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3 Respiration and ammonia excretion by marine metazooplankton taxa: synthesis toward
4 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):

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

$a_3 \times \ln \text{Depth} - \text{TAXA}$, 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 ($\pm 16.5, \text{SD}$) 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 ($1000/\text{K}$) 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_{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 ammonium (as NH₄-N) excretion data

Taxa	Code	Species	Depth (m)	T°C	Range/Std	DW (mg)	C (mg)	N (mg)	Reference
COPE	51	<i>Calanus propinqua</i>	2	-1.0	0.007	1.043	0.41	0.12	Baño et al. (2003)
COPE	52	<i>Calanoides acutus</i> CS	2	-0.2	0.019	0.794	0.19	0.03	
COPE	53	<i>Calanoides calanoides</i> CA CS	2	-0.5	0.014	0.708	0.10	0.02	
COPE	54	<i>Rhinocalanus gigas</i>	50	-1.7	0.113	1.080	0.50	0.11	
COPE	55	<i>Mesocyclops perdurans</i>	2	-1.4	0.031	0.265	0.11	0.027	
COPE	56	<i>Calanus finmarchicus</i> CFP	2	0.1	0.013	0.307	0.21	0.030	
COPE	57	<i>Calanus placidus</i> CFP	50	2.3	0.030	0.474	0.22	0.050	
COPE	58	<i>Calanus hyperboreus</i> CFP	50	2.0	0.049	0.50	2.24	0.28	
COPE	59	<i>Calanus hyperboreus</i> CS (biont)	50	0.9	0.051	1.94	1.12	0.14	
COPE	510	<i>Calanus hyperboreus</i> CS (late bloom)	50	-0.3	0.030	2.277	1.63	0.18	
COPE	511	<i>Mesocyclops</i> CFP	50	0.1	0.023	0.353	0.17	0.027	
COPE	512	<i>Noeclema planchensis</i> CS	2	7.3	0.017	0.785	0.45	0.063	
COPE	513	<i>Noeclema planchensis</i> CA	2	5.6	0.057	0.205	0.15	0.023	
COPE	514	<i>Noeclema planchensis</i>	2	15.1	0.066	0.294	0.14	0.026	
COPE	515	<i>Noeclema crassius</i>	2	6.3	0.164	1.59	0.79	0.13	
COPE	516	<i>Acetabularia</i> CFP	2	4.0	0.058	0.40	0.10	0.03	
COPE	517	<i>Paracalanus elongatus</i>	2	8.6	0.002	0.016	0.003	0.004	
COPE	518	<i>Mesocyclops</i> CFP	2	0.2	0.033	0.146	0.064	0.017	
COPE	519	<i>Mesocyclops</i> CFP	2	13.0	0.023	0.094	0.043	0.013	
COPE	520	<i>Acetabularia</i> CFP	2	14.8	0.006	0.008	0.003	0.003	
COPE	521	<i>Acetabularia</i> CFP	2	9.6	0.002	0.008	0.003	0.003	
COPE	522	<i>Termona discoloratus</i>	2	7.0	0.008	0.057	0.025	0.006	
COPE	523	<i>Canthocamptus paucis</i> CFP	2	22.0	0.014	0.014	0.014	0.003	
COPE	524	<i>Noeclema pumilus</i>	2	19.7	0.052	0.500	0.254	0.051	
COPE	525	<i>Undinula vulgaris</i>	2	23.0	0.074	0.185	0.077	0.018	
COPE	526	<i>Arctocalanus gibbus</i> CFP	22.0	0.011	0.023	0.009	0.002	0.002	
COPE	527	<i>Paracalanus parvus</i>	2	22.0	0.015	0.014	0.014	0.003	
COPE	528	<i>Acetabularia suberosus</i> CFP	2	22.0	0.024	0.103	0.043	0.009	
COPE	529	<i>Arctocalanus</i> CFP	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 brevicornis</i>	2	17.3	0.011	0.020	0.002	0.002	
COPE	532	<i>Termona</i> CFP	2	22.0	0.005	0.006	0.006	0.003	
COPE	533	<i>Calanopsis affinis</i> CFP	2	22.0	0.017	0.077	0.032	0.007	
COPE	534	<i>Labidocera</i> sp.	22.0	0.070	0.136	0.070	0.014	0.004	
COPE	535	<i>Termona gracilis</i> CFP	2	22.0	0.010	0.028	0.012	0.003	
COPE	536	<i>Acetabularia</i> CFP	22.0	0.006	0.017	0.010	0.001	0.001	
COPE	537	<i>Acetabularia</i> CFP	2	22.0	0.006	0.007	0.003	0.003	
COPE	538	<i>Corycaeus</i> sp.	2	22.0	0.013	0.032	0.013	0.003	
COPE	539	<i>Stomatoceros</i> CFP	2	26.0	0.021	0.048	0.021	0.005	
COPE	540	<i>Undinula vulgaris</i>	2	27.6	0.118	0.167	0.070	0.018	
COPE	541	<i>Acetabularia suberosus</i> CFP	2	27.7	0.027	0.029	0.017	0.004	
COPE	542	<i>Undinula vulgaris</i>	2	24.0	0.021	0.104	0.043	0.010	
COPE	543	<i>Acetabularia suberosus</i>	2	27.4	0.070	0.137	0.054	0.013	
COPE	544	<i>Paracalanus aculeatus</i>	2	28.0	0.084	0.077	0.037	0.012	
COPE	545	<i>Arctocalanus gibbus</i> CFP	2	28.7	0.022	0.010	0.004	0.001	
COPE	546	<i>Termona</i> CFP	2	27.0	0.010	0.005	0.002	0.001	
COPE	547	<i>Centropages furcatus</i> CCM	2	27.0	0.016	0.010	0.002	0.002	
COPE	548	<i>Calanopsis affinis</i> CFP	2	26.0	0.020	0.036	0.023	0.005	
COPE	549	<i>Calanopsis affinis</i> CFP	2	27.4	0.024	0.040	0.020	0.005	
COPE	550	<i>Labidocera</i> sp.	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</i> sp.	2	26.4	0.139	0.220	0.095	0.027	
COPE	553	<i>Labidocera</i> sp. CFP	2	28.5	0.037	0.024	0.010	0.002	
COPE	554	<i>Acetabularia</i> CFP	2	25.0	0.044	0.005	0.004	0.001	
COPE	555	<i>Acetabularia</i> CFP	2	27.0	0.004	0.017	0.007	0.002	
COPE	556	<i>Acetabularia</i> CFP	2	27.8	0.012	0.018	0.008	0.002	
COPE	557	<i>Termona gracilis</i> CCM	2	26.0	0.010	0.010	0.002	0.002	
COPE	558	<i>Termona gracilis</i> CCM	2	29.0	0.058	0.113	0.063	0.012	
COPE	559	<i>Labidocera</i> sp.	2	25.0	0.160	0.160	0.066	0.016	
COPE	560	<i>Undinula vulgaris</i>	25	25.5	0.080	0.220	0.099	0.026	
COPE	561	<i>Paracalanus indicus</i>	1	23.0	0.019	0.072	0.032	0.008	
COPE	562	<i>Microsetella pusilla</i>	1	25.0	0.029	0.060	0.030	0.005	
COPE	563	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	564	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	565	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	566	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	567	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	568	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	569	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	570	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	571	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	572	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	573	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	574	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	575	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	576	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	577	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	578	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	579	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	580	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	581	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	582	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	583	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	584	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	585	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	586	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	587	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	588	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	589	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	590	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	591	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	592	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	593	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	594	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	595	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	596	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	597	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	598	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	599	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	600	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	601	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	602	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	603	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	604	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	605	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	606	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	607	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	608	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	609	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	610	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	611	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	612	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	613	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	614	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	615	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	616	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	617	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	618	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	619	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	620	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	621	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	622	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	623	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	624	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	625	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	626	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	627	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	628	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	629	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	630	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	631	<i>Obolus subdilatatus</i>	1	24.0	0.005	0.012	0.003	0.001	
COPE	632	<i>Obolus subdilatatus</i>	1	24.0					

S1. Summary of ON ratio data

COPE	Code	Species	Depth (m)	Reference					Taxa	Code	Species	Depth (m)	Reference							
				T (°C)	ON (by atom)	DW(mg)	C (mg)	N (mg)					T (°C)	ON (by atom)	DW(mg)	C (mg)	N (mg)			
	S1	<i>Calanus propinquus</i>	2	-1.0	13.8	1.04	0.109	0.118	Beck et al. (2001)	40a	see S4	767	9	11.8	444	32.9	0.89	Beck (2014a)		
	S2	<i>Calanoides acutus</i>	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		41	see S4	2	15.7	85.6	61.8	7.12	1.91			
	S4	<i>Rhincalanus gigas</i>	50	-1.7	4.8	1.06	0.503	0.066		42b	see S4	2	15	17.2	52.1	5.89	1.93			
	S5	<i>Metridia percheri</i>	2	-1.4	12.9	0.265	0.106	0.027		43a	see S4	10	25	10.7	7.6	2.83	0.75			
	S6	<i>Calanus finmarchicus</i> C6F	2	0.1	30.6	0.387	0.215	0.030		44	see S4	2	-0.8	14.7	40.9	8.7	9.4			
	S7	<i>Calanus glacialis</i> C6F	50	2.3	25.7	0.474	0.223	0.020		45	see S4	1	-1.6	14.9	1362	76.0	20.9			
	S8	<i>Calanus hyperboreus</i> C6F	50	1.3	37.9	3.95	2.338	0.263		47	see S4	1	22	15.4	224	24.6	0.76			
	S9	<i>Calanus hyperboreus</i> C5 (boom)	50	0.9	25.4	1.94	1.117	0.144		48	see S4	1	14.4	17.6	30.0	9.5	0.87			
	S10	<i>Calanus hyperboreus</i> C5 (late boom)	50	-0.3	44.5	2.68	1.634	0.180		49	see S4	5	1	20.2	232	19.5	4.25			
	S11	<i>Metridia longa</i> C6F	50	0.1	22.1	0.353	0.168	0.037		50	see S4	10	25	12.2	20.2	1.78	0.48			
	S12	<i>Noecalanus planchrus</i> C5	2	7.3	50.0	0.785	0.452	0.063		51	see S4	1	0	14.0	380	19.5	4.87			
	S13	<i>Noecalanus planchrus</i> C4	2	5.6	48.8	0.263	0.148	0.021		52	see S4	1	-1.6	24.2	93.7	10.5	2.25			
	S14	<i>Noecalanus planchrus</i>	2	15.1	10.5	0.794	0.135	0.026		53a	see S4	1	20	13.0	300	5.10	1.50			
	S15	<i>Noecalanus cristatus</i>	2	6.3	12.7	1.59	0.790	0.133		54	see S4	1	11.3	11.8	720	16.3	2.46			
	S16	<i>Eucalanus bangii</i> C6F	2	6.0	17.3	1.01	0.404	0.099		55	see S4	10	25	11.8	1263	28.7	8.1			
	S17	<i>Pseudocalanus elongatus</i>	2	8.6	21.9	0.016	0.003	0.004		56	see S4	10	25	15.8	141	1.66	0.42			
	S18	<i>Metridia pacifica</i>	2	8.2	35.6	0.148	0.065	0.016		57	see S4	2	25	11.2	92.3	14.7	0.44			
	S19	<i>Metridia pacifica</i>	2	13.0	14.7	0.094	0.043	0.011		59	see S4	767	9	17.5	1840	93.8	26.4			
		S20	<i>Acartia clausi</i>	2	14.8	4.6	0.0085	0.0035	0.0010		MOLL	1a	see S4	2	27.4	13.1	16.65	4.84	0.83	Beck (2014b)
		S21	<i>Acartia longiremis</i>	2	9.6	16.2	0.0107	0.0051	0.0010		1b	see S4	2	27.4	11.8	14.34	2.77	0.40		
		S22	<i>Torulus discoidatus</i>	2	7.0	19.6	0.057	0.025	0.006		14	see S4	1	19.7	14.1	18.0	4.94	0.88		
		S23	<i>Noecalanus gracilis</i>	2	19.7	20.1	0.500	0.234	0.051		5	see S4	2	22.4	14.5	30.00	7.83	1.34		
		S24	<i>Udula vulgaris</i>	2	23.5	16.3	0.185	0.077	0.018		6b	see S4	15	20	28.5	2.05	0.53	0.10		
		S25	<i>Euchaeta marina</i>	2	24.0	27.4	0.291	0.121	0.028		11a	see S4	2	22.4	11.6	10.8	20.15	4.45		
		S26	<i>Centropages brevistylus</i>	2	17.3	13.1	0.0198	0.0082	0.0020		9	see S4	15	26	100.0	100.0	25.5	4.1		
		S27	<i>Acartia tonsa</i>	2	22.0	12.5	0.0072	0.0030	0.0007		11a	see S4	2	24.5	20.8	1.62	0.40	0.07		
		S28	<i>Nannocalanus minor</i>	2	26.9	12.7	0.040	0.017	0.005		11c	see S4	7.5	3.0	15.2	0.34	0.10	0.03		
		S29	<i>Udula vulgaris</i>	2	27.6	14.8	0.167	0.070	0.018		11d	see S4	1	19	8.5	0.44	0.11	0.02		
		S30	<i>Eucalanus subsecutus</i> C6F	2	24.0	39.5	0.104	0.043	0.010		12	see S4	15	20	29.8	1.53	0.39	0.07		
		S31	<i>Eucalanus attenuatus</i>	2	27.4	16.2	0.137	0.054	0.013		13	see S4	2	22.4	19.5	4.00	3.78	0.65		
		S32	<i>Calanopia elliptica</i> C6F	2	26.0	17.4	0.056	0.023	0.005		16a	see S4	2	27	11.8	87.1	2.13	0.35		
		S33	<i>Labidocera acuta</i>	2	24.0	14.4	0.233	0.097	0.022		16b	see S4	15	20	20.1	1.85	0.48	0.09		
		S34	<i>Labidocera acuta</i>	2	28.5	17.6	0.228	0.098	0.028		17a	see S4	2	27.4	12.8	12.26	2.99	0.48		
		S35	<i>Labidocera seri</i>	2	26.4	13.6	0.221	0.095	0.027		19	see S4	15	20	26.6	2.36	0.61	0.11		
		S36	<i>Acartia australis</i>	2	25.0	15.5	0.0091	0.0038	0.0009		20a	see S4	2	-0.91	10.7	6.45	2.33	0.52		
		S37	<i>Torulus gracilis</i> C6M	2	26.0	17.8	0.024	0.0098	0.0023		20b	see S4	75	0	85.8	38.25	10.40	1.91		
		S38	<i>Labidocera fernalii</i>	25	25.0	13.5	0.160	0.057	0.016	Beck and McKinnon (2012)	22c	see S4	75	0	78.8	0.59	0.22	0.05		
		S39	<i>Udula vulgaris</i>	25	25.5	17.8	0.229	0.094	0.026		26a	see S4	2	12.7	8.3	22.53	6.33	1.37		
		S40	<i>Panacalanus indicus</i>	1	23.0	21.7	0.0072	0.0032	0.0008		26b	see S4	75	0	85.8	38.25	10.40	1.91		
		S41	<i>Macrostella gracilis</i>	1	25.0	18.2	0.0065	0.0024	0.0005		27a	see S4	2	22.4	19.5	4.00	3.78	0.65		
		S42	<i>Oithona niladhi</i>	2	24.0	11.8	0.0032	0.0014	0.0004		27c	see S4	1	-1.8	6.2	24.94	5.05	1.19		
		1a	see S4	400	-5.5	41.4	60.0	25.5	3.8	Beck (2013a)	29	see S4	2	27.4	13.0	13.7	1.27	0.28		
		2a	see S4	10	-1.6	42.0	30.8	14.0	3.4		30	see S4	2	27.4	14.5	14.6	1.91	0.19		
		2b	see S4	5	-1.3	34.5	10.1	3.82	1.06		34b	see S4	2	28.4	29.6	7.75	2.43	0.56		
		3	see S4	2	26	19.1	1.89	0.78	0.20		36	see S4	15	26	7.9	10.0	2.5	0.4		
		4	see S4	2	27	16.3	5.54	1.40	0.38		THAL	S1	<i>Diaptomus</i>	2	-1.0	18.5	39.94	1.11	0.30	Beck and Michel (1982)
		5	see S4	1	28	22.6	3.29	1.37	0.27		82	<i>Salpa thomasi</i>	2	-1.10	18.6	115.07	5.59	1.32		
		7	see S4	2	19.7	14.5	0.287	0.117	0.029		S3	<i>Thalia</i> dem.	2	17.30	12.09	2.97	0.23	0.05	Beck (1974)	
		8	see S4	40	12.5	15.4	5.00	2.02	0.54		84	<i>Salpa fusca</i>	2	17.84	14.5	14.6	1.91	0.19		
		9	see S4	1	28	11.3	1.82	0.74	0.21		85	<i>Isala thomasi</i>	2	27	45.4	4.94	0.386	0.083		
	10a	see S4	2	13	23.1	4.97	2.06	0.54		86	<i>Pegusa pegus</i>	2	25.70	9.5	89.96	6.41	1.37			
	10b	see S4	100	5	90.0	12.8	4.6	1.2		87	<i>Salpa fusca</i>	2	27.40	27.8	4.88	0.38	0.08			
	10c	see S4	100	5	76.0	11.5	4.0	1.1		88	<i>Pyrosoma</i> sp.	2	25.70	9.5	60.02	5.08	1.09			
	11a	see S4	35	-1.1	16.6	36.3	14.4	8.8		89	<i>Salpa thomasi</i>	1	-1.61	28.2	70.32	33.84	7.54	Beck and Bruce (1986)		
	11c	see S4	3	-1.7	34.1	40.3	16.4	4.8		90	<i>Salpa thomasi</i>	1	1.30	18.1	10.0	5.87	1.49	Beck and Bruce (2004)		
	11c	see S4	35	-1.1	17.3	247.1	115.9	24.7		91		1	11.00	91	104.16	3.34	0.62	Modin and Purcell (1992)		
	11d	see S4	1.7	29.3	30.5	32.5	9.6	9.6		92	<i>Cyclopsylla</i>	15	24.50	24.9	12.79	1.00	0.24	Cetin et al. (1986)		
	11a	see S4	3	-1.7	31.9	97.7	39.5	11.4		93	<i>Cyclopsylla</i>	15	24.50	21.7	12.79	1.00	0.22			
	12	see S4	2	27	13.9	0.77	0.31	0.08		94	<i>Cyclopsylla</i>	15	24.50	16.9	12.79	1.00	0.23			
	13a	see S4	100	-0.8	12.4	23.0	9.5	2.7		95	<i>Pegusa pegus</i>	15	24.50	95.3	12.79	1.00	0.21			
	13b	see S4	600	0	29.0	82.8	39.2	8.9		96	<i>Salpa cylind</i>	15	24.50	27.2	12.79	1.00	0.23			
	14a	see S4	250	4	42.0	74.1	25.9	7.6		97	<i>Salpa cylind</i>	15	16.50	19.5	12.79	1.00	0.23			
	14b	see S4	190	17	4.7	12.50	12.4	1.7		98	<i>Salpa fusca</i>	15	16.50	27.2	12.79	1.00	0.24			
	14c	see S4	50	4	15.7	45.8	17.0	5.0		99	<i>Salpa munda</i>	15	24.50	23.2	12.79	1.00	0.22			
	15	see S4	2	15	21.6	2.00	0.87	0.232		100	<i>Salpa munda</i>	15	26	20.8	7.5	5.89	1.20	Biggs (1977)		
	17	see S4	1	44.3	17.3	4.9	1.5	1.5		101	<i>Salpa cylind</i>	15	26	25.7	7.5	5.89	1.13			
	18a	see S4	2	-0.4	26.3	0.47	0.20	0.05		102	<i>Salpa cylind</i>	15	26	23.3	7.5	5.89	1.26			
	18b	see S4	2	-1.7	27.1	5.49	2.23	0.54		103	<i>Salpa munda</i>	15	26	14.6	7.5	5.89	1.26			
	18c	see S4	2	-0.46	22.3	0.49	0.26	0.05		104	<i>Pegusa pegus</i>	15	26	49.3	7.5	5.89	1.26			
	20	see S4	15	20	32.0	5.00	2.10	0.53		105	<i>Pegusa pegus</i>	15	26	31.3	7.5	5.89	0.13			
	21a	see S4	100	5	42.0	12.2	4.5	1.2		106	<i>Salpa thomasi</i>	15	26	38.7	7.5	5.89	0.13			
	21b	see S4	100	5	35.0	7.02	2.40	0.71		APPE	S1	<i>Oithona</i>	1	15	16.7	0.00112	0.00065	0.00011	Gosky et al. (1987)	
	21	see S4	26	30.7	12.8	5.4	1.6			S2		1	20	12.3	0.00121	0.00071	0.00014			
	13	see S4	2	27	26.3	2.44	0.99	0.10	Beck (2013b)	S3		2	30.2	0.00126	0.00074	0.00014				
	3	see S4	2	26	15.9	1.62	0.41	0.07		POLY										

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
1	COPE	<i>Pachyphthalma pacifica</i>	C6F	151		<i>Scaphocalanus affinis</i>	C5F	6		<i>Acanthopheora similis</i>	C5F	9		<i>Colobomonas sericeum</i>	
2		<i>Laciniaria bicornata</i>	C6M	152		<i>Amalothrix inornata</i>	C6F	7a		<i>Hymenodora frontalis</i>	C6F	10		<i>Crossota</i> sp.	
3		<i>Laciniaria grandis</i>	C5F	153		<i>Scolochalcis</i> sp.	C6F	7b		<i>Hymenodora frontalis</i>	C6F	11a		<i>Easteria cellulata</i>	
4		<i>Merridia asymmetrica</i>	C6F	154		<i>Scotocalanus scutifrons</i>	C6F	7c		<i>Hymenodora frontalis</i>	C6F	11b		<i>Easteria cellulata</i>	
5		<i>Merridia curvicauda</i>	C6F	155		<i>Bythocalanus bradyi</i>	C6F	8		<i>Janicella spinicauda</i>	C6F	12		<i>Eperomus typus</i>	
6		<i>Merridia okoteana</i>	C6F	156		<i>Bythocalanus bradyi</i>	C6F	9		<i>Nematocarcinus lanceopes</i>	C6F	13		<i>Eatonina indicans</i>	
7		<i>Platromma scutellata</i>	C6M	157		<i>Bythocalanus magnus</i>	C6F	10		<i>Nototomus elegans</i>	C6F	14		<i>Goniomoma vertens</i>	
8			C6F	158		<i>Arctidopsis rostrata</i>	C6F	11		<i>Nototomus gibbosus</i>	C6F	15		<i>Liriope tetrastylus</i>	
9		<i>Platromma siphonis</i>	C6F	159		<i>Amalothrix inornata</i>	CSM	12		<i>Nototomus</i> sp.	C6F	16		<i>Nemopsis hachei</i>	
10		<i>Candacia columbica</i>	CSM	160		<i>Amalothrix inornata</i>	C6F	13a		<i>Opilophora graciliorstris</i>	C6F	17		<i>Panathogenus haeckeli</i>	
11		<i>Arctidopsis rostrata</i>	CSM	161		<i>Bartholomaeus lamellata</i>	CSM	13b		<i>Opilophora graciliorstris</i>	C6F	18a		<i>Phialidium gregarium</i>	
12		<i>Chiridius pacificus</i>	C6F	162		<i>Bartholomaeus lamellata</i>	C6F	14a		<i>Opilophora spinosa</i>	C6F	18b		<i>Phialidium gregarium</i>	
13		<i>Chiridius atrevis</i>	C6F	163		<i>Bartholomaeus lamellata</i>	CSM	14b		<i>Opilophora spinosa</i>	C6F	19		<i>Phialidium ionae</i>	
14		<i>Euchirella brevis</i>	C6F	164		<i>Bartholomaeus bradyi</i>	C3	15a		<i>Parapandalus richardi</i>	C6F	20		<i>Seria princeps</i>	
15		<i>Euchirella yulensis</i>	C6F	165		<i>Bartholomaeus bradyi</i>	C5	15b		<i>Parapandalus richardi</i>	C6F	21		<i>Solmisia incisa</i>	
16		<i>Euchirella meschiensis</i>	C6F	166		<i>Benthomorphia pullulata</i>	C6M	16		<i>Parapandanus sulcifrons</i>	C6F	22a		<i>Somatoeca atra</i>	
17		<i>Euchirella rostrata</i>	C6F	167		<i>Chiridella abyssalis</i>	C6F	17a		<i>Pauphous chacei</i>	C6F	23b		<i>Somatoeca atra</i>	
18		<i>Euchirella truncata</i>	C6M	168		<i>Chiridella pacifica</i>	C6F	17b		<i>Pauphous chacei</i>	C6F	23		<i>Atelopsis tetragona</i>	
19		<i>Gadilus brevirostris</i>	C6F	169		<i>Gastanus parvicornis</i>	C6F	18a		<i>Pauphous emarginata</i>	C6F	24		<i>Chelophyes appendiculata</i>	
20			C6F	170		<i>Gadilus pungens</i>	C6F	18b		<i>Pauphous emarginata</i>	C6F	25a		<i>Diphyes antarcica</i>	
21		<i>Gastanus robustus</i>	C6F	171		<i>Gastanus robustus</i>	C6F	20		<i>Pauphous multidentata</i>	C6F	26		<i>Diphyes</i> sp.	
22		<i>Gadilus tenuispinus</i>	C5F	172		<i>Merridia ornata</i>	CSM	21a		<i>Pauphous scotiae</i>	C6F	27		19 species	
23			C6F	173		<i>Merridia ornata</i>	C6F	21b		<i>Pauphous scotiae</i>	C6F	28a		<i>Aurelia aurita</i>	
24		<i>Gadilus variabilis</i>	CSM	174		<i>Merridia ornata</i>	C6M	22		<i>Systellapsis braveri</i>	C6F	29b		<i>Aurelia aurita</i>	
25			C5F	175		<i>Miscocalanus robustus</i>	C6F	23a		<i>Systellapsis cristata</i>	C6F	29c		<i>Aurelia aurita</i>	
26			C6F	176		<i>Onchocalanus magnus</i>	C5F	23b		<i>Systellapsis cristata</i>	C6F	29d		<i>Aurelia aurita</i>	
27		<i>Pseudochirella pacifica</i>	CSM	177		<i>Onchocalanus magnus</i>	C6F	24a		<i>Systellapsis debilis</i>	C6F	30a		<i>Cystosopa samachana</i>	
28		<i>Pseudochirella spinifera</i>	CSM	178		<i>Paracantha rubra</i>	C4F	24b		<i>Systellapsis debilis</i>	C6F	30b		<i>Cystosopa samachana</i>	
29			CSM	179		<i>Pseudochirella pacifica</i>	CSM	24c		<i>Systellapsis debilis</i>	C6F	31		<i>Gastropylus muscicus</i>	
30		<i>Undinucha plamosa</i>	C6F	180		<i>Pseudochirella polyopina</i>	C6F	24d		<i>Systellapsis debilis</i>	C6F	32		<i>Chrysaster gaudichaudii</i>	
31		<i>Paracantha rubra</i>	C6F	181		<i>Scaphocalanus magnus</i>	C6F	25		<i>Funchalia villosa</i>	C6F	33a		<i>Cymus capillatus</i>	
32		<i>Paracantha brevispinis</i>	CSM	182		<i>Spinocalanus magnus</i>	C6F	26		<i>Gennadas copensis</i>	C6F	33b		<i>Cymus capillatus</i>	
33			C6F	183		<i>Undinucha acuta</i>	C6F	27a		<i>Gennadas kempii</i>	C6F	33c		<i>Cymus capillatus</i>	
34			C6F	184		<i>Undinucha major</i>	C6F	27b		<i>Gennadas kempii</i>	C6F	34		<i>Mastigias</i> sp.	
35		<i>Paracantha brevispinis</i>	C6F	185		<i>Undinucha plamosa</i>	C5F	28a		<i>Gennadas propinquus</i>	C6F	35a		<i>Pelagia noctiluca</i>	
36		<i>Paracantha elongata</i>	CSM	186		<i>Undinucha plamosa</i>	C6F	28b		<i>Gennadas propinquus</i>	C6F	35b		<i>Pelagia noctiluca</i>	
37			C6F	187		<i>Valdeleylla imperfecta</i>	C6F	29		<i>Gennadas scutatus</i>	C6F	36		<i>Propellia periphras</i>	
38			CSM	188		<i>Xanthocalanus karlensis</i>	C6F	30		<i>Gennadas valens</i>	C6F	37a		<i>Poralla refecens</i>	
39			CSM	189		<i>Calanus propinquus</i>	C6F	31a		<i>Acetes ibigues australis</i>	C6F	37b		<i>Poralla refecens</i>	
40			C6F	190		<i>Merridia perlucida</i>	C6F	31b		<i>Acetes ibigues australis</i>	C6F	37c		<i>Poralla refecens</i>	
41			C6F	191		<i>Calanoides acutus</i>	C5	32a		<i>Eusergestes similis</i>	C6F	38		<i>Somolophus melagris</i>	
42			C6F	192		<i>Calanoides acutus</i>	C4.5	32b		<i>Eusergestes similis</i>	C6F	38		<i>Somolophus melagris</i>	
43			C6F	193		<i>Calanus finmarchicus</i>	C6F	35		<i>Leuope</i> sp.	C6F	39		<i>Aganippe portogallensis</i>	
44		<i>Paracantha modesta</i>	C6F	194		<i>Calanus glacialis</i>	C6F	36		<i>Parasergestes armatus</i>	C6F	40a		<i>Bathocyroe fovei</i>	
45		<i>Paracantha orientalis</i>	C6F	195		<i>Calanus hyperboreus</i>	C6F	37		<i>Petalidium foliaceum</i>	C6F	40b		<i>Bathocyroe fovei</i>	
46		<i>Paracantha pseudomimulus</i>	CSM	196		<i>Calanus hyperboreus</i>	C6F	38		<i>Sergestes corvina</i>	C6F	40c		<i>Bathocyroe fovei</i>	
47			C6F	197		<i>Calanus hyperboreus</i>	C5	39		<i>Sergestes edax</i>	C6F	41		<i>Boreo</i> sp. B	
48		<i>Paracantha rubra</i>	CSM	198		<i>Merridia longa</i>	C6F	40		<i>Sergia bialata</i>	C6F	42		<i>Eirene mollis</i>	
49			C6F	199		<i>Riccalanus riggsi</i>	C6F	41		<i>Sergia splendens</i>	C6F	43a		<i>Halicara bigelowi</i>	
50		<i>Amalothrix valida</i>	CSM	200		<i>Noctocalanus crinitus</i>	C5	42		<i>Sergia splendens</i>	C6F	43b		<i>Halicara bigelowi</i>	
51			C6F	201		<i>Noctocalanus planchus</i>	C4	43a		<i>Sergia phorca</i>	C6F	44		<i>Haliphrops maui</i>	
52		<i>Miscocalanus robustus</i>	C6F	202		<i>Noctocalanus planchus</i>	C5	43b		<i>Sergia phorca</i>	C6F	45		<i>Panathogenus</i> sp. A	
53		<i>Scaphocalanus medius</i>	C6F	203		<i>Eucaulus longi</i>	C6F	44		<i>Sergia tenuis</i>	C6F	46		<i>Tetrasia erythrogaster</i>	
54		<i>Spinocalanus stellatus</i>	C6F	204		<i>Pseudocalanus elongatus</i>	C6F	45		<i>Sergestes tenuis</i>	C6F	47		<i>Valoniopsis albertensis</i>	
55		<i>Pachyphthalma pacifica</i>	C6F	205		<i>Merridia pacifica</i>	C6F	46		<i>Sergia grandis</i>	C6F	48		<i>Vampyrocera childei</i>	
56		<i>Laciniaria inornata</i>	C6F	206		<i>Acartia longirostris</i>	C6F	47		<i>Sergia robusta</i>	C6F	49		<i>Arctidopsis</i> sp. A	
57		<i>Laciniaria grandis</i>	C6M	207		<i>Tortanus discoidalis</i>	C6F	48		<i>Sergia splendens</i>	C6F	50		<i>Arctidopsis</i> sp. A	
58		<i>Laciniaria pacifica</i>	C6F	208		<i>Merridia pacifica</i>	C6F	49		<i>Sergia talismani</i>	C6F	51		<i>Panophyllina ranaui</i>	
59			C6F	209		<i>Miscocalanus tenuicornis</i>	C6F	50		<i>Platromma planchus</i>	C6F	52		<i>Paraphyllina pacifica</i>	
60		<i>Merridia asymmetrica</i>	C6F	210		<i>Paracalanus parvus</i>	C5	AMPH	1	<i>Chionella spinifera</i>	C6F	CTEN	39	<i>Aganippe portogallensis</i>	
61			C6F	211		<i>Centropages abdominalis</i>	C6F	2		<i>Cyllopus lucasi</i>	C6F	40a		<i>Bathocyroe fovei</i>	
62		<i>Merridia curvicauda</i>	C6F	212		<i>Pseudodiplopus marinus</i>	C6F	3		<i>Hemiphipps tenuissimus</i>	C6F	40b		<i>Bathocyroe fovei</i>	
63		<i>Merridia ornata</i>	C6F	213		<i>Noctocalanus planchus</i>	C6F	4		<i>Hyperia galba</i>	C6F	40c		<i>Bathocyroe fovei</i>	
64		<i>Arctidopsis rostrata</i>	CSM	214		<i>Acartia clausi</i>	C6F	5		<i>Hyperia gaudichaudii</i>	C6F	41		<i>Boreo</i> sp. B	
65			C5F	215		<i>Noctocalanus gracilis</i>	C6F	6		<i>Leucopeia brevis</i>	C6F	42a		<i>Boreo</i> sp. B	
66		<i>Bradydium pacificum</i>	C6F	216		<i>Centropages brevispinis</i>	C6F	7a		<i>Oryctophagus clausi</i>	C6F	42b		<i>Boreo</i> sp. B	
67		<i>Euchirella rostrata</i>	C6F	217		<i>Acartia tonsa</i>	C6F	7b		<i>Oryctophagus clausi</i>	C6F	43a		<i>Boreo</i> sp. B	
68			C6F	218		<i>Undinula vulgaris</i>	C6F	8a		<i>Phronima sedentaria</i>	C6F	43b		<i>Boreo</i> sp. B	
69		<i>Gadilus brevirostris</i>	C6F	219		<i>Euchaeta marina</i>	C6F	8b		<i>Phronima sedentaria</i>	C6F	44		<i>Boreo</i> sp. B	
70		<i>Gadilus variabilis</i>	C6F	220		<i>Acartia pacifica</i>	C6F	8c		<i>Phronima sedentaria</i>	C6F	45		<i>Boreo</i> sp. B	
71			C6F	221		<i>Calanopsis elliptica</i>	C6F	9a		<i>Primo abyssalis</i>	C6F	46		<i>Bolnopsis infundibulum</i>	
72		<i>Pseudochirella pacifica</i>	CSM	222		<i>Tortanus gracilis</i>	C6F	9b		<i>Primo abyssalis</i>	C6F	47		<i>Bolnopsis infundibulum</i>	
73			C6F	223		<i>Eucaulus subvexus</i>	C6F	10		<i>Primo abyssalis</i>	C6F	48		<i>Bolnopsis infundibulum</i>	
74			C6F	224		<i>Labidocera acuta</i>	C6F	11		<i>Scina borealis</i>	C6F	49		<i>Callinura antarctica</i>	
75		<i>Pseudochirella polyopina</i>	C6F	225		<i>Acartia australis</i>	C6F	12		<i>Scina borealis</i>	C6F	50		<i>Euphrasiaus vacillans</i>	
76			C6F	226		<i>Noctocalanus crinitus</i>	C6F	13		<i>Thomopsis rostrata</i>	C6F	51		<i>Mertensia ovum</i>	
77		<i>Pseudochirella spinifera</i>	C5F	227		<i>Undinula vulgaris</i>	C6F	14		<i>Thomopsis compressa</i>	C6F	52		<i>Mertensia ovum</i>	
78			C6M	228		<i>Eucaulus attenuatus</i>	C6F	15a		<i>Thomopsis gaudichaudii</i>	C6F	53a		<i>Mertensia ovum</i>	
79			CSM	229		<i>Labidocera acuta</i>	C6F	15b		<i>Thomopsis gaudichaudii</i>	C6F	53b		<i>Mertensia ovum</i>	
80		<i>Undinucha major</i>	C6F	230		<i>Labidocera tenuis</i>	C6F	15c		<i>Thomopsis gaudichaudii</i>	C6F	54		<i>Mertensia ovum</i>	
81			C6F	231		<i>Pontella danse</i>	C6F	16a		<i>Thomopsis japonica</i>	C6F	55		<i>Ocyropsis maculata</i>	
82		<i>Undinucha plamosa</i>	C6F	232		<i>Noctocalanus crinitus</i>	C5	16b		<i>Thomopsis japonica</i>	C6F	56		<i>Ocyropsis maculata</i>	
83		<i>Paracantha brevispinis</i>	C6F	233		<i>Calanus marshalli</i>	C6F	16c		<i>Thomopsis japonica</i>	C6F	57a		<i>Platromma pilosus</i>	
84			C6M	234		<i>Noctocalanus planchus</i>	C5	17		<i>Thomopsis libellula</i>	C6F	57b		<i>Platromma pilosus</i>	
85			C6M	235		<i>Noctocalanus planchus</i>	C5	18		<i>Thomopsis pacifica</i>	C6F	58		<i>Platromma pilosus</i>	
86			C6F	236		<i>Miscocalanus tenuicornis</i>	C6F	19		<i>Vibilia</i> sp.	C6F	59		<i>Platromma pilosus</i>	
87			C6F	237		<i>Merridia pacifica</i>	C6F	20		<i>Vibilia propinqua</i>	C6F	60		<i>Platromma pilosus</i>	
88		<i>Paracantha brevispinis</i>	C6F	238		<i>Merridia pacifica</i>	C6F	21		<i>Vibilia strobili</i>	C6F	61		<i>Platromma pilosus</i>	
89		<i>Paracantha elongata</i>	CSM	239		<i>Platromma scutellata</i>	C6F	22a		<i>Cyphocaris challengeri</i>	C6F	62		<i>Platromma pilosus</i>	
90			C5F	240		<i>Platromma scutellata</i>	C6F	22b		<i>Cyphocaris challengeri</i>	C6F	63		<i>Platromma pilosus</i>	
91		<i>Paracantha pseudomimulus</i>	C6F	241		<i>Platromma scutellata</i>	C6F	23		<i>Cyphocaris fovei</i>	C6F	64		<i>Platromma pilosus</i>	
92			CSM	242		<i>Platromma scutellata</i>	C6F	24		<i>Cyphocaris richardi</i>	C6F	65		<i>Platromma pilosus</i>	
93			C6F	243		<i>Platromma scutellata</i>	C6F	25		<i>Cyphocaris sp. A</i>	C6F	66		<i>Platromma pilosus</i>	
94			C6M	244		<i>Gast</i>									