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Respiration and ammonia excretion by marine metazooplankton taxa: synthesis toward
a global-bathymetric model

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Abstract For thirteen representative taxa of metazooplankton from various depth horizons ($< 4,200$ m) of the world's oceans, respiration rate (681 datasets on 390 species) and ammonia excretion rate (266 datasets on 190 species) are compiled and analyzed as a function of body mass (dry mass, carbon or nitrogen), habitat temperature, habitat depth and taxon. Stepwise-regression analyses reveal that body mass is the most important parameter, followed by habitat temperature and habitat depth, whereas taxon is of lesser importance for both rates. The resultant multiple regression equations show that both respiration rate and ammonia excretion rate (per individual) increase with increase in body mass and habitat temperature, but decrease with habitat depth. Some taxa are characterized by significantly higher or lower rates of respiration or ammonia excretion than the others. Overall, the global bathymetric models explain 93.4–94.2% of the variance of respiration data, and 80.8–89.7% of the variance of ammonia excretion data. The atomic O:N ratios (respiration/ammonia excretion) are largely independent of body mass, habitat temperature, habitat depth and taxon, with a median of 17.8. The present results are discussed in the light of the methodological constraints and the standing hypotheses for the relationship between metabolic rate and temperature. Perspectives for model improvement and possible application of it to plankton-imaging systems for rapid assessment of the role of metazooplankton in C or N cycles in the pelagic ecosystem are briefly discussed.

Introduction

Metazoans belonging to a broad variety of taxonomic groups occur as zooplankton in marine ecosystems, and they are an important link between primary production and production at higher trophic levels. Because of their ubiquitous distribution, high abundance and trophic importance, physiological rates of metazooplankton are of particular relevance to understanding oceanic biogeochemical cycles of carbon and other elements (Ikeda and Motoda 1978; Al-Mutairi and Landry 2001; Hidaka et al. 2001; Yamaguchi et al. 2002; Hernandez-Leon and Ikeda 2005; Buitenhuis et al. 2006; López-Urrutia et al. 2006). Zooplankton respiration (measured as oxygen consumption) and nitrogen excretion as ammonium are direct measures of mineralization, and have been extensively documented as functions of body mass and habitat temperature for epipelagic metazooplankton (Ivleva 1980; Vidal and Whitledge 1982; Ikeda 1974, 1985).

The importance of body mass and temperature to the variation of metabolic rates of marine epipelagic mesozooplankton has been well documented. Their importance is also well studied for a broad range of non-marine taxa, including microbes, ectotherms and endotherms (Hemmingsen 1960; Gillooly et al. 2001). However, application of epipelagic mass and temperature correlations to animals living in the ocean interior may introduce a bias, since metabolic rates significantly lower than predicted by those models have been found for metazooplankton and micronekton in the mesopelagic and bathypelagic zones (Childress 1975; Quetin et al. 1980; Ikeda 1988, 2012; Torres et al. 1994; Ikeda et al. 2006a; Seibel and Drazon 2007; Kruse et al. 2010; Brey et al. 2010; Ikeda and Takahashi 2012). For the progressive decline of respiration rates in deeper-living micronekton and zooplankton, the “visual-interactions hypothesis”

(Childress 1995) and “predation-mediated selection hypothesis” (Ikeda et al. 2007) have been proposed. These hypotheses both interpret the phenomenon as being a result of lowered selective pressure for high activity at depth because of the decrease in visual predators in the dark. However, they are different in that the former applies strictly to micronekton with functional eyes, whereas the latter applies to micronekton and zooplankton both with and without functional eyes.

In addition to body mass, habitat temperature and habitat depth, taxonomic differences may be a source of variance in the metabolic rates of mesozooplankton taxa, which exhibit strong dissimilarities in body design, behavior, locomotory activity, physiology and nutrition. As body mass units, selection of carbon (C) or nitrogen (N) instead of wet mass (WM) or dry mass (DM) is a way to reduce such the between-taxon differences in metabolic rates of marine metazooplankton (Ikeda 1985; Schneider 1990). Nevertheless, respiration rates of pteropods, copepods, amphipods, euphausiids and chaetognaths from the epipelagic zones of arctic and antarctic waters standardized to a body size of 1 mgN and at 0°C were not the same, but varied from 1.7 to 8.5 $\mu\text{l O}_2$ (mgN)^{-0.85} h⁻¹ (Ikeda 1989). These between-taxon differences by a factor of 5 may account for a good share of residual variation of metabolic rates, but are unexplored in the previous studies (Ivleva 1980; Ikeda 1985). In place of taxonomic distinctions, Brey (2010) has used lifestyle features (feeding type, mobility type and vision type) and physiological states (fed or starved, and activity level) of animals along with body mass, temperature and water depth as parameters in his predictive model of aquatic invertebrate respiration. Brey’s (2010) model can be applied to metazooplankton through the proper translation of the features of each taxon as mobility (as swimmer in contrast with crawler or sessile for benthos), feeding (carnivore or non-carnivore) and

vision types (with or without functional eyes). Since accuracy and generality are contradistinctive objectives in predictive models (cf. Brey 2010), application of the general model developed for aquatic invertebrates to marine metazooplankton may lead to biased results.

In the present study, I have compiled published data on respiration and ammonia excretion rates of major marine metazooplankton taxa and constructed empirical, global, bathymetric models as a function of body mass, habitat temperature and depth applicable to thirteen metazooplankton taxa. The results are discussed in light of the relative importance of these parameters, the between-taxon differences and the standing hypotheses for the temperature sensitivities. As an approach to further research, it is suggested that complex metazooplankton-mediated carbon or nitrogen flows in marine pelagic ecosystems can be assessed rapidly and continuously at fine time and spatial scales by combining the present model with the automated plankton identification, counting and sizing systems under development.

Materials and methods

The data

Published species-structured data compilations on pelagic copepods (Ikeda et al. 2007), chaetognaths (Ikeda and Takahashi 2012), euphausiids (Ikeda 2013a), amphipods (Ikeda 2013b), mysids (Ikeda 2013c), decapods (Ikeda 2013d), medusae and ctenophores (Ikeda 2014a) and pelagic molluscs (Ikeda 2014b), have been combined with new compilations for ostracods, thaliaceans, appendicularians and polychaetes. The data covers a total of 13 major metazooplankton taxa (Table 1) to which the present analyses are applied. Criteria applied for the selection of these datasets were:

1. Data represent post-larvae (juveniles and adults) collected from the field and used for experiments without considerable time delay (mostly < 24 h). As a notable exception, data from laboratory-raised specimens were used for appendicularians (Gorsky et al. 1987; Lombard et al. 2005), since no data are available for wild specimens.

2. Measurements were made in the absence of food at near *in situ* temperatures and at surface hydrostatic pressures (1 atm) in the dark. For most metazooplankton taxa, hydrostatic pressure is well established to have small effects on their respiration rates over the range that the species encounter in natural habitats (cf. review by Ikeda et al. 2000). Exceptions are the data for delicate, deep-sea medusae and ctenophores from *in situ* capture and incubation using submersibles (Bailey et al. 1994, 1995) or a decapod from autonomous landers (Bailey et al. 2005). Divergence from these procedures, including the use of natural seawater for *in situ* incubation of gelatinous species by SCUBA divers (Biggs 1977) or a flow-through system for a pteropod (Gerber and Gerber 1979) were assumed to yield no appreciable differences in the results. The metabolic rates measured in this manner on pelagic animals with uncontrolled but minimum motor activity are defined as “routine” metabolism (Ikeda et al. 2000).

3. O:N ratios were computed from simultaneous measurements of respiration rates and ammonia excretion rates.

4. Body mass in terms of wet mass (WM), dry mass (DM), carbon (C), nitrogen (N) or protein (PRO) units were given together with metabolic data (note: body-mass specific rates without body-mass data are not useful). Body composition (water content, ash, C, N, or PRO) were obtained with standard methods (Omori and Ikeda 1984; Postel et al. 2000).

5. The depth of sampling of animals was described or deducible from the known

vertical distribution pattern of the species studied.

Using those criteria, totals of 687 datasets on respiration rates for 393 species, 268 datasets on ammonia excretion rates for 191 species and 232 datasets on O:N ratios for 169 species were selected and analyzed (Tables 1, 2). Datasets for the same species from different locations were treated as independent, although mere repetition of the data on the same species was carefully avoided. The entire datasets of respiration rate, ammonia excretion rate and O:N ratio are summarized as supporting materials (S1, S2 and S3, respectively).

Regression models

Global-bathymetric models used for specific metazooplankton taxa (Ikeda et al. 2007; Ikeda and Takahashi 2012; Ikeda 2013a, 2013b, 2013c, 2013d) were modified by taking into account possible between-taxon differences (quantified relative to Copepoda) as independent variables. On the premise that the effects of body mass, habitat temperature and habitat depth are common across the taxa, and the datum of each species is independent each other (or “phylogenetic inertia” is absent, cf. Felsenstein 1985), the model is described as:

$$\ln Y = a_0 + a_1 \times \ln BM + a_2 \times 1000/Temp + a_3 \times \ln Depth + a_4 \times EUPH + a_5 \times AMPH + a_6 \times DECA + a_7 \times MYSI + a_8 \times OSTR + a_9 \times CHAE + a_{10} \times CNID + a_{11} \times CTEN + a_{12} \times MOLL + a_{13} \times THAL + a_{14} \times APPE + a_{15} \times POLY$$

where $\ln Y$ is the logarithm (base e) of respiration rate (R : $\mu\text{lO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$), ammonia-N

excretion rate (E : $\mu\text{gN ind.}^{-1} \text{h}^{-1}$) or O:N atomic ratios (O:N, no dimension), $\ln\text{BM}$ is the logarithm of body mass (DM, C or N), Temp is habitat temperature (K), $\ln\text{Depth}$ is the logarithm of sampling or habitat depth (meters), and EUPH, AMPH, DECA, MYSI, OSTR, CHAE, CNID, CTEN, MOLL, THAL, APPE and POLY are dummy (binary) variables for Euphausiacea, Amphipoda, Decapoda, Mysidacea, Ostracoda, Chaetognath, Cnidaria, Ctenophora, Mollusca, Thaliacea, Appendicularia and Polychaeta, respectively (Table 1). For the data from a given taxon its dummy variable takes a value 1 or 0 otherwise. The data for Copepoda (COPE), which do not appear in the regression equation, take values of 0 in either case (Table 2). As an index of temperature effects, the activation energy (E_a) is calculated from the coefficient a_2 [$= -E_a/k$, where k is the Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV/K}$); $E_a = a_2 \times 1000 \times 8.62 \times 10^{-5}$]. Temperature effects on physiological rates have usually been expressed by Q_{10} instead of E_a . By defining a temperature range (t_1 and t_2 , both in $^{\circ}\text{C}$), E_a can be converted to Q_{10} as;

$$Q_{10} = \exp(10 \times E_a / (k \times (273 + t_1) \times (273 + t_2))) \text{ (Ivleva 1980).}$$

Sampling depth (= habitat depth) was represented by mid-range values for discrete samplings. The depth of near surface collections was assigned as 1 m. The attributes of these variables were analyzed simultaneously by using a stepwise multiple-regression (forward selection) method (Sokal and Rohlf 1995). Independent variables were added and removed at the $p = 0.05$ level; therefore, partial regression coefficients from the

resultant equations are all significant ($p \leq 0.05$), unless otherwise noted. The calculation was conducted using a linear regression program in SYSTAT version 10.2. When the program detected outliers (based on Studentized residuals), they were excluded from the regression calculation.

Results

Respiration and ammonia excretion

Across 13 metazooplankton taxa considered in the present analyses (Table 3), habitat depth ranged from 1 to 1300 m (ammonia excretion data) or to 4200 m (respiration data); the temperature range was -1.7 to 30°C ; and body mass (DM) ranged from 0.0011 to 25200 mg (respiration data) or 90762 mg (ammonia excretion data). All these respiration and ammonia excretion data are plotted against DM, disregarding the differences in habitat temperatures and depths (Fig. 1).

The overall results of the stepwise multiple regressions showed that body mass, habitat temperature, habitat depth and some taxa were significant variables, accounting for 93.4–94.2% (adjusted $R^2 = 0.934$ – 0.942) and 80.8–89.7% (adjusted $R^2 = 0.808$ – 0.897) of the variances in respiration and ammonia excretion rates, respectively, depending on the choice of body mass units (Table 4). Thus, both rates of respiration and ammonia excretion increase with the increase in body mass and with greater habitat temperature, but they both decrease downward in the water column. Multicollinearity between these variables is considered to be small, since the variation inflation factors (VIF) of these variables (1.12–2.15) were < 5 (cf. Kutner et al. 2004). Irrespective of the choice of body mass units, the coefficient a_1 (the scaling exponent of the body mass

effect) was significantly less than unity (0.766–0.857 for respiration rates, and 0.771–0.796 for ammonia excretion rates, all $p < 0.0001$). With regard to the effect of habitat temperature, the E_a (eV) calculated from the coefficient a_2 varied depending on the choice of body mass units from 0.453 to 0.547 (equivalent to 1.90–2.17 in terms of Q_{10} between -2 and 30°C) for respiration rates and from 0.432 to 0.518 (Q_{10} of 1.84 to 2.08) for ammonia excretion rates.

By the definition of dummy variables (Table 2), respiration rates and/or ammonia excretion rates of the taxon for which regression coefficients were not significant ($p > 0.05$, blanks in Table 4) are equivalent to the rates of Copepoda. Among the taxon groups for which coefficients were significant, those of Euphausiacea (EUPH), Amphipoda (AMPH) and Appendicularia (APPE) for respiration rates or only Appendicularia (APPE) for ammonia excretion rates were positive regardless of the choice of body mass units. That suggests that their respiration rates and excretion rates are consistently higher than those of Copepoda. As indices of the relative contribution of each variable to the variance, the standardized coefficients (Std Coeff) suggest that the most important variable affecting both rates is body mass, followed by habitat temperature and depth. The differences among taxa are of lesser importance.

Among the 13 independent variables designated in the present multiple regression analyses, the effects on R or E of body mass, habitat temperature or habitat depth can be extracted from the regression statistics (Table 4) by calculating standardized R (R_{std}) and E (E_{std}), which are free from the effects of the other independent variables. For the effect of body mass (represented by DM):

$$\ln R_{\text{std}} \text{ or } \ln E_{\text{std}} = a_0 + a_1 \times \ln DM, \text{ where } \ln R_{\text{std}} \text{ or } \ln E_{\text{std}} = \ln R \text{ or } \ln E - a_2 \times 1000/\text{Temp} -$$

$a_3 \times \ln \text{Depth} - \text{TAXA}$, where $\text{TAXA} = a_4 \times \text{EUPH} + a_5 \times \text{AMPH} + a_6 \times \text{DECA} + a_7 \times$
 $\text{MYSI} - a_8 \times \text{OSTR} + a_9 \times \text{CHAE} + a_{10} \times \text{CNID} + a_{11} \times \text{CTEN} + a_{12} \times \text{MOLL} + a_{13} \times$
 $\text{THAL} + a_{14} \times \text{APPE} + a_{15} \times \text{POLY}$.

A scatter diagram combining $\ln R_{\text{std}}$ and $\ln E_{\text{std}}$ versus $\ln \text{DM}$ is shown in Fig. 2A. In the
same way, the generalized effects of habitat temperature on R_{std} and E_{std} and of habitat
depth on R_{std} and E_{std} were analyzed by replacing $\ln \text{DM}$ in the right side of the equation
by $1000/\text{Temp}$ and by $\ln \text{Depth}$, respectively. Thus, I obtained scatter diagrams of R_{std}
and E_{std} versus habitat temperature and of R_{std} and E_{std} versus habitat depth (Figs 2B and
C, respectively).

Original datasets (DM, Temp, Depth) for each taxon were substituted in the
resultant regression models from the analyses (Table 4) to predict R or E. Then,
residuals (predicted – observed) were calculated and plotted against predicted R or E
(Fig. 3). The random distribution of the residuals across the range of predicted rates
implies there is no obvious bias inherent in the models.

O:N ratios

A total of 231 O:N ratios from 169 metazooplankton species ranged from 4.8 to 100,
with a mean of 23.0 (± 16.5 , SD) and a median 17.8. Further regression analyses revealed
that neither body mass (DM) nor habitat temperature (Temp) were significant variables
(Table 4). Among significant variables, $\ln \text{Depth}$, EUPH and AMPH were positive, while
CHAE and CTEN were negative. From the regression statistics in Table 4, standardized
O:N ratios [$\ln(\text{O:N}_{\text{std}})$] were computed as,

$\ln\text{O:N}_{\text{std}} = a_0 + a_3 \times \ln\text{Depth}$, where $\ln\text{O:N}_{\text{std}} = \ln\text{O:N} - a_1 \times \ln\text{DM} - a_2 \times 1000/\text{Temp} - \text{TAXA}$,

which was plotted against $\ln\text{Depth}$ (Fig. 4). The combined reduction by $\ln\text{Depth}$ and the other significant variables of the variance of the O:N ratios was only 16.3% (Adjusted $R^2 = 0.163$).

Discussion

Methodological constraints

The respiration, ammonia excretion and O:N ratio data for metazooplankton listed in Table 1 are derived almost exclusively from experiments in which they were placed in filtered seawater, a common practice when using the sealed-chamber method (Ikeda et al. 2000). Use of filtered seawater is imperative to determine the rates of respiration and ammonia excretion accurately without corrections for complex uptake/release of oxygen and ammonia by food organisms (Ikeda et al. 2000), but starvation of metazooplanktons may influence their normal metabolism. Specific dynamic action (SDA) is a widespread phenomenon across diverse animals, and is interpreted as an energy expenditure for ingestion, digestion, absorption and assimilation of food (Secor 2009). Experimental evaluation of SDA effects on metabolic rates of laboratory-raised or wild zooplankton has yielded variable results, including depression and no effects (cf. review by Ikeda et al. 2000). According to recent studies, Thor (2002) observed that the copepod *Calanus finmarchicus* fed *Rhodomonas baltica* during experiments (8 h) increased its respiration rates on the order of 1.6 times those prior to feeding, and the high rates lasted the next 10–15 h. Respiration and ammonia excretion rates of *Oithona davisae* fed satiating

concentrations of a dinoflagellate (*Oxyrrhis marina*) for 16 h at 20°C were 2.3 and 1.4 times the rates of the control (non-feeding *O. davisae*) (Almeda et al. 2011). The corresponding increase in the O:N ratios from feeding was 1.6-fold. Almeda et al. (2011) interpreted the increase in the O:N ratios to be a result from enhanced lipid-metabolism due to feeding on the lipid-rich *O. marina*.

Since the duration and magnitude of SDA are a function of feeding duration and meal size (Secor 2009), the kind of natural prey, daily ration and feeding history prior to experiments all need to be taken into account for proper correction of sealed-chamber metabolic data for wild metazooplankton. In practice, inability to define those conditions for wild metazooplankton species at the time of collection hinders appropriate correction of measured rates. Analyzing SDA data over 85 invertebrates (including some marine planktonic crustaceans), Secor (2009) concluded that the maximal increase in respiration rates by SDA averaged 2.45 (± 0.12 , 1SD) times the rates of non-feeding animals. Thus, a factor $\times 2.45$ may be taken as the maximum for respiration rate of wild zooplankton engaging in feeding for 24 hours daily, but the factor would be much less for other zooplankton that feed only, say, at night.

Body mass effects

Basal or standard metabolic rates of organisms from a broad variety of taxa and of many different sizes [10^{-13} g wet mass (WM) of bacteria to 10^8 g WM of large mammals] have been documented to be a power function (the scaling exponent is approximately 0.75) of body mass (Hemmingsen 1960). Since West et al. (1997) provided a theoretical foundation (fractal network theory) for this empirical law, the theory has evoked active controversy with regard to the validity of its mathematical and methodological bases

(Kozłowski and Konarzewski 2004, 2005), but also enhanced verification by the data (Dodd et al. 2001; Bokma 2004). While the debate is not resolved, alternative analytic theories that are free from the constraint of a fixed scaling exponent have also been proposed (Agutter and Tuszynski 2011).

The first report on the relationship between respiration rate and body mass (WM, DM) of marine metazooplankton was for medusae, ctenophores and salps by Vernon (1896). To date, the relationship has been investigated for diverse metazooplankton taxa using various body mass units, including WM, DM and ash-free DM (= organic matter)(Ivleva 1980), DM and lipid-free DM (Vidal and Whitledge 1982), protein (Biggs 1977), DM, C and N (Ikeda 1985) or calories (Musayeva and Shushkina 1978). Unlike large invertebrates and vertebrates, WM of mesozooplankton is often difficult, if not impossible, to measure in shipboard experiments without the use of special balances, and small specimens are highly susceptible to immediate dehydration in the air during weighing. In addition, metazooplankton are characterized by extremely heterogeneous body structures [gelatinous or non-gelatinous (Schneider 1990) and having or lacking large lipid droplets (Lee et al. 2006)]. Adding technical simplicity and biological rationale to these issues, N and C, instead of WM, DM or protein, have been proposed as common currencies for body mass to obtain meaningful, interspecific, metabolic comparisons (Schneider 1990; Ikeda 2008). Nevertheless, the choice of body mass units only slightly affects the resultant scaling exponents for mesozooplankton, most of which fall within the range between 0.7 and 0.9. Perhaps, this is unsurprising because all of these different body mass units are correlated, and the wider the range of body masses in any units, the tighter the correlations.

The present results show that the metabolic scaling exponent with body mass

varies some extent depending on the body mass units; from 0.767 (DM) to 0.857 (N) for respiration rates, and from 0.771 (C) to 0.796 (DM) for ammonia excretion rates (Table 4), both of which are in good agreement with results of previous studies mentioned above. As judged by adjusted R^2 values, there is no consistent pattern in the performance of the three body units at yielding a best fit to the global-bathymetric model. Previous results have shown that C or N rather than DM yields a best fit to the metabolic model for mixed metazooplankton taxa (Ikeda 1985), and the present result, that the number of taxa involved in the respective regression equations decreased in the order DM to C to N (Table 4), are equivalent in terms of modulation of between-taxon differences in metabolic rates. The present results for scaling exponents are consistent with those (0.7–0.9) of empirical global-bathymetric models for copepods, chaetognaths, euphausiids, amphipods, mysids, decapods and pelagic molluscs (Ikeda et al. 2007; Ikeda and Takahashi 2012; Ikeda 2013a, 2013b, 2013c, 2013d, 2014b) with only the exception of medusae and ctenophores (Ikeda 2014a). According to Ikeda (2014a), the scaling exponent with body mass of both rates of respiration and ammonia excretion of medusae and ctenophores were 0.8 when expressed by DM units but 1 for C or N units, reflecting decreases in relative C and N content with the increase in DM. This DM dependence of C and N composition is a unique feature of medusae, ctenophores and salps, and it has not been observed in the other zooplankton taxa (Ikeda 2014a). This aspect of gelatinous metazooplankton is well mixed with the C and N relation to DM of other metazooplankton taxa, and is overwhelmed in the present regression model that assumes a common scaling exponent with body mass across the 13 metazooplankton taxa (see “Regression models” Section).

Temperature effects

Habitat temperature is the second most important parameter affecting the metabolic rates of marine metazooplankton (Table 4), and its effect (converted to Q_{10}) estimated from the coefficient of the regression equations based on DM body mass is 1.90 (95%CI: 1.78–2.02, Table 5) for respiration rates and 1.84 (1.67–2.03) for ammonia excretion rates. Gillooly et al. (2001) analyzed the relationship between body-mass normalized resting metabolic rates (the rates adjusted to 1 g WM) and temperature for a broad suite of organisms including unicells, plants, invertebrates and vertebrates, and they concluded that the magnitude of the effect of temperature on the rates was relatively constant and expressed by the activation energy (E_a) of 0.6–0.7 eV, which is equivalent to $Q_{10} = 2.3$ –2.7 for the temperature range of -0.2 to 30°C [the quantitative range they accept within their “universal temperature dependence” (UTD) hypothesis (Gillooly et al. 2001, 2006)]. Thus, the range of Q_{10} for metabolic rates of metazooplankton estimated in the present study (1.8–1.9) is significantly less than that (2.3–2.7) from the UTD hypothesis.

Clarke (1987) distinguished intraspecific (within-species) Q_{10} from interspecific (between-species) Q_{10} ; the former represents the adjustment of an organism to a new temperature in the laboratory (acclimation), and the latter the evolutionary adjustment of an organism’s physiology to the environment (adaptation). Acclimated (intraspecific) Q_{10} is interpreted as reflecting the acute thermodynamic effect of temperature, adapted (interspecific) Q_{10} as an evolutionary optimization of each species. Data presented by Clarke and Johnston (1999) support the conclusion that acclimated $Q_{10} >$ adapted Q_{10} . Clarke and Fraser (2004) termed this the “evolutionary trade-off” (ET) hypothesis. They developed the ET hypothesis from their compilation of the resting respiration data

for 69 teleost fishes from a global range of habitat temperature spanning 40°C (acclimated $Q_{10} = 2.40 > \text{adapted } Q_{10} = 1.83$, Clarke and Johnston 1999). In contrast to the ET hypothesis, the UTD hypothesis is based on the notion of a biochemical mechanism (Boltzmann kinetics) in common both within- and between-species, thereby implying that acclimated $Q_{10} = \text{adapted } Q_{10}$ (Clarke 2006). The different temperature sensitivities of metabolism in marine metazooplankton, compared with the organisms studied by Gillooly et al. (2001), leads me to examine whether the ET hypothesis applies for marine metazooplankton.

Taxon-specific Q_{10} values for respiration rates are available from studies of global or global-bathymetric models for nine (adapted Q_{10} data) or eight (acclimated Q_{10} data) mesozooplankton taxa (Table 5). It is noted that acclimated Q_{10} data were derived from experiments in which individual species were placed at graded temperatures within the range of their natural habitats. Across the taxa, adapted (between-species) Q_{10} values ranged from 1.45 to 2.69, and acclimated (within-species) Q_{10} values from 1.81 to 3.28. Taking into account possible taxon-specific differences in temperature sensitivity, the null hypothesis that

$$\text{Adapted } Q_{10} = \text{Acclimated } Q_{10}$$

was tested by a paired Student *t*-test and rejected at $p = 0.013$ ($t = -3.311$, $df = 7$). The result remained unchanged ($p = 0.025$) using a non-parametric test (Wilcoxon Signed Ranks test). Thus, the presently available data support the ET hypothesis for the eight metazooplankton taxa as a group.

Acclimated Q_{10} data for ammonia excretion rates remain too limited for marine metazooplankton species to allow a comparison with the adapted Q_{10} data obtained in the present study.

Habitat depth effects

Analyzing the reduced respiration rates of deeper-living crustacean zooplankton (amphipods, decapods, euphausiids, isopods, mysids and ostracods) off California, the Gulf of Mexico, off Hawaii and in Antarctic waters, Torres et al. (1994) noted that the reduction in the rates [standardized to a body size of 1 mg wet mass by using the body mass exponent of 0.75, and at 0.5°C by assuming $Q_{10} = 2.0$] of species at 1000 m depth were reduced to comparable near-surface counterparts by factors of 0.1 to 0.5. Similar calculations for other mesozooplankton taxa reveal that the respiration rate of specimens from 1000 m are 0.3 times those for copepods from 1 m (Fig. 2 in Ikeda et al. 2006a), and the comparison was 0.1–0.2 times for chaetognaths (Ikeda and Takahashi 2012). The present global-bathymetric model (Table 4) shows that the reduction in respiration rates is 0.4–0.5 times, depending on the choice of DM, C or N for body mass unit. That is at the upper range of the values of the previous studies. Like respiration rates, the depth-related decline in ammonia excretion rates has been documented for crustacean plankton (amphipods, decapods, euphausiids, isopods, mysids and copepods) off California (Quetin et al. 1980) and in Antarctic waters (Ikeda 1988). The magnitude of the decline from 1 m depth to 1000 m depth is more variable; ranging from 0.04 of surface species (95%CI: 0.01–0.16) off California to 0.29 in Antarctic waters. Predicted reduction in ammonia excretion by the increase of habitat depth from 1 to 1000 m in the present model, in which the data of those two previous studies are included, is 0.45–0.57 of surface rates (Table 4). The present results (Fig. 2C) show clearly that the decline with increasing habitat depth in ammonia excretion rates is nearly in parallel with that of respiration rates, implying that the proportion of protein in the total

metabolic substrate of metazooplankton is little affected by their habitat depths (see below).

O:N ratios

The atomic ratio of respiratory oxygen consumption rate to ammonia-nitrogen excretion rate (O:N ratio) is 7 when only protein is metabolized, and is calculated, respectively, as 21 or 13 when protein-and-lipid or protein-and-carbohydrate are catabolized in equal quantities simultaneously (Table 10.3 in Ikeda et al. 2000). Thus, the large variations in the O:N ratios (4.8–100) of the 169 zooplankton species in the present study reflect species-specific or taxon-specific variations in their metabolic substrates. Nevertheless, the O:N ratios overall (median: 17.8) fall between these two hypothetical ratios for the mixed substrates (21 and 13), which suggests that marine zooplankton taxa favor protein-lipid or protein-carbohydrate oriented metabolism. Among the 13 zooplankton taxa analyzed, the results of multiple regression analyses showed that the O:N ratios of euphausiids and amphipods are greater than the average, whereas those of chaetognaths and ctenophores O:N ratios are less (Table 4). Assuming that the methodological constraints in the measurements mentioned above are common across the mesozooplankton taxa analyzed, these results are consistent with food habits of euphausiids (a mixture of herbivores, omnivores and carnivores, Mauchline and Fisher 1967), chaetognaths (carnivores only, Feigenbaum 1991) and ctenophores (carnivores only, Purcell 1991). Amphipods are considered to be primarily carnivores (Ikeda 2013b, and literature therein), and their high O:N ratios cannot be explained by their food habits. In addition to food habits, the nitrogen composition of food is known to affect O:N ratios of marine invertebrate catabolism (Mukai et al. 1989; Ikeda and McKinnon

2012). Since the largest O:N ratios of amphipods were measured in deep-sea species,
N-poor and/or C-rich prey animals at depth (mostly copepods) may be considered as a
possible cause (Ikeda 2013b).

Future aspects

In the light of variations in metazooplankton community composition from one
ecosystem to the next, the global bathymetric model built in the present study is capable
of integrating respiration or ammonia excretion over all component species by taking
into account their taxonomic differences and habitat depths, which was not possible
with previous global models for just epipelagic metazooplankton (Ikeda 1985). The data
coverage of taxa from a variety of habitats across the world's oceans leaves
appendicularians (1 versus 64 described species, cf. Census of Marine Zooplankton
2004) and ostracods (8 versus 169 described species) clearly under-represented in the
model (Table 1). There is an urgent need to collect data on these taxa to improve the
model. With those groups more fully represented, the global bathymetric model could
be coupled with automated plankton identification, counting and sizing systems under
development (Davies et al. 2004; Grosjean et al. 2004; Culverhouse et al. 2006;
Benfield et al. 2007) for rapid and continuous assessment at fine time-space scales in
the field of carbon or nitrogen flows mediated by complex zooplankton communities. In
practice, the size data of identified species or taxa generated optically in the form of
biovolume (BV) could be converted to DM, C or N by using taxon-specific factors. To
achieve this, BV can be converted first to WM taking into account the specific gravity
of seawater (1.03), then to DM using taxon-specific water content data via $DM = WM \times$
 $(100 - \text{Water content})/100$. Fortunately, no appreciable variations of body mass with

habitat temperature or depth have been detected for most metazooplankton, including copepods. The same is true of the whole-animal fractional water content of most metazooplankton:

copepods [mean: 81.4 % ($\pm$ 5.1, SD) of WM, Båmstedt 1986, Ikeda et al. 2006b], chaetognaths [90.2% ($\pm$ 3.1), Ikeda and Takahashi 2012], euphausiids [76.9 % ($\pm$ 3.7), Ikeda 2013a], amphipods [78.7% ($\pm$ 8.3), Ikeda 2013b], mysids [77.6% ($\pm$ 5.4), Ikeda 2013c], decapods [73.9% ($\pm$ 5.2), Ikeda 2013d], medusae and ctenophores [95.8% ($\pm$ 0.7), Ikeda 2014a] and molluscs [83.9% ($\pm$ 8.7), Ikeda 2014b].

As an alternative approach to translate digitized images to body mass without using water content data, empirical relationships between body length or area to DM, C or N has been established for some metazooplankton taxa in subtropical and Antarctic waters (Lehette and Hernández-León 2009) and for those from the California Current (Gorsky et al. 2010). In this way, study of metazooplankton, which has lagged behind physical and chemical oceanography from the lack of effective, rapid data-gathering and analysis tools, could provide insights in timely fashion regarding their roles in carbon and nitrogen cycles and ecosystem trophodynamics, as they respond to ever-changing environmental conditions.

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Figure captions

Fig. 1. Scatter diagram of (A) respiration rates (R) versus body mass (BM in terms of DM) and (B) ammonia excretion rates (E) versus DM for 390 and 190 species, respectively, both belonging to 13 marine metazooplankton taxa from widely different habitat temperatures (-2 to 30°C) and habitat depth (1 to 4200 m) of the world's oceans. For abbreviations of taxa see Table 1.

Fig. 2. Scatter diagram of standardized respiration rates (R_{std}) and ammonia excretion rates (E_{std}) versus (A) body mass (BM), (B) habitat temperature ($1000/K$) and (C) habitat depth (Depth).

Fig. 3. Plots of (A) residuals versus predicted respiration rates (R_{std}) and (B) ammonia excretion rates (E_{std}) from the respective models constructed in the present study (Table 4). To facilitate comparison, residual = 0 (observed - predicted) lines are superimposed as horizontal dashed lines in A and B.

Fig. 4. Scatter diagram of standardized O:N ratios ($O:N_{\text{std}}$) and habitat depth (Depth) of 169 species belonging to 13 marine metazooplankton taxa.

Table 1. Zooplankton taxonomic groups, the number of species and data for which respiration rate, ammonia excretion rate or O:N ratio data compiled in this study.

Taxon	Abbreviation	Respiration		Ammonia excretion		O:N		Data source*
		N _{data}	N _{species}	N _{data}	N _{species}	N _{data}	N _{species}	
Copepoda	COPE	264	109	63	43	42	33	1
Euphausiacea	EUPH	39	24	35	21	32	19	2
Amphipoda	AMPH	41	32	22	18	22	17	3
Decapoda	DECA	55	43	19	18	14	13	4
Mysidacea	MYSI	39	32	15	13	15	13	5
Ostracoda	OSTR	16	8	4	1	4	1	6
Chaetognath	CHAE	35	23	13	10	12	10	7
Cnidaria	CNID	69	45	16	12	13	9	8
Ctenophora	CTEN	24	20	21	19	19	18	9
Mollusca	MOLL	58	32	27	20	27	20	10
Thaliacea	THAL	31	15	27	12	26	12	11
Appendicularia	APPE	4	1	3	1	3	1	12
Polychaeta	POLY	12	9	3	3	3	3	13
Total		687	393	268	191	232	169	
Outliers		6	3	2	1	1	0	

* 1. Ikeda et al. (2001, 2007, unpublished data), Ikeda and McKinnon (2012), 2. Roger (1988), Ikeda (2013a), 3. Ikeda (2013b), 4. Quetin et al. (1980), Roger (1988), Ikeda (2013c), 5. Ikeda (2013d), 6. Childress (1975), Båmstedt (1979), Ikeda (1988, 1990), Torres et al. (1994), Kaeriyama and Ikeda (2004), Ikeda (2012), 7. Reeve et al. (1970), Ikeda (1974, unpublished), Szyper (1981), Ikeda and Skjoldal (1989), Ikeda and Kirkwood (1989), Ikeda and McKinnon (2012), Ikeda and Takahashi (2012), 8. Ikeda (2014a), 9. Ikeda (2014a), 10. Ikeda (2014b), 11. Nival et al. (1972), Mayzaud and Dallot (1973), Ikeda (1974), Biggs (1977), Ikeda and Mitchell (1982), Ikeda and Bruce (1986), Cetta et al. (1986), Madin and Purcell (1992), Iguchi and Ikeda (2004), Köster et al. (2010), 12. Gorsky et al. (1987), Lombard et al. (2005), 13. Ikeda (1974), Båmstedt (1979), Ikeda and Mitchell (1982), Thuesen and Childress (1993), Donnelly et al. (2004), Ikeda (2012)

Table 2. Definitions of dummy variables. The zooplankton taxa were categorized into 12 categories.

Taxon category	EUPH	AMPH	DECA	MYSD	OSTR	CHAE	CNID	CTEN	MOLL	THAL	APPE	POLY
Copepoda	0	0	0	0	0	0	0	0	0	0	0	0
Euphausiacea	1	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	0	1	0	0	0	0	0	0	0	0	0	0
Decapoda	0	0	1	0	0	0	0	0	0	0	0	0
Mysidacea	0	0	0	1	0	0	0	0	0	0	0	0
Ostracoda	0	0	0	0	1	0	0	0	0	0	0	0
Chaetognath	0	0	0	0	0	1	0	0	0	0	0	0
Cnidaria	0	0	0	0	0	0	1	0	0	0	0	0
Ctenophora	0	0	0	0	0	0	0	1	0	0	0	0
Mollusca	0	0	0	0	0	0	0	0	1	0	0	0
Thaliacea	0	0	0	0	0	0	0	0	0	1	0	0
Appendicularia	0	0	0	0	0	0	0	0	0	0	1	0
Polychaeta	0	0	0	0	0	0	0	0	0	0	0	1

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Table 3. Zooplankton taxonomic groups and the ranges of independent variables [habitat depth, temperature and body mass (DM)] for which respiration, ammonia excretion and O:N ratio data compiled in this study.

Taxa	Respiration						Ammonia excretion					
	Habitat depth (m)		Temp (°C)		DM (mg)		Habitat depth (m)		Temp (°C)		DM (mg)	
	min	max	min	max	min	max	min	max	min	max	min	max
COPE	1	4000	-1.7	28.5	0.0012	34.5	1	50	-1.7	29.0	0.0012	3.95
EUPH	1	4000	-1.7	28.0	0.29	1405	1	600	-1.7	28.0	0.29	247
AMPH	1	4000	-1.6	27.8	1.00	344	1	600	-1.6	27.8	1.0	193
DECA	1	4200	0.2	30.0	6.5	5944	1	600	0.2	30.0	0.014	840
MYSI	1	1250	0.2	28.8	0.071	1040	1	600	0.2	28.5	0.16	1040
OSTR	100	4000	-1	5.5	0.028	160	500	500	-1.0	0.2	48.0	160
CHAE	2	2500	-1.3	27.5	0.084	35.3	1	100	-1.0	27.5	0.053	35.3
CNID	1	1300	-0.7	30.0	0.48	25200	1	1300	-0.7	27.0	0.48	90762
CTEN	1	767	-1.6	25.0	3.4	18400	1	767	-1.6	25.0	5.2	18400
MOLL	1	500	-2.0	30.0	0.028	625	1	75	-1.8	30.0	0.34	100
THAL	1	15	-1.6	27.4	0.25	763	1	15	-1.6	27.4	2.97	763
APPE	1	1	15.0	24.0	0.0011	0.0013	1	1	15.0	24.0	0.0011	0.0013
POLY	2	4000	-0.9	28.4	2.4	859	2	3	-0.9	28.4	2.44	63.1

Table 4. Regression statistics derived from stepwise (forward selection, $P_{in} = P_{out} = 0.05$) multiple regression analyses of respiration rates, ammonia-N excretion rates, or O:N atomic ratios (Y : $\mu\text{l O}_2$ individual $^{-1}\text{h}^{-1}$, $\mu\text{gNH}_4\text{-N}$ individual $^{-1}\text{h}^{-1}$, or no dimension) of marine zooplankton on body mass [BM, in terms of dry mass (DM), carbon (C) or nitrogen (N), all mg], habitat temperature (Temp, K), habitat depth (Depth, m) and 13 taxa (see Table 1). Full model; $\ln Y = a_0 + a_1 \times \ln BM + a_2 \times (1000/\text{Temp}) + a_3 \times \ln \text{Depth} + a_4 \times \text{EUPH} + a_5 \times \text{AMPH} + a_6 \times \text{DECA} + a_7 \times \text{MYSI} + a_8 \times \text{OSTR} + a_9 \times \text{CHAE} + a_{10} \times \text{CNID} + a_{11} \times \text{CTEN} + a_{12} \times \text{MOLL} + a_{13} \times \text{THAL} + a_{14} \times \text{APPE} + a_{15} \times \text{POLY}$. Blank: coefficient $p > 0.05$. Among 681 respiration-DM datasets analyzed, appropriate information about C and N composition was not available for three polychaetes therefore $N = 678$ for respiration-C and N datasets. Regression statistics of O:N ratios based on C and N body mass units are the same to those based on DM unit therefore not shown.

Dependent Variable (lnY)	Body mass unit		
	DM	C	N
Respiration			
N	681	678	678
Adjusted R ²	0.934	0.934	0.942
Coefficient (Std Error; Std Coeff)			
	a_0 18.775 (0.940; 0.000)	23.079 (0.970; 0.000)	24.808 (0.885; 0.000)
	a_1 0.766 (0.012; 0.907)	0.813 (0.013; 0.877)	0.857 (0.009; 0.919)
	a_2 -5.256 (0.274; -0.259)	-6.248 (0.280; -0.309)	-6.342 (0.257; -0.313)
	a_3 -0.113 (0.011; -0.143)	-0.136 (0.011; -0.172)	-0.108 (0.010; -0.136)
	a_4 0.697 (0.105; 0.070)	0.600 (0.108; 0.061)	0.212 (0.094; 0.022)
	a_5 0.416 (0.101; 0.043)	0.421 (0.104; 0.044)	0.344 (0.091; 0.036)
	a_6 0.631 (0.104; 0.075)	0.333 (0.113; 0.040)	
	a_7 0.393 (0.103; 0.040)	0.230 (0.106; 0.023)	
	a_8 -0.395 (0.151; -0.026)		-0.394 (0.142; -0.026)
	a_9 -0.448 (0.105; -0.043)	-0.345 (0.106; -0.033)	-0.673 (0.097; -0.065)
	a_{10} -0.480 (0.092; -0.062)	0.425 (0.091; 0.055)	
	a_{11} -1.257 (0.145; -0.097)	0.547 (0.139; 0.042)	
	a_{12}		
	a_{13}	1.079 (0.121; 0.097)	0.899 (0.107; 0.080)
	a_{14} 1.604 (0.308; 0.053)	1.456 (0.309; 0.049)	1.780 (0.288; 0.059)
	a_{15} 0.382 (0.175; 0.022)	0.484 (0.202; 0.024)	
Ammonia-N excretion			
N	266	266	266
Adjusted R ²	0.897	0.808	0.812
Coefficient (Std Error; Std Coeff)			
	a_0 15.567 (1.410; 0.000)	17.945 (1.953; 0.000)	20.648 (1.864; 0.000)
	a_1 0.796 (0.020; 1.168)	0.771 (0.028; 1.000)	0.778 (0.025; 0.999)
	a_2 -5.010 (0.410; -0.295)	-5.528 (0.556; -0.325)	-6.004 (0.530; -0.353)
	a_3 -0.115 (0.028; -0.106)	-0.082 (0.038; -0.075)	(-0.104)*
	a_4		
	a_5		
	a_6		
	a_7		
	a_8 -1.356 (0.384; -0.072)	-1.054 (0.524; -0.056)	-1.551 (0.512; -0.080)
	a_9		
	a_{10} -0.558 (0.206; -0.058)	0.655 (0.268; 0.068)	
	a_{11} -1.397 (0.195; -0.165)	0.878 (0.236; 0.103)	0.659 (0.233; 0.078)
	a_{12} -0.550 (0.158; -0.073)		
	a_{13} -0.564 (0.169; -0.073)	0.871 (0.214; 0.113)	0.808 (0.211; 0.105)
	a_{14} 1.633 (0.445; 0.075)	1.267 (0.607; 0.058)	1.521 (0.604; 0.070)
	a_{15}		
O:N ratio (by atoms)			
N	231		
Adjusted R ²	0.163		
Coefficient (Std Error; Std Coeff)			
	a_0 2.818 (0.056; 0.000)		
	a_1		
	a_2		
	a_3 0.055 (0.017; 0.201)		
	a_4 0.311 (0.106; 0.182)		
	a_5 0.262 (0.122; 0.132)		
	a_6		
	a_7		
	a_8		
	a_9 -0.514 (0.161; -0.196)		
	a_{10}		
	a_{11} -0.350 (0.130; -0.165)		
	a_{12}		
	a_{13}		
	a_{14}		
	a_{15}		

* $p = 0.094$

Table 5. Effects of temperature (as Q_{10}) on respiration rates of various marine metazooplankton taxa, as evaluated adapted (interspecific, based on DM body mass units) and acclimated (intraspecific) comparison. N_{data} = the number of data, $N_{species}$ = the number of species studied.

Zooplankton taxa	Adapted Q_{10} Mean (95%CI)	Temp range (°C)	N_{data}	$N_{species}$	Data source*	Acclimated Q_{10} Mean (SD)	Temp range (°C)	N_{data}	$N_{species}$	Data source*
Copepoda	1.90 (1.67–2.17)	–1.7 to 28	253	108	1	3.28 (1.24)	0 to 22	9	8	11
Euphausiacea	1.70 (1.50–1.92)	–1.7 to 28	39	24	2	2.59 (0.40)	0 to 25	11	9	2
Amphipoda	1.45 (1.11–1.88)	–1.6 to 28	41	32	3	2.29 (0.37)	0 to 12	6	4	3
Decapoda	2.69 (2.12–3.42)	0.2–30	55	46	4	2.37 (0.57)	5 to 20	16	16	4
Mysidacea	2.12 (1.47–2.60)	–1.6 to 29	42	31	5	2.54 (0.59)	0 to 20	6	5	5
Chaetognath	1.67 (1.36–2.44)	–1 to 28	35	23	6					
Cnidaria/Ctenophora	1.80 (1.48–2.20)	–1.6 to 27	93	71	7	2.97 (0.69)	2 to 28	8	8	7
Mollusca	1.58 (1.30–1.94)	–2 to 30	57	31	8	1.81 (0.54)	5 to 25	14	12	8
Thaliacea	2.36 (1.64–3.41)	–1.6 to 27	30	14	9	2.87 (0.06)	10 to 24	2	2	12
Mixed	1.90 (1.78–2.02)	–2 to 30	681	386	10					

*1. Ikeda et al. (2007), 2. Ikeda (2013a), 3. Ikeda (2013b), 4. Ikeda (2013c), 5. Ikeda (2013d), 6. Ikeda and Takahashi (2012), 7. Ikeda (2014a), 8. Ikeda (2014b), 9. modified from Iguchi and Ikeda (2004), 10. from Table 4 of this study, 11. Hirche (1984, 1987), Svetlichny et al. (2000), Castellani et al. (2005), 12. Vernon (1896)

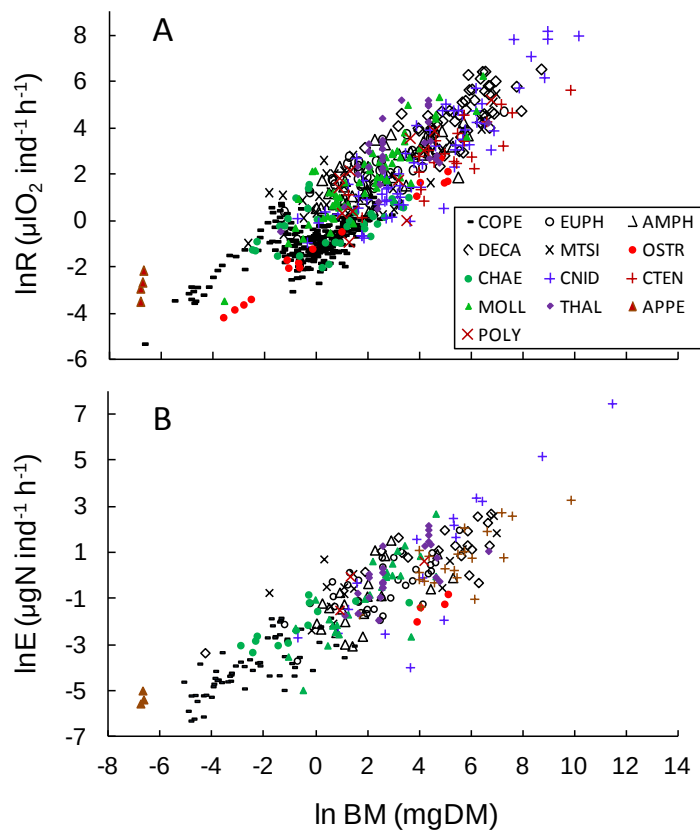


Fig. 1 Ikeda

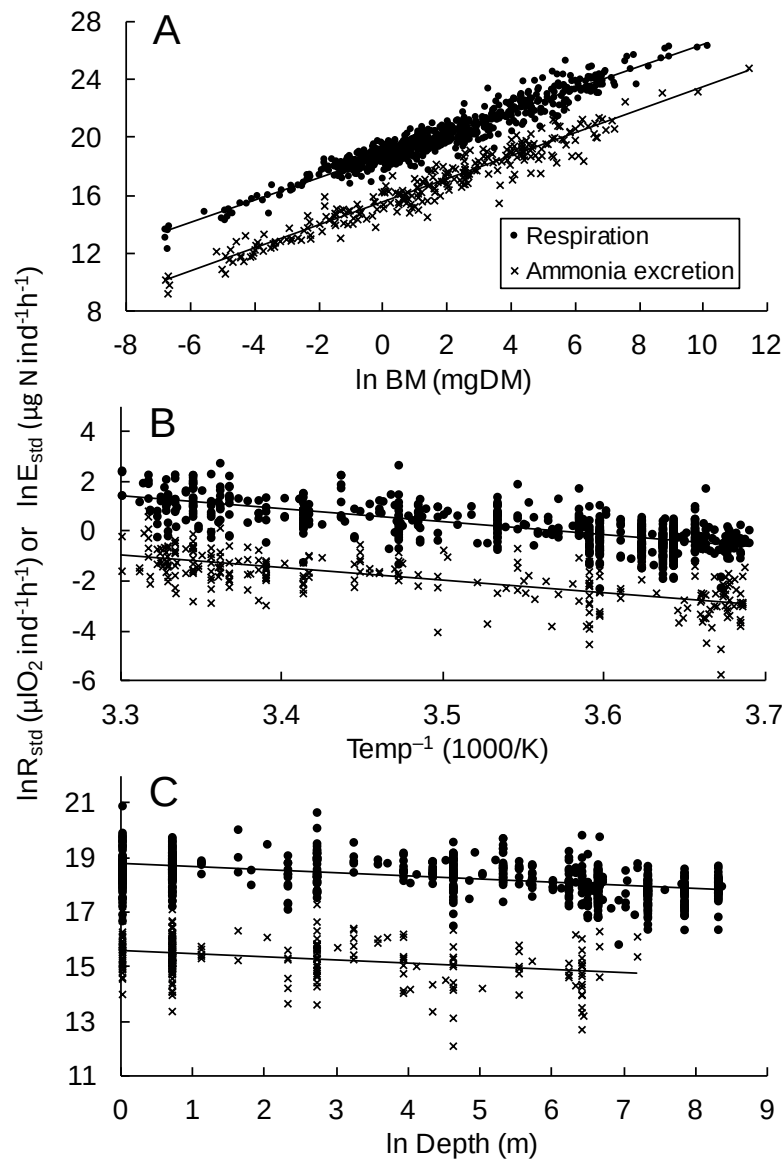


Fig. 2 Ikeda

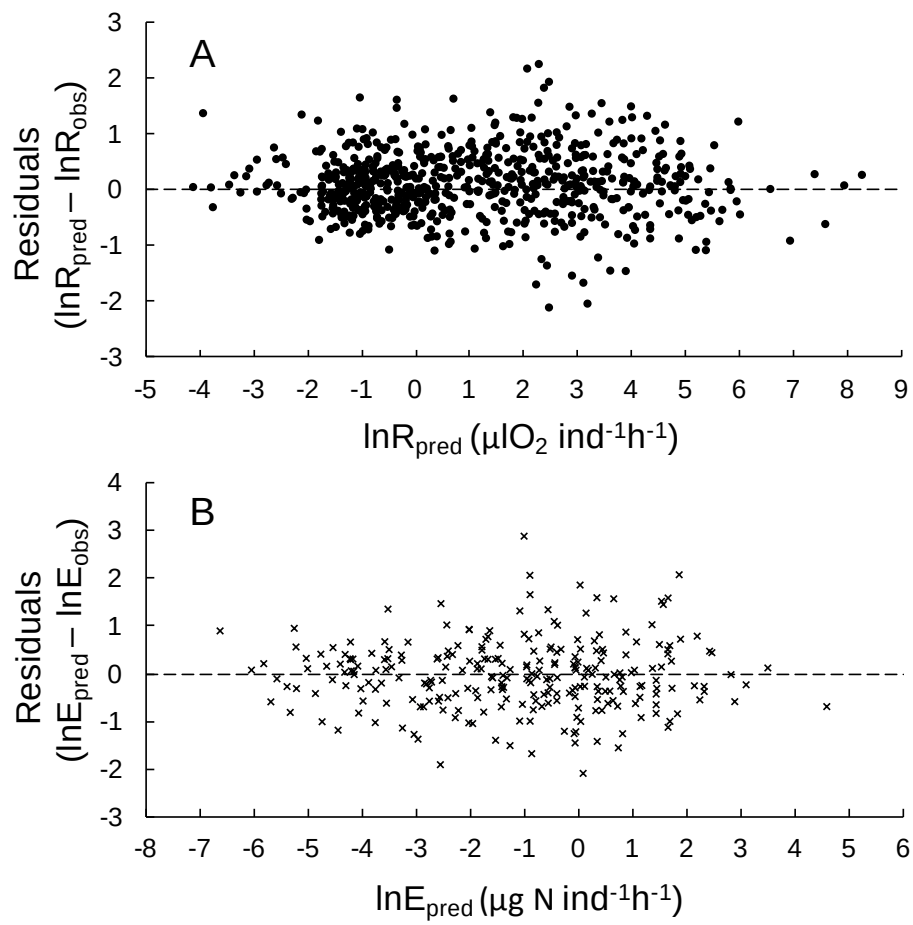


Fig. 3 Ikeda

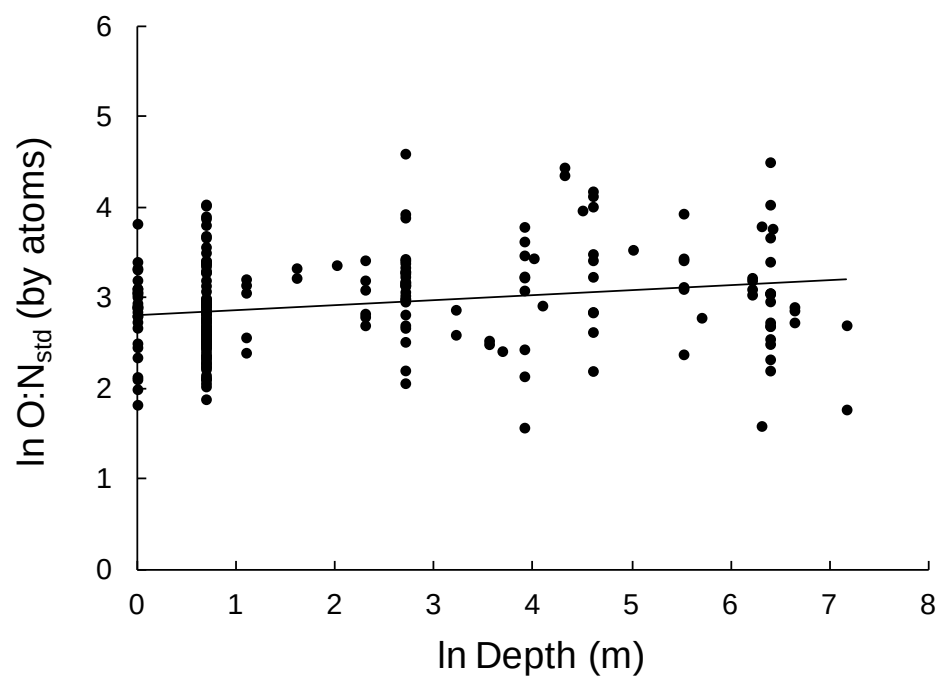


Fig. 4 Ikeda

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S2. Summary of ammonia (as NH4-N) excretion data

Taxa	Code	Species	Depth (m)	T (°C)	Excretion (mmol N m ⁻² d ⁻¹)	Depth (m)	T (°C)	C (mg)	N (mg)	Reference
COPE	51	<i>Calanus propinquus</i>	2	-1.0	0.07	1.64	0.4	0.12	0.01	Baer et al. (2003)
COPE	52	<i>Calanoides acutus</i> CS	2	-0.2	0.019	0.394	0.19	0.03		
COPE	53	<i>Calanoides acutus</i> CA CS	2	-0.5	0.044	0.208	0.10	0.02		
COPE	54	<i>Rhabdosoma gigas</i>	50	-1.7	0.113	1.080	0.50	0.11		
COPE	55	<i>Mesocyclops giesbrei</i>	2	-1.4	0.033	0.265	0.11	0.027		
COPE	56	<i>Calanus (seneculus) CCF</i>	2	0.1	0.013	0.307	0.21	0.030		
COPE	57	<i>Calanus glacialis</i> CCF	50	2.3	0.030	0.474	0.22	0.050		
COPE	58	<i>Calanus hyperboreus</i> CCF	50	2.0	0.040	2.05	2.24	0.28		
COPE	59	<i>Calanus hyperboreus</i> CS (bloom)	50	0.9	0.053	1.34	1.12	0.14		
COPE	510	<i>Calanus hyperboreus</i> CS (see bloom)	50	-0.3	0.030	2.077	1.63	0.18		
COPE	511	<i>Mesocyclops giesbrei</i> CCF	50	0.1	0.023	0.320	0.17	0.027		
COPE	512	<i>Neocalanus planifrons</i> CS	2	7.3	0.017	0.765	0.45	0.063		
COPE	513	<i>Neocalanus planifrons</i> CA	2	5.6	0.007	0.205	0.15	0.023		
COPE	514	<i>Neocalanus planifrons</i>	2	15.1	0.065	0.294	0.14	0.036		
COPE	515	<i>Neocalanus cristatus</i>	2	6.3	0.164	1.59	0.79	0.13		
COPE	516	<i>Neocalanus homotri</i> CCF	2	6.0	0.050	1.09	0.40	0.10		
COPE	517	<i>Pseudocalanus elongatus</i>	2	8.6	0.002	0.016	0.003	0.004		
COPE	518	<i>Mesocyclops pacificus</i>	2	8.2	0.023	0.146	0.054	0.010		
COPE	519	<i>Mesocyclops pacificus</i>	2	13.0	0.023	0.094	0.043	0.013		
COPE	520	<i>Acartia clausi</i>	2	14.8	0.006	0.005	0.001	0.001		
COPE	521	<i>Acartia inaquatica</i>	2	9.6	0.002	0.008	0.001	0.001		
COPE	522	<i>Tarameus disciculatus</i>	2	7.0	0.008	0.057	0.025	0.006		
COPE	523	<i>Canthocamptus pauper</i> CCF	2	22.0	0.014	0.014	0.004	0.003		
COPE	524	<i>Neocalanus gracilis</i>	2	18.7	0.102	0.508	0.254	0.051		
COPE	525	<i>Undinula vulgaris</i>	2	21.5	0.074	0.185	0.077	0.018		
COPE	526	<i>Arctocyclops gibber</i> CCF	2	22.0	0.011	0.021	0.009	0.002		
COPE	527	<i>Pseudocalanus parvus</i>	2	22.0	0.015	0.014	0.004	0.003		
COPE	528	<i>Neocalanus subrecessus</i> CCF	2	22.0	0.024	0.103	0.043	0.010		
COPE	529	<i>Eurytemora aestiva</i>	2	24.0	0.061	0.290	0.121	0.028		
COPE	530	<i>Centropages furcatus</i> CCM	2	22.0	0.011	0.033	0.014	0.003		
COPE	531	<i>Centropages brevispinis</i>	2	17.3	0.011	0.030	0.002	0.002		
COPE	532	<i>Temora turbinata</i>	2	22.0	0.005	0.016	0.006	0.001		
COPE	533	<i>Calanopsis affligens</i> CCF	2	22.0	0.017	0.017	0.012	0.007		
COPE	534	<i>Labidocera</i> sp.	2	22.0	0.070	0.136	0.070	0.018		
COPE	535	<i>Temora gracilis</i> CCF	2	22.0	0.010	0.028	0.012	0.003		
COPE	536	<i>Acartia australis</i> CCF	2	22.0	0.006	0.017	0.004	0.001		
COPE	537	<i>Acartia tonsa</i>	2	22.0	0.006	0.007	0.003	0.000		
COPE	538	<i>Cyclopoida</i> sp.	2	22.0	0.013	0.012	0.011	0.003		
COPE	539	<i>Remaneocanthurus</i>	2	26.0	0.021	0.046	0.021	0.005		
COPE	540	<i>Undinula vulgaris</i>	2	27.6	0.118	0.167	0.070	0.018		
COPE	541	<i>Eurytemora subrecessus</i> CCF	2	27.0	0.027	0.029	0.013	0.003		
COPE	542	<i>Eurytemora subrecessus</i> CCF	2	24.0	0.021	0.104	0.043	0.010		
COPE	543	<i>Eurytemora subrecessus</i>	2	27.4	0.070	0.137	0.054	0.013		
COPE	544	<i>Pseudocalanus aculeatus</i>	2	28.0	0.084	0.017	0.007	0.002		
COPE	545	<i>Arctocyclops gibber</i> CCF	2	28.7	0.022	0.030	0.004	0.001		
COPE	546	<i>Temora turbinata</i>	2	27.0	0.010	0.005	0.002	0.000		
COPE	547	<i>Centropages furcatus</i> CCM	2	27.0	0.016	0.010	0.002	0.002		
COPE	548	<i>Calanopsis affligens</i> CCF	2	26.0	0.020	0.036	0.023	0.005		
COPE	549	<i>Calanopsis affligens</i> CCF	2	27.4	0.024	0.040	0.020	0.005		
COPE	550	<i>Labidocera acuta</i>	2	24.0	0.164	0.231	0.097	0.022		
COPE	551	<i>Labidocera acuta</i>	2	28.5	0.147	0.228	0.098	0.028		
COPE	552	<i>Labidocera acuta</i>	2	26.4	0.130	0.220	0.095	0.027		
COPE	553	<i>Labidocera</i> sp. CCF	2	28.5	0.037	0.024	0.010	0.002		
COPE	554	<i>Acartia australis</i>	2	25.0	0.004	0.005	0.004	0.001		
COPE	555	<i>Acartia tonsa</i>	2	27.0	0.004	0.017	0.007	0.002		
COPE	556	<i>Acartia pacifica</i> CCF	2	27.8	0.012	0.018	0.008	0.002		
COPE	557	<i>Temora gracilis</i> CCM	2	26.0	0.010	0.014	0.002	0.002		
COPE	558	<i>Temora gracilis</i> CCM	2	29.0	0.050	0.113	0.053	0.012		
COPE	559	<i>Labidocera</i> sp.	2	25.0	0.100	0.160	0.050	0.016		
COPE	560	<i>Undinula vulgaris</i>	25	25.5	0.080	0.220	0.090	0.026		
COPE	561	<i>Pseudocalanus indicus</i>	1	23.0	0.010	0.007	0.002	0.000		
COPE	562	<i>Microsetella gracilis</i>	25.0	0.020	0.002	0.002	0.000	0.000		
COPE	563	<i>Onchocella subdila</i>	1	24.0	0.005	0.002	0.000	0.001		
COPE	564	<i>Onchocella subdila</i>	1	26.0	0.005	0.002	0.000	0.001		
COPE	565	<i>Onchocella subdila</i>	1	28.0	0.005	0.002	0.000	0.001		
COPE	566	<i>Onchocella subdila</i>	1	30.0	0.005	0.002	0.000	0.001		
COPE	567	<i>Onchocella subdila</i>	1	32.0	0.005	0.002	0.000	0.001		
COPE	568	<i>Onchocella subdila</i>	1	34.0	0.005	0.002	0.000	0.001		
COPE	569	<i>Onchocella subdila</i>	1	36.0	0.005	0.002	0.000	0.001		
COPE	570	<i>Onchocella subdila</i>	1	38.0	0.005	0.002	0.000	0.001		
COPE	571	<i>Onchocella subdila</i>	1	40.0	0.005	0.002	0.000	0.001		
COPE	572	<i>Onchocella subdila</i>	1	42.0	0.005	0.002	0.000	0.001		
COPE	573	<i>Onchocella subdila</i>	1	44.0	0.005	0.002	0.000	0.001		
COPE	574	<i>Onchocella subdila</i>	1	46.0	0.005	0.002	0.000	0.001		
COPE	575	<i>Onchocella subdila</i>	1	48.0	0.005	0.002	0.000	0.001		
COPE	576	<i>Onchocella subdila</i>	1	50.0	0.005	0.002	0.000	0.001		
COPE	577	<i>Onchocella subdila</i>	1	52.0	0.005	0.002	0.000	0.001		
COPE	578	<i>Onchocella subdila</i>	1	54.0	0.005	0.002	0.000	0.001		
COPE	579	<i>Onchocella subdila</i>	1	56.0	0.005	0.002	0.000	0.001		
COPE	580	<i>Onchocella subdila</i>	1	58.0	0.005	0.002	0.000	0.001		
COPE	581	<i>Onchocella subdila</i>	1	60.0	0.005	0.002	0.000	0.001		
COPE	582	<i>Onchocella subdila</i>	1	62.0	0.005	0.002	0.000	0.001		
COPE	583	<i>Onchocella subdila</i>	1	64.0	0.005	0.002	0.000	0.001		
COPE	584	<i>Onchocella subdila</i>	1	66.0	0.005	0.002	0.000	0.001		
COPE	585	<i>Onchocella subdila</i>	1	68.0	0.005	0.002	0.000	0.001		
COPE	586	<i>Onchocella subdila</i>	1	70.0	0.005	0.002	0.000	0.001		
COPE	587	<i>Onchocella subdila</i>	1	72.0	0.005	0.002	0.000	0.001		
COPE	588	<i>Onchocella subdila</i>	1	74.0	0.005	0.002	0.000	0.001		
COPE	589	<i>Onchocella subdila</i>	1	76.0	0.005	0.002	0.000	0.001		
COPE	590	<i>Onchocella subdila</i>	1	78.0	0.005	0.002	0.000	0.001		
COPE	591	<i>Onchocella subdila</i>	1	80.0	0.005	0.002	0.000	0.001		
COPE	592	<i>Onchocella subdila</i>	1	82.0	0.005	0.002	0.000	0.001		
COPE	593	<i>Onchocella subdila</i>	1	84.0	0.005	0.002	0.000	0.001		
COPE	594	<i>Onchocella subdila</i>	1	86.0	0.005	0.002	0.000	0.001		
COPE	595	<i>Onchocella subdila</i>	1	88.0	0.005	0.002	0.000	0.001		
COPE	596	<i>Onchocella subdila</i>	1	90.0	0.005	0.002	0.000	0.001		
COPE	597	<i>Onchocella subdila</i>	1	92.0	0.005	0.002	0.000	0.001		
COPE	598	<i>Onchocella subdila</i>	1	94.0	0.005	0.002	0.000	0.001		
COPE	599	<i>Onchocella subdila</i>	1	96.0	0.005	0.002	0.000	0.001		
COPE	600	<i>Onchocella subdila</i>	1	98.0	0.005	0.002	0.000	0.001		
COPE	601	<i>Onchocella subdila</i>	1	100.0	0.005	0.002	0.000	0.001		
COPE	602	<i>Onchocella subdila</i>	1	102.0	0.005	0.002	0.000	0.001		
COPE	603	<i>Onchocella subdila</i>	1	104.0	0.005	0.002	0.000	0.001		
COPE	604	<i>Onchocella subdila</i>	1	106.0	0.005	0.002	0.000	0.001		
COPE	605	<i>Onchocella subdila</i>	1	108.0	0.005	0.002	0.000	0.001		
COPE	606	<i>Onchocella subdila</i>	1	110.0	0.005	0.002	0.000	0.001		
COPE	607	<i>Onchocella subdila</i>	1	112.0	0.005	0.002	0.000	0.001		
COPE	608	<i>Onchocella subdila</i>	1	114.0	0.005	0.002	0.000	0.001		
COPE	609	<i>Onchocella subdila</i>	1	116.0	0.005	0.002	0.000	0.001		
COPE	610	<i>Onchocella subdila</i>	1	118.0	0.005	0.002	0.000	0.001		
COPE	611	<i>Onchocella subdila</i>	1	120.0	0.005	0.002	0.000	0.001		
COPE	612	<i>Onchocella subdila</i>	1	122.0	0.005	0.002	0.000	0.001		
COPE	613	<i>Onchocella subdila</i>	1	124.0	0.005	0.002	0.000	0.001		
COPE	614	<i>Onchocella subdila</i>	1	126.0	0.005	0.002	0.000	0.001		
COPE	615	<i>Onchocella subdila</i>	1	128.0	0.005	0.002	0.000	0.001		
COPE	616	<i>Onchocella subdila</i>	1	130.0	0.005	0.002	0.000	0.001		
COPE	617	<i>Onchocella subdila</i>	1	132.0	0.005	0.002	0.000	0.001		
COPE	618	<i>Onchocella subdila</i>	1	134.0	0.005	0.002	0.000	0.001		
COPE	619	<i>Onchocella subdila</i>	1	136.0	0.005	0.002	0.000	0.001		
COPE	620	<i>Onchocella subdila</i>	1	138.0	0.005	0.002	0.000	0.001		
COPE	621	<i>Onchocella subdila</i>	1	140.0	0.005	0.002	0.000	0.001		
COPE	622	<i>Onchocella subdila</i>	1	142.0	0.005	0.002	0.000	0.001		
COPE										

S1. Summary of O/N ratio data

Code	Species	Depth (m)	T (°C)	O/N (by atoms)	DW(mg)	C (mg)	N (mg)	Reference	
CEPHE	S1	<i>Calanus propinquus</i>	2	-1.0	13.8	1.04	0.499	0.118	Bieda et al. (2001)
	S2	<i>Calanoides acutus</i> C5	2	-0.2	13.6	0.394	0.193	0.033	
	S3	<i>Calanoides acutus</i> C4, C5	2	-0.5	12.0	0.218	0.096	0.018	
	S4	<i>Rhincalanus gigas</i>	50	-1.7	4.8	1.06	0.503	0.106	
	S5	<i>Meridia percheri</i>	2	-1.4	12.9	0.265	0.106	0.027	
	S6	<i>Calanus finmarchicus</i> C6F	2	0.1	30.6	0.387	0.215	0.030	
	S7	<i>Calanus glacialis</i> C6F	50	2.3	25.7	0.474	0.223	0.050	
	S8	<i>Calanus hyperboreus</i> C5	50	1.3	37.9	3.95	2.538	0.263	
	S9	<i>Calanus hyperboreus</i> C5 (bloom)	50	0.9	25.4	1.94	1.117	0.144	
	S10	<i>Calanus hyperboreus</i> C5 (no bloom)	50	-0.3	44.5	2.68	1.634	0.180	
	S11	<i>Meridia longae</i> C6F	30	0.1	22.1	0.353	0.168	0.027	
	S12	<i>Noecalanus planchrus</i> C5	2	7.3	50.0	0.785	0.452	0.063	
	S13	<i>Noecalanus planchrus</i> C4	2	5.6	48.8	0.263	0.148	0.021	
	S14	<i>Noecalanus planchrus</i>	2	15.1	10.5	0.294	0.135	0.026	
	S15	<i>Noecalanus cristatus</i>	2	6.3	12.7	1.59	0.790	0.133	
	S16	<i>Eucalanus bangii</i> C6F	2	6.0	17.3	1.01	0.404	0.099	
	S17	<i>Pseudocalanus elongatus</i>	2	8.6	21.9	0.0116	0.0053	0.0014	
	S18	<i>Meridia pacifica</i>	2	8.2	35.6	0.148	0.065	0.016	
	S19	<i>Meridia pacifica</i>	2	13.0	14.7	0.094	0.043	0.011	
	S20	<i>Acartia clausi</i>	2	14.8	4.6	0.0085	0.0035	0.0010	
	S21	<i>Acartia longiremis</i>	2	9.6	16.9	0.0081	0.0035	0.0010	
	S22	<i>Torulus discoidulus</i>	2	7.0	19.6	0.057	0.025	0.006	
	S23	<i>Noecalanus gracilis</i>	2	19.7	20.1	0.500	0.234	0.051	
	S24	<i>Udinus vulgaris</i>	2	23.5	16.3	0.185	0.077	0.018	
	S25	<i>Euchaeta marina</i>	2	24.0	27.4	0.291	0.121	0.028	
	S26	<i>Centropages brachyurus</i>	2	17.3	13.1	0.0108	0.0062	0.0020	
	S27	<i>Acartia tonsa</i>	2	22.0	12.5	0.0072	0.0030	0.0007	
	S28	<i>Nannocalanus minor</i>	2	26.9	12.7	0.040	0.017	0.005	
	S29	<i>Udinus vulgaris</i>	2	27.6	14.8	0.167	0.070	0.018	
	S30	<i>Eucalanus suberectus</i> C6F	2	24.0	39.5	0.104	0.043	0.010	
	S31	<i>Eucalanus attenuatus</i>	2	27.4	16.2	0.137	0.054	0.013	
	S32	<i>Calanopia elliptica</i> C6F	2	26.0	17.4	0.056	0.023	0.005	
	S33	<i>Lahidocera acuta</i>	2	24.0	14.4	0.233	0.097	0.022	
	S34	<i>Lahidocera acuta</i>	2	28.5	17.6	0.228	0.098	0.028	
	S35	<i>Lahidocera seri</i>	2	26.4	13.6	0.221	0.095	0.027	
	S36	<i>Acartia australis</i>	2	25.0	15.5	0.0059	0.0028	0.0009	
	S37	<i>Torulus gracilis</i> GIM	2	26.0	17.8	0.024	0.0098	0.0023	
	S38	<i>Lahidocera fermani</i>	25	25.0	13.5	0.160	0.057	0.016	Bieda and McKinnon (2012)
	S39	<i>Udinus vulgaris</i>	25	25.5	17.8	0.220	0.094	0.026	
	S40	<i>Paracalanus parvus</i>	1	23.0	21.7	0.0072	0.0032	0.0008	
	S41	<i>Microsetella gracilis</i>	1	25.0	18.2	0.0065	0.0024	0.0005	
	S42	<i>Oithona niphidius</i>	2	24.0	11.8	0.0032	0.0016	0.0004	
EUPHI	1	see S4	600	-5.5	41.4	60.0	23.5	3.8	Bieda (2013a)
	2a	see S4	10	-1.6	42.0	30.8	14.0	3.4	
	2b	see S4	24.5	3.3	31.0	34.2	1.06	0.2	
	3	see S4	2	26	19.1	1.89	0.78	0.20	
	4	see S4	2	27	16.3	3.54	1.40	0.38	
	5	see S4	1	28	22.6	3.29	1.37	0.37	
	7	see S4	2	19.7	14.5	0.267	0.117	0.029	
	8	see S4	40	12.5	15.4	5.00	2.02	0.54	
	1	see S4	1	28	11.3	1.82	0.74	0.21	
	10a	see S4	2	13	23.1	4.97	2.06	0.54	
	10b	see S4	100	5	90.0	12.8	4.6	1.2	
	10c	see S4	100	5	76.0	11.5	4.0	1.1	
	11a	see S4	35	-1.1	16.6	86.3	1.4	0.8	
	11b	see S4	3	-1.7	34.1	40.3	16.4	4.8	
	11c	see S4	35	-1.1	17.3	247.1	115.9	24.7	
	11d	see S4	3	-1.7	29.3	80.3	32.5	9.6	
	11e	see S4	3	-1.7	31.9	97.7	39.5	11.4	
	12	see S4	2	27	13.9	0.77	0.31	0.08	
	13a	see S4	100	0	12.4	23.0	9.5	2.7	
	13b	see S4	600	0	29.0	82.8	39.2	8.9	
	14a	see S4	250	4	42.0	74.1	25.9	7.6	
	14b	see S4	300	12	4.7	32.50	12.8	3.7	
	14c	see S4	50	4	15.7	45.8	17.0	5.0	
	15	see S4	2	15	21.6	2.00	0.87	0.232	
	17	see S4	1	44.3	17.3	4.9	1.5	0.5	
	18a	see S4	2	-0.4	26.3	0.47	0.20	0.05	
	18b	see S4	2	-1.7	27.1	5.49	2.23	0.54	
	18c	see S4	-0.46	22.3	6.89	2.56	0.61	0.16	
	20	see S4	15	20	32.0	5.00	2.10	0.53	
	21a	see S4	100	5	42.0	12.2	4.5	1.2	
	21b	see S4	100	5	35.0	7.02	2.40	0.71	
	24	see S4	1	26	30.7	12.6	5.4	1.6	
AMPHI	13	see S4	2	27	26.3	2.44	0.59	0.10	Bieda (2013b)
	3	see S4	2	26	15.9	1.62	0.41	0.07	
	5	see S4	1	-0.8	14.4	105.3	49.2	7.5	
	7a	see S4	1	28	13.7	13.98	3.56	0.87	
	7b	see S4	2	27	10.8	17.67	4.26	0.97	
	8a	see S4	2	27	12.8	9.48	2.26	0.48	
	8b	see S4	20	17.4	7.29	1.74	0.37	0.08	
	9b	see S4	250	5	40.8	6.15	3.28	0.46	
	12	see S4	22	20.3	2.99	1.25	0.30	0.09	
	14	see S4	250	4	29.1	2.13	0.98	0.20	
	15a	see S4	2	-0.9	13.7	7.06	2.67	0.58	
	15c	see S4	2	15	16.2	1.90	0.38	0.08	
	16a	see S4	2	9	24.2	2.90	1.19	0.23	
	10b	see S4	250	5	14.1	2.65	1.23	0.23	
	17	see S4	30	-0.1	60.3	2.98	1.14	0.24	
	18	see S4	250	5	29.8	1.18	0.56	0.10	
	19	see S4	22	28	22.7	1.24	0.44	0.09	
	20	see S4	2	-1.1	18.4	12.14	4.90	0.99	
	22a	see S4	2	13	73.1	3.96	1.62	0.32	
	22b	see S4	250	5	66.9	5.90	2.17	0.40	
	28	see S4	30	-1.6	40.8	193.1	87.6	12.2	
	25	see S4	600	0.2	12.9	81.4	38.5	5.7	
DECA	21a	see S4	600	0.2	21.4	265	122.2	21.2	Bieda (2013b)
	27b	see S4	600	0.2	15.8	139	156.1	27.1	
	31b	see S4	1	30	48.1	26.7	12.3	3.2	
	39	see S4	1	27.5	14.6	23.5	10.8	2.8	
	31a	see S4	1	24.5	24.7	6.49	2.99	0.77	
	S1	<i>Acanthephyra carolinensis</i>	600	5.5	14.9	840			Quetin et al. 1980
	S2	<i>Hymenodora frontalis</i>	600	5.5	12.2	400			
	S3	<i>Parapolydora sulcatifrons</i>	600	5.5	91.0	520			
	S4	<i>Psiphospha chacei</i>	100	5.5	11.2	340			
	S5	<i>Psiphospha emarginata</i>	600	5.5	21.4	790			
	S6	<i>Synallogia cristata</i>	600	5.5	8.1	740			
	S7	<i>Gammarus propinquus</i>	600	5.5	19.3	140			
	S8	<i>Sergestes similis</i>	100	5.5	33.0	110			
	S9	<i>Sergestes phorax</i>	600	5.5	12.9	500			
MYSI	2	see S4	2	14.9	8.6	2.88	1.27	0.32	Bieda (2013c)
	6	see S4	60	-1.6	18.7	171	75.3	17.9	
	12	see S4	600	5.5	18.5	280	143	38.3	
	15a	see S4	600	0.15	39.6	127	52.6	9.2	
	16	see S4	600	5.5	14.9	930	479	57.7	
	17	see S4	550	5.5	44.8	1040	512	66.0	
	19	see S4	1	14	21.1	0.82	0.32	0.10	
	20a	see S4	1	14	15.6	1.72	0.68	0.20	
	20b	see S4	1	16	20.5	4.20	1.70	0.47	
	20c	see S4	1	16	22.5	2.90	1.17	0.33	
	32a	see S4	2	28.5	8.4	0.16	0.069	0.017	
	32b	see S4	2	28.5	7.9	1.33	0.59	0.14	
	36	see S4	1	28.5	18.5	4.09	1.79	0.45	
	38a	see S4	2	27.8	14.7	1.47	0.59	0.15	
OSTR	S1	<i>Gigamysopsis mulleri</i>	500	0.2	24.6	54.9	17.7	4.5	Bieda (1988)
	S2	<i>Gigamysopsis mulleri</i>	500	0.2	22.4	103.1	36.7	14.9	
	S3	<i>Gigamysopsis mulleri</i>	500	-0.9	25.4	48.0	14.2	3.9	
	S4	<i>Gigamysopsis mulleri</i>	500	-1	21.0	193.7	44.4	11.7	
CHAE	S1	<i>Adiantopsis neopacifica</i>	2	23	17.7	0.224	0.070	0.020	Bieda and McKinnon (2012)
	S2	<i>Ferrosagitta hispida</i>	2	24	27.2	0.330	0.134	0.037	Bieda (unpublished data)
	S3		2	26	6.8	0.100	0.041	0.011	Reeve et al. (1970)
	S4	<i>Ferrosagitta robusta</i>	2	27	6.0	0.790	0.291	0.074	Bieda (1974)
	S5	<i>Flaccisagitta enflata</i>	2	27	20.7	0.710	0.249	0.056	Bieda (unpublished data)
	S6	<i>Mesosagitta minima</i>	2	15	7.2	0.094	0.034	0.010	Bieda (1974)
	S7	<i>Ferrosagitta elegans</i>	2	9	9.7	1.03	0.42	0.12	Bieda (1974)
	S8		30	-0.4	8.1	4.50	1.73	0.47	Bieda and Skjoldal (1989)
	S9	<i>Pseudosagitta gazellae</i>	100	-1	13.1	35.3	7.1	2.0	Bieda and Kikwood (1989)
	S10	<i>Sagitta bipunctata</i>	2	27.5	9.2	0.450	0.175	0.044	Bieda (1974)
S11	<i>Serratosagitta serratosetata</i>	2	27	8.1	0.730	0.283	0.072	Bieda (1974)	
S12	<i>Zoeosagitta lundii</i> minor	2	24	10.1	0.084	0.032	0.010	Bieda and McKinnon (2012)	
CHNI	2	see S4	2	8.5	24.9	3.39	1.02	0.32	Bieda (2014a)
	3b	see S4	150	11	44.2	14.00	2.34	0.80	
	7b	see S4	9	16.8	200	16.4	5.4	5.4	
	7a	see S4	100	-0.7	17.6	136	12.9	3.3	
	15	see S4	2	27	18.7	2.27			

S4. Data code and species. C = Copepodid, F = Female, M = Male, J = Juvenile, A = Adult, FG = Gravid female.

Index	Data Code	Species	Stage/Sex	Index	Data Code	Species	Stage/Sex	Index	Data Code	Species	Stage/Sex	Index	Data Code	Species	Stage/Sex
COPE	1	<i>Pachypeltis pacificus</i>	C:FG	151	<i>Scaphocalanus affinis</i>	C:FG	7	<i>Acanthephyra similis</i>	C:FG	9	<i>Colobanoma sericeum</i>	9	<i>Colobanoma sericeum</i>	9	<i>Colobanoma sericeum</i>
2	<i>Lucicutia bicornuta</i>	C:GM	152	<i>Amaltheia incornuta</i>	C:FG	7a	<i>Hymenodora frontalis</i>	7a	<i>Hymenodora frontalis</i>	10	<i>Crossota</i> sp.	10	<i>Crossota</i> sp.	10	<i>Crossota</i> sp.
3	<i>Lucicutia grandis</i>	C:FG	153	<i>Scotocalanus</i> sp.	C:FG	7b	<i>Hymenodora frontalis</i>	7b	<i>Hymenodora frontalis</i>	11a	<i>Eutima cellularia</i>	11a	<i>Eutima cellularia</i>	11a	<i>Eutima cellularia</i>
4	<i>Meridia asymmetrica</i>	C:FG	154	<i>Scotocalanus securifrons</i>	C:FG	7c	<i>Hymenodora frontalis</i>	7c	<i>Hymenodora frontalis</i>	11b	<i>Eutima cellularia</i>	11b	<i>Eutima cellularia</i>	11b	<i>Eutima cellularia</i>
5	<i>Meridia curvicauda</i>	C:FG	155	<i>Bathycalanus bradyi</i>	C:FG	8	<i>Janicella spinicauda</i>	8	<i>Janicella spinicauda</i>	12	<i>Eperomus typus</i>	12	<i>Eperomus typus</i>	12	<i>Eperomus typus</i>
6	<i>Meridia okutanensis</i>	C:FG	156	<i>Bathycalanus bradyi</i>	C:FG	9	<i>Nematosquilla lanceipes</i>	9	<i>Nematosquilla lanceipes</i>	13	<i>Eutima indicans</i>	13	<i>Eutima indicans</i>	13	<i>Eutima indicans</i>
7	<i>Pleuronemma scutellata</i>	C:GM	157	<i>Spinocalanus magnus</i>	C:FG	10	<i>Notostomus elegans</i>	10	<i>Notostomus elegans</i>	14	<i>Goniomus vortens</i>	14	<i>Goniomus vortens</i>	14	<i>Goniomus vortens</i>
8		C:FG	158	<i>Acridospis rostrata</i>	C:FG	11	<i>Notostomus gibbosus</i>	11	<i>Notostomus gibbosus</i>	15	<i>Lirapia tetraphylla</i>	15	<i>Lirapia tetraphylla</i>	15	<i>Lirapia tetraphylla</i>
9	<i>Pleuronemma siphonis</i>	C:FG	159	<i>Amaltheia incornuta</i>	C:GM	12	<i>Notostomus</i> sp.	12	<i>Notostomus</i> sp.	16	<i>Nemopsis bachei</i>	16	<i>Nemopsis bachei</i>	16	<i>Nemopsis bachei</i>
10	<i>Conducia columbica</i>	C:GM	160	<i>Amaltheia incornuta</i>	C:FG	13a	<i>Ophephorus gracilirostris</i>	13a	<i>Ophephorus gracilirostris</i>	17	<i>Pantachogon haeckeli</i>	17	<i>Pantachogon haeckeli</i>	17	<i>Pantachogon haeckeli</i>
11	<i>Acridospis rostrata</i>	C:GM	161	<i>Bathycharta lamellata</i>	C:GM	13b	<i>Ophephorus gracilirostris</i>	13b	<i>Ophephorus gracilirostris</i>	18a	<i>Phialidium gregarium</i>	18a	<i>Phialidium gregarium</i>	18a	<i>Phialidium gregarium</i>
12	<i>Chiridius pacificus</i>	C:FG	162	<i>Bathycharta lamellata</i>	C:GM	14a	<i>Ophephorus spinosus</i>	14a	<i>Ophephorus spinosus</i>	18b	<i>Phialidium gregarium</i>	18b	<i>Phialidium gregarium</i>	18b	<i>Phialidium gregarium</i>
13	<i>Chiridius strepsi</i>	C:FG	163	<i>Bathycharta lamellata</i>	C:GM	14b	<i>Ophephorus spinosus</i>	14b	<i>Ophephorus spinosus</i>	19	<i>Phialidium lense</i>	19	<i>Phialidium lense</i>	19	<i>Phialidium lense</i>
14	<i>Euchirella brevis</i>	C:FG	164	<i>Bathycalanus bradyi</i>	C:3	15a	<i>Parapandalus richardi</i>	15a	<i>Parapandalus richardi</i>	20	<i>Sergia princeps</i>	20	<i>Sergia princeps</i>	20	<i>Sergia princeps</i>
15	<i>Euchirella galathea</i>	C:FG	165	<i>Bathycalanus bradyi</i>	C:5	15b	<i>Parapandalus richardi</i>	15b	<i>Parapandalus richardi</i>	21	<i>Solmisia incisa</i>	21	<i>Solmisia incisa</i>	21	<i>Solmisia incisa</i>
16	<i>Euchirella messiensis</i>	C:FG	166	<i>Benthomphala pallidula</i>	C:GM	16	<i>Parapandanus sulcifrons</i>	16	<i>Parapandanus sulcifrons</i>	22a	<i>Somostoma atra</i>	22a	<i>Somostoma atra</i>	22a	<i>Somostoma atra</i>
17	<i>Euchirella rostrata</i>	C:FG	167	<i>Chiridella abyssalis</i>	C:FG	17a	<i>Pauphara chacei</i>	17a	<i>Pauphara chacei</i>	22b	<i>Somostoma atra</i>	22b	<i>Somostoma atra</i>	22b	<i>Somostoma atra</i>
18	<i>Euchirella truncata</i>	C:4M	168	<i>Chiridella pacifica</i>	C:FG	17b	<i>Pauphara chacei</i>	17b	<i>Pauphara chacei</i>	23	<i>Athyopsis tetragona</i>	23	<i>Athyopsis tetragona</i>	23	<i>Athyopsis tetragona</i>
19	<i>Gaidius brevirostris</i>	C:FG	169	<i>Gastanus parvicornis</i>	C:FG	18a	<i>Pauphara emarginata</i>	18a	<i>Pauphara emarginata</i>	24	<i>Chelephyes appendiculata</i>	24	<i>Chelephyes appendiculata</i>	24	<i>Chelephyes appendiculata</i>
20		C:FG	170	<i>Gaidius pungens</i>	C:FG	18b	<i>Pauphara emarginata</i>	18b	<i>Pauphara emarginata</i>	25a	<i>Diphyes antarctica</i>	25a	<i>Diphyes antarctica</i>	25a	<i>Diphyes antarctica</i>
21	<i>Gastanus robustus</i>	C:4F	171	<i>Gastanus robustus</i>	C:FG	20	<i>Pauphara multidentata</i>	20	<i>Pauphara multidentata</i>	26	<i>Diphyes</i> sp.	26	<i>Diphyes</i> sp.	26	<i>Diphyes</i> sp.
22	<i>Gaidius tenuirostris</i>	C:5F	172	<i>Meridia ornata</i>	C:GM	21a	<i>Pauphara scotiae</i>	21a	<i>Pauphara scotiae</i>	27	19 species	27	19 species	27	19 species
23		C:FG	173	<i>Meridia ornata</i>	C:FG	21b	<i>Pauphara scotiae</i>	21b	<i>Pauphara scotiae</i>	28a	<i>Aurelia aurita</i>	28a	<i>Aurelia aurita</i>	28a	<i>Aurelia aurita</i>
24	<i>Gaidius variabilis</i>	C:GM	174	<i>Meridia ornata</i>	C:GM	22	<i>Systellaspis debilis</i>	22	<i>Systellaspis debilis</i>	29a	<i>Aurelia aurita</i>	29a	<i>Aurelia aurita</i>	29a	<i>Aurelia aurita</i>
25		C:FG	175	<i>Mitocalanus robustus</i>	C:FG	23a	<i>Systellaspis cristata</i>	23a	<i>Systellaspis cristata</i>	29c	<i>Aurelia aurita</i>	29c	<i>Aurelia aurita</i>	29c	<i>Aurelia aurita</i>
26		C:FG	176	<i>Ochrocalanus magnus</i>	C:FG	23b	<i>Systellaspis cristata</i>	23b	<i>Systellaspis cristata</i>	29d	<i>Aurelia aurita</i>	29d	<i>Aurelia aurita</i>	29d	<i>Aurelia aurita</i>
27	<i>Pseudochirella pacifica</i>	C:GM	177	<i>Ochrocalanus magnus</i>	C:FG	24a	<i>Systellaspis debilis</i>	24a	<i>Systellaspis debilis</i>	30a	<i>Cassiopea samachana</i>	30a	<i>Cassiopea samachana</i>	30a	<i>Cassiopea samachana</i>
28	<i>Pseudochirella spinifera</i>	C:GM	178	<i>Paracantha rubra</i>	C:4F	24b	<i>Systellaspis debilis</i>	24b	<i>Systellaspis debilis</i>	30b	<i>Cassiopea samachana</i>	30b	<i>Cassiopea samachana</i>	30b	<i>Cassiopea samachana</i>
29		C:GM	179	<i>Pseudochirella pacifica</i>	C:GM	24c	<i>Systellaspis debilis</i>	24c	<i>Systellaspis debilis</i>	31	<i>Cassiopea samachana</i>	31	<i>Cassiopea samachana</i>	31	<i>Cassiopea samachana</i>
30	<i>Undeucharta plumosa</i>	C:FG	180	<i>Pseudochirella polyzona</i>	C:FG	24d	<i>Systellaspis debilis</i>	24d	<i>Systellaspis debilis</i>	32	<i>Chrysaster quinquevittatus</i>	32	<i>Chrysaster quinquevittatus</i>	32	<i>Chrysaster quinquevittatus</i>
31	<i>Paraneucharta barbata</i>	C:FG	181	<i>Scaphocalanus magnus</i>	C:FG	25	<i>Furchella villosa</i>	25	<i>Furchella villosa</i>	33a	<i>Cyanea capillata</i>	33a	<i>Cyanea capillata</i>	33a	<i>Cyanea capillata</i>
32	<i>Paraneucharta brevis</i>	C:GM	182	<i>Spinocalanus magnus</i>	C:FG	26	<i>Gennadas copensis</i>	26	<i>Gennadas copensis</i>	33b	<i>Cyanea capillata</i>	33b	<i>Cyanea capillata</i>	33b	<i>Cyanea capillata</i>
33	<i>Undeucharta brevis</i>	C:FG	183	<i>Undeucharta brevis</i>	C:FG	27a	<i>Gennadas kempii</i>	27a	<i>Gennadas kempii</i>	33c	<i>Cyanea capillata</i>	33c	<i>Cyanea capillata</i>	33c	<i>Cyanea capillata</i>
34		C:FG	184	<i>Undeucharta major</i>	C:FG	27b	<i>Gennadas kempii</i>	27b	<i>Gennadas kempii</i>	34	<i>Metastigis</i> sp.	34	<i>Metastigis</i> sp.	34	<i>Metastigis</i> sp.
35	<i>Paraneucharta brevis</i>	C:FG	185	<i>Undeucharta plumosa</i>	C:FG	28a	<i>Gennadas propinquus</i>	28a	<i>Gennadas propinquus</i>	35a	<i>Pelagia noctiluca</i>	35a	<i>Pelagia noctiluca</i>	35a	<i>Pelagia noctiluca</i>
36	<i>Paraneucharta elongata</i>	C:4M	186	<i>Undeucharta plumosa</i>	C:FG	28b	<i>Gennadas propinquus</i>	28b	<i>Gennadas propinquus</i>	35b	<i>Pelagia noctiluca</i>	35b	<i>Pelagia noctiluca</i>	35b	<i>Pelagia noctiluca</i>
37		C:FG	187	<i>Valdivia imperforata</i>	C:FG	29	<i>Gennadas scutatus</i>	29	<i>Gennadas scutatus</i>	36	<i>Peripatella peripatella</i>	36	<i>Peripatella peripatella</i>	36	<i>Peripatella peripatella</i>
38		C:GM	188	<i>Xanthocalanus kurileensis</i>	C:FG	30	<i>Gennadas valens</i>	30	<i>Gennadas valens</i>	37a	<i>Porallia rufescens</i>	37a	<i>Porallia rufescens</i>	37a	<i>Porallia rufescens</i>
39		C:GM	189	<i>Calanus propinquus</i>	C:FG	31a	<i>Acetes ibogae australis</i>	31a	<i>Acetes ibogae australis</i>	37b	<i>Porallia rufescens</i>	37b	<i>Porallia rufescens</i>	37b	<i>Porallia rufescens</i>
40		C:FG	190	<i>Meridia gracilis</i>	C:FG	31b	<i>Acetes ibogae australis</i>	31b	<i>Acetes ibogae australis</i>	37c	<i>Porallia rufescens</i>	37c	<i>Porallia rufescens</i>	37c	<i>Porallia rufescens</i>
41		C:FG	191	<i>Calanoides acutus</i>	C:5	32a	<i>Eusergestes similis</i>	32a	<i>Eusergestes similis</i>	38	<i>Stomatopoda melanops</i>	38	<i>Stomatopoda melanops</i>	38	<i>Stomatopoda melanops</i>
42		C:FG	192	<i>Calanoides acutus</i>	C:4.5	32b	<i>Eusergestes similis</i>	32b	<i>Eusergestes similis</i>	TC1	<i>Aegina citrea</i>	TC1	<i>Aegina citrea</i>	TC1	<i>Aegina citrea</i>
43		C:FG	193	<i>Calanus finmarchicus</i>	C:FG	35	<i>Leucope</i> sp.	35	<i>Leucope</i> sp.	TC2	<i>Byrrhina brucei</i>	TC2	<i>Byrrhina brucei</i>	TC2	<i>Byrrhina brucei</i>
44	<i>Paraneucharta modesta</i>	C:FG	194	<i>Calanus glacialis</i>	C:FG	36	<i>Parasergestes armatus</i>	36	<i>Parasergestes armatus</i>	TC3	<i>Colobanoma sericeum</i>	TC3	<i>Colobanoma sericeum</i>	TC3	<i>Colobanoma sericeum</i>
45	<i>Paraneucharta orientalis</i>	C:FG	195	<i>Calanus hyperboreus</i>	C:FG	37	<i>Petalidium foliaceum</i>	37	<i>Petalidium foliaceum</i>	TC4	<i>Crossota</i> sp.	TC4	<i>Crossota</i> sp.	TC4	<i>Crossota</i> sp.
46	<i>Paraneucharta pseudotumidula</i>	C:GM	196	<i>Calanus hyperboreus</i>	C:5	38	<i>Sesocentropus curvicauda</i>	38	<i>Sesocentropus curvicauda</i>	TC5	<i>Crossota rufotumida</i>	TC5	<i>Crossota rufotumida</i>	TC5	<i>Crossota rufotumida</i>
47		C:FG	197	<i>Calanus hyperboreus</i>	C:5	39	<i>Sergestes calanoides</i>	39	<i>Sergestes calanoides</i>	TC6	<i>Crossota</i> sp. A	TC6	<i>Crossota</i> sp. A	TC6	<i>Crossota</i> sp. A
48	<i>Paraneucharta rubra</i>	C:GM	198	<i>Meridia longa</i>	C:FG	40	<i>Sergia biulcata</i>	40	<i>Sergia biulcata</i>	TC7	<i>Eirene mollis</i>	TC7	<i>Eirene mollis</i>	TC7	<i>Eirene mollis</i>
49		C:FG	199	<i>Riccalanus gigas</i>	C:5	41	<i>Sergia splendens</i>	41	<i>Sergia splendens</i>	TC8	<i>Haliscera ligetovi</i>	TC8	<i>Haliscera ligetovi</i>	TC8	<i>Haliscera ligetovi</i>
50	<i>Anallathia valida</i>	C:GM	200	<i>Neocalanus cristatus</i>	C:5	42	<i>Sergia splendens</i>	42	<i>Sergia splendens</i>	TC9	<i>Haliscera ligetovi</i>	TC9	<i>Haliscera ligetovi</i>	TC9	<i>Haliscera ligetovi</i>
51		C:FG	201	<i>Neocalanus planchus</i>	C:4	43a	<i>Sergia phorca</i>	43a	<i>Sergia phorca</i>	TC10	<i>Pantachogon</i> sp. A	TC10	<i>Pantachogon</i> sp. A	TC10	<i>Pantachogon</i> sp. A
52	<i>Mitocalanus robustus</i>	C:FG	202	<i>Neocalanus planchus</i>	C:5	43b	<i>Sergia phorca</i>	43b	<i>Sergia phorca</i>	TC11	<i>Tetrasia erythrogaster</i>	TC11	<i>Tetrasia erythrogaster</i>	TC11	<i>Tetrasia erythrogaster</i>
53	<i>Scaphocalanus medius</i>	C:FG	203	<i>Eucalanus longi</i>	C:GM	44	<i>Sergia incurrens</i>	44	<i>Sergia incurrens</i>	TC12	<i>Valoniopsis subterreus</i>	TC12	<i>Valoniopsis subterreus</i>	TC12	<i>Valoniopsis subterreus</i>
54	<i>Spinocalanus stellatus</i>	C:FG	204	<i>Pseudocalanus elongatus</i>	C:FG	45	<i>Sergestes tenuirostris</i>	45	<i>Sergestes tenuirostris</i>	TC13	<i>Vampyrocera</i> sp.	TC13	<i>Vampyrocera</i> sp.	TC13	<i>Vampyrocera</i> sp.
55	<i>Pachypeltis pacificus</i>	C:FG	205	<i>Meridia pacifica</i>	C:FG	46	<i>Sergia grandis</i>	46	<i>Sergia grandis</i>	TC14	<i>Arctia vanthoffi</i>	TC14	<i>Arctia vanthoffi</i>	TC14	<i>Arctia vanthoffi</i>
56	<i>Lucicutia incornuta</i>	C:FG	206	<i>Acetia longirostris</i>	C:FG	47	<i>Sergia robusta</i>	47	<i>Sergia robusta</i>	TC15	<i>Arctia vanthoffi</i>	TC15	<i>Arctia vanthoffi</i>	TC15	<i>Arctia vanthoffi</i>
57	<i>Lucicutia grandis</i>	C:GM	207	<i>Tortanus dilucidatus</i>	C:FG	48	<i>Sergia splendens</i>	48	<i>Sergia splendens</i>	TC16	<i>Nauclerus</i> sp.	TC16	<i>Nauclerus</i> sp.	TC16	<i>Nauclerus</i> sp.
58	<i>Lucicutia pacifica</i>	C:FG	208	<i>Meridia pacifica</i>	C:FG	49	<i>Sergia italiamai</i>	49	<i>Sergia italiamai</i>	TC17	<i>Paraphyllina ramosi</i>	TC17	<i>Paraphyllina ramosi</i>	TC17	<i>Paraphyllina ramosi</i>
59		C:FG	209	<i>Mitocalanus tenuicornis</i>	C:5	50	<i>Pleurocystidia planifrons</i>	50	<i>Pleurocystidia planifrons</i>	TC18	<i>Paraphyllina ramosi</i>	TC18	<i>Paraphyllina ramosi</i>	TC18	<i>Paraphyllina ramosi</i>
60	<i>Meridia asymmetrica</i>	C:FG	210	<i>Paracalanus parvus</i>	C:5	1	<i>Chionella spinifera</i>	1	<i>Chionella spinifera</i>	CTEN	<i>Aganippe</i> sp.	CTEN	<i>Aganippe</i> sp.	CTEN	<i>Aganippe</i> sp.
61		C:FG	211	<i>Centropages abdominalis</i>	C:5	2	<i>Cyllipsus lacini</i>	2	<i>Cyllipsus lacini</i>	40a	<i>Bathocyroe foveata</i>	40a	<i>Bathocyroe foveata</i>	40a	<i>Bathocyroe foveata</i>
62	<i>Meridia curvicauda</i>	C:FG	212	<i>Pseudodiplopus marinus</i>	C:5	3	<i>Hemiphaedusa tenuirostris</i>	3	<i>Hemiphaedusa tenuirostris</i>	40b	<i>Bathocyroe foveata</i>	40b	<i>Bathocyroe foveata</i>	40b	<i>Bathocyroe foveata</i>
63	<i>Meridia ornata</i>	C:5	213	<i>Neocalanus planchus</i>	C:5	4	<i>Hyperia gallica</i>	4	<i>Hyperia gallica</i>	40c	<i>Bathocyroe foveata</i>	40c	<i>Bathocyroe foveata</i>	40c	<i>Bathocyroe foveata</i>
64	<i>Acetia clausi</i>	C:GM	214	<i>Acetia clausi</i>	C:5	5	<i>Hyperia gallica</i>	5	<i>Hyperia gallica</i>	41	<i>Boreo abyssicola</i>	41	<i>Boreo abyssicola</i>	41	<i>Boreo abyssicola</i>
65		C:FG	215	<i>Neocalanus gracilis</i>	C:5	6	<i>Leucope</i> sp.	6	<i>Leucope</i> sp.	42a	<i>Boreo curvicauda</i>	42a	<i>Boreo curvicauda</i>	42a	<i>Boreo curvicauda</i>
66	<i>Bradydium pacificum</i>	C:FG	216	<i>Centropages brachyatus</i>	C:5	7a	<i>Oxycephalus clausi</i>	7a	<i>Oxycephalus clausi</i>	42b	<i>Boreo curvicauda</i>	42b	<i>Boreo curvicauda</i>	42b	<i>Boreo curvicauda</i>
67	<i>Euchirella rostrata</i>	C:FG	217	<i>Acetia clausi</i>	C:5	7b	<i>Oxycephalus clausi</i>	7b	<i>Oxycephalus clausi</i>	43a	<i>Boreo curvicauda</i>	43a	<i>Boreo curvicauda</i>	43a	<i>Boreo curvicauda</i>
68		C:FG	218	<i>Undinula vulgaris</i>	C:5	8a	<i>Phronima sedentaria</i>	8a	<i>Phronima sedentaria</i>	43b	<i>Boreo curvicauda</i>	43b	<i>Boreo curvicauda</i>	43b	<i>Boreo curvicauda</i>
69	<i>Gaidius brevirostris</i>	C:FG	219	<i>Eucharta marina</i>	C:5	8b	<i>Phronima sedentaria</i>	8b	<i>Phronima sedentaria</i>	44	<i>Boreo curvicauda</i>	44	<i>Boreo curvicauda</i>	44	<i>Boreo curvicauda</i>
70	<i>Gaidius variabilis</i>	C:FG	220	<i>Acetia pacifica</i>	C:5	9	<i>Phronima sedentaria</i>	9	<i>Phronima sedentaria</i>	45	<i>Boreo curvicauda</i>	45	<i>Boreo curvicauda</i>	45	<i>Boreo curvicauda</i>
71		C:FG	221	<i>Calanopsis elliptica</i>	C:5	9a	<i>Phronima sedentaria</i>	9a	<i>Phronima sedentaria</i>	46	<i>Bolnopsis infundibulum</i>	46	<i>Bolnopsis infundibulum</i>	46	<i>Bolnopsis infundibulum</i>
72															