Respiration in marine pelagic copepods: a global-bathymetric model

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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 2 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 for 72 to 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 leading to a negative effect of depth and a positive effect of oxygen saturation on respiration rates are thought to be due to 'predation-mediated selection' and the lack of specialized respiratory organs (i.e. oxygen diffusion through the body surface), respectively.

KEY WORDS: Respiration · Copepods · Global · Bathymetric · Model

INTRODUCTION

Copepods are the major component of marine meso-zooplankton and may be the most numerous multicellular organisms on 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 for understanding oceanic biogeochemical cycles of carbon and other elements (Aristegui et al. 2005, Hernandez-Leon & Ikeda 2005, Buitenhuis et al. 2006). Copepod respiration (= oxygen consumption) is a direct measure of mineralization and has been shown to be a function of body mass and habitat temperature for epipelagic copepods (Ivleva 1980, Ikeda et al. 2001); this principle has now been expanded to apply to all organisms on earth (Gillooly et al. 2001). While the ultimate importance of body mass and habitat temperature as determinants of copepod respiration (hereafter referred as

the 'global' respiration model) was derived from statistical analyses of large datasets on epipelagic copepods collected from the world's oceans, its application to those living in the ocean's interior is currently inappropriate since a recent study indicated significantly lower respiration rates for copepods in the mesopelagic and bathypelagic zones of the ocean (Ikeda et al. 2006a). As a basis for advancing 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 over many years (1970–2004) using standardized methods (sealed-chamber method, cf. Ikeda et al. 2000) at various locations in the world's oceans (Fig. 1) (Ikeda et al.
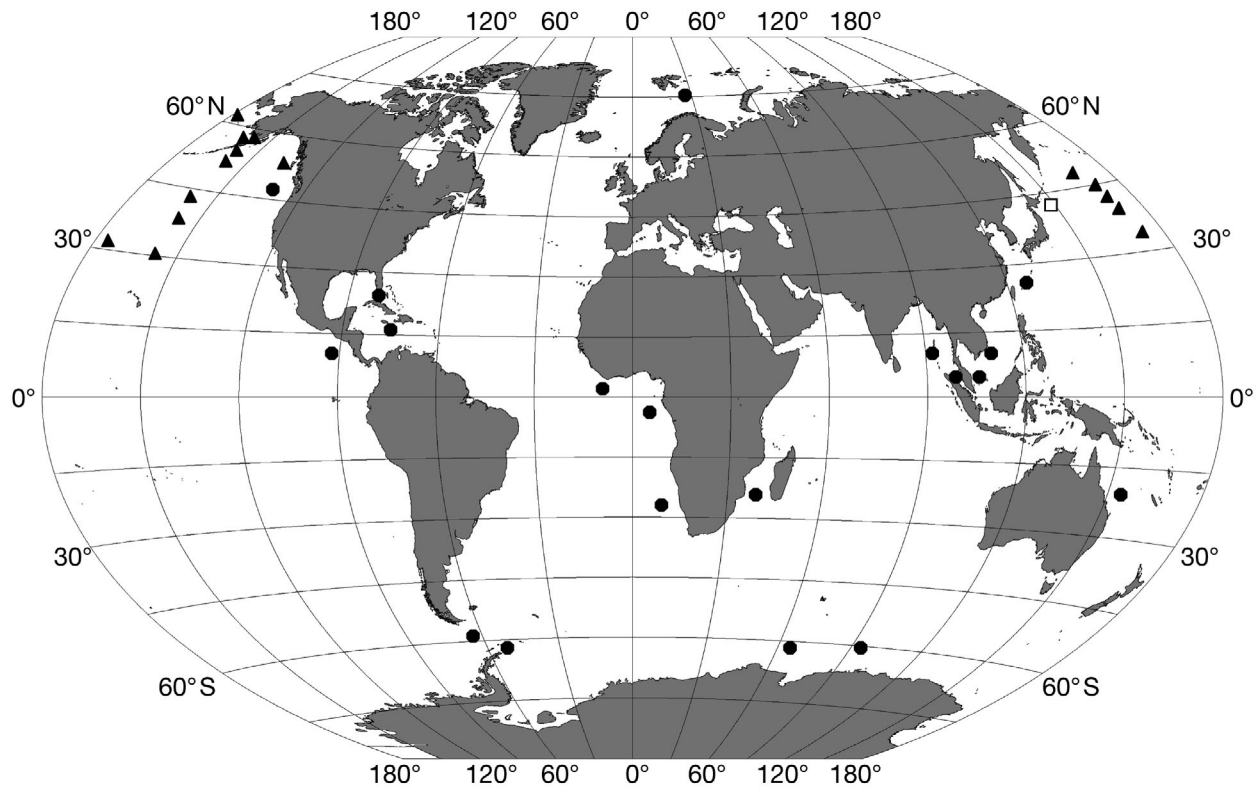
Fig. 1. Geographical distribution of study sites of copepod respiration, including those for epipelagic species (●: Ikeda et al. 2001; ▲: F. Sano & T. Ikeda unpubl. data) and mesopelagic through bathypelagic (Ikeda et al. 2006) and abyssopelagic species (Ikeda unpubl.) in the western North Pacific Ocean (□)

2001, 2004, F. Sano & T. Ikeda unpubl. data). In these epipelagic datasets, the temperatures of the water where the copepods were collected ranged from sea-water near the point of freezing (–1.7°C) in the polar seas to tropically warm water (28.5°C). The 188 deep-sea respiration datasets were from the mesopelagic (500 to 1000 m), upper-bathypelagic (1000 to 2000 m) and lower-bathypelagic (2000 to 3000 m) (Ikeda et al. 2006a) supplemented by the abyssopelagic (3000 to 5000 m) zones (T. Ikeda unpubl.), all in the western North Pacific Ocean (Fig. 1). Respiration rates of cope-pods from these bathymetric zones were determined at the mean temperatures of each zone (1.5 to 3°C) and at near ambient oxygen concentrations (see below) by using fresh seawater from the mid-sampling depth of each zone collected just prior to the experiment (for details of the procedures, see Ikeda et al. 2006a). No decompression effect was taken into account for the experiment on deep-sea copepods, since a lack of appreciable hydrostatic pressure effects on the respi-ration 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 or from deeper zones was confirmed by the enzyme activities of the

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 gen-era and 108 species of marine pelagic copepods was used in our analysis (see Appendix 1 at: www.int-res.com/articles/suppl/m339p215_app.pdf). In terms of dried body mass (DM), the smallest copepod was *Para-calanus parvus* (0.0038 mg) and the largest was *Bathy-calanus bradyi* (34.5 mg).

In addition to the 2 conventional independent vari-ables (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), 2 new inde-pendent variables (x_3: oxygen saturation; and x_4: depth of occurrence) were introduced to the global-bathy-metric model of the present 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 4 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

Table 1. Stepwise (forward selection) multiple regression analyses of respiration rates (y: μl O_2 ind.$^{-1}$ h^{-1}) on body mass (x_1: mg ind.$^{-1}$), 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 (N = 253). Theoretical regression equation: $\ln(y/x_1^{0.75}) = a_0 + a_2(1000x_2^{-1}) + a_3x_3 + a_4\ln x_4$; empirical regression equation: $\ln y = a_0 + a_1\ln x_1 + a_2x_2 + a_3x_3 + a_4\ln x_4$. DM: dry mass; NM: nitrogen; CM: carbon; R^2: correlation coefficient

Regression model	Body mass unit	Step	Equation coefficients					R^2
			a_0	a_1	a_2	a_3	a_4	
Theoretical	DM	1	30.874		−8.800			0.668
		2	19.348		−5.355		−0.146	0.746
		3	18.305		−5.227	0.537	−0.089	0.760
	NM	1	29.710		−7.966			0.675
		2	21.350		−5.746	0.813		0.750
		3	18.887		−4.907	0.512	−0.070	0.762
	CM	1	33.499		−9.385			0.669
		2	21.364		−5.758		−0.155	0.746
		3	20.230		−5.619	0.584	−0.092	0.761
Empirical	DM	1	−0.894	0.367				0.364
		2	−1.289	0.649	0.094			0.669
		3	−0.258	0.737	0.064		−0.145	0.737
		4	−0.815	0.750	0.064	0.539	−0.091	0.752
	NM	1	0.146	0.421				0.420
		2	0.456	0.705	0.092			0.729
		3	0.359	0.777	0.072	0.855		0.791
		4	1.073	0.796	0.063	0.543	−0.079	0.803
	CM	1	−0.667	0.337				0.344
		2	−0.878	0.606	0.094			0.644
		3	−1.116	0.678	0.075	0.878		0.708
		4	−0.392	0.700	0.065	0.549	−0.085	0.722

sampling from the mesopelagic zone (500 to 1000 m), 1500 m from the upper-bathypelagic zone (1000 to 2000 m) and so on. x_1 was expressed as DM, nitrogen (NM) or carbon (CM) since the choice of the 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 a theoretical model characterized by the scaling exponent of 3/4 (or 0.75) and the Arrhenius relationship for the temperature effect ($R = R_0M^{3/4}e^{-E/kT}$, 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 Boltzmann's constant and R_0 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 a number of criticisms of the theoretical model above have been expressed. One of 2 components of the model, the scaling exponent 3/4 (or 0.75) has been questioned from the viewpoint of its theoretical justification and verification by the data (Dodds et al. 2001). The other component, the Arrhenius relationship, implies that there is an automatic increase in respiration rate with increasing temperature, with no provision for laboratory acclimation, seasonal acclimation 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_0) of specimens weighing 1 mg DM ($R_0 = R$ 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_0) at 10°C of epipelagic, mesopelagic, upper-bathypelagic, lower-bathypelagic and abyssopelagic
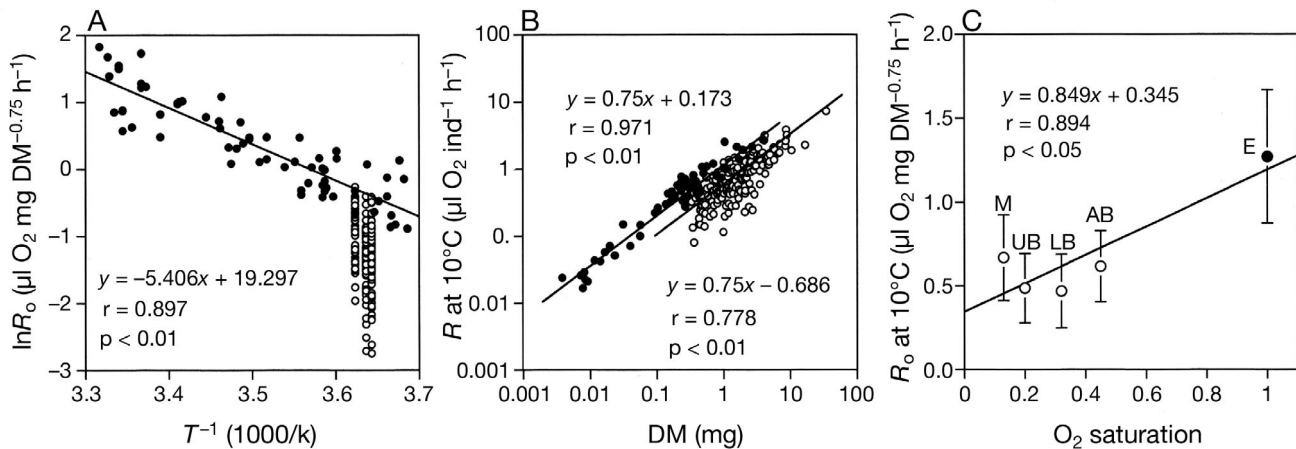
Fig. 2. Copepod respiration rates and variables. (A) Relationship between the respiration rate of copepods standardized to a body size of 1 mg dry mass (DM), (R_o) and inverse temperature (T^{-1}); fitted least square regression line only for epipelagic copepod data. (B) Relationship between respiration rate standardized to the rate (R) at 10°C and 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°C and oxygen concentration (O_2 saturation), and fitted least square regression line. ●: epipelagic copepods; O: mesopelagic through abyssopelagic copepods. Bathymetric abbreviations: E = epipelagic, M = mesopelagic, UB = upper-bathypelagic, LB = lower-bathypelagic, AB = 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 3 out of the 4 individual variables on the respiration rates (Fig. 2), the attributes of these 4 variables were analyzed simultaneously by using stepwise multiple regression (forward selection) method (Sokal & Rohlf 1995). Independent variables were added if $p < 0.05$ and removed if $p > 0.10$. The calculation was conducted using SYSTAT version 10.2. The results show that the 4 independent variables were all significant although the priority of addition oxygen saturation (x_3) or depth of occurrence (x_4) differed depending on the choice of the body mass unit in both models (Table 1). The choice of body mass unit also affected the correlation coefficients derived from the empirical model ($R^2 = 0.72$ to 0.80 for the regression equations at Step 4, Table 1), but this was not the case in the theoretical model ($R^2 = 0.76$ for those at Step 3).

DISCUSSION

Our results indicate clearly that not only body mass and temperature but also the depth of occurrence and ambient oxygen saturation contributed significantly to the variance of the copepod respiration data from the epipelagic through the abyssepelagic zones (Table 1). When compared with the equivalent body mass unit,

there was little difference in the partial regression coefficients of each variable (excepting those of the temperature, the effect of which was expressed as different mathematical forms in each model) and the correlation coefficients between the theoretical and empirical models. While the best fit regression equation was that of the empirical model in which body mass was expressed by the nitrogen unit ($R^2 = 0.80$, cf. Table 1), the differences from the rest of the 5 full regression equations ($R^2 = 0.72$ to 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's oceans 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 determined 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, USA, 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) which live in or in close proximity to the minimum oxygen zone are able 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 supports the 'predation-mediated selection' hypothesis (Ikeda et al. 2006a). According to this hypothesis, the lower levels of respiration in deeper-living copepods is a result of low selective pressure for high activity in copepods in the deep-sea. 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 also need to be active enough to avoid predation risk. A recent observation of a progressive decline in the nitrogen (= muscle) concentration in copepods living in the epipelagic through the abyssopelagic zones supports the hypothesis (Ikeda et al. 2006b). It is noted that the 'visual-interactions' hypothesis (Childress 1995) which has been proposed to explain the 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 the respiration rates of pelagic copepods. The lower respiration rates of mesopelagic through abyssopelagic copepods found here supports the predictions of that hypothesis.

Compared with the previous global respiration model (Ikeda et al. 2001), the global-bathymetric respiration model (Table 1) described in the present study is an advanced version, which provides 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 4 independent variables (x_1, x_2, x_3 and x_4), the present global-bathymetric model explained 72 to 80% of the variance in the epipelagic through abyssopelagic respiration data. The amount of explained variance by the 4 variables in the global-bathymetric model is less than that (93 to 96%) of the global model, which has only 2 variables (Ikeda et al. 2001). This may be partially due to the low precision of the respiration data for copepods from the mesopelagic through the abyssopelagic zones, since most of the mesopelagic data 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. In the future, the global-bathymetric model can be improved by the addition of new respiration datasets of copepods from other extreme deep-sea environments characterized by a high temperature and/or high oxygen saturation (the present data are of low temperature and low oxygen in the western subarctic Pacific); possible candidates for such study sites are the Arabian Sea, the Sulu Sea and the entire North Atlantic Ocean.

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