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Hypoxia effects on females and early stages of *Calanus chilensis* in the Humboldt Current ecosystem (23°S)

P.M. Ruz[a,b], P. Hidalgo[b,*], R. Escribano[b], J.E. Keister[c], L. Yebra[d], B. Franco-Cisterna[b,e]

[a] *Programa de Doctorado en Oceanografía, Departamento de Oceanografía, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile*

[b] *Instituto Milenio de Oceanografía and Departamento de Oceanografía, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, P.O. Box 160 C, Concepción, Chile*

[c] *School of Oceanography, University of Washington, Box 357940, Seattle, WA 98195, USA*

[d] *Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Puerto Pesquero s/n, 29640 Fuengirola, Málaga, Spain*

[e] *Programa de Magister en Oceanografía, Departamento de Oceanografía, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile*

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A B S T R A C T

Deoxygenation of the ocean has become a critical issue in coastal upwelling systems, which are subjected to shallow Oxygen Minimum Zones (OMZs). The OMZ can expand into the photic zone, causing hypoxic conditions and affecting pelagic organisms. During the winters 2013 and 2014, the copepod *Calanus chilensis* was collected off northern Chile to evaluate how oxygen conditions may affect its vital rates and to assess the physiological responses of developmental stages to oxygen. Adult females, eggs, and early nauplii (N1 to N3) were exposed to hypoxia (~32.6 μmol kg^{-1}, ~2.5 kPa) and normoxia (~252.2 μmol kg^{-1}, ~19.9 kPa) in the laboratory. Survival of females and their egg production were not affected by hypoxia. No significant differences in female somatic growth and potential respiration between hypoxic and normoxic conditions were found. Early stages, however, were strongly affected by hypoxia. Hatching success diminished by at least 29% from normoxia (72.3 ± 6.6% and 55.5 ± 3.7%) to hypoxia (22.9 ± 9.7% and 26.8 ± 6.8%). Naupliar growth was significantly lower under hypoxia (0.15 ± 0.02 d^{-1}) than normoxia (0.24 ± 0.01 d^{-1}). These findings suggest that expansion of OMZs in upwelling systems may substantially influence copepod dynamics by suppressing growth and survival of early life stages.

1. Introduction

Ocean deoxygenation has become a crucial issue in coastal upwelling systems. Global warming and eutrophication processes, caused by anthropogenic activity, are causing the spread of hypoxic and anoxic conditions in coastal and open oceans (Ekau et al., 2010; Keeling et al., 2010; Stramma et al., 2010). Expansion, intensification, and shoaling of Oxygen Minimum Zones (OMZs) is a main concern related to global warming because on the negative impacts on survival of some pelagic species, affecting the ecosystem structure, vertical fluxes, and productivity of Eastern Boundary Upwelling Systems (EBUS) (Ekau et al., 2010; Keeling et al., 2010; Seibel, 2011).

Oxygen availability is critical for the successful development of aerobic marine biota (Marcus et al., 2004) and plays a direct role in the biogeochemical cycling of nutrients (Feely et al., 2004); therefore, the capacity of organisms to avoid or to adapt to stressful oxygen conditions may be vital to promoting their continued success in a changing ocean. One of the major effects of the increasing hypoxia in OMZs is the compression of the oxygenated surface layer, where organisms tend to concentrate to avoid low oxygen conditions (Escribano et al., 2009; Hidalgo et al., 2010; Ekau et al., 2010; Teuber et al., 2013). The shoaling of OMZs diminishes the extent of the usable habitat of zooplankton (Manríquez et al., 2009), small-pelagic (Bertrand et al., 2010) and large size fishes such as billfishes and tunas that have been shown to decrease their diving depths, thus possibly increasing their exposure to overfishing because of their shallower distribution (Stramma et al., 2011).

The OMZs present in EBUS may be considered as natural laboratories to understand how organisms can deal with and inhabit oxygen-poor environments. The OMZs are mid-depth regions of the water column which contain low oxygen concentrations due to the natural decomposition of sinking organic material and aerobic respiration; they mostly occur in the eastern boundaries of the Pacific and Atlantic oceans (Wyrtki, 1962). Due to climate-related deoxygenation, the

* Corresponding author.
E-mail address: pahidalg@udec.cl (P. Hidalgo).

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hypoxic conditions of OMZs are intensifying and, consequently, expanding their distribution area at faster rates than the natural OMZ formation in the modern ocean (Keeling et al., 2010; Wang et al., 2015). Moreover, the intensification of upwelling-favorable winds due to global warming may even strengthen the shoaling of these low-oxygen layers, and thus vertically compress the normally oxygenated surface layer and affect zooplankton and fishes inhabiting these waters (Gilly et al., 2013). This in turn may change ecosystem structure, vertical fluxes, the biological pump, distribution, behavior, and metabolic rates of marine organisms, bentho-pelagic coupling, and fisheries (Levin, 2003; Paulmier et al., 2008; Ekau et al., 2010; Stramma et al., 2010; Seibel, 2011; Wishner et al., 2013).

OMZs have been described as effective barriers that restrict the vertical distribution of most zooplankton and benthic macrofauna (Wishner et al., 1995; Levin, 2003; Escribano et al., 2009), where only some species that perform diel or ontogenetic vertical migration can move into them (Hidalgo et al., 2005a, 2005b; Escribano et al., 2009; Wishner et al., 2013; Hirche et al., 2014). In epipelagic environments associated with an OMZ, the aggregation of zooplankton in waters just above the OMZ may also contribute to oxygen loss through enhanced respiration at the base of the oxycline (Donoso and Escribano, 2014). Non-vertically migrating zooplankton may be more limited in their ability to avoid hypoxia than vertically migrating species, increasing the chance that they are negatively affected by the vertical movements of the OMZ (Bakun, 1990; Rykaczewski and Checkley, 2008; Wang et al., 2015). Hidalgo et al. (2010) described that species diversity and richness are higher in oxygenated shallow waters than in deeper hypoxic waters. Therefore, the vertical intrusion of the OMZ into the surface layer may lead to natural mortality of species that inhabit shallow waters, like the copepods *Paracalanus* cf. *indicus* (Yáñez et al., 2012) and *Acartia tonsa* who decrease hatching success and female survival at concentrations < 0.9 mL O_2 L^{-1} (~1.3 mg O_2 L^{-1}, ~40.6 μmol kg^{-1}) (Ruz et al., 2015). Similar effects also have been reported for *A. tonsa* in environments dominated by seasonal bottom hypoxia (Richmond et al., 2006; Marcus et al., 2004). On the other hand, some species have developed metabolic adaptations (e.g. low aerobic or anabolic metabolism) to successfully inhabit or take refuge from predation inside the OMZ. Some copepods of the families Eucalanidae and Metridinidae (Hidalgo et al., 2005b; Auel and Verheye, 2007; Teuber et al., 2013) may be less affected by ocean deoxygenation if these adaptations occur in the early stages as well as adults.

The Mejillones Bay is one of the most important upwelling centers off northern Chile (Marín et al., 2001; Thiel et al., 2007) that is characterized by a shallow OMZ (≤ 26 m) as result of a semi-permanent upwelling regime (Pizarro et al., 1994; Morales et al., 1999; Sobarzo et al., 2007; Piñones et al., 2007; Thiel et al., 2007; Hidalgo and Escribano, 2008; Ruz et al., 2015). Dissolved oxygen (DO) often reaches very lower concentrations (< ~21.7 μmol kg^{-1}, ~0.71 mg O_2 L^{-1}, ~0.5 mL O_2 L^{-1}) or even total anoxia (Ulloa et al., 2012). In this zone, most of the copepod abundance and biomass are retained in well-oxygenated surface waters above the upper boundary of the OMZ, defined by the depth where the DO concentration is ~43.5 μmol kg^{-1} (~1.39 mg O_2 L^{-1}, ~1 mL O_2 L^{-1}) (Morales et al., 1999; Hidalgo et al., 2005b; Hidalgo and Escribano, 2008; Escribano et al., 2012; Ruz et al., 2015).

Copepods correspond to approximately 80% of zooplankton abundance in Mejillones Bay and have been considered a model group to evaluate changes in bio-oceanography, especially for their rapid response to changing conditions such as temperature, food quantity and quality, oxygen, changes in upwelling intensity and El Niño Southern Oscillation (Escribano and Hidalgo, 2000; Hidalgo and Escribano, 2001; Vargas et al., 2006; Hidalgo et al., 2010; Aguilera et al., 2011; Escribano et al., 2012, 2014). However, in EBUS like the Humboldt Current System (HCS), early life stages (including eggs) have rarely been studied to evaluate population changes in abundance, growth and distributions (Torres and Escribano, 2003; Hidalgo et al., 2005a; Vargas et al., 2006; Hidalgo and Escribano, 2007, 2008; Ruz et al., 2015, 2017). Early stages are a key component for zooplankton dynamics and production, especially in areas where hypoxia can be a selective force for the zooplankton of coastal waters (Dam, 2013). Understanding how copepods and their early stages may cope with oxygen-deficient water seems highly relevant to comprehend how their populations respond to a changing ocean.

The ontogenetic development of copepods includes shifts in swimming speed and nutritional demands; therefore, metabolism and growth rate are stage-specific and play a relevant role in the depths inhabited by copepods (Mauchline, 1998; Hidalgo et al., 2005b; Hidalgo and Escribano, 2008). Among the copepod community in the HCS, *Calanus chilensis* Brodsky 1959 is one of the dominant species (Hidalgo et al., 2010; Escribano et al., 2012). *C. chilensis* exhibits continuous reproduction year-round (Hidalgo and Escribano, 2008; Ruz et al., 2015), and seems to be vertically restricted by the shallow OMZ to the well-oxygenated surface layer (50 m depth), with few individuals entering hypoxic waters (Escribano et al., 2009). However, recent evidence shows that later life stages of *C. chilensis* may be able to inhabit the OMZ off southern Peru (Hirche et al., 2014), and that adult females off northern Chile (23°S) are able to tolerate short-term exposure to hypoxia (Ruz et al., 2015). This suggests that *C. chilensis* may be a suitable species to assess the effect of hypoxia associated with the OMZ, and the potential effects of low-oxygen conditions through the species' ontogeny.

The main goal of this research was to determine whether survival and stage-specific vital rates of the copepod *C. chilensis* are affected by low oxygen concentrations associated with the OMZ. We hypothesized that low oxygen conditions would limit the metabolism of *C. chilensis* and that responses to hypoxia would be stage-specific, reflected in a potential reduction of metabolic and survival rates. Thus low oxygen may affect population dynamics of *C. chilensis* within a scenario of expansion and intensification of the OMZ in northern Chile.

2. Methods

2.1. Sampling

Experiments on female metabolism, egg production rate (EPR), egg hatching success, naupliar growth, and naupliar development rate of the copepod *C. chilensis* were conducted from zooplankton collected at Station 3 (23° 00.2′ S, 70° 28.2′ W; maximum depth = 120 m) in Mejillones Bay during austral winters 2013 and 2014. Station 3 corresponds to the outermost station along a coast to ocean transect of the Antofagasta Zooplankton Time Series Program conducted by the University of Concepción (Fig. 1 in Escribano et al., 2012).

Prior to each zooplankton sampling, a CTD-O (Conductivity, Temperature, Depth and DO) Seabird 19 plus and a YSI EXO2 multiparameter sonde (C, T and DO) were deployed to 90 m depth, to assess the depth of the upper boundary of the OMZ; profiles were immediately visualized onboard from the YSI EXO2 multiparameter data. Once the oxygen profile was analyzed, seawater for experiments was collected from the oxygenated layer (for normoxic treatments) at ~10 m depth and from inside the OMZ (for hypoxic treatments) at ~60 m depth using a 10 L Niskin Bottle to try to maintain chemical characteristics, temperature, and salinity of in situ seawater. A summary of the in situ field conditions is included as supplementary material. Zooplankton were collected by gentle oblique trawls with a WP-2 net (200 μm mesh size) within the oxygenated upper layer. Once onboard, live zooplankton was kept in an insulated cooler diluted with surface seawater and transported to the laboratory within 2 h.

Copepods and media were stored in a cold room at 14 °C, which is the typical mean in situ temperature of the ~30 m layer during non-El Niño years (Ruz et al., 2015). Within the first 2 h after returning to the laboratory, healthy ovigerous females of *C. chilensis* were carefully picked from the live samples under a stereoscopic microscope. Groups