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Ecological characteristics of eucalanoid copepods of the eastern tropical North Pacific Ocean: Adaptations for life within a low oxygen system

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ABSTRACT

The eastern tropical North Pacific Ocean (ETNP) is home to one of the largest and most severe mid-water oxygen minimum zones (OMZs). Members of the copepod family Eucalanidae are abundant in this region and display varied vertical distributions throughout the OMZ. This research assessed the diversity of ecological strategies used by these copepods to cope with the presence of the OMZ based on their biochemical, physiological, and behavioral characteristics. Five species of copepods (*Eucalanus inermis*, *Pareucalanus attenuatus*, *Rhincalanus nasutus*, *Rhincalanus rostrifrons*, and *Subeucalanus subtenuis*) were collected at the Costa Rica Dome (9°N, 90°W) and Tehuantepec Bowl (13°N, 105°W) during cruises in fall of 2007 and winter of 2008–2009. Adult females of all species were collected and analyzed for water, ash, carbon, nitrogen, hydrogen, phosphorus, protein and lipid content, lactate dehydrogenase (LDH) activity, and survivorship when exposed to prolonged low-oxygen conditions. Four distinct ecological strategies were observed for the five species based on genus. *E. inermis*, found throughout the OMZ and surface waters, had very high water content (94% of wet weight (WW)), leading to low organic content per unit WW. However, when corrected to ash-free dry weight (AFDW), protein and storage lipid contents of this species had intermediate (46 and 8% of AFDW, respectively) values compared to other species. *E. inermis* demonstrated high survivorship under low-oxygen conditions (>90%), and had detectable levels of LDH, indicating an ability to rely on anaerobic pathways. *Rhincalanus* spp., found primarily in the lower-oxygen subsurface waters, also had detectable LDH activity and high survivorship under low-oxygen conditions (>85%), but had much higher storage lipid levels (>37% of AFDW), very low protein levels (28–33% of AFDW), and low water content (87% of WW). *S. subtenuis* and *P. attenuatus* are both distributed primarily in surface waters, but showed distinct ecological strategies. *S. subtenuis* protein levels were very high (67% AFDW), storage lipid levels low (0%), and water content low (87% of WW). They also had very low survivorship under low-oxygen conditions (22%) and no detectable LDH activity. *P. attenuatus* also did not have detectable LDH activity or large lipid stores. *P. attenuatus*, however, had much lower protein content (30% AFDW) and higher water content (89% of WW), indicating a distinct ecological strategy. Comparisons of ETNP individuals with conspecifics or congeners from higher-oxygen environments suggest that low protein levels (indicative of lower overall activity) seen in some groups may be an adaptation for survival in lower-oxygen regions.

1. Introduction

The oceans are decreasing in oxygen in response to global warming, primarily through surface heating and increased stratification (Emerson et al., 2004; Keeling and Garcia, 2002). Additionally, regions of the ocean having oxygen minimum zones (OMZs), which are characterized by oxygen deficient waters at intermediate depths, appear to be expanding (Stramma et al., 2008, 2010). The suboxic regions in open water OMZs are typically maintained as a result of poor ventilation, sluggish circulation, oxygen-poor source waters, and decomposition of sinking particles (Wyrtki, 1962). Most tropical and subtropical regions in the Atlantic and western Pacific oceans have moderate OMZs, with minimum oxygen levels of 60 to 80 μM (Paulmier and Ruiz-Pino, 2009). One of the largest and most severe open water OMZs is located in the eastern tropical North Pacific (ETNP) (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 often reach <4.5 μM in the OMZ core (the region of lowest oxygen concentrations) (Brinton, 1979; Levin et al., 1991; Saltzman and Wishner, 1997b; Vinogradov et al., 1991). Some oxygen levels have been reported below 0.5 μM (Chen, 1986; Levin et al., 1991; Sameoto, 1986). The vertical oxygen gradients in OMZs structure biological assemblages and

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biogeochemical processes. As a result, habitats of organisms intolerant to low oxygen may be compressed into the shallow, near-surface oxygenated waters (Prince and Goodyear, 2006).

Members of the family Eucalanidae are dominant copepods in the ETNP, and include all four genera (*Rhincalanus*, *Eucalanus*, *Subeucalanus* and *Pareucalanus*) (Chen, 1986; Longhurst, 1985; Saltzman and Wishner, 1997a; Sameoto, 1986). Like many other zooplankters in the region, these copepods display a variety of vertical distributions that are likely related to the oxygen environment (Chen, 1986; Saltzman and Wishner, 1997a; Sameoto, 1986; Vinogradov et al., 1991). *Eucalanus inermis* (Giesbrecht, 1892), endemic to the ETNP, is found throughout the upper 1000 m, often with maximum concentrations in the chlorophyll maximum and the upper and lower edges of the OMZ core. *Subeucalanus subtenuis* (Giesbrecht, 1888), *Subeucalanus subcrassus* (Giesbrecht, 1888), *Subeucalanus pileatus* (Giesbrecht, 1888), and *Pareucalanus attenuatus* (Dana, 1849) are usually concentrated in the shallow euphotic zone. *Rhincalanus rostrifrons* (Dana, 1849) [sometimes referred to as *Rhincalanus cornutus rostrifrons* (Lang, 1965)] and *Rhincalanus nasutus* (Giesbrecht, 1888), on the other hand, are often absent from the surface mixed layer, and instead are concentrated above and below the OMZ core. This suggests that a variety of ecological strategies occur within this family in the ETNP region.

Even though eucalanoid copepods are abundant in the ETNP, little is known about their ecology. As severe OMZ regions appear to be expanding (Stramma et al., 2008, 2010), understanding the strategies employed by zooplankton in current OMZ systems may help us to predict the effects of decreasing oxygen on marine ecosystems in other regions of the ocean. Eucalanidae is a relatively small family of copepods (24 described species) that are distributed throughout a majority of the world's oceans and occur in coastal and open water systems (Bradford-Grieve et al., 1999; Goetze, 2003; Grice, 1962; Lang, 1965). The abundance of eucalanoid copepods in the ETNP system, coupled with their broad distribution in other regions, make them a useful group for comparative studies within and between ecosystems. These copepods also have been the focus of several recent genetic studies, which aimed to further describe separate lineages within species (Goetze, 2003, 2005, 2006, 2010; Goetze and Ohman, 2010). Consequently, their phylogeny is fairly well described, which provides a basis for understanding differences in ecological characteristics between species and populations within the family.

The primary objective of this study was to assess whether eucalanoid copepods employed different ecological strategies in the ETNP OMZ system based on their biochemical, physiological and behavioral characteristics. Based on published vertical distributions in this region (Chen, 1986; Saltzman and Wishner, 1997a; Sameoto, 1986; Vinogradov et al., 1991), it was hypothesized that *P. attenuatus* and *S. subtenuis* would have similar characteristics and strategies, and *R. nasutus* and *R. rostrifrons* would be similar to each other, whereas *E. inermis* would have different strategies relative to the other two groups. The results of our study were compared with findings for eucalanoid copepods in other regions of the world to assess whether the observed characteristics were adaptations to the OMZ system, or simply general features of a species or genus.

Additional attention was paid to *E. inermis*, which is one of the most abundant and widely vertically distributed copepods in this region (Chen, 1986; Longhurst, 1985; Saltzman and Wishner, 1997a; Wishner et al., 2013). Adult females occur in near-surface waters, but a large resident population also occurs in the upper and lower oxyclines and in the OMZ. Their occurrence at low oxygen depths may be due to an ontogenetic migration, possibly related to their reproductive cycle (Wishner et al., 2013). However, this hypothesis has not been well substantiated in the literature. We hoped to learn more about how individuals taking part in this migration may differ from conspecifics in shallower depths to better understand the role of such a migration within a tropical system. Also, differences in vertical distribution have been documented between adult males and females, with adult males often concentrated at shallower depths than females (Longhurst, 1985; K. Wishner, personal communication). Therefore, the ecological strategies of both males and females were examined.

2. Methods

2.1. Collection site and methods

Copepods were collected during two cruises to the eastern tropical North Pacific (ETNP) during 18 October–17 November 2007 aboard the R/V *Seward Johnson* and 8 December 2008–6 January 2009 aboard the R/V *Knorr*. Sampling occurred primarily at the Costa Rica Dome (9°N, 90°W) and to a lesser extent the Tehuantepec Bowl (13°N, 105°W) (Fig. 1). Copepods were collected using bongo tows, Tucker trawls, and MOCNESS (Multiple Opening/Closing Net and Environmental Sampling System) (Wiebe et al., 1976) tows at depths of high abundances. Adult female *S. subtenuis* and *P. attenuatus* were collected from the upper 50 m, while *R. rostrifrons* and *R. nasutus* were collected in the 200–300 m range. *E. inermis* adult females were collected at both shallow and deep depths and adult males collected in the upper 50 m. In addition, adult female *R. cornutus* were obtained during a cruise to the Gulf of Mexico (GOM) at a station offshore of Florida (27°N, 86°W) during June 25–29 2007 aboard the R/V *Suncoaster*. Adult female *R. nasutus* individuals also were collected from the Guaymas Basin, Gulf of California (GOC) (approximate location 27°N, 111°W) during June 4–12 2007 aboard the R/V *New Horizon*. These *R. cornutus* and *R. nasutus* were both collected using a Tucker trawl.

Immediately after capture, adult copepods were sorted and individuals of each species were separated into small containers containing 0.2 μm filtered seawater at in situ temperature. Copepods were kept at in situ temperatures for approximately 3–12 h to allow them to empty their guts. Once their guts were emptied, copepods collected in the ETNP were divided up for various analyses. Most individuals were frozen at −80 °C for later body content, enzyme, and weight analyses. Some individuals of *S. subtenuis*, *R. rostrifrons*, and *E. inermis* were used for metabolic end point incubation experiments (see Cass and Daly, 2014). All *Rhincalanus* spp. collected during the GOM and GOC cruises were frozen at sea, either in liquid nitrogen (GOM) or a −80 °C freezer (GOC).

2.2. Body composition

Subsets of individuals from each species were used for carbon/hydrogen/nitrogen (CHN) content analyses. Copepods were thawed,

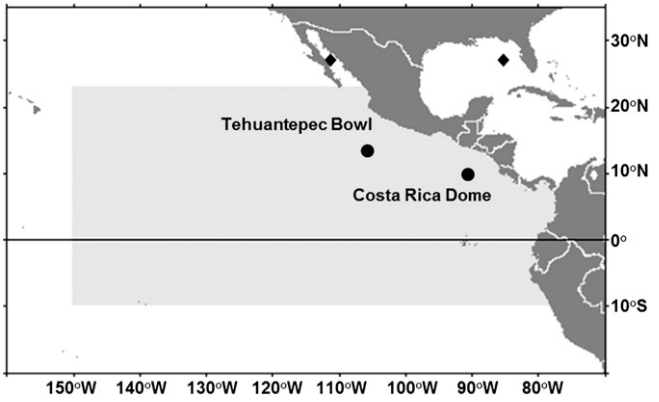

Fig. 1. Map of sampling sites. Black dots show the two main sampling regions, the Tehuantepec Bowl and Costa Rica Dome, in the eastern tropical North Pacific. Black diamonds show the Gulf of California and Gulf of Mexico sites. Gray area denotes the extent of the eastern tropical Pacific Ocean as designated by Fiedler and Lavín (2006). Map modified from SWFSC NOAA website (http://swfsc.noaa.gov/).