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Metabolic activity of pelagic copepods from 5000-7000 m depth of the western  
subarctic Pacific, as inferred from electron-transfer-system (ETS) activity

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Pacific

Running head: ETS activity of pelagic copepods from 5000-7000 m depth

## Abstract

This study demonstrates reduced electron transfer system (ETS) activity of mixed copepods collected from 5,000 to 7,000 m depths [ $3.21 \pm 1.25 \mu\text{l O}_2 (\text{mg protein})^{-1} \text{h}^{-1}$  at  $10^\circ\text{C}$ ] as compared with mixed copepods from 0 to 200 m depths [ $5.93 \pm 1.66 \mu\text{l O}_2 (\text{mg protein})^{-1} \text{h}^{-1}$  at  $10^\circ\text{C}$ ] of the western subarctic Pacific. At the in situ temperature of  $1.5^\circ\text{C}$ , the 5,000–7,000 m ETS data, in terms of wet mass (WM)-specific respiration rates (R), is equivalent to [ $0.052 \pm 0.021 \mu\text{l O}_2 (\text{mg WM})^{-1} \text{h}^{-1}$ ] which is similar to or greater than those reported for selected copepods or mixed mesozooplankton from 5,000 m depth by previous workers.

## 1. Introduction

Copepods are the major component of marine mesozooplankton and may be the most numerous multicellular organisms on the earth (Longhurst 1985; Mauchline 1998). Because of their ubiquitous distribution, high abundance and trophic importance, vital rates of copepods and other mesozooplankton are of particular relevance to understanding oceanic biogeochemical cycles of carbon and other elements (Hernandez-Leon and Ikeda 2005; Aristegui et al. 2005; Buitenhuis et al. 2006). Copepod respiration (=oxygen consumption) is a direct measure of mineralization, and voluminous data has been accumulated on the epipelagic copepods of the world's oceans (Ivleva 1980; Ikeda et al. 2001). In contrast, from the mesopelagic and bathypelagic zones, little respiration is currently available for live copepods except for two studies; one off California (Thuesen et al. 1998) and the other in the western subarctic Pacific (Ikeda et al. 2006a, 2007a). This paucity of information about respiration in deep-sea copepods reflects the technical difficulty in retrieving live specimens from depth in good enough condition for incubation experiments. To date, the maximum depth from which copepods have been retrieved for incubation experiments is 3000-5000 m (Ikeda et al. 2007a). Copepods living below 5000 m are known to be characterized by smaller body size than those distributing above (Vinogradov 1962; Mauchline 1972) but their respiration rates have not been studied.

An enzyme assay of intermediary metabolism can be a measure of potential respiration. Its advantage over a physiological measurement on deep-sea copepods is its freedom from problems associated with recovery of live copepods from depth. This is because the cellular enzyme concentration in a specimen does not vary appreciably on a short time scale (cf. Ikeda et al. 2000). If the enzyme is constitutive, this is especially

true. The intermediary enzymes, citrate synthase (CS), lactate dehydrogenase (LDH) and pyruvate kinase (PK) have been used as indices of respiration as well as indicators of aerobic metabolism, anaerobic metabolism and glycolytic flux, respectively, in deep-sea pelagic animals (see review of Childress 1995). However, both LDH and CS activities were poorly correlated with respiration rates of the deep-sea copepods (Thuesen et al. 1998). Furthermore, as indicators of respiratory O<sub>2</sub> consumption or CO<sub>2</sub> production, they are poor choices because they are not associated closely with the reactions of either O<sub>2</sub> consumption or with CO<sub>2</sub> production. As an alternative, enzyme activities of electron-transfer-system (ETS), the enzyme system that is known from all biochemistry text-books to control the respiratory O<sub>2</sub> consumption, have been shown to be closely associated with respiration rates of marine zooplankton (Packard et al. 1975; King and Packard 1975a; Packard and Gómez 2008). ETS activity has been used as a practical method to estimate community metabolism of deep-sea zooplankton (King et al. 1978; Koppelman et al. 2004; Hernández-León and Ikeda 2005). Theoretically, according to enzyme kinetics, the ratio of ETS activity to respiration is 2 (Owens and King 1975; King and Packard 1975a) and is little affected by temperature and body mass of zooplankton tested (King and Packard 1975a).

As part of a deep-sea zooplankton metabolism project (Ikeda et al. 2006a and b, 2007a and b), I determined potential respiration rates (ETS activity) of copepods living below 5000 m of the subarctic Pacific to gain insight into their metabolic characteristics.

## **2. Materials and methods**

## 2.1 Zooplankton sampling

Copepods were collected from 5,000-7,000 m depth at station D (42°40'N 147°58'E) off the east coast of Hokkaido during RS Tansei-Marui Cruise KT-05-12 to the western subarctic Pacific on June 3, 2005 (Fig. 1). A vertical closing net [80 cm diameter, 0.3 mm mesh size; modified from Kawamura (1968)] equipped with a large cod-end (2 l capacity) was used to retrieve zooplankton from depth. The closing net was towed from 7,000 to 5,000 m at a speed of 0.5 m sec<sup>-1</sup>, closed and raised to the surface at 2 m sec<sup>-1</sup>. The depth the net reached was estimated by the length of winch wire paid out on the basis of a linear relationship between the wire length and the depth of the net reached; the linear relationship was confirmed repeatedly by using a RMD depth meter (Rigosha Co. Ltd.) monitoring the net at depths above 5000 m [note: the maximum depth to which the depth meter withstands was 5,000 m]. The distance towed of the open net (2,000 m) was confirmed by a flow-meter (Rigosha Co. Ltd.) attached to the mouth-ring of the net. The flow meter reading was 14,328 revolutions which compared well with 14,171 (±1,770, SD, N = 4) revolutions, the value obtained by calibrating the net in a vertical haul from 5,000 m to 3,000 m. After closing the mouth of the net at 5,000 m, the net reached the surface in 42 min. As a control, shallow-living copepods were collected with a Norpac net (0.3 mm mesh) which was towed from 200 m to the surface at station S (40°29'N 142°30'E, Fig. 1) off the northeast coast of Honshu on June 6 during the same cruise.

Upon retrieval of the net, zooplankton samples were passed through 1.4 mm mesh netting to remove gelatinous material. Undamaged copepods in the filtrate were sorted immediately into chilled seawater which had been collected from 6,000 m depth with 20

1 Niskin bottles or from the surface with a bucket just prior to zooplankton collection.

Temperature, salinity and dissolved oxygen profiles were determined by using a CTD

system down to 5,000 m.

## 2.2 ETS activity

Batches of copepods (10-30 specimens each) were placed on 0.2 mm mesh nettings, blotted on filter paper, preserved immediately in liquid nitrogen on board the ship, and brought back to the land laboratory for ETS analysis. Within one month after the cruise, each batch of frozen copepods was homogenized with a small piece of glass fiber filter in a glass-teflon tissue homogenizer. The Owens and King (1975) ETS assay was used. However, the final reaction volume was reduced from 6 ml to 1.5 ml. One ml of each homogenized sample was centrifuged yielding a cell-free extract that was used for the ETS assay. Preliminary tests indicated that the ETS activities from 5,000-7,000 m depth were too low to measure at *in situ* temperature (1.5°C). To overcome this problem, the reaction temperature of the assays was raised to 10°C. ETS activities were determined on two 0.25 ml aliquots of cell-free extract from each subsample. The effect of hydrostatic pressure on ETS activities of crustacean plankton has been demonstrated to be not significant at least down to 265 atm (King and Packard 1975b). As an indicator of copepod biomass, protein concentrations were determined on each homogenate to standardize ETS activities. Protein was determined in duplicate by the method of Lowry et al. (1951) using bovine serum albumin as a standard.

## 2.3 Taxonomy/biometry

Part of each fresh subsample was preserved in 10% formalin-seawater for microscopic observation. Part of each frozen subsample was used to establish mean wet mass (WM), dry mass (DM) and the protein of individual copepods. DM was obtained by freeze-drying the subsamples.

### 3. Results and discussion

#### 3.1 ETS activity of copepods from 5000-7000 m versus those from 0-200 m

Copepods from 5,000-7,000 m depth (Fig. 2) were composed of *Spinocalanus* spp. (33%, the total N = 91), *Scaphocalanus* spp. (11%), *Microcalanus* spp. (9%), *Lucicutia* spp. (8%) and others (39%), and those from 0-200 m depth *Pseudocalanus* spp. (28%, the total N = 72), *Metridia pacifica* (24%), *Neocalanus plumchrus* (21%), *Eucalanus bungii* (18%) and others (9%).

Mean WM, DM and protein content were 0.328 mg individual<sup>-1</sup>, 0.066 mg individual<sup>-1</sup> and 6.71 % of WM, respectively, for copepods from the 5000-7000 m, and were 0.394 mg individual<sup>-1</sup>, 0.058 mg individual<sup>-1</sup> and 7.19% of WM, respectively, for those from the 0-200 m (Table 1).

ETS activity determined at 10°C was  $3.21 \pm 1.25 \mu\text{l O}_2 (\text{mg protein})^{-1}\text{h}^{-1}$  (N = 16) for the 5,000-7,000 m copepods and  $5.93 \pm 1.66 \mu\text{l O}_2 (\text{mg protein})^{-1}\text{h}^{-1}$  (N = 15) for the 0-200 m copepods (Fig. 3). On the basis that each dataset was normally distributed (Chi-square test,  $p > 0.1$ ) and the variance of both datasets did not differ significantly (F-test,  $p > 0.05$ ), Student t-test detected a significant difference between the two means

( $p < 0.001$ ).

The body mass and temperature have been documented as two major parameters affecting the metabolic rates of pelagic copepods across diverse species (Ikeda et al. 2001). From this, combined with an intimate relationship between respiration rates and ETS activity (Packard et al. 1975; King and Packard 1975a), mixed copepods from 5,000-7,000 m and 0-200 m of this study were anticipated to yield similar ETS activities since the body mass of each component copepod was effectively the same (Table 1) and all the assays were made at the same temperature (10°C, Fig. 3). However, the observed ETS activities of the copepods from 5,000-7,000 m were about one half that of those from 0-200 m (Fig. 3), implying the presence of important parameter(s) other than temperature and body mass. This negative effect of habitat depth on body mass specific  $R_s$  (standardized by body mass and temperature) has already been documented for deeper-living micronektonic fishes, crustaceans and cephalopods with functional eyes (Childress, 1995). According to Childress (1995), the vision-aided reaction distance in prey-predator relationships decreases downward due to diminishing light; thus, progressively less energy expenditure is required for vision-aided prey/predator reactions with increasing depth (“visual interactions hypothesis”). For pelagic copepods with no functional eyes, there are conflicting reports of neutral (Thuesen et al. 1998) and negative effects of habitat depth (Ikeda et al. 2006a; Ikeda 2008). The results here favor the view of Ikeda et al. (2006a) and Ikeda (2008). Because pelagic copepods lack functional eyes, the negative effect of habitat depth on the metabolism of pelagic copepods cannot be explained by the “visual interactions hypothesis”. Ikeda et al. (2006a) proposed a new “predation-mediated selection hypothesis” that explained reduced respiration rates of deeper-living copepods to be a result of lowered selective

pressure for high activity at these depths because of the decrease in visual predators in the dark. Reduced metabolic rates of deep-sea copepods are in concert with their lower protein synthesis activities (= growth rates) as evidenced by their lower RNA:DNA ratios (Ikeda et al. 2007b).

### 3.2 ETS-respiration of copepods/mesozooplankton

Previously (Table 2), ETS activities have been determined on selected copepods from 0-5,000 m in the western subarctic Pacific (Ikeda et al. 2006a; Ikeda unpublished), on mixed mesozooplankton from 0-3,000 m in the tropical North Pacific (King et al. 1978), and on mixed mesozooplankton from 2,500-4,000 m in the eastern Mediterranean and Arabian Sea (Koppelman et al. 2004). ETS data ( $ETS_{\text{assay}}$ ) derived from various assay temperatures were corrected to 1.5°C (= near *in situ* temperature at 6000 m of this study, Table 1) by the Arrhenius equation;  $ETS = ETS_{\text{assay}} \times \exp [E_a(T_{\text{assay}}^{-1} - T^{-1}) / R_g]$ , where  $E_a$  is an activation energy (16 and 13.2 kcal mole<sup>-1</sup> for epipelagic and bathypelagic zooplankton, respectively, Packard et al. 1975),  $R_g$  is the gas constant ( $1.987 \times 10^{-3}$  kcal mole<sup>-1</sup>),  $T$  is the absolute temperature (K). Given the temperature range of this study (1.5-10°C), the  $E_a = 16$  or 13.2 kcal mole<sup>-1</sup> of the Arrhenius equation is equivalent to  $Q_{10} = 2.82$  or 2.35 of van't Hoff rule. Corrected ETS data were converted to respiration rates ( $R$ ) on the basis of  $R = 0.5 \times ETS$  (Owens and King 1975; King and Packard 1975a).  $R$ s expressed per mg protein were re-expressed per mg WM by multiplying by the appropriate conversion factors (protein contents of 6.71 or 7.19% of WM for the present data, Table 1). For comparing metabolic activities, N or protein is superior to WM as body mass unit (Ikeda 2008), but WM is used in this comparison since little is

known about the conversion factor of WM to N or protein for mixed mesozooplankton from depth. The sensitivity of ETS assay differs due to the use of different components in the homogenate buffer, with or without the detergent (Triton X-100), dissimilar pH and/or substrate concentrations (Christensen and Packard 1979). In this regard, the data of Koppelman et al. (2004) derived from Kenner and Ahmed (1975)'s assay method are comparable to the present data (Christensen and Packard, 1979) but those of King et al. (1978) derived from Packard (1971)'s assay method need to be multiplied by 3.3 (Owens and King 1975). The ETS data for copepods and mixed mesozooplankton from the epipelagic layer from several regions of the world's oceans thus standardized to WM-specific R ( $\mu\text{l O}_2 (\text{mg WM})^{-1}\text{h}^{-1}$ ) at 1.5°C ranged from 0.084 to 0.229 (Table 2).

While selected copepods by Ikeda et al. (2007a) and Ikeda (unpublished) exhibited a wide range of data and were composed of much larger specimens than those of mixed copepods in this study, their mean WM-specific Rs at 1.5°C were similar to the present results if the sampling depth is considered. Mesozooplankton Rs were compared with copepod Rs on the premise that the latter is the major component of the former in ocean interiors (Vinogradov 1970; Yamaguchi et al. 2004). Compared with the present results on 5,000-7,000 m copepods, mesozooplankton data from 2,000-3,000 m in the tropical North Pacific (King et al. 1978) are comparable, but those from 2,750-4,250 m in the eastern Mediterranean and the Arabian Sea (Koppelmann et al. 2004) are less than the present 5,000-7,000 m data by a factor of 0.16-0.52 (Table 2). Consistently lower Rs of Koppelmann et al. (2004) may be due to the overestimation of mesozooplankton biomass by detritus. Russian workers have been defining "seston" mass (detritus plus organisms) to be the entire net samples, and plankton biomass to be a sum of individual organisms in the sample (Rudiyakov and Tseitlin 1992; Kitain et al.

1995). The proportion of detritus in plankton samples has been known to vary with mesh size of net used, study region, season and depth (Rudyakov and Tseitlin 1992; Koppelman 1994). By using the Russian term mentioned above, it is noted that the prime objective of Koppelmann et al. (2004) is to calculate mesozooplankton community respiration by combining WM-specific seston respiration and seston mass, for which separation of organisms and detritus is of little importance. In addition to detritus, possible dissimilar regional physical, chemical and biological conditions of their deep habitats could also affect ETS activities of resident zooplankton, but our knowledge about deep-sea zooplankton metabolism at present is too limited to allow rigorous inter-comparison among the regional data.

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## References

- Aristegui J, Agustí S, Middleburg JJ, Duarte CM (2005) Zooplankton respiration. In: del Giorgio PA, leB. Williams PJ (eds) .Respiration in aquatic ecosystems. Oxford Univ Press, Oxford, pp 181-205
- Buitenhuis E, Quere CL, Aumont Q, Beaugrand G, Bunker A, Hirst A, Ikeda T, O'Brien T, Pointkovski S, Straile D (2006) Biogeochemical fluxes through mesozooplankton. *Global Biogeochem Cycles* 20: GB2003, doi:10.1029/2005GB002511
- Childress JJ (1995) Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *TREE* 10: 30-36
- Christensen JP, Packard TT (1979) Respiratory electron transport activities in phytoplankton and bacteria: Comparison of methods. *Limnol Oceanogr* 24: 576-583
- Hernández-León S, Ikeda T (2005) A global assessment of mesozooplankton respiration in the ocean. *J Plankton Res* 27: 153-158
- Ikeda T (2008) Metabolism in mesopelagic and bathypelagic copepods: Reply to Childress et al. (2008). *Mar Ecol Prog Ser* 373: 193-198
- Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar Biol* 139: 587-596
- Ikeda T, Sano F, Yamaguchi A, Matsuishi T (2006a) Metabolism of mesopelagic and bathypelagic copepods in the western North Pacific Ocean. *Mar Ecol Prog Ser* 322: 199-211
- Ikeda T, Sano F, Yamaguchi A (2007a) Respiration in marine pelagic copepods: a global-bathymetric model. *Mar Ecol Prog Ser* 339: 215-219

289 Ikeda T, Sano F, Yamaguchi A, Matsuishi T (2007b) RNA:DNA ratios of calanoid  
 290 copepods from the epipelagic through abyssopelagic zones of the North Pacific  
 291 Ocean. *Aquat Biol* 1: 99-108  
 292 Ikeda T, Torres JJ, Hernández-León S, Geiger SP (2000) Metabolism. In Harris RP et al.  
 293 (eds) ICES zooplankton methodology manual. Academic Press, San Diego, pp.  
 294 455-532  
 295 Ikeda T, Yamaguchi A, Matsuishi T (2006b) Chemical composition and energy content  
 296 of deep-sea calanoid copepods in the western North Pacific Ocean. *Deep-Sea*  
 297 *Res I* 53: 1791-1809  
 298 Ivleva IV (1980) The dependence of crustacean respiration rate on body mass and  
 299 habitat temperature. *Int Revue ges Hydrobiol* 65: 1-47  
 300 Kawamura A (1968) Performance of Peterson type closing net. *Bull Plankton Soc Jpn*  
 301 15: 11-12  
 302 Kenner RA, Ahmed SI (1975) Measurements of electron transport activities in marine  
 303 phytoplankton. *Mar Biol* 33: 119-127  
 304 King FD, Packard TT (1975a) Respiration and the activity of the respiratory electron  
 305 transport system in marine zooplankton. *Limnol Oceanor* 20: 849-853  
 306 King, F.D. and Packard, T.T. (1975b): The effect of hydrostatic pressure on respiratory  
 307 electron transport system activity in marine zooplankton. *Deep-Sea Res.*, **22**,  
 308 99-105.  
 309 King FD, Devol AH, Packard TT (1978) Plankton metabolic activity in the eastern  
 310 tropical North Pacific. *Deep-Sea Res* 25: 689-704  
 311 Kitain Vya, Rudyakov YuA, Tseitlin VB (1995) Seston and zooplankton of the Bering  
 312 Sea and the northwestern Pacific. *Oceanology* 35: 66-68

313 Koppelman R (1994) Distribution and composition of gelatinous detrital material from  
 314 closing net hauls in the NE Atlantic. *Mar Biol* 118: 755-759

315 Koppelman R, Weikert H, Halsband-Lenk C, Jennerjahn T (2004) Mesozooplankton  
 316 community respiration and its relation to particle flux in the oligotrophic eastern  
 317 Mediterranean. *Global Biogeochem Cycles* 18: GB1039,  
 318 doi:10.1029/2003GB002121

319 Longhurst AR (1985) The structure and evolution of plankton communities. *Prog*  
 320 *Oceanogr* 15: 1-35

321 Lowry OH, Rosebrough NJ, Farr AL, Randall RJ (1951) Protein measurement with the  
 322 Folin Phenol reagent. *J. Biol. Chem* 193: 265-275

323 Mauchline J (1972) The biology of bathypelagic organisms, especially Crustacea.  
 324 *Deep-Sea Res* 19: 753-780

325 Mauchline J (1998) The biology of calanoid copepods. *Adv Mar.Biol* 33: 1-710

326 Owens TG, King FD (1975) The measurement of respiratory electron-transport system  
 327 activity in marine zooplankton. *Mar Biol* 30: 27-36

328 Packard TT (1971) The measurement of respiratory electron transport activity in marine  
 329 phytoplankton. *J Mar Res* 28: 235-244

330 Packard TT, Devol AH, King FD (1975):The effect of temperature on the respiratory  
 331 electron transport system in marine plankton. *Deep-Sea Res* 22: 237-249

332 Packard TT, Gómes M. (2008) Exploring a first-principles-based model for zooplankton  
 333 respiration. *ICES J Mar.Sci* 65: 371-378

334 Rudyakov YuA, Tseitlin VB (1992) Biomass ratio of seston and zooplankton.  
 335 *Oceanology* 32: 618-620

336 Thuesen EV, Miller CB, Childress JJ (1998) Ecophysiological interpretation of oxygen

337 consumption rates and enzymatic activities of deep-sea copepod. Mar Ecol Prog  
 338 Ser 168: 95-107  
 339 Vinogradov ME (1962) Feeding of the deep-sea zooplankton. Rapp R-v Réun Cons  
 340 perm int Explor Mer 153: 114-120  
 341 Vinogradov ME (1970) Vertical distribution of oceanic zooplankton. Israel Program for  
 342 Scientific Translations, Jerusalem, pp 339  
 343 Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J,  
 344 Ikeda T, Takahashi MM (2004) Latitudinal differences in the planktonic biomass  
 345 and community structure down to the great depths in the western North Pacific.  
 346 J Oceanogr 60: 773-787  
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**Table 1** Summary of sampling data, biomass (WM and DM) and potein contents of copepods from the western subarctic Pacific. Means  $\pm$  SD, with the number of replicates in parentheses.

| Mid-sampling<br>depth (m)  | <i>In situ</i> T<br>(°C) | WM<br>(mg indiv <sup>-1</sup> ) | DM<br>(mg indiv <sup>-1</sup> ) | Protein<br>(% of WM) |
|----------------------------|--------------------------|---------------------------------|---------------------------------|----------------------|
| 100 (control) <sup>a</sup> | 3.6                      | 0.394 $\pm$ 0.045(4)            | 0.058 $\pm$ 0.006(4)            | 7.19 $\pm$ 1.11(4)   |
| 6,000 <sup>b</sup>         | 1.5 <sup>c</sup>         | 0.328 $\pm$ 0.074(3)            | 0.066 $\pm$ 0.023(3)            | 6.71 $\pm$ 1.86(3)   |

<sup>a</sup> 0-200 m

<sup>b</sup> 5,000-7,000 m

<sup>c</sup> substituted by the data at 5,000 m

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**Table 2** ETS-respiration (R) data of zooplankton from various depths and regions of the world's oceans. ETS data reported by various units were re-calculated and expressed as WM-specific R at 1.5°C. Values are means or means  $\pm$  SD. N denotes the number of replicates (gothic) or species/stage/sex structured data (italic). ND = No data. See text for details.

| Sampling depth (m) | Region               | Zooplankton                | Mean body mass (mgWM indiv <sup>-1</sup> ) | Assay T (°C) | Original unit                                         | N  | R at 1.5°C ( $\mu\text{LO}_2(\text{mgWM})^{-1}\text{h}^{-1}$ ) | Reference               |
|--------------------|----------------------|----------------------------|--------------------------------------------|--------------|-------------------------------------------------------|----|----------------------------------------------------------------|-------------------------|
| euphotic zone      | Tropical N Pacific   | Mixed mesozooplankton      | ND                                         | 20           | $\mu\text{LO}_2(\text{mgDM})^{-1}\text{h}^{-1}$       | 27 | $0.229 \pm 0.073^b$                                            | King et al. (1978)      |
| 0-250              | W. subarctic Pacific | Selected calanoid copepods | 4.45                                       | 10           | $\mu\text{LO}_2(\text{mg protein})^{-1}\text{h}^{-1}$ | 17 | $0.105 \pm 0.042^a$                                            | Ikeda et al. (2006a)    |
| 0-200              | W. subarctic Pacific | Mixed copepods             | 0.394                                      | 10           | $\mu\text{LO}_2(\text{mg protein})^{-1}\text{h}^{-1}$ | 15 | $0.088 \pm 0.025$                                              | This study              |
| 2,000-3,000        | Tropical N Pacific   | Mixed mesozooplankton      | ND                                         | 20           | $\mu\text{LO}_2(\text{mgDM})^{-1}\text{h}^{-1}$       | 1  | $0.067^b$                                                      | King et al. (1978)      |
| 2,750              | E. Mediterranean     | Mixed mesozooplankton      | ND                                         | 15           | $\mu\text{gC}(\text{gWM})^{-1}\text{d}^{-1}$          | 2  | 0.027                                                          | Koppelman et al. (2004) |
| 4,250              | E. Mediterranean     | Mixed mesozooplankton      | ND                                         | 15           | $\mu\text{gC}(\text{gWM})^{-1}\text{d}^{-1}$          | 2  | 0.0084                                                         | Koppelman et al. (2004) |
| 2,500              | Arabian Sea          | Mixed mesozooplankton      | ND                                         | 15           | $\mu\text{gC}(\text{gWM})^{-1}\text{d}^{-1}$          | 2  | 0.023                                                          | Koppelman et al. (2004) |
| 4,000              | Arabian Sea          | Mixed mesozooplankton      | ND                                         | 15           | $\mu\text{gC}(\text{gWM})^{-1}\text{d}^{-1}$          | 2  | 0.014                                                          | Koppelman et al. (2004) |
| 2,000-3,000        | W. subarctic Pacific | Selected calanoid copepods | 4.64                                       | 10           | $\mu\text{LO}_2(\text{mg protein})^{-1}\text{h}^{-1}$ | 31 | $0.062 \pm 0.043^a$                                            | Ikeda et al. (2006a)    |
| 3,000-5,000        | W. subarctic Pacific | Selected calanoid copepods | 4.46                                       | 10           | $\mu\text{LO}_2(\text{mg protein})^{-1}\text{h}^{-1}$ | 35 | $0.062 (0.024-0.158)^c$                                        | Ikeda unpublished       |
| 5,000-7,000        | W. subarctic Pacific | Mixed copepods             | 0.328                                      | 10           | $\mu\text{LO}_2(\text{mg protein})^{-1}\text{h}^{-1}$ | 16 | $0.052 \pm 0.021$                                              | This study              |

<sup>a</sup> Protein =  $0.11 \times \text{WM}$  (Ikeda, unpublished)

<sup>b</sup> DM =  $0.24 \times \text{WM}$  (Ikeda et al. 2006b)

<sup>c</sup> normalized by log-transformation (mean  $\pm$  SD range)

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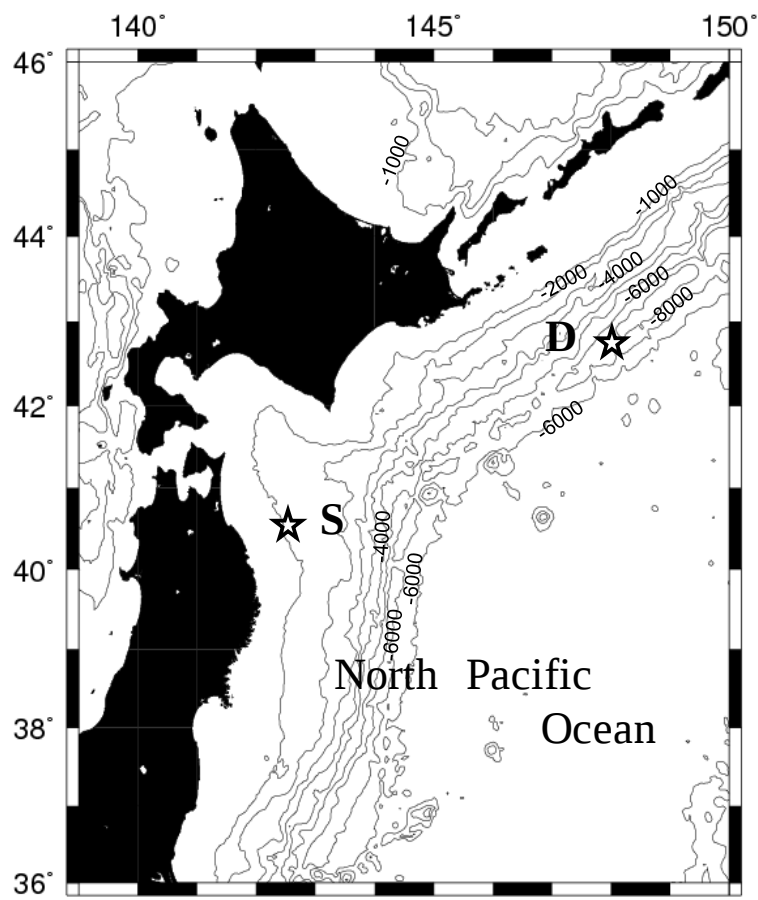
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Figure caption

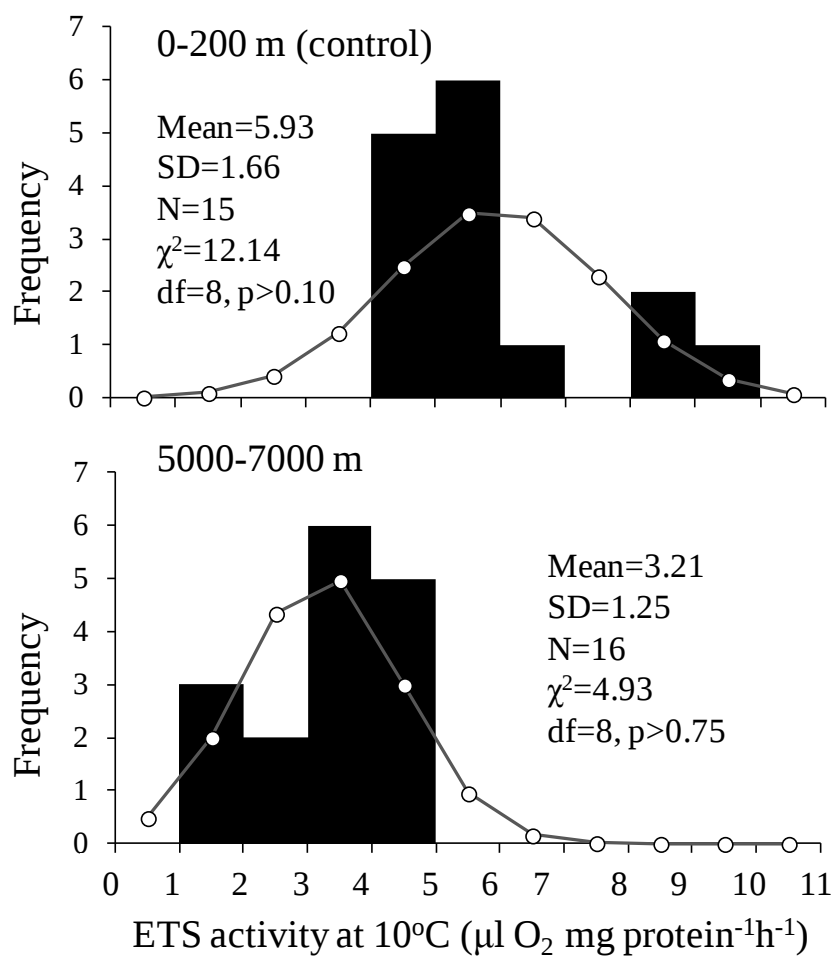
**Fig. 1** Sampling stations (star) at where zooplankton was collected from 5,000-7,000 m (D) and 0-200 m depth (S) in the subarctic western North Pacific Ocean. Depth contours (1,000, 2,000, 3,000, 4,000, 5,000, 6,000, 7,000 and 8,000 m) are superimposed.

**Fig. 2** Frequency distribution of ETS activities determined at 10°C of mixed copepods from 0-200 m (top) and 5,000-7,000 m (bottom) in the western subarctic Pacific Ocean (histograms). The data fit to theoretical normal distribution curves, as was confirmed the Chi-square tests.



Ikeda Fig. 1

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Ikeda Fig. 2