 4(a)–(c)).

At subtropical stations, heterotrophic bacteria and protozooplankton, instead of metazooplankton, were the

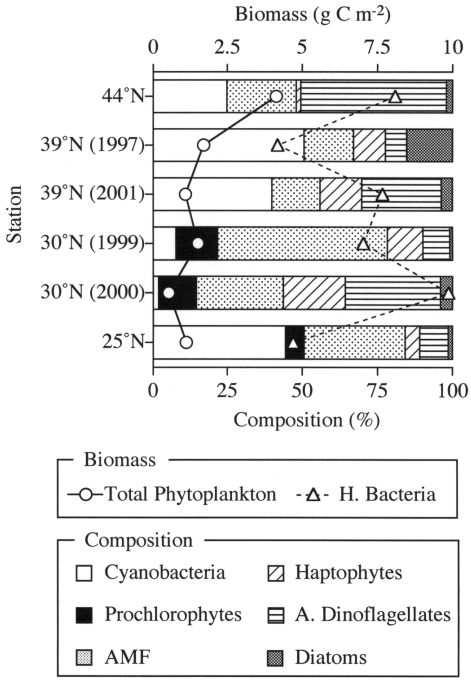

Fig. 5. Water-column integrated biomasses of phytoplankton and heterotrophic bacteria and taxonomic compositions of phytoplankton in each sampling station. AMF: autotrophic microflagellates, A.: autotrophic.

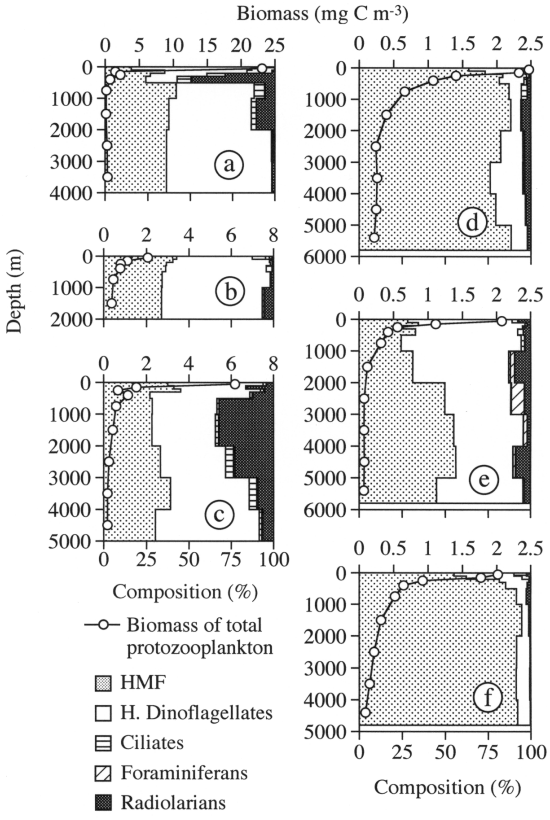

Fig. 6. Vertical distribution of protozooplankton biomass and its taxonomic composition at four stations in the western North Pacific Ocean. HMF: heterotrophic microflagellates, H.: heterotrophic. (a): 44°N, (b): 39°N (1997), (c): 39°N (2001), (d): 30°N (1999), (e): 30°N (2000), (f): 25°N.

most important groups contributing to the total plankton biomass (Figs. 4(d)–(f)). The relative importance of these two groups did not change greatly with depth. In the entire water column, heterotrophic bacteria and protozooplankton contributed ca. 60% and 20%, respectively, of total plankton biomass. Within the same station (30°N), relative composition of heterotrophic bacteria and protozooplankton varied with the year studied; heterotrophic bacteria predominated (ca. 80%) in October 2000 (Fig. 4(e)) but it did not in October 1999 (Fig. 4(d)).

3.4 Plankton biomass vs. latitude

Latitudinal variations in plankton biomass of the four taxonomic groups were analyzed by calculating integrated biomass of each taxonomic group over the great depth (Table 3). In this calculation, the data sets collected in November 1997 at 39°N were omitted because the maximum depth sampled (2000 m) was much shallower than that in the other samplings (4000–5800 m), and because the sampling season was more advanced (November) as compared with other samplings (August–October). From grand mean biomass across the four stations thus computed for each taxonomic group, the most important group contributing to the total plankton biomass was heterotrophic bacteria (47.1%), followed by metazooplankton (28.2%), protozooplankton (14.1%) and phytoplankton (10.6%). Between-station variation, as judged by coefficient of variation (CV, %), was greatest in metazooplankton (134%), followed by phytoplankton (84.7%), protozooplankton (44.3%) and bacteria (25.1%) (Table 3). Standing stock of each taxonomic group, transformed to the logarithm (base 10), was regressed on the latitudes. As a result, significant correlation was found only for metazooplankton biomass ($p < 0.01$). This result may be due to the greater degree of freedom for metazooplankton data sets as collected both day and night at given stations (N = 10), as compared with those of the other taxonomic groups which were sampled only during day time at each station (N = 5), but the result remained unchanged when the day and night data of metazooplankton were combined and its means (i.e. N = 5) were used for the calculation of correlation coefficients ($r = 0.935$, $p < 0.05$). Thus, a latitudinal biomass pattern characterized by progressive decline toward southern latitudes was confirmed only for metazooplankton.

Table 4. Metazooplankton biomass and their taxonomic composition at each depth layer of four stations in the western North Pacific Ocean. For copepods, composition of "diapausing copepods" (=*Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri* and *Eucalanus bungii* distributed below 200 m depths) were shown in the parentheses. Values of total water columns were shown in *italic* letters. Chaeto: Chaetognaths.

Depth	Biomass	Taxonomic composition (%)				Biomass	Taxonomic composition (%)			
(m)	(mg C m^{-3})	Copepods	Chaeto	Cnidarians	Others	(mg C m^{-3})	Copepods	Chaeto	Cnidarians	Others
	44°N, 155°E (1998, day)					44°N, 155°E (1998, night)				
0–100	7.53	71 (0)	17	6	6	21.82	79 (0)	15	1	6
100–200	9.27	53 (0)	38	7	2	5.91	70 (0)	24	3	3
200–300	45.98	76 (28)	15	2	8	76.87	77 (27)	19	2	2
300–500	15.61	87 (8)	8	0	3	11.81	81 (16)	15	0	3
500–1000	2.09	85 (29)	9	0	5	2.38	82 (45)	14	1	3
1000–2000	1.84	76 (67)	23	0	1	1.86	73 (51)	19	0	7
2000–3000	1.53	40 (12)	58	0	2	0.99	39 (24)	57	0	4
3000–4000	0.10	79 (0)	6	9	6	0.10	55 (0)	2	6	37
0–4000	*3.48*	*73 (23)*	*20*	*1*	*5*	*4.24*	*75 (25)*	*20*	*1*	*4*
	39°N, 147°E (1997, night)									
0–100	20.87	26 (0)	13	43	18					
100–200	0.31	85 (0)	6	6	3					
200–300	0.69	37 (0)	40	18	4					
300–500	6.59	18 (1)	42	39	1					
500–1000	3.45	32 (5)	44	20	4					
1000–2000	1.62	49 (6)	16	33	2					
0–2000	*3.42*	*32 (3)*	*27*	*34*	*7*					
	39°N, 147°E (2001, day)					39°N, 147°E (2001, night)				
0–100	4.981	27 (0)	66	0	6	8.412	78 (0)	12	3	7
100–200	4.976	27 (0)	66	0	6	1.286	42 (0)	22	0	36
200–300	0.822	30 (9)	65	0	5	0.753	26 (8)	71	0	4
300–500	3.466	69 (19)	17	1	14	3.043	75 (36)	23	0	2
500–1000	2.227	82 (51)	16	0	2	2.235	79 (64)	17	1	3
1000–2000	1.354	83 (55)	14	0	3	0.835	89 (56)	9	0	2
2000–3000	0.385	76 (55)	18	0	6	0.421	80 (56)	18	0	2
3000–4000	0.029	93 (25)	2	3	3	0.022	57 (0)	2	0	41
4000–5000	0.008	90 (0)	0	0	10	0.013	69 (0)	4	0	26
0–5000	*0.932*	*67 (36)*	*27*	*0*	*5*	*0.813*	*78 (40)*	*17*	*1*	*4*

3.5 Components of each taxonomic group

As a component of phytoplankton biomass, prochlorophytes distributed only in the south of 30°N (Fig. 5). At most of the stations, pico- to nano-size fractions (Cyanobacteria, prochlorophytes and autotrophic microflagellates [AMF]) were dominated in phytoplankton community. However, the pico- to nano-size fractions were the least at 30°N in 2000 (<50% of total phytoplankton biomass), which were caused by the dominance of large-sized haptophytes and autotrophic dinoflagellates (Fig. 5).

In the subarctic and transitional stations (44°N and 39°N), heterotrophic microflagellates (HMF) and heterotrophic dinoflagellates were two major components of protozooplankton biomass, occupying near similar proportions throughout the water column (Figs. 6(a)–(c)). Radiolarians made up the third dominant group in the subarctic and transitional stations. In contrast, only HMF predominated (ca. 80% of total protozoa biomass) throughout the water column in the subtropical stations (30°N in 1999 and 25°N) (Figs. 6(d) and (f)). At 30°N station, protozooplankton assemblages were different between 1999 (Fig. 6(d)) and 2000 (Fig. 6(e)), as was observed for overall planktonic community structure and phytoplankton assemblages (Figs. 4 and 5) mentioned above. Protozooplankton assemblages at 30°N station was dominated by HMF and heterotrophic dinoflagellates in 2000 (Fig. 6(e)), a feature that was similar to that at the subarctic stations rather than that at the subtropical stations.

Table 4. (continued).

Depth	Biomass	Taxonomic composition (%)				Biomass	Taxonomic composition (%)			
(m)	(mg C m^{-3})	Copepods	Chaeto	Cnidarians	Others	(mg C m^{-3})	Copepods	Chaeto	Cnidarians	Others
	30°N, 147°E (1999, day)					30°N, 147°E (1999, night)				
0–100	0.885	60 (0)	20	2	17	1.123	77 (0)	6	1	15
100–200	0.550	78 (0)	6	1	15	0.367	69 (0)	12	2	17
200–300	0.288	50 (0)	30	2	19	0.114	72 (0)	6	1	21
300–500	0.674	65 (0)	23	0	12	0.349	28 (0)	62	1	9
500–1000	0.440	65 (0)	25	1	10	0.398	71 (0)	17	3	10
1000–2000	0.154	60 (2)	36	0	4	0.087	83 (8)	13	0	4
2000–3000	0.043	76 (0)	22	0	2	0.012	84 (0)	5	6	5
3000–4000	0.016	90 (0)	5	4	1	0.014	98 (0)	2	0	0
4000–5000	0.004	93 (0)	0	1	7	0.003	94 (0)	0	0	6
5000–5800	0.002	65 (0)	3	2	29	0.003	95 (0)	1	1	4
0–5800	*0.128*	*65 (0)*	*24*	*1*	*10*	*0.095*	*70 (1)*	*18*	*2*	*10*
	30°N, 147°E (2000, day)					30°N, 147°E (2000, night)				
0–100	1.949	35 (0)	49	3	14	2.890	29 (0)	48	3	21
100–200	0.388	28 (0)	62	1	8	0.938	29 (0)	12	0	59
200–300	0.659	40 (0)	53	0	7	0.741	13 (0)	24	0	63
300–500	0.186	55 (0)	9	1	35	0.643	14 (0)	52	2	33
500–1000	0.648	59 (1)	23	1	18	0.752	43 (6)	47	1	9
1000–2000	0.122	55 (14)	40	0	5	0.155	67 (27)	24	1	8
2000–3000	0.008	29 (0)	59	4	8	0.013	88 (0)	4	1	6
3000–4000	0.022	7 (0)	1	1	92	0.010	53 (0)	2	5	40
4000–5000	0.001	22 (0)	0	5	73	0.001	70 (0)	1	13	17
5000–5800	0.003	21 (0)	2	0	77	0.004	80 (0)	17	0	3
0–5800	*0.141*	*48 (2)*	*35*	*1*	*17*	*0.197*	*37 (6)*	*39*	*1*	*22*
	25°N, 137°E (day)					25°N, 137°E (night)				
0–100	3.1866	16 (0)	5	71	9	3.4962	25 (0)	2	56	17
100–200	3.2531	10 (0)	14	72	4	0.6680	13 (0)	18	65	4
200–300	0.8376	16 (0)	46	25	14	0.6801	13 (0)	73	2	13
300–500	0.6793	29 (0)	33	23	15	0.2672	23 (0)	31	22	24
500–1000	0.4661	66 (0)	11	1	22	0.2711	21 (0)	20	45	15
1000–2000	0.0564	55 (0)	16	27	2	0.0360	30 (0)	2	66	2
2000–3000	0.0088	96 (0)	0	0	3	0.0253	80 (0)	17	2	1
3000–4000	0.0302	6 (0)	0	94	0	0.0029	69 (0)	0	24	8
4000–4800	0.0002	98 (0)	0	0	2	0.0002	23 (0)	68	0	8
0–4800	*0.2484*	*28 (0)*	*15*	*47*	*10*	*0.1537*	*24 (0)*	*16*	*46*	*14*

Metazooplankton biomass were predominated by copepods (mostly >50%), followed by chaetognaths (>15%) or often by cnidarians and showed a clear north to south differences (Table 4). In the subarctic and transitional stations (44°N and 39°N), diapausing copepods (such as *Neocalanus* species) were dominated at meso- to bathypelagic layers (200–3000 m) (Table 4). The diapausing copepods also occurred at 30°N station in small quantities but did not at 25°N station. The rapid/irregular changes in the community structure below 3000 m depth (such as 30°N in 2000 and 25°N) might be due to very low abundance of metazooplankton.

4. Discussion

4.1 Latitude vs. water column plankton biomass

From sediment trap experiments, the ratio of the organic carbon flux in the deep sea to surface primary productivity in the western subarctic Pacific has been reported to be much higher than the other oceanic regions (cf. Honda *et al.*, 2002). Because of increased organic matter supply to the depth, it is anticipated that plankton biomass in the entire water column in the subarctic regions would be greater as compared with those at transitional and subtropical regions. Our simultaneous estima-

tion of integrated biomass over the greater depth of heterotrophic bacteria, phytoplankton, protozooplankton and metazooplankton at the four stations located at 25°–44°N in the western North Pacific showed a significant latitudinal effect (a reduction toward south), which was seen in metazooplankon, but not in the other three taxonomic groups mentioned above (Table 3).

Since the present field sampling was limited once per year at four stations, and only two out of four stations were visited twice, the observed differences between the four stations are attributed not only by dissimilar latitudes but also by the season or the year sampled. Our classification of subarctic (44°N station, cf. Fig. 1), transitional (39°N station) and subtropical regions (30°N and 25°N stations) of this study corresponds to "Pacific Subarctic Gyres (PSAG)", "Kuroshio Current Province (KURO)", and "North Pacific Tropical Gyre Province (NPTG)", respectively, of ecological province proposed by Longhurst (1998). Because of physical forcing of biological processes, which differs one province to the next, spring phytoplankton bloom, followed by zooplankton biomass peak in early summer, are annual events pronounced in PSAG and moderately pronounced in KURO, but these are not the case in NPTG (Longhurst, 1998). It is noted however that the seasonal variations in plankton biomass and its community structure referred in the past are largely on those occurring in shallow layers, and only limited information is currently available for plankton in mesopelagic and bathypelagic zones of the ocean.

Tanaka and Rassoulzadegan (2002) studied depth profile of microbial biomasses down to 2000 m depth at a station (43°25.2′ N) in the NW Mediterranean Sea monthly over one year. According to their results, the range of seasonal variations in the biomass integrated over the water column were one order magnitude for heterotrophic bacteria, two orders of magnitude for heterotrophic nanoflagellates (HNF), and three orders of magnitude for ciliates. Assuming that interannual variations are negligible and the seasonal variations in the present stations in the western North Pacific are similar order to those in the NW Mediterranean Sea mentioned above, the effect of slightly different sampling seasons on the heterotrophic bacteria and protozooplankton biomass between the four stations (August, September or October cf. Table 3) of this study would be not appreciable. In subarctic and transitional regions of this study, annual peaks of phytoplankton and metazooplankton are considered to occur largely in April–June (Odate, 1994; Imai *et al*., 2002; Kobari *et al*., 2003), thereby the present data collected in August–October represent a transient phase from these peaks to winter minimum. The decrease in metazooplankton biomass (mostly composed of *Neocalanus* copepods) from the peak season is due to sinking to depth (500–2000 or 3000 m, cf. Table 4), where they enter in diapause and reproduction (as discussed below). It is noted that the bulk of these interzonal copepods, which disappear from the upper layer, is captured in our sampling from greater depths, thereby our sampling, if continued throughout the year, would show an extremely reduced seasonal variation pattern of metazooplankton biomass (Kobari *et al*., 2003) as compared with those having been reported from shallow layer samplings in the subarctic region (Odate, 1994). Apart from North Pacific, seasonal differences (April vs. August) in vertical profiles of metazooplankton biomass down to 4000 m have been examined at a station in NE Atlantic (Koppelmann and Weikert, 1999). According to the results of Koppelmann and Weikert (1999), who observed some seasonal differences in the biomass depending on the depth intervals, the entire biomasses (0–4000 m) in April and August were similar to each other.

Combining all these results by previous workers, we consider that the effects of different sampling seasons at the four stations located in subarctic, transitional and subtropical regions in this study, would vary relatively small as compared with the effect of latitudes (or ecological province, cf. Longhurst, 1998). Incidentally, our data at 30°N in October 1999 and October 2000 (Table 3) suggest possible between-year variations in plankton biomass at an oceanic station, but the order of its magnitude (less than ×3) is too small to affect to the between-latitude variations (×30). Recent studies have revealed that the interannual variations in pelagic ecosystems are a consequence of climate changes of various time scales (for subtropical region of this study, see Nakata and Hidaka, 2003).

Our conclusion of the latitudial pattern in metazooplankton biomass is consistent with that of Vinogradov (1968, figure 55), who mapped metazooplankton biomass data down to greater depths from 60°N to 60°S in the Pacific Ocean. Other than metazooplankton, heterotrophic bacterial biomass data down to 4000 or 5000 m depth at stations in tropical through subarctic North Pacific (0° to 57°N) region were reported by Nagata *et al*. (2000). While the data compiled by Nagata *et al*. (2000) were those collected during different seasons of dissimilar years, a latitudinal pattern of higher biomass (integrated over 1000–4000 m) at stations in higher latitudes was observed in contrast to our results. These contradictory results may partly be explained by narrower latitudinal coverage of this study (25–44°N) as compared with that Nagata *et al*.'s (0–57°N), e.g. the pattern was masked by the scatter of data of each station in this study.

4.2 Latitude vs. community structure

Despite the fact that the latitudinal effects were seen in integrated biomass over the greater depth sampled of

metazooplankton only, as described above, the taxonomic composition of plankton assemblages and components of each taxonomic group changed greatly from subarctic to subtropical stations. Yamaguchi *et al*. (2002a) have noted the phenomena based on preliminary data of WEST-COSMIC Phase I.

Firstly, the dominant taxonomic group was heterotrophic bacteria and metazooplankton in the subarctic and transitional stations, while it was heterotrophic bacteria and protozooplankton in the subtropical stations (Fig. 4). At subarctic and transitional stations, the relative composition of metazooplankton in the total plankton peaked at mesopelagic layer (200–1000 m) then heterotrophic bacteria increased its proportion with increasing depth (Figs. 4(a)–(c)). Secondary, HMF and heterotrophic dinoflagellates were the two predominant components of protozooplankton assemblages in the subarctic and transitional stations, while only HMF predominated in protozooplankton assemblages in the subtropical stations (Fig. 6). Thirdly, diapausing copepods dominated in metazooplankton assemblages at meso- to bathypelagic layer (200–3000 m) of subarctic and transitional station, while they were absent in the southernmost station (Table 4).

Among these latitudinal differences in plankton community structure, the first (metazooplankton dominated in subarctic and transitional station) is related to the third (diapausing copepods dominated in metazooplankton at subarctic and transitional station). This is because metazooplankton at subarctic and transitional stations includes dormant stages of large grazing copepods (*Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri* and *Eucalanus bungii*), all characterized by ceased feeding, lowered metabolism and a large accumulation of lipids in their body (Miller *et al*., 1984; Kobari and Ikeda, 1999). These copepods grow rapidly to pre-adult stages in the upper layers during the productive spring-early summer season and sink to the meso- or bathypelagic zone in mid- or late summer for transforming into adults and entering reproduction. Vinogradov and Arashkevich (1969) noted that composition of dormant copepods to mesozooplankton biomass was the largest upper 2000 m and their composition decreased rapidly below 2000 m in the western subarctic Pacific. In the present data, the maximum contribution of these dormant copepods to the total plankton biomass was 46% at 1500–2000 m at 44°N, but only 4% at 1000–2000 m at 30°N, near the southern edge of the normal distribution range of these cold-water copepods. No diapausing copepods were detected at 25°N. Diapausing copepods have been reported to be transported southward by submerged Oyashio current, of which the density is higher than that of the warm Kuroshio current (Omori, 1967). This explains why the vertical profiles of metazooplankton biomass at transitional station (39°N) was characterized by a subtropical feature (lower biomass) in the epipelagic layer, but by a subarctic feature (higher biomass) below the mesopelagic layer (Fig. 3(d)).

Not only the integrated biomass over the greater depth discussed above, the components of metazooplankton may also be altered by the season studied. In the subarctic and transitional regions, the present study season (August–November) corresponds to the period when all diapausing copepods nearly or totally completed migration from the surface layer to mesopelatic/bathypelagic zones (Miller *et al*., 1984). Thus, the present data of the relative proportion of dormant copepods (contributed 23–25% of the metazooplankton biomass at 44°N station, Table 4) may represent an annual maximum value. According to Vinogradov and Arashkevich (1969), the interzonal copepods contributed as high as 57–92% of mesozooplankton biomass at Kurile-Kamchatka region in July–August. Since some dormant copepods are known to continue reproduction throughout the year (Kobari and Ikeda, 1999), the high proportion of dormant copepods in the total metazooplankton biomass may remain throughout the year in the subarctic and transitional regions.

4.3 Microbial loop in deep sea

Microbial loop such as "the sinking POC-DOC-heterotrophic bacteria-HMF-ciliates" has been considered in the aphotic layer in the NW Mediterranean Sea (Tanaka and Rassoulzadegan, 2002). A close relationship between heterotrophic bacteria biomass and protozooplankton biomass has been found in the western North Pacific (cf. figure 6 of Yamaguchi *et al*., 2002a). Taking into account that the proportion of ciliates was lower than that of the heterotrophic dinoflagellates in the present study (Fig. 6), the Tanaka and Rassoulzadegan's microbial schema can be modified as "the sinking POC-DOC-heterotrophic bacteria-HMF-heterotrophic dinoflagellates" in the deep sea of the western North Pacific.

In the present study, biomass ratios between heterotrophic bacteria: HMF: heterotrophic Dinoflagellates showed clear north and south differences (Table 5). High heterotrophic bacteria: HMF ratios (5.0–16.2) throughout the water column in the subarctic and transitional stations indicate favorable food condition for HMF at that region. High heterotrophic dinoflagellates: HMF ratio (1.1–1.8) at these stations implies that high nutrition supply to the deep supports enough energy transfer to reach the heterotrophic dinoflagellates there. In the subtropical stations, low heterotrophic bacteria: HMF ratio (1.8–8.9) and heterotrophic dinoflagellates: HMF ratio (0.1–0.6) were the case except for 30°N in 2000 (Table 5). In addition, heterotrophic bacteria: HMF ratio in these subtropical stations decreased with increasing depth. These facts indicate that nutrient condition of HMF are severe at sub-

Table 5. Ratios of biomass between heterotrophic bacteria: heterotrophic microfragellates (HMF): heterotrophic dinoflagellates at different depth strata and geographical location. Ratios were calculated based on the biomass of HMF as 1. Depth strata were integrated into four depths: epipelagic (0–200 m), mesopelagic (200–1000 m), bathypelagic (1000–3000 m) and abyssopelagic (>3000 m). nd: no data.

Depth strata	44°N	39°N (1997)	39°N (2001)	30°N (1999)	30°N (2000)	25°N
Epipelagic	5.0:1:4.3	9.8:1:1.2	5.5:1:1.4	6.7:1:0.4	14.2:1:2.0	8.9:1:0.6
Mesopelagic	16.2:1:1.1	9.1:1:1.8	10.0:1:1.6	3.5:1:0.1	22.9:1:2.5	3.1:1:0.1
Bathypelagic	16.0:1:1.5	11.3:1:1.8	12.0:1:1.3	3.3:1:0.1	40.5:1:1.3	2.1:1:0.1
Abyssopelagic	14.3:1:1.7	nd	15.6:1:1.6	1.8:1:0.2	32.8:1:0.8	1.9:1:0.1

tropical region especially in the deep layer. As compared with subarctic regions, lower POC flux to deep sea at subtropical region (cf. Honda *et al*., 2002) is considered as a cause of predominance of HMF in protozooplankton community at that region (Figs. 6(d) and (f)). Limited nutrition in the subtropical region and long the pathway of "sinking POC-DOC-heterotrophic bacteria-HMF-heterotrophic dinoflagellates" may imply that the energy reaching heterotrophic dinoflagellates is very few.

4.4 "Biological pump"; an implication

The pattern of decline in planktonic biomass with increasing depth was expressed by a straight line on $\log_{10}$–$\log_{10}$ graph, omitting data from <100 m depth (Fig. 3), as was attempted by Yamaguchi *et al*. (2002a) and confirmed with larger data sets in this study (Table 2). The greater of negative slope values (*b*) indicate a more rapid decrease in biomass with increasing depth. Among the slopes of the four taxa compared, the slowest decline seen in heterotrophic bacteria (Table 2) may be interpreted by the limitation of nutrient (DOC) supply that is not severe throughout the water column as compared with other taxonomic groups. Protozooplankton feeds on heterotrophic bacteria so that their biomasses decrease toward greater depth with moderate slope. In contrast, phytoplankton biomass decreased most rapidly with depth because of light limitation. Since several trophic levels are needed for the nutrient (started as DOC) to reach metazooplankton, the rapid reduction in metazooplankton biomass is suggestive of food limitation which becomes severe progressively toward greater depth. As a special feature detected in the general biomass decline with depth, biomass sub-minimum was observed in the vertical profiles of metazooplankton at 100–300 m depth (Fig. 3(d)), which has been known as the effects of cold intermediate water in the western North Pacific (Vinogradov, 1968).

Judging by the slope of depth-related decline in biomass, heterotrophic bacteria and protozooplankton are in parallel, but metazooplankton decreases more rapidly than these two taxa do (Fig. 3, Table 2), suggesting that the above mentioned food chain (sinking POC-DOC-heterotrophic bacteria-HMF-heterotrophic dinoflagellates) cannot supply enough nutrition for metazooplankton at greater depth. Since metazooplankton biomass in meso- and bathypelagic zones has already been demonstrated to be correlated with those of the epipelagic zone across the world's oceans (cf. Vinogradov, 1968), sinking fecal pellets egested by metazooplankton from the upper layers may be an another source of food supply to the deep metazooplankton. Sasaki *et al*. (1988) and Yamaguchi *et al*. (2002b) have evaluated this process called "repacking" and concluded that a 32–38% of gravity POC flux is consumed by calanoid copepods distributing between 0–1000 m or 0–4000 m water column in the western North Pacific. According to the recent review by Koppelmann *et al*. (2004), POC consumption by metazooplankton in the 1000–4000 m water column has been estimated as 4–23% in the oceanic regions of the world oceans.

From the viewpoint of biological pump, dominance of dormant copepods in meso- and bathypelagic zones at the subarctic station (Table 4) is of special interest. Dormant copepods do not feed, instead they are eaten by deep-sea pelagic carnivores such as micronektonic fish (Beamish *et al*., 1999). Since these copepods are primary grazers grown in the upper layers, they are an integral component of deep-water communities as a link between particulate carbon produced photosynthetically in the surface layer and nutrition of deep-water communities. This export carbon flux mediated by ontogenetic vertical migration of *Neocalanus* spp. in the subarctic Pacific (*N. cristatus*, *N. plumchrus* and *N. flemingeri*) and in the subantarctic waters (*N. tonsus*) has been estimated to be similar to or larger than the sedimentary passive flux at 1000 m (Bradford-Grieve *et al*., 2001; Kobari *et al*., 2003).

Compared with subarctic and subantarctic regions, the schema of zooplankton-mediated active carbon flux to the deep in subtropical and tropical regions is completely different. Because of the lack of ontogenetic vertical migrating zooplankton (for subtropical regions, see Table 4), organic materials ingested in the surface layer, that is then defecated or assimilated (subsequently excreted as CO_2) at depth by 'diel' migrating zooplankton and micronekton, are important agents of active transport of carbon vertically in the subtropical and tropical

region (Longhurst *et al*., 1990; Dam *et al*., 1995; Hidaka *et al*., 2001; Al-Mutairi and Landry, 2001). Such active carbon flux by 'diel' vertical migrators has been estimated to be ca. 20–25% for zooplankton (Dam *et al*., 1995; Al-Mutairi and Landry, 2001) and 28–55% for micronekton (Hidaka *et al*., 2001) of the passive carbon flux out of the euphotic zone.

Carbon pathways within epipelagic plankton communities at selected regions have been analyzed by combining the abundance of trophically grouped organisms with their consumption-production rates, the latter being estimated from empirical body size-rates relationships. Compared with epipelagic plankton, physiological data presently available for those living in meso- and bathypelagic zones are scarce, so that the validity of the direct application of epipelagic data to deep-sea plankton organisms is questionable. The metabolism of most fish and crustacean micronekton living in the deep sea appears to be greatly reduced compared with shallow-living counterparts (see review of Childress, 1995). For the paucity of physiological data for heterotrophic bacteria and protozooplankton living at greater depths of the ocean, see Nagata *et al*. (2000, 2001) and Cho *et al*. (2000), respectively. For deep-sea metazooplankton, extensive information is now available for the metabolism of copepods (Thuesen *et al*., 1998), but such information is quite limited for non-copepod metazooplankton taxa. Clearly, there is an urgent need for the collection of appropriate biological and physiological data, together with biomass data over various time scales (seasonal, annual), on planktonic organisms living at greater depths in the world's oceans to deepen our understanding about nature and functions of the biological pump operating at global scales.

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