Title	Respiration in marine pelagic copepods: a global-bathymetric model
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Citation	Marine Ecology Progress Series, 339, 215-219 https://doi.org/10.3354/meps339215
Issue Date	2007-06-06
Doc URL	http://hdl.handle.net/2115/28416
Type	article (author version)
File Information	MEPS339.pdf

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Respiration in marine pelagic copepods: a global-bathymetric model

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Running head: Global-bathymetric model for copepod respiration

Key words: Respiration·Copepods·Global·Bathymetric·Model

Abstract

Historical global respiration datasets of epipelagic copepods and recent bathymetric respiration datasets of mesopelagic, upper- and lower bathypelagic and abyssopelagic copepods were combined to build a global-bathymetric respiration model by adopting two regression models (theoretical and empirical ones). Designated independent variables including body mass (expressed as dry mass, carbon or nitrogen), habitat temperature, ambient oxygen saturation and the depth of occurrence were all significant, accounting 72-80% in the variation in these respiration data. Both theoretical and empirical regression models yielded similar results, but the latter was sensitive to the choice of body mass. The mechanisms for the negative effect of the depth of occurrence and the positive effect of ambient oxygen saturation on the respiration rates are discussed.

Introduction

Copepods are the major component of marine mesozooplankton and may be the most numerous multicellular organisms on the earth (Longhurst 1985, Mauchline 1998). In marine pelagic ecosystems, copepods are an important link between primary production and production of organisms at higher trophic levels. Because of their ubiquitous distribution, high abundance and trophic importance, vital rates of copepods and other mesozooplankton are of particular relevance to understanding oceanic biogeochemical cycles of carbon and other elements (Hernandez-Leon & Ikeda 2005, Aristegui et al. 2005, Buitenhuis et al. 2006). Copepod respiration (=oxygen consumption) is a direct measure of mineralization, and has been documented as a function of body mass and habitat temperature for epipelagic copepods (Ivleva 1980, Ikeda et al. 2001), the principle now expanded to all organisms on the earth (Gillooly et al. 2001). While this conclusion was derived from statistical analyses of large datasets on epipelagic copepods collected from the world ocean (hereafter referred as "global" respiration model), its application to those living in the ocean interior is currently inappropriate since a recent study indicated significantly lower respiration rates of copepods in the mesopelagic and bathypelagic zones of the ocean (Ikeda et al. 2006a). As a basis to advance our understanding about the role of marine pelagic copepods in the entire ocean, the existing global respiration model needs to be modified to a global-bathymetric model by incorporating new datasets of deep-sea copepods.

Materials and methods

The 65 epipelagic respiration datasets were a compilation of rates measured at *in situ* temperatures using standardized methods (sealed-chamber method, cf. Ikeda et al. 2000) at various locations in the world ocean (Fig. 1) over many years (1970-2004) (Ikeda et al. 2001, unpublished data). Of these epipelagic datasets, water temperatures from where copepods were collected ranged from near freezing point of seawater (-1.7^{o}C) in polar seas to the tropical warmth (28.5^{o}C). The 188 deep-sea respiration datasets were from the mesopelagic (500-1000 m), upper-bathypelagic (1000-2000 m) and lower-bathypelagic (2000-3000 m)(Ikeda et al. 2006a) supplemented by the

abyssopelagic (3000-5000 m) zones (Ikeda, unpublished), all in the western North Pacific Ocean (Fig. 1). Respiration rates of copepods from these bathymetric zones were determined at mean temperature of each zone (1.5-3°C) and near ambient oxygen concentrations (see below) by using fresh seawater from mid-sampling depth of each zone collected just prior to experiment (for detail procedure, see Ikeda et al. 2006a). No de-compression effect was taken into account for the experiment on deep-sea copepods, since the lack of appreciable hydrostatic pressure effects on the respiration rates has been confirmed experimentally on bathypelagic copepods and other zooplankton (cf. Ikeda et al. 2001, 2006a). The validity of respiration data on copepods from the mesopelagic zone or more deeper zones was confirmed with enzyme activities of Electron-Transfer-System (ETS) of copepods from the same zone; i.e. the ratios of ETS to respiration were close to the theoretical value of 2 (Ikeda et al. 2006a). A total of 253 datasets representing 21 families, 51 genera and 108 species of marine pelagic copepods was used in our analysis (Appendix). In terms of dried body mass (DM), the smallest copepod was *Paracalanus parvus* (0.0038 mg) and the largest was *Bathycalanus bradyi* (34.5 mg).

In addition to the two conventional independent variables (X_1: body mass, and X_2: habitat temperature) used in the global respiration model for marine epipelagic copepods (Ivleva 1980, Ikeda et al. 2001), two new independent variables (X_3: oxygen saturation, and X_4: the depth of occurrence) were introduced to the global-bathymetric model of this study (Table 1). X_3 was expressed as a fraction of saturation (full saturation = 1.00), and respective saturation values for epipelagic, mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic zones were 1.00, 0.13, 0.20, 0.32 and 0.45 (the last four values are the means of respective strata based on our own measurements in the western subarctic Pacific, cf. Fig. 1). X_4 was expressed as mid-depth of each sampling stratum, e.g. 750 m for the sampling from the mesopelagic zone (500 - 1000 m), 1500 m from the upper-bathypelagic zone (1000 - 2000 m) and so on. X_1 was expressed as dry mass (DM), nitrogen (NM) or carbon (CM) since the choice of body mass unit is known to cause somewhat different results (Ivleva 1980, Ikeda et al. 2001). Two regression models were adopted as a basis to build a

global-bathymetry model for respiration in pelagic copepods; one was theoretical model characterized by the scaling exponent of 3/4 (or 0.75) and the Arrehenius relationship for the temperature effect ($R = R_o M^{3/4} e^{-E/kT}$, where R is respiration rate, M is body mass, T is absolute temperature, E is an average activation energy for the rate-limiting enzyme-catalyzed biochemical reactions of metabolism, k is the Boltzmann's constant and R_o is a normalization constant, cf. Gillooly et al. 2001) and the other was empirical model characterized by undefined scaling exponent and the Van't Hoff rule (Q_{10}) for the temperature effect (Ikeda et al. 2001) (Table 1).

It is noted that there several critical views against the theoretical model above at present. As one of two components of the model, the scaling exponent 3/4 (or 0.75) has been questioned from the viewpoints of theoretical justifications and verifications by the data (Dodds et al. 2001). The other component, the Arrehenius relationship, implies the increase in respiration rate with increasing temperature automatically, with no provision for laboratory acclimation, seasonal acclimatization or evolutionary adaptation known for respiration-temperature relationships for marine animals (Clarke & Fraser 2004).

Results

Preliminary analysis was made to determine the coefficient a_2 ($= {}^- E\, k^{-1}$) of temperature X_2 of the theoretical model first, by plotting the epipelagic respiration rate standardized to the rate (R_o) of specimens weighing 1 mg DM ($R_o = R\, DM^{-0.75}$) against inverse temperature (1000/K)(Fig. 2a). The resultant slope (-5.406) for epipelagic copepods was used to compute respiration rate at a given temperature (designated as 10°C) of both epipelagic and mesopelagic-abyssopelagic copepods, which was plotted against copepod DM (Fig. 2b). In both figures, it is clear that the mesopelagic-abyssopelagic rate values only partially overlap the epipelagic values, and the former distribute well below the latter at equivalent inverse temperature and body mass. The standardized respiration rates (R_o) at 10°C of epipelagic, mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic copepods were plotted against oxygen saturations of respective bathymetric zones (Fig. 2c). While the

respiration data were rather biased to lower oxygen saturation, there was a significant positive correlation ($p < 0.05$) between the two.

After confirming significant effects of the three out of the four individual variables on the respiration rates (Fig. 2a,b,c), the attributes of these four variables were analyzed simultaneously by using stepwise multiple regression (Forward Selection) method (Sokal & Rohlf 1995). Independent variables were added if $p \leq 0.05$ and removed if $p \geq 0.10$. The calculation was conducted using SYSTAT ver. 10.2. The results show that the four independent variables were all significant although the priority of addition oxygen saturation (X_3) or the depth of occurrence (X_4) differed depending on the choice of body mass unit in both models (Table 1). The choice of body mass unit also affected the correlation coefficients derived from the empirical model ($R^2 = 0.72$-0.80 for the regression equations at Step 4, Table 1), but this were not the case in the theoretical model ($R^2 = 0.76$ for those at Step 3).

Discussion

The present results indicate clearly that not only body mass and temperature but also the depth of occurrence and ambient oxygen saturation were attributed significantly to the variance of the copepod respiration data from epipelagic through abyssepelagic zones (Table 1). When compared with equivalent body mass unit, the differences in partial regression coefficients of each variable (excepting those of the temperature of which effect was expressed as different mathematical forms in each model) and correlation coefficients between the theoretical and empirical models were little. While the best fit regression equation was that of empirical model in which body mass was expressed by nitrogen unit ($R^2 = 0.80$, cf. Table 1), the differences from the rest of the five full regression equations ($R^2 = 0.72$ - 0.76) were not marked.

The positive effect of oxygen concentration (X_3) was not considered in the previous global respiration model of marine pelagic copepods because the epipelagic environments of the world ocean are oxygen saturated throughout. Nevertheless, a significant effect of oxygen saturation on respiration in copepods is to be expected since copepods lack respiratory organs such as gills and their respiration is achieved by the

gradient of oxygen concentration through body integuments (Wolvekamp & Waterman 1960). Respiration rates of micronektonic crustaceans living in the oxygen-poor mesopelagic zone off South California have been reported to be one-half those of oxygen-rich mesopelagic zones of Antarctic waters (Ikeda 1988). Some pelagic crustaceans with respiratory organs (gills) and living in or in close proximity to oxygen minimum zone exhibit the capacity to respire at low oxygen concentrations (Childress & Seibel 1998).

The negative effect of the depth of occurrence (X_4) on the respiration of marine pelagic copepods in the present analysis is in support the "Predation-mediated selection" hypothesis (Ikeda et al. 2006a). According to the hypothesis, lower respiration of deeper-living copepods is a result from low selective pressure for high activity in copepods in deep-sea. The pelagic life is characterized by the lack of shelters. Copepods living in the illuminated epipelagic zone have the advantage of a rich food supply, but must also need to be active enough to avoid predation risk. A recent observation of progressive decline in nitrogen (=muscle) concentration in copepods living in the epipelagic through abyssopelagic zones supports the hypothesis (Ikeda et al. 2006b). It is noted that the "visual-interactions" hypothesis (Childress 1995) being proposed for reduced respiration rates of deeper-living micronektonic fishes, crustaceans and cephalopods with well developed visual perception systems (eyes) does not apply to pelagic animals without visual perception systems such as copepods, but it predicts the lack of depth-related changes in respiration rates of pelagic copepods. The lower respiration rates of mesopelagic through abyssopelagic copepods found here argues the predictions of that hypothesis.

Compared with the previous global respiration model (Ikeda et al. 2001), the global-bathymetric respiration model (Table 1) built in this study is an advanced version, providing a solid basis for assessing energy flux and biogeochemical cycles of carbon via copepod communities in the marine pelagic realm at larger spatial scales. Taking into account the four independent variables (X_1, X_2, X_3 and X_4), the present global-bathymetric model explained 72-80% of the variance in the epipelagic through abyssopelagic respiration data. The amount of explained variance by the four variable

in the global-bathymetric model is less than that (93-96%) of the global model which has only two variables (Ikeda et al. 2001). Part of reason may be due to low precision of the respiration data of copepods from the mesopelagic through abyssopelagic zones, since most of former were based on measurements using single specimens (Ikeda et al. 2006a). This reflects the extremely low abundance of most deep-sea copepods as compared with shallow-living copepods. As a future aspect, the global-bathymetric model can be improved by the addition of new respiration datasets of copepods from another extreme deep-sea environments characterized by high temperature and/or high oxygen saturation (present data are of low temperature and low oxygen in the western subarctic Pacific), and possible candidates of such the study sites are the Arabian Sea, Sulu Sea and broad North Atlantic Ocean.

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Table 1. Stepwise (forward selection) multiple regression analyses of respiration rates (Y: µl O_2 individual^{-1}h^{-1}) on body mass (X_1: mg individual^{-1}), habitat temperature (X_2: K for theoretical model, °C for empirical model), oxygen saturation (X_3: 1.00 for full saturation) and habitat depth (X_4: m) for marine planktonic copepods. R^2=correlation coefficient.

Regression model	Body mass unit	N	Step	Full regression equation: Theoretical: $\ln(Y/X_1^{0.75}) = a_0 + a_2(1000X_2^{-1}) + a_3X_3 + a_4\ln X_4$ Empirical: $\ln Y = a_0 + a_1\ln X_1 + a_2X_2 + a_3X_3 + a_4\ln X_4$						R^2
				a_0	a_1	a_2	a_3	a_4	
Theoretical	DM	253	1	30.874		-8.800			0.668
		253	2	19.348		-5.355		-0.146	0.746
		253	3	18.305		-5.227	0.537	-0.089	0.760
	NM	253	1	29.710		-7.966			0.675
		253	2	21.350		-5.746	0.813		0.750
		253	3	18.887		-4.907	0.512	-0.070	0.762
	CM	253	1	33.499		-9.385			0.669
		253	2	21.364		-5.758		-0.155	0.746
		253	3	20.230		-5.619	0.584	-0.092	0.761
Empirical	DM	253	1	-0.894	0.367				0.364
		253	2	-1.289	0.649	0.094			0.669
		253	3	-0.258	0.737	0.064		-0.145	0.737
		253	4	-0.815	0.750	0.064	0.539	-0.091	0.752
	NM	253	1	0.146	0.421				0.420
		253	2	0.456	0.705	0.092			0.729
		253	3	0.359	0.777	0.072	0.855		0.791
		253	4	1.073	0.796	0.063	0.543	-0.079	0.803
	CM	253	1	-0.667	0.337				0.344
		253	2	-0.878	0.606	0.094			0.644
		253	3	-1.116	0.678	0.075	0.878		0.708
		253	4	-0.392	0.700	0.065	0.549	-0.085	0.722

Figure captions

Figure 1. Geographical distribution of study sites of copepod respiration, including those for epipelagic species (closed circles are those in Ikeda et al. 2001, closed triangles those in Sano and Ikeda, unpublished data) and mesopelagic through bathypelagic (Ikeda et al. 2006) and abyssopelagic species (Ikeda, unpublished) in the western North Pacific Ocean (an open rectangle).

Figure 2. Copepod respiration rates and variables. A. Relationship between respiration rate of copepods standardized to a body size of 1 mg DM (R_o) and inverse temperature (T^{-1}), and fitted least square regression line only for epipelagic copepod data, B. Relationship between respiration rate standardized to a body size of 1 mg DM (R_o) at 10^oC and dry mass (DM), and fitted regression lines with preset slope (0.75) for epipelagic and mesopelagic-abyssopelagic copepod data, C. Relationship between respiration rates standardized to a body size of 1 mg DM (R_o) and at 10^oC and oxygen concentration (O_2 saturation), and fitted least square regression line.   Closed circles are epipelagic copepods, open circles are mesopelagic through abyssopelagic copepods. Bathymetric abbreviations; E=Epipelagic, M=Mesopelagic, UB=Upper-Bathypelagic, LB=Lower-Bathypelagic, AB=Abyssopelagic.

Ikeda et al. Fig. 1

A

$\ln R_0$ ($\mu l\ O_2$ mg $DM^{-0.75}\ h^{-1}$)

T^{-1} (1000 / K)

$Y = -5.406X + 19.297$
$r = 0.897$
$p < 0.01$

B

R at 10°C ($\mu l\ O_2$ ind$^{-1}\ h^{-1}$)

DM (mg)

$Y = 0.75X + 0.173$
$r = 0.971$
$p < 0.01$

$Y = 0.75X - 0.686$
$r = 0.778$
$p < 0.01$

C

R_0 at 10°C ($\mu l\ O_2$ mg $DM^{-0.75}\ h^{-1}$)

O_2 saturation

$Y = 0.849X + 0.345$
$r = 0.894$
$p < 0.05$

M UB LB AB E
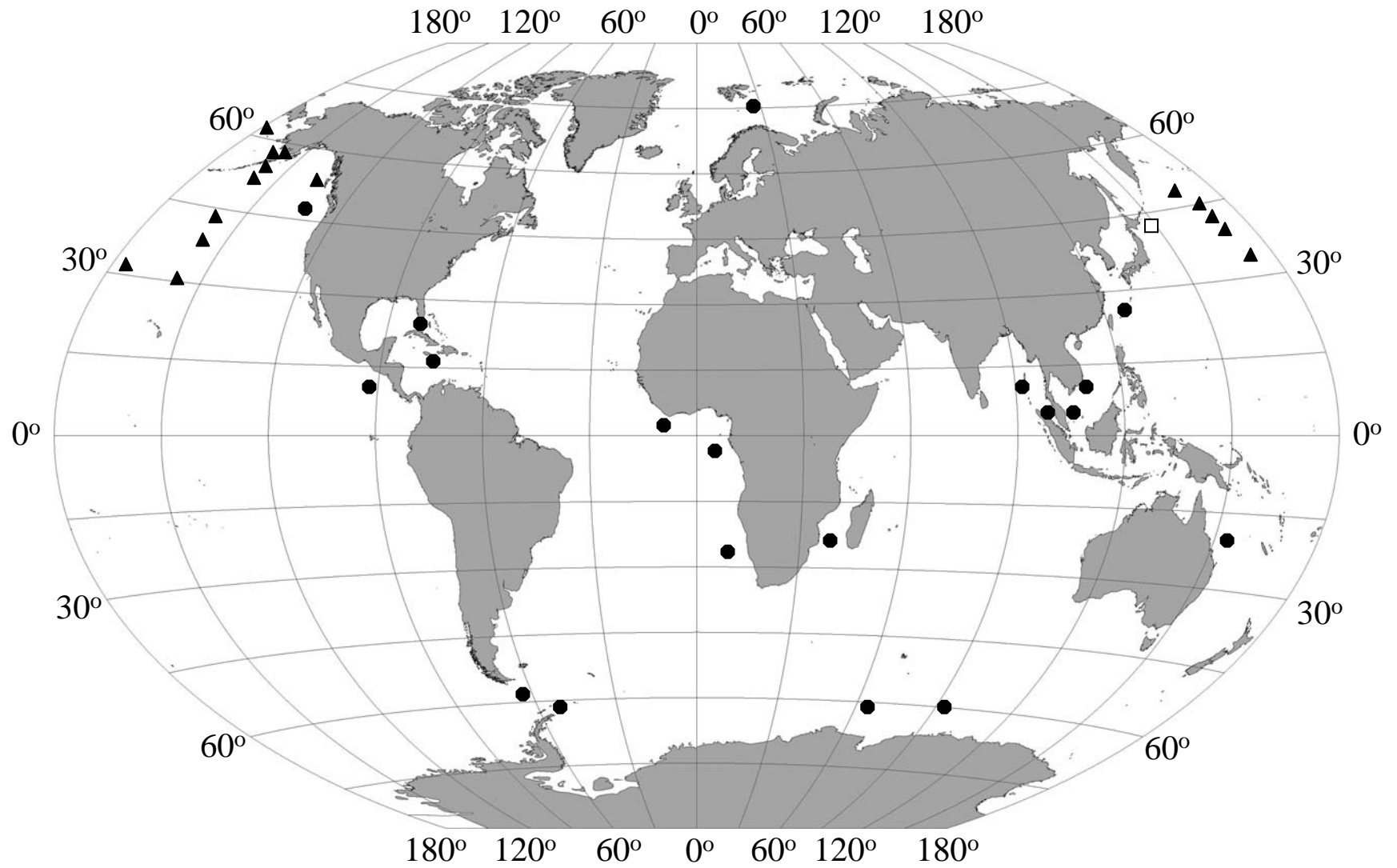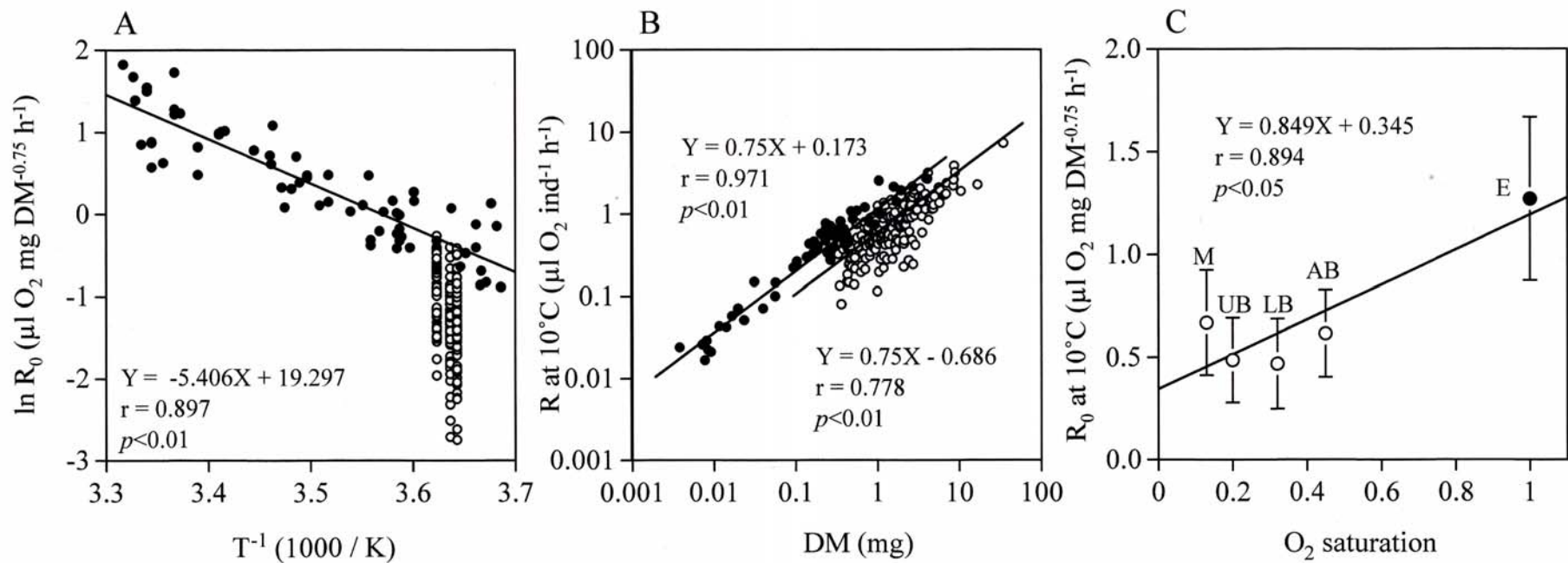
Ikeda et al. Fig. 2

Appendix. Copepodid stage/sex (M: male, F: female), respiration rate, body mass (DW, N or C), experimental (=habitat) temperature, depth of occurrence and ambient oxygen concentration (full saturation=1.00) of copepods.

Data No.	Copepods	Stage	Depth of occurrence (m)	Expt. Temp. (oC)	Oxygen saturation	Respiration rate (μlO$_2$ ind^{-1} h^{-1})	Body mass DW(mg)	N (mg)	C (mg)
1	Pachyptilus pacificus	C6F	750	3	0.13	0.463	2.065	0.129	0.892
2	Lucicutia bicornuta	C6M	750	3	0.13	0.121	0.625	0.05	0.253
3	Lucicutia grandis	C5F	750	3	0.13	0.113	0.429	0.032	0.188
4	Metridia asymmetrica	C6F	750	3	0.13	0.175	0.457	0.033	0.242
5	Metridia curticauda	C6F	750	3	0.13	0.141	0.484	0.034	0.27
6	Metridia okhotensis	C6F	750	3	0.13	0.292	0.713	0.05	0.429
7	Pleuromamma scutullata	C6M	750	3	0.13	0.316	0.564	0.067	0.251
8		C6F	750	3	0.13	0.276	0.429	0.031	0.218
9	Pleuromamma xiphias	C6F	750	3	0.13	0.472	0.563	0.067	0.24
10	Candacia columbiae	C6M	750	3	0.13	0.231	0.435	0.05	0.179
11	Aetideopsis rostrata	C5M	750	3	0.13	0.397	0.762	0.08	0.335
12	Chiridius pacificus	C6F	750	3	0.13	0.42	0.692	0.08	0.316
13	Chirundina streetsi	C6F	750	3	0.13	0.787	1.237	0.158	0.538
14	Euchirella brevis	C6F	750	3	0.13	0.51	0.952	0.084	0.506
15	Euchirella galeata	C6F	750	3	0.13	1.139	2.459	0.28	1.126
16	Euchirella messinensis	C6F	750	3	0.13	1.02	1.917	0.215	0.863
17	Euchirella rostrata	C6F	750	3	0.13	0.558	0.93	0.086	0.455
18	Euchirella truncata	C4M	750	3	0.13	0.086	0.517	0.054	0.241
19	Gaidius brevispinus	C6F	750	3	0.13	0.432	0.914	0.077	0.439
20		C6F	750	3	0.13	0.362	0.949	0.104	0.419
21	Gaidius robustus	C4F	750	3	0.13	0.228	0.381	0.041	0.18
22	Gaidius tenuispinus	C5F	750	3	0.13	0.77	1.238	0.117	0.624
23		C6F	750	3	0.13	0.251	0.436	0.053	0.197
24	Gaidius variabilis	C5M	750	3	0.13	0.237	0.488	0.051	0.223
25		C5F	750	3	0.13	0.225	0.323	0.034	0.13
26		C6F	750	3	0.13	0.295	0.509	0.055	0.243
27	Pseudochirella pacifica	C5M	750	3	0.13	0.488	0.7	0.071	0.296
28	Pseudochirella spinifera	C5M	750	3	0.13	0.583	1.592	0.125	0.923
29		C5M	750	3	0.13	0.632	1.275	0.109	0.687
30	Undeuchaeta plumosa	C6F	750	3	0.13	1.273	3.332	0.322	1.696
31	Paraeuchaeta barbata	C6F	750	3	0.13	0.703	3.862	0.246	2.394
32	Paraeuchaeta birostrata	C5M	750	3	0.13	0.366	1.351	0.095	0.762
33		C5F	750	3	0.13	0.448	1.793	0.131	1.038
34		C6F	750	3	0.13	0.796	4.852	0.363	2.834
35	Paraeuchaeta brevirostris	C6F	750	3	0.13	1.009	4.969	0.357	2.877
36	Paraeuchaeta elongata	C4M	750	3	0.13	0.176	0.714	0.052	0.407
37		C4F	750	3	0.13	0.244	0.939	0.066	0.55
38		C5M	750	3	0.13	0.314	1.122	0.079	0.66
39		C5M	750	3	0.13	0.261	1.245	0.096	0.684
40		C5F	750	3	0.13	0.286	1.192	0.083	0.653
41		C5F	750	3	0.13	0.55	2.38	0.174	1.383
42		C6F	750	3	0.13	0.846	5.715	0.384	3.412
43		C6F	750	3	0.13	1.03	1.943	0.185	0.999
44	Paraeuchaeta modesta	C6F	750	3	0.13	1.08	3.867	0.287	2.27
45	Paraeuchaeta orientalis	C6F	750	3	0.13	1.617	8.557	0.529	4.723
46	Paraeuchaeta pseudotumidula	C6M	750	3	0.13	0.54	2.272	0.171	1.331
47		C6F	750	3	0.13	0.796	2.585	0.173	1.543
48	Paraeuchaeta rubra	C5M	750	3	0.13	0.491	1.902	0.1316	1.143
49		C6F	750	3	0.13	0.58	3.498	0.2728	1.959
50	Amallothrix valida	C5M	750	3	0.13	0.281	0.684	0.0548	0.384
51		C6F	750	3	0.13	0.562	0.872	0.0942	0.416
52	Mixtocalanus robstus	C6F	750	3	0.13	0.774	1.008	0.1119	0.475
53	Scaphocalanus medius	C6F	750	3	0.13	0.411	1.062	0.0787	0.609
54	Spinocalanus stellatus	C6F	750	3	0.13	0.503	0.818	0.0592	0.356
55	Pachyptilus pacificus	C6F	1500	2	0.20	0.157	2.41	0.1824	1.125
56	Lucicutia bicornuta	C6F	1500	2	0.20	0.247	1.017	0.0755	0.537
57	Lucicutia grandis	C6M	1500	2	0.20	0.408	2.192	0.1903	1.19
58	Lucicutia pacifica	C6F	1500	2	0.20	0.268	1.81	0.1314	0.853
59		C6F	1500	2	0.20	0.451	1.634	0.1186	0.77
60	Metridia asymmetrica	C6F	1500	2	0.20	0.046	0.36	0.0271	0.188
61		C6F	1500	2	0.20	0.077	0.344	0.0249	0.162
62	Metridia curticauda	C6F	1500	2	0.20	0.066	0.99	0.0729	0.471
63	Metridia ornata	C6F	1500	2	0.20	0.241	2.9	0.232	1.465
64	Aetideopsis rostrata	C5M	1500	2	0.20	0.42	1.84	0.106	0.96
65		C5F	1500	2	0.20	0.122	0.707	0.0578	0.369
66	Bradyidius pacificus	C5M	1500	2	0.20	0.225	0.89	0.0779	0.451
67	Euchirella rostrata	C6F	1500	2	0.20	0.242	0.804	0.09	0.356
68		C6F	1500	2	0.20	0.511	0.82	0.1025	0.344
69	Gaidius brevispinus	C6F	1500	2	0.20	0.27	0.971	0.099	0.425
70	Gaidius variabilis	C6F	1500	2	0.20	0.187	0.672	0.0672	0.296
71		C6F	1500	2	0.20	0.3	0.935	0.1	0.43
72	Pseudochirella pacifica	C5M	1500	2	0.20	0.43	0.554	0.0514	0.294
73		C5F	1500	2	0.20	0.513	1.945	0.1502	1.05
74		C5F	1500	2	0.20	0.6	1.637	0.1445	0.925
75	Pseudochirella polyspina	C6F	1500	2	0.20	0.85	2.525	0.2626	1.167
76		C6F	1500	2	0.20	0.645	3.057	0.291	1.623
77	Pseudochirella spinifera	C5F	1500	2	0.20	0.422	1.79	0.1475	0.977
78		C6M	1500	2	0.20	0.176	1.2	0.1081	0.64
79		C6M	1500	2	0.20	0.29	1.363	0.1022	0.837
80	Undeuchaeta major	C6F	1500	2	0.20	0.834	3.35	0.271	1.745
81		C6F	1500	2	0.20	0.706	2.477	0.2576	1.241
82	Undeuchaeta plumosa	C6F	1500	2	0.20	1.128	2.82	0.2752	1.449
83	Paraeuchaeta birostrata	C5M	1500	2	0.20	0.34	3.527	0.2793	2.155
84		C6M	1500	2	0.20	0.6	2.472	0.1869	1.523
85		C6M	1500	2	0.20	0.35	2.455	0.1846	1.488
86		C6F	1500	2	0.20	0.49	4.217	0.2986	2.387
87		C6F	1500	2	0.20	0.812	4.46	0.3403	2.649
88	Paraeuchaeta brevirostris	C6F	1500	2	0.20	0.668	4.808	0.3649	2.866
89	Paraeuchaeta elongata	C5M	1500	2	0.20	0.445	2.152	0.173	1.259
90		C5F	1500	2	0.20	0.74	2.13	0.1879	1.125
91	Paraeuchaeta pseudotumidula	C6F	1500	2	0.20	0.634	2.977	0.2152	1.712
92	Paraeuchaeta rubra	C5M	1500	2	0.20	0.25	2.098	0.1569	1.276
93		C5F	1500	2	0.20	0.39	1.904	0.17	1.144
94		C6M	1500	2	0.20	0.238	1.65	0.1241	1.096
95		C6F	1500	2	0.20	0.66	4.625	0.293	2.636
96	Cornucalanus indicus	C5F	1500	2	0.20	0.962	3.55	0.2989	1.818
97		C6F	1500	2	0.20	1.017	6.919	0.5494	3.812

98	*Onchocalanus magnus*	C5F	1500	2	0.20	0.983	6.596	0.4789	3.971
99		C6F	1500	2	0.20	1.131	5.77	0.4206	2.827
100	*Amallothrix inornata*	C6M	1500	2	0.20	0.166	0.524	0.0422	0.291
101		C5M	1500	2	0.20	0.363	0.912	0.0658	0.553
102		C6F	1500	2	0.20	0.21	0.946	0.0759	0.522
103	*Amallothrix paravalida*	C6F	1500	2	0.20	0.26	0.664	0.0473	0.369
104	*Amallothrix valida*	C5F	1500	2	0.20	0.287	1	0.0748	0.568
105		C6F	1500	2	0.20	0.316	1.094	0.0788	0.66
106	*Lophothrix frontalis*	C6F	1500	2	0.20	0.922	3.19	0.3031	1.451
107		C6F	1500	2	0.20	0.607	1.416	0.1284	0.797
108	*Scaphocalanus magnus*	C6F	1500	2	0.20	0.44	1.166	0.1159	0.596
109	*Scaphocalanus medius*	C6F	1500	2	0.20	0.263	1.115	0.0798	0.682
110	*Scottocalanus securifrons*	C6F	1500	2	0.20	0.537	1.452	0.1626	0.716
111	*Bathycalanus bradyi*	C6F	1500	2	0.20	4.17	34.49	2.3798	21.798
112	*Euaugaptilus pseudaffinis*	C6F	2500	1.5	0.32	0.202	1.681	0.1273	0.884
113	*Pachyptilus pacificus*	C6F	2500	1.5	0.32	0.136	2.724	0.1882	1.22
114	*Heterostylites major*	C6F	2500	1.5	0.32	0.162	0.528	0.0495	0.228
115	*Lucicutia ellipsoidalis*	C6F	2500	1.5	0.32	0.271	0.777	0.049	0.412
116	*Lucicutia grandis*	C6M	2500	1.5	0.32	0.157	1.528	0.0935	0.877
117		C6F	2500	1.5	0.32	0.238	1.398	0.0931	0.717
118	*Lucicutia longifurca*	C5	2500	1.5	0.32	0.122	1.189	0.0949	0.6
119		C6M	2500	1.5	0.32	0.291	1.534	0.0923	0.913
120	*Lucicutia pacifica*	C6F	2500	1.5	0.32	0.271	1.705	0.132	0.856
121	*Metridia asymmetrica*	C6F	2500	1.5	0.32	0.083	0.425	0.0317	0.23
122		C6F	2500	1.5	0.32	0.138	0.453	0.0369	0.25
123	*Metridia ornata*	C5F	2500	1.5	0.32	0.4	1.906	0.162	0.93
124		C6M	2500	1.5	0.32	0.226	0.868	0.0717	0.422
125		C6M	2500	1.5	0.32	0.191	0.818	0.0627	0.402
126		C6F	2500	1.5	0.32	0.276	1.267	0.1022	0.646
127	*Gaetanus paracurvicornis*	C6F	2500	1.5	0.32	0.222	0.735	0.0694	0.343
128	*Gaidius robustus*	C5M	2500	1.5	0.32	0.251	0.708	0.0678	0.301
129		C5M	2500	1.5	0.32	0.785	3.444	0.2094	2.17
130		C5M	2500	1.5	0.32	0.346	1.261	0.1042	0.463
131		C6F	2500	1.5	0.32	1.322	7.03	0.6721	3.494
132	*Gaidius variabilis*	C5F	2500	1.5	0.32	0.258	0.835	0.0852	0.416
133		C6F	2500	1.5	0.32	0.155	1.316	0.1017	0.738
134	*Pseudochirella pacifica*	C5	2500	1.5	0.32	1.495	4.074	0.3312	2.151
135		C6F	2500	1.5	0.32	1	2.772	0.3105	1.239
136	*Pseudochirella polyspina*	C5F	2500	1.5	0.32	0.156	1.085	0.0697	0.589
137		C6F	2500	1.5	0.32	0.89	2.688	0.2556	1.333
138		C6F	2500	1.5	0.32	1.762	4.146	0.4519	2.019
139		C6F	2500	1.5	0.32	0.922	2.533	0.2609	1.251
140	*Pseudochirella spinifera*	C5M	2500	1.5	0.32	0.935	3.639	0.2351	2.202
141	*Undeuchaeta major*	C5F	2500	1.5	0.32	0.082	0.445	0.0454	0.21
142	*Paraeuchaeta birostrata*	C6M	2500	1.5	0.32	0.556	2.155	0.1476	1.297
143		C6F	2500	1.5	0.32	1.787	8.892	0.7745	4.917
144	*Paraeuchaeta pseudotumidula*	C6F	2500	1.5	0.32	0.31	1.157	0.0899	0.702
145	*Paraeuchaeta rubra*	C5M	2500	1.5	0.32	0.269	2.64	0.1753	1.632
146		C5F	2500	1.5	0.32	0.264	2.125	0.1494	1.245
147		C6F	2500	1.5	0.32	0.839	4.638	0.3386	2.843
148	*Xanthocalanus kurilensis*	C6F	2500	1.5	0.32	0.109	1.041	0.0937	0.579
149	*Amallothrix inornata*	C6F	2500	1.5	0.32	0.433	0.803	0.0835	0.391
150		C6F	2500	1.5	0.32	0.369	1.029	0.107	0.546
151	*Scaphocalanus affinis*	C5F	2500	1.5	0.32	0.503	2.577	0.1425	1.649
152		C6F	2500	1.5	0.32	0.373	1.524	0.1372	0.823
153	*Scolecithricella sp.*	C6F	2500	1.5	0.32	0.135	0.447	0.0384	0.229
154	*Scottocalanus securifrons*	C6F	2500	1.5	0.32	1.162	5.64	0.4856	3.141
155	*Bathycalanus bradyi*	C6F	2500	1.5	0.32	1.259	16.78	1.1947	9.934
156		C6F	2500	1.5	0.32	1.052	10.52	0.9152	4.9865
157	*Spinocalanus magnus*	C6F	2500	1.5	0.32	0.232	0.868	0.0606	0.5199
158	*Aetideopsis rostrata*	C6F	4000	1.5	0.45	0.35	0.975	0.0713	0.4602
159	*Amallothrix inornata*	C5M	4000	1.5	0.45	0.2	0.471	0.031	0.241
160	*Amallothrix inornata*	C6F	4000	1.5	0.45	0.22	0.581	0.039	0.288
161	*Batheuchaeta lamellata*	C5M	4000	1.5	0.45	0.13	0.647	0.0421	0.3856
162	*Batheuchaeta lamellata*	C6F	4000	1.5	0.45	0.31	1.317	0.1037	0.6873
163	*Batheuchaeta lamellata*	C6M	4000	1.5	0.45	0.38	0.765	0.0564	0.427
164	*Bathycalanus bradyi*	C3	4000	1.5	0.45	0.76	1.2	0.123	0.5563
165	*Bathycalanus bradyi*	C5	4000	1.5	0.45	2.14	8.686	0.5446	5.0952
166	*Benthomisophria palliata*	C6M	4000	1.5	0.45	0.12	0.53	0.0351	0.1972
167	*Chiridiella abyssalis*	C6F	4000	1.5	0.45	0.17	0.806	0.0542	0.4267
168	*Chiridiella pacifica*	C6F	4000	1.5	0.45	0.3	1.198	0.0757	0.4732
169	*Gaetanus paracurvicornis*	C6F	4000	1.5	0.45	0.26	0.685	0.0572	0.3171
170	*Gaidius pungens*	C6F	4000	1.5	0.45	0.3	0.641	0.0458	0.3365
171	*Gaidius robustus*	C6F	4000	1.5	0.45	1.23	8.478	0.7393	4.5273
172	*Metridia ornata*	C5M	4000	1.5	0.45	0.18	0.33	0.0237	0.1158
173	*Metridia ornata*	C6F	4000	1.5	0.45	0.32	1.666	0.1445	0.7233
174	*Metridia ornata*	C6M	4000	1.5	0.45	0.35	0.936	0.0823	0.3965
175	*Mixtocalanus robustus*	C6F	4000	1.5	0.45	0.39	1.06	0.0799	0.572
176	*Onchocalanus magnus*	C5F	4000	1.5	0.45	0.62	2.014	0.111	1.236
177	*Onchocalanus magnus*	C6F	4000	1.5	0.45	0.82	1.47	0.1391	0.7575
178	*Paraeuchaeta rubra*	C4F	4000	1.5	0.45	0.18	0.492	0.0329	0.254
179	*Pseudochirella pacifica*	C5M	4000	1.5	0.45	0.37	0.948	0.054	0.561
180	*Pseudochirella polyspina*	C6F	4000	1.5	0.45	0.41	2.23	0.1561	1.1878
181	*Scaphocalanus magnus*	C6F	4000	1.5	0.45	0.51	1.35	0.1292	0.6761
182	*Spinocalanus magnus*	C6F	4000	1.5	0.45	0.24	0.358	0.029	0.1622
183	*Undeuchaeta incisa*	C5M	4000	1.5	0.45	0.53	2.843	0.1746	1.7172
184	*Undeuchaeta major*	C6F	4000	1.5	0.45	0.49	1.183	0.1355	0.5406
185	*Undeuchaeta plumosa*	C5F	4000	1.5	0.45	0.16	0.475	0.0418	0.2166
186	*Undeuchaeta plumosa*	C6F	4000	1.5	0.45	0.31	1.378	0.0908	0.7882
187	*Valdeviella imperfecta*	C5F	4000	1.5	0.45	0.25	0.894	0.0655	0.4946
188	*Xanthocalanus kurilensis*	C6F	4000	1.5	0.45	0.18	0.66	0.0479	0.3565
189	*Calanus propinquus*		2	-1	1.00	1.1789	1.0425	0.1301	0.455
190	*Metridia gerlachei*		2	-1.4	1.00	0.3195	0.2654	0.0304	0.12
191	*Calanoides acutus*	C5	2	-0.2	1.00	0.2108	0.3936	0.0335	0.1934
192	*Calanoides acutus*	C4,5	2	-0.6	1.00	0.1625	0.266	0.0212	0.1208
193	*Calanus finmarchicus*	C6F	2	0.1	1.00	0.3279	0.3865	0.0295	0.2146
194	*Calanus glacialis*	C6F	50	1.9	1.00	0.6158	0.4736	0.0503	0.2227
195	*Calanus hyperboreus*	C6F	50	1.3	1.00	1.485	3.95	0.2825	2.3375
196	*Calanus hyperboreus*	C5	50	0.9	1.00	1.0277	1.943	0.1438	1.117
197	*Calanus hyperboreus*	C5	50	-0.3	1.00	1.054	2.677	0.18	1.634
198	*Metridia longa*	C6F	50	0.1	1.00	0.4058	0.353	0.037	0.1675
199	*Rincalanus gigas*		50	-1.7	1.00	0.437	1.08	0.1063	0.5033
200	*Neocalanus cristatus*	C5	2	6.3	1.00	1.67	1.5873	0.1333	0.7905
201	*Neocalanus plumchrus*	C4	2	5.6	1.00	0.28	0.2633	0.0208	0.148

202	*Neocalanus plumchrus*	C5	2	7.3	1.00	0.68	0.7852	0.0628	0.4523
203	*Eucalanus bungii*		2	6	1.00	0.795	1.01	0.099	0.404
204	*Pseudocalanus elongatus*		2	8.6	1.00	0.0397	0.0116	0.0014	0.0053
205	*Metridia pacifica*		2	8.2	1.00	0.3822	0.1476	0.0164	0.0654
206	*Acartia longiremis*		2	9.6	1.00	0.028	0.0081	0.001	0.0035
207	*Tortanus discaudatus*		2	7	1.00	0.12	0.0569	0.0064	0.025
208	*Metridia pacifica*		2	13	1.00	0.2737	0.094	0.0113	0.0433
209	*Mesocalanus tenuicornis*		2	15.8	1.00	0.22	0.0313	0.0038	0.0123
210	*Paracalanus parvus*		2	13.9	1.00	0.031	0.0038	0.0005	0.0016
211	*Centropages abdominaris*		2	15.9	1.00	0.0855	0.0167	0.002	0.0067
212	*Pseudodiaptomus marinus*		2	14.3	1.00	0.0563	0.0142	0.0017	0.0057
213	*Neocalanus plumchrus*		2	15.1	1.00	0.555	0.294	0.0262	0.1353
214	*Acartia clausi*		2	14.8	1.00	0.0305	0.0085	0.0011	0.0035
215	*Neocalanus gracilis*		2	19.7	1.00	1.64	0.5	0.051	0.2335
216	*Centropages brachiatus*		2	17.3	1.00	0.115	0.0198	0.002	0.0083
217	*Acartia tonsa*		2	22	1.00	0.0564	0.0072	0.0007	0.003
218	*Undinula vulgaris*		2	23.5	1.00	0.9663	0.1854	0.0178	0.0771
219	*Euchaeta marina*		2	24	1.00	1.3375	0.2905	0.028	0.1209
220	*Acartia pacifica*		2	26	1.00	0.0464	0.0078	0.0008	0.0032
221	*Calanopia elliptica*		2	26	1.00	0.2803	0.0563	0.0054	0.0234
222	*Tortanus gracilis*		2	26	1.00	0.1433	0.0235	0.0023	0.0098
223	*Eucalanus subcrassus*		2	24	1.00	0.655	0.1037	0.01	0.0431
224	*Labidocera acuta*		2	24	1.00	1.89	0.2334	0.0224	0.0971
225	*Acartia australis*		2	25	1.00	0.0553	0.0091	0.0009	0.0038
226	*Nannocalanus minor*		2	26.9	1.00	0.21	0.0401	0.0045	0.017
227	*Undinula vulgaris*		2	27.6	1.00	1.3989	0.1673	0.0181	0.0698
228	*Eucalanus attenuatus*		2	27.4	1.00	0.905	0.1374	0.0128	0.0541
229	*Labidocera acuta*		2	28.5	1.00	2.07	0.2315	0.0283	0.0998
230	*Labidocera nerii*		2	26.4	1.00	1.515	0.221	0.027	0.0953
231	*Pontella danae*		2	26.4	1.00	3.43	0.7	0.084	0.2996
232	*Neocalanus cristatus*	C5	25	5	1.00	1	1.72	0.1651	0.676
233	*Calanus marshallae*	C5	15	8	1.00	0.3829	0.4211	0.0356	0.239
234	*Neocalanus plumchrus*	C5	75	5.8	1.00	0.251	0.244	0.0187	0.1113
235	*Neocalanus plumchrus*	C5	15	8	1.00	0.6478	0.9278	0.0696	0.5511
236	*Mesocalanus tennuicornis*	C6F	15	22	1.00	0.5993	0.265	0.0281	0.1226
237	*Metridia pacifica*	C6F	135	4.7	1.00	0.3975	0.2032	0.0245	0.0946
238	*Metridia pacifica*	C6F	75	5.8	1.00	0.2775	0.183	0.0215	0.0824
239	*Pleuromamma scutullata*	C6F	75	6	1.00	0.4335	0.3223	0.0352	0.1464
240	*Pleuromamma scutullata*	C6F	75	5.8	1.00	0.423	0.4025	0.0432	0.1962
241	*Pleuromamma scutullata*	C6F	100	3	1.00	0.336	0.3588	0.0358	0.1799
242	*Pleuromamma abdominaris*	C6F	100	13.6	1.00	0.6835	0.3585	0.0427	0.1545
243	*Pleuromamma xiphias*	C6F	100	12	1.00	0.5488	0.3873	0.0445	0.1599
244	*Gaetanus simplex*	C6F	75	6	1.00	0.3635	0.4508	0.0524	0.2176
245	*Gaetanus simplex*	C6F	100	3	1.00	0.2723	0.4343	0.0477	0.2295
246	*Euchaeta marina*	C6F	100	11.3	1.00	0.6028	0.415	0.044	0.205
247	*Euchaeta marina*	C6F	15	20.2	1.00	0.743	0.18	0.0196	0.0862
248	*Euchaeta marina*	C6F	100	20	1.00	0.9085	0.23	0.0281	0.104
249	*Euchaeta marina*	C6F	100	16	1.00	0.9036	0.335	0.0409	0.1514
250	*Candacia bipinnata*	C6F	100	11.3	1.00	0.7088	0.3325	0.0371	0.1438
251	*Candacia bipinnata*	C6F	15	20.2	1.00	0.4763	0.1017	0.0117	0.0444
252	*Candacia bipinnata*	C6F	100	13	1.00	0.4041	0.1636	0.0193	0.07
253	*Candacia clombidea*	C6F	100	4.7	1.00	0.7603	0.5589	0.066	0.2541

Source of data
1-157: Ikeda et al. Mar. Ecol. Prog. Ser. 322: 199-211(2006)(a datum of *Euaugaptilus parabullifer* C6F from 2500m was omitted as an outlier)
158-188: Ikeda, unpublished
189-231: Ikeda et al. Mar. Biol. 139:587-596 (2001)
232: Ikeda et al. Mar. Biol. 145: 1181-1190 (2004), S3 data
233-253: Sano and Ikeda, ubpublished