
Eucalanoid copepod metabolic rates in the oxygen minimum zone of the eastern tropical north Pacific: Effects of oxygen and temperature

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abstract

The eastern tropical north Pacific Ocean (ETNP) contains one of the world's most severe oxygen minimum zones (OMZs), where oxygen concentrations are less than 2 mmol kg^{-1} . OMZs cause habitat compression, whereby species intolerant of low oxygen are restricted to near-surface oxygenated waters. Copepods belonging to the family Eucalanidae are dominant zooplankters in this region and inhabit a variety of vertical habitats within the OMZ. The purpose of this study was to compare the metabolic responses of three species of eucalanoid copepods, *Eucalanus inermis*, *Rhincalanus rostrifrons* and *Subeucalanus subtenius* to changes in temperature and environmental oxygen concentrations. Oxygen consumption and urea, ammonium, and phosphate excretion rates were measured via end-point experiments at three temperatures (10, 17, and $23 \text{ }^{\circ}\text{C}$) and two oxygen concentrations (100% and 15% air saturation). *S. subtenius* which occurred primarily in the upper 50 m of the water column at our study site, inhabiting well-oxygenated to upper oxycline conditions, had the highest metabolic rates per unit weight, while *E. inermis*, which was found throughout the water column to about 600 m depth in low oxygen waters, typically had the lowest metabolic rates. Rates for *R. rostrifrons*

known, however, about the effects of OMZs and hypoxic coastal regions on carbon and nitrogen cycles, marine biota, and the efficiency of the biological pump.

Metabolic rates of marine organisms, in particular, will be sensitive to changing ocean conditions. Increasing water temperatures and decreasing O_2 and pH levels will exceed physiological tolerances of many marine organisms and eventually limit suitable habitats (Prince and Goodyear, 2006). Metabolic rates of marine zooplankton are known to be influenced by a number of different factors, including temperature (e.g., Childress, 1977; Hirche, 1987; Ikeda et al., 2001), body mass (Conover and Gustavson, 1999; Ikeda et al., 2001), salinity (Barber and Blake, 1985), season (Conover, 1959; Conover and Gustavson, 1999; Torres et al., 1994), depth of occurrence (Childress, 1975; Seibel and Drazen, 2007; Torres et al., 1994), life strategy (Company and Sardà, 1998), feeding activity or feeding history (Bohrer and Lampert, 1988; Ikeda, 1971, 1977; Mayzaud, 1976), swimming activity (Childress, 1968; Swadling et al., 2005; Torres and Childress, 1983), and in situ oxygen concentrations (Childress, 1975, 1977; Cowles et al., 1991; Donnelly and Torres, 1988). Other metabolic parameters, such as ammonia, urea, and phosphate excretion rates also may be influenced by many of the same factors, including temperature (e.g., Aarset and Aunaas, 1990; Ikeda et al., 2001; Quarmby, 1985), salinity (Barber and Blake, 1985), body mass (Conover and Gustavson, 1999; Ikeda et al., 2001) and feeding history (Ikeda, 1977; Mayzaud, 1976; Miller and Roman, 2008; Saba et al., 2009). The metabolic ratios of O:N, N:P and O:P (which compare the molar ratios of oxygen consumed and ammonium and phosphate excreted) are useful as indicators of metabolic substrate catabolized during respiration (primarily lipids, proteins, and/or carbohydrates), and have been documented to vary with season (Gaudy et al., 2003; Hatcher, 1991; Snow and Williams, 1971), timing in reproductive cycle (Barber and Blake, 1985), dry weight (Ikeda et al., 2001), feeding history (Hatcher, 1991; Ikeda, 1977; Mayzaud and Conover, 1988; Quetin et al., 1980), and temperature (Aarset and Aunaas, 1990). Unlike respiration rates, however, excretion rates and metabolic ratios have rarely been examined in relation to variable in situ oxygen concentrations.

The lethal and sublethal effects of coastal hypoxic oxygen concentrations are well documented for many benthic organisms (Vaquer-Sunyer and Duarte, 2008), and some work has examined deleterious effects of low oxygen levels on pelagic crustaceans (Ekau et al., 2010). Crustacean studies on effects of low oxygen have largely concentrated on changes in oxygen consumption rates, egg production, growth, development, activity rates and survival (

2007 aboard the R/V Seward Johnson and 8 December 2008–6
January 2009 aboard the R/V Knorr. Primary sampling locations

at lower oxygen concentrations (5% saturation; 8 –

were most abundant mid-thermocline, in the vicinity of the chlorophyll maximum (CRD site: 25 m; $T=16\text{ }^{\circ}\text{C}$; $60\text{ }\mu\text{M O}_2$) as illustrated in [Fig. 2](#). *R. rostrifrons* females were largely observed slightly above the base of the upper oxycline, just above the core of the OMZ at 275 m ($T=11\text{ }^{\circ}\text{C}$; $6\text{ }\mu\text{M O}_2$). *E. inermis* had a peak maximum abundance at 325 m, also near the base of the upper oxycline ($T=10\text{ }^{\circ}\text{C}$; $2\text{ }\mu\text{M O}_2$), and extending through the OMZ in low concentrations to the top of the lower oxycline. In addition, adult females of this species had a secondary peak in the thermocline near the chlorophyll maximum at 35 m ($T=15\text{ }^{\circ}\text{C}$; $35\text{ }\mu\text{M O}_2$).

3.2. Comparison of rates among species

At both 10 and 17 $^{\circ}\text{C}$, *E. inermis* had significantly lower oxygen consumption ([Table 3](#)) and ammonium, urea and total measured nitrogen excretion rates (rates per mg wet weight; [Tables 4 and 5](#)) than *S. subtenuis*. *E. inermis* also had signi

The few experiments carried out at approximately 5% saturation at 10 °C showed, on average, lower oxygen consumption rates (0.83, 1.04, 1.06 nmol O₂ (mg WW)⁻¹ h⁻¹) for *E. inermis* at 10 °C versus rates measured at 15–20% and 100% saturation (median of 1.71 nmol O₂ (mg WW)⁻¹ h⁻¹ with 25th to 75th quartile ranges of

activity or expression of relevant enzymes in response to different oxygen environments is possible in crustaceans.

oxygen supply through decreased activity and, therefore, decreased metabolic demand. Large lipid reserves also contributed towards its metabolic needs. When excretion rates were examined as daily body N or P turnover rates, however, species differences largely disappeared, indicating that there was not necessarily a functional metabolic difference among these species.

As *S. subtenuis* and *R. rostrifrons* are circum-tropical and subtropical species, it would be interesting to see if the results from this study hold for individuals found in areas without such severe oxygen limitations. It has been suggested that some characteristics observed in organisms inhabiting oceanic low oxygen regions are not necessarily adaptations specifically for life at low oxygen, but rather general taxonomic features that allow them to exploit such a lifestyle (Childress and Seibel, 1998). A regional comparison would help to illuminate whether these copepods respond to low oxygen in this manner due to adaptation, or genetic pre-disposition.

One of the most interesting new findings of this study was the relationship between temperature, oxygen level, and nitrogen excretion in these species (Fig. 3). At 10 °C, low oxygen led to an increase in the amount of urea nitrogen produced relative to ammonium nitrogen in *E. inermis* and *R. rostrifrons*. The opposite trend was true at 17 °C for *E. inermis* and *S. subtenuis*. While the general pathways of urea and ammonia production in crustaceans are known, the mechanisms that regulate the relative amount of each produced are woefully understudied. Other studies have investigated relationships between urea, ammonium, and amino acid excretion with factors like food source, species, temperature, and life stage (Conover and Cota, 1985; Dagg et al., 1980; Miller and Roman, 2008; Mitamura and Saijo, 1980; Quarmby, 1985; Saba et al., 2009). Their findings illustrated that nitrogen excretion is complex and variable among individuals and species. Thus, our examination of three dominant copepod species only represents a small portion of the overall community picture. It is particularly important to understand the factors influencing nitrogen cycles in OMZ regions. It is thought that such regions contribute up to 50% of total nitrogen lost from the oceans to the atmosphere (Codispoti et al., 2001; Gruber and Sarmiento, 1997), primarily through denitrification and anaerobic ammonium oxidation (anammox) pathways. Our oceans are currently seeing decreases in oxygen concentrations, increases in temperatures, and expansion of OMZ systems (Bograd et al., 2008; Emerson et al., 2004; Gilly et al., 2013; Keeling and Garcia, 2002; Stramma et al., 2008, 2010). Thus, it is particularly important to understand the relationships between temperature, oxygen levels, and zooplankton excretory products as well as their impacts on OMZ food webs. Future work in this area should include more examination of enzyme levels to better understand how pathways themselves are affected, not just the end products.

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