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Chemical composition and energy content of deep-sea calanoid copepods in the western North Pacific Ocean

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## Abstract

Condition factor index [ $CFI=1000 \times DW/(PL)^3$ ; DW: dry weight, PL: prosome length], water content, carbon (C), nitrogen (N), ash and energy content were determined on a total of 69 copepod species caught from the mesopelagic (500-1000 m), upper-bathypelagic (1000-2000 m), lower-bathypelagic (2000-3000 m) and abyssopelagic (3000-5000 m) zones of the western subarctic Pacific. Resultant data were grouped into these four sampling zones, four developmental stage/sex categories (C4, C5 and C6 females and males), three feeding types (carnivore, detritivore and suspension feeder), or two reaction speed groups by the presence/absence of myelinated sheath enveloping axons (fast and slow reacting species). Zone-structured data showed the overall ranges were 3.8-4.6 mm for PL, 1.6-2.6 mg for DW, 21.4-25.0 for CFI, 75.0-78.6% of wet weight (WW) for water, 51.3-53.7% of DW for C, 7.7-8.8% of DW for N, 6.2-7.0 (by weight) for C/N, 6.9-9.6% of DW for ash and 25.3-27.4 J mg<sup>-1</sup> DW for energy. Among these components, N and ash exhibited significant between-zone differences characterized by gradual decrease downward for the former, and only the upper-bathypelagic zone > abyssopelagic zone for the latter. Stage/sex-structured data showed no significant differences among them, but energy content of C5 was higher than that of C6 females. From the analyses of feeding type-structured data, carnivores were shown to have lower water, N, ash, but higher C, C/N and energy contents than suspension feeders do. Reaction speed-structured data indicated that slow-reacting species have significantly higher water but lower CFI, C, N and energy contents than fast-reacting species. Designating these grouping criteria, PL and DW as independent variables, the attributes of these variables to the CFI, chemical composition or energy contents were evaluated by stepwise-multiple regression analysis, showing the most pronounced effect of suspension-feeder, followed by the presence of myelinated sheath, DW, C6 females and the abyssopelagic zone. Further analysis of zone-structured data, by adding epipelagic copepod data from identical thermal habitats (Arctic/Antarctic waters), revealed a more marked decline in N content from the epipelagic zone to the abyssopelagic zone, accompanied by an increase in C/N ratios downward. The decline in N (=protein or muscle) contents with depth cannot be

explained by the "visual interactions" hypotheses being proposed for the metabolism of pelagic visual predators, but is consistent with the "predation-mediated selection" hypothesis for the metabolism of pelagic copepods.

## Introduction

Among various taxa occurring as zooplankton in the pelagic realm of the world ocean, copepods are the most numerous (55-95% of individuals in samples, Longhurst, 1985). Because of their ubiquitous distribution through the ocean interior, high abundance and trophic importance in pelagic food webs, information about their physiology and biochemistry is a basis for our better understanding of their roles in energy flow and biogeochemical cycles in the ocean.

While studies of elemental composition of marine zooplankton go back to the early 1910s (Vinogradov, 1953), the first comprehensive study on the carbon (C) and nitrogen (N) composition of marine zooplankton is that of Omori (1969), who determined the composition for 33 species (including 15 copepod species) predominating in the North Pacific Ocean. Since then, Ikeda (1974) reported C and N content of a total of 111 zooplankton species (including 41 copepod species) from temperate-tropical waters of the Pacific, Indian and Atlantic Oceans. Båmstedt (1986) reviewed literature data on chemical composition (not only C and N, but also water, ash, protein, lipid, carbohydrate, and energy contents) of marine pelagic copepods, separating data from three habitats (high, low and medium latitude seas) and splitting each habitat further into two depth strata (“surface” and “deep”). His analysis showed higher C or energy accumulation (in the form of lipids) by copepods inhabiting higher latitude seas, a pattern especially marked in the “surface” dataset but less so in the “deep” datasets. Nevertheless, the differences between “surface” and “deep” datasets were not clear, because the latter represented specimens largely from < 1000 m deep and they only numbered < 8 over the designated three latitudinal ranges. The deepest sampling for the study of chemical composition of pelagic copepods ever made is that (1300-2500 m in the eastern North Pacific) of Lee et al. (1971), but their analysis was limited to lipid composition only.

Regarding depth-related patterns of body chemical composition of marine pelagic animals generally, Childress and Nygaard (1973) demonstrated a rapid increase in water and decrease in protein and energy contents with increasing depth of occurrence for micronektonic fishes. Further, Childress and Nygaard (1974) noted that while water

contents did not increase, protein contents of micronektonic crustaceans (decapods, mysids, euphausiids etc.) decrease with increasing depth of occurrence. Morris and Hopkins (1983) investigated biochemical composition of pelagic crustaceans (mostly copepods and euphausiids) caught at various depths between the surface and 1000 m and noted a depth-related pattern in water and protein contents similar to those of micronektonic fishes. The decrease in protein concentration in the body with increasing depth is considered to be in line with the "visual interactions" hypothesis proposed for a rapid decline in metabolic activity of pelagic visual predators such as micronektonic fishes, crustaceans and cephalopods (cf. Childress, 1995).

In this study, we determined the prosome length (PL), dry weight (DW), condition factor index (CFI), water, carbon, nitrogen, ash and energy contents on various copepods retrieved from mesopelagic (500 - 1000 m), upper-bathypelagic (1000 - 2000 m), lower-bathypelagic (2000 - 3000 m) and abyssopelagic (3000 - 5000 m) zones in the western subarctic Pacific. The objectives of this study were to (1) establish the depth-related patterns of these body measures and chemical composition/energy units of copepods in cold-thermal regimes, (2) explore major biological attributes (feeding habits, reaction speeds, body sizes etc.) to the interspecific variations in chemical composition/energy units of deep-sea copepods, and (3) determine whether or not the observed depth-related patterns of chemical composition/energy units fit the visual interactions hypothesis.

## 2. Materials and methods

### 2.1. Copepods:

Specimens were collected at stations in the western subarctic Pacific, including Site H (41°30'N 145°50'E) and Station Knot (44°00'N 155°00'E), during T/S Oshoro-Maru Cruises 124A (June) in 2002; 133D (March), 136A (June) and 142A (December) in 2003; 143B (February) and 144A (March) in 2004; and 155 (March) in 2005, and during R/S Tansei-Maru cruise KT-04-18 (August) in 2004. A vertical closing net (mouth diameter 80 cm, mesh aperture 0.3 mm; modified from Kawamura 1968) equipped with a large cod-end (1-2 l capacity) was used to collect zooplankton

from the mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic zones. The closing net was towed from the bottom through the top of a designated depth stratum at a speed of 1 m sec<sup>-1</sup>, closed and retrieved to the surface at 2 m sec<sup>-1</sup>. The depth the net reached was read from the record of an RMD depth meter (Rigosha Co. Ltd.) attached to the suspender cable of the net. During this study, a closing cod-end was developed (Ikeda unpublished) to maintain near *in situ* temperature of the zooplankton samples during net retrieval, and it was used when the water temperature at the surface layer exceeded 10°C. Upon retrieval of the net, undamaged specimens of copepods were sorted immediately. Most of the copepods (excluding those from the abyssopelagic zone) used in the present study were those on which respiration rates were determined (Ikeda et al., in press). Temperature and salinity profiles were determined with a CTD system.

## 2.2. Analytical procedures

On board the ship, individual specimens were rinsed briefly with a small amount of chilled distilled water, blotted on filter paper and frozen at -60°C. In a land laboratory, frozen specimens were weighed quickly on a microbalance (WW), freeze-dried then oven-dried at 60°C for 0.5-1 h to obtain dry weight (DW). Specimens were observed under a dissecting microscope for species, developmental stage and sex identification. At the same time, the prosome length (PL) was read to the nearest 0.05 mm with an eye-piece micrometer. For 26 freshly collected copepods, the effect of freeze-drying on the prosome length was examined by repeating measurement before (PL<sub>before</sub>) and after (PL<sub>after</sub>) freeze-drying. Since the differences between the two measurements were very small (PL<sub>after</sub>/PL<sub>before</sub> = 0.97 ± 0.02), no correction for the effect was made in this study. From each cruise, specimens of the same species, depth, stage and sex were pooled for C and N composition analysis with a CHN elemental analyzer (Elementar vario EL) using acetanilide, antipyrine or phenacetin as a standard. Weighed fractions of specimens were incinerated at 480°C for 5 h and reweighed for ash (ASH) determination. A specimen or a batch of specimens weighing <1.5 mg DW was used for single or duplicate measurement of C

and N composition, and replicate ash measurements were made only for the samples weighing >1.5 mg DW. Precision (CV) of these measurements was 3% for C, 7% for N and 10% for ash.

Condition Factor Index (CFI) of copepods was defined as  $CFI = 1000 \times DW / (PL)^3$  (cf. Mauchline, 1998). Water content (WATER) was computed as:  $WATER = 100(WW - DW) / WW$ , and thus as a percentage of WW. Ash-free dry weight (AFDW) was computed as:  $AFDW = DW - ASH$ . The energy content was calculated by using the formula of Gnaiger (1983), amended by Gnaiger and Shick (1985):  $J = 66.265W_c + 4.436W_n - 11.2$ , where J is an energy content in  $J\ mg^{-1}AFDW$ , and  $W_c$  and  $W_n$  are fractions of C and N, respectively, on an AFDW basis. J was expressed also as  $J\ mg^{-1}DW (= J\ mg^{-1}AFDW \times AFDW/DW)$ .

### 2.3. Data analysis

Individual data representing one or a batch of a few specimens from various seasons of the year were grouped into four sampling zones (mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic), four developmental stage/sex categories (C4, C5 and C6 females and males), three feeding types as judged by morphology (carnivore, detritivore and suspension feeder, cf. Yamaguchi et al., 2002), or two reaction speed groups (fast and slow reacting species) based on presence/absence of myelinated sheath enveloping axons (Lenz et al., 2000). All species belonging to the superfamilies Arietelloidea and Centropagoidea were assumed to lack myelinated sheath enveloping the axons according to the study of Lenz et al. (2000). The depth of occurrence of the four zone copepods was represented by the mid-point of the sampling interval, i.e. 750 m for the mesopelagic zone (500-1000 m), 1500 m for the upper-bathypelagic zone (1000-2000 m), 2500 m for the lower-bathypelagic zone (2000-3000 m) and 4000 m for the abyssopelagic zone (3000-5000 m).

## 3. Results

### 3.1. Mesopelagic through abyssopelagic environments

With the increase in depth from 500 m to 5000 m in the western subarctic Pacific, water temperatures decrease from 3 to 1.5°C, and salinities increase from 34.0 to 34.7. These features are almost constant throughout the year (Fig. 1). The 1000-2000 m depth is characterized by low oxygen [1.0-2.0 ml O<sub>2</sub> l<sup>-1</sup>, or 10-30% saturation, Favorite et al. (1976)].

### 3.2. Copepods

Calanoid copepod species belonging to the five Superfamilies and 11 Families were used for the present analyses (Table 1). Species belonging to the Families Eucalanidae (*Eucalanus bungii*) and Calanidae (*Neocalanus cristatus* and *N. plumchrus*) are known to undergo an extensive ontogenetic vertical migration (Vinogradov and Tseitlin, 1983), and those occurring in the mesopelagic through abyssopelagic zones were in diapause phase (characterized by a large accumulation of lipids, cf. Ikeda et al. 2004) and were not used in the present study. The number of datasets (DW, C and N data) was 54 for 36 mesopelagic zone species, 57 for 33 upper-bathypelagic zone species, 49 for 28 lower-bathypelagic zone species and 30 for 25 abyssopelagic zone species (Table 2). Of a total of 69 species which ranged from 2.5 mm (*Metridia asymmetrica*) to 10.8 mm (*Bathycalanus bradyi*) in PL, or from 0.30 mg (*Scaphocalanus subelongatus*) to 27.3 mg (*B. bradyi*) DW, many species occurred from two or three neighbouring bathymetric zones, and two (*Lucicutia gracilis* and *Pseudochirella spinifera*) occurred in all bathymetric zones.

### 3.3. WATER

Water contents varied little among the four bathymetric zone groups (75.0-78.6% of WW, Table 3) and the developmental stage/sex categories (74.3-77.7% of WW)(one-way ANOVA,  $p > 0.05$ , Table 3). Among the three feeding types, suspension feeders contained more water (78.1% of WW) than carnivores and detritivores did (74.5-74.6% of WW)(one-way ANOVA and followed Bonferroni-test,  $p < 0.05$ ). We found a significant difference between copepods with (74.8% of WW) and without (83.0% of WW) a myelin sheath enveloping their axons (one-way ANOVA,

$p < 0.001$ ).

#### 3.4. CFI

Similarly to WATER, no significant differences in CFI were seen among the four bathymetric zone groups (21.5-25.0) or the four developmental stage/sex groups (22.7-26.5)(one-way ANOVA,  $p > 0.06$ , Table 3). CFI values changed significantly among the three feeding types (one-way ANOVA,  $p = 0.001$ ), and a significant difference was seen between carnivores (27.1) and suspension feeders (22.2)(Bonferroni-test,  $p < 0.05$ ). Copepods with myelinated axons exhibited greater CFI (25.4) than those without myelinated sheath (18.6) (one-way ANOVA,  $p < 0.001$ ).

#### 3.5. C and N

While C composition of the four bathymetric zone groups (51.3-53.7% of DW), and C and N composition (51.5-55.1% of DW and 7.9-8.9% of DW, respectively) among the four developmental stage/sex groups did not vary significantly (one-way ANOVA,  $p > 0.06$ , Table 3), N content showed one significant difference between bathymetric groups (one-way ANOVA,  $p < 0.02$ ), and subsequent test showed the mesopelagic zone  $>$  the abyssopelagic zone (Bonferroni-test,  $p < 0.05$ ). With regard to feeding types, suspension feeders were characterized by lower C (50.2% of DW) composition but higher N (8.6% of DW) composition, as compared with those of the other two feeding types (54.3-56.0% and 7.6-8.4% of DW, respectively)(one-way ANOVA,  $p < 0.001$ ). Copepods without myelinated axons contained less C (49.1% of DW) and N (7.8% of DW) as compared with those with myelinated axons (53.3 and 8.4% of DW, respectively) (one-way ANOVA,  $p < 0.025$ ).

#### 3.6. C/N

Because of differential patterns of C and N composition within each designated group or type, variation in resultant C/N ratios is expected to be dissimilar from that of C or N composition mentioned above. No significant between-group differences were shown among the four bathymetric zone groups (6.2-7.0), among the four

development/sex groups (6.4-7.3), or between those with and without myelinated axons (6.3-7.3)(one-way ANOVA,  $p > 0.06$ , Table 3). C/N ratios were significantly different among the three feeding types (one-way ANOVA,  $p < 0.001$ ), and subsequent tests showed that the ratio of carnivores (7.5) was significantly greater than that (6.2) of suspension feeders (Bonferroni-test,  $p < 0.05$ ).

### 3.7. ASH

Because of limited sample size and its preferential use for C and N composition, the number of data sets of ASH was much less than those of WATER, C or N. Despite fewer datasets, ASH differed significantly among the four bathymetric zone groups (one-way ANOVA,  $p < 0.01$ , Table 3), and the upper-bathypelagic zone (9.6% of DW) was significantly greater than that (6.9% of DW) of the abyssopelagic zone (Bonferroni-test,  $p < 0.05$ ). No significant differences were seen among the four developmental stage/sex groups (7.5-9.0% of DW) or copepods with and without myelinated axons (8.2-10.3% of DW)(one-way ANOVA,  $p > 0.05$ ). ASH varied significantly among the three feeding types (one-way ANOVA,  $p < 0.01$ ), and ASH of suspension feeders (9.4) was significantly greater than that (7.2) of carnivores (Bonferroni-test,  $p < 0.05$ ).

### 3.8. Energy

No significant differences were seen among the four bathymetric zone groups (27.1-29.5 J AFDW<sup>-1</sup>)(one-way ANOVA,  $p > 0.50$ , Table 3). On the other hand, there were significant differences among the three developmental stage/sex groups, among the three feeding types and the groups with and without myelinated axons (one-way ANOVA,  $p < 0.02$ ). Within each designated group or type, significant differences were detected between C5 (30.0) and C6 female (27.2), between carnivores (30.5) and suspension feeders (26.2), and between copepods with (28.4) and without (25.1) myelinated sheath (Bonferroni-test,  $p < 0.05$ ). These results remained unchanged if the energy unit was changed from J AFDW<sup>-1</sup> to J DW<sup>-1</sup> (Table 3).

### 3.9. Relative importance of various parameters

Designating the depth of occurrence, stage/sex, feeding type, presence/absence of myelinated sheath, *PL* and *DW* as independent variables, the attributes of these variables to each dependent variable (*Y*: CFI, WATER, C, N, ASH, C/N, J/AFDW or J/DW) of copepods from the mesopelagic through abyssopelagic zones (Table 2) were analyzed by stepwise multiple regression (Sokal and Rohlf, 1995). The full model of the multiple regression adopted was

$$Y=UB+LB+AB+C5+C6F+C6M+DETR+SUS+MYEL+PL+DW+constant,$$

where *UB*, *LB* and *AB* are dummy variables on depth; *C5*, *C6F*, *C6M* are on stage; *DETR* and *SUS* are on feeding type. Details of the definitions of these dummy variables are summarized in the Appendix. The dummy variable *MYEL* was defined as 1 when a myelinated sheath was present, and 0 when it was absent. The independent variable *PL* and *DW* were the value of *PL* in mm and *DW* in mg. Predictor variables were added if  $p \leq 0.05$  and removed if  $p \geq 0.10$ . The calculation was conducted using SPSS ver 11.5.

The stepwise regression analyses distinguished significant independent variables which varied from one dependent variable to the next (Table 4). Among 11 independent variables tested, the feeding type (*SUS* or not) was the most important one, affecting all dependent variables (CFI, chemical composition and energy contents). As one of the other independent variables, the presence of myelinated sheath (*MYEL*) influenced CFI, WATER and N. Of depth zones, *LB* was not a significant variable, but *UB* was associated positively with ASH, and *AB* negatively with N (then positively with C/N). As stage/sex, all *C5*, *C6F* and *C6M* contributed negatively the chemical composition and energy contents. Overall, the regression analysis yielded results similar to those of one-way ANOVA (Table 3) in which the chemical composition and energy content data were grouped based on single criteria (depth, stage/sex, feeding type or myelinated sheath) and where other criteria were regarded as random variables. It is noted that *PL* and *DW* were newly designated independent variables for the regression analysis. *PL* affected negatively CFI, C and C/N but *DW* affected positively these variables plus energy content units, the latter indicating greater accumulation of C or

energy rich material (=lipids) in copepods with greater DW (Table 4).

## 4. Discussion

### 4.1. Comparison with previous data

Since the data of C and N composition and energy contents of copepods living down to 5000 m depth were first obtained in this study, it is of great interest to compare the present results with those of previous studies on copepods reviewed by Båmstedt (1986). Båmstedt (1986) split the entire dataset into three latitudinal groups (high, medium and low), and each latitudinal group was divided further into two bathymetric levels (“surface” and “deep”), thus yielding six subgroups. His “deep” data are from copepods living at < 1000 m depth, and the sample size for that group was very small (< 8 for C and N). Comparison of the present data for deep-sea copepods (the data of mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic zone copepods pooled) with those (the six subgroups pooled) of Båmstedt showed partial overlap of the water content ranges [75.0-78.6% (this study) vs. 78.3-91.5% of WW (Båmstedt) ], characterized by extension to lower values in our data, and ash ranges [25.3-27.4 (this study) vs. 15.8-27.1 J mg<sup>-1</sup> DW (Båmstedt)] characterized by the wider spread of Båmstedt’s data. The present data for C (51.3-53.7% of DW), N (7.7-8.8% of DW) and ASH (6.9-9.6% of DW) of deep-sea copepods fell well within the ranges (C and N) or showed partial overlap of the range (ASH) (37.2-54.7%, 6.4-12.6% and 8.5-16.9%, respectively, of DW) of Båmstedt’s data. Energy contents of deep-sea copepods (25.3-27.4 J mg<sup>-1</sup> DW) were close to the upper range of Båmstedt’s data (15.8-27.1 J mg<sup>-1</sup> DW). Overall implications gained from this broad comparison with previously reported data are that; (1) the mesopelagic through abyssopelagic zone copepods from the western subarctic Pacific of this study are not especially unique as compared with previous data for the epipelagic/mesopelagic zone copepods from high to low latitude seas compiled by Båmstedt; (2) compared with the data compiled by Båmstedt, lesser variations of each component in the present data may reflect the narrower ranges of variations in environmental factors (temperature, food abundance, etc) affecting the body composition of copepods, directly or indirectly, in the deep sea.

While comparable data are not available in Båmstedt (1986), the present analysis shows that water, C, N and ash contents did not vary significantly among C4, C5, C6F and C6M (Table 3). It must be borne in mind that all the data in Table 2 of this study represent single specimens or a batch of a few specimens of each stage or stage/sex combination of a given species; therefore statistically meaningful tests are limited to interspecific differences only. Our results showed no significant effects of sex on the C and N composition of C6 specimens (Table 3). Intraspecifically, the effect of sex on the C and N composition of copepods has been documented as variable: some species exhibit higher C and lower N in males than females, but the reverse pattern or no sexual difference has also been reported on copepods living in coastal regions (Uye, 1982; Lee et al., 2001).

Our stepwise regression analysis revealed positive and negative effects of body size (*PL* and *DW*) on C, N, C/N and/or energy contents but negative effects on N of deep-sea copepods (Table 3). Because of narrow ranges of these size measures (*PL*: 2.5-10.8 mm, *DW*: 0.3 to 27.3 mg, cf. Table 2) the generalization of the results needs caution. Previously, no *DW* effects have been recognized on C and N composition in the broad analyses of marine zooplankton including copepods (*DW* range: 0.005 to 100 mg, Ikeda 1974).

Previously, the CFI was computed as 8-13 (re-calculated with the equation of this study) for *Acartia clausi* by Durbin and Durbin (1978) as a possible index sensitive to change in food and other environmental conditions for this small neritic copepod. Durbin et al. (1983) demonstrated experimentally that the CFI of *A. tonsa* increased with increasing phytoplankton concentrations and reached a saturated CFI value (18). While the between-species variations in CFI values were large, CFIs computed for mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic zone copepods (21.5 - 25.0, cf. Table 3) of this study are higher than those (8 - 18) of *Acartia* spp. Since the body shape of copepods varies species-specifically, between-species differences in CFI values can not be used as an indication of relative nutritional conditions experienced by the species. If one assumes a typical copepod *Calanus finmarchicus* of which prosome is ellipsoid in shape [ $PL = 2 \times \text{long axis (a mm)}$ ];

prosoma width =  $0.3 \times PL$ ] and with a water content of 75% of WW (cf. Table 3), the CFI can be computed as 11.8 from the equation used in the present study [ $4\pi a^3 \times 1000 \times 0.3^2 \times 0.25 / (3 \times (2a)^3)$ ]. Judging from the CFI value, the prosoma shape of *Acartia* spp. is close to that of this hypothetical *C. finmarchicus* but that of the deep-sea copepods of this study is more solid than *C. finmarchicus*. The lack of significant differences among the zone-structured data of this study (Table 3) indicates that the prosoma shapes of copepods living in the mesopelagic through abyssopelagic zones are more or less similar. Besides the prosoma shape, CFI may be used as an index of feeding type or phylogenetic position of the species (cf. Table 4).

#### 4.2. Copepods vs. net plankton

While the previous data mentioned above are limited to depths above 1000 m, chemical composition data from net-plankton samples collected with a 90 $\mu$ m mesh net from epipelagic through abyssopelagic zones in the western subarctic Pacific (the present study site) were reported recently by Yamaguchi et al. (2005). Compared with the present results (Fig. 2), marked differences are seen in the net-plankton data from the epipelagic and abyssopelagic zones. Net-plankton in the epipelagic and abyssopelagic zones characterized by high water (91-92% of WW) and ash (27- 44% of DW) contents, yet markedly low C (25-35% of DW), N (4-8% of DW) and energy (12-16 J mg<sup>-1</sup> DW) contents, suggest that an appreciable fraction of net-plankton is detritus (and phytoplankton in the epipelagic zone samples). The proportion of detritus in the total net-plankton biomass increased with depth and often exceeded zooplankton biomass below 1000 m depth in the western subarctic Pacific (Yamaguchi et al., 2005). According to Rudyakov and Tseitlin (1992), seston (detritus+plankton): plankton mass ratios determined with a 178  $\mu$ m 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%). In the mesopelagic, upper-bathypelagic and lower-bathypelagic zones, differences in chemical composition between copepods and net-plankton were not appreciable. Yamaguchi et al. (2004) noted that copepods were the major component

(40-87%) of zooplankton biomass in these depth strata, and *Neocalanus* spp. in diapause often dominated (0-67%) in copepod biomass. *Neocalanus* spp. in diapause contain even more C and energy (as great as 64% of DW and 32 J mg<sup>-1</sup>DW, cf. Ikeda et al., 2004) than those of the mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic copepods of this study (51 – 53% of DW and 25 - 27 J mg<sup>-1</sup>DW, cf. Table 2). In the comparison of the data shown in Fig. 2, *Neocalanus* spp. were excluded from mesopelagic through abyssopelagic zone copepod data of this study, but were included in net-plankton data of Yamaguchi et al. (2005). Therefore, apparent agreements seen in the mesopelagic and upper-bathypelagic zone (ca. 500 and 1500 m) data between these two studies may be that the negative effect of detritus and gelatinous zooplankton containing less organic matter (by high water and high ash contents) was offset by the positive effect of organic-rich *Neocalanus* (low water and low ash contents).

Nevertheless, we present the first evidence for differences between net-plankton samples and copepods (hypothesized major component of net-plankton) in chemical composition and energy content, which was highlighted typically in the data of water, C, N, ash and energy contents at the abyssopelagic zone (Fig. 2).

#### 4.3. Feeding types and reaction speed types

Our stepwise regression analyses revealed that of 11 independent variables tested, the one affecting broadly the chemical composition and energy contents of deep-sea copepods was a feeding type (suspension feeder)(Table 4). Since the effects of detritivore to these variables are neutral, the effects of non-suspension feeder (e.g. carnivore) would be the reverse to those of suspension-feeder. For shallow-living zooplankton in higher latitude seas, herbivores (=suspension feeders) are known to accumulate a large amount of lipid in the body as an energy reserve to cope with the phytoplankton-depleted winter season. In contrast, such accumulation of lipid is not usually the case for carnivores, because they take animal food (including herbivores), which is a more stable food resource than phytoplankton (Ikeda, 1974; Båmstedt, 1986). C contents as high as >45% of DW are an indication of accumulation of lipids in the

body of marine zooplankton (Ikeda, 1974). From this view, all deep-sea copepods grouped into the three feeding types of this study (50-56% C of DW, Table 3) contain large amounts of lipids. In the present analysis of deep-sea copepods, carnivores showed higher C and lower ash contents (Table 3) and therefore contain larger energy reserves than detritivores and suspension feeders do. If one assumes a continuous food supply for carnivores as in shallow-water environments, the possession of energy reserves in carnivorous copepods of this study do not make sense. As a plausible explanation, food supply for carnivores is discontinuous in the deep-sea. Lee et al. (1971) found a large accumulation of wax esters in mesopelagic and bathypelagic copepods (without separating into feeding types), and considered their role as an energy reserve in these food-limited deep environments. Considering that prey zooplankton biomass decreases rapidly toward greater depths (Vinogradov and Tseitlin, 1983; Yamaguchi et al., 2005), carnivorous feeding appears to be not a feeding trait well adapted to deep-sea regimes relative to detritivorous or suspension feeding. In analyzing the trophic structure of zooplankton communities (copepods plus non-copepods) to great depths in the western subarctic Pacific, Vinogradov and Tseitlin (1983) noted that the proportion of carnivores increases from the surface to around 2000 m, then decreases rapidly toward 6000 m. In the present analysis, the mean depth of occurrence of carnivores (1605 m) was shown to be significantly less than that (2089 m) of suspension feeders (Table 3).

The presence of myelinated sheath (*MYEL*) was found to be another parameter affecting moderately some chemical composition units and energy contents of deep-sea copepods (Table 4). The presence of myelinated sheath enveloping axons implies fast escape reactions against the stimuli of predators (Lenz et al., 2000), and its positive effects on C and N composition and energy contents but negative effect on water contents altogether suggest rich musculature and organic matter in the body to support active swimming. Of a total of 190 datasets in Table 2, those with myelinated sheath were 148 (78%). If one assumes binomial distribution, the probability of 50 carnivores, which were sampled at random from the 190 copepods, to have as high as 41 incidences (or 82%) of specimens with myelinated sheath is 0.11 or quite low

$[f(41)=_{50}C_{41}(148/190)^{41}((190-148)/190)^{50-41}=0.112$ , cf. Sokal and Rohlf, 1995]. Perhaps carnivorous copepods in the deep sea do not necessarily need to react quickly, as specialized feeding mechanisms such as venom or anaesthetic injection, mucus jets etc. have been known on some carnivorous copepods in the deep sea to capture prey animals (cf. Nishida and Ohtsuka 1996). Compared with fast-reacting species (myelin sheath present), special features of slow-reacting species are less CFI, C, N and energy contents but higher water levels. However, these features of deep-sea copepods with/without myelinated sheath cannot be generalized to shallow-living copepods; i.e., among dominant copepods occurring in the surface water of high-latitude seas those with (*Calanus* spp., *Neocalanus* spp.) and without (*Metridia longa*, *M. pacificus*) myelinated sheath do not show appreciable differences in water content or C and N compositions (Ikeda and Skjoldal, 1989; Ikeda and Hirakawa, 1998).

#### 4.4. Depth-related pattern

In order to avoid an obvious effect of thermal regimes on the chemical composition and energy contents (Båmstedt, 1986), the data for the epipelagic copepods living at near-zero or at subzero temperatures, such as *Calanus propinquus*, *Calanoides acutus*, *Rhincalanus gigas* and *Metridia gerlachei* in Antarctic waters (Ikeda and Mitchell, 1982; Ikeda unpublished data), and *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus* and *M. longa* in Arctic waters (Ikeda and Skjoldal, 1989) were combined with mesopelagic through abyssopelagic data of this study to evaluate depth-related patterns, if any (Table 3, Fig. 2). Not all available Arctic data (Ikeda and Skjoldal, 1989) and no *R. gigas* data (Ikeda, unpublished) from the Antarctic are included in the review by Båmstedt (1986). The combined data of this study show no significant depth-related pattern in water level, C, ash or energy contents. At the same time, the significant pattern of decline with increasing depth becomes more marked in N content, and a reversed pattern (increase with depth) emerged newly in the C/N ratios (Fig. 2). Since the C composition did not show significant depth-related patterns, the pattern newly emerged in the C/N ratios was caused by the reduced N content of deeper-living copepods.

An increase in water content and a decrease in N content (per WW) with increasing depth of occurrence (ca. 1000 m at most) has been observed for micronektonic fishes off southern California (Childress and Nygaard, 1973) and crustaceans (copepods and euphausiids) in the eastern Gulf of Mexico (Morris and Hopkins, 1983). On the other hand, only a decline in N content (per WW) was observed for large crustaceans (mysids, decapods etc.) off southern California (Childress and Nygaard, 1974). Our re-calculation indicates that the depth-related decline in N content, expressed as % of WW by Childress and Nygaard (1973, 1974), disappears when expressed as % of DW, but the pattern remains in the results of Morris and Hopkins (1983). The present results for pelagic copepods (Fig. 2) are in agreement with Childress and Nygaard's (1974) for water content, and with Morris and Hopkins's for N content. Unlike copepods, fishes have well-developed visual perception systems and are strict predators among the species studied by Childress and Nygaard (1973). The increased water content in deeper-living micronektonic fishes may be interpreted by a "visual interactions" hypothesis (Childress, 1995), i.e., the progressive decline in visual perception range as darkness increases at depth is accompanied by reduction in their locomotive activity/body musculature (implied by increasing water content). Dissimilar results for water content, and similar results for N content between pelagic crustaceans found by Morris and Hopkins (1983) and in the copepods by us are difficult to interpret, because copepods are a taxon included in both studies. As a possible explanation, inclusion of deep eucalanidae (*Eucalanus* spp.), characterized by high water contents (as high as 92% of WW), in Morris and Hopkins's study may be considered. Eucalanid copepods, characterized by high water content but low N content, occurred frequently in the present samples from the mesopelagic zone (e.g. *Eucalanus bungi* containing water 91% of WW and N 7.4% of DW, Ikeda unpublished data), but they were not included in the present analyses because of their unusual physiological states (e.g., diapause) (see Methods and Materials section).

Among various chemical components of pelagic copepods examined, why does only N content decline with increasing depth? As mentioned above, the decline in N content means a reduction in their locomotive activity/body musculature for visual

predators such as micronektonic fishes. From the “visual interactions” hypothesis, no depth-related changes in chemical composition may be predicted for copepods, since they do not have visual perception systems, at least none useful in predation or escape from predators. Recently, the rapid decline in respiration rates with increasing depth of occurrence, which has been reported on pelagic visual predators only, was observed on pelagic copepods (non-visual predators) by Ikeda et al. (in press). They interpreted this as a consequence of lowered selective pressure for activity in deep-sea copepods, reflecting progressive reduction in predation pressure downward (“predation-mediated selection” hypothesis in contrast to “visual interactions” hypothesis). The decline in N content observed in this study is consistent with the predation-mediated selection hypothesis. In the light of high diversity of non-visual pelagic animals in the ocean, further study on animals other than copepods is needed to prove/disprove this new “predation-mediated selection” hypothesis.

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Appendix: Definitions of dummy variables

The depth was categorized into mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic, and the independent variables *UB*, *LB*, *AB* were defined as dummy variables as in Table A1. The stage/sex was categorized into Category 4, Category 5, Category 6 Female and Category 6 Male, and dummy variables *C5*, *C6F*, *C6M* were defined as in Table A2. Feeding type was categorized as carnivore, detritivore, and suspension-feeder, and dummy variables *DETR*, and *SUS* were defined as in Table A3. The dummy variable *MYELI* was defined as 1 if myelinated sheath was present and otherwise *MYEL* was defined as 0.

Table A1. Definition of dummy variables on depth

| Depth category     | <i>UB</i> | <i>LB</i> | <i>AB</i> |
|--------------------|-----------|-----------|-----------|
| Mesopelagic        | 0         | 0         | 0         |
| Upper-bathypelagic | 1         | 0         | 0         |
| Lower-bathypelagic | 0         | 1         | 0         |
| Abyssopelagic..    | 0         | 0         | 1         |

Table A2. Definition of dummy variables on stage/sex

| Stage/sex Category | <i>C5</i> | <i>C6F</i> | <i>C6M</i> |
|--------------------|-----------|------------|------------|
| Category 4         | 0         | 0          | 0          |
| Category 5         | 1         | 0          | 0          |
| Category 6 Female  | 0         | 1          | 0          |
| Category 6 Male    | 0         | 0          | 1          |

Table A3. Definition of dummy variables on feeding type

| Feeding Type      | <i>DETR</i> | <i>SUS</i> |
|-------------------|-------------|------------|
| Carnivore         | 0           | 0          |
| Detritivore       | 1           | 0          |
| Suspension Feeder | 0           | 1          |

Table 1. A list of copepod superfamily, family and genus used in the present study (\*Arctic/Antarctic copepods, see text for details).

| Superfamily          | Family                  | Genus                 |                      |
|----------------------|-------------------------|-----------------------|----------------------|
| Arietelloidea        | Augaptilidae            | <i>Euaugaptilus</i>   |                      |
|                      |                         | <i>Pachyptilus</i>    |                      |
|                      | Heterorhabdidae         | <i>Heterostylites</i> |                      |
|                      | Lucicutiidae            | <i>Lucicutia</i>      |                      |
|                      | Metridinidae            | <i>Metridia</i>       |                      |
| <i>Pleuromamma</i>   |                         |                       |                      |
| Centropagoidea       | Candaciidae             | <i>Candacia</i>       |                      |
| Clausocalanoidea     | Aetideidae              | <i>Aetideopsis</i>    |                      |
|                      |                         | <i>Bradyidius</i>     |                      |
|                      |                         | <i>Batheuchaeta</i>   |                      |
|                      |                         | <i>Chiridiella</i>    |                      |
|                      |                         | <i>Chiridius</i>      |                      |
|                      |                         | <i>Euchirella</i>     |                      |
|                      |                         | <i>Gaetanus</i>       |                      |
|                      |                         | <i>Gaidius</i>        |                      |
|                      |                         | <i>Pseudochirella</i> |                      |
|                      |                         | <i>Undeuchaeta</i>    |                      |
|                      |                         | <i>Valdiviella</i>    |                      |
|                      |                         | Euchaetidae           | <i>Paraeuchaeta</i>  |
|                      |                         | Phaennidae            | <i>Cornucalanus</i>  |
|                      |                         |                       | <i>Onchocalanus</i>  |
|                      |                         |                       | <i>Xanthocalanus</i> |
|                      |                         | Scolecitrichidae      | <i>Amalothrix</i>    |
|                      |                         |                       | <i>Lophothrix</i>    |
|                      |                         |                       | <i>Mixtocalanus</i>  |
|                      |                         |                       | <i>Scaphocalanus</i> |
|                      | <i>Scolecithricella</i> |                       |                      |
| <i>Scottocalanus</i> |                         |                       |                      |
| Eucalanidea          | Eucalanudae             | <i>Rhincalanus</i> *  |                      |
| Megacalanoidea       | Calanidae               | <i>Calanoides</i> *   |                      |
|                      |                         | <i>Calanus</i> *      |                      |
|                      | Megacalanidae           | <i>Megacalanus</i>    |                      |
|                      |                         | <i>Bathycalanus</i>   |                      |
| Spinocalanoidea      | Spinocalanidae          | <i>Spinocalanus</i>   |                      |

Table 2. Prosome length (PL), dry weight (DW), condition factor index (CFI), water, carbon (C) and nitrogen (N) composition, ash contents, C/N ratio (by weight) and energy contents of copepods from mesopelagic through abyssopelagic zones in the western subtropical Pacific. Associated features of each species including Copepodid stage/sex (F: female, M: male), feeding type (C: carnivore, D: detritivore, S: suspension feeder) and presence/absence of myelinated sheath enveloping nerve fiber axons are noted. For details see text.

| Species                          | Date   | Stage | Feeding type | A: absent<br>P: present | Myelinated sheath |         | DW(mg) | CFI      | Water |      | Composition (%DW) |      | J/AFDW | J/DW |       |       |
|----------------------------------|--------|-------|--------------|-------------------------|-------------------|---------|--------|----------|-------|------|-------------------|------|--------|------|-------|-------|
|                                  |        |       |              |                         | PL(nm)            | SD(n)   |        |          | Mean  | SD   | Mean              | SD   |        |      | C     | N     |
| Mesopelagic (500-1000 m)         |        |       |              |                         |                   |         |        |          |       |      |                   |      |        |      |       |       |
| <i>Pachypitius pacificus</i>     | Jun-03 | C6F   | C            | A                       | 4.8               |         | 2.065  | 18.67    | 88.5  |      | 43.2              | 6.25 | 6.91   |      |       |       |
| <i>Lucicutia bicornata</i>       | Jun-03 | C6F   | S            | A                       | 3.5               |         | 0.625  | 14.58    | 89.1  |      | 40.5              | 8.02 | 5.05   |      |       |       |
| <i>Lucicutia grandis</i>         | Jun-03 | C5F   | S            | A                       | 3.2               |         | 0.429  | 13.09    | 88.4  |      | 43.9              | 7.35 | 5.97   |      |       |       |
| <i>Metridia asymmetrica</i>      | Mar-03 | C6F   | S            | A                       | 2.9               | 0.08(5) | 0.457  | 0.016(2) | 13.36 | 82.2 | 1.5               | 53.0 | 7.28   | 7.9  | 27.28 |       |
| <i>Metridia curticauda</i>       | Jun-03 | C6F   | S            | A                       | 2.6               | 0.49(2) | 0.484  |          | 29.19 | 77.2 |                   | 55.7 | 7.03   | 7.92 |       |       |
| <i>Metridia okhotsensis</i>      | Oct-03 | C5F   | S            | A                       |                   |         | 0.713  | 0.107(8) |       | 68.7 | 3.9               | 60.2 | 6.96   | 5.0  | 36.65 |       |
| <i>Pleuronomma scutellata</i>    | Jun-03 | C6M   | S            | A                       | 3.2               | 0.05(7) | 0.564  | 0.032(6) | 17.71 | 79.0 | 0.6               | 44.5 | 11.90  | 8.0  | 3.74  | 21.43 |
|                                  | Jun-03 | C6F   | S            | A                       | 2.9               | 0.2(3)  | 0.429  | 0.003(2) | 17.59 | 81.5 | 3                 | 50.8 | 7.25   | 8.1  | 7.01  | 25.78 |
| <i>Pleuronomma xiphias</i>       | Jun-03 | C6F   | S            | A                       |                   |         | 0.563  | 0.016(4) |       |      |                   | 42.7 | 11.90  | 13.3 | 3.59  | 22.04 |
| <i>Conchoecia columbiana</i>     | Jun-03 | C6M   | C            | A                       | 2.6               | 0.49(2) | 0.435  |          | 26.23 | 81.3 |                   | 41.1 | 11.50  |      | 3.57  |       |
| <i>Aetiideopsis rostrata</i>     | Jun-03 | C5M   | S            | P                       | 3.6               |         | 0.762  |          | 16.33 | 82.4 |                   | 44.0 | 10.50  |      | 4.19  |       |
| <i>Chirudina pacificus</i>       | Jun-03 | C6F   | S            | P                       | 3.0               | 0.21(2) | 0.692  | 0.257(2) | 26.96 | 77.4 | 2.3               | 45.7 | 11.50  |      | 3.97  |       |
| <i>Chirudina strosti</i>         | Jun-03 | C6F   | S            | P                       | 4.2               | 0.00(2) | 1.237  | 0.057(2) | 16.70 | 78.2 | 0.3               | 43.5 | 12.80  |      | 3.4   |       |
| <i>Euchirella brevis</i>         | Jun-03 | C6F   | S            | P                       | 3.2               | 0.14(2) | 0.952  | 0.063(2) | 29.05 | 74.9 | 6.2               | 53.1 | 8.79   |      | 6.04  |       |
| <i>Euchirella galathea</i>       | Jun-03 | C6F   | S            | P                       | 5.0               |         | 2.459  |          | 19.67 | 87.6 |                   | 45.8 | 11.40  |      | 4.02  |       |
| <i>Euchirella messinensis</i>    | Jun-03 | C6F   | S            | P                       | 4.3               | 0.35(2) | 1.917  | 0.373(2) | 24.97 | 79.6 | 1.3               | 45.0 | 11.20  |      | 4.02  |       |
| <i>Euchirella rostrata</i>       | Jun-03 | C6F   | S            | P                       | 3.0               | 0.04(5) | 0.930  | 0.09(4)  | 33.76 | 75.1 | 2.1               | 48.9 | 9.23   | 8.1  | 5.3   | 24.51 |
| <i>Euchirella transcaucasica</i> | Jun-03 | C4M   | S            | P                       | 2.8               |         | 0.517  |          | 23.55 | 76.4 |                   | 46.6 | 10.40  |      | 4.48  |       |
| <i>Gaidius brevirostris</i>      | Mar-03 | C5F   | S            | P                       | 3.6               |         | 0.914  |          | 19.59 | 82.1 |                   | 48.0 | 8.46   |      | 5.67  |       |
|                                  | Jun-03 | C6F   | S            | P                       | 3.6               | 0.00(3) | 0.949  | 0.006(3) | 20.34 | 82.3 | 0.8               | 44.2 | 11.00  | 11.2 | 4.02  | 22.33 |
| <i>Gaidius robustus</i>          | Jun-03 | C4F   | S            | P                       | 2.7               |         | 0.381  |          | 19.36 | 81.2 |                   | 47.3 | 10.70  |      | 4.42  |       |
| <i>Gaidius tenuispinus</i>       | Jun-03 | C5F   | S            | P                       | 3.7               |         | 1.238  |          | 24.44 | 76.6 |                   | 50.4 | 9.47   |      | 5.32  |       |
|                                  | Jun-03 | C6F   | S            | P                       | 2.8               | 0.04(5) | 0.436  | 0.022(3) | 19.44 | 80.7 | 1.4               | 45.1 | 12.10  | 8.8  | 3.73  | 22.16 |
| <i>Gaidius variabilis</i>        | Jun-03 | C5M   | S            | P                       | 2.9               |         | 0.488  |          | 21.08 | 80.5 |                   | 45.6 | 10.40  |      | 4.38  |       |
|                                  | Jun-03 | C5F   | S            | P                       | 2.8               |         | 0.323  |          | 14.71 | 84.4 |                   | 40.4 | 10.50  |      | 3.85  |       |
|                                  | Jun-03 | C6F   | S            | P                       | 2.7               | 0.21(6) | 0.509  | 0.039(5) | 25.29 | 77.2 | 1.3               | 47.8 | 10.80  | 7.2  | 4.43  | 23.45 |
| <i>Pseudocharella pacifica</i>   | Jun-03 | C5M   | S            | P                       | 3.7               |         | 0.700  |          | 13.82 | 84.7 |                   | 42.3 | 10.10  |      | 4.19  |       |
| <i>Pseudocharella spinifera</i>  | Mar-03 | C5M   | S            | P                       | 3.6               |         | 1.592  |          | 34.12 | 67.9 |                   | 58.0 | 7.84   |      | 7.4   |       |
|                                  | Jun-03 | C5M   | S            | P                       | 3.5               |         | 1.275  |          | 29.74 | 73.4 |                   | 53.9 | 8.51   |      | 6.33  |       |
| <i>Undeuchata plumosa</i>        | Jun-03 | C6F   | S            | P                       | 4.9               |         | 3.332  |          | 28.32 | 73.1 |                   | 50.9 | 9.65   | 6.8  | 5.27  | 25.45 |
| <i>Paraeuchaeta barbata</i>      | Jun-03 | C6F   | C            | P                       | 4.9               |         | 3.862  |          | 32.83 | 66.5 |                   | 62.0 | 6.36   | 4.1  | 9.75  | 31.93 |
| <i>Paraeuchaeta breirostrata</i> | Mar-03 | C5M   | C            | P                       | 4.0               |         | 1.351  |          | 21.11 | 78.9 |                   | 56.4 | 7.04   | 5.0  | 8.01  | 28.47 |
|                                  | Mar-03 | C5F   | C            | P                       | 4.0               |         | 1.793  |          | 28.02 | 73.6 |                   | 57.9 | 7.33   |      | 7.9   |       |
|                                  | Jun-03 | C6F   | C            | P                       | 5.5               | 0.06(3) | 4.852  | 0.437(3) | 29.65 | 71.8 | 1.4               | 58.4 | 7.48   | 4.9  | 7.81  | 29.84 |
| <i>Paraeuchaeta brevirostris</i> | Mar-03 | C6F   | C            | P                       | 5.6               |         | 4.969  |          | 28.29 | 69.6 |                   | 57.9 | 7.19   | 3.7  | 8.05  | 28.97 |
| <i>Paraeuchaeta elongata</i>     | Jun-03 | C4M   | C            | P                       | 3.0               | 0.14(2) | 0.714  | 0.042(2) | 26.44 | 76.0 | 2.5               | 57.0 | 7.25   |      | 7.86  |       |
|                                  | Jun-03 | C4F   | C            | P                       | 3.2               |         | 0.939  |          | 28.06 | 70.8 |                   | 58.6 | 7.64   |      | 8.32  |       |
|                                  | Mar-03 | C5M   | C            | P                       | 4.2               |         | 1.122  |          | 15.14 | 82.8 |                   | 58.8 | 7.03   |      | 8.36  |       |
|                                  | Jun-03 | C5M   | C            | P                       | 4.0               |         | 1.245  |          | 19.45 | 79.2 |                   | 54.9 | 7.69   |      | 7.14  |       |
|                                  | Mar-03 | C5F   | C            | P                       | 3.6               |         | 1.192  |          | 25.55 | 78.8 |                   | 54.8 | 6.99   |      | 7.84  |       |
|                                  | Jun-03 | C5F   | C            | P                       | 3.2               |         | 2.380  |          | 72.63 | 70.6 |                   | 58.1 | 7.29   | 5.3  | 7.97  | 29.80 |
|                                  | Mar-03 | C6F   | C            | P                       | 5.6               | 0.06(4) | 5.715  | 0.412(4) | 32.03 | 67.7 | 1.3               | 59.7 | 6.72   | 4.0  | 8.88  | 30.32 |
|                                  | Jun-03 | C6F   | C            | P                       | 4.6               | 0.1(3)  | 1.943  | 0.281(3) | 19.96 | 78.1 | 2.7               | 51.4 | 9.52   | 6.0  | 5.4   | 25.48 |
| <i>Paraeuchaeta modesta</i>      | Jun-03 | C6F   | C            | P                       | 5.1               | 0.66(3) | 3.867  | 1.584(3) | 29.67 | 69.3 | 6.2               | 58.7 | 7.43   | 5.7  | 7.19  | 30.40 |
| <i>Paraeuchaeta orientalis</i>   | Mar-03 | C6F   | C            | P                       | 7.8               |         | 8.557  |          | 18.03 | 80.1 |                   | 55.2 | 6.18   | 13.4 | 8.93  | 31.35 |
| <i>Paraeuchaeta pseudotumida</i> | Jun-03 | C6M   | C            | P                       | 4.3               | 0.85(2) | 2.272  | 1.006(2) | 28.58 | 67.5 | 4                 | 58.6 | 7.54   | 5.1  | 7.77  | 30.07 |
| <i>Paraeuchaeta rubra</i>        | Jan-00 | C6F   | C            | P                       | 4.7               |         | 2.585  |          | 24.90 | 70.7 |                   | 59.7 | 6.69   |      | 8.92  |       |
|                                  | Jun-03 | C5M   | C            | P                       | 3.9               |         | 1.902  |          | 32.06 | 69.3 |                   | 60.1 | 6.92   |      | 8.68  |       |
|                                  | Jun-03 | C6F   | C            | P                       | 5.1               | 0.21(2) | 3.498  | 0.296(2) | 27.16 | 75.0 | 1.2               | 56.0 | 7.80   | 6.5  | 7.18  | 28.86 |
| <i>Amalobrix valida</i>          | Jun-03 | C5M   | D            | P                       | 2.8               |         | 0.684  |          | 31.16 | 67.9 |                   | 56.1 | 8.01   |      | 7     |       |
|                                  | Jun-03 | C6F   | D            | P                       | 3.2               |         | 0.872  |          | 26.61 | 75.8 |                   | 47.7 | 10.80  |      | 4.42  |       |
| <i>Mistocalanus robetus</i>      | Jun-03 | C6F   | D            | P                       | 3.4               |         | 1.008  |          | 25.65 | 72.9 |                   | 47.1 | 11.10  |      | 4.24  |       |
| <i>Scaphocalanus medius</i>      | Jun-03 | C6F   | D            | P                       | 3.2               |         | 1.062  |          | 32.41 | 68.7 |                   | 57.3 | 7.41   |      | 7.73  |       |
| <i>Spinocalanus stellatus</i>    | Jun-03 | C6F   | S            | P                       | 3.2               |         | 0.818  |          | 24.96 | 75.9 |                   | 43.5 | 7.24   |      | 6.01  |       |
| Upper-bathypelagic (1000-2000 m) |        |       |              |                         |                   |         |        |          |       |      |                   |      |        |      |       |       |
| <i>Pachypitius pacificus</i>     | Jun-02 | C6F   | C            | A                       | 4.7               | 0.14(3) | 2.410  | 0.465(3) | 22.77 | 86.3 | 2.6               | 46.7 | 7.57   | 15.6 | 6.17  | 25.86 |
| <i>Lucicutia bicornata</i>       | Jun-03 | C6F   | S            | A                       | 3.4               |         | 1.017  |          | 25.88 | 81.5 |                   | 52.8 | 7.42   |      | 7.12  |       |
| <i>Lucicutia gracilis</i>        | Mar-02 | C6M   | S            | A                       | 3.8               |         | 0.984  | 0.192(2) | 18.66 | 87.0 | 4.5               | 45.4 | 7.38   | 16.6 | 6.15  | 25.26 |
| <i>Lucicutia grandis</i>         | Jun-04 | C6M   | S            | A                       | 4.8               |         | 2.192  |          | 19.82 | 79.9 |                   | 54.3 | 8.68   |      | 6.26  |       |
| <i>Lucicutia pacifica</i>        | Jun-02 | C6F   | S            | A                       | 4.8               |         | 1.810  |          | 16.89 | 82.1 |                   | 47.1 | 7.26   |      | 6.49  |       |
| <i>Metridia asymmetrica</i>      | Jun-03 | C6F   | S            | A                       | 4.5               |         | 1.634  |          | 17.93 | 84.0 |                   | 47.1 | 7.26   |      | 6.49  |       |
| <i>Metridia curticauda</i>       | Jun-02 | C6F   | S            | A                       | 2.7               | 0.06(4) | 0.360  | 0.071(2) | 19.34 | 74.8 | 5                 | 52.3 | 7.54   |      | 6.94  |       |
| <i>Metridia ornata</i>           | Jun-03 | C6F   | S            | A                       | 2.6               | 0.00(2) | 0.344  |          | 19.57 | 84.9 |                   | 47.1 | 7.24   |      | 6.51  |       |
| <i>Metridia rostrata</i>         | Jun-02 | C6F   | S            | A                       | 4.1               |         | 0.990  |          | 14.36 | 88.4 |                   | 47.6 | 7.36   |      | 6.47  |       |
| <i>Aetiideopsis rostrata</i>     | Jun-02 | C5M   | S            | P                       | 3.8               | 0.14(2) | 1.840  | 0.071(2) | 34.89 | 70.7 | 6.2               | 52.2 | 8.18   | 8.6  | 6.38  | 27.04 |
| <i>Bradydus pacificus</i>        | Mar-04 | C5M   | S            | P                       | 3.9               |         | 0.890  |          | 15.00 | 81.2 |                   | 50.7 | 8.75   |      | 5.79  |       |
| <i>Euchirella rostrata</i>       | Jun-02 | C6F   | S            | P                       | 3.0               | 0.06(6) | 0.804  | 0.116(6) | 30.38 | 78.8 | 2.9               | 44.3 | 11.20  | 8.8  | 3.96  | 21.53 |
| <i>Gaidius brevirostris</i>      | Jun-02 | C6F   | S            | P                       | 3.6               | 0.07(2) | 0.971  | 0.211(2) | 20.81 | 80.7 | 3.8               | 43.8 | 10.20  | 9.1  | 4.29  | 21.23 |
| <i>Gaidius variabilis</i>        | Jun-02 | C6F   | S            | P                       | 3.1               | 0.37(3) | 0.672  | 0.371(2) | 22.13 | 81.3 | 2.3               | 44.1 | 10.00  | 14.8 | 4.41  | 23.62 |
|                                  | Mar-04 | C6F   | S            | P                       | 3.6               | 0.06(3) | 0.935  | 0.274(3) | 20.55 | 82.7 | 4.3               | 46.0 | 10.70  | 14.1 | 4.3   | 24.84 |
| <i>Pseudocharella pacifica</i>   | Mar-04 | C5M   | S            | P                       | 3.2               | 0.64(3) | 0.554  | 0.051(2) | 16.91 | 81.3 | 8.2               | 53.0 | 9.27   | 11.7 | 5.72  | 29.04 |
|                                  | Jun-02 | C5F   | S            | P                       | 3.8               | 0.00(2) | 1.945  | 0.148(2) | 35.45 | 63.5 | 7.5               | 54.0 | 7.72   |      | 6.99  |       |
|                                  | Mar-04 | C5F   | S            | P                       | 3.9               | 0.04(2) | 1.637  | 0.114(2) | 28.24 | 72.7 | 2.3               | 56.5 | 8.83   |      | 6.4   |       |
| <i>Pseudocharella polyospina</i> | Jun-02 | C6F   | S            | P                       | 4.7               | 0.04(2) | 2.525  | 0.389(2) | 24.79 | 77.4 | 3.6               | 46.2 | 10.40  | 9.8  | 4.44  | 23.25 |
|                                  | Mar-04 | C6F   | S            | P                       | 4.8               | 0.11(4) | 3.057  | 0.358(4) | 27.84 | 75.8 | 1.5               | 53.1 | 9.52   | 9.7  | 5.58  | 28.23 |
| <i>Pseudocharella spinifera</i>  | Jun-02 | C5F   | S            | P                       | 3.8               |         | 1.790  |          | 32.62 | 69.1 |                   | 54.6 | 8.24   |      | 6.63  |       |
|                                  | Jun-02 | C6M   | S            | P                       | 3.8               |         | 1.200  |          | 21.87 | 75.0 |                   | 53.3 | 9.01   |      | 5.92  |       |
|                                  | Mar-04 | C6M   | S            | P                       | 3.7               |         | 1.363  | 0.482(2) | 26.48 | 71.8 | 8.7(2)            | 61.4 | 7.50   | 8.19 | 34.28 |       |



Table 3. Summary of CFI, chemical composition and energy content data of copepods in Table 2 grouped into 4 bathymetric zones, 4 development/sex categories, 3 feeding types or 2 presence/absence types of myelinated sheath enveloping axons. For the latter three groups, associated depth zones were calculated and showed in the last column (mean depth only for the "Depth zone" group). Epipelagic copepod data from Arctic/Antarctic waters are shown in *italic*. Differences among groups were tested by one-way ANOVA, combined with Bonferroni-test for between means. *NS*: not significant ( $p>0.05$ )

|              |                   | PL     | DW                  | CFI                 | Water               | C                   | N                   | Ash                 | C/N                 | J/AFDW              | J/DW                | Depth               |                     |
|--------------|-------------------|--------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| Depth zone   | <i>E*</i>         |        |                     |                     | <i>74.24</i>        | <i>49.54</i>        | <i>9.14</i>         | <i>8.40</i>         | <i>5.74</i>         | <i>27.34</i>        | <i>23.10</i>        | <i>50</i>           |                     |
|              |                   |        |                     |                     | <i>1.81</i>         | <i>6.61</i>         | <i>1.84</i>         | <i>1.61</i>         | <i>1.81</i>         | <i>3.67</i>         | <i>3.86</i>         |                     |                     |
|              |                   |        |                     |                     | <i>7</i>            | <i>14</i>           | <i>14</i>           | <i>8</i>            | <i>14</i>           | <i>8</i>            | <i>8</i>            |                     |                     |
|              | M                 | Mean   | 3.79                | 1.62                | 24.95               | 76.78               | 51.26               | 8.76                | 7.05                | 6.23                | 27.19               | 25.34               | 750                 |
|              |                   | SD     | 1.02                | 1.60                | 8.91                | 6.01                | 6.48                | 1.90                | 2.79                | 1.87                | 3.48                | 3.51                |                     |
|              |                   | N      | 52                  | 54                  | 52                  | 53                  | 54                  | 54                  | 21                  | 54                  | 21                  | 18                  |                     |
|              | UB                | Mean   | 4.28                | 2.17                | 24.82               | 75.58               | 53.74               | 8.24                | 9.58                | 6.68                | 28.19               | 25.71               | 1500                |
|              |                   | SD     | 1.02                | 1.51                | 6.54                | 6.20                | 5.61                | 1.16                | 2.82                | 1.29                | 3.86                | 3.82                |                     |
|              |                   | N      | 57                  | 57                  | 57                  | 57                  | 57                  | 57                  | 29                  | 57                  | 30                  | 29                  |                     |
|              | LB                | Mean   | 4.56                | 2.54                | 23.41               | 78.60               | 52.46               | 8.18                | 8.94                | 6.70                | 28.18               | 25.69               | 2500                |
|              |                   | SD     | 1.61                | 2.95                | 9.24                | 7.26                | 6.15                | 1.45                | 2.64                | 1.84                | 3.81                | 3.76                |                     |
|              |                   | N      | 48                  | 49                  | 48                  | 49                  | 49                  | 49                  | 13                  | 49                  | 13                  | 13                  |                     |
| AB           | Mean              | 4.27   | 2.60                | 21.47               | 74.98               | 51.85               | 7.68                | 6.92                | 6.96                | 29.47               | 27.43               | 4000                |                     |
|              | SD                | 1.68   | 5.09                | 8.19                | 8.88                | 7.34                | 1.20                | 1.88                | 1.68                | 2.57                | 2.44                |                     |                     |
|              | N                 | 30     | 30                  | 30                  | 30                  | 30                  | 30                  | 5                   | 30                  | 5                   | 5                   |                     |                     |
| <i>p</i>     |                   | 0.033  | 0.300 <sup>NS</sup> | 0.231 <sup>NS</sup> | 0.076 <sup>NS</sup> | 0.209 <sup>NS</sup> | 0.015               | 0.009               | 0.225 <sup>NS</sup> | 0.590 <sup>NS</sup> | 0.723 <sup>NS</sup> |                     |                     |
|              |                   |        | LB>M                |                     |                     |                     | M>AB                | UB>AB               |                     |                     |                     |                     |                     |
| Stage/sex    | C4                | Mean   | 2.93                | 0.64                | 24.50               | 76.10               | 52.38               | 8.85                |                     | 6.27                |                     | 750                 |                     |
|              |                   | SD     | 0.22                | 0.24                | 4.02                | 4.25                | 6.30                | 1.97                |                     | 2.11                |                     | 0                   |                     |
|              |                   | N      | 4                   | 4                   | 4                   | 4                   | 4                   | 4                   | 4                   | 0                   | 0                   | 4                   |                     |
|              | C5                | Mean   | 3.87                | 1.68                | 26.52               | 75.04               | 53.47               | 8.04                | 7.51                | 6.89                | 30.03               | 27.77               | 1870                |
|              |                   | SD     | 0.69                | 1.18                | 11.31               | 7.68                | 7.30                | 1.24                | 2.09                | 1.78                | 3.04                | 2.81                | 1096                |
|              |                   | N      | 50                  | 50                  | 50                  | 50                  | 50                  | 50                  | 14                  | 50                  | 14                  | 14                  | 50                  |
|              | C6F               | Mean   | 4.46                | 2.56                | 22.95               | 77.67               | 51.51               | 8.43                | 8.69                | 6.38                | 27.21               | 24.92               | 2002                |
|              |                   | SD     | 1.57                | 3.39                | 6.91                | 6.45                | 5.55                | 1.58                | 2.97                | 1.55                | 3.38                | 3.44                | 1118                |
|              |                   | N      | 115                 | 117                 | 114                 | 116                 | 117                 | 117                 | 48                  | 117                 | 49                  | 49                  | 117                 |
|              | C6M               | Mean   | 3.90                | 1.46                | 23.16               | 74.31               | 55.11               | 7.93                | 9.07                | 7.28                | 29.48               | 26.86               | 1987                |
|              |                   | SD     | 0.65                | 0.73                | 5.43                | 7.83                | 7.28                | 1.56                | 4.01                | 1.95                | 5.11                | 5.10                | 1052                |
|              |                   | N      | 19                  | 19                  | 19                  | 19                  | 19                  | 19                  | 6                   | 19                  | 6                   | 6                   | 19                  |
| <i>p</i>     |                   | 0.006  | 0.098 <sup>NS</sup> | 0.080 <sup>NS</sup> | 0.062 <sup>NS</sup> | 0.063 <sup>NS</sup> | 0.260 <sup>NS</sup> | 0.362 <sup>NS</sup> | 0.067 <sup>NS</sup> | 0.020               | 0.023               | 0.154 <sup>NS</sup> |                     |
|              |                   |        | C6F>C5              |                     |                     |                     |                     |                     |                     | C5>C6F              | C5>C6F              |                     |                     |
| Feeding type | Camivore          | Mean   | 4.66                | 2.88                | 27.06               | 74.54               | 56.01               | 7.62                | 7.19                | 7.49                | 30.45               | 28.31               | 1605                |
|              |                   | SD     | 1.17                | 1.99                | 10.3                | 7.18                | 6.21                | 0.98                | 2.76                | 1.31                | 2.33                | 2.22                | 982                 |
|              |                   | N      | 50                  | 50                  | 50                  | 50                  | 50                  | 50                  | 26                  | 50                  | 26                  | 25                  | 50                  |
|              | Detritivore       | Mean   | 4.02                | 1.86                | 25.02               | 74.63               | 54.28               | 8.4                 | 8.14                | 6.71                | 28.28               | 26                  | 1952                |
|              |                   | SD     | 1.3                 | 1.86                | 7.17                | 6.49                | 4.82                | 1.42                | 2.21                | 1.62                | 2.42                | 2.67                | 965                 |
|              |                   | N      | 30                  | 31                  | 30                  | 31                  | 31                  | 31                  | 5                   | 31                  | 5                   | 5                   | 31                  |
|              | Suspension feeder | Mean   | 4.06                | 1.94                | 22.21               | 78.13               | 50.22               | 8.56                | 9.44                | 6.16                | 26.24               | 23.86               | 2089                |
|              |                   | SD     | 1.38                | 3.23                | 6.99                | 6.7                 | 5.84                | 1.65                | 2.8                 | 1.7                 | 3.56                | 3.4                 | 1166                |
|              |                   | N      | 107                 | 109                 | 107                 | 108                 | 109                 | 109                 | 37                  | 109                 | 38                  | 35                  | 109                 |
|              | <i>p</i>          |        | 0.020               | 0.112 <sup>NS</sup> | 0.002               | 0.002               | <0.001              | <0.001              | 0.008               | <0.001              | <0.001              | <0.001              | 0.036               |
|              |                   |        |                     | C>S                 | C>S                 | S>C=D               | C=D>S               | S>C                 | S>C                 | C>S                 | C>S                 | C>S                 | S>C                 |
|              | Myelinated sheath | Absent | Mean                | 4.04                | 1.25                | 18.61               | 82.96               | 49.12               | 7.83                | 10.31               | 6.48                | 25.08               | 22.31               |
|              |                   | SD     | 1.12                | 0.76                | 5.79                | 4.6                 | 5.44                | 1.37                | 4.24                | 1.41                | 2.99                | 1.92                | 971                 |
|              |                   | N      | 40                  | 42                  | 40                  | 41                  | 42                  | 42                  | 8                   | 42                  | 9                   | 6                   | 42                  |
| Present      |                   | Mean   | 4.26                | 2.44                | 25.41               | 74.84               | 53.34               | 8.42                | 8.24                | 6.64                | 28.41               | 26.08               | 1926                |
|              |                   | SD     | 1.39                | 3.07                | 8.25                | 6.5                 | 6.25                | 1.53                | 2.65                | 1.75                | 3.55                | 3.56                | 1141                |
|              |                   | N      | 147                 | 148                 | 147                 | 148                 | 148                 | 148                 | 60                  | 148                 | 60                  | 59                  | 148                 |
| <i>p</i>     |                   |        | 0.342 <sup>NS</sup> | 0.013               | <0.001              | <0.001              | <0.001              | 0.025               | 0.058 <sup>NS</sup> | 0.603 <sup>NS</sup> | 0.011               | 0.013               | 0.747 <sup>NS</sup> |
|              |                   |        |                     | P>A                 | P>A                 | A>P                 | P>A                 | P>A                 |                     |                     | P>A                 | P>A                 |                     |

Table 4. Attributes of the depth (UB, LB or AB), stage/sex (C5, C6F or C6M), feeding type (DETR or SUS), presence/absence of myelinated axons (MYEL), prosome length (PL) and dry weight (DW) to CFI, chemical composition (WATER, C, N, ASH or C/N) or energy content (*I*/AFDW or *J*/DW) of mesopelagic through abyssopelagic copepods. + + +, + + or + indicates the coefficients are all positive and significant at  $p < 0.001$ ,  $p < 0.01$  and  $p < 0.05$ , respectively. - - -, - - or - indicates the coefficients are all negative and significant at  $p < 0.001$ ,  $p < 0.01$  and  $p < 0.05$ , respectively.

| Independent variable | UB  | LB | AB  | C5 | C6F | C6M | DETR | SUS | MYEL | PL  | DW  |
|----------------------|-----|----|-----|----|-----|-----|------|-----|------|-----|-----|
| CFI                  |     |    | -   |    |     |     | --   | --- | +++  | --- | +++ |
| WATER                |     |    |     |    |     | --  |      | ++  | ---  |     |     |
| C                    |     |    |     |    | --  |     |      | --- | +    | --- | +++ |
| N                    |     |    | --- | -- |     |     |      | +++ | +++  |     | -   |
| ASH                  | +++ |    |     |    |     |     |      | +++ |      |     |     |
| C/N                  |     |    | +   |    | --  |     |      | --- |      | -   | ++  |
| <i>I</i> /AFDW       |     |    |     |    | --- |     |      | --- | +    |     | ++  |
| <i>J</i> /DW         |     |    |     |    | --- |     |      | --- | +    |     | +++ |

### Figure caption

Fig. 1. Location of sampling stations (solid circles; Site H, KNOT and others) in the western North Pacific Ocean. Depth contours (1000 to 6000 m) are superimposed.

Fig. 2. Temperature and salinity profiles at Site H (40°30'N 145°50'E), one of the major sampling sites of this study. Note that both temperature and salinity below 500 m are nearly stable throughout the year.

Fig. 3. Changes with the depth of occurrence in (top) water content, carbon (C), nitrogen (N), (bottom) C:N ratio, ash and energy of pelagic copepods in the western subarctic Pacific (including epipelagic data of Arctic/Antarctic copepods). The depth represents mid-range of the epipelagic (50 m for 0-100 m), mesopelagic (750 for 500-1000 m), upper-bathypelagic (1500 for 1000-2000 m), lower-bathypelagic (2500 for 2000-3000 m) and abyssopelagic (4000 for 3000-5000 m) zones. For statistically significant cases, a best-fit regression line was superimposed:  $N = 9.06 - 0.00038 \times \text{Depth}$  ( $r = 0.964$ ), and  $C/N = 0.635 \log_{10} \text{Depth} + 4.60$  ( $r = 0.967$ ). The figure includes the “surface” (designated as 75 m) and “deep” (1000 m) copepod data from “high” latitude seas by Båmstedt (1986), and net-plankton data at 100, 600, 1500 and 4000 m by Yamaguchi et al. (2005). Symbols and horizontal bars denote means and 1 SD.

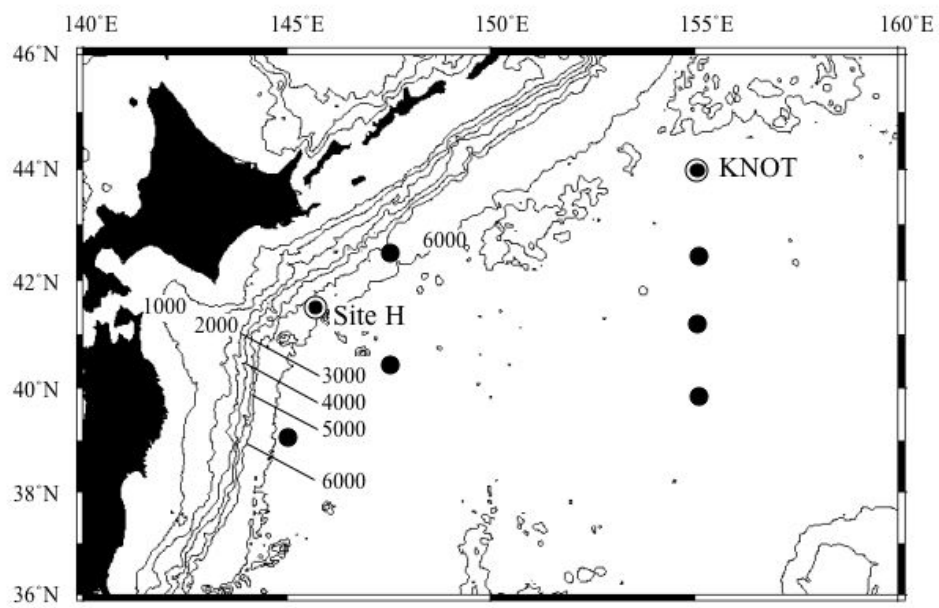


Fig. 1 (Ikeda et al.)

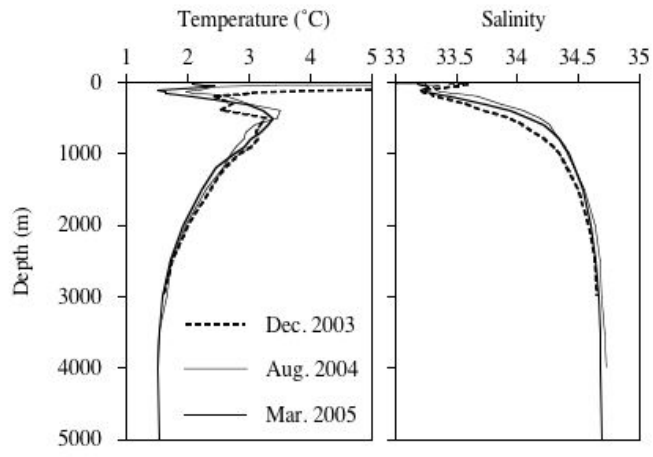


Fig. 2 (Ikeda et al.)

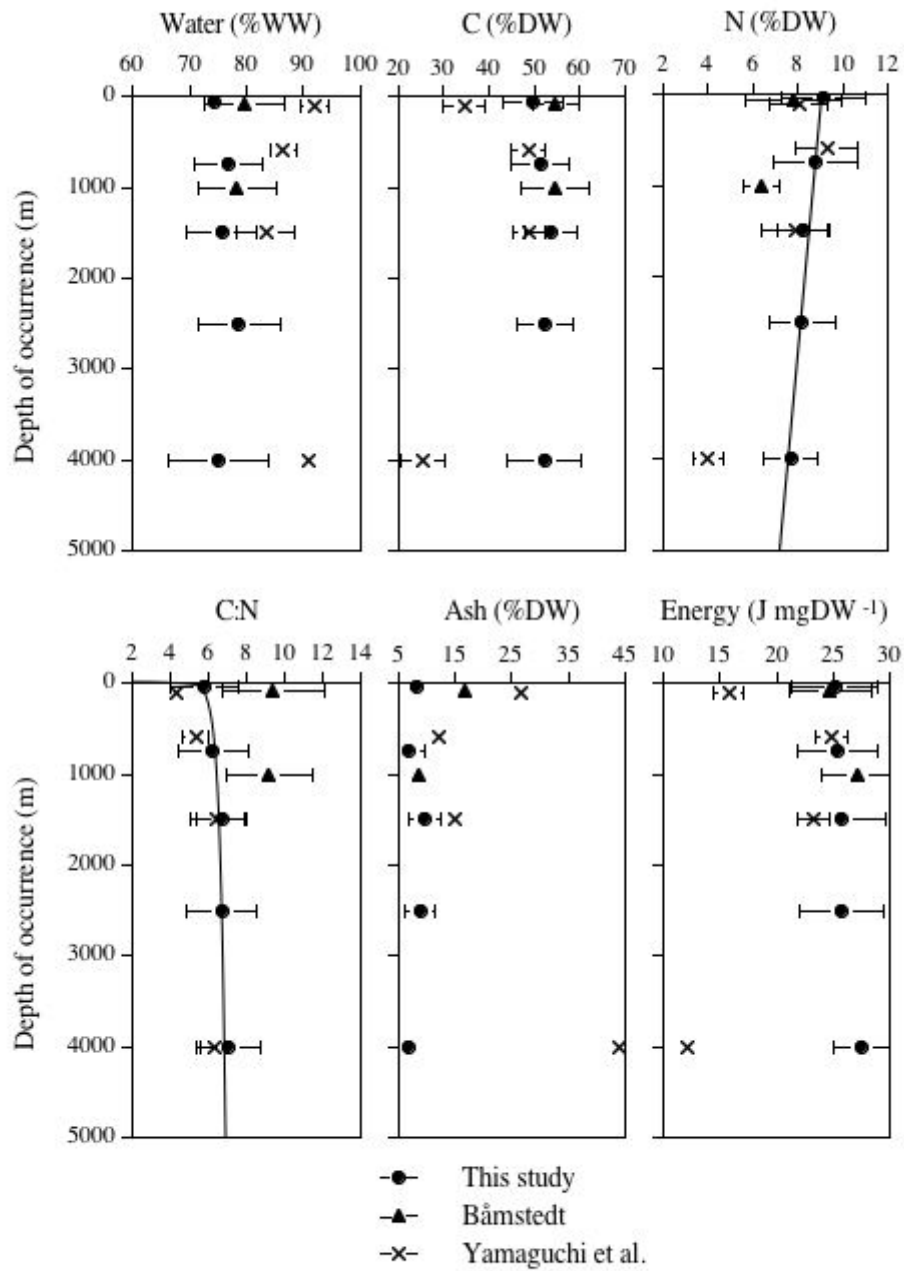


Fig. 3 (Ikeda et al.)