



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 $2 \mu\text{mol kg}^{-1}$. 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 °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* (found primarily between 200 and 300 m depth) were intermediate between the other two species and more variable. Metabolic ratios suggested that *R. rostrifrons* relied more heavily on lipids to fuel metabolism than the other two species. *S. subtenius* was the only species that demonstrated a decrease in oxygen consumption rates (at intermediate 17 °C temperature treatment) when environmental oxygen concentrations were lowered. The percentage of total measured nitrogen excreted as urea (% urea-N), as well as overall urea excretion rates, responded in a complex manner to changes in temperature and oxygen concentration. *R. rostrifrons* and *E. inermis* excreted a significantly higher % of urea-N in low oxygen treatments at 10 °C. At 17 °C, the opposite trend was observed as *E. inermis* and *S. subtenius* excreted a higher % of urea-N in the high oxygen treatment. This unique relationship has not been documented previously for crustacean zooplankton, and warrants additional research into regulation of metabolic pathways to better understand nitrogen cycling in marine systems. This study also compared metabolic data for *E. inermis* individuals captured near the surface versus those that were resident in the deeper OMZ. Deeper-dwelling individuals had significantly higher nitrogen excretion rates and O:N ratios, suggesting an increased reliance on lipids for energy while residing in the food-poor waters of the OMZ.

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1. Introduction

Recent studies indicate that the oceans are decreasing in oxygen in response to climate change, primarily through surface heating and increased stratification (Emerson et al., 2004; Keeling and Garcia, 2002; Keeling et al., 2010). In addition, regions of the ocean classified as oxygen minimum zones (OMZs), which are

layers of oxygen deficient waters at intermediate depths, appear to be expanding and are characterized by having a greater than average decrease in oxygen concentrations (Bograd et al., 2008; Gilly et al., 2013; Stramma et al., 2008, 2010). These OMZs ($\text{O}_2 < 20 \mu\text{M}$) occupy about 7% of total ocean volume (Paulmier and Ruiz-Pino, 2009) and are typically maintained as a result of poor ventilation, sluggish circulation, oxygen-poor sources waters, and decomposition of sinking particles (Keeling et al., 2010; Wyrski, 1962). The extent of low oxygen or hypoxic waters in coastal regions (usually defined as $\text{O}_2 < 2 \text{ mg l}^{-1}$ or $< 60 \mu\text{M}$) also has increased in the last three decades due to natural and human activities (Helly and Levin, 2004; Rabalais et al., 2009). Little is

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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 O₂ 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 (Auel and Verheye, 2007; Svetlichny and Hubareva, 2002; Svetlichny et al., 2000). Few studies, if any, have examined the effects of low oxygen conditions on ammonia, urea or phosphate excretion rates or on metabolic substrate use. One study on white shrimp (*Penaeus setiferus*) found that protein catabolism dominated at low oxygen, whereas substrate use switched to a combination of lipid and protein catabolism at higher oxygen levels (Rosas et al., 1999). Thus, low *in situ* oxygen concentrations have the potential to influence other metabolic parameters besides respiration rates, and changes in metabolic pathways could influence the composition of excreted by-products and, therefore, impact elemental cycling.

The eastern tropical north Pacific (ETNP) is the largest low oxygen oceanic biome (Paulmier and Ruiz-Pino, 2009). The ETNP is characterized by a strong, shallow pycnocline and a pronounced oxycline (Fiedler and Talley, 2006), where chlorophyll, primary production, and copepod maxima occur (Herman, 1989). Oxygen concentrations < 50 μM occur as shallow as 40 m and can reach values as low as 0.5 μM in the OMZ core (Brinton, 1979; Levin et al., 1991; Saltzman and Wishner, 1997a; Vinogradov et al., 1991). Studies examining the vertical distribution of organisms within

the ETNP have found that all taxa, from zooplankton to micro-nekton to benthic fauna, seem to have distinct layers of peak abundance often related to oxygen concentrations (e.g., Brinton, 1979; Sameoto, 1986; Wishner et al., 1995, 2013).

Members of the copepod family Eucalanidae are among the dominant zooplankton in this region and adult females have a broad depth distribution (Chen, 1986; Longhurst, 1985; Saltzman and Wishner, 1997b; Sameoto, 1986). The most abundant members of the group, *Subeucalanus subtenius* (formerly *Eucalanus subtenius* (Geletin, 1976)) and *Eucalanus inermis*, are consistently in the top 10–12 most abundant copepod species in this region. Recorded abundances are extremely variable, but these two species can each comprise 2% to more than 50% of the total copepod population in the region, and occur in densities of tens to several hundred individuals per cubic meter. *S. subtenius* females are found in highest abundance in the shallow euphotic zone, while *E. inermis* adult females have a vertical range which spans much of the upper 1000 m, with peaks in abundance near the chlorophyll maximum, the upper oxycline and the lower oxycline. This species is also present in small numbers throughout the core of the OMZ, where oxygen levels are nearly zero. It is thought that the presence of these females at depths below 200 m represent an ontogenetic migration (Wishner et al., 2013). Neither of these species has been reported to have diel vertical migration patterns in the ETNP. *Rhincalanus rostrifrons* is less abundant than *E. inermis* and *S. subtenius*. *R. rostrifrons* often occurs in densities of 5–10 individuals per cubic meter and has maximum abundances in the upper oxycline. The occurrence of diel vertical migration does not seem to be consistent for this species, but one study did report migration to deeper depths at night (modal depth change from 97 to 193 m) (Longhurst, 1985). Such differences in vertical distributions allow us to examine the metabolic response of closely related species, or even different life history stages, to low *in situ* oxygen concentrations in the open ocean. Members of this family occurring in other low-oxygen regions have a variety of responses to the presence of the OMZ, including avoidance, dormancy, reduced metabolic rates, and the presence of anaerobic pathways (e.g., Flint et al., 1991; Ohman et al., 1998; Teuber et al., 2013b; Wishner et al., 2008).

Distributions of microbial (Podlaska et al., 2012), microzooplankton (Olson and Daly, 2013), and zooplankton communities (Wishner et al., 2013) were previously reported for our study. In addition, the results of Maas et al. (2012) indicated that metabolic suppression occurred in the mesozooplankton pteropods, as an effect of low temperature and hypoxia. The goal of this study was to assess respiration and excretion rates of the eucalanoid copepods *S. subtenius*, *R. rostrifrons* and *E. inermis* in order to investigate the metabolic responses of these three closely related species to low oxygen concentrations in the ETNP OMZ system. To our knowledge, no metabolic rates have been previously measured for *R. rostrifrons*, and only oxygen consumption rates for *S. subtenius* from the Atlantic Ocean have been recently reported (Teuber et al., 2013a). Herein, we present results on oxygen consumption, and ammonium, phosphate, and urea excretion rates, as well as O:N, N:P, and O:P metabolic ratios. Measurements were obtained at high (100% saturation) and low (15–20% saturation) oxygen concentrations at representative temperatures for this study site, in order to compare baseline metabolic rates between these three species and assess their strategies to cope with a low oxygen environment.

2. Methods

2.1. Study area

Sample collection for this work occurred during two cruises to the eastern tropical north Pacific (ETNP) from 18 October to 17 November

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