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Research Article

Diel vertical migration of *Nannocalanus minor* and *Eucalanus inermis* (Copepoda: Calanoidea) associated with the oxygen minimum zone in northern Chile

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ABSTRACT. The semi-permanent coastal upwelling system within the Humboldt Current System (HCS) off northern Chile provides nutrient-rich, oxygen-poor water to the euphotic zone that contributes to high levels of primary production and restricts the vertical distribution of most zooplankton species according to their tolerance to hypoxia within this highly heterogeneous environment. The day/night vertical distributions of two calanoid copepods, *Eucalanus inermis* and *Nannocalanus minor*, were studied concerning the presence of oxygen-poor water associated with the Oxygen minimum zone (OMZ) at a coastal and an offshore station off northern Chile (~20°S), by stratified sampling from the surface to a depth of 600 m. At the coastal station, most of the population of both species remained above the OMZ, whereas at the offshore station, most populations remained at the edge of the OMZ. Both species exhibited reverse diel vertical migration between day and night and were positively correlated with dissolved oxygen and chlorophyll-a, suggesting that both species may prefer oxygenated waters and avoid the OMZ. However, *E. inermis* and *N. minor* exhibited distinct behavior, with *E. inermis* displaying significant variations among stations and strata and *N. minor* showing differences only among strata, particularly in the upper strata where it was more aggregated. The results helped us understand the behavior and distribution of zooplankton related to OMZ and how they may change as ocean temperature increases worldwide.

Keywords: copepods; diel vertical migration; oxygen minimum zone; Humboldt Current System

INTRODUCTION

The Humboldt Current System (HCS), a major Eastern Boundary Upwelling System (EBUS) located off the southeastern Pacific coasts (5-42°S), sustains high levels of fish production. The HCS has been recognized as the most productive EBUS (Chávez et al. 2008), with a total fishery landing of 7.8 million tons in 2019 (FAO 2022). This major ecosystem is associated with the presence of Equatorial Subsurface Water (ESSW), characterized by low dissolved Oxygen (DO) concentrations (<44.6 µmol L^{-1} yr^{-1}) that form the oxygen minimum zone (OMZ), which can even reach anoxic conditions (Morales et al. 1999, Ulloa et al. 2012).

The ESSW originates at 200-500 m in depth, rising to 10 m or shallower as it approaches the coast, owing to offshore Ekman transport of surface water driven by southwesterly winds along the coast (Hidalgo et al.

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2005a, Thiel et al. 2007, Ruz et al. 2017). These upwelling events favour the ascent of nutrient-rich, oxygen-poor water from the OMZ to the surface layer (Fuenzalida et al. 2009, Jacob et al. 2011), coupled with the irregular coastline topography, generates local upwelling centers such as bays, which favor the retention of nutrients that enhance primary productivity (PP) (Daneri et al. 2000, Escribano et al. 2012). As a result, these areas serve as vital habitats for the reproduction, growth, and development of zooplankton in neritic waters (Escribano 1998, Hidalgo & Escribano 2001, Escribano et al. 2009).

Upwelling events occur year-round in northern Chile with higher intensity during the spring-summer period, which promotes nutrition intrusion into the photic zone (Morales et al. 1999), sustain high levels of PP (~3000 mg m^{-2} d^{-1}, Iriarte et al. 2007), and contribute to oxygen depletion in subsurface waters by zooplankton respiration and degradation of organic matter sedimented out from the surface (Donoso & Escribano 2014). Wind-driven advection transports nutrients and plankton from the coast to the open ocean (Marín et al. 2001), which plays an important role in zooplankton population dynamics in the well-oxygenated offshore waters (Escribano et al. 2007, 2009, 2012).

The OMZ can be a challenging environment for most aerobic species. Only a few species are adapted (e.g. metabolic suppression and resting stages) to these hypoxic waters throughout their complete life cycle or just parts of it (Hidalgo et al. 2005a, Escribano et al. 2009, Seibel 2010, Wishner et al. 2018, 2020). Consequently, most zooplankton associated with OMZ environments avoid low-oxygen conditions and aggregate in highly oxygenated surface waters. Their higher diversity and abundance substantiate this behavior (Escribano et al. 2009, Paulmier & Ruiz-Pino 2009, Wishner et al. 2013, 2018). Zooplankton abundance decreases significantly at depths with less than 44.6 µM O_2, where the OMZ is located (Ruz-Moreno et al. 2023). A succession of taxa adapted to hypoxic conditions can be found within this environment, resulting in lower species richness, abundance of zooplankton, and higher trophic levels (Wishner et al. 2013, Donoso & Escribano 2014). Below the OMZ, these community structure parameters increase along with the gradual increment of DO in the lower oxycline, indicating that metabolic constraints directly influence the community structure and population parameters of zooplankton due to hypoxia and other physical and biogeochemical parameters in OMZ environments (Paulmier & Ruiz-Pino 2009, Wishner et al. 2018, 2020).

The chitinous zooplankton community structure off northern Chile (18-28°S) has been previously studied by various authors, ranging from shallow waters (30 m) to a depth of 400 m (Hidalgo & Escribano 2001, Escribano et al. 2009, Hidalgo et al. 2010). Among the dominant zooplankton species, Calanoid copepods such as *Acartia tonsa*, *Calanus chilensis*, *Centropages brachiatus*, *Eucalanus inermis*, and *Paracalanus* cf. *indicus* maintain their permanency and abundance throughout the year (Hidalgo & Escribano 2008, Escribano et al. 2009). Most studies on the biology and ecology of zooplankton in the HCS have been focusing on coastal waters, resulting in a gap in our understanding of the taxonomy, diversity, and ecological patterns (e.g. Diel vertical migration; DVM) of zooplankton in offshore waters and how they may be affected by the OMZ.

In the OMZ, it is common to find abundant and large zooplankton species. These include calanoid copepods such as *Eucalanus attenuatus* and *E. inermis*, as well as the euphausiid *Euphausia mucronata*, all of which show DVM throughout the OMZ. In contrast, certain calanoid species, such as *Aetideus bradyi*, *C. chilensis*, and *P. cf. indicu*s, do not enter the OMZ (Escribano et al. 2009).

It has been shown that zooplankton communities respond to changes in temperature, seasonal upwelling intensity, and interannual fluctuations by shifting dominance, abundance, diversity, and species richness (Hidalgo & Escribano 2007, 2008, Escribano et al. 2009, 2012, Hugget et al. 2009, Hidalgo et al. 2010, 2012). Additionally, some studies have shown that environmental features directly affect the ontogeny development of certain calanoid species such as *E. inermis* (Hidalgo et al. 2005a,b, Criales-Hernández et al. 2007, Wishner et al. 2020), *C. chilensis*, and *A. tonsa* and their growth rates (Torres & Escribano 2003, Ruz et al. 2015, 2017, Ruz-Moreno et al. 2023). The vertical zonation of zooplankton has allowed for the description and understanding of the response of the copepod community off the coastal zone of Chile.

The present study focused on the calanoid species *E. inermis* and *Nannocalanus minor*, widely distributed in the Pacific Ocean (Ashjian & Wishner 1993). These copepods exhibit DVM, with *E. inermis* covering distances of 500 m and *N. minor* up to 150 m within the water column. It is well documented that *E. inermis* can enter diapause in low-oxygen water, especially in female adults and late copepodite stages (Hidalgo et al. 2005a, Wishner et al. 2020). In contrast, *N. minor* is typically associated with well-oxygenated waters (Saltzman & Wishner 1997). *E. inermis* has been found at as deep as 1000 m, but it is primarily distributed between 100 and 600 m depth, overlapping the OMZ (Hidalgo et al. 2005a,b, Jackson & Smith 2016, Wishner et al. 2018). Meanwhile, the mid-sized *N. minor* inhabit the upper 300 m depth, gathering around the chlorophyll-a (Chl-*a*) peaks along warmer isotherms. These species can also respond rapidly when primary productivity increases, producing over five generations year-round (Ashjian & Wishner 1993, Saltzman & Wishner 1997).

This research compared the DVM patterns of two important species in the HCS, spanning a depth range of 600 m. The research was conducted during the Lowphox I expedition from the spring to summer of 2015. We hypothesized that the diel vertical distribution differs between *N. minor* and *E. inermis*, which reflects how they spread out and use the habitat differently throughout the OMZ.

MATERIALS AND METHODS

Study area

During late spring (November) and early summer (December) 2015, onboard the AGS-61 Cabo de Hornos, the Lowphox I expedition of the Instituto Milenio de Oceanografía (IMO, www.imo-chile.cl) was carried out off the coast of Iquique in northern Chile. Two stations were sampled in two consecutive day/night periods: the coastal station T3 (20°07'S - 70°25'W) was located 15 nm from the coast with a maximum depth of approximately 1000 m; the offshore station T5 (20°05'S, 70°53'W) was 43 nm from the coast with a maximum depth of 2800 m (Fig. 1). At each station, water temperature (T), salinity (S), DO, and fluorescence (Chl-*a*) were recorded using a CTD-rosette Seabird SBE-25.

Zooplankton sampling

Zooplankton samples were obtained using a Multiple Plankton Sampler net (Multinet Midi TYPE, Hydro-Bios) equipped with an integrated flowmeter and five nets with a mesh size of 200 µm, with pre-programmed closure on board before deployment. The five strata were defined based on the objectives of this study about the bathymetry of the stations, setting the maximum sampling depth at 600 m: 600-400, 400-150, 150-90, 90-30, and 30-0 m. On board, the zooplankton samples were preserved in 10% formalin immediately after arrival on deck.

Taxonomy analysis

Under a stereomicroscope, copepod species *N. minor* (range of size for females:1.45-2.45 mm, and males: 1.17-2.06 mm) and *E. inermis* (range of size for females: 5.53-6.65 mm, and males: 4.30-5.50 mm) were meticulously identified and counted according to standard methods (Bradford-Grieve et al. 1999, Razouls et al. 2018). The abundance was expressed as individuals per cubic meter (ind m^{-3}). Only the late copepodite stage (C5) and adults were considered in this study to avoid potential biases resulting from misidentification of juvenile stages.

Data analysis

The potential density (kg m^{-3}) was derived from *in situ* T and S using Ocean Data View 4 (ODV) software to identify the mixed layer (ML) as proposed by Griffies et al. (2016), which considers a threshold concentration of 0.03 kg m^{-3} difference from the surface. According to the oxygen vertical profile, three strata were categorized: i) the oxycline located at depths with a gradient of >2.05 µM m^{-1} (~2.1 µM m^{-1}; Paulmier & Ruiz-Pino 2009) above the OMZ; ii) the OMZ defined by concentrations <43.6 µM m^{-1} (1 mL L^{-1}, Ruz et al. 2017) and its core with DO concentrations ca. 1.8 µmol L^{-1} (~0.04 mL L^{-1}, Wishner et al. 2013); and iii) the lower oxycline (LO) with increasing DO gradient below the OMZ.

A single parameter was calculated for the abundance of each species to represent the population center of gravity (centroid) over the water column following the equation used by Hidalgo et al. (2005b) and Ruz et al. (2017; Eq. 2). These values were correlated with the environmental variables considered in this study.

Pycnoclines were utilized to identify water masses, following the classification method proposed by Blanco et al. (2001) for waters off northern Chile. Water masses were identified using T-S diagrams generated in ODV software, using *in situ* water temperature and salinity. Differences in abundance among stations (T3 and T5), strata (600-400, 400-150, 150-90, 90-30, 30-0 m), sampling period (day-night), and water masses (Subtropical Water (STW), Equatorial Subsurface Water (ESSW), and Antarctic Water) were tested using ANOSIM performed in PRIMER 6 statistical software. Bray-Curtis dissimilarity analysis was used to quantify species composition dissimilarity between strata. Linear regression analysis was used to test the linear relationships between abundances and in situ environmental parameters per stratum using Minitab16 statistical software.

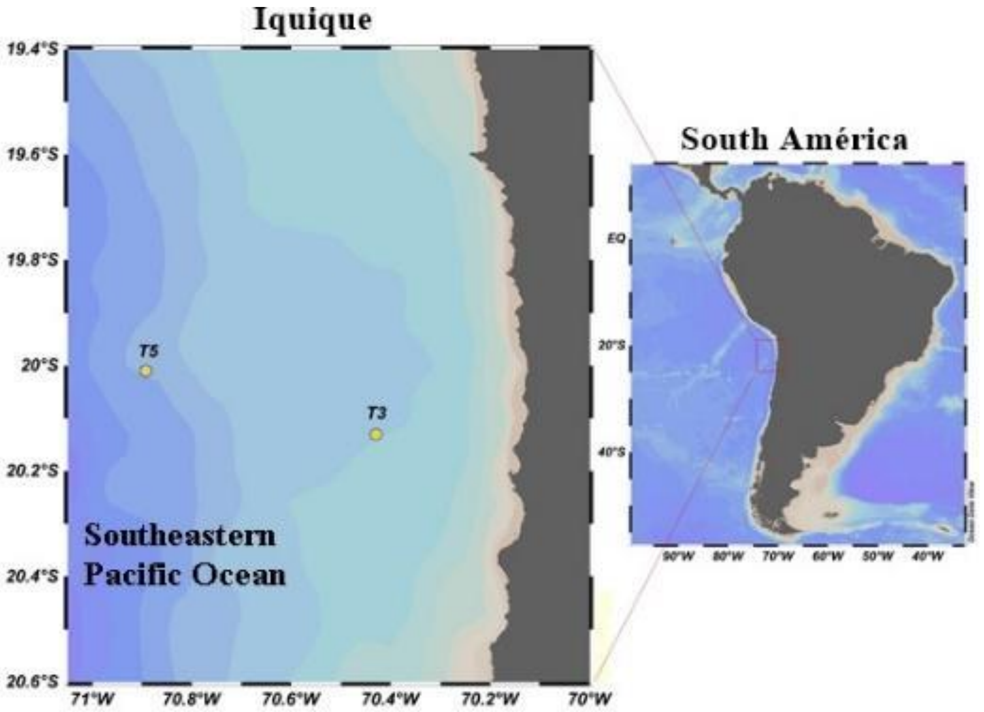

Figure 1. Map of the study area in northern Chile during the Lowphox I expedition in November - December 2015. Yellow circles represent sampling stations.

RESULTS

Oceanographic conditions

The average seawater temperature during the sampling period was 11.65 ± 2.94°C (range 6.87-21.30°C) (Figs. 2a, 3a). The mean salinity was 34.79 ± 0.18 (range 34.48 - 35.38) (Figs. 2b, 3b). The mixed layer was at 14 m at the coastal station (24.74 kg m^{-3}) and at 9 m at the offshore station (24.73 kg m^{-3}) (Figs. 2b, 3b). The identified water masses were STW, Subantarctic Water (SAAW), ESSW, and Antarctic Intermediate Water (AAIW). The surface layer was filled mainly by a mixture of the three water masses STW, SAAW, and ESSW, whereas the intermediate and bottom layers were filled mainly by ESSW mixed with AAIW and SAAW (Fig. 4).

The DO in the mixed layer averaged 248.54 ± 0.749 µM (range 247.64-250.25 µM) at the coastal station, and a slightly lower DO mean value 242.10 ± 1.28 µM; (range 240.72-243.62 µM) occurred offshore. Principal disparities in the oxygen profiles between coastal and offshore stations were observed at the oxycline. At the coastal station, the oxycline was between 15 and 32 m, above the OMZ (60 m) (Fig. 2c). In contrast, at the offshore station, the oxycline extended into the OMZ (43.76 µM O$_2$ at 67 m) until it reached 82 m (Fig. 3c), also reflected by its shallower slope of the oxycline than at the coastal station (Fig. 5). Below the oxycline and within the OMZ, similar DO concentrations occurred with a mean value of 8.34 ± 10.73 µM (range 1.77-43.6 µM), with its core maintaining a mean concentration of 2.09 ± 0.12 µM (range 1.77-2.37 µM). The lower oxycline started at 442 m depth with a mean DO value of 22.60 ± 14.55 µM (range 1.93-52.99 µM).

The Chl-*a* concentration averaged 0.62 ± 0.98 mg m^{-3} (range 4.58-0.03 mg m^{-3}) between the surface and 144 m, including the mixed layer and the upper oxycline. Below this depth, the Chl-*a* concentration was negligible (Figs. 2d, 3d). At the coastal station, the maximum Chl-*a* concentration was recorded at 16 m (3.48 mg m^{-3}), which is slightly below the ML (Fig. 2d). In the offshore station, the primary Chl-*a* maximum occurred at 20 m (4.58 mg m^{-3}), and a secondary Chl-*a* peak was observed at 48 m (1.12 mg Chl-*a* m^{-3}), coincident with a DO level of 106.38 µM above the beginning of the OMZ (Fig. 3d).

Species patterns and dial vertical migration

The total abundance of *E. inermis* was 49.10 ind m^{-3} at station T3 and 10.72 ind m^{-3} at station T5. The total abundance of *N. minor* was 42.35 and 14.45 ind m^{-3} at T3 and T5, respectively. Both species were more

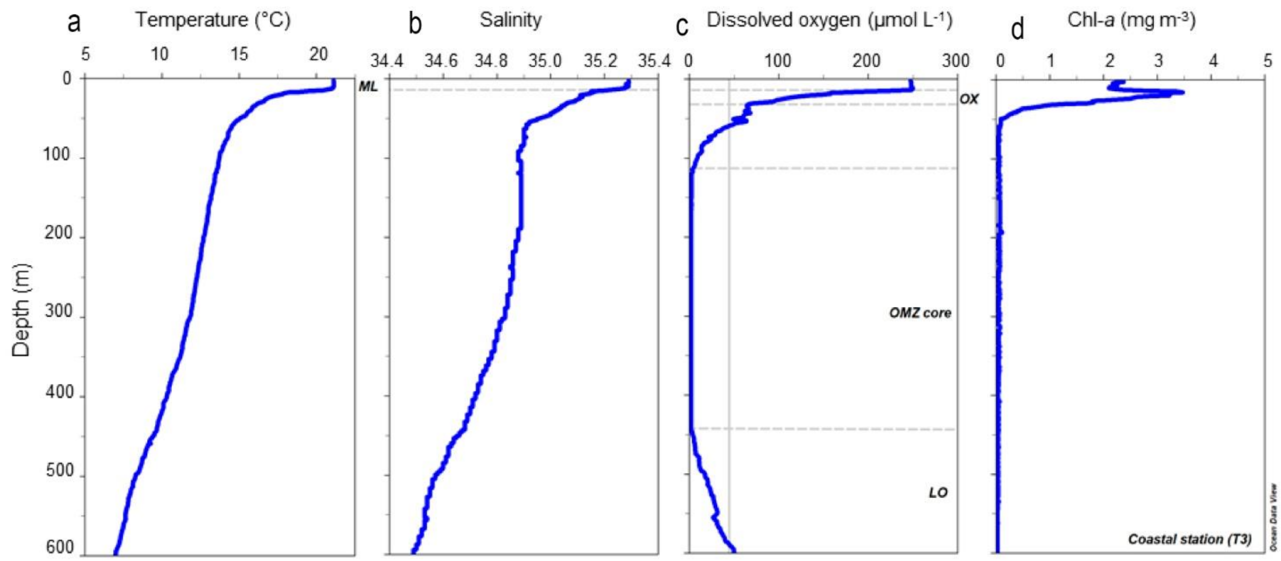

Figure 2. Vertical profiles of a) temperature (°C), b) salinity, c) dissolved oxygen (µmol L^{-1}), including the boundary oxygen concentration of the oxygen minimum zone (OMZ, indicated by the vertical gray solid line at 44.6 µM), and the DO strata: oxycline (OX), the core of the OMZ (OMZ core; ≤4.0 µM, indicated by a grey dashed line), followed by the lower oxycline (LO); and d) chlorophyll-a (Chl-*a*; mg m^{-3}) at coastal station T3 during the Lowphox I expedition. The mixed layer (ML) is shown in panel b and c (grey dashed line).

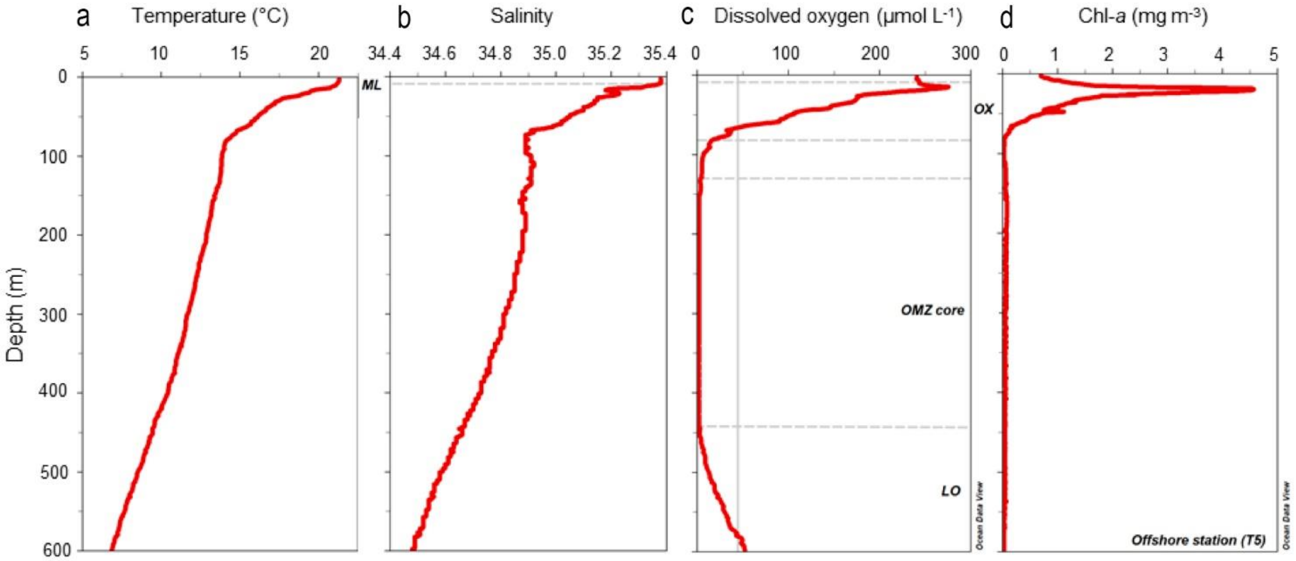

Figure 3. Vertical profiles of a) temperature (°C), b) salinity, c) dissolved oxygen (µmol L^{-1}), including the boundary oxygen concentration of the oxygen minimum zone (OMZ, indicated by the vertical gray solid line at 44.6 µM), and the DO strata: oxycline (OX), the core of the OMZ (OMZ core; ≤4.0 µM, indicated by a grey dashed line), followed by the lower oxycline (LO); and d) chlorophyll-a (Chl-*a*; mg m^{-3}) at coastal station T5 during the Lowphox I expedition. The mixed layer (ML) is shown in panel b and c (grey dashed line).

abundant in the surface layers of coastal waters than in offshore waters (Table 1, Fig. 6).

Significant variations in the abundance of *E. inermis* were observed in terms of spatial distribution, strata, and water masses, although no discernible differences were noted between day and night. The species exhibited higher abundances within the oxycline than the OMZ, with a slight increase in the lower oxycline

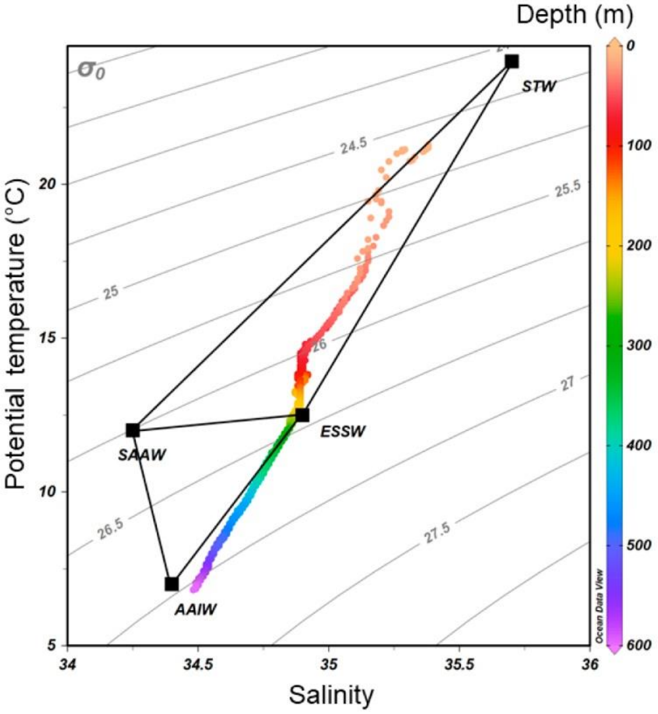

Figure 4. T-S diagrams describing the water masses present off Iquique at stations T3 and T5. STW: Subtropical Water, SAAW: Subantarctic Water, and ESSW: Equatorial Subsurface Water.

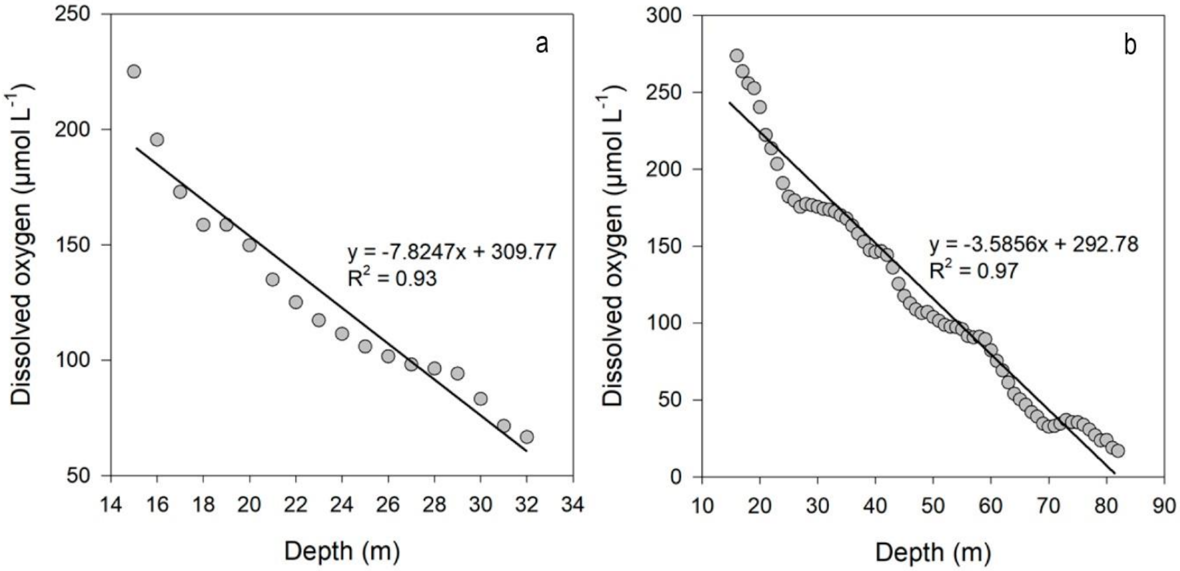

Figure 5. Linear regression analysis for the first layer of the upper oxycline at each station: a) coastal station T3, where the depths ranged between 15 to 32 m; and b) offshore station T5, where the depths ranged from 15 to 82 m.

(Figs. 6a-b). The abundance of *E. inermis* were significantly different between stations (ANOSIM, R = 0.09, *P* <0.01), depth strata (ANOSIM, R = 0.24, *P* < 0.01) and water mass (ANOSIM, R = 0.20, *P* < 0.01) but not between day and night. The main differences in abundances among strata were observed between the ML (30 - 0 m) and the OMZ (400 - 150 m) (Pairwise, ML-OMZ, R = 0.65 *P* < 0.01). The differences among water masses were given between STW and ESSW (Pairwise, R = 0.39 *P* < 0.01). In the other hand, *N. minor* abundances were significantly different among depth strata (ANOSIM, R = 0.40, *P* < 0.01) and water

Table 1. Oceanographic variables (mean ± standard deviation) were measured at stations T3 and T5 during the Lowphox I expedition and averaged from the day and night profiles. The mid-depths of each sampling stratum are indicated in parentheses.

Stratum (m)	Temperature (°C)		Salinity		Oxygen (µM)		Chl-*a* (mg m^{-3})	
	T3	T5	T3	T5	T3	T5	T3	T5
30-0 (15)	19.10 ± 1.95	19.70 ± 1.35	35.19 ± 0.08	35.26 ± 0.09	186.19 ± 65.60	228.55 ± 32.41	2.45 ± 0.50	2.14 ± 1.29
90-30 (60)	14.79 ± 0.72	15.47 ± 1.08	34.94 ± 0.06	35.00 ± 0.09	24.42 ± 19.91	78.96 ± 53.23	0.20 ± 0.27	0.51 ± 0.46
150-90 (120)	13.49 ± 0.20	13.14 ± 0.15	34.89 ± 0.00	34.90 ± 0.05	5.21 ± 3.53	5.72 ± 2.49	0.06 ± 0.01	0.05 ± 0.01
400-150 (275)	11.92 ± 0.80	11.98 ± 0.86	34.81 ± 0.05	34.83 ± 0.05	2.06 ± 0.12	2.01 ± 0.12	0.06 ± 0.01	0.06 ± 0.01
600-400 (500)	8.48 ± 1.00	8.56 ± 1.02	34.59 ± 0.07	34.59 ± 0.07	18.50 ± 14.64	18.22 ± 16.21	0.04 ± 0.01	0.04 ± 0.01

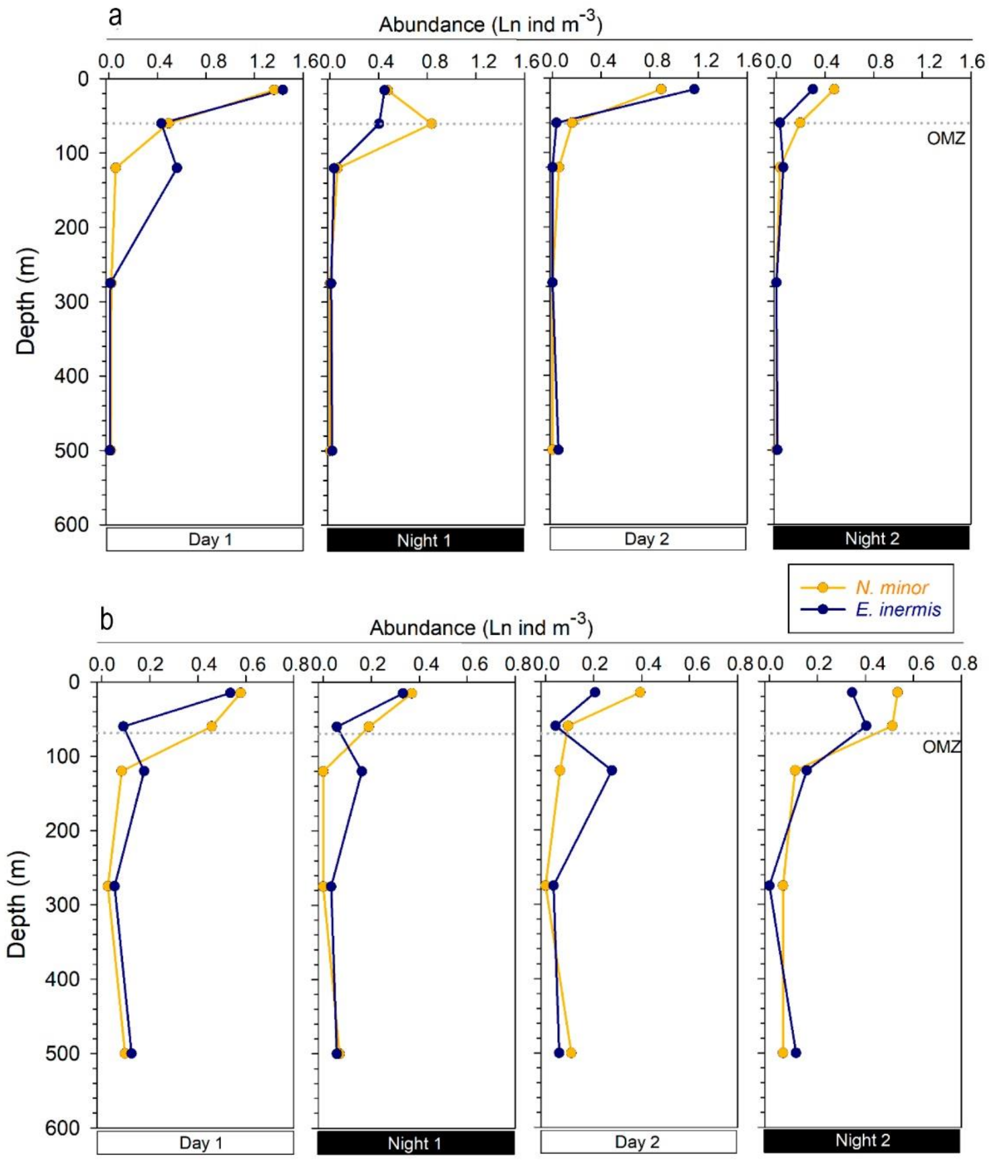

Figure 6. Day and night vertical distribution abundances for the copepods *Nannocalanus minor* and *Eucalanus inermis* at a) coastal station T3 and b) offshore station T5. The upper boundary of the Oxygen minimum zone (OMZ, indicated by the gray dotted line at 44.6 µM) was followed by the OMZ. The abundances were plotted at the mid-depth of each sampling stratum, as indicated in Table 1.

masses (ANOSIM, R = 0.37, $P < 0.01$). The differences within strata were given between the ML, UO (90-30 m) and the OMZ (Pairwise, ML-OMZ, R = 0.84 $P < 0.01$; UO-OMZ, R = 0.74 $P < 0.01$). The main differences between water masses were detected also between STW and ESSW (Pairwise, R = 0.63 $P < 0.01$).

The abundance of *E. inermis* was significantly associated with the oceanographic variables included in this study. The highest positive association were with DO ($R^2 = 0.65$, $P < 0.001$) and salinity ($R^2 = 0.64$, $P < 0.001$), followed by temperature ($R^2 = 0.63$, $P < 0.001$).

The abundance of *N. minor* significantly differed among the depth strata and water masses but not between stations or day/night periods. Variations within strata were observed, especially between the shallowest strata (30-0 and 90-30 m) and the OMZ, suggesting that *N. minor* predominantly resides in oxygenated waters above the OMZ (Table 2). The exception was the second night sampled, where the population centroid was recorded at 90.51 m. (Table 3). The abundance of *N. minor* was positively associated with temperature ($R^2 = 0.79$, $P < 0.001$) and DO ($R^2 = 0.81$, $P < 0.001$), followed by salinity ($R^2 = 0.78$, $P < 0.001$), indicating that this species aggregated in oxygenated waters above the OMZ. This species showed a strong negative regression with water density ($R^2 = -0.72$, $P < 0.001$) and was more aggregated within the STW.

Throughout most of the sampling period, both species displayed a pattern of ascending to shallower waters near the surface during the day and descending to deeper waters at night, indicating reverse DVM, except for the second day at the offshore station. Higher copepod abundance and homogeneous distribution between each stratum were found at the offshore station, where both species showed deeper distributions than in coastal waters (Figs. 7a-b). *E. inermis* and *N. minor* presented higher abundances outside the OMZ at both stations. *E. inermis* showed a vertical movement towards deeper waters than *N. minor*, especially at the offshore station (Fig. 7b).

E. inermis remained without major changes in its distribution during the sampling period except for the second night, when a slight descending movement toward the second stratum was observed (Fig. 6b). On the other hand, *N. minor* was absent from the OMZ during the first sampling night. However, it was present in the entire water column (0-600 m) during the second day, especially within the OMZ. During the second night of sampling, *N. minor* went up towards the oxycline (Figs. 7a-b).

Adult populations of *E. inermis* and *N. minor* predominantly inhabited the upper strata (0-90 m), especially at the coastal station closer to the continental shelf (15 nm). Both species exhibited a slight downward trend during the first night. However, during the nighttime, these calanoid species were situated approximately 20 m deeper than during the daytime at the same coastal station (Figs. 7a-b). Conversely, at station T5, both species were found at nearly the same depth during the initial sampling period (day and night). According to the centroids, both populations barely shifted during the first sampling period (day and night) (Fig. 7b). However, on the second night, they migrated to depths below 90 m (Fig. 7b). This observation suggests that, as the OMZ deepened at the offshore station, the population centroid also moved deeper. In contrast, at the coastal station where the OMZ was shallower, the population centroid showed minimal movement within the oxycline (Figs. 7a-b).

DISCUSSION

Our results suggest that despite the biology of each species, *E. inermis* and *N. minor* were mostly restricted to well-oxygenated waters above the OMZ, with a more restricted distribution in *N. minor* than in *E. inermis*.

E. inermis is a highly abundant species found in the eastern south and northern Pacific (Hidalgo et al. 2005b, Jackson & Smith 2016), where it appears to be more abundant above 90 m depth. Its behavior includes a DVM from depths close to 200 to 60 m in the ML (Hidalgo et al. 2005a, Escribano et al. 2009). Although different abundances of *E. inermis* were observed in association with the DO gradient, this species was distributed throughout the water column but with higher abundances in well-oxygenated waters. In contrast with previous studies in the Arabian Sea, this species was concentrated in poorly oxygenated waters, surpassing the OMZ (Wishner et al. 2013), which is more consistent with its population centroid at the offshore station in this study (Fig. 7b).

N. minor is mostly found within the well-oxygenated surface waters in the north Pacific (Saltzman & Wishner 1997), which is consistent with our observations, where large copepodites (C5) and the adult fraction of *N. minor* was mostly found between 20 and 60 m depth. Although *N. minor* is mainly restricted to the upper layers, this species has been found to inhabit the OMZ with higher abundances than other related calanoids in the Arabian Sea, such as *Rhincalanus cornutus*, *Paraeucalanus attenuatus*, and

Table 2. Numerical and relative abundances of *Eucalanus inermis* and *Nannocalanus minor* at stations T3 and T5 during the Lowphox I expedition. The data are presented by station, period, and strata. This period corresponds to the time of day (D1 and D2) or night (N1 and N2) when the samples were collected.

			E. inermis		*N. minor*	
Station	Period	Stratum (m)	Abundance (ind m^{-3})	Relative abundance (%)	Abundance (ind m^{-3})	Relative abundance (%)
T3	D1	30-0	26.08	85.56	21.96	90.41
		90-30	1.71	5.61	2.10	8.65
		150-90	2.64	8.66	0.14	0.58
		400-150	0.03	0.10	0.05	0.21
		600-400	0.02	0.07	0.04	0.16
	N1	30-0	1.81	52.01	1.98	24.81
		90-30	1.53	43.97	5.85	73.31
		150-90	0.08	2.30	0.15	1.88
		400-150	0.02	0.57	0.00	0.00
		600-400	0.04	1.15	0.00	0.00
	D2	30-0	13.71	98.56	6.86	92.20
		90-30	0.08	0.58	0.45	6.05
		150-90	0.00	0.00	0.13	1.75
		400-150	0.00	0.00	0.00	0.00
		600-400	0.12	0.86	0.00	0.00
	N2	30-0	1.00	81.30	2.00	75.76
		90-30	0.07	5.69	0.57	21.59
		150-90	0.14	11.38	0.07	2.65
		400-150	0.00	0.00	0.00	0.00
		600-400	0.02	1.63	0.00	0.00
T5	D1	30-0	2.43	67.13	2.79	53.86
		90-30	0.23	6.35	1.87	36.10
		150-90	0.50	13.81	0.21	4.05
		400-150	0.13	3.59	0.06	1.16
		600-400	0.33	9.12	0.25	4.83
	N1	30-0	1.15	58.67	1.34	65.05
		90-30	0.14	7.14	0.55	26.70
		150-90	0.45	22.96	0.00	0.00
		400-150	0.08	4.08	0.00	0.00
		600-400	0.14	7.14	0.17	8.25
	D2	30-0	0.61	33.52	1.48	68.84
		90-30	0.10	5.49	0.24	11.16
		150-90	0.89	48.90	0.15	6.98
		400-150	0.08	4.40	0.00	0.00
		600-400	0.14	7.69	0.28	13.02
	N2	30-0	1.21	34.97	2.42	46.27
		90-30	1.53	44.22	2.25	43.02
		150-90	0.43	12.43	0.28	5.35
		400-150	0.00	0.00	0.14	2.68
		600-400	0.29	8.38	0.14	2.68

Haloptilus chierchiae, which are strictly associated with more oxygenated waters of the photic zone (Wishner et al. 2013). Similarly, off northern Chile, a few individuals of *N. minor* were found in the OMZ, mainly during the nighttime at the offshore station, and like most zooplankton associated with OMZ areas, *E. inermis* and *N. minor* tended to avoid the low oxygen concentrations in the core of the OMZ (Hidalgo et al. 2005a, 2009, Wishner et al. 2013).

Table 3. Centroids of *Eucalanus inermis* and *Nannocalanus minor* at coastal (T3) and offshore (T5) stations during two consecutive sampling of day (D1 and D2) and night (N1 and N2) periods.

Sampling	Coastal station		Offshore station	
	E. inermis	*N. minor*	*E. inermis*	*N. minor*
D1	27.19	20.83	85.91	61.92
N1	44.27	49.96	87.58	67.04
D2	19.44	19.56	117.55	90.51
D2	37.40	27.50	88.60	59.92

Both species were located near the surface at the offshore station (T5), which could be related to the high concentrations of Chl-*a* in the oxygen-rich water (Saltzman & Wishner 1997, Escribano et al. 2009). None of the calanoids in the present study were prominently present in the OMZ according to their DVM, contrary to previous findings (Hidalgo et al. 2005a, Escribano et al. 2009), evidencing that *E. inermis* may display a wide range of DVM and also inhabit the OMZ core and that *N. minor* also can be found in both rich and poor-oxygenated waters. The results suggest that the OMZ conditioned the developmental stages studied because both species increased their vertical distribution range when the oxycline was less steep, and consequently, the OMZ was deeper.

Other related species of the Eucalanidae, such as *Subecalanus subtenuis*, *Paraeucalanus attenuatus*, and *Rhincalanus* sp. of the eastern tropical north Pacific Ocean, have different ecological strategies. They avoid the OMZ core and stay in oxygenated water at ca. 100 m depth, so they do not suppress their metabolism as *E. inermis* does, allowing them to stay within the OMZ at ca. 400-450 m depth (Jackson & Smith 2016). The low abundance of *E. inermis* could be related to seasonal patterns because this species is associated with high Chl-*a* peaks (Saltzman & Wishner 1997) in the cold than the warm periods in austral regions (Hidalgo & Escribano 2001). The abundance of *E. inermis* might have been different in a different scenario because this species is associated with intense upwelling in coastal waters in northern Chile's late spring and early summer (Hidalgo et al. 2005b).

By occupying the mid-depth, *E. inermis* could move rapidly to the ML, where there was more available DO and nutrients. This species also seemed to remain at similar depths, as indicated by previous reports (Hidalgo et al. 2005a, Jackson & Smith 2016). When *E. inermis* moves towards the ML, carrying nutrients from depth strata, phytoplankton can take these nutrients in the photic zone and eventually return to the food web. Likewise, zooplanktonic communities in hypoxic strata could also benefit from this organic matter input (Hidalgo et al. 2005a, Ekau et al. 2010), which has great ecological implications.

N. minor is prevalent off Peru and is considered as abundant as its congener, *Calanus chilensis*, perhaps because of similar environmental requirements (Hirche et al. 2014). Other studies on zooplankton communities have demonstrated that different copepod species associate with different water masses (Smoot & Hopcroft 2016).

This study shows that there is a negative correlation between temperature and the abundance of *N. minor*, this can be interpreted as the species' association with lower density and warmer waters such as STW. Nevertheless, the water masses had a different vertical distribution according to the depth strata, which was not a key factor determining the DVM of copepods because each stratum's isopycnals seemed similar. In the Lowphox I expedition, other environmental variables, such as current flow, wind intensity, or nitrite concentration, are not considered but might influence these copepods' distribution and DVM patterns.

Our findings suggest four migration patterns: 1) there was a clear DVM between strata, especially in the ML and upper oxycline; 2) both species seemed to avoid the OMZ when the oxycline was steeper, especially *N. minor*, despite a few incursions into the OMZ at station T5; 3) *N. minor* seemed to be associated with STW because of its high correlation with low-density water; and 4) both species showed reverse DVM, except during the second day at station T5, where the two species moved downwards and *E. inermis* was closer to the upper limit of the OMZ, which seemed to be a common behavior in calanoids (Wishner et al. 2018).

In a different scenario, with stronger upwelling and constant input of colder waters (Rykaczewski et al. 2015), *N. minor* would have had a higher abundance due to its affinity to upwelling environments, contrary to the austral oceanic waters in central-southern Chile, where conditions are more oligotrophic (Morales et al. 2010). Although the OMZ is a physical threshold for zooplankton, it can also provide shelter to certain species adapted to these conditions. Different community compositions at different vertical ranges may significantly affect the trophic dynamics of the ecosystem (Ekau et al. 2010, Wishner et al. 2020).

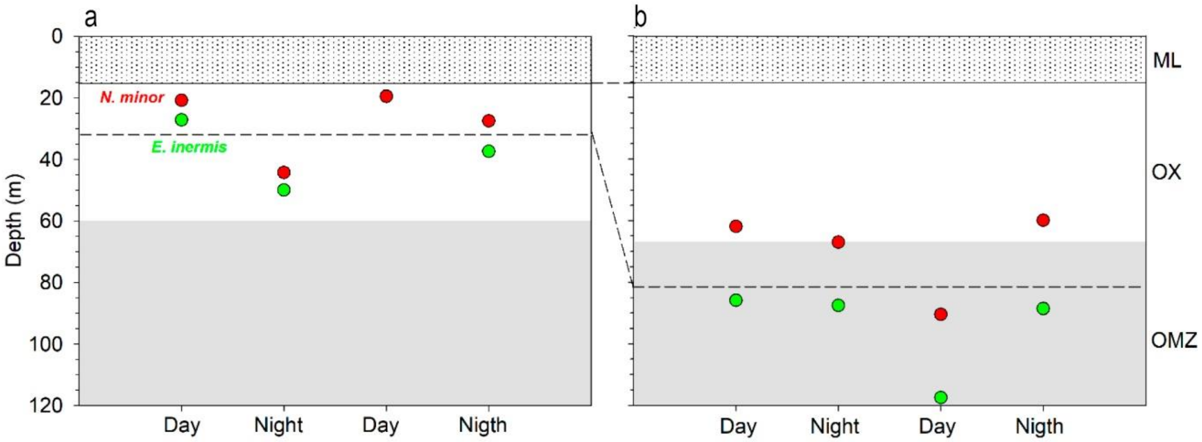

Figure 7. Diel vertical migration patterns are denoted by the centroid of the population of *Eucalanus inermis* (green dots) and *Nannocalanus minor* (red dots) for a) the coastal station (T3) and b) the offshore station (T5), during two consecutive days and nights. ML: mixed layer, OX: oxycline, and OMZ: oxygen minimum zone.

Additional observations, including an extended sampling period and more sampling stations, could provide information about oceanographic features that have played crucial roles in uncovering other key factors driving different zooplankton behaviors related to the OMZ.

It should be noted that studies of this nature hold promise for predicting the behavior and distribution of zooplankton under a global climate change scenario as mean sea temperature increases. Nevertheless, it is essential to recognize that copepods and their ecological zones, defined by oxygen concentrations, do not strictly adhere to predefined rules (Criales-Hernández 2007). Therefore, it is imperative to collaborate in diverse coastal and oceanic environments better to understand the dynamics of zooplankton communities in upwelling ecosystems.

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REFERENCES

Ashjian, C.J. & Wishner, K.F. 1993. Temporal and spatial changes in body size and reproductive state of *Nannocalanus minor* (Copepoda) females across and along the Gulf Stream. Journal of Plankton Research, 15: 67-98. doi: 10.1093/plankt/15.1.67

Blanco, J.L., Thomas, A.C., Carr, M.E. & Strubb, P.T. 2001. Seasonal climatology of hydrographic conditions in the upwelling region off northern Chile. Journal of Geophysical Research, 106: 11451-11467. doi: 10.1029/2000JC000540

Bradford-Grieve, J., Markhaseva, E., Rocha, C. & Abiahy, B. 1999. South Atlantic zooplankton. Backhuys Publisher, Leiden, pp. 869-1098.

Chávez, F.P., Bertrand, A., Guevara-Carrasco, R., Soler, P. & Csirke, J. 2008. The northern Humboldt Current System: Brief history, present status and a view towards the future. Progress in Oceanography, 79: 95-105. doi: 10.1016/j.pocean.2008.10.012

Criales-Hernández, M., Schwomborn, I.R., Graco, M., Ayón, P., Hirche, J.H. & Wolff, M. 2007. Zooplankton vertical distribution and migration off Central Peru in relation to the oxygen minimum layer. Helgoland Marine Research, 62: 85-100. doi: 10.1007/s10152-007-0094-3

Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P. & Ulloa, O. 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. Marine

Ecology Progress Series, 197: 41-49. doi: 10.3354/meps197041

Donoso, K. & Escribano, R. 2014. Mass-specific respiration of mesozooplankton and its role in the maintenance of an oxygen-deficient ecological barrier (BEDOX) in the upwelling zone off Chile upon presence of a shallow oxygen minimum zone. Journal of Marine Systems, 129: 166-177. doi: 10.1016/j.jmarsys.2013.05.011

Ekau, W., Auel, H., Pörtner, H.O. & Gilbert, D. 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates, and fish). Biogeosciences, 7: 1669-1699. doi: 10.5194/bg-7-1669-2010

Escribano, R. 1998. Population dynamics of *Calanus chilensis* in the Chilean Eastern Boundary Humboldt Current. Fisheries Oceanography, 7: 245-251. doi: 10.1046/j.1365-2419.1998.00078.x

Escribano, R., Hidalgo, P. & Krautz, C. 2009. Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000. Deep-Sea Research, 56: 1083-1094. doi: 10.1016/j.dsr2.2008.09.009

Escribano, R., Hidalgo, P., Fuentes, M. & Donoso, K. 2012. Zooplankton time series in the coastal zone off Chile: Variation in upwelling and responses of the copepod community. Progress in Oceanography, 97-100: 174-186. doi: 10.1016/j.pocean.2011.11.006

Escribano, R., Hidalgo, P., González, H., Gieseke, R., Riquelme-Bugueño, R. & Manríquez, K. 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Progress in Oceanography, 75: 470-485. doi: 10.1016/j.pocean.2007.08.027

Fuenzalida, R., Schneider, W., Garcés-Vargas, J., Bravo, L. & Lange, C. 2009. Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. Deep-Sea Research II, 56: 1027-1038. doi: 10.1016/j.dsr2.2008.11.001

Griffies, S.M., Danabasoglu, G., Durack, P.J., Adcroft, A.J., Balaji, V., Böning, C.W., et al. 2016. OMIP contribution to CMIP6: experimental and diagnostic protocol for the physical component of the Ocean Model Intercomparison Project. Geoscientific Model Development, 9: 3231-3296. doi: 10.5194/gmd-9-3231-2016, 2016

Hidalgo, P. & Escribano, R. 2001. Succession of pelagic copepod species in coastal waters off northern Chile: the influence of the 1997-98 El Niño. Hidrobiología, 453-454: 153-160. doi: 10.1023/A:1013188522222

Hidalgo, P. & Escribano, R. 2007. The coupling of life cycles of the copepods *Calanus chilensis* and *Centropages brachiatus* to upwelling variability in the central-south upwelling region off Chile. Progress in Oceanography, 75: 501-517. doi: 10.1016/j.pocean.2007.08.028

Hidalgo, P. & Escribano, R. 2008. The life cycles of two coexisting copepods, *Calanus chilensis* and *Centropages brachiatus*, in the upwelling zone off northern Chile (23ºS). Marine Biology, 155: 429-442. doi: 10.1007/s00227-008-1041-9

Hidalgo, P., Escribano, R. & Morales, C.E. 2005a. Annual life cycle of the copepod *Eucalanus inermis* at a coastal upwelling site off Mejillones (23°S), northern Chile. Marine Biology, 146: 995-1003. doi: 10.1007/s00227-004-1487-3

Hidalgo, P., Escribano, R. & Morales, C.E. 2005b. Ontogenetic vertical distribution and diel migration of the copepod *Eucalanus inermis* in the oxygen minimum zone off northern Chile (20-21°S). Journal of Plankton Research, 45: 519-529. doi: 10.1093/plankt/fbi025

Hidalgo, P., Escribano, R., Fuentes, M., Jorquera, E. & Vergara, O. 2012. How coastal upwelling influences spatial patterns of size-structured diversity of copepods off central-southern Chile (summer 2009). Progress in Oceanography, 92-95: 134-145. doi: 10.1016/j.pocean.2011.07.012

Hidalgo, P., Escribano, R., Vergara, O., Jorquera, E., Donoso, K. & Mendoza, P. 2010. Patterns of copepod diversity in the Chilean coastal upwelling system. Deep-Sea Research II, 57: 2089-2097. doi: 10.1016/j.dsr2.2010.09.012

Hirche, H.J., Barz, K., Ayon, P. & Schulz, J. 2014. High-resolution vertical distribution of the copepod *Calanus chilensis* in relation to the shallow oxygen minimum zone off northern Peru using LOKI, a new plankton imaging system. Deep-Sea Research Part I: Oceanographic Research Papers, 88: 63-73. doi: 10.1016/j.dsr.2014.03.001

Iriarte, J.L., González, H.E., Liu, K.K., Rivas, C. & Valenzuela, C. 2007. Spatial and temporal variability of chlorophyll and primary productivity in surface waters of southern Chile (41.5-43°S). Estuarine, Coastal and Shelf Science, 74: 471-480. doi: 10.1016/j.ecss.2007.05.015

Jackson, M.L. & Smith, S.L. 2016. Vertical distribution of Eucalanoid copepods within the Costa Rica Dome area of the Eastern Tropical Pacific. Journal of Plankton Research, 38: 305-316. doi: 10.1093/plankt/fbv117

Jacob, B., Daneri, G., Quiñones, R.A. & Sobarzo, M. 2011. Community metabolism, phytoplankton size structure and heterotrophic prokaryote production in a highly productive upwelling zone off northern Chile. Ecology Letters, 430: 23-34. doi: 10.3354/meps09074

Marín, V.H., Escribano, R., Delgado, L.E., Olivares, G. & Hidalgo, P. 2001. Nearshore circulation in a coastal upwelling site off the Northern Humboldt current system. Continental Shelf Research, 21: 1317-1329. doi: 10.1016/S0278-4343(01)00022-X

Morales, C.E., Hormazábal, S.E. & Blanco, J.L. 1999. Interannual variability in the mesoscale distribution of the depth of the upper boundary of the oxygen minimum layer off northern Chile (18-24°S): Implications for the pelagic system and biogeochemical cycling. Journal of Marine Research, 57: 909-932. doi: 10.1357/002224099321514097

Morales, C.E., Torreblanca, M.L., Hormazabal, S., Correa-Ramírez, M., Núñez, S. & Hidalgo, P. 2010. Mesoscale structure of copepod assemblages in the coastal transition zone and oceanic waters off central-southern Chile. Progress in Oceanography, 84: 158-173. doi: 10.1016/j.pocean.2009.12.001

Paulmier, A. & Ruiz-Pino, D. 2009. Oxygen minimum zones (OMZs) in the modern ocean. Progress in Oceanography, 80: 113-128. doi: 10.1016/j.pocean.2008.08.001

Razouls, C., De Bovée, F., Kouwenberg, J. & Desreumaux, N. 2018. Diversity and geographic distribution of marine planktonic copepods. [http://copepodes.obs-banyuls.fr/en]. Reviewed: August, 9, 2015.

Ruz, P.M., Hidalgo, P., Riquelme-Bugueño, R., Franco-Cisterna, B. & Cornejo, M. 2017. Vertical distribution of copepod eggs in the oxygen minimum zone off Mejillones Bay (23°S) in the Humboldt Current System. Marine Ecology Progress Series, 571: 83-96. doi: 10.3354/meps12117

Ruz, P.M., Hidalgo, P., Yáñez, S., Escribano, R. & Keister, J.E. 2015. Egg production and hatching success of *Calanus chilensis* and *Acartia tonsa* in the northern Chile upwelling zone (23°S), Humboldt Current System. Journal of Marine Systems, 148: 200-212. doi: 10.1016/j.jmarsys.2015.03.007

Ruz-Moreno, P.M., Hidalgo, P., Cornejo-D'Ottone, M., Fierro-González, P., Babbonney, J. & Tank, K.W. 2023. Potential effects of shoaling of oxygen minimum zone on the population of *Acartia* (*Acanthacartia*) *tonsa* in the Humboldt Current Upwelling System (23°S). Journal of Sea Research, 193: 102372. doi: 10.1016/j.seares.2023.102372

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Rykaczewski, R.R., Dunne, J.P., Sydeman, W.J., García-Reyes, M., Black, B.A. & Bograd, S.J. 2015. Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. Geophysical Research Letters, 42: 6424-6431. doi: 10.1002/2015GL064694

Saltzman, J. & Wishner, K.F. 1997. Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 2. Vertical distribution of copepods. Deep-Sea Research I, 44: 931-954. doi: 10.1016/S0967-0637(97)00007-1

Seibel, B.A. 2010. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. Journal of Experimental Biology, 214: 326-336. doi: 10.1242/jeb.049171

Smoot, C.A. & Hopcroft, R.R. 2016. Depth-stratified community structure of Beaufort Sea slope zooplankton and its relations to water masses. Journal of Plankton Research, 39: 79-91. doi: 10.1093/plankt/fbw087

Thiel, M., Macaya, E.C., Acuña, E., Arntz, W.E., Bastias, H., Brokordt, K., et al. 2007. The Humboldt Current System of northern and central Chile. Oceanographic processes, ecological interactions and socioeconomic feedback. Oceanography and Marine Biology - An Annual Review, 45: 195-344. doi: 10.1201/9781420050943.ch6

Torres, C.G. & Escribano, R. 2003. Growth and development of *Calanus chilensis* nauplii reared under laboratory conditions: testing the effects of temperature and food resources. Journal of Experimental Marine Biology and Ecology, 294: 81-99. doi: 10.1016/S0022-0981(03)00261-2

Ulloa, O., Canfield, D.E., DeLong, E.F., Letellier, R.M. & Steward, F.J. 2012. Microbial oceanography of anoxic oxygen minimum zones. Proceedings of the National Academy of Sciences of the United States of America, 109: 15996-16003. doi: 10.1073/pnas.1205009109

Wishner, K.F., Seibel, B. & Outram, D. 2020. Ocean deoxygenation and copepods: coping with oxygen minimum zone variability. Biogeosciences, 17: 2315-2339. doi: 10.5194/bg-17-2315-2020

Wishner, K.F., Outram, D.M., Seibel, B.A. & Daly, K.L. 2013. Zooplankton in the eastern tropical north Pacific: Boundary effects of oxygen minimum zone expansion. Deep-Sea Research I, 79: 122-140. doi: 10.1016/j.dsr.2013.05.012

Wishner, K.F., Seibel, B.A., Roman, C., Deutsch, C., Outram, D., Shaw, C.T., et al. 2018. Ocean deoxygenation and zooplankton: Very small oxygen differences matter. Science Advances, 4: 12. doi: 10.1126/sciadv.aau5180