Zooplankton diel vertical migration and downward C into the Oxygen Minimum Zone in the highly productive upwelling region off Northern Chile

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10 **Abstract.** The daily vertical movement of zooplankton, known as diel vertical migration (DVM), can enhance the vertical flux of carbon (C) and so contributing to the functioning of the biological pump. The magnitude and efficiency of this active transport of C may depend on the size and taxonomic structure of the migrant zooplankton. However, the impact that a variable community structure can have on zooplankton-mediated downward C has not been properly addressed. This taxonomic effect may become critically important in highly productive eastern boundary upwelling systems (EBUS), where zooplankton

15 biomass becomes aggregated in the coastal zone, but comprised by a highly variable community structure (size-composition). In these systems, presence of a subsurface oxygen minimum zone (OMZ) can impose an additional constraint to vertical migration and so influencing the downward C export. Here, we address these issues based on a high-resolution plankton sampling at three stations off northern Chile (20°S-30°S) during November 2015. Automated analysis of zooplankton composition and taxa-structured biomass allowed us to estimate daily migrant biomass by taxa, amplitude of migration and

20 daily rate of migration, defined as the daily exchange of biomass between the upper mixed layer and below the thermocline. We found that high biomass aggregates above the oxycline, associated with more oxygenated surface waters and this condition was more evident upon a more intense OMZ. Some taxa however, were found closely associated with the OMZ. We found that most taxa were able to perform DVM in the upwelling zone withstanding severe hypoxia. Even, several strong migrants, such as copepods Eucalanidae and Euphausiids, can exhibit a large migration amplitude (~500 m), remaining either temporarily

25 or permanently during the day or night condition within the core of the OMZ and so contributing to the release of C below the thermocline. Our estimates of DVM-mediated C flux showed that migrant biomass (5099 ± 2701 mg C m^{-2} d^{-1}) may contribute with about 678 ± 465 mg C m^{-2} d^{-1} to the OMZ system through respiration, mortality, and production of fecal pellets, implying the existence of a very efficient mechanism to incorporate freshly produced C into the OMZ. This downward C by zooplankton is however strongly depending on taxonomic structure due to variable migration amplitude and behavior affecting the daily

30 rate of diel vertical migration.

1 Introduction

The Oxygen Minimum Zone (OMZ) in the eastern South Pacific Ocean, the fourth largest of the six permanent hypoxic regions in the world oceans (Paulmier *et al.,* 2006), is a key component of the water column and a permanent feature intruding the coastal zone of Ecuador, Peru and Chile (Fuenzalida *et al.,* 2009; Paulmier *et al.,* 2006). In the highly productive upwelling

5 region of Northern Chile the OMZ is closely linked to wind-driven upwelling in the coastal area and associated to Equatorial Subsurface Water (ESSW), which is transported from north to south along the continental slope by the Peru-Chile Undercurrent (PUC) as far south as 48°S (Fuenzalida et al., 2009; Morales et al., 1996; Silva and Neshyba, 1979). Off Iquique (20°S) the OMZ is characterized by being thick (500 m), very intense (< 20 µmol kg^{-1}) and O$_2$ concentrations in the core of OMZ at 21ºS are among the lowest found in the global ocean reaching the detection limit (<1 µM) (Ulloa and Pantoja, 2009), whereas that

10 off Coquimbo at 30ºS becomes thinner (Paulmier *et al.,* 2006).

During the last decades, the OMZ systems have attracted much scientific interest because of evidence showing that hypoxic and anoxic conditions in coastal areas are expanding and becoming more intense (Ekau *et al.,* 2010; Stramma *et al.,* 2008). At present, ongoing ocean deoxygenation is widely recognized as linked to global warming and it is rising much concern in modern oceanography (Breitburg *et al.,* 2018)

15 The presence of oxygen-depleted water becomes a critical physiological constraint for pelagic and benthic organisms inhabiting the upwelling zone, impacting their biomass and productivity, the species diversity, distribution and behavior (Wishner *et al.,* 2018; Ekau *et al.,* 2010; Grantham *et al.,* 2004;). For instance, diel vertical migration (DVM), a common feature of the various size groups of zooplankton and also one of the most important movements of biomass in the ocean, can also be affected by the OMZ intensity and variation (Wishner *et al.,* 2013; Escribano *et al.,* 2009; Hidalgo *et al.,* 2005; Morales

20 *et al.,* 1996; Judkins, 1980). The OMZ can act as an effective barrier for vertical distribution of many organisms, confining most zooplankton to a narrow (50 m) upper layer, as in the coastal upwelling zone off Chile in according to the works of Escribano (2006) and Donoso and Escribano (2014), or by limiting them to the upper 150 or 300 m as found in copepods of the eastern tropical north Pacific (Wishner *et al.* 2013). However, the OMZ can also offer refuge for species adapted to live there, creating microhabitats of differing oxygen concentration that are characterized by layers of high zooplankton biomass

25 and abundance, with distinct species zonation (Antezana, 2009; Wishner *et al.,* 2008), which, in turn, may have important consequences for carbon (C) cycling and its vertical flux. For example, it is known that zooplankton in the coastal upwelling region off northern Chile may play a significant biogeochemical role by promoting carbon flux into the subsurface OMZ (Escribano *et al.,* 2009). Therefore a significant proportion of the vertical material flux from the euphotic zone to the deep sea (> 200 m) and within the food chain could be determined by DVM of zooplankton (Longhurst and Williams, 1992; Steinberg

30 and Landry, 2017).

As important contributors to functioning of the biological pump, diel zooplankton migrants can actively increase the magnitude of C export by transporting surface-ingested material in their guts to deep waters where it can be metabolized (Steinberg and Landry, 2017). Zooplankton molting or mortality at depth can also contribute to the transportation of assimilated organic

biomass into the deep waters (Ducklow *et al.,* 2001). The biological pump process is also thought to be related to the size structure of dominant zooplankton. This because some groups with large body sizes may exhibit a greater range of vertical migration and sometimes higher levels of biomass, and so influencing the biogeochemical fluxes (Dai e*t al.,* 2016; Ducklow *et al.,* 2001). However, the effect of variable size structure on DVM performance and its consequence for active C transport

5   has not indeed been assessed. Size-structure is certainly related to zooplankton composition which has hardly been properly addressed when examining the role of DVM on C flux. For instance, in areas with hypoxic subsurface layers some species are more active migrants and thus more efficient C-transporters, because they have developed adaptations to low oxygen conditions and can even use the OMZ as their habitat, either temporarily or permanently (Escribano et al., 2009; Gonzalez and Quiñones, 2002; Seibel, 2011).

10   C-export to depth may also depend on the amount of biomass being produced in the photic zone. Primary production promotes zooplankton feeding and growth and therefore determining C availability for both passive and active transport to depth. In this context, highly productive upwelling zones can be assumed as systems where the C-flux mediated by zooplankton DVM can be enhanced, although certainly depending on the size and taxonomic structure of zooplankton. In these regions, a shallow OMZ might exert a further impact on the C-flux by affecting DVM or zooplankton metabolism at depth. In the present study,

15   based on high resolution sampling and automated analysis of mesozooplankton, we assessed zooplankton vertical migration and downward C to the OMZ in the highly productive upwelling region of Northern Chile. We aimed at understanding the role that taxonomic and size-structure can play in the magnitude and variability of the DMV behavior interacting with a shallow OMZ, and the implications this interaction can have in the magnitude of downward C in a highly productive coastal upwelling zone

20   **2 Methods**

2.1 Study Area

The study area was located in the eastern South Pacific Ocean and covered the coastal zone of the northern upwelling region of Chile (21-29ºS) (Fig. 1) which is a region known to be subjected to wind-driven upwelling throughout the year and containing an intense and shallow OMZ (Ulloa *et al.,* 2012). The sampling design comprised three stations: Two stations (St.

25   T3 and St.T5) across a zonal section off Iquique (20ºS) and a coastal station (St. L6) off Coquimbo (29ºS). The study was carried out during the LowPhox cruise conducted in October 2015 onboard the R/V *Cabo de Hornos*. At each station, temperature, salinity and dissolved oxygen (DO) were recorded from 1000 m (Sts. T5-T3) and 356 m (St. L6) using an oceanographic rosette equipped with SeaBird 911 (SBE 911 plus). Discrete water samples were also obtained for chemical measurements of oxygen and Chlorophyll-*a* concentration.

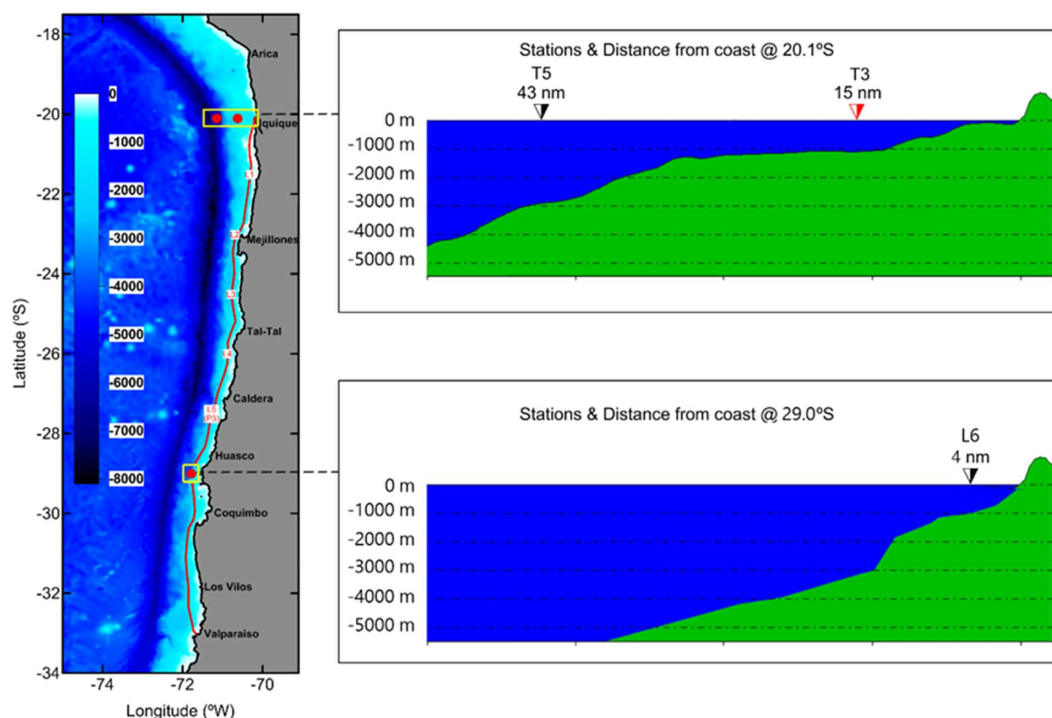



Figure 1. Study area indicating stations sampled during the LowPhox cruise performed in October 2015 onboard the R/V *Cabo de Hornos*.

2.2 Zooplankton sampling

5 Zooplankton samples were collected during daytime and nighttime conditions in two consecutive days at three stations off northern Chile (T5-T3-L6) (Fig. 1), also as indicated in Table. 1. Zooplankton hauls were performed from 600 to 0 m depth with a Multi Plankton Sampler Hydro-Bios MultiNet system with a 0.25 m² opening area and equipped with 200-µm mesh-size nets. The MultiNet towing speed was 1 m s⁻¹ and the flowmeter was located in the mouth of the MultiNet to estimate the volume of filtered water. At each station, 40 discrete samples were obtained from 600 to 0 m depth. Each sample corresponded

10 to a different depth stratum (30-0, 90-30, 150-90, 400-150 and 600–400m). The thickness of these strata was defined according to distribution of oxygen concentration and localization of the OZM. These strata were assumed to represent the near surface oxygenated later, the upper oxycline, the upper OMZ, the OMZ core and below the OMZ. Once onboard the collected zooplankton samples were preserved immediately in 5% buffered formalin-seawater solution.

Table 1. Sampling data for Multinet tows by day (D) and at night (N) for five depth strata at three stations off northern Chile, during spring 2015.

Station	Haul	Date	Time	Latitude	Longitude	Sampling Depth (m)
St. T5	D1a	29/11/2015	9:30	-20.05	-70.53	0-600
	D1b	29/11/2015	16:30	-20.05	-70.53	0-600
	N1a	30/11/2015	2:30	-20.05	-70.53	0-600
	N1b	30/11/2015	4:30	-20.05	-70.53	0-600
	D2a	30/11/2015	10:30	-20.05	-70.53	0-600
	D2b	30/11/2015	15:00	-20.05	-70.53	0-600
	N2a	30/11/2015	22:30	-20.05	-70.53	0-600
	N2b	01/12/2015	4:30	-20.05	-70.53	0-600
St. T3	D1a	02/12/2015	14:30	-20.07	-70.25	0-600
	D1b	02/12/2015	18:00	-20.07	-70.25	0-600
	N1a	03/12/2015	0:15	-20.07	-70.25	0-600
	N1b	03/12/2015	5:00	-20.07	-70.25	0-600
	D2a	03/12/2015	12:00	-20.07	-70.25	0-600
	D2b	03/12/2015	16:00	-20.07	-70.25	0-600
	N2a	04/12/2015	23:30	-20.07	-70.25	0-600
	N2b	05/12/2015	0:15	-20.07	-70.25	0-600
St. L6	D1	09/12/2015	10:31	-29.29	-71.36	0-600
	N1	09/12/2015	22:30	-29.29	-71.36	0-600
	D2	10/12/2015	8:14	-29.29	-71.36	0-600
	N2	10/12/2015	5:00	-29.29	-71.36	0-600

2.3 Taxonomic and size measurements

Taxonomic identification and enumeration were carried out by analysis of digitized images obtained with the Hydroptic
5 ZooScan digital imaging system (Gorsky *et al.,* 2010). Each sample was wet-sieved through a 1000 µm mesh into two size
fractions. Then, each size-fraction subsample was fractionated separately with a Motoda splitter until the zooplankton
concentration was sufficiently diluted to avoid contact between organisms on the ZooScan scanning frame. Separation of the
small and large objects and consequent separate image acquisition of the two size classes prevented underestimates of large-
rare objects which may need less fractioning (Gorsky *et al.,* 2010). 179 subsamples were scanned and digitized at a resolution
10 of 2400 dpi after manual separation of objects on the scanning tray. After processing the samples with Zooprocess, each of the
objects was automatically sorted with the help of a learning set, and then the sorting was visually validated by an expert (for
details, see Chang *et al.,* 2012; Gorsky *et al.,* 2010). Organisms making up the ZooScan datasets were enumerated, measured,

biomass-estimated and classified into 27 taxonomic groups, such as copepods, chaetognaths, euphausiid, gelatinous and other zooplankton (Table 2). The abundance (ind. m^{-3}) of total zooplankton or of each taxonomic group was calculated following Eq. (1):

$$Abundance/m^3 = \frac{N*Subpart}{Vol*Townb},$$ (1)

5 were, N is the number of individuals with same prediction (e.g., in last column written "copepod"), Subpart is the splitting ratio, Vol is net volume and Townb is the number of net tows in a sample.

2.4 Biomass estimates

The ZooScan Integrated System also provided zooplankton body size. Then the ellipsoidal biovolume (EBv) was computed instead of equivalent spherical diameter (ESD). Biovolume was used because most of the zooplankton shapes were elongated,

10 and also because ESD overestimates biovolume since spheres have a higher volume: cross-sectional-area ratio than other shapes (García-Comas *et al.,* 2014; Herman and Harvey, 2006; Sprules *et al., 1*998). Ellipsoidal biovolume EBv (mm^3) was calculated following Eq. (2):

$$EBv = \frac{4}{3} * \pi \left(\frac{Major}{2}\right) * \left(\frac{Minor}{2}\right),$$ (2)

where, the EBv corresponds to the biovolume of a prolate ellipsoid, Major is longest axis of the object and Minor is minor axis

15 of a perfect ellipse of the same area of the object measured, both axes are in mm and were provided by ZooScan. We used EBv (mm^3) for estimating biomass (mg C) for all taxonomic group. Conversion from the EBv to carbon were made in three steps: First EBv was converted into wet weight (WW), assuming 1 mm^{-3} was equivalent to 1 mg WW (Wiebe *et al.,* 1975). Then WW was converted to dry weight (DW) assuming that the water content of zooplankton was 90% (DM = 0.1 × WW), as shown by Matsuno *et al.* (2009). Finally Individual biomass was converted to carbon using published regression equations relating

20 organism size, area or volume to individual weight.

To calculate the migrant biomass we subtracted each night profile from the corresponding day profile to show only daily changes involving migrants as in Putzeys *et al.* (2011). The negative values of the biomass day-minus-night profile correspond to migrant biomass that reached the epipelagic layer at night including organisms inhabiting above and below 600 m by day.

2.5 Patterns of vertical distribution of migrating zooplankton

25 For the analysis of vertical distribution of organisms, the density estimates of the organisms were standardized to number of individuals per 1000 m*3* (for each stratum) or per m*2* (for the entire water column explored). In order to quantify the presence and extent of DVM of various taxa at each station, we calculated both night: day (N:D) ratios in each stratum and weighted mean depth (WMD) for zooplankton biomass and for abundance, as a measure of the center of gravity of a population's vertical distribution for each taxon and haul, in according to Andersen *et al.* (2004) following Eq. (3):

30 $$WMD = \frac{\Sigma(ni*zi*di)}{\Sigma(ni*zi)},$$ (3)

where, *di* is the depth of a sample *i* (centre of the depth interval), *zi* the thickness of the stratum and *ni* the number of individuals per 1000 m³ at that depth.

We calculated the amplitude of vertical migration (ΔDVM) as the difference between the mean depth of the organism *i* during the day and the night. To determine the DVM behavior, the difference of the average values of WMD between day and night

5 for each taxon was assessed. Positive values indicated normal DVM (pattern of nocturnal ascent by individuals that reside at depth by day) and negative values indicated reverse DVM (pattern of nocturnal descent by individuals that reside near the surface by day). The individuals that occupied the same depth stratum by day and by night, whether near the surface or at depth were considered as non migrant in according to Ohman (1990).

2.6 Multivariate analysis

10 For statistical analysis, as a criterion for determining if the DVM was significant, we tested for differences in the WMD mean between day and night using a two-tailed t test. We considered the occurrence of DVM when the difference in the WMD mean between day and night was significant ($p < 0.05$). In order to evaluate the similarity/dissimilarity in the abundance and biomass among station, strata, and day–night conditions, the multivariate grouping techniques were applied ("cluster analysis"), ANOSIM (Two-Way Crossed Analysis) tests and multidimensional scaling (MDS) with the data transformed in PRIMER v

15 6.1.16 (2013), prior to the application of the Bray-Curtis similarity index (Bray and Curtis, 1957). In general, WMD for taxa did not exhibiting a pronounced bimodal vertical distribution.

3 Results

3.1 Hydrographic conditions

Vertical profiles of temperature, DO, and sigma-t show general oceanographic conditions in all stations (Fig. 2), as such as,

20 the structure of OMZ. By looking the vertical profiles of oxygen different layers were defined: A well oxygenated stratum with oxygen approaching air saturation (>250 µmol kg⁻¹ O₂) defined as oxic mixed layer (OX-ML), an upper O₂ gradient (oxycline), defined by the level where O₂< 4% of O₂ surface is intense (Paulmier *et al.,* 2006); at whose base is located the upper boundary of the OMZ (45 µmol O₂ isoline, OMZ-UB) (Escribano *et al.,* 2009; Hidalgo *et al.,* 2005; Morales *et al.,* 1999*)*; the OMZ core defined by a upper boundary (OMZ-UC) with lowest concentration of O₂ (<20−1 µmol kg⁻¹ O₂) and

25 lower boundary (OMZ-LC) (1−<20 µmol kg⁻¹ O₂) and finally a lower O₂ gradient (OMZ-LW). The thickness of each of these strata was variable among the stations and it was determined in according to described by Paulmier *et al.* (2006).

Across the zonal section off Iquique the offshore station (St. T5) and onshore station (St. T3) showed two contrasting hydrographic regimes with regard to the OMZ. Station T5 usually had a less pronounced and thicker OMZ than station T3. At

30 both stations of 5 strata were well defined in the water column (Fig. 2). The OX-ML (>250 µmol kg⁻¹ O₂) was present at 18 m (St. T5) -15 m (St. T3) of depth. The oxycline exhibited a continuum decrease from oxic (~250 µmol kg⁻¹ O₂) to suboxic (<20

µmol kg^{-1} O^2) conditions associated with a strong stratification at about 80 m depth on average in both stations. The 45 µmol O$_2$ isoline (OMZ -UB) was present at the base of the oxycline at 70 m (St. T5) and 59 m (St. T3). The OMZ core (<20 µmol kg^{-1} O^2) was located below the thermocline and below the 26.5 kg/m3 isopycnal according to Paulmier *et al.* (2006). In in the oceanic station (St. T5) it was located between 80 to 514, while in the coastal station (St. T3) it was between 80 to 507 m of

5   depth with 423 m thickness. The O$_2$ concentrations in the core was 1 µmol kg^{-1} O^2. The OMZ-LW at both stations was delimited above the core and below the depth where the O$_2$ slope changes significantly (slope break >20 µmol /m) (Fig. 2).

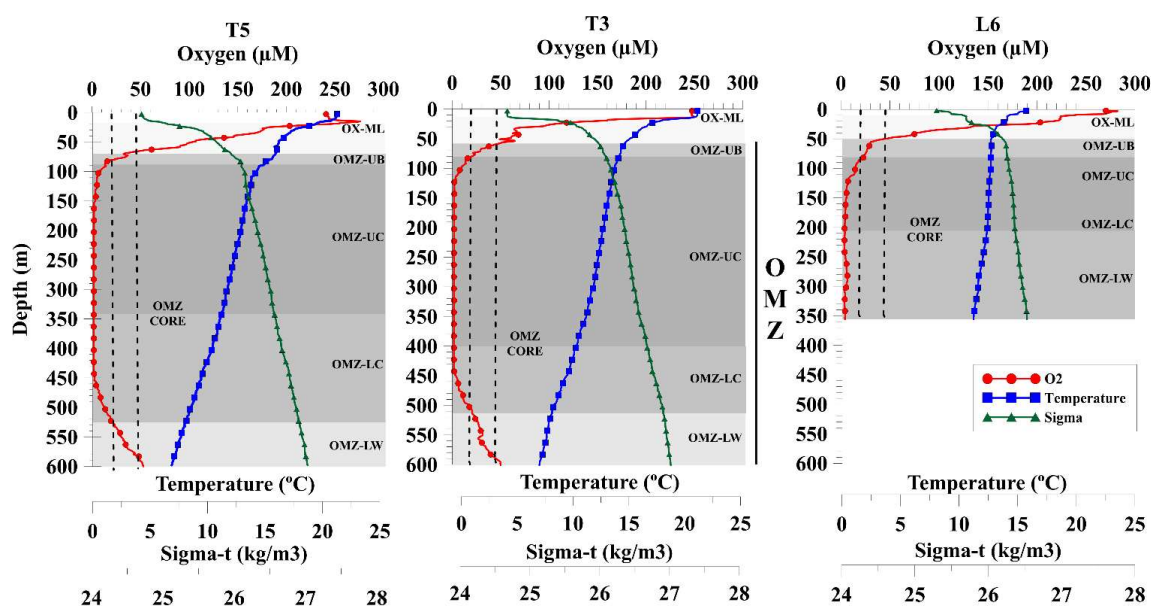



Figure 2. Vertical profiles of dissolved oxygen (O*2*), temperature and sigma-t at 3 stations off northern Chile, during spring 2015. The dashed line represent the 20 and the 45 µmol O2 isoline, respectively.

The structure of OMZ at the coastal station (St. L6) off Coquimbo (29ºS) (Fig.1), exhibited similar characteristics to St. T3 (21ºS), but in this area the OMZ was deeper and thinner. The OX-ML was present at 10 m. The OMZ -UB (45 µmol O$_2$) in the base of oxycline was down to 50 m. The low O$_2$ concentrations in the core was less intense than at 21ºS (4 to 20 µmol kg^{-1} O^2) and it was located below 90 m (Fig. 2). The OMZ-LW could be recorder, but according to Paulmier *et al.* (2006) generally

15   it was delimited above the core and below the depth where the O2 slope changes significantly (>4 µmol /m).

3.2 Zooplankton composition and abundance

A total of 27 zooplankton taxa were identified during the study period **(Table 2).** The number of taxa varied among stations and strata (Table 2). Across to zonal section off Iquique the number of taxonomic groups fluctuated between 23 (St. T3) and 26 (St. T5), whereas 25 taxa were present off 29ºS (St. L6). The most dominant taxa in each stations both daytime and night

5 conditions, were: Copepods (Small (SC.), Large (LC.), Eucalanidae (EC.) and Acartia (AC.)) constituting 86% (in St. T5), 80% (in St. T3) and 67% (in St. L6); Eggs Fish (EF.) constituting 2% (in St. T5), 5% (in St. T3) and 6% (in St. L6); Nauplius Larvae (NL) 1% (in St. T5), 1% (in St. T3) and 7% (in St. L6); Appendicularia (AP.)5% (in St. T5), 4% (in St. T3) and 3% (in St. L6). The remaining 19 groups only constituting 5% (in St. T5) 8% (in St. T3) and 12% (St. L6). (Fig. 3). Because these 7 taxonomic groups represented 91% of the average of the total abundance in the study area, we hereafter assumed that they

10 represented the whole zooplankton community and therefore we used them for the vertical distribution analysis. The total integrated abundance of zooplankton in the study area ranged from 254,171 to 742,469 ind. m^{-2} (mean 480.037 ind. m^{-2}). As based on a Two-Way Crossed Analysis ANOSIM test, this water-column integrated abundance showed no significant differences between day and night samples ($p > 0.05$).

15 **Table 2-** Daily average of relative abundance (ind. m^{-2}) for the 27 zooplankton groups sorted in this study during daytime/ night condition at three stations off northern Chile, during spring 2015. Each depth stratum represents a specific oxygen condition

Taxa	OX ML	OMZ				Total	OX ML	OMZ				Total	OX ML	OMZ				Total
		St. T5						**St. T3**						**St. L6**				
		UB	UC	LC	LW			UB	UC	LC	LW			UB	UC	LC	LW	
						Major Groups												
SC.	46	27	4	1	2	81	47	17	8	1	2	75	32	17	5	3	4	62
LC.	3	2	< 1	< 1	< 1	5	3	1	< 1	< 1	< 1	5	3	3	1	< 1	1	7
AC.	0	< 1	0	0	0	< 1	0	0	0	0	0	0	< 1	0	< 1	0	0	< 1
EC.	0	0	0	< 1	< 1	< 1	0	< 1	0	0	< 1	< 1	< 1	0	< 1	< 1	0	< 1
EF.	1	< 1	< 1	< 1	< 1	2	2	1	< 1	1	< 1	5	2	3	< 1	< 1	< 1	6
NL.	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	6	1	< 1	< 1	< 1	7
AP.	3	1	< 1	< 1	< 1	5	4	< 1	< 1	< 1	< 1	4	2	1	< 1	< 1	< 1	3
Others	3	2	1	1	< 1	6	5	3	1	1	< 1	11	6	6	1	1	1	15

Regional difference among stations (Two-Way Crossed Analysis ANOSIM $p < 0.05$) were found, therefore, the different stations were treated independently. In general, across to zonal section off Iquique the abundance showed the lowest values at

onshore station (St. T3- 18%), which was characterized by the strongest and most extensive OMZ in the study area, these values increased at the offshore station (St. T5- 31%), where the OMZ was less pronounced and thicker than in St. T3. Unlike the zonal section, the onshore station off 29ºS (St. L6) had a weaker and less extensive OMZ showing the highest abundance (51%) (Table 2).

3.3 Diel vertical migration (DVM) and Vertical Distribution

3.3.1 Main migrant groups of zooplankton

The diel vertical migration of 27 zooplankton taxa in the 0–600 m water column is shown in **Figure 3**. These taxa were classified into four groups in according to their ΔDVM **(Table 3)**: **1) Stronger migrants**, represented by taxa that exhibited a strong DVM and showed a broad range of ΔDVM 225 -99 m (in St.T5), 440-84 m (in St. T3) and 208 -87 m (in St. L6). This group constituting 70% of taxa with higher ΔDVM. The composition of taxa in this group was variable at each station **(Table 3)**, but in general it was represented by Eucalanidae Copepods (EC.), Euphausiids (EU.), Acartia Copepods (AC.), Ctenophores (CT.), Decapoda (DC.), Annelida (AN.), Bryozoan (BR.), Pteropoda (PT.) and Chaetognatha (CH.). These taxa were mostly concentrated in the oxic surface stratum (**OX-ML),** and **OMZ core** showing a strong interaction both with **OMZ-UC** and the **OMZ-LC** strata, changing from normoxia to hypoxia condition and vice versa between 0 to 550 m **(Fig. 3). 2) Intermediate migrants,** represented by taxa that exhibited a moderate DVM and showed a range of ΔDVM 73 -34 m (in St. T5), 70-27 m (in St. T3) and 49 -22 m (in St. L6). This group constituting 23% of taxa with moderate ΔDVM. The composition of taxa in this group was also variable at each station **(Table 3)**, but in general it was represented by small (SC.) and large Copepods (LC.), Amphipoda (AM.), Cirripedia Larvae (CL.), Gastropoda (GA.), Siphonophora (SIP), Appendicularia (AP). These taxa were mostly concentrated in the oxic surface strata (**OX-ML),** and **OMZ-UC** showing some interaction with **OMZ core,** spatially changing from normoxia to hypoxia condition, and vice versa between 0 to 200 m**. 3) Weaker migrants,** represented by taxa that exhibited a weak DVM and showed a range of ΔDVM 24-18 m (in St.T5), 23 -12 m (in St.T3) and 21 -11 m (in St. L6). This group constituted 5% of taxa of low range of ΔDVM. The composition of taxa in this group was also variable at each station **(Table 3)**, but in general it was represented by Hydrozoa (HY.), Salps (SA.), Platyhelminthes (PT.), Decapoda Larvae (DL.), Ostracoda (OS.), Nauplius Larvae (NL.) and Ichthyoplankton (IC.). These taxa were concentrated mainly in the oxic surface strata (**OX-ML)** and **OMZ-UP,** but also in **OMZ-UC** at the onshore station (Sts. T3-L6), showing much less interaction with **OMZ core,** while spatially moving from normoxia to hypoxia condition and vice versa between 0 to 100 m**. 4) Non migrants,** represented by taxa that did not exhibit DVM and showed a range of ΔDVM 16-0 m (in St. T5), 7-0 m (in St. T3) and 6 -0 m (in St. L6). This group constituting 1% of taxa with not significant ΔDVM. The composition of taxa in this group was also variable at each station **(Table 3)**, but in general it was represented by Egg Fish (EF.), Radiolarians (RA.) and Echinoderm Larvae (EL.).

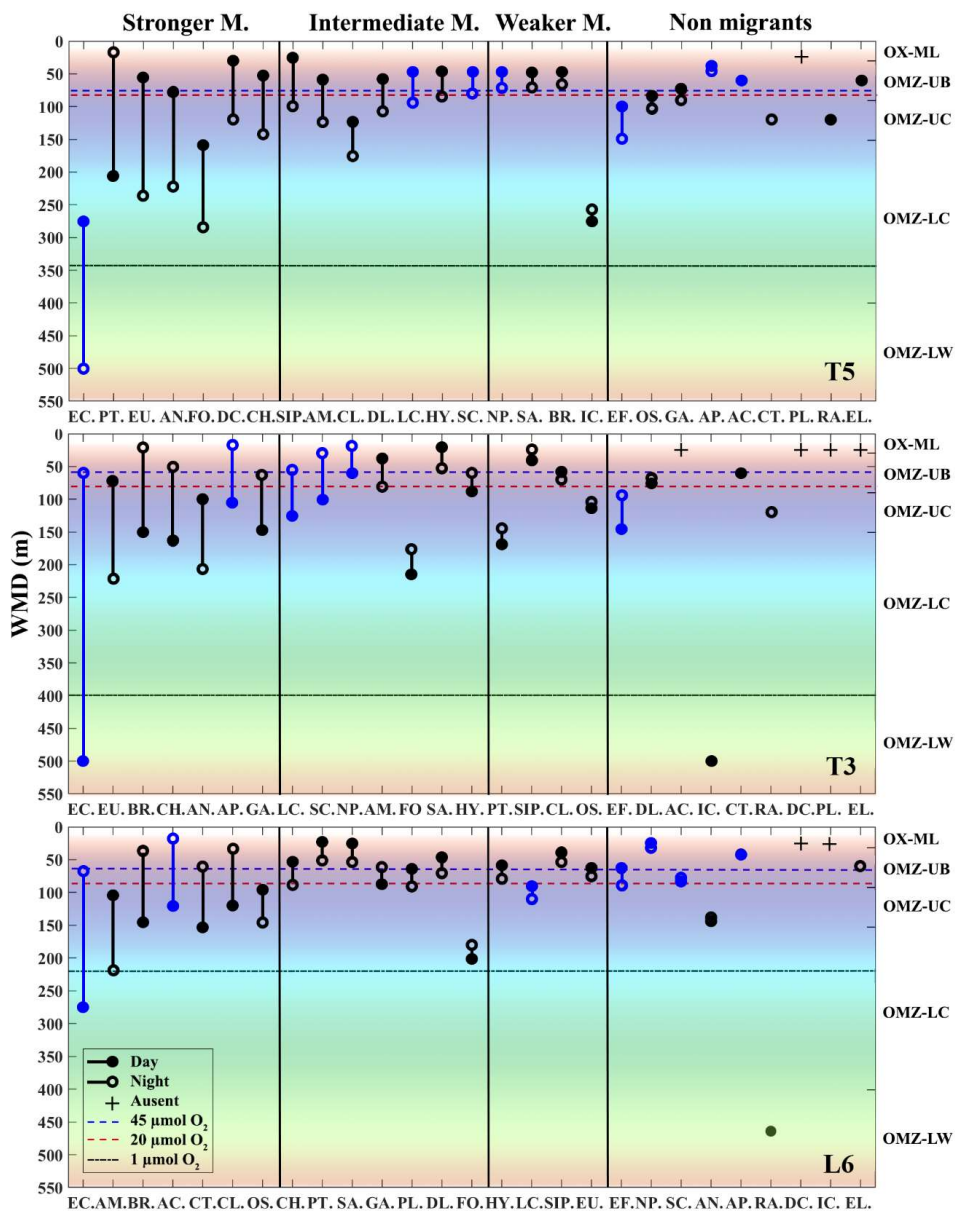



Figure 3. Weighed mean depth distribution (WMD) of zooplankton community within and outside to the OMZ off Iquique (Sts.T5-T3) and Coquimbo (St. L6) during 2015. The blue symbols represent major group of zooplankton. Background colour represents variable levels of oxygen as defined for each layer.

3.3.2 Distribution and DVM of major groups

Vertical distributions of zooplankton for the major taxonomic group sampled: Copepods Small (SC.), Large (LC.), Eucalanidae

5   (EC.) and Acartia (AC.), Eggs Fish (EF.), Nauplius Larvae (NL) and Appendicularia (AP.), as well as their patterns of strata–station–abundance relationships are illustrated in **Figure 4.** The abundance of zooplankton regarding depth strata was variable (ANOSIM $p<0.05$) at each station **(Table 2),** and therefore represented distinctive microhabitats characterized by specific depth and oxygen concentration feature. In general, the higher abundance was in the shallower strata and well oxygenated **(OX-ML - OMZ UP >50%)** (>250 μmol kg^{-1} O$_2$), and then decreased rapidly in the strata associated to OMZ core **(OMZ-UC**

10   **- OMZ-LC**). Below this stratum a slight peak in abundance was present at **OMZ-LW** at all stations, occurring between 400-600 m, both daytime and night condition. (Fig. 4).

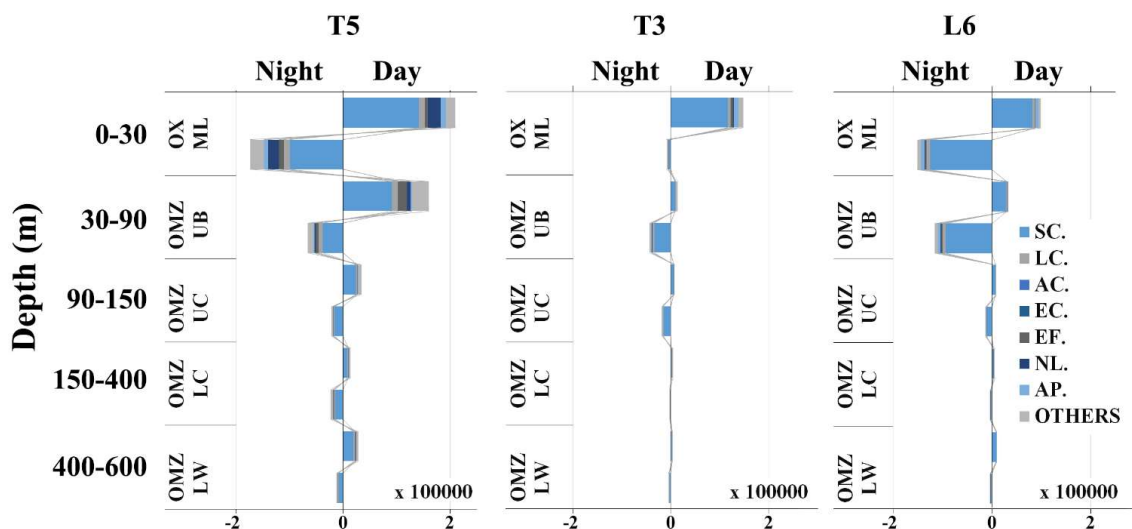



Figure 4. Vertical distributions of zooplankton for the major taxonomic group off Iquique (Sts. T5 and T3) and Coquimbo (St. L6) during consecutive days in spring 2015.

As expected, copepods dominated numerically the zooplankton community both within and outside to the OMZ **(Fig. 4).** The SC. were the most abundant copepods, followed by LC. **(Table 2),** whereas AC. and EC. showed the lowest abundance. The largest aggregation of theses group during the entire study period was observed at the offshore station St. T5 (86%), where abundances reaching up to 384,176 ind. m^{-2} were found **(Fig. 4).** Across of zonal section off Iquique, the highest abundances

20   and biomass were in the shallower strata **(OX-ML)** St. T5 (49%) and St. T3 (47%), and they were reduced in the core of the

OMZ St. T5 (4-1%) and T3 (8-1%) between 90-400 m, where oxygen had the lowest (< 20 μM -1μM). The abundances showed slight increase in the **OMZ-LW** stratum during daytime, where oxygen conditions started to restore again. At the onshore station off 29ºS (St. L6) with a weaker less extensive OMZ, the abundance showed similar vertical distribution. However the abundance of copepods was lowest in this station (67%) in comparison with stations off Iquique.

5   Diel vertical migration of copepods was pronounced at onshore stations (Sts. T3-L6), but the strength of migration was higher overall at St. T3 off Iquique, as indicated by the overall N:D ratio of SC. (3.29), LC. (2.28) and EC. (8.33), and by the migration indices (WMD- ΔDVM) **(Table 3).** The WMD for biomass and for abundance of these taxa showed over a broad range (17–500 m), which varied significantly among copepods groups and stations, both day and night samples (p < 0.05) **(Fig. 5A-5B).** During the night, at the offshore station (St. T5) most of the copepods exhibited normal DVM and they were concentrated mainly in the oxic surface strata (**OX-ML),** and **OMZ-UB** (40-60 m) without interacting with the OMZ; except for Eucalanidae which concentrated deeper in the **OMZ-LC** stratum, associated to the lower core of the OMZ and showed a high ΔDVM (225m). During the day, these four groups tended to live deeper in the stratum associated to the lower core of OMZ (**OMZ-UC**) and Lower O_2 gradient (OMZ-LW) except for small copepods that remained at the **OMZ-UB** stratum and showed a less ΔWMD (34 m). At offshore stations (Sts.T3-L6) the most of the copepods exhibited inverse DVM, except for Large C. that showed slight normal DVM at St. L6 off 29ºS. At night copepods tended to concentrate deeper in the stratum associated to lower core of OMZ (**OMZ-UC**) and Lower O2 gradient (**OMZ-LW),** in special Eucalanidae C. that exhibited a strong DVM with high ΔWMD 440 m (St. T3) and 208 m (St. L6) and Acartia 103 m (St. L6) **(Table 3)**, whereas at St. L6 SC. were caught in abundance at the **OMZ-UB** stratum down to 82–90 m depth, respectively **(Fig. 5A-5B).** During the day however copepods tended to remain shallower than at night, although they concentrated at different depths. Small copepods tended to concentrate in the oxic surface strata **OX-ML** (St. T3) and remained in the upper boundary of the OMZ (St. L6) without a detectable DVM, as judging by the small difference between their day- and night-time distributions (ADVM – 4 m), LC, as expected showed a normal migration and tended to stay inside the OMZ and concentrated in the **OMZ-UC** stratum (St. L6) and **OMZ-UB** (St. T3). Eucalanidae that exhibited a strong DVM tended to distribute in the **OMZ-UC (**St.T3**)** and **OMZ UB** (St. L6) **(Fig. 5A-5B).**

25   The second most abundant taxa of zooplankton, Egg fish showed the largest aggregation at the onshore station St. L6 (6%), with a weaker less extensive OMZ, where abundances made up to 41695 ind. m^{-2} **(Fig. 4)**. The WMD of Fish Eggs showed a range between 64 and 149 m depth **(Table 3)** and appeared to aggregate deeper in the whole study area, also present in the OMZ **(Fig. 5)**. The abundance and biomass of this group were mainly concentrated in the lower core of OMZ (**OMZ-UC**) both by day and at night. Off 29ºS (St. L6) during daytime they tended to concentrate in the stratum associated with the **OMZ-UB (Fig. 5A-5B).**

30   Similarly, most of the individuals of Nauplius Larvae showed the largest aggregation at the onshore station St. L6 (7%), where abundances up to 41695 ind. m^{-2} were found **(Fig. 4)**. The abundance and biomass of this group increased in the oxic surface strata **OX-ML** both by day and at night. No DVM was discernible in this station **(Fig. 4)**, because of the slight difference between their day- and night-time distributions. By contrast, at onshore station St.T3 they appeared to perform a weak DVM

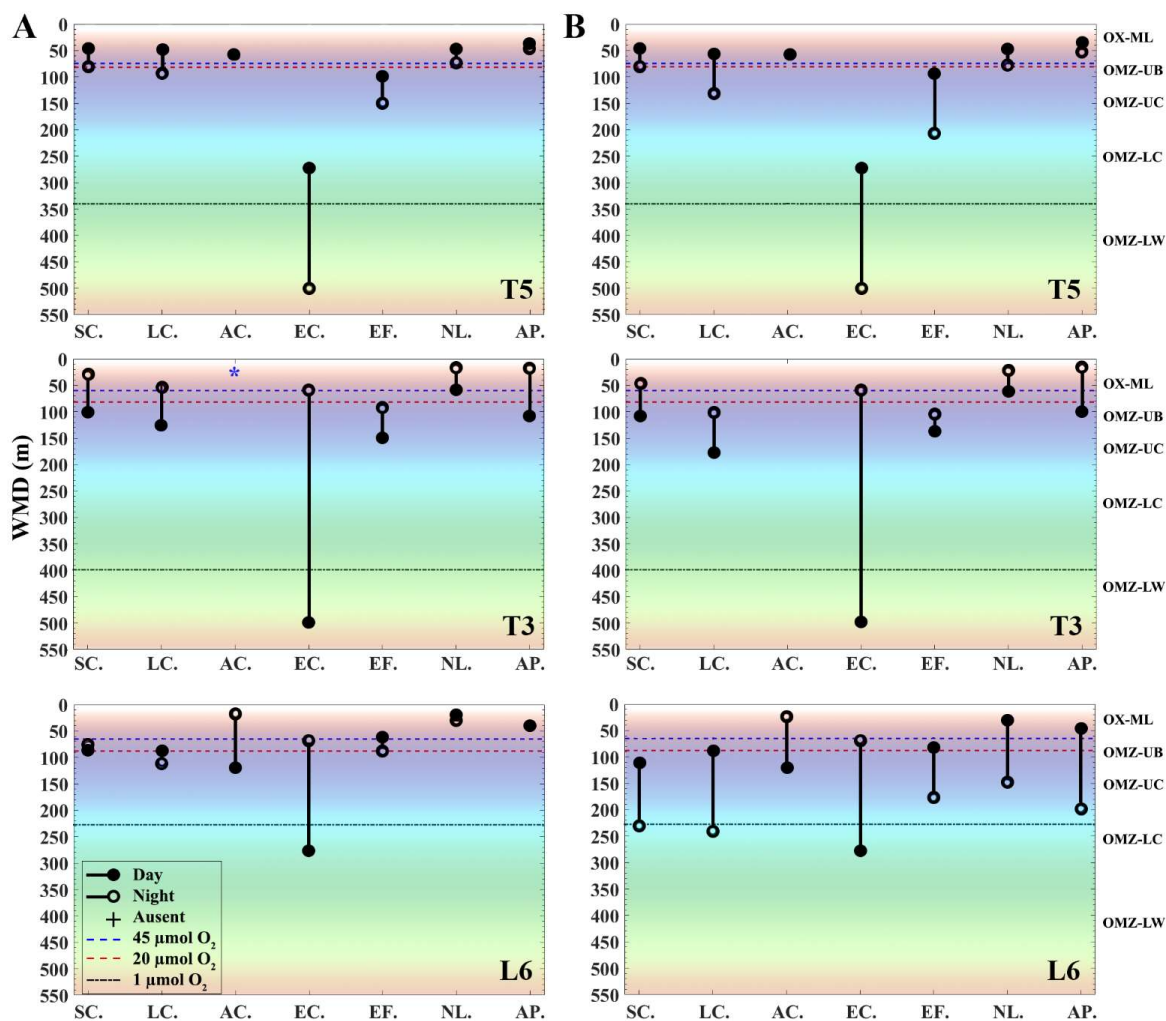
in the **OMZ-UB** stratum at night, as indicated by the overall N:D ratio (3.31) and by the migration indices (WMD-ΔDVM) **(Table 3).**

5 **Figure 5.** Dominant habitat and daily movements of zooplankton major taxa within and outside to the OMZ structure off Iquique (T5-T3) and Coquimbo (L6) during two consecutive days in 2015. **A** WMD of abundance of zooplankton community and **B** WMD of biomass of zooplankton community. Background colour represents variable levels of oxygen as defined for each layer.

Table 3- Diel vertical migration indices for 27 taxa sorted in this study at 3 stations off northern Chile, during spring 2015. Average of weighted mean depth, WMD (m) for daytime (D) and night (N) (see methods). Amplitude of the migration, ΔDVM (m). Positive values indicate normal DVM and negative values indicate reverse DVM.

T5-WMD				T3-WMD				L6-WMD				MIGRANTS
TAXA	D	N	ADVM	TAXA	D	N	ADVM	TAXA	D	N	ADVM	
EC.	500	275	225	EC.	60	500	-440	EC.	68	275	-208	Stronger Migrants > 5%
PT.	17	205	-188	EU.	222	73	149	AM.	219	104	115	
EU.	236	56	181	BR.	22	150	-129	BR.	38	145	-107	
AN.	222	77	145	CH.	51	164	-114	AC.	17	120	-103	
FO	285	159	126	AN.	206	101	105	CT.	60	154	-94	
DC.	120	30	90	AP.	18	106	-88	CL.	33	121	-87	
CH.	142	54	88	GA.	63	147	-84	OS.	145	96	49	
SIP.	99	26	73	LC.	55	125	-70	CH.	88	54	35	Intermediate Migrants > 2%
AM.	124	60	64	SC	31	101	-70	PT.	52	23	29	
CL.	175	124	51	NP.	18	61	-42	SA.	54	25	29	
DL.	108	58	50	AM.	80	39	42	GA.	61	88	-27	
LC.	94	47	47	FO	176	214	-38	PL	90	64	26	
HY.	85	46	39	SA.	52	20	32	DL.	70	48	22	
SC	80	47	34	HY.	60	88	-27	FO	180	202	-22	
NP.	71	47	24	PT.	145	168	-23	HY.	79	58	21	Weaker Migrants > 1%
SA.	71	48	23	SIP.	24	39	-15	LC.	109	90	19	
BR.	66	47	18	CL.	71	59	12	SIP.	53	38	15	
IC.	258	275	-18	OS.	105	114	-9	EU.	74	63	11	
EF	149	100	49	EF	94	146	-52	EF	89	64	25	Non Migrants <1%
OS.	101	85	16	*DL.*	69	76	-7	NP.	31	25	6	
GA.	90	75	15	AC.	-	-	-	SC	78	82	-4	
AP.	46	39	7	IC.	-	500	-	AN.	138	143	-4	
AC.		60	-	CT.	-	60	-	AP.	43	41	2	
CT.	120	-	-	RA.	120	-	-	RA.		464	-	
PL.	-	-	-	DC.	-	-	-	DC.	-	-	-	
RA.	-	120	-	PL.	-	-	-	IC.	-	-	-	
EL.	-	60	-	*EL.*	-	-	-	*EL.*	60	-	-	

The other main taxa, Appendicularia showed the largest aggregation at the onshore station T5 (5%), where abundances reached up to 21848 ind. m^{-2} were found **(Fig. 4)**. The abundance and biomass of this group were mainly concentrated in the oxic surface strata **OX-ML** at St. T5 and St. L6 both by day and at night. No DVM was attributed in these stations, judging by the

5 small difference between their day- and night-time distributions, while at onshore station St. T3 appeared to perform a strong inverse DVM in **OMZ-UC** stratum at night, as indicated by the overall N:D ratio (5.91) and by the migration indices (WMD-ΔDVM) **(Table 3).** The WMD at this station showed a range between 18 and 106 m depth and ΔDVM of 88 m depth **(Fig. 4)**.

3.3.3 Others groups with vertical distribution associated to OMZ UC

The remaining 19 groups that only constituting 5% (in St.T5) 8% (in St.T3) and 12% (in St.L6) in abundance, they showed

10 different behaviors at each station: Normal DVM (in St.T5) and inverse DVM (in Sts.T3-L6) **(Table 3).** These groups clearly exhibited different daytime and night depths associated to **OMZ core (OMZ UC-LC).** Overall they tended to live deeper by day and shallower by night at in St. T5 than at the other sites **(Fig.3).**

3.4 Distribution of biomass and Migrant biomass

The vertical distribution and daytime vs. nighttime variability of zooplankton biomass showed distinctive features associated

15 to OMZ structure, with significant difference ($p<0.05$) between strata in both daytime and nighttime sampling as based on the ANOSIM test. In the whole area most of the biomass was concentrated in a narrow band within the OX-ML and OMZ UB strata, associated with more oxygenated surface waters, with reduced values in deeper waters associated with the OMZ core, in special at the onshore station off Iquique (St. T3) (Fig.6). Overall, we observed that highest values of biomass were present during the night, and they were concentrated above 150 m (negative values), whereas in the deeper strata it was weakened, as

20 expected from the effect of the DVM. Despite the fact that the zooplankton showed higher biomass during the night (**Fig.6**), the two-Way Crossed Analysis ANOSIM did not reveal a significant day–night difference ($p>0.05$). We observed a slight differences between day and night samples when comparing total biomass regardless the effects of strata suggesting that a small percentage of the zooplankton biomass migrated out of the upper 150 m during the day. However, these results can be underestimated due complex DVM behaviours (Normal-Inverse) (**Table 3**) that exhibit the taxa, depending on the species

25 composition in each station.

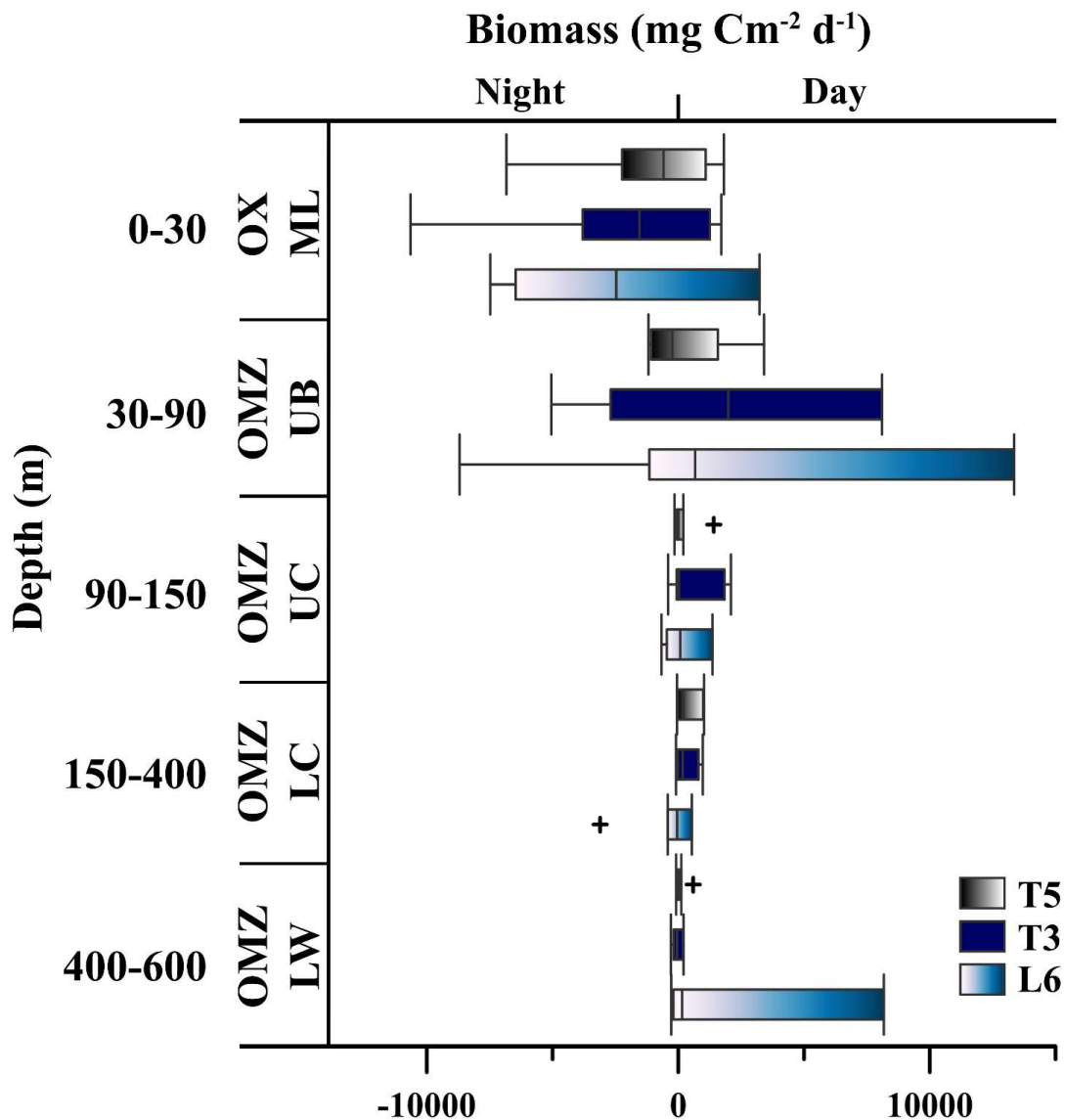
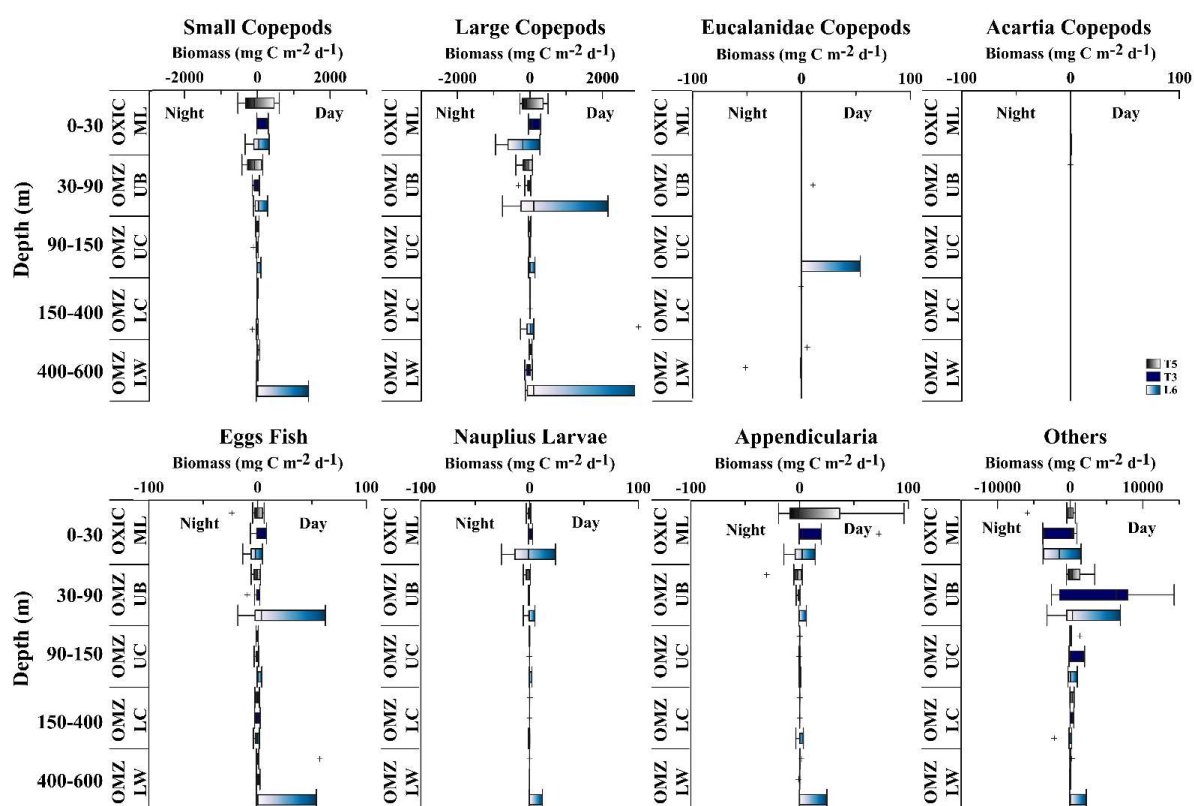



Figure 6. Differences in zooplankton biomass distribution between daytime and night in 3 station off Iquique (Sts.T5-T3) and Coquimbo (St. L6) during two consecutive days in 2015 are averaged in a boxplot, with error bars indicating the range. In each

box, the central black line represent the mean, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme data points not considered outliers and outliers are plotted individually (+).

Vertical distributions of zooplankton for the major taxonomic group sampled (Copepods, fish eggs, Nauplius larvae and
5   appendicularia) as well as the patterns of strata–station–biomass relationships are illustrated in Figure 7. Biomass of Copepods was several orders of magnitude more than other 6 groups, specially accounted by large and small Copepods. Although Eucalanidae and Acartia copepods showed a high ΔDVM (ca. 440 - 208 m), they had low biomass throughout water column in all stations.

10   **Figure 7.** Biomass profiles of the zooplankton major taxa off Iquique (Sts. T5-T3) and Coquimbo (St. L6) during consecutive days in spring 2015. Each depth stratum represents a specific oxygen condition.

3.4.1 Migrant biomass spatial patchiness of the major zooplankton taxa

The migrant biomass and spatial patchiness of the zooplankton taxa was reflected in the day-minus-night biomass profiles **(Fig. 8).** Biomass of these taxa was, in most situations, two orders of magnitude greater than the biomass of copepods. Biomass of Copepods was an order of magnitude more than other groups **(Fig. 8).** Some of these taxa, such as small and large copepods,

5 exhibited very strong migration in special at the onshore station off Iquique (St. T3), showing the highest biomass in a narrow band within the oxycline, but also in the OMZ-UB (St. T3). The magnitude of this migration also changed across of zonal section off Iquique (20ºS) specially at the offshore station (St. T5), which showed the lowest biomass in the whole study area. Subsurface mesopelagic peaks were present at onshore station off 29ºS (St. L6), occurring mainly between 400-600m, mirroring the mesopelagic peaks in total zooplankton biomass in this stratum **(Fig. 8).**

10 The Nauplius larvae and appendicularia showed the same behavior in all stations, with a slight increase of migrant biomass in the OX-ML stratum, except for appendicularia that also showed a subsurface peaks at the onshore station off 29ºS, occurring mainly between 30-90m.

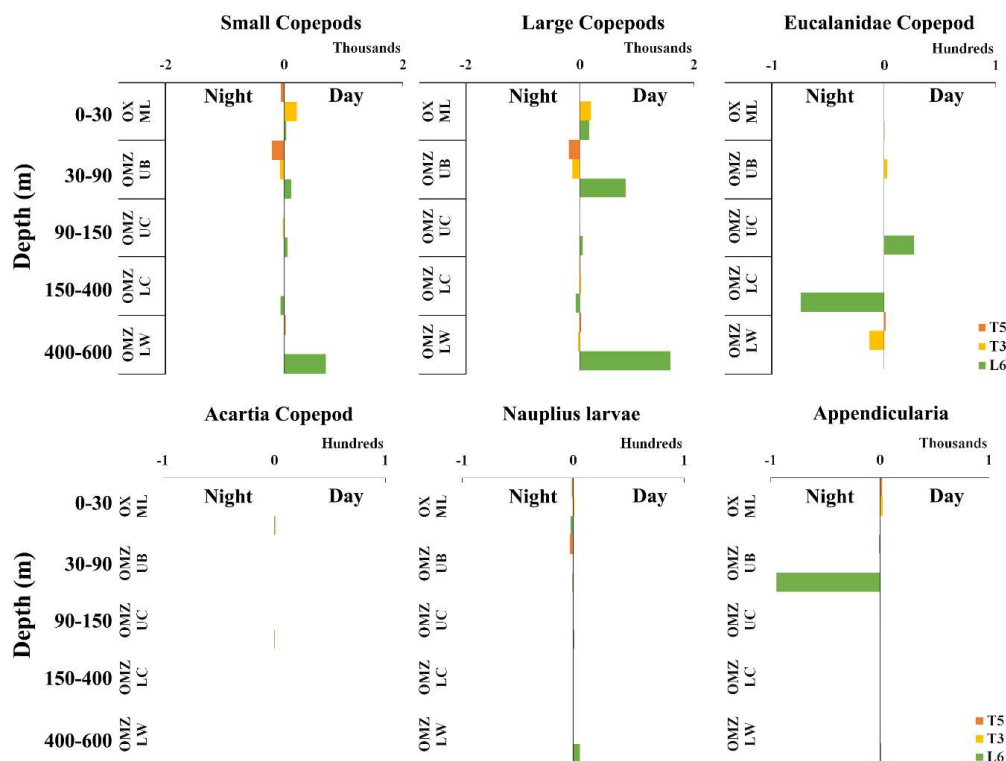



Figure 8. Migrant biomass (mg C m^{-2}): Day-minus-night profiles of average daily biomass in the water column off Iquique

15 (Sts. T5-T3) and Coquimbo (St. L6) during two consecutive days in 2015.

Table 4- Vertical distributions of mean biomass and migrant biomass (mg C m^{-3}) for the 27 zooplankton groups sorted by strata during daytime and night-time conditions.

Station		T5			T3			L6		
Strata		Day	Night	Migrant Biomass	Day	Night	Migrant Biomass	Day	Night	Migrant Biomass
30	0	29.36	101.37	-72.01	31.64	207.71	-176.07	53.71	156.89	-103.18
90	30	24.14	14.62	9.52	146.41	43.47	102.93	92.78	40.77	52.01
150	90	1.73	1.21	0.52	16.72	2.08	14.64	13.74	5.53	8.21
400	150	1.70	0.10	1.60	1.50	0.09	1.42	1.18	6.05	-4.88
600	400	0.75	0.19	0.56	0.57	0.73	-0.16	2.48	0.99	1.49

3.4.2 Rate of diel vertical migration

The rate of diel vertical migration (DVMR) is defined here as the net biomass (mg C m^{-3} day^{-1}) transferred daily from the upper mixed waters to below the thermocline (into the OMZ in our study). This movement of biomass in and out of the OMZ, mainly derived from the migrating behaviour of zooplankton with large migration amplitudes, implies the existence of a very efficient mechanism to incorporate freshly produced C into the OMZ system. In according to the groups previously defined by their ΔDVM (Stronger migrants, Intermediate migrants, weaker migrants and Non migrant) **(Table 5).** Overall, the highest DVMR (60%) was estimated at the onshore station (St. T3) off Iquique, characterized by the strongest and most extensive OMZ in the study area. The rate of migration was lower upon a decrease in intensity and extension of the OMZ at T5 (16%) and L6 (24%) station, which usually had a less pronounced and thicker OMZ than station T3, as it can be seen in **Figure 9**. The taxa with a highest DVMR varied at each stations, but in general they were represented by: Salps (37%), Chaetognatha (26%), Decapoda (7%), Appendicularia (6%), Euphausiids (5%), Large Copepods (5%) and Hydrozoa (5%).

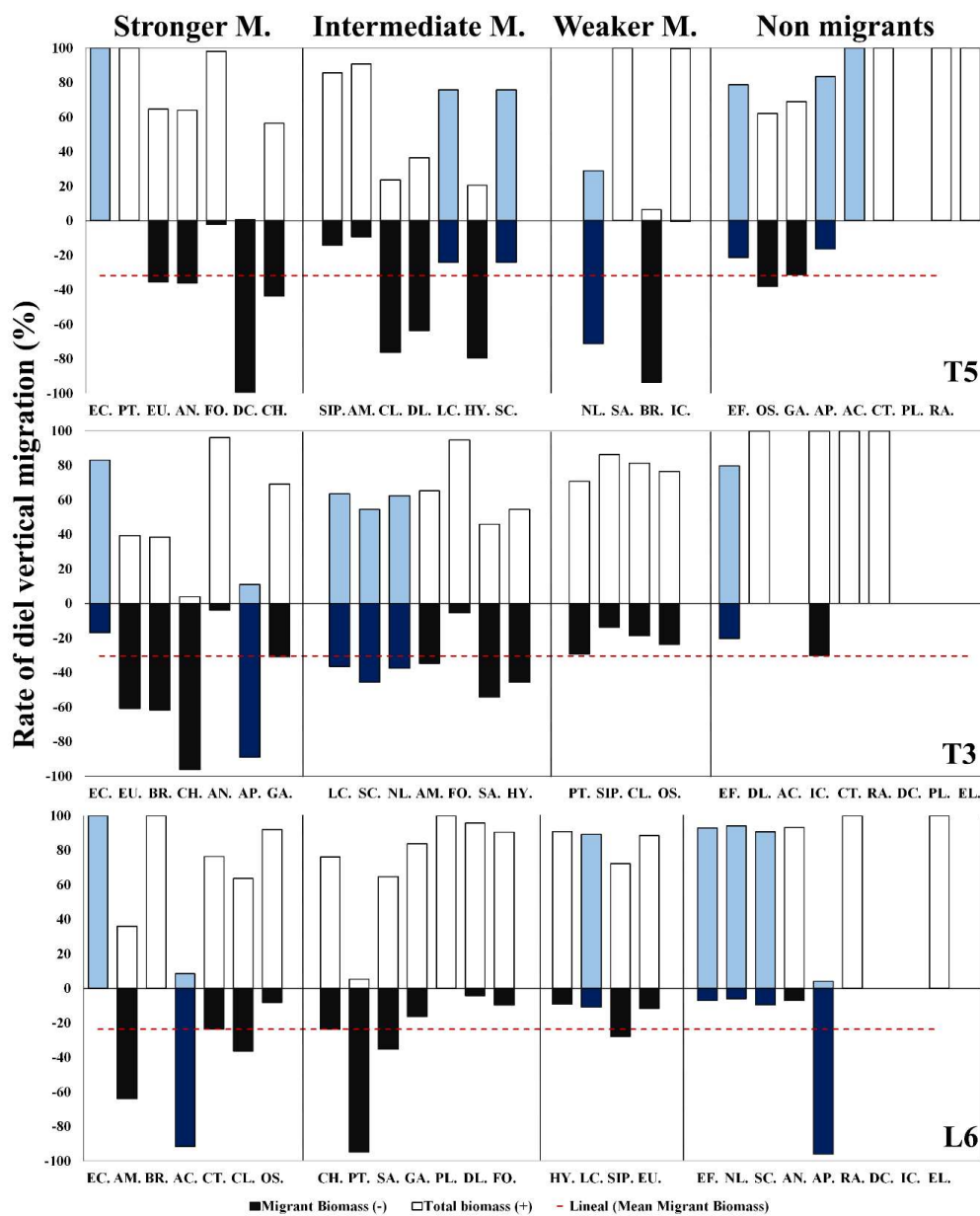



Figure 9. Rate of diel vertical migration for the 27 zooplankton groups sorted off Iquique (T5-T3) and Coquimbo (L6) during 2015. Gray bars represent the migrant biomass of zooplankton major groups

5 **Table 5-** Rate of diel vertical migration of biomass for the 27 zooplankton groups sorted off Iquique (T5-T3) and Coquimbo (L6) during 2015.

TAXA	T5	T3	L6	RATE OF DVM (mg C m² d⁻¹)
Salps	0.00	5851.57	675.60	2175.72
Chaetognatha	188.26	3462.59	1070.04	1573.63
Decapoda	1296.57	0.00	0.00	432.19
Appendicularia	9.96	26.30	1043.57	359.94
Euphausiids	209.63	531.44	212.29	317.79
Large Copepods	202.92	198.18	532.35	311.15
Hydrozoa	438.57	331.59	145.72	305.29
Small Copepods	266.81	210.54	155.92	211.09
Siphonophora	129.37	99.90	69.27	99.51
Annelida	51.36	8.28	145.27	68.30
Amphipoda	1.97	35.60	38.74	25.44
Decapoda Larvae	27.76	0.00	46.54	24.77
Ctenoforos	0.00	0.00	48.51	16.17
Ostracoda	9.07	7.76	28.57	15.13
Pteropoda	5.22	0.52	8.10	4.61
Nauplius Larvae	4.42	1.06	3.04	2.84
Cirripedia Larvae	0.38	0.05	2.97	1.13
Eucalanidae Copepod	0.00	2.65	0.03	0.89
Gastropoda	0.59	0.35	1.11	0.68
Foraminifera	0.05	0.01	1.73	0.60
Bryozoa	1.50	0.24	0.00	0.58
Acartia Copepod	0.00	0.00	0.81	0.27
Ictioplancton	0.06	0.00	0.00	0.02
Echinoderm Larvae	0.00	0.00	0.00	0.00
Platyhelminthes	0.00	0.00	0.00	0.00
Radiolario	0.00	0.00	0.00	0.00
TOTAL	2851.97	10772.97	4236.76	5946.86

4 Discussion

Studies on zooplankton DVM and active transport of C have been documented previously for the Pacific Ocean and other areas of the world's ocean, as we summarized in Table 6. However, downward C due to DVM in highly productive upwelling regions, such as northern Chile, which is characterized by severe subsurface hypoxic conditions associated with the OMZ, is

5 still poorly understood. Some studies have shown that hypoxic conditions can interfere with DMV of many meso- and macrozooplankton species (Wishner *et al.,* 2013; Ekau *et al.,* 2010; Escribano *et al.,* 2009; Apablaza and Palma, 2006; Antezana, 2002; Escribano, 1998). Studies show that small differences in oxygen concentration can make a large difference for zooplankton behavior, physiology and adaptation (Wishner *et al.,* 2018; Kiko *et al.,* 2016; Seibel, 2011; Gonzalez and Quiñones, 2002; Escribano, 1998). Therefore, it seems that the OMZ can plan a very significant role influencing vertical

10 distribution, DVM and ultimately the downward C mediated by zooplankton. For instance, the extension and intensity of DVM, in terms of the total amount of zooplankton biomass which can daily be exchanged between the mixed layer and the subsurface stratum below the thermocline, could greatly affect the magnitude of the downward C being released at depth.

Our approach to assess downward C into the Oxygen Minimum Zone, based on estimates of the migrant biomass and our proposed migration indices, allowed us on one hand to examine the contribution that zooplankton can have for vertical flux

15 and export production, and in the other hand to assess zooplankton responses (e.g. vertical distribution and DVM performance) to changes in environmental conditions over the vertical gradient, such as temperature, water density and the abrupt changes in oxygenation levels. In this subtropical upwelling region, vertical gradients are much stronger than in temperate upwelling zones. For example, the coastal zone in this region is more stratified and with a very shallow OMZ (<50 m) with a weak seasonal signal and moderate upwelling throughout the year (Paulmier and Ruiz-Pino, 2009; Fuenzalida *et al.,* 2009; Escribano

20 *et al.,* 2004). This means that zooplankton must cope with hypoxic conditions during their entire life cycle, except for some species that may reside in near surface water (<30 m), such as *C. chilensis* and *C. brachiatus* which have been reported as mostly restricted to the upper layer without performing any substantial DVM (Escribano *et al.,* 2012, 2009; Escribano and Hidalgo, 2000; Escribano, 1998).

The vertical distribution and diurnal variability of zooplankton biomass seem to be disturbed by the OMZ, such that high

25 biomass aggregates above the oxycline in a narrow band within the OX-ML and OMZ-UB layers, associated with more oxygenated surface waters, whereas extremely low biomass reside in deeper waters, in particular within the OMZ core. This condition was more evident in the coastal station off Iquique (St.T3), characterized by the most intense OMZ in the whole study area. In the eastern tropical north Pacific biomass distribution seemed different, exhibiting a secondary peak at depth during the daytime within the upper oxycline or OMZ core (Wishner *et al.,* 2013).

30 Despite the apparently hostile oxygen-deficient habitat, associated with the OMZ, we found that most taxa were able to perform DVM in the upwelling zone withstanding severe hypoxia. Even, several zooplankton groups are strong migrants, exhibiting large DVM amplitude (~500 m). Among them, a key migrant group is comprised by the copepods Eucalanidae which have been described as even being able to enter the core of the OMZ, and then migrate downward to the lower limit of the OMZ,

which is slightly more oxygenated (Hidalgo *et al.*, 2005). In our study however, their contribution to total migrant biomass was small (ca. 2.6 mg C m-² d⁻¹), as compared to the estimate made by Hidalgo *et al.* (2005). Other taxa, such as Euphausiids, Acartia spp., other copepods, Ctenophores, Decapoda, Annelida, Bryozoan, Pteropoda and Chaetognatha concentrated their populations inside the OMZ core showing a strong link to the OMZ with important movement through the water column.

5   Antezana (2010) showed that *E. mucronata*, an endemic and abundant euphausiid in the coastal upwelling zone off Chile, is a well-adapted species to vertically migrate into the core of the OMZ. In fact, the euphausiids studied here showed a large DVM amplitude (~250 m), descending into the core of the OMZ and below 250 m each day. In general, all strong migrants taxa seem to show a strong interaction with the core of OMZ, remaining there either temporarily or permanently during the day or night condition, contributing in this way to the release of C below the thermocline, despite presence of hypoxic conditions.

10   Our estimates of DVM-mediated fluxes showed that migrant biomass (5099 ±2701 mg C m⁻² d⁻¹) and C flux estimates (678± 465 mg C m⁻² d⁻¹) of the major taxa performing DVM, were greater than those reported for the Pacific Ocean, both in oligotrophic, such as Hawaii, and mesotrophic waters, as the subarctic North Pacific(Steinberg *et al.*, 2008), and even greater than that informed by Yebra *et al.* (2005) within eddies with enhanced biological production. Most of these previous estimates have not been done in regions with severe hypoxia or anoxia at midwater depths (eg. Kiko *et al.*, 2016), such as the highly

15   productive upwelling region of the coastal zone off northern of Chile, where the oxygen concentrations may fall below <1 µmol in the core of OMZ (Paulmier and Ruiz-Pino, 2009). Moreover only few works have considered the whole zooplankton community (Table 6). High productivity and strong aggregation of zooplankton in coastal areas of this region (Escribano *et al.,* 2000; Escribano and Hidalgo, 2000) may favour a greater availability of migrant biomass. This requires however that DVM should not be majorly constrained by presence of the DMV and that most migrant taxa are tolerant to low-oxygen. Our

20   estimates of downward C were substantially lower than previous ones reported off northern Chile by Hidalgo *et al.* (2005) for *E. inermis* alone (14.1 mg C m⁻² d⁻¹) and for copepods by Escribano *et al.* (2009) (7200 mg C m⁻² d⁻¹) (Table 7). Although, such previous estimates may exceed the level of primary production (~1000 mg C m⁻² d⁻¹) (Daneri *et al.*, 2000), suggesting that previous works may have overestimated active transport of C. The work of Escribano *et al.* (2009) was based on samples obtained with a Tucker Trawl net, which can be more efficient in capturing large-sized zooplankton or macrozooplankton

25   (Escribano *et al.,* 2007), as compared with the vertically towed Multinet. This means that our estimates mainly based on mesozooplankton may not include the contribution of macrozooplankton, and therefore such values may be greater.

Table 6. Comparison of active transport of carbon (AC) by vertically migratory taxa in Pacific Ocean. Diel vertically migratory taxa (DVM), productivity primary (PP), migrant biomass (MB), respiratory loss (R), faecal (F) and mortality (M). Where given by the author, estimated passive export (POC) is listed. Fluxes refers to carbon export beneath the epipelagic zone (150–200 m depth, depending on the study) in mg C m^{-2} d^{-1}

Location	Taxa	PP	MB	AC	RF	EF	MF	% POC	References
N. Hawaii ALOHA	DVM Zooplankton		108–216	7.1	2.6–4.8			12–18	Al-Mutairi and Landry (2001)
N. Hawaii ALOHA			157.9	3.2–13.6	3.7			18	Steinberg *et al.* (2008)
N.W. Pac.	DVM Metridia	418	144	9	3	5	1	23.1–61.8	Kobari *et al.* (2008)
N.W. Pac.	DVM copepods			8				22.3	Takahashi *et al.* (2009)
N.E. Pac.	Mesopelagic fishes	170			23.9				Davison *et al.* (2013)
Eastern Equator			96.0± 25.2		4.2± 1.2		2.9±0.8	18.4	Zhang and Dam (1997)
Eastern Equator	DVM zooplankton		154.8± 32.4		7.3± 1.4		5.4±1.1	25.4	Zhang and Dam (1997)
Central Equator (HNLC)			52.9		6		−	4	Rodier and Le Borgne (1997)
Western Equator			46.9		3		−	6	Rodier and Le Borgne (1997)
E. Eq. Pac.	DVM Zooplankton		1214	7.1	7.1			204	Rodier and Le Borgne (1997)
Western Equator	DVM Zooplankton		144–447	23.53-9.97	7.3–19.1		2.6–4.4	13–35	Hidaka *et al.* (2002)
Equator divergence			2.8–21.8		0.9–1.2			<1-2	Roman *et al.* (2002)
Oligotrophic area			30.2–33.8		1.3–1.7			4	Roman *et al.* (2002)
E.S.Pac. N.Chile		5503							Gonzalez *et al.* (1998)
E.S.Pac. N.Chile		10000							Daneri *et al.* (2000)
E.S.Pac. N.Chile	DVM Eucalanus		8.0 -34	14.1					Hidalgo *et al.* (2005)
E.S.Pac. N.Chile	DVM zooplankton		37810	7200		6700			Escribano *et al.* (2009)
E.S.Pac. N.Chile	DVM zooplankton		5099 ±2701	678± 465					This study

5   Even although the OMZ did not greatly prevent DVM migration, zooplankton behaviour appeared as disrupted, or exhibited reversed patterns, depending on vertical distribution of OMZ and on the taxonomic group being considered. This behaviour was more evident in the onshore stations (Sts.T3-L6), but in particular in the station off Iquique (St. T3) that also showed higher migration rate (60%). In according to Ekau *et al.* (2010) other indirect effects could also be caused by the hypoxia

conditions, such as changes in prey availability, prey size or predation risk, as well as changes in species composition, the strength of which depends on the duration and amplitude of the hypoxic events. This could explain why individuals within a single population can perform reverse, normal, or non DVM, apparently depending on the more important source of mortality: predation by nocturnally feeding normally migrating carnivorous zooplankton, or visually hunting planktivorous fish (Ohman,

5   1990). These kind of DVM behaviors can only be better assessed and understood when looking at the population level. Concerning C fluxes, our estimates of active transport of carbon by zooplankton were greater than estimates of passive C sinking obtained off northern Chile at 60 m depth by Gonzalez *et al.* (1998) based on sediment traps (125 to 176 mg C m^{-2} d^{-1}). Our estimates represented 7±5 % of export of Carbon resulting from primary production in the upwelling region calculated as ~1000 mg C m^{-2} d^{-1} (Table 7). If we consider this is accounted only by mesozooplankton, then an important

10   fraction of freshly produced C can be taken downward by zooplankton, and this zooplankton-mediated C flux ought to be taking into account when and analysing and modelling the C budget in the upwelling zone.

Table 7. Mean primary production rate and estimates of daily downward C flux due to passive sinking and mediated by diel vertical migration of mesozooplankton at three stations in the coastal upwelling region off northern Chile during the spring

15   2015.

Station	T5	T3	L6	Mean ± SD		
Primary Production mg C m-2 d-1			10000			
Passive Carbon Flux mg C m^{-2} d^{-2}				151	±	36
Abundance ind. m^{-2} (0–600 m)	44347	25417	74247	48004	±	24620
Σ Total biomass mg C m^{-2} d^{-1} (0–600m)	7403	20571	22142	16705	±	8094
Epipelagic biomass mg C m^{-2} d^{-1} (0–90m)	6251	18781	15357	13463	±	6476
Migrant biomass mg C m^{-2} d^{-1}	2847	8093	4357	5099	±	2701
Rate of Biomass migration %	77	79	39	65	±	23
Active Carbon Flux mg C m^{-2} d^{-2}	427	1214	392	678	±	465
Total Active Carbon exported %	4	12	4	7	±	5

5 Conclusion

The vertical distribution and diurnal variability of biomass of 27 taxonomic groups seem to be disturbed by the OMZ in the coastal zone off northern Chile, such that high biomass aggregates above the oxycline in a narrow band within the near-surface

20   oxygenated layer, whereas much lower biomass resides in deeper waters, in particular within the OMZ. Many taxa, however, were found closely associated with the OMZ, and capable of performing DVM withstanding severe hypoxia. Even, several

zooplankton groups are strong migrants, exhibiting a large DVM amplitude (~500 m). Among them, a key migrant group is comprised by the copepods Eucalanidae and euphausiids which can even enter the core of the OMZ, and then migrate downward to the lower limit of the OMZ, which is slightly more oxygenated. The variable behaviour among taxa reflected in different amplitudes of vertical migration can greatly affect the daily rate of migrant biomass, indicating that estimates of

5   downward C must take into account taxonomic structure of the zooplankton community.

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