



Potential effects of shoaling of oxygen minimum zone on the population of *Acartia (Acanthacartia) tonsa* in the Humboldt Current Upwelling System (23°S)

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ABSTRACT

Expansion and shoaling of the Oxygen Minimum Zone (OMZ) in coastal upwelling systems due to climate change can have dire consequences on the ecosystem structure and productivity. The OMZ restricts the habitat range of most zooplankton, and species with low tolerance to hypoxia may suffer physiological stress and mortality as a result. During 2013 and 2014, the copepod *Acartia tonsa* collected off northern Chile was used to evaluate how hypoxia may affect its survival and vital rates. Exposure of gravid females to severe hypoxia ($\sim 0.2 \text{ mL L}^{-1}$ dissolved oxygen) resulted in total mortality. Hypoxia at $\sim 0.5 \text{ mL L}^{-1}$ decreased female survival to $\sim 20\%$ and egg production to nil. Hypoxia at $\sim 0.8 \text{ mL L}^{-1}$ decreased survival to $\sim 50\%$ but no change in egg production rate compared to the normoxia treatment. Egg hatching success was $\sim 68\%$ and naupliar development time was $\sim 36\%$ lower in hypoxia than normoxia. The critical and lethal oxygen levels for the species were estimated to be 1.78 and 0.73 mL L^{-1} , respectively. Based on modeled historical data, the 1.5 mL L^{-1} isopleth has been moving upward at a rate of $1.3\text{--}2.0 \text{ m}$ per year in northern Chile, barring interruptions during El Niño events. The long-term, gradual shoaling of the OMZ is expected to have significant impacts on the zooplankton community and productivity in the region.

1. Introduction

Since the 1960s scientists have recognized the spreading threat of deoxygenation in coastal seas caused by eutrophication (Díaz and Rosenberg, 2008), and the problem is further exacerbated by climate change (Altieri and Gedan, 2014), with wide-ranging effects on biodiversity, ecosystem services, and socioeconomic wellbeing (Díaz and Rosenberg, 2011). Deoxygenation of seawater can also occur offshore within the Oxygen Minimum Zone (OMZ) found in, e.g., Eastern South Pacific, Eastern North Pacific, the Arabian Sea, and the Bay of Bengal

(Paulmier and Ruiz-Pino, 2009), where oxygen in the mid-water column becomes depleted due to limited ventilation combined with high remineralization of organic matters sedimented out from the productive surface layer (Wyrski, 1962; Keeling et al., 2010). The intensity of OMZ is modulated by the local physical and biological processes, creating different OMZ areal coverage and thickness (Paulmier and Ruiz-Pino, 2009), but the characteristic oxygen concentrations are usually below 0.5 mL L^{-1} ($\sim 24.7 \mu\text{mol kg}^{-1}$) (Keeling et al., 2010; Stramma et al., 2010) to total anoxia (Ulloa et al., 2012).

The Humboldt Current System (HCS) is one of four major Eastern

Abbreviations: EBUS, Eastern Boundary Upwelling sSystems; OMZ, Oxygen Minimum Zone; HCS, Humboldt Current System; DO, Dissolved oxygen; EPR, Egg production rate; CET, cumulative Ekman transport.

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Boundary Upwelling Systems (EBUS) in the world (Thiel et al., 2007). In Mejillones Bay (23°S) off northern Chile, prevailing winds induce year-round upwelling of subsurface water and maintain a shallow OMZ (Piñones et al., 2007; Sobarzo et al., 2007). Therefore, the organisms inhabit a highly heterogeneous environment, subjected to changes in temperature, stratification, upwelling intensity, and hypoxia associated with the vertical movements of the OMZ (Escribano et al., 1998, 2012, 2014; Hidalgo and Escribano, 2008; Ruz et al., 2017).

Copepods account for ~80% of the zooplankton in Mejillones Bay, of which the dominant species include *Acartia* (*Acanthacartia*) *tonsa* Dana 1849, *Centropages brachiatus* Dana 1849, *Paracalanus* cf. *indicus* Wolfenden 1905 and *Calanus chilensis* Brodsky 1959 (Escribano et al., 2009; Hidalgo et al., 2010). The copepods provide a main food source for small pelagic fish, contributing ca. 50% and 30% of the diet of sardines and anchovies, respectively (Escribano et al., 2009). Therefore, changes to copepod production due to changes in OMZ intensity can have dire consequences on the fisheries in the region. The upwelling intensity within HCS is predicted to increase due to climate change (Echevin et al., 2012), which would lead to shoaling of OMZ and compress the habitat range for the copepods. Under such a scenario, copepod species with a low tolerance to hypoxia may suffer physiological impairment and non-predation mortality; conversely, avoidance of the encroaching OMZ may increase encounter probability with predators within the dwindling upper pelagic zone (Elliott et al., 2013a).

An earlier study showed that *C. chilensis* adult female survival, egg production, and growth were not affected by hypoxic treatment (Ruz et al., 2018), which seems to be consistent with field observations that *C. chilensis* female and egg vertical distribution extend deeper into the oxycline (Ruz et al., 2017). Nevertheless, egg hatching success and naupliar survival were negatively impacted by hypoxia in the same study (Ruz et al., 2018), suggesting that hypoxia tolerance may vary among developmental stages.

Another dominant copepod species in Mejillones Bay, *A. tonsa*, occurs in higher abundances than *C. chilensis* (Yáñez et al., 2018) but is largely concentrated above the OMZ (Ruz et al., 2017), suggesting that *A. tonsa* may be more sensitive to hypoxia than *C. chilensis*. Interestingly, the peak abundances of *A. tonsa* adults were observed in early Spring and late Summer (Yáñez et al., 2018) when strong upwelling brought hypoxic water higher up in the water column (Yáñez et al., 2019). To resolve these seemingly contradicting observations and to attain a better understanding of how *A. tonsa* will be affected by expanding OMZ, we conducted experiments where we exposed *A. tonsa* from Mejillones Bay to different dissolved oxygen conditions and measured its adult female survival, egg production, egg hatching success, and naupliar growth. We then combined our experimental results with literature data on OMZ intensity to estimate the past and future changes in copepod populations in HCS.

2. Materials and methods

2.1. Water and zooplankton collection

Field sampling was conducted in Mejillones Bay (23° 00.2' S, 70° 28.2' W; maximum depth = 120 m) in 2013 and 2014 as a part of the Antofagasta Zooplankton Time Series Program operated by the University of Concepción (Fig. 1). In each sampling campaign, the water temperature profile (0–90 m) was measured by a CTD-O Seabird 19 plus and a YSI EXO2 sonde. The YSI EXO2 oxygen profiles were immediately visualized onboard to assess the depth of the upper boundary of the OMZ. Waters from ~10 m depth (corresponding to the surface layer) and ~60 m depth (corresponding to the OMZ) were then collected with 10-L Niskin bottles and maintained at in situ temperatures until use. Zooplankton was collected by oblique trawls with a WP-2 net (200 µm mesh size) within the oxygenated upper layer; kept in diluted surface seawater in an insulated cooler and transported to the laboratory within 2 h.

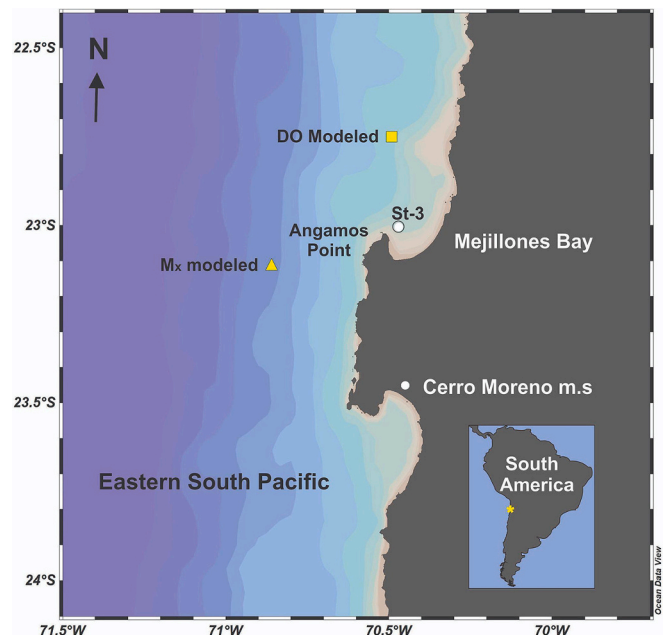


Fig. 1. Study area in Mejillones Bay in the Eastern South Pacific, showing the sampling station (St. 3) and Cerro Moreno meteorological station (m.s) (white dots), the locations for the extraction of dissolved oxygen (DO) modeled data from Copernicus (yellow square) and the Ekman transport (M_x) modeled data (yellow triangle). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In the laboratory, field samples were stored at 14 °C, which was the average temperature of the ~30 m layer during non-El Niño years (Ruz et al., 2015). Healthy gravid females of *A. tonsa* were carefully picked out under a microscope for experiments. Groups of ten females were placed into 500-mL glass jars filled with 0.7-µm filtered seawater at 14 °C and allowed to acclimate for two hours before experiments.

To remove ambient particles, seawater from 60 m (hypoxic) and 10 m (normoxic) depths were filtered through 0.7-µm glass fiber filters into separate carboys. Because the filtration procedure may introduce oxygen into the seawater, we bubbled the filtered 60-m seawater with high-purity nitrogen gas (N_2) to the desired hypoxic conditions, and the dissolved oxygen (DO) concentrations were checked using a PreSens Micro-Optode OXY-4 sensor (calibrated according to manufacturer's instructions): low dissolved oxygen treatment 1 (LDO-1 = ~0.2 mL L⁻¹), treatment 2 (LDO-2 = ~0.5 mL L⁻¹), treatment 3 (LDO-3 = 0.8 mL L⁻¹) and normoxia (~6.0 mL L⁻¹).

For each experiment, seawater of a specific DO condition was siphoned slowly into 100-mL vials until overflowing. The actual initial DO concentrations in the vials were measured by the PreSens sensor; copepods or eggs were then added carefully with a pipette with a very trace amount of water to start the incubation (see below). The vials were hermetically sealed with rubber stoppers and aluminum crimp-seal, and placed in a water bath at a constant temperature of 14 °C.

2.2. Egg production experiments

Egg production rate (EPR) and survival of the copepods during 24 h were measured according to Runge and Roff (2000). The first experiment was run in lethal hypoxia and normoxia, whereas the next seven experiments were run in sub-lethal hypoxia and normoxia. Each experiment had 8 to 34 replicate vials per DO treatment, with 1 gravid copepod per vial, depending on the availability of copepods (Table 1).

After the 24-h incubations, the vials were opened one by one, and the copepod and eggs were carefully collected on a 23-µm sieve and counted. Copepod survival and egg abundance were examined under a

Table 1

Summary of the experiments indicating the number of vials as replicates, the stage initially incubated, the number of individuals per vial (n), and the incubation time in days.

Experiment	Date	No. of vials			Stage	n	Days
		Lethal hypoxia	Sub-lethal hypoxia	Normoxia			
Egg production rate							
	01/03/2013	34	–	23	Female	1	1
	13/03/2013	–	8	8	Female	1	1
	14/03/2013	–	8	–	Female	1	1
	15/03/2013	–	8	8	Female	1	1
	11/07/2014	–	22	23	Female	1	1
	14/07/2014	–	9	–	Female	1	1
	25/07/2014	–	17	9	Female	1	1
Hatching success, and naupliar growth and development							
	15/07/2013	–	4	3	Eggs	20–50	1–3
	20/07/2013	–	2	–	Eggs	50	1–3
	19/07/2014	–	3	3	Eggs	20	1–3
	25/07/2014	–	8	10	Eggs	20–50	1–3

stereomicroscope and then preserved in a 4% formalin solution (see section 2.4). At least three vials were randomly selected to measure the final DO concentrations between the vial opening and the collection of the copepod and eggs.

2.3. Hatching success and naupliar growth

To obtain a sufficient number of eggs for these experiments, we put 50–100 gravid female copepods in a 3-L bucket with a 200- μ m sieve false bottom (to prevent cannibalism on eggs) in a normoxic condition for 24-h. The eggs produced by the copepods were collected from the bottom of the bucket with a pipette and separated into groups of eggs for incubations. Because the previous experiments showed that the copepods only produced eggs under LDO-3 and normoxia treatments, egg hatching success and naupliar growth were measured under those two conditions. Each DO treatment had 2–13 replicate vials, each vial with 3–100 eggs depending on the availability of eggs, and the incubation lasted 1–3 days (Table 1). Every 24 h, at least three vials were randomly selected to measure the final DO concentrations and to collect any unhatched eggs and nauplii on a 23- μ m sieve for enumeration. Hatching success was expressed as percent eggs hatched per day.

2.4. Live-dead status and growth measurements

The live-dead status of the eggs and female copepods at the end of the incubation was assessed by the Neutral Red method adjusted for the local species (Yáñez et al., 2012). The Neutral Red method allowed the discrimination of live (red-stained) vs. dead (non-stained) organisms (Elliott and Tang, 2009; Yáñez et al., 2012). The eggs and copepods in 2 mL of seawater were stained by adding 0.1 mL of Neutral Red solution [0.5% p/v, 1:1000] (Ruz et al., 2018). After 10 min, the samples were preserved in 4% formaldehyde in a seawater solution buffered with sodium acetate for later analysis. The samples were analyzed within two months of the experiments to avoid degradation of the stain. Before transferring the samples into counting chambers, they were rinsed on a 200- μ m mesh screen to remove the formaldehyde solution. The samples were then acidified to pH < 7 by the addition of ~0.5 mL of acetic acid (C₂H₄O₂) to develop the red stain's color in organisms that were alive at the end of the experiments (Yáñez et al., 2012; Ruz et al., 2018).

The naupliar stages were identified under a microscope (10 \times –40 \times), following the characteristics of the developmental stages described by Murphy and Cohen (1978) and Alver et al. (2011). Egg diameter and cephalosome length and width of nauplii (N1 and N2) were measured (μ m \pm 1 SD) under a stereomicroscope (40 \times –80 \times) equipped with a digital camera and the software Micrometric SE Premium 4. The egg and naupliar biovolumes were calculated from linear dimensions according

to Torres and Escribano (2003) and Ruz et al. (2018), and then converted to biomass using the factor 0.045 mg C μ L⁻¹ (Ikeda and Omori, 1984). The weight-specific growth rates were calculated from the estimated naupliar weights (μ g C) of consecutive stages and the incubation time (Runge and Roff, 2000).

2.5. Water masses and experimental data analysis

The water masses in the study station were identified by potential temperature and salinity using the mixing triangle methodology in TS diagrams, considering the end-members values according to Silva et al. (2009).

The relationships between female copepod survival, EPR, egg hatching success and the dissolved oxygen concentrations were tested with a Chi-square or G-Test of independence (α = 0.05). Additionally, differences among egg production experiments were analyzed with a General Linear Model (GLM), and egg hatching success, naupliar growth, naupliar development, egg and naupliar sizes among the DO treatments were tested with Student's Test (α = 0.05) after normality and homoscedasticity of the data were checked (Zar, 1999). All experimental data were reported as mean \pm SE (standard error), whereas morphological parameters such as size, weight, and biovolume were reported as mean \pm SD (standard deviation).

2.6. Model analysis

To identify the variability of oxygen levels throughout the year in surface waters (10 m) and the intermediate layer (60 m) in the study area, the monthly average oxygen data were obtained from the numerical model of global ocean biogeochemistry hindcast in Copernicus (<https://data.marine.copernicus.eu/>). The available data covers the years 1993 to 2020 from a station 28 km offshore (22.75°S; 70.50°W) from our sampling station (Fig. 1). In situ dissolved oxygen measurements at 10 m and 50 m depths of the Mejillones Time Series (2010–2015) were used to compare with modeled data.

The modeled and in situ Ekman transport was derived using the procedure described by Mann and Lazier (1991). To show coastal upwelling favorable conditions the cumulative Ekman transport (CET) was used. The CET is described as the cumulative transport effect over time and it corresponds to the wind-generated mass transport per unit of width over the depth of the Ekman layer, which is expressed in kg m⁻¹ s⁻¹ (a transport of 1000 kg m⁻¹ s⁻¹ is typically for a wind stress of 0.1 N m⁻² at 45°; Tomczak and Godfrey, 2003). The CET was integrated monthly between the years 2015 and 2021 and annually between the years 2015 and 2100 forecast.

To identify the variability of Ekman transport, the output scenario

modeling SSP585 was analyzed from six numerical models CMIP6 (NorESM2-MM, ESM1-2-HR, CM2-SR5, CMCC-ESM2, INM-CM5-0, INMCM48) of the World Climate Research Programme (WCRP; <https://esgfnode.ipsl.upmc.fr/search/cmip6-ipsl/>). The selection criteria of the models used were the availability of the surface tension towards the north (tauv) with a 100 km resolution. The available data covers the years 2015 to 2100 from an offshore station (23.09°S; 71.25°S) at Angamos Point. An average of the six models were carried out on a multi-model database to calculate Ekman transport. In situ wind measurements were taken from Cerro Moreno meteorological station (23.45°S;70.45°W) of the General Directorate of Civil Aviation of Chile (<https://climatologia.meteochile.gob.cl/application/informacion/inventarioComponentesPorEstacion/230001/28/60>) (Fig. 1). The CET derived from in situ data was used to contrast it with CET from modeled data between 2015 and 2022.

3. Results

3.1. Oceanographic conditions

The seawater temperature at 10 and 60 m depths during the sampling period averaged 14.40 ± 0.44 °C (range 13.74–14.76 °C) and 12.93 ± 0.10 °C (range 12.82–13.05 °C), respectively. The mean salinity was 34.64 ± 0.26 (range 34.39–34.94) at 10 m and 37.76 ± 0.20 (range 34.47–34.91) at 60 m. The identified water masses were Subtropical Water (STW), Subantarctic Water (SAAW) and Equatorial Subsurface Water (ESSW) (Fig. 2). The intermediate and bottom layers were filled mainly by ESSW, whereas the surface layer was a mixture of ESSW, STW and SAAW, depending on the sampled period.

The dissolved oxygen concentration at the 10 m depth had a mean value of 3.09 ± 1.41 mL L⁻¹ (range 1.26–4.71 mL L⁻¹) (Table 2). At 60 m depth, the OMZ was present the entire study period with a mean concentration of 0.24 ± 0.26 mL L⁻¹ (range 0.06–0.63 mL L⁻¹) (Table 2).

Table 2

In situ oceanographic conditions at 10 and 60 m depths at Mejillones Bay during zooplankton sampling.

	Temperature (°C)		Salinity		Dissolved oxygen (mL L ⁻¹)	
	10 m	60 m	10 m	60 m	10 m	60 m
March 2013	14.22	12.91	34.39	34.80	3.25	0.19
July 2013	14.76	12.82	34.46	34.47	4.71	0.63
January 2014	13.74	12.93	34.76	34.85	1.26	0.06
July 2014	14.49	13.05	34.94	34.91	3.15	0.10
Mean	14.30	12.93	34.64	34.76	3.09	0.24
SD.	0.44	0.10	0.26	0.20	1.41	0.26

3.2. Female survival and egg production rate

The survival of *Acartia tonsa* was measured in 173 gravid females and it was dependent on the dissolved oxygen concentration (Chi-square = 110.8; d.f. = 3; $p < 0.001$). The survival was $92.7 \pm 2.52\%$ ($n = 6$) in normoxia, $53.6 \pm 11.06\%$ ($n = 3$) in low-oxygen treatment LDO2, $19.0 \pm 19.05\%$ ($n = 3$) in LDO3, and no survival (0%; $n = 33$) in LDO1 (Fig. 3). The oxygen concentrations measured during the experiments are given in Table 3.

Among the surviving females in LDO-2, LDO-3 and normoxia, their egg production rates (EPR; eggs female⁻¹ d⁻¹) varied significantly (GLM; $F = 6.94$; $P = 0.002$). Normoxia (4.7 ± 0.55 ; range 0–16; $n = 49$) and LDO-3 (5.7 ± 1.82 ; range 0–13; $n = 7$) were comparable ($T = -0.41$, $p = 0.913$), but surviving females in LDO-2 did not produce eggs ($n = 4$) (Tuckey test LDO-3 versus LDO-2, $T = 3.29$, $p = 0.005$; Normoxia versus LDO-2, $T = 3.65$, $P = 0.002$) (Fig. 4).

3.3. Hatching success and naupliar growth

Between the two conditions where egg production occurred (LDO-3 and normoxia), the egg hatching success (HS) was significantly higher in normoxia ($35.7 \pm 8.04\%$; range 18–60%; $n = 6$) than in LDO-3 ($11.4 \pm 2.74\%$; range 0–24%; $n = 8$) (T-Student: $T = -3.21$; $GL = 12$; $p = 0.008$) (Fig. 5). After hatching, the development from egg to N1 was similar between LDO-3 and normoxia treatments. However, further development was more successful under normoxia, evidenced by 18.9% of the eggs reaching N2 within three days, versus only 2% in LDO-3 treatment (Table 4). The survival of *A. tonsa* early stages (G-test; $G = 218.4$; d.f. = 1; $p < 0.001$) and hatching success (G-Test; $G = 44.5$; d.f. = 1; $p < 0.001$) were both dependent on the dissolved oxygen concentration.

The egg diameter (Test-T; $T = 2.13$; d.f. = 133; $p = 0.035$), N1 body length (Test-T; $T = 4.22$; d.f. = 140; $p < 0.001$) and N2 body length

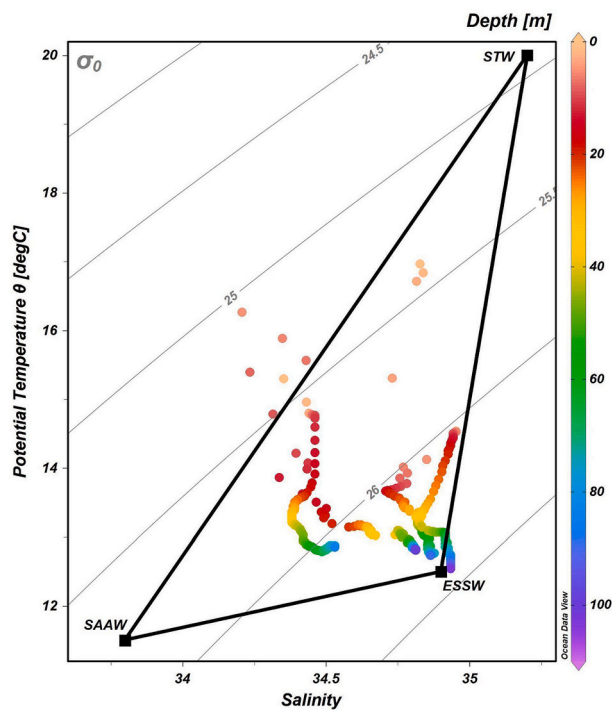


Fig. 2. Seawater mixing triangle at Mejillones Bay. The identified water masses were Subtropical Water (STW), Subantarctic Water (SAAW) and Equatorial Subsurface Water (ESSW).

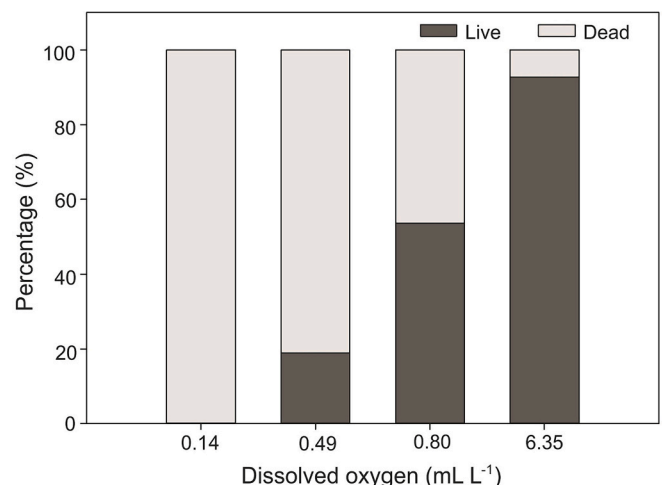


Fig. 3. Live and dead percentages of *Acartia tonsa* gravid females.

Table 3

Experimental dissolved oxygen concentrations (mL L^{-1}) and kPa equivalences. Mean, standard error (SE), and range (min. - max. value) among the different vials are presented. Treatments are low dissolved oxygen (LDO) and normoxia.

Treatment	n	Dissolved oxygen			
		mL L^{-1} Mean \pm SE	mL L^{-1} Min. - Max.	kPa Mean \pm SE	kPa Min. - Max.
LDO-1	33	0.14 ± 0.07	0.00–0.44	0.47 ± 0.24	0.00–1.49
LDO-2	38	0.49 ± 0.05	0.34–0.59	1.66 ± 0.17	1.15–2.00
LDO-3	17	0.80 ± 0.13	0.31–1.24	2.71 ± 0.44	1.05–4.21
Normoxia	85	6.35 ± 0.48	4.81–7.09	21.55 ± 1.63	16.32–24.06

(Test-T; $T = 3.29$; d.f. = 41; $p = 0.002$) were significantly different between LDO-3 and normoxia. However, the biovolume of eggs and nauplii was not significantly affected by the dissolved oxygen concentration. The carbon content of early-state *A. tonsa* only showed significant differences for N2 exposed to LDO-3 vs. normoxia (Test-T; $T = 2.39$; d.f. = 41; $p = 0.021$) (Table 5). The growth rate from N1 to N2 was lower in LDO-3 (0.55 d^{-1}) than normoxia (0.86 d^{-1}); the equivalent development time was 1.82 d in LDO-3 and 1.16 d in normoxia.

3.4. Model environmental parameters

According to the offshore historical modeled oxygen data (Fig. 3), the first 10 m always contained well oxygenated surface layer. The modeled oxygen data from Copernicus for 10 m depth were in the range of 2.6 to 5.5 mL L^{-1} (Fig. 6a). There were differences of up to 270% between in situ and modeled data, likely because the modeled data is a monthly average oxygen concentration and because of the distance between the studied and modeled stations. The modeled data for the 60 m depth showed a wider range of oxygen concentrations, from 0.07 to 3.82 mL L^{-1} (Fig. 6a). The vertical distribution of the oxygen concentration presented a high temporal variability modulated at the seasonal and interannual scales. For example, oxygenation of the water column was observed to be associated with El Niño events (Fig. 6a and b). The shoaling of OMZ was interrupted by El Niño events (1997/98 and 2015/16) when oxygenation of the water column deepened the 1.5 mL L^{-1}

isopleth down to 120 m (Fig. 6b).

The multimodel time series of monthly CET (2015–2021) fluctuated between $0.7 \times 10^4 \text{ kg m}^{-1} \text{ s}^{-1}$ and $1.6 \times 10^4 \text{ kg m}^{-1} \text{ s}^{-1}$, with the maximum value during 2016 and the minimum at the beginning of 2018. In general, the CET was higher in the winter and spring seasons, decreasing towards the summer, with positive values in the entire series. In addition to the seasonal variations typical for this region (strongest in mid-year; Bravo et al., 2016), there was a slight increasing trend in CET over time (Fig. 7). This became more obvious in the forecast of CET from the multi-model data showing a positive trend in the next 80 years, which would drive the shoaling of OMZ in Mejillones Bay (Fig. 8). The cross-correlation coefficient between modeled DO versus modeled CET (Fig. S1) is shown in the supplementary material, followed by the monthly CET for multi-modeled data versus in situ data from Cerro Moreno meteorological station (Fig. S2) and its respective cross-correlation analysis (Fig. S3).

4. Discussion

Oxygen plays a key role in ecosystem structure and spatio-temporal distribution patterns of marine organisms (Gilly et al., 2013). In upwelling systems, many species congregate within the surface oxygen-rich layer above the OMZ (EEscribano et al., 2009; Hidalgo et al., 2010). Due to climate change, the expansion and shoaling of OMZ restrict the habitat of pelagic organisms to shallower waters (Bertrand et al., 2010; Stramma et al., 2010). Some species have developed metabolic adaptations (e.g., metabolic suppression); some perform diel vertical migration (DVM) to seek refuge within the OMZ from predation, or inhabit inside the OMZ, as has been observed in some copepods (e.g., Family Calanidae, Metridinidae, and Eucalanidae) (Hidalgo et al., 2005; Auel and Verheye, 2007; Teuber et al., 2013). However, the intensification of favorable upwelling winds (Bakun, 1990; Rykaczewski and Checkley, 2008; Wang et al., 2015) may affect the capacity to avoid hypoxic events associated with the vertical movements of the OMZ, changes that could disadvantage species that have low tolerance to hypoxic condition.

Due to the coastal deoxygenation processes that are facing the pelagic ecosystems in upwelling areas, understanding how the

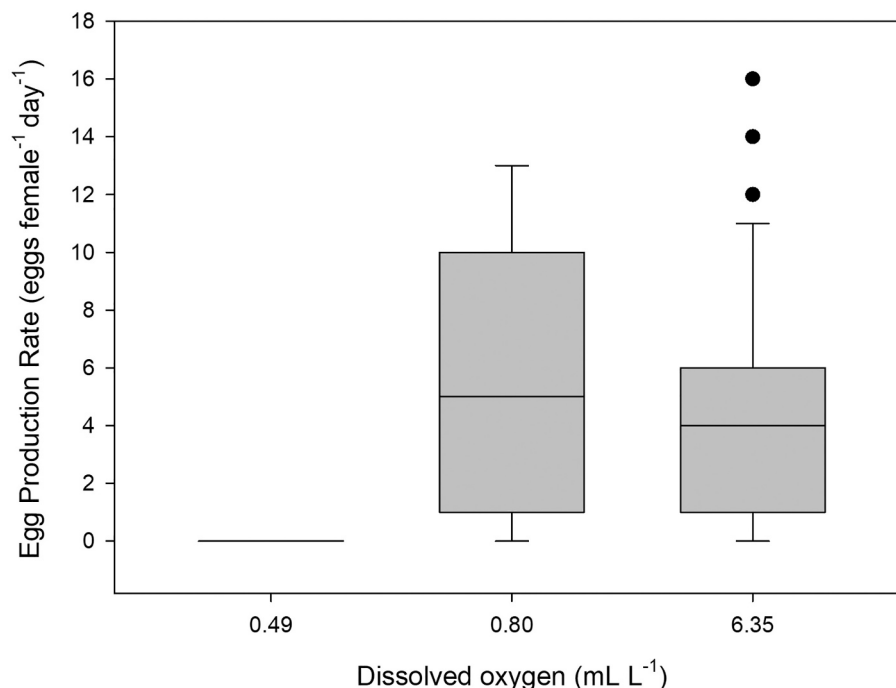


Fig. 4. Box plot of Egg Production Rate ($\text{eggs female}^{-1} \text{ d}^{-1}$) of surviving *Acartia tonsa* under different oxygen conditions.

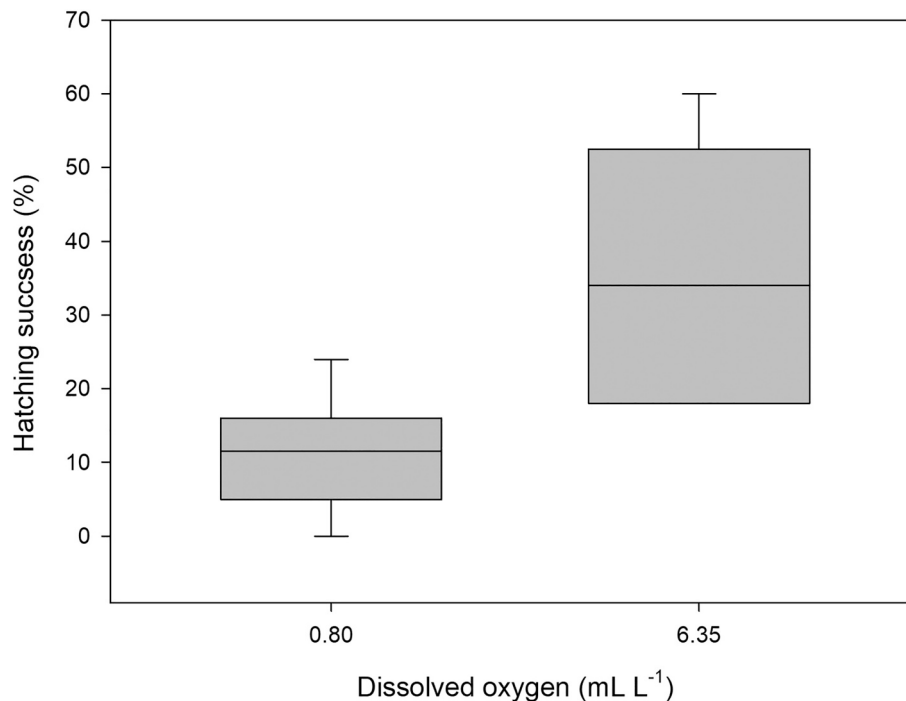


Fig. 5. Box plot of the hatching success of *Acartia tonsa* eggs exposed to sub-lethal hypoxia (LDO-3) and normoxia.

Table 4

Initial eggs (N_i) were incubated to determine naupliar growth to naupliar stage 1 (N1) and naupliar stage 2 (N2). The final count for each stage is (N_f) and its percentage is indicated between brackets (%).

	Eggs		Naupliar stage 1	Naupliar stage 2
	N_i	N_f	N_f	N_f
Hypoxia (LDO-3)				
Day 1	20	7 (35.0%)	6 (30.0%)	0 (0.0%)
Day 2	120	42 (35.0%)	17 (14.2%)	2 (1.7%)
Day 3	50	14 (28%)	7 (14.0%)	1 (2.0%)
Normoxia				
Day 1	70	37 (52.9%)	18 (25.7%)	1 (1.4%)
Day 2	50	13 (26.0%)	5(10.0%)	4 (1.8%)
Day 3	90	24 (26.7%)	14 (15.6%)	17 (18.9%)

Table 5

Estimates of nauplii volume and weight (mean \pm SD) of *A. tonsa* under experimental oxygen conditions (normoxia and LDO-3) reared at constant temperature (14 °C). Significant differences between dissolved oxygen treatments are shown in bold.

	N1	N2
Normoxia		
Length (μm)	106.64 \pm 8.35	134.22 \pm 6.06
Width (μm)	53.61 \pm 5.71	62.99 \pm 5.46
Volume ($10^5 \mu\text{m}^3$)	1.64 \pm 0.44	2.81 \pm 0.54
Weight ($\mu\text{g C}$)	0.007 \pm 0.002	0.013 \pm 0.002
n	63	34
LDO-3		
Length (μm)	100.38 \pm 11.24	127.02 \pm 4.79
Width (μm)	52.63 \pm 8.16	60.34 \pm 7.80
Volume ($10^5 \mu\text{m}^3$)	1.49 \pm 0.56	2.47 \pm 0.76
Weight ($\mu\text{g C}$)	0.007 \pm 0.003	0.011 \pm 0.003
n	79	9

upwelling ecosystems respond to the oxygen decrease is essential to project changes from population to ecosystem structure in these environments. This paper contributes to analyzing the response of a key copepod species in the upwelling zone in Mejillones Bay in northern

Chile. Under normoxia and sub-lethal hypoxia, the egg production rate that we measured (0–16 eggs female⁻¹ day⁻¹) was within the range of previous values reported for this species in the HCS: ca. 0–60 (Vargas et al., 2006), 0–50 (Aguilera et al., 2011, 2013) and 21 \pm 4 eggs female⁻¹ day⁻¹ (Ruz et al., 2015), whereas severe hypoxia (0.14 \pm 0.07 mL L⁻¹) was lethal to the copepod in our experiments, similar to the 100% mortality of *A. tonsa* in bottom hypoxia (0.11 mL L⁻¹, partial pressure of \sim 1.85 KPa) at 18 °C in the Chesapeake Bay (Elliott et al., 2013a). In the EPR experiments, we did not separate the eggs from the female in the incubation, which could have resulted in underestimation of EPR due to egg cannibalism. Nevertheless, we did not find any crumpled eggs or empty egg membranes that would have indicated cannibalism (Besiktepe and Dam, 2020); therefore, we consider egg cannibalism to be negligible in our experiments.

The hypoxia below the critical oxygen level (P_{crit}) of 2.24 mL L⁻¹ (\sim 8.08 KPa) limits the respiration of *A. tonsa*, whereas the lethal oxygen level (P_{leth}) for this species at 18 °C was reported to be 0.89 mL L⁻¹ (\sim 3.20 KPa) in Chesapeake Bay (Elliott et al., 2013b). The seasonal bottom hypoxia also decreases the growth and increases the mortality of other copepod species (Stalder and Marcus, 1997; Marcus et al., 2004; Richmond et al., 2006). In Mejillones Bay, the semi-permanent upwelling regime leads to a cooler surface temperature (average \sim 14 °C). Based on the equations of Elliott et al., 2013b, eq. 3 and 4), we estimated that at 14 °C the theoretical P_{crit} and P_{leth} for *A. tonsa* in Mejillones Bay would be 1.78 mL L⁻¹ (\sim 6.03 KPa) and 0.73 mL L⁻¹ (\sim 2.49 KPa), respectively (supplementary material). These values are close to our experimental oxygen conditions (Table 2). Hypoxia-induced mortality in copepods in the HCS has been reported for *Calanus chilensis* (Ruz et al., 2018), *Paracalanus* cf. *indicus* (Yáñez et al., 2012) and *A. tonsa* (Ruz et al., 2015; this study). Our results showed that survival of female *A. tonsa* was decreased by \sim 70% under sub-lethal hypoxia (LDO-2 = 0.49 \pm 0.05 mL L⁻¹), and \sim 40% (LDO-3 = 0.80 \pm 0.13 mL L⁻¹) compared to normoxia, consistent with previous report of non-predatory mortality of ca. 44% for this species in Mejillones Bay upwelling zone (Yáñez et al., 2019). Lethal and sublethal oxygen concentrations for *A. tonsa* that we observed were lower than the reported values for the same species in seasonal bottom hypoxia in nearshore environments (Roman et al., 1993; Richmond et al., 2006; Elliott et al., 2013b). Colder

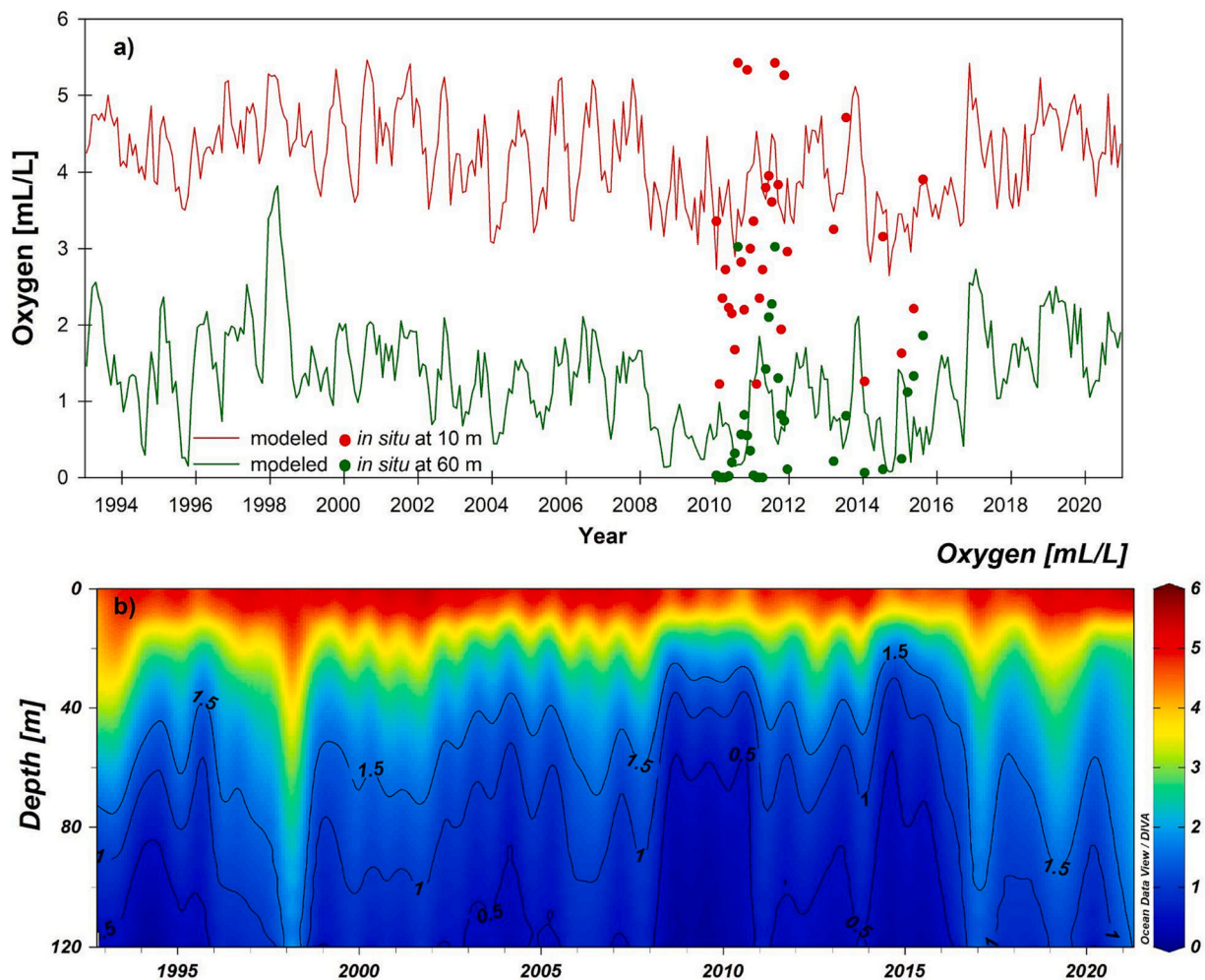


Fig. 6. a) Historical dissolved oxygen (mL L^{-1}) modeled data from Copernicus (lines) and in situ oxygen concentrations (dots) for Mejillones Bay at 10 and 60 m (upper panel) and b) modeled data between 0 and 120 m depths (lower panel) between 1993 and 2020.

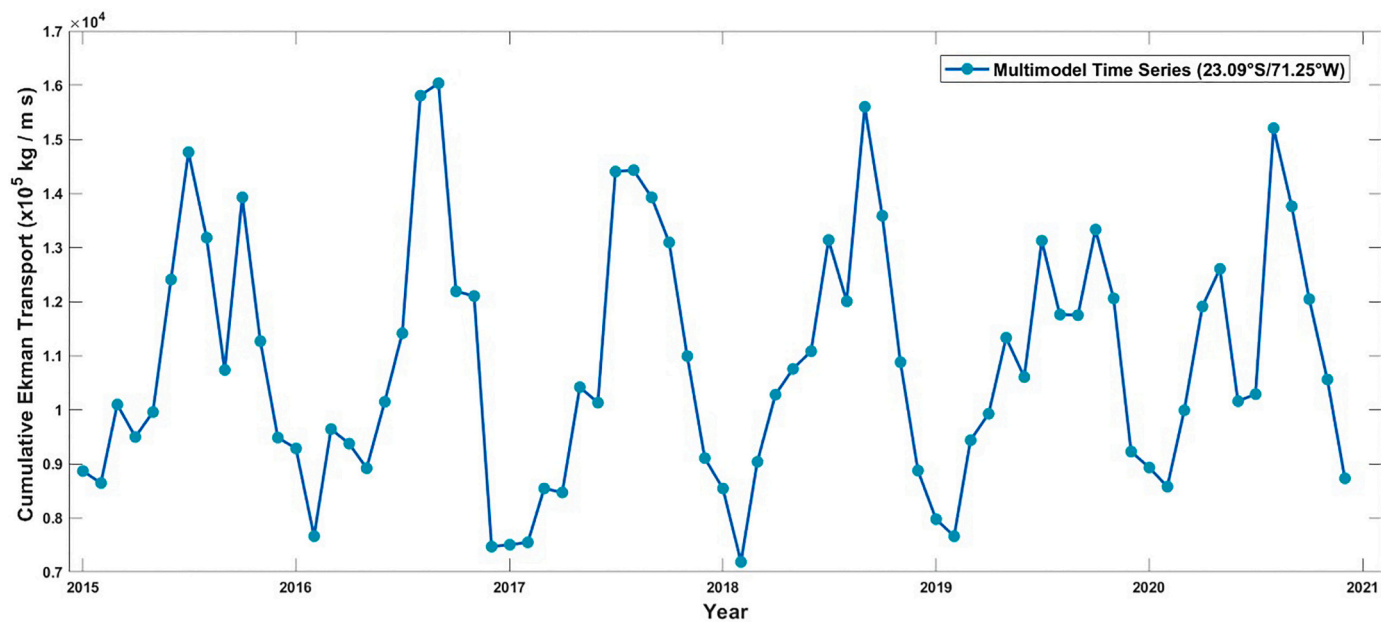


Fig. 7. The monthly variability of Ekman transport between the years 2015 and 2021 from the modeled data of the World Climate Research Programme.

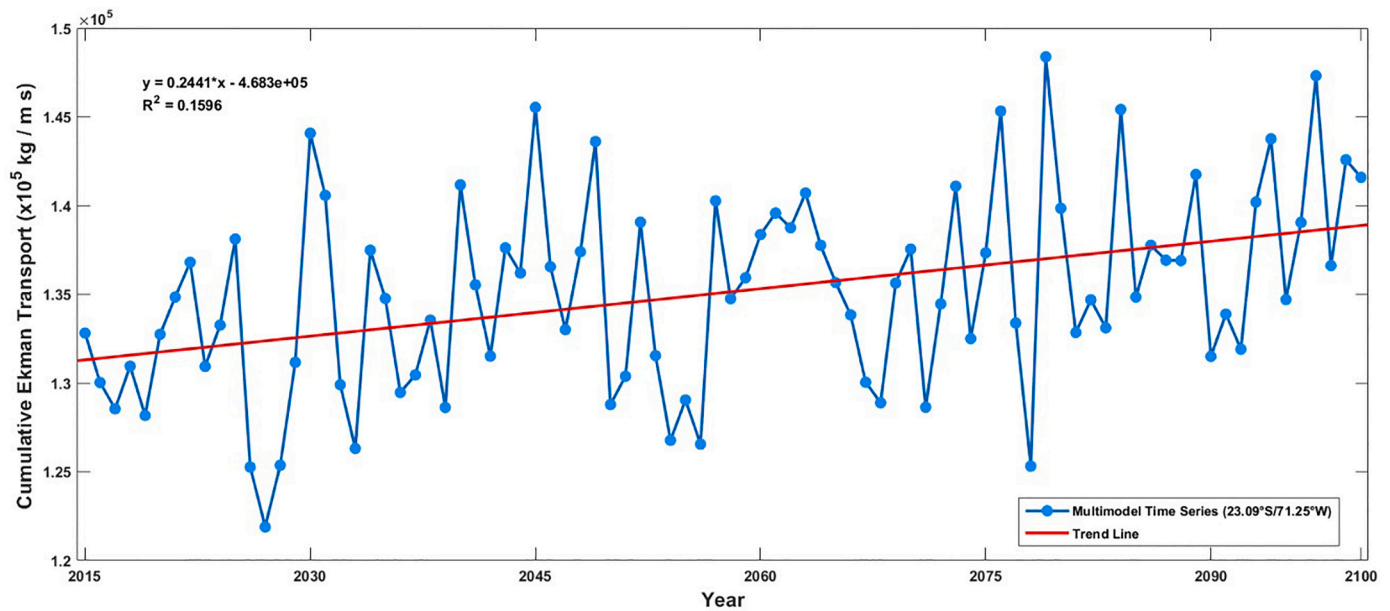


Fig. 8. Forecast of the Multimodel Time Series using the annual average of cumulative Ekman transport from data of the World Climate Research Programme, between the years 2015 to 2100.

water will increase oxygen solubility (oxygen availability) while decrease oxygen demand (respiration) of the zooplankton. As our study region presents lower temperatures (higher oxygen saturations/lower oxygen demand), the tolerance of *A. tonsa* to lower dissolved oxygen concentrations should be higher than in other areas. However, it is relevant to consider the oxygen demand to compare the different oxygen thresholds, along with the probability that it results from the more intense hypoxia or even anoxia of the HCS acting as a selection pressure on the *A. tonsa* population off northern Chile, as has also been suggested for *C. chilensis* (Ruz et al., 2018).

Oxygen conditions above 1.78 mL L^{-1} are mainly found from the surface to the oxycline above the OMZ, where oxygen level decreases from 1 mL L^{-1} to near anoxia (EEscribano et al., 2009; Ulloa et al., 2012). Lower oxygen concentration constrains the physiology of this species. However, under the projected intensification and expansion of the OMZ, species capable of surviving sublethal hypoxia would be able to sustain future generations in the HCS. The females of *A. tonsa* seem to be more vulnerable to hypoxia than *C. chilensis* in northern Chile, showing species-specific responses (Ruz et al., 2015). *C. chilensis* also shows stage-specific responses to hypoxia: females are present within the OMZ off Perú (Hirche et al., 2014) and survive the exposure to low-oxygen experimental waters from northern Chile (Ruz et al., 2015), whereas egg hatching success and naupliar growth (N1–N3) diminish in hypoxia (Ruz et al., 2018). Our results showed that the egg hatching success of *A. tonsa* exposed to sub-lethal hypoxia decreased by ca. 30%, agreeing with previous estimates for this species from Mejillones Bay (Ruz et al., 2015). Additionally, the naupliar growth of *A. tonsa* was affected by hypoxia in our experiments, similar to earlier observations for *C. chilensis* (Ruz et al., 2018) and *A. tonsa* (Richmond et al., 2006). Thus, the negative hypoxia effect over the *A. tonsa* population occurs in females, egg and naupliar physiology, growth and survival. A smaller size of copepods may induce long-term changes in the pelagic food webs, mainly due to changes in predatory pressure on smaller phytoplankton species (Richmond et al., 2006) (e.g., a dietary shift from nano-phytoplankton to picophytoplankton). Roman and Pierson (2022) discussed the synergistic effect increasing temperature and decreasing oxygen on copepod diversity, favoring smaller size species in warmer coastal seas. In contrast, the HCS of northern Chile faces a coastal cooling process with the shoaling of hypoxic waters. Here we showed that these conditions will also contribute to the shrinking of the size of

copepods, which could affect the pelagic food webs and fishery.

Dissolved oxygen as a modulator of ecosystem structure may determine the habitat availability for species that inhabit well-oxygenated water. According to the historical modeled data and the dissolved oxygen thresholds derived from our experimental data, *A. tonsa* has a habitat range that varies between 22 m and the entire water column in Mejillones Bay. The thickness of this layer should diminish closer to the coast because of the greater influence of the OMZ. Our modeled data showed a shallowing of the 1.5 mL L^{-1} oxygen concentration isopleth between 1993 and 2015. Considering the 1.5 mL L^{-1} threshold on a monthly basis (i.e., all months of January from 1993 to 2015, all months of February from 1993 to 2015, etc., Fig. S4 and S5 of supplementary material), the shallowing rate varied between 1.3 and 2.0 m per year. This phenomenon would concentrate copepods and other zooplankters in the surface waters, enhancing predation-prey interactions, and potentially increase organic carbon burial in coastal upwelling ecosystems due to the combined effect of increased production in surface waters and strong preservation of organic matter in shallower and more intense OMZ in the next 200 years (Ruvalcaba et al., 2020). Additionally, copepod eggs will reach low-oxygen waters faster if the OMZ is found at shallower depths, which should decrease hatching success and naupliar growth, resulting in a reduced population size of copepods. However, in coastal upwelling ecosystems, the vertical Ekman transport counteracts the sinking of copepod eggs, and allows the retention of eggs from small copepods, such as *P. cf. indicus* and *A. tonsa*, above the oxycline, in contrast with bigger eggs (e.g., *C. chilensis*) that are dense enough to sink and reach the core of the OMZ (Ruz et al., 2017). At a longer time scale, our model forecast showed an increasing trend of Ekman transport until the end of the century (Fig. 8), which is expected to lead to the shoaling of the OMZ and cooling of the surface waters (Wang et al., 2015; Schneider et al., 2017). Although the HCS copepods may not increase their oxygen demand from the cooling effect, our data showed that *A. tonsa* was highly vulnerable in adult and egg stages to the hypoxia associated with the OMZ; therefore, long-term OMZ shoaling and intrusion of hypoxic water may negatively impact *A. tonsa* population in the ecosystem. Further research is needed to understand better the oxygen-critical values for *A. tonsa* and other dominant copepod species and/or taxa (e.g., euphausiids, chaetognaths, salps, decapods larvae, pteropods) in the HCS. Understanding how the zooplankton populations may respond and adapt to hypoxia in the HCS may help to

generate a better prediction of the changes in the ecosystem structure and productivity in response to ocean deoxygenation induced by climate change in upwelling ecosystems.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2023.102372>.

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