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Egg production and hatching success of *Calanus chilensis* and *Acartia tonsa* in the northern Chile upwelling zone (23°S), Humboldt Current System

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ABSTRACT

Oxygen Minimum Zones (OMZ's) are expanding and intensifying as result of climate change, affecting Eastern Boundary Upwelling Systems. Local effects of vertical movements of OMZ's that result from changes in upwelling intensity could reduce or expand the oxygenated surface layer that most zooplanktonic species inhabit in coastal areas. Using the copepods *Calanus chilensis* and *Acartia tonsa* as model organisms, an experimental test of the impact of different dissolved oxygen (DO) concentrations (between 0.5 and 5 ml L^{-1}) on egg production and hatching success was carried out and compared with field estimations of egg production, female and egg abundance in Mejillones Bay (23°S). Abundance of *C. chilensis* was highly variability and no consistent pattern in egg production and hatching success was found across DO levels, whereas *A. tonsa* egg production had maximum values between 2.6 and 4.7 ml O_2 L^{-1} and hatching success was positively correlated with DO ($r = 0.75$). In the field, temperature was the main factor controlling the dynamics of both species, while Chl-*a* and DO were also correlated with *C. chilensis* and *A. tonsa*, respectively. Principal Component Analysis showed that abundances of both copepods were controlled by temperature, stratification, OMZ depth, and Ekman transport, which together explained more than 70% of the total variance and were the main factors that modulated the populations of *C. chilensis* and *A. tonsa* in the upwelling zone of northern Chile (23°S). The differential responses of *C. chilensis* and *A. tonsa* to changes in DO concentrations associated with vertical movements of the OMZ suggest that *C. chilensis* may be better adapted to hypoxic conditions than *A. tonsa*, however both species are successful and persistent all year-round. We suggest that physiological responses of copepods could be used to evaluate population dynamics affected by the shoaling of OMZ's and the repercussions to trophic food webs of eastern boundary current systems.

1. Introduction

Nowadays, one of the main focuses of study in marine sciences is to understand how climate change affects the chemistry, physics and biology of the ocean. As a result, we known that chemical transformations occur in the ocean, principally acidification, deoxygenation, and expansion of Oxygen Minimum Zones (OMZ's) (Keeling et al., 2010; Pelejero et al., 2010). Physical conditions in the oceans that are affected by climate change include an increase in stratification due to the warming of the ocean surface (Bograd et al., 2008; Richardson, 2008) and favorable intensification of upwelling winds at eastern boundary currents, which cools coastal areas and shoals the low oxygen water of OMZ's (Bakun, 1990; Rykaczewski and Checkley, 2008). The changes in the ocean biology could be expressed as a consequence of the physicochemistry shifts of the ocean, where plankton distribution, abundance, and phenology are important aspects of the ecosystems that can be used to understand and quantify ecological changes caused by CO_2-induced climate change (Hays et al., 2005).

The Humboldt Current System (HCS) in northern Chile has high biological productivity throughout the year. This production is driven by frequent upwelling events, which cause shoaling of the oxygen poor Equatorial Subsurface Water (ESSW) that forms the OMZ in the South Eastern Pacific, resulting in low levels of dissolved oxygen (<0.5 ml L^{-1}) near the surface (Escribano, 1998; Mann and Lazier,

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Abbreviations: HCS, Humboldt Current System; DO, dissolved oxygen; OMZ, Oxygen Minimum Zone; EPR, Egg Production Rate; EPR_{exp}, Experimental Egg Production Rate; HS, Hatching Success.

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1991; Morales et al., 1999). The upper boundary of the OMZ is defined as the depth with dissolved oxygen (DO) concentrations of 1 ml L^{-1}, which in this area, is normally close to surface waters (<50 m) (Fuenzalida et al., 2009; Hidalgo et al., 2005; Morales et al., 1999). Below these depths, the dissolved oxygen concentration decreases markedly to very low values (<0.1 ml L^{-1}) and even to the total absence of oxygen (Ulloa et al., 2012). The upper boundary of the OMZ acts as a physical–chemical barrier to vertical distribution of most aerobic planktonic organisms in the water column (Hidalgo and Escribano, 2001; Morales et al., 1999). The OMZ is considered an Oxygen-Deficient Ecological Barrier (BEDOX) that concentrates the abundance, biomass and diversity of plankton into the oxygenated and food-rich surface water within the photic zone (Donoso and Escribano, 2014), promoting more efficient carbon flux through pelagic food webs due to higher overlap of primary production, grazers, and predators (Escribano et al., 2009; Hidalgo and Escribano, 2001; Hidalgo et al., 2010; Manríquez et al., 2009), either by direct herbivory or a heterotrophic pathway (Vargas et al., 2007).

Copepods constitute about 80% of the zooplankton biomass in the HCS (Escribano and Hidalgo, 2000; Escribano et al., 2007; Hidalgo and Escribano, 2001). About 118 species have been identified in this system; the calanoid copepods *Acartia tonsa*, *Calanus chilensis*, *Centropages brachiatus* and *Paracalanus cf. indicus* are the most abundant species (Hidalgo and Escribano, 2001; Hidalgo et al., 2010). Production and growth rates of copepods in the HCS show high temporal and spatial variability and are controlled by temperature (Escribano et al., 1998), food quality and quantity (Poulet et al., 2007; Torres and Escribano, 2003; Vargas et al., 2006), advection (Escribano, 1998), and upwelling intensity (Escribano et al., 2012). Previous studies in other systems have shown that hypoxic conditions could negatively affect *A. tonsa* egg production, hatching success and survival (Marcus et al., 2004; Richmond et al., 2006) while other copepods and their different developmental stages, like *Calanoides carinatus*, are able to tolerate low DO concentrations (Auel and Verheye, 2007). Understanding how copepod growth and reproduction respond to stress and environmental variability would greatly improve our understanding of how populations and ecosystems function (Runge and Roff, 2000).

The Antofagasta Peninsula and Mejillones Bay are characterized by cold and oxygen-poor subsurface waters due to semi-permanent upwelling throughout the year (Marín and Olivares, 1999) and an upper boundary of the OMZ located on average at 26 m depth (Hidalgo et al., 2005). In this area, year-round copepod reproduction indicates they may not be limited by food availability; the main factors affecting their life cycles and distribution are changes in temperature and DO associated with upwelling intensity (Escribano et al., 1998, 2012; Hidalgo and Escribano, 2008; Hidalgo et al., 2010). However, direct effects of the vertical displacement of the OMZ on the abundance and production rates of different copepod species remain unknown. Also, no direct measurements of the effect of different DO concentrations on production, and specifically, on copepod egg production and egg viability, are available in the HCS.

The main goal of this study was to determine whether vital rates of dominant copepods in the HCS are affected by DO concentrations that occur in the field. Vertical movements of the OMZ that result from changes in upwelling intensity could reduce or expand the oxygenated surface layer that most copepods inhabit, especially in areas where upwelling intensity and the OMZ's extension is increasing due to climate change. We hypothesize that these vertical movements would expose the copepods to lower oxygen conditions than necessary for their physiological requirements, and therefore reduce production and growth rates. To evaluate this hypothesis, several oxygen-controlled experiments were conducted to test the Egg Production Rates (EPR) and hatching success (HS) of *C. chilensis* and *A. tonsa* during spring and summer 2010. The laboratory results were complemented with a one-year time series of monthly *in situ* abundances of females and eggs, *in situ* egg production rates, and oceanographic parameters.

2. Materials and methods

2.1. Field studies

In order to study the temporal and spatial variability of zooplankton in the coastal upwelling zone of Mejillones Bay (23°S), we conducted monthly hydrographic surveys, net tows and Niskin samples during 2010. Three stations located along a coast-to-ocean transect were sampled monthly from January to December (St-1: 23° 04.2′ S, 70° 25.8′ W, station depth (z_{max}) = 60 m; St-2: 23° 02.4′ S, 70° 27.0′ W, z_{max} = 90 m; and St-3: 23° 00.2′ S, 70° 28.2′ W, z_{max} = 120 m) (Fig. 1). At each station, an autonomous oceanographic profiler CTD-O SeaBird 19 was used to obtain conductivity, temperature, density, and DO measurements.

To assess zooplankton abundance and composition, samples were obtained at each station using vertical hauls of a WP-2 net (57 cm ring diameter and 200 μm mesh) equipped with a flowmeter. The vertical hauls were conducted from 30 m to surface to ensure sampling of the upper boundary of the OMZ layer, which has been shown to have an average depth of 26 m (Hidalgo et al., 2005). Zooplankton samples were preserved in 4% buffered formalin solution for later composition analysis.

Water samples at 10 m depth were collected with a Niskin bottle (10 L) to obtain microplankton samples to estimate copepod egg abundance and Chlorophyll-*a* (Chl-*a*). This depth was chosen based on studies that showed that the Chl-*a* maximum is typically located above 15 m depth (Iriarte et al., 2000) and that changes in copepod egg abundance between 10 and 15 m is a good index of overall changes in eggs throughout the water column due to the presence of very low oxygen waters below those depths (Hidalgo and Escribano, 2007, 2008). Approximately 9.6 L of the sample was 20-μm sieved to collect microplankton samples that were preserved in 2% buffered formalin solution for later composition analysis. Chl-*a* was determined by filtering 200 ml subsamples onto GF/F filters (0.7 μm pore diameter) and analyzing by the fluorometric method (Anabalón et al., 2014; Holm-Hansen et al., 1965).

2.2. Oceanographic data

To assess the relationship between upwelling intensity and the vertical distribution of the OMZ, upwelling was estimated from Ekman transport using the equation described by Mann and Lazier (1991):

$$M_x = \tau_y / f$$

where, M_x is Ekman transport ($m^3\ s^{-1}\ km^{-1}$), f is the Coriolis parameter, and τ_y is the along-shore wind stress (Pa). M_x is positive for south winds (upwelling) and negative for north winds (downwelling), and Tau (τ) was estimated as:

$$\tau_y = \rho_a * C_d * (V_y|V_y|)$$

where, ρ_a correspond to air density (1.21 kg m^{-3}), C_d is the empirical constant known as drag coefficient (=0.0014) and V_y represents the along-shore wind velocity (m s^{-1}). Daily wind data were taken from the Meteorological Station of Cerro Moreno (latitude–longitude: 23° 27′ S–70° 26′ W) maintained by the Dirección Meteorológica de Chile (http://164.77.222.61/climatologia/).

Water column stratification was estimated from density profiles obtained with the CTD-O as the geopotential energy anomaly (ϕ_{50}) (J m^{-3}) described by Bowden (1983) and applied in the HCS (Hidalgo and Escribano, 2007, 2008; Torres et al., 2002):

$$\phi_{50} = 1/H\int_{-H}^{0}(\rho_m - \rho)gz\ dz$$

where, ρ_m is the mean density of the water column, ρ is the density at a given depth z, g is acceleration due to gravity, and H = 50 m. The