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Biomass and chemical composition of net-plankton down to greater depths (0–5800 m) in the western North Pacific Ocean

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Abstract

As part of the research program Western Pacific Environment Study on CO_2 Ocean Sequestration for Mitigation of Climate Change (WEST-COSMIC), plankton sampling was carried out down to great depths (maximum: 5800 m) at four stations (44°N, 155°E; 39°N, 147°E; 30°N, 147°E and 25°N, 137°E) located in the western North Pacific Ocean. Ranges of plankton standing stock integrated over the water columns were wet mass (WM) 22–256 g m^{-2}, dry mass (DM) 1.3–27.4 g m^{-2}, carbon (C) 0.4–12.3 g C m^{-2}, nitrogen (N) 0.10–2.44 g N m^{-2}, ash (ash) 0.43–4.35 g m^{-2}, ash-free dry mass (AFDM) 0.9–21.8 g m^{-2} and energy 20–582 kJ m^{-2}. Log-linear equations were computed to allow interconversions among measurements in different mass units. Plankton mass was greater at higher latitudes. At each station, plankton mass decreased exponentially with increasing depth. This decrease was greater at subarctic (44°N) and subtropical (30°N and 25°N) stations than that at the transitional station (39°N) due to high amounts of diapausing copepods in meso- and bathypelagic depths at the latter station. Water content (% of WM), C:N ratios and ash (% of DM) increased with increasing depth, while C, N, AFDM (% of DM) and energy contents (J mg^{-1} DM) showed an opposite pattern. Extremely low C (24–25% of DM), N (3.2–4.4% of DM), AFDM (48–56% of DM) and energy contents (10–12 J mg^{-1} DM), accompanied by high C:N ratios (5.7–8.0 by weight), of plankton samples from depths below 3000 m suggest possible dominance of detritus in samples from that layer. The overall effect of detritus in measuring chemical composition of plankton samples is discussed.

Keywords: Abyssopelagic zone; Bathypelagic zone; Biochemical composition; Detritus; Energy; Zooplankton

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1. Introduction

For quantitative evaluation of the function of the biological pump in the ocean, deep-sea metazooplankton biomass must be estimated (Angel, 1989). Biomass of metazooplankton has been studied mainly in neritic regions and epipelagic zones of the ocean, while little work has been done on deep-sea metazooplankton because of logistic and technical difficulties in collecting them from deeper zones. Studies on the biomass of metazooplankton in meso- and bathypelagic zones before 1990 include those in the North Pacific Ocean (Vinogradov, 1968; Murano et al., 1976; Kikuchi and Omori, 1985; Sameoto, 1986), North Atlantic Ocean (Grice and Hülsemann, 1965; Angel and Baker, 1982; Roe, 1988), Indian Ocean (Vinogradov, 1968), Mediterranean Sea (Scotto di Carlo et al., 1984), off Bermuda (Deevey and Brooks, 1971), and Red Sea (Weikert, 1982). During the last two decades, the development of new sampling gears, such as the RMT 1+8 (Roe and Shale, 1979), BIONESS (Sameoto et al., 1980) and MOCNESS (Wiebe et al., 1985) has enabled the easy and precise sampling of metazooplankton at meso- and bathypelagic depths. As a result, our knowledge has advanced rapidly (Wiebe et al., 1988; Weikert and Trinkaus, 1990; Koppelmann and Weikert, 1992, 1997, 1999; Koppelmann, 1994; Böttger-Schnack, 1996; Yamaguchi et al., 2002a, b). Nevertheless, most of the previous determinations of metazooplankton biomass have been expressed as wet mass, so little is yet known about its chemical composition. Full understanding of trophodynamics and biogeochemical cycles in the ocean will require information about plankton biomass and its chemical composition at various depths of the ocean.

In the present study, we investigate deep-sea net-plankton mass (wet, dry, carbon and nitrogen, ash and ash-free dry masses) and energy density down to 5800 m at four stations in the western North Pacific Ocean. Vertical profiles of chemical composition of plankton are established and plankton masses are expressed as a function of depth. Observed patterns of chemical composition and energy content of plankton with depth and latitude are discussed in light of the taxonomic composition of zooplankton and detritus in the samples.

2. Material and methods

As part of the research program (Western Pacific Environment Assessment Study on CO_2 Ocean Sequestration for Mitigation of Climate Change WEST-COSMIC; cf. Ishizaka, 1999), a total of 13 plankton samplings to great depths was made at four stations (44°N, 155°E; 39°N, 147°E; 30°N, 147°E and 25°N, 137°E, Fig. 1) in the western North Pacific Ocean during August to October of 1998–2001 (Table 1). Plankton was collected from 0–100 and 100–200 m with closing NORPAC nets (mouth opening 0.16 m^2, cf. Motoda, 1957), and with Vertical Multiple Plankton Sampler (VMPS, mouth opening 1.0 m^2, Tsurumi Seiki Co. Ltd., cf. Terazaki and Tomatsu, 1997) from >200 m depth. Mesh size of both nets was 90 μm and towing speeds were 1.0 m s^{-1}. A flowmeter (Rigosha Co. Ltd.) was mounted in the mouth of the net to register the volume of water passed through the net. Most of the filtration efficiencies calculated were greater than 90%. After net retrieval, any large (>2 cm) animals

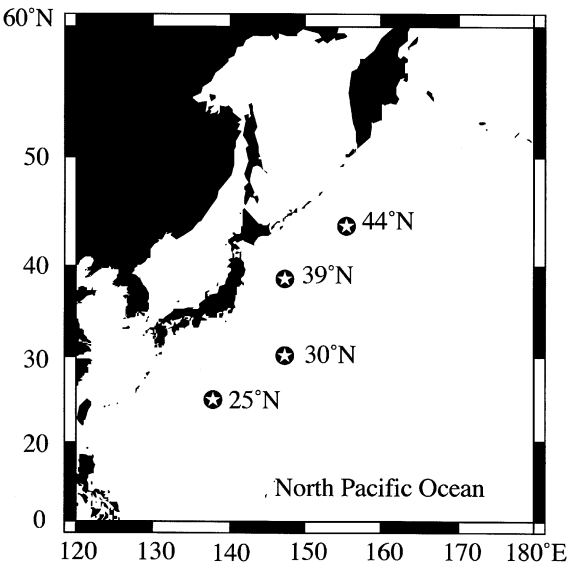

Fig. 1. Location of sampling stations in the western North Pacific Ocean.

Table 1
Plankton sampling data in the western North Pacific

Date	Day/Night	Location	Sampling layer (m)	Cast code	Ash measurement
19 Aug. 1998	Day	44°00′N, 155°00′E	0–4000 (9)	44N-1	
19 Aug. 1998	Night	44°00′N, 155°00′E	0–4000 (9)	44N-2	●
25 Sep. 2000	Night	44°00′N, 155°00′E	0–5000 (10)	44N-3	
15 Aug. 2001	Night	39°00′N, 147°00′E	0–5000 (9)	39N-1	●
16 Aug. 2001	Day	39°00′N, 147°00′E	0–5000 (8)	39N-2	
17 Aug. 2001	Night	39°00′N, 147°00′E	0–5000 (9)	39N-3	
18 Aug. 2001	Day	39°00′N, 147°00′E	0–5000 (8)	39N-4	
4 Oct. 1999	Day	30°00′N, 147°00′E	0–5800 (10)	30N-1	
5–6 Oct. 1999	Night	30°00′N, 147°00′E	0–5800 (10)	30N-2	●
15 Oct. 2000	Day	30°00′N, 147°00′E	0–5800 (10)	30N-3	
13–14 Oct. 2000	Night	30°00′N, 147°00′E	0–5800 (10)	30N-4	
21 Sep. 1999	Day	25°00′N, 137°00′E	0–4800 (9)	25N-1	●
20 Sep. 1999	Night	25°00′N, 137°00′E	0–4800 (9)	25N-2	

The number of discrete sampling depths is shown in parentheses aside sampling layer. Note that WM, DM, C and N were determined on all samples, while ash was determined on marked samples only.

were removed (and not determined mass) the remaining samples were split with a Motoda splitting device (Motoda, 1959). A $\frac{1}{2}$ aliquot of the samples was preserved in 5% formalin–seawater buffered with borax for later microscopic observations, and the remaining $\frac{1}{2}$ aliquot was filtered through preweighed pieces of 50 μm mesh net under vacuum. Samples were then briefly rinsed with distilled water while still under vacuum, wrapped with aluminum foil, placed into sealed plastic bags, and stored in a deep freezer (−80 °C).

In the land laboratory, frozen samples were weighed (wet mass WM) and then freeze-dried to obtain dry mass (DM). Water content in the samples was calculated from the difference between WM and DM, and expressed as a percentage of WM. Dried samples were ground into a fine powder with a ceramic mortar and pestle and used for analyses of carbon and nitrogen (Yanaco CHN Corder). Selecting one cast from those made at each sampling station (see Table 1), a weighed fraction of each sample was incinerated at 480 °C for 5 h and reweighed for ash determination (ash), and ash-free dry mass (AFDM) fraction was calculated (AFDM = DM−ash). The energy content was calculated by using a formulae given by Gnaiger (1983), amended by Gnaiger and Shick (1985): $J = 66.265W_C + 4.436W_N - 11.2$, where J is an energy content in J mg^{-1} AFDM, and W_C and W_N are fractions of C and N, respectively, on an AFDM basis.

3. Results

3.1. Hydrography

Temperature profiles in the upper 1000 m varied among sampling stations (Fig. 2A). The profile at 44°N station was the coldest on average (integrated mean temperature of 0–1000 m was 3.1 °C) and these means increased gradually toward the south: 12.4 °C at 30°N and 13.2 °C at 25°N. Below 1000 m depth, there was little temperature difference among stations and all profiles showed a slight decrease from ca. 3.0 °C at 1000 m to 1.6 °C at 5800 m. Salinity profiles differed also in the upper 1000 m (Fig. 2B) across stations. Salinity was the lowest at the 44°N station (integrated mean 0–1000 m salinity was 33.9). Salinities were highest at the 25°N and 30°N stations (both had integrated mean salinity of 34.5), followed by that (34.2) at the 39°N station. Below 1000 m, among-station differences in salinities were small, with a slight increase from ca. 34.3 at 1000 m to 34.7 at 5800 m. From temperature and salinity profiles in the upper 1000 m, the stations were divided into

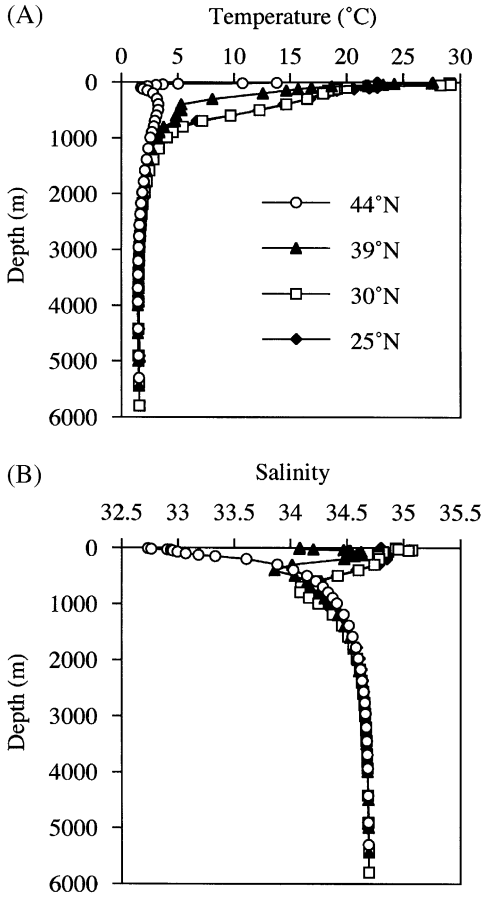

Fig. 2. (A) Temperature and (B) salinity profiles at sampling stations in the western North Pacific Ocean.

three groups: the subarctic station (44°N) characterized by lower temperature and salinity, the subtropical stations (25°N and 30°N) with higher temperature and salinity, and the transitional station (39°N) with intermediate temperature and salinity.

3.2. Biomass

Plankton mass expressed as WM, DM, C, N, ash, AFDM or energy density decreased exponentially with increasing depth at all the stations. This reduction in biomass from shallow to great depth was 3–4 orders of magnitude (Fig. 3). The highest biomass throughout the entire water column was observed at the subarctic station (44°N) with 18.9–27.4 g DM m^{-2}, and the lowest biomass was detected at the subtropical stations (25°N and 30°N) with 1.3–2.1 g DM m^{-2} (Table 2). At the transitional station (39°N), the standing stock of 5.9–7.5 g DM m^{-2} fell between those of the subarctic and subtropical stations in the upper 1000 m, but was similar to that at the subarctic station below 1000 m (Fig. 3).

Day vs. night differences in bathymetric distributions of plankton mass (DM) were evident within the same station (Table 2). The percentage of the total DM integrated over 0 to >3000 m that was captured in the epipelagic zone (0–200 m) was greater at night than in the daytime at most of the stations with exceptions of casts 44N-2 and 30N-3 (Table 2). The percentage in the bathypelagic zone (1000–3000 m) at the transitional station (39°N) was anomalously high (36–45%) compared to that at the other stations (8–24%). Among the other stations, the fraction of biomass in the bathypelagic zone was higher at the subarctic station and lower at the subtropical stations, especially at the southernmost station.

The consistent pattern of decrease in plankton masses (Y: mg m^{-3}) with increasing depth (Z: m), was fitted station-by-station to the equation: $\log_{10} Y = a - b \times Z$, where a and b are fitting constants (Table 3). The resultant equations were all significant ($p<0.01$), as judged by the correlation coefficients between the two parameters (Y and Z). Within stations, the slopes (b) calculated using various units showed that the nitrogen yielded the greatest value (Table 3), indicating that nitrogen decreases more rapidly than the other mass constituents with increasing depth. Inter-station comparison showed that the slopes (b) of the equation were the least at 39°N (b: $3.5–5.1 \times 10^{-4}$) and 30°N ($3.5–5.5 \times 10^{-4}$).

All measures of plankton biomass, including WM, DM, C, N, ash, AFDM and energy, were highly correlated with each other ($p<0.0001$) (Table 4).

3.3. Chemical composition

The overall ranges of the chemical composition and energy content of plankton samples were

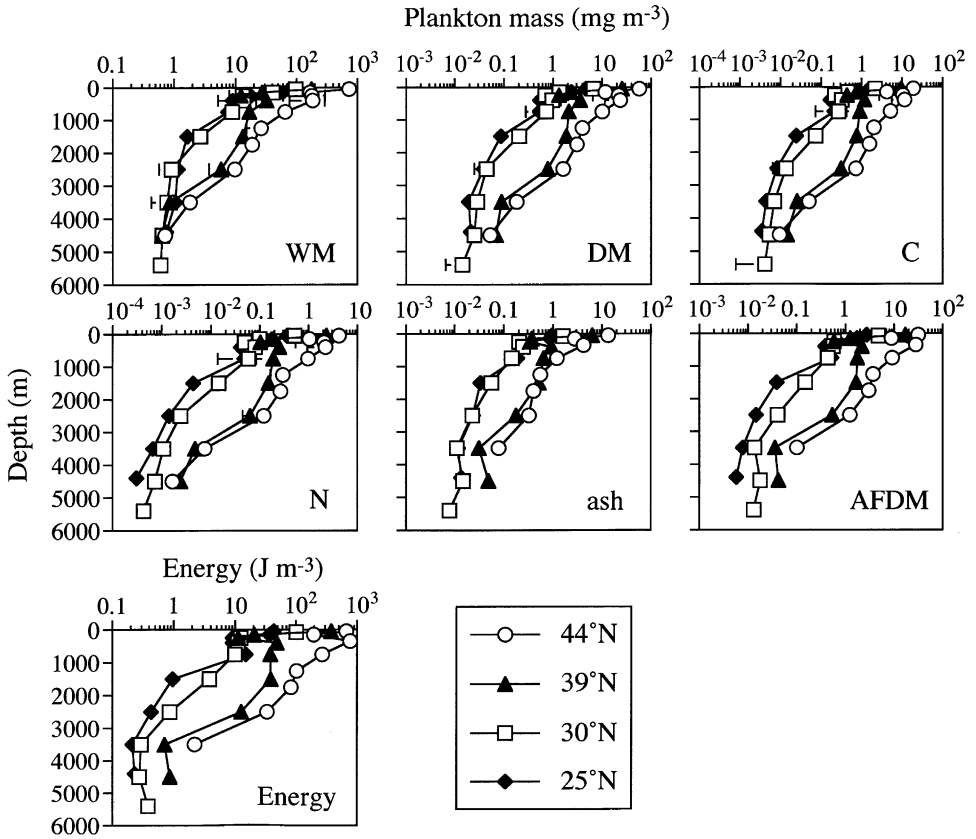

Fig. 3. Vertical distributions of plankton mass in terms of (*top*) wet mass (WM), dry mass (DM), carbon (C), (*middle*) nitrogen (N), ash (ash), ash-free dry mass (AFDM), and (*bottom*) energy density ($J\,m^{-3}$) at each station in the western North Pacific Ocean. Bars indicate standard deviations. Note that the *X*-axis ($mg\,m^{-3}$ or $J\,m^{-3}$) is on log-scales (base 10).

Table 2
Bathymetric distribution of fractions (%) of plankton mass standing stock integrated over the water column (for cast code, see Table 1)

Cast code (Day/night)	%				Standing stock ($g\,DM\,m^{-2}$)
	Epipelagic	Mesopelagic	Bathypelagic	Abyssopelagic	
44N-1 (D)	21.7	53.5	23.9	0.9	27.4
44N-2 (N)	21.6	57.0	20.7	0.7	26.2
44N-3 (N)	48.6	32.8	17.7	0.8	18.9
39N-1 (N)	33.4	25.7	38.7	2.1	7.47
39N-2 (D)	12.8	42.9	41.8	2.5	5.88
39N-3 (N)	44.8	16.0	36.2	3.0	6.92
39N-4 (D)	18.2	34.3	45.3	2.1	5.86
30N-1 (D)	28.1	46.9	20.6	4.4	1.45
30N-2 (N)	46.1	32.6	16.7	4.6	1.62
30N-3 (D)	52.2	34.6	10.0	3.2	1.78
30N-4 (N)	54.1	31.6	11.6	2.7	2.07
25N-1 (D)	46.7	42.4	8.3	2.6	1.35
25N-2 (N)	59.5	26.9	10.8	2.9	1.31

Note: Epipelagic: 0–200 m, Mesopelagic: 200–1000 m, Bathypelagic: 1000–3000 m, Abyssopelagic: >3000 m.

Table 3
Slopes (b) of regression lines of biomass (Y: WM, DM, C, N, ash, AFDM in mg m^{-3} and energy in J m^{-3}) on depth (Z: m) for each cast

Cast code	Slope (b)						
	WM	DM	C	N	Ash	AFDM	Energy
44N-1	6.6×10^{-4}	5.7×10^{-4}	5.8×10^{-4}	6.2×10^{-4}			
44N-2	6.6×10^{-4}	6.2×10^{-4}	6.5×10^{-4}	7.3×10^{-4}	5.4×10^{-4}	6.3×10^{-4}	6.3×10^{-4}
44N-3	5.4×10^{-4}	5.8×10^{-4}	6.5×10^{-4}	6.6×10^{-4}			
39N-1	4.2×10^{-4}	4.1×10^{-4}	4.4×10^{-4}	4.7×10^{-4}	3.5×10^{-4}	4.4×10^{-4}	4.4×10^{-4}
39N-2	4.0×10^{-4}	4.7×10^{-4}	5.0×10^{-4}	5.1×10^{-4}			
39N-3	3.8×10^{-4}	3.7×10^{-4}	4.2×10^{-4}	4.5×10^{-4}			
39N-4	4.1×10^{-4}	4.4×10^{-4}	4.8×10^{-4}	5.0×10^{-4}			
30N-1	4.1×10^{-4}	4.4×10^{-4}	4.7×10^{-4}	5.2×10^{-4}			
30N-2	3.6×10^{-4}	3.9×10^{-4}	4.2×10^{-4}	5.0×10^{-4}	3.5×10^{-4}	4.2×10^{-4}	4.1×10^{-4}
30N-3	3.6×10^{-4}	4.5×10^{-4}	5.1×10^{-4}	5.5×10^{-4}			
30N-4	3.8×10^{-4}	4.8×10^{-4}	5.0×10^{-4}	5.4×10^{-4}			
25N-1	4.3×10^{-4}	5.2×10^{-4}	5.6×10^{-4}	6.3×10^{-4}	4.2×10^{-4}	6.1×10^{-4}	5.4×10^{-4}
25N-2	4.1×10^{-4}	5.0×10^{-4}	5.9×10^{-4}	6.9×10^{-4}			

Regression model: $\log_{10} Y = a - b \times Z$. Note that ash, AFDM and energy were investigated in four casts only. For cast code, see Table 1. All the regressions were significant at $p<0.01$.

Table 4
Interrelationships between various measures of mass and energy of plankton samples in the western North Pacific Ocean (regression model: $\mathrm{Log}_{10}\, Y=a+b\times\log 10\, X$, where Y and X are in mg m^{-3} for mass or in J m^{-3} for energy, a and b are fitted constants)

		Intercept	Slope			
Y	X	a	b	(95% CI)	r^2	N
DM	WM	−1.22	1.11	(1.06–1.17)	0.93	117
C	WM	−1.79	1.20	(1.13–1.27)	0.91	117
N	WM	−2.57	1.26	(1.19–1.34)	0.91	117
Ash	WM	−1.65	0.95	(0.87–1.03)	0.94	35
AFDM	WM	−1.55	1.20	(1.08–1.32)	0.92	35
Energy	WM	−0.18	1.18	(1.05–1.31)	0.91	35
C	DM	−0.47	1.09	(1.07–1.11)	0.99	117
N	DM	−1.18	1.14	(1.12–1.17)	0.99	117
Ash	DM	−0.56	0.84	(0.80–0.89)	0.98	35
AFDM	DM	−0.17	1.08	(1.06–1.11)	1.00	35
Energy	DM	1.18	1.07	(1.03–1.11)	0.99	35
N	C	−0.69	1.05	(1.03–1.06)	0.99	117
Ash	C	−0.20	0.77	(0.71–0.83)	0.95	35
AFDM	C	0.29	1.01	(0.98–1.03)	1.00	35
Energy	C	1.64	1.00	(0.98–1.01)	1.00	35
Ash	N	0.30	0.72	(0.67–0.78)	0.95	35
AFDM	N	0.94	0.94	(0.90–0.97)	0.99	35
Energy	N	2.28	0.93	(0.89–0.97)	0.99	35
AFDM	ash	0.51	1.24	(1.15–1.34)	0.96	35
Energy	ash	1.86	1.23	(1.13–1.33)	0.95	35
Energy	AFDM	1.35	0.99	(0.96–1.02)	0.99	35

In this calculation, differences in depths and locations were disregarded. Note that all the regressions are highly significant ($p<0.0001$). Range of masses (all in mg m^{-3}): WM: 0.4–773, DM: 0.006–83, C: 0.002–30, N: 0.0002–6.6, ash: 0.008–13, AFDM: 0.006–31. Range of energy: 0.2–774 J m^{-3}.

82–98% water of WM, 18–51% C of DM, 1.6–9.6% N of DM, 11–70% ash of DM, 30–89% AFDM of DM and 8.4–25.9 J mg^{-1} DM for energy content (Fig. 4). The C:N ratio (on a weight basis) varied from 4.0 to 11.8. Water content of plankton at 30°N and 25°N was markedly higher than at 44°N and 39°N. It decreased with increasing depth to 2000 or 3000 m then increased again at the two more northerly stations, but it increased downward rather monotonously at the two more southerly ones (Fig. 4). The vertical profiles of C and N content mirror the profile of water content. The C and N contents at 44°N and 39°N were higher than those at 30°N and 25°N. With increasing depth, the C and N contents (% of DM) showed more or less marked peaks at 1000–2000 m depth at all stations (Fig. 4), then decreased steadily downward (apart from a slight rise at >5000 m at 30°N). The C:N ratios increased with depth at all stations without showing appreciable between-station variations. Since both C and N content decreased with increasing depth, the consistent increase of C:N ratios with depth implies the reduction in N contents is more rapid than that of C content (cf. Table 3). The patterns of ash content with increasing depth resembled those of water content (Fig. 4). More water implies greater salt content and, thus, more ash. AFDM content mirrored ash content (AFDM = DM−ash) or C

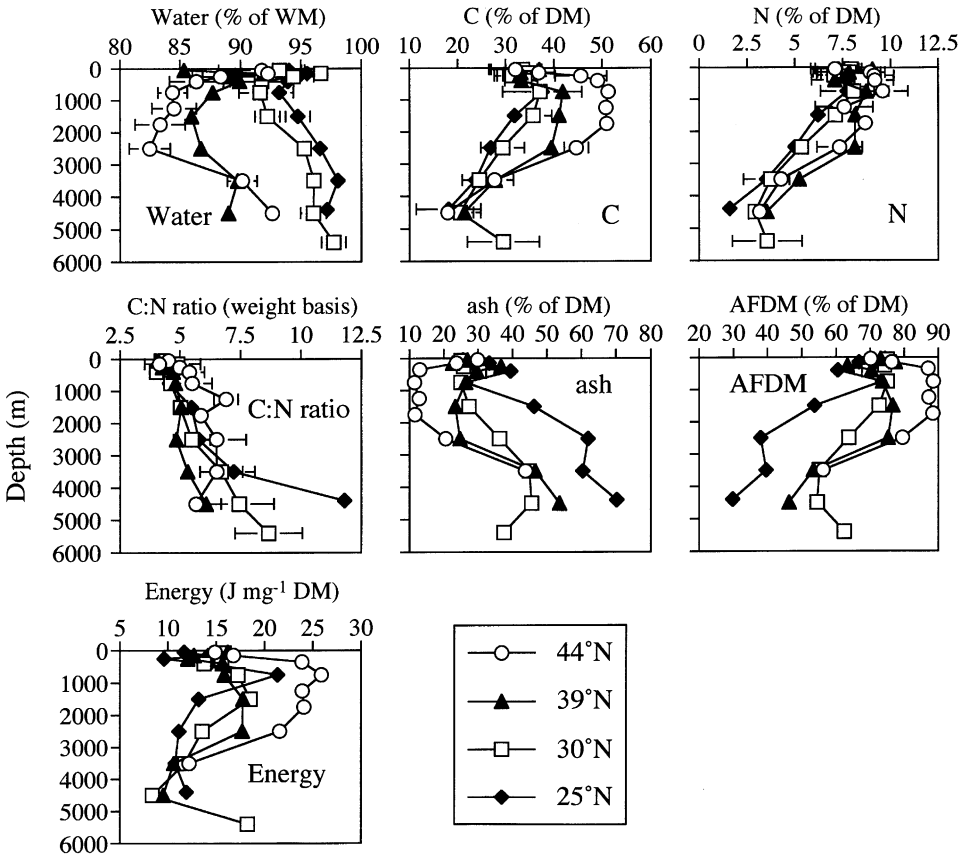

Fig. 4. Vertical distribution of chemical composition and energy contents of plankton in terms of (*top*) water content (% of WM), C (% of DM), N (% of DM), (*middle*) C:N ratio (weight basis), ash (% of DM), AFDM (% of DM) and (*bottom*) energy content (J mg^{-1} DM) at each station in the western North Pacific Ocean. Bars indicate standard deviations.

content (as the major component of AFDM) and thus decreased with increasing depth (Fig. 4). Samples from 200 to 2000 m at 44°N had markedly high AFDM (ca. 88% of DM). Vertical profiles of energy content of plankton materials paralleled those of AFDM or C content simply because these two components are the input terms of the energy content calculations. Common to all the stations, energy content peaked in the meso- to bathypelagic zone (200–3000 m), and rapidly decreased with or without recovery in the abyssopelagic zone (>3000 m). These depth-related changes in chemical composition and energy content at stations in subarctic (44°N), transitional (39°N) and subtropical (30°N and 25°N) regions are summarized in Table 5, designating the depths of sampling as epipelagic (0–200 m), mesopelagic (200–1000 m), bathypelagic (1000–3000 m) and abyssopelagic zones (>3000 m).

4. Discussion

4.1. Plankton mass versus depth

The decrease of plankton mass with increasing depth was fitted to an exponential model in this study (Table 3). Two models have been proposed for the depth-related reduction in zooplankton biomass below 1000 m depth. One is an exponential model applied by Vinogradov (1968), $\log_{10} Y = a - b \times Z$, where Y is zooplankton biomass, Z is depth, and a and b are fitted constants, and the other is a power model applied by Koppelmann and Weikert (1992), $Y = a' \times Z^{b'}$ or $\log_{10} Y = a' + b' \times \log_{10} Z$, where a' and b' are fitted constants. Koppelmann and Weikert reported that bathypelagic zooplankton biomass data were better fitted by the power model than by the exponential model. In the present study, we applied the exponential model to the plankton mass data not only from >1000 m depth but over the whole water column. As mentioned above, this is because the sample size below 1000 m depth was small in this study. Despite this difference in the kind of data incorporated, the results showed that the data from all casts are fitted well by the model (Table 3). We also applied the same data sets on the power regression model and found values significantly lower than for the exponential model (all $p<0.01$ in the case of the exponential model, but in only 51 out of 64 cases for the power model). Thus, the exponential model is superior to the power model to express depth-related changes in plankton mass in the present study. The choice of the model may depend on the kind of data. For example, numerical data for copepods throughout the water column (0–4000 m) in the subarctic Pacific were fit best by the power model, while their biomass data were fit better by the exponential model (Yamaguchi et al., 2002a).

In the exponential model described above, the constant b denotes the magnitude of the reduction of zooplankton biomass with increasing depth. Vinogradov (1968) noted that b determined in tropical regions (Marianas and Bougainville trenches) was constant ($b = 8.5 \times 10^{-4}$), and higher than in the subarctic regions (Kurile-Kamchatka trench, $b = 6.5 \times 10^{-4}$). In the present study, the b value at 39°N was less than at stations to either the north or south. This result for 39°N is due to the greater bathypelagic biomass at that station (Table 2), which was caused by the occurrence of large calanoid copepods (subarctic species such as *Neocalanus* spp. and *Eucalanus bungii*) in diapause (for details see Table 4 of Yamaguchi et al., 2004). Life cycles of these copepods are characterized by a long diapause phase in deep layers (cf. Miller et al., 1984), and their diapausing stages are known to be transported to subtropical latitudes by the submerging Oyashio current (Omori, 1967; Omori and Tanaka, 1967). The southern limit of their occurrence has been seen to extend to 28°N, 134°E (Omori, 1967). Higher standing stocks (plankton mass integrated throughout the water column) at northern stations in this study may be related in part to the southward transport of these copepods. The latitudinal change in standing stocks is appreciable for mesozooplankton, but not for pico-sized heterotrophic bacteria. Over the 19° of latitude covered in our study, the depth-integrated standing stocks of net-plankton changed 21-fold (27.4/1.3 mg DM m^{-2}, Table 2) as compared with only 4-fold for the whole (pico to meso size) plankton biomass (Yamaguchi et al., 2002b, 2004).

Table 5
Summary of chemical composition and energy content data in Fig. 4, classifying the stations into subarctic (44°N), transitional (39°N) and subtropical (30 and 25°N), then the data sets into epipelagic (0–200 m), mesopelagic (200–1000 m), bathypelagic (1000–3000 m) and abyssopelagic (>3000 m) zones

Region Depth zone	Water (% of WM)	C (% of DM)	N (% of DM)	C:N ratio (weight base)	AFDM (% of DM)	Energy contents (J mg^{-1} DM)
Subarctic						
Epipelagic	92.0±2.6 (6)	34.5±4.5 (6)	8.02±1.29 (6)	4.33±0.30 (6)	73.2±4.4 (2)	15.8±1.3 (2)
Mesopelagic	86.4±2.3 (9)	48.7±3.8 (9)	9.30±1.38 (9)	5.30±0.65 (9)	87.8±1.1 (3)	24.9±1.4 (3)
Bathypelagic	83.4±5.1 (9)	48.8±3.4 (9)	7.86±1.47 (9)	6.43±1.41 (9)	85.0±4.9 (3)	23.2±1.4 (3)
Abyssopelagic	90.8±1.6 (4)	25.3±4.9 (4)	4.00±0.69 (4)	6.31±0.71 (4)	56.2 (1)	12.2 (1)
Transitional						
Epipelagic	87.3±4.6 (6)	34.2±2.5 (6)	7.71±1.95 (6)	4.70±1.3 (6)	75.3±3.1 (2)	14.5±2.4 (2)
Mesopelagic	88.9±2.9 (12)	36.0±7.1 (12)	7.84±1.55 (12)	4.60±0.33 (12)	69.1±5.3 (3)	14.5±2.1 (3)
Bathypelagic	86.4±0.8 (8)	40.3±1.5 (8)	8.14±0.28 (8)	4.96±0.18 (8)	75.9±0.9 (2)	17.7±0.1 (2)
Abyssopelagic	89.4±0.7 (8)	24.7±4.8 (8)	4.38±1.04 (8)	5.70±0.63 (8)	49.9±5.0 (2)	10.1±0.8 (2)
Subtropical						
Epipelagic	94.9±1.7 (12)	34.0±3.7 (12)	7.79±1.48 (12)	4.51±0.59 (12)	72.6±3.9 (4)	14.3±1.9 (4)
Mesopelagic	93.1±2.0 (18)	33.8±4.0 (18)	7.76±1.07 (18)	4.39±0.32 (18)	70.7±6.1 (5)	15.3±4.4 (5)
Bathypelagic	94.4±1.9 (12)	30.0±5.9 (12)	5.65±1.23 (12)	5.39±0.56 (12)	57.0±14.8 (5)	14.1±3.1 (5)
Abyssopelagic	96.8±1.2 (16)	23.5±6.9 (16)	3.17±1.12 (16)	8.04±2.38 (16)	48.3±13.3 (5)	12.2±3.7 (5)
one-way ANOVA						
Subarctic						
df, F	3, 8.79	3, 47.07	3, 14.79	3, 7.05	3, 16.78	3, 29.60
p	0.0004	<0.0001	<0.0001	0.0015	0.0099	0.0034
Fisher's PLSD	B M A E	A E M B	A B E M	E M A B	A E B M	A E B M
Transitional						
df, F	3, 2.59	3, 13.89	3, 14.30	3, 5.12	3, 16.35	3, 6.36
p	0.072 (ns)	<0.0001	<0.0001	0.0056	0.0051	0.0370
Fisher's PLSD		A E M B	A E M B	M E B A	A M E B	A E M B
Subtropical						
df, F	3, 12.77	3, 12.77	3, 49.17	3, 26.09	3, 5.59	3, 1.750
p	<0.0001	<0.0001	<0.0001	<0.0001	0.0098	0.206 (ns)
Fisher's PLSD	M B E A	A B M E	A B M E	M E B A	A B M E	

Values are mean±1sd. The number of data points is shown in parentheses. Differences between depth zones were tested by one-way ANOVA and Fisher's PLSD. Any two zones not connected by underlining are significantly different (Fisher's PLSD, $p<0.05$). (ns): not significant.

4.2. Chemical composition versus depth

Not only plankton mass, but also its chemical composition and energy content varied with station and depth (Table 5, Fig. 4). On the premise that the plankton mass determined on the samples collected with the 90 μm mesh net of this study is composed mainly of crustacean copepods (the predominant group of mesozooplankton, cf. Longhurst (1985)), the overall ranges of each chemical component and energy content obtained in this study (Table 5) can be compared with those summarized by Childress and Nygaard (1974) and Båmstedt (1986). Båmstedt (1986) separated the data on pelagic copepods by depth of occurrence (shallow and deep, but not exceeding 1000 m) and geographical location (high, low and intermediate latitudes). As shown in Table 6, with the exception of water content, the ranges in this study of all of these variables fell well within those of pelagic crustaceans or copepods, suggesting that the major components of the present plankton samples are copepods or other zooplankton with similar body composition. A similar comparison of the present results for bathypelagic and abyssopelagic plankton samples with Childress and Nygaard's and Båmstedt's upper water column data showed partial overlaps of C, N and AFDM ranges characterized by extended lower-end values in our data. Water and energy contents did not follow this trend. An implication from this comparison is that deep net haul contents include more material with lower AFDM, possibly "detritus" (see discussion below).

The general pattern of change in chemical composition of plankton samples with increasing depth is that C, N and AFDM decreased toward greater depth, while water content, C:N ratio and ash increased with increasing depth (Fig. 4). However, we observed several exceptions to this pattern: (1) low water content and ash accompanied with high C, AFDM and energy content of samples from 200 to 3000 m depths at 44°N, and (2) high ash (or low AFDM) and C:N of samples from >2000 m at 25°N (particularly of samples from 4500 m, Fig. 4). The anomalous features of deep samples from the 44°N station can be explained by the dominance of large *Neocalanus* copepods in diapause that contain a large amount of lipids. Fraction of diapausing copepods to metazooplankton biomass exceeded 60% at 1000–2000 m depths at that station (Table 4 of Yamaguchi et al., 2004). Ikeda et al. (2004) has observed water content as low as 61% of WM and C as high as 60% of DM for *N. cristatus* in diapause. The vertical distribution of *Neocalanus* spp. is known to be <3000 m in the subarctic North Pacific (Vinogradov and Arashkevich, 1969), which will explain why vertical profile patterns of water, C, ash, AFDM and energy content changed rapidly below 3000 m (Fig. 4). Diapausing copepods are known to be transported to the subtropical region by the submerging Oyashio, as mentioned above. In our previous study on latitudinal changes in the fraction of diapausing copepods in the whole planktonic biomass (from pico to meso size), we noted that the fraction was 46% at 1500–2000 m at 44°N, but only 4% at 500–1000 m at 39°N (Yamaguchi et al.,

Table 6
Comparison of the overall ranges of chemical component and energy content of various zooplankton taxa and net-plankton

Taxa Depth range (m)	Crustaceans 0–1200	Copepods 0–1000	Net-plankton 0–1000	Net-plankton >1000
Water content (% of WM)	64–96	67–92	86–95	83–97
AFDM (% of DM)	30–93	70–98	69–88	48–85
Carbon (% of DM)	11–51	28–63	34–49	24–49
Nitrogen (% of DM)	2.9–12.3	5.2–15.8	7.7–9.3	3.2–8.1
C:N ratio (weight base)	3–17	3–13	4–5	5–8
Energy content ($J\,mg^{-1}$ DM)	—	9–31	14–25	10–23
Source	Childress and Nygaard (1974)	Båmstedt (1986)	Present study	Present study

2002b, 2004). The effect of copepods in diapause, though reduced, may be seen as low water content and high C values of samples from meso- to bathypelagic zones at 39°N (Fig. 4).

Low AFDM yet high C:N in samples from >2000 m at the 25°N station may indicate that a predominant fraction of the filtered material is biogenic detritus. Nitrogen associated with biogenic detritus is solubilised preferentially to carbon, resulting in elevation of the detrital C:N ratio in the course of sinking to depth (Smith et al., 1992). At St. ALOHA (22°45′N, 158°W) in the north-central Pacific Gyre, Karl et al. (1996) observed C:N ratios (by weight) of ca. 6.9 and >8.6 of particles collected with drifting traps at 150 and 500 m depth, respectively. Incidence of detritus in plankton samples has been well documented. Russian workers have been making a distinction between "seston" mass (detritus plus plankton) determined by weighing the entire net sample, and plankton biomass as a sum of individual organisms in the sample (Rudyakov and Tseitlin, 1992; Kitain et al., 1995). According to Rudyakov and Tseitlin (1992), seston:plankton mass ratios determined with a 178 μm mesh net change slightly with depth, but vary more strongly among regions: 2.4 in the Peru upwelling region (the fraction of detritus in total sample is 58%), 1.9 in the Indian Ocean (47%) and 1.4 in the Bering Sea (29%). Subsequent studies on the quantification of the amount of detritus filtered by nets showed that the amount of detritus changes with season in the 0–100 m layer of the Bering Sea (Kitain et al., 1995, using 178 μm mesh nets), and with depth and season in the NE Atlantic (Koppelmann, 1994, using 333 μm mesh nets). While the mesh size (90 μm) of the net used in this study is much smaller than those used in these previous studies, our preliminary observation of samples from 30°N shows that the proportion of detritus in total plankton mass increases with depth and often exceeds zooplankton biomass below 1000 m (Yamaguchi, unpublished data). Since the observation of detritus in the samples collected in this study is currently limited, we are unable to evaluate its effects on the overall results from the present study.

4.3. Plankton equivalents

Interrelationships or conversion equations among various mass units and energy densities for marine plankton samples have been reported by several workers (see review of Postel et al., 2000). Compared with the previous studies, which largely dealt with neritic or epipelagic plankton, samples used in the present study were from nearly the entire water column in the western North Pacific. As we have shown above, mass and energy density of plankton measured in different units changes differently with depth at the same station. In order to compare the differences among values predicted from the relationships/equations established in this study from relationships established by other workers, we calculated the predicted carbon content in 80 mg of plankton DM. We found 40.2 mg C from our C–DM relationship (Table 4), 26.1 mg C from Wiebe's (1988) result for plankton in the North Atlantic and 29.7 mg C from the analysis by Bode et al. (1998) of plankton collected off NW Spain. Thus, the C–DM relationship of this study yields 1.3–1.5 times higher carbon content than those of Wiebe (1988) and Bode et al. (1998). This higher C of this study appears to result from the incidence of large, lipid-rich copepods (such as *Neocalanus* spp.) in our plankton samples (Yamaguchi et al., 2004). All these results indicate that the validity of the interrelationship or conversion equations between various mass units and energy density is primarily limited to the region from which the samples derive. From this viewpoint, the interrelationships established in this study are applicable to the plankton samples collected from the surface layer to the great depth in the North Pacific Ocean, provided that seasonal variations in the detritus fraction are not appreciable.

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