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

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Abstract. The daily vertical movement of zooplankton, known as diel vertical migration (DVM), can enhance the vertical flux of carbon (C) and so contribute to the functioning of the biological pump in the ocean. 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 flux has not been properly addressed. This taxonomic effect may become critically important in highly productive eastern boundary upwelling systems (EBUS), where high levels of zooplankton biomass are found in the coastal zone and composed by a diverse community with variable DVM behavior. In these systems, presence of a subsurface oxygen minimum zone (OMZ) can impose an additional constraint to vertical migration and so influence the downward C export. Here, we address these issues based on a high-resolution zooplankton sampling at three stations off northern Chile (20°S-30°S) during November-December 2015. Automated analysis of zooplankton composition and taxa-structured biomass allowed us to estimate daily migrant biomass by taxa and their amplitude of migration. We found that a higher biomass aggregates above the oxycline, associated with more oxygenated surface waters and this was more evident upon a more intense OMZ. Some taxonomic groups, however, were found closely associated with the OMZ. Most taxa were able to perform DVM in the upwelling zone withstanding severe hypoxia. Also, strong migrants, such as Copepods Eucalanidae and Euphausiids, can exhibit a large migration amplitude (~500 m), remaining either temporarily 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 suggested that a mean migrant biomass of ca. 958 mg C m^{-2} d^{-1} may contribute with about 71.3mg C m^{-2} d^{-1} to the OMZ system through respiration, mortality and C excretion at depth, accounting for ca. 4% of the net primary production, and so implying the existence of an efficient mechanism to incorporate freshly produced C into the OMZ. This downward C flux mediated by zooplankton is however strongly variable in the space and mostly dependent on the taxonomic structure due to variable migration amplitude and DVM behavior.

1 Introduction

The Oxygen Minimum Zone (OMZ) in the Southeast Pacific, 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 region of Northern Chile, the OMZ is closely linked to wind-driven upwelling in the coastal area and associated to the Equatorial Subsurface Water (ESSW), which is transported southward along the continental shelf by the Peru-Chile Undercurrent (PUC), as far south as 48°S (Fuenzalida et al., 2009; Morales et al., 1996a; Silva and Neshyba, 1979). Off Iquique (20°S) the OMZ is characterized by being thick (500 m), very intense (< 20 µmol kg^{-1}) and with O_2 concentrations in the core of OMZ among the lowest found in the global ocean reaching the current detection limit (<1 µM) (Ulloa and Pantoja, 2009), although it becomes thinner at about 30ºS (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).

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, behaviour and metabolic activity (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 changes in intensity and distribution of the OMZ (Wishner *et al.,* 2018, 2013; Escribano *et al.,* 2009; Fernández-Álamo and Färber-Lorda, 2006; Hidalgo *et al.,* 2005; Morales *et al.,* 1996; Judkins, 1980). The OMZ can act as an ecological barrier for vertical distribution of many organisms, constraining most zooplankton to a narrow (50 m) upper layer, as shown in the coastal upwelling zone off Chile according to the works of Escribano (2006) and Donoso and Escribano (2014). Zooplankton also become limited to the upper 150 or 300 min 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 and abundance, with distinct species zonation (Antezana, 2009; Wishner *et al.,* 2008; Fernández-Álamo and Färber-Lorda, 2006), 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 and Landry, 2017).

As important contributors to the 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 moults 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 *et al.,* 2016; Ducklow *et al.,* 2001). However, the effect of variable size structure on DVM performance and its consequence for active C transport 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). Adaptation may include in some cases reduction of aerobic metabolism by more than 50% during exposure to hypoxia conditions, as a mechanism to facilitate low oxygen tolerance, an so reducing dramatically energy expenditure during daytime within low oxygen waters, and therefore affecting the carbon C flux in areas subjected to low concentrations of oxygen (Seibel *et al.,* 2016).

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, 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 DVM behaviour interacting with a shallow OMZ, and the implications this interaction can have on the magnitude of the downward C flux in a highly productive coastal upwelling zone

2Methods

2.1Study Area

The study area was located in the Southeast 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. 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 November-December 2015 onboard the R/V *Cabo de Hornos*. At each station, temperature, salinity and dissolved oxygen (DO) were recorded from 1000 m (St.T5 and St.T3) and only 356 m (St.

L6) using an oceanographic rosette with a CTD SeaBird 911 (SBE 911 plus)equipped with a SeaBird SBE-43 oxygen sensor and a Seatech Fluorometer. Discrete water samples were also obtained for chemical measurements of oxygen.

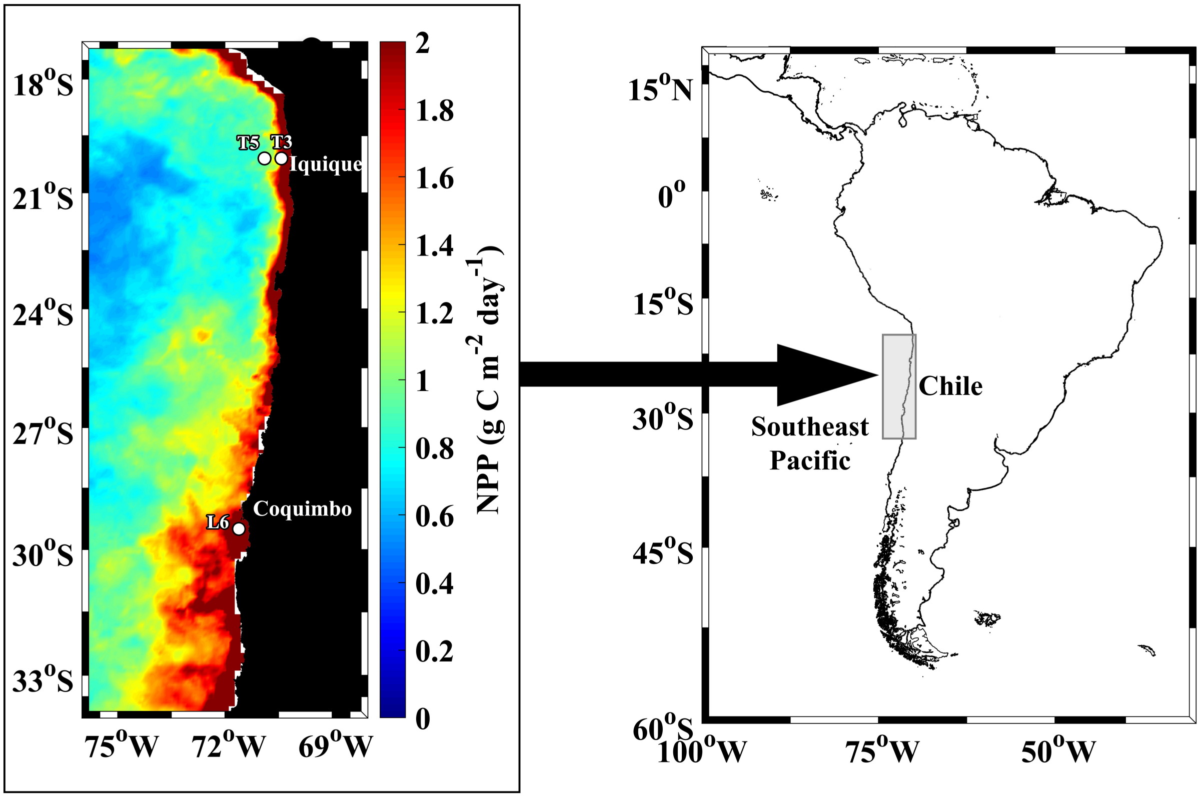

Fig.1. Study area at the northern upwelling region of Chile, indicating sampling stations during the LowpHox cruise conducted in November-December 2015 onboard the R/V *Cabo de Hornos*. Satellite estimated Net Primary Production (NPP), averaged for November-December 2015 is shown. NPP was obtained from http://science.oregonstate.edu.ocean.productivity.

2.2 Zooplankton sampling

Zooplankton samples were collected during daytime and night-time conditions in two consecutive days at the three stations off northern Chile (T5-T3-L6) (**Fig. 1**), also as indicated in **Table S1 (Supplemental Material).** Vertical hauls of zooplankton were performed from 600 to 0 m depth with a Multi Plankton Sampler Hydro-Bios Multinet system with a 0.25 m^2 opening area and equipped with 200-µm mesh-size nets. The Multinet towing speed was 1 m s^{-1} and the flowmeter was in the mouth of the Multinet to estimate the volume of filtered water. Once onboard the collected zooplankton samples were preserved immediately in 5% buffered formalin-seawater solution. At each station, 40 discrete samples were obtained from 600 to 0 m depth. Each sample corresponded to a different depth stratum (30-0, 90-30, 150-90, 400-150 and 600–400m depth). These strata were defined in according to distribution of oxygen concentration and localization of the OMZ (**Fig. 2**).

Then, from the vertical profiles of oxygen and coinciding with the sampled layers of the Multinet, strata were defined as: A well oxygenated stratum with oxygen approaching air saturation (>250 µmol O_2 kg^{-1}) was defined as the oxic mixed layer (OX-ML), an upper O_2 gradient (oxycline), defined by the level where O_2 reaches 4% of the surface O_2 (Paulmier *et al.,* 2006), at whose base is located the upper boundary of the OMZ (45 µmol O_2 isoline, OMZ-UB) (Escribano *et al.,* 2009; Hidalgo *et al.,* 2005; Morales *et al.,* 1999*)*; the OMZ core defined by an upper boundary (OMZ-UC) with the lowest concentration of O_2 (<20 µmol O_2 kg^{-1}) and a lower boundary (OMZ-LC) (1 to<20 µmol O_2 kg^{-1}), and finally a lower O_2 gradient (OMZ-LW). Depth ranges and oxygen levels for these strata are detailed in **Table S2 (Supplemental Material)**.

2.3Taxonomic and size measurements

Taxonomic identification and enumeration of taxa were carried out by analysis of digitized images obtained with the Hydroptic 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 was fractionated again separately with a Motoda splitter until the zooplankton concentration was sufficiently diluted to avoid contact between organisms in the ZooScan scanning frame. Fractioning into small and large organisms 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 of 2400 dpi after manual separation of objects on the scanning tray. After processing the samples with ZooProcess software, 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. The abundance (ind. m^{-3}) of total zooplankton or of each taxonomic group was calculated following Eq. (1):

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

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 tows in a sample. Townb =1 in our case because of a single tow per sample. Stratum-integrated abundance (ind. m^{-2}) was obtained after multiplying by width (m) of a given stratum.

2.4 Biomass estimates and Carbon fluxes

The ZooScan Integrated System also provided zooplankton body size in terms of area (mm^2) or volume (mm^3)for each organism. We used these organisms´ area or volume to estimate dry weight of each individual of different taxonomic groups using published regression equations relating organism size, area or volume to individual weight as detailed in **Table S3**

(Supplemental Material). Mass unit conversions between dry weight (DW) and carbon content (C) were performed using averaged conversion factors obtained for different zooplankton groups (Kiørboe, 2013) and ichthyoplankton (Childress and Nygaard, 1973) (Table S3 Supplemental Material). Added biomasses (µg C ind.$^{-1}$) of individuals within taxonomic categories identified by ZooScan allowed us to estimate total biomass per taxa (mg C m^{-3}) for each sample by station, daytime vs night-time condition, and depth strata. Integrated values of biomass per depth strata (mg C m^{-2}) and taxa were calculated multiplying by strata width (m).

To calculate the migrant biomass, we integrated biomass in the upper 90 m layer from our two sampled strata 0-30 m and 30-60 m. This 0-90 m stratum was considered the approximate above-oxycline layer after examining the vertical profiles of oxygen. Biomass at night was thus subtracted from the corresponding day biomass in this layer to assess daily changes involving migrants as in Putzeys *et al.*(2011). Thus, the negative values of the day-minus-night biomass corresponded to migrant biomass that reached the epipelagic layer at night including organisms inhabiting above and below the oxycline. The proportion of migrant biomass with respect to observed biomass in the upper 90 m of a given taxonomic group was defined at the rate of migration on a daily basis. This rate of migration could thus be used as an index of DMV behaviour for a taxonomic group.

To estimate the active C flux at each sampling station, we considered three processes contributing to C at depth mediated by migrant zooplankton: respiration (R), excretion (E) and mortality (M) at depth. Respiration at depth (>90 m) was estimated using the equation provided by Ikeda (1985) which relates individual respiration rate with body mass and temperature, independently of taxonomic category which may have a minor effect on R in according to a more recent assessment (Ikeda, 2014). Mean body mass (µg C) for each taxonomic group from ZooScan estimates and mean in situ temperature were used to obtain integrated R at each depth strata. Estimates of R for each taxonomic group are shown in Table S6 (Supplemental Material). Integrated R per station for the 0-600 depth strata along with the corresponding integrated biomass was then used to estimate the fraction of C being respired at depth by zooplankton. The contribution of C by excretion (E) at depth was assumed to be 31% of R as suggested by (Steinberg *et al.,* 2000) and daily mortality at depth (M) was considered to be in the range of 0.3 and 0.5 as suggested by Edvardsen *et al.* (2002), so that a median value of 0.4 as a fraction of migrant biomass was assumed. Vertical C flux mediated by zooplankton was thus estimated as,

$$\text{C Flux} = \text{MB} \times [(R + M + 0.31R)/2)] \qquad (2)$$

where MB is the migrant biomass (mg C m^{-2}), R and M are daily Respiration and Mortality, and C excretion expressed as 0.31R. The three processes are divided by 2 assuming a 12 h incursion at depth.

2.5 Patterns of vertical distribution of migrating zooplankton

For the analysis of vertical distribution of organisms, the density estimates of the organisms were standardized to number of individuals per m^3 (for each stratum) or per m^2 (for integrated values). In order to quantify the presence and extent of DVM of various taxa at each station, we calculated weighted mean depth (WMD) for zooplankton abundance, as a measure of the center of gravity of a population's vertical distribution for each taxon and haul, according to Andersen *et al.*(2004) following Eq. (3):

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

where *d* is the mean depth of the strata (m), *z* the width (m) of the strata and *ni* the abundance (ind. m^{-3}) of a given *i* taxonomic group.

We calculated the amplitude of vertical migration (ΔDVM) as the difference between the WMD of the organisms during the day and the night and therefore this ΔDVM was considered as the criterion to assess the DVM behaviour for each taxonomic group. 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 Statistical analysis

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

3 Results

3.1 Hydrographic conditions

Across the zonal section off Iquique the offshore station (St. T5) and onshore station (St. T3) showed two contrasting hydrographic regimes regarding the OMZ. Station T5 had a less pronounced and thicker OMZ than station T3. At both stations the 5 strata were well defined in the water column (**Fig. 2**). The OX-ML (>250 µmol O_2 kg^{-1}) was present at 18 m (St. T5) and 15 m (St. T3). The oxycline gradually decreased from oxic (~250 µmol O_2 kg^{-1}) to suboxic (<20 µmol O2 µmol O_2 kg^{-1}) conditions associated with a strong stratification in the upper 80 m depth. The 45 µmol O_2 isoline (OMZ -UB) was at the base of the oxycline at 70 m (St. T5) and 59 m (St. T3). The OMZ core (<20 µmol µmol O_2 kg^{-1}) was below the thermocline and below the 26.5 kgm^{-3}isopycnal following description of Paulmier*et al.* (2006).In the oceanic station (St. T5) the OMZ core was between 80 to 514 m, while in the coastal station (St. T3) it was between 80 to 507 m with 423 m thickness. The O_2 concentration in the OMZ core was ca. 1 µmol O_2 kg^{-1}. The OMZ-LW at both stations was delimited above the core and below the depth where the O_2 slope changed significantly (slope break >20 µmol /m) (**Fig. 2**).

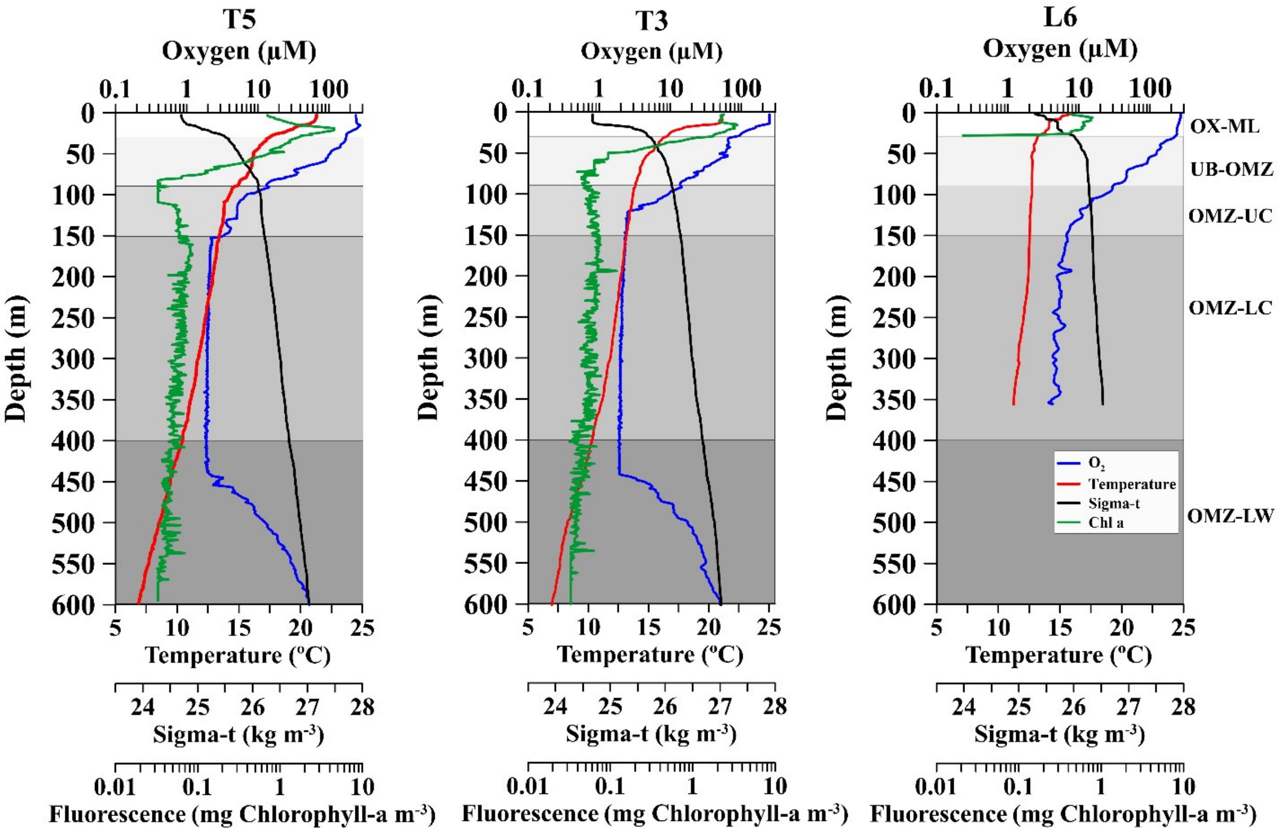

Fig. 2. Vertical profiles of dissolved oxygen (O_2), temperature, Chlorophyll-a and water density (sigma-t), at 3 stations off northern Chile (see **Fig. 1**) during the LowpHox Cruise in the austral spring 2015. Shaded areas represent different layers defined according to oxygen concentration. OX-M= Oxic mixed layer, OMZ-UB= Upper boundary of the oxygen minimum zone, OMZ-UC= Upper core of the oxygen minimum zone, OMZ-LC= Lower core of the OMZ and OMZ-LW=lower oxygen gradient.

The structure of the OMZ at the coastal station (St. L6) off Coquimbo (29ºS) (**Fig.1**), was similar to St. T3 (21ºS), but in this area the OMZ was deeper and thinner. The OX-ML was shallower. The OMZ -UB (45 µmol O_2) in the base of the oxycline was down to 80 m. The low O_2 concentrations in the core were less intense than at 21ºS (4 to 20 µmol O_2kg^{-1}) and it was located below 100 m (**Fig. 2**). The OMZ-LW could not be assessed because of lack of CTD data below 350 m.

Additional oceanographic variables showed a surface warming (>20 °C) and strongly stratified conditions at the three stations with a sharp thermocline in the upper 100 m, coinciding with the oxycline, whereas Chlorophyll-a maximum (>5 mg Chlorophyll-a $m^{-3}$was in the upper 20 m (**Fig. 2**).

3.2 Zooplankton composition and abundance

A total of 27 zooplankton taxa were identified by the ZooScan and ZooProcess **(Table S4 Supplemental Material).** The number of taxa varied among stations and strata. Across the zonal section off Iquique the number of taxonomic groups fluctuated between 23 (St. T3) and 26 (St. T5), whereas 25 taxa were off 29ºS (St. L6). The most dominant taxa both daytime and night conditions, were: Copepods87% (in St. T5), 79% (in St. T3) and 69% (in St. L6). This group was constituted by small Copepods, large Copepods, the Copepods Eucalanidae and the Copepods *Acartia* spp; fish eggs constituting 2% (in St. T5), 5% (in St. T3) and 6% (in St. L6); Nauplii being <1% (in St. T5), <1% (in St. T3) and 7% (in St. L6); Appendicularia 5% (in St. T5), 4% (in St. T3) and 3% (in St. L6) **(Table S5 Supplemental Material).** The remaining 19 pooled groups only constituted<6% (in St. T5),11% (in St. T3) and 15% (in St. L6). The total integrated abundances of zooplankton (0-600 m) by sampling station are in **Table S4** (Supplemental Material). As based on a Two-Way Crossed Analysis ANOSIM test, this water-column integrated abundance did not show significant differences between day and night samples ($p>0.05$). However, the abundance of these zooplankton groups regarding stations was significantly different (Two-Way Crossed Analysis ANOSIM $p<0.05$), so that the stations were treated independently. Off Iquique the abundance was the lowest at the onshore station (St. T3 with 18% lower), which was characterized by the strongest and most extensive OMZ in the study area. These values increased at the offshore station (St. T5 with 31% greater), where the OMZ was less pronounced and thicker. Unlike stations T3 and T5, the onshore station off 29ºS (St. L6) had a weaker and less extensive OMZ showing the highest zooplankton abundance (51% greater).

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 in **Fig. 3**. These taxa were classified into four groups according to their amplitude of migration (ΔDVM) **(Table 1)**: **1) Strong migrants**, represented by taxa with a strong DVM and a broad range of ΔDVM from 225 to 99 m (in St.T5), 440 to 84 m (in St. T3) and 208 to 87 m (in St. L6). This group constituted 70% of taxa with higher ΔDVM. The composition of taxa in this group was variable at each station **(Table 1)**, but in general was well represented by Eucalanidae Copepods (EC), Euphausiids (EU), *Acartia* Copepods (AC), Ctenophores (CT), Decapods (DC), Annelids (AN), Bryozoan L (BR), Pteropods (PT) and Chaetognaths (CH). These taxa were mostly concentrated in the oxic surface stratum (**OX-ML),** and the **OMZ core** showing a strong interaction with both the **OMZ-UC** and the **OMZ-LC**, and so changing from normoxia to hypoxia condition and vice versa between 0 to 550 m

(Fig. 3), 2) Intermediate migrants, represented by taxa with a moderate DVM and a range of ΔDVM from 73 to 34 m (in St. T5),70 to 27 m (in St. T3) and 49 to 22 m (in St. L6). This group constituted 23% of taxa with moderate ΔDVM. The composition of taxa in this group was also variable at each station **(Table 1)**, but it was mostly represented by small (SC) and large Copepods (LC), Amphipods (AM), Cirripedia Larvae (CL), Gastropods (GA), Siphonophores (SIP) and Appendicularia (AP). These taxa were mostly concentrated in the oxic surface strata (**OX-ML)** and in the **OMZ-UC** showing some interaction with the **OMZ core** and vertically changing from normoxia to hypoxia condition, and vice versa between 0 to 200 m, **3) Weak migrants,** represented by taxa that with a weak DVM and a range of ΔDVM of 24 to 18 m (in St.T5),23 to 12 m (in St.T3) and 21 to 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 1)**, but in general it was represented by Hydrozoa (HY),Salps (SA), Platyhelminthes (PT), Decapoda Larvae (DL), Ostracods (OS), Nauplii (NL) and Ichthyoplankton (IC). These taxa were concentrated mainly in the oxic surface strata (**OX-ML)**andin the **OMZ-UP,** but also in the **OMZ-UC**at the onshore stations (Station T3 and Station L6),showing much less interaction with the **OMZ core,** while spatially moving from normoxia to hypoxia condition and vice versa between 0 to 100 m, and **4) Non-migrants,** represented by taxa which did not exhibit a significant DVM and had a range of ΔDVM from 16 to 0 m (in St. T5),7 to 0 m (in St. T3) and 6 to 0 m (in St. L6). This group constituted 1% of taxa with not significant ΔDVM. The composition of taxa in this group was also variable at each station **(Table 1)**, but in general it was represented by fish eggs (FE), Radiolarian (RA) and Echinoderm larvae (EL).

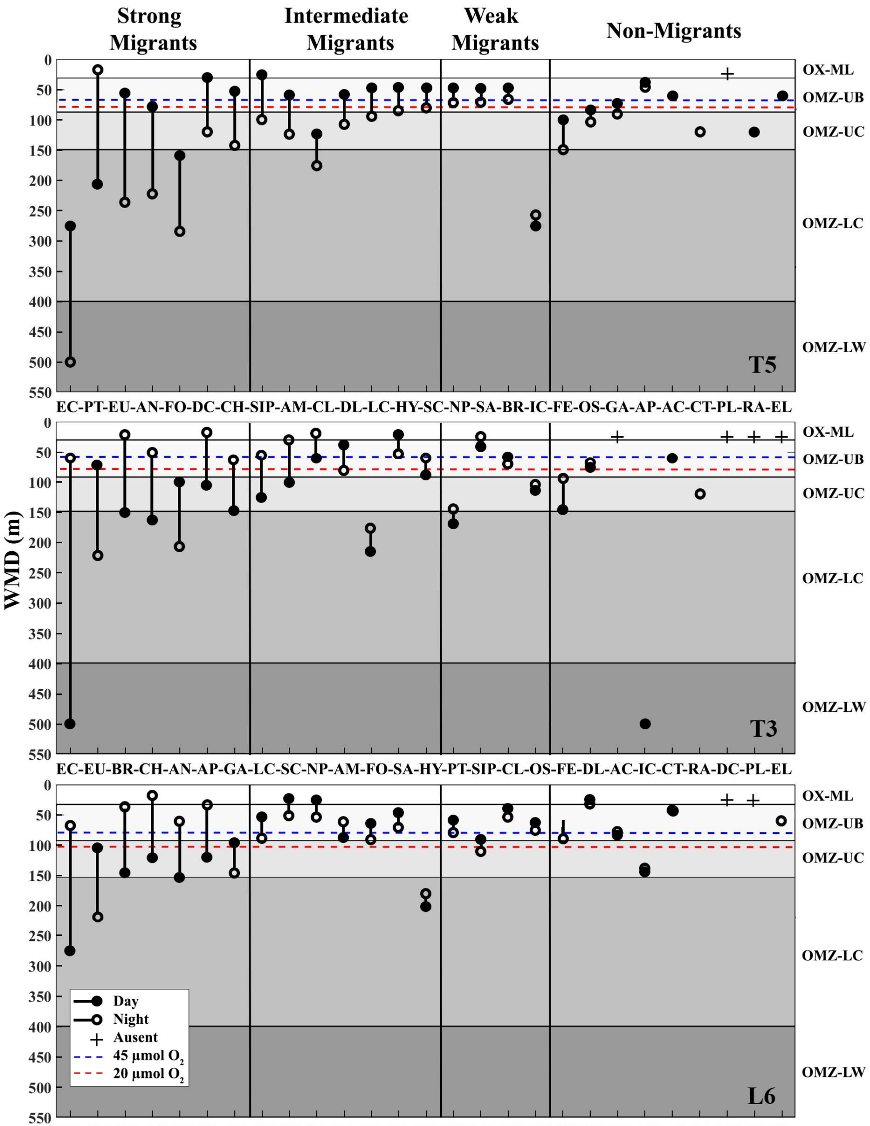

Fig.3. Weighed mean depth distribution (WMD) of the zooplankton community interacting with the OMZ off Iquique (Stations T5 and T3) and off Coquimbo (StationL6) at the northern upwelling area of Chile during the austral spring 2015. Shaded gray areas represent different layers defined by their oxygen levels (defined in Methods). The taxonomic groups were classified by automated analysis (ZooScan): EC= Eucalanidae Copepods, AM= amphipods, BR=Bryzoa larvae, AC= *Acartia* Copepods, CT= Ctenophores, CL=Cirripedia larvae, OS=Ostracods, CH=Chaetognaths, PT= Pteropods, SA=salps, GA= Gastropods, PL= Platyhelminthes, DL= Decapoda larvae, FO=Foraminifera HY=Hydrozoa, LC=Large Copepods, SIP=Siphonophores, EU=Euphausiids, FE=fish eggs, NP=Nauplii, SC=Small copepods, AN= Annelids, AP=Appendicularia, RA=Radiolarian, DC=Decapods, IC=ichthyoplankton, EL=Echinoderm larvae.

Table 1- Diel vertical migration indices for 27 taxonomic groups (TAXA) identified and sorted by ZooScan at 3 stations off northern Chile (see **Fig. 1** for acronyms), during the austral spring 2015.Amplitude of migration (ΔDVM) is in meters. Positive values indicate normal DVM and negative values indicate reverse DVM (see Methods).. Four groups are defined in according to DVM behaviour. Relative abundances are shown in %.

T5			T3			L6			
TAXA	**ΔDVM**	**%**	**TAXA**	**ΔDVM**	**%**	**TAXA**	**ΔDVM**	**%**	**MIGRANTS**
EC.	225	14	**EC.**	-440	28	**EC.**	-208	20	**STRONG MIGRANTS > 5%**
PT.	-188	12	**EU.**	149	10	**AM.**	115	11	
EU.	181	11	**BR.**	-129	8	**BR.**	-107	10	
AN.	145	9	**CH.**	-114	7	**AC.**	-103	10	
FO	126	8	**AN.**	105	7	**CT.**	-94	9	
DC.	90	6	**AP.**	-88	6	**CL.**	-87	8	
CH.	88	6	**GA.**	-84	5	**OS.**	49	5	
SIP.	73	5	**LC.**	-70	5	**CH.**	35	3	**INTERMEDIATE MIGRANTS > 2%**
AM.	64	4	**SC**	-70	5	**PT.**	29	3	
CL.	51	3	**NP.**	-42	3	**SA.**	29	3	
DL.	50	3	**AM.**	42	3	**GA.**	-27	3	
LC.	47	3	**FO**	-38	2	**PL.**	26	2	
HY.	39	2	**SA.**	32	2	**DL.**	22	2	
SC	34	2	**HY.**	-27	2	***FO***	-22	2	
NP.	24	2	**PT.**	-23	1	**HY.**	21	2	**WEAK MIGRANTS > 1%**
SA.	23	1	**SIP.**	-15	1	**LC.**	19	2	
BR.	18	1	**CL.**	12	1	**SIP.**	15	1	
IC.	-18	1	**OS.**	-9	1	**EU.**	11	1	
FE	49	3	**FE**	-52	3	**FE**	25	2	**NON-MIGRANTS <1%**
OS.	16	1	***DL.***	-7	0	**NP.**	6	1	
GA.	15	1	**AC.**	-	-	**SC**	-4	0	
AP.	7	0	**IC.**	-	-	**AN.**	-4	0	
AC.	-	-	**CT.**	-	-	**AP.**	2	0	
CT.	-	-	**RA.**	-	-	**RA.**	-	-	
PL.	-	-	**DC.**	-	-	**DC.**	-	-	
RA.	-	-	**PL.**	-	-	**IC.**	-	-	
EL.	-	-	***EL.***	-	-	***EL.***	-	-	

3.2 Vertical distribution and DVM of dominant groups.

Vertical distributions of zooplankton were assessed for 5 taxonomic groups, which represented 80% of total abundance in average: Copepods represented by small Copepods, Large Copepods, Eucalanidae Copepods and *Acartia* Copepods; Euphausiids; Decapods Larvae; Chaetognaths and Annelids, as well as their patterns of strata–station–abundance relationships are detailed in **Table S4 (Supplemental Material).** The abundance of these zooplankton groups regarding depth strata was significantly different (ANOSIM, $p<0.05$) at each station**,** and therefore representing distinctive microhabitats characterized by specific depth and oxygen concentration**.** In general, the higher abundance (>80%) was found in the shallower strata and well oxygenated layers **(OX-ML and OMZ UB)** (>250 μmol O_2 kg^{-1}), and then it decreased rapidly in the strata associated with the OMZ core (**OMZ-UC** and **OMZ-LC**). Below this stratum a second slight peak in abundance was in the **OMZ-LW** in special at Sts. T5 and L6, occurring between 400-600 m, both daytime and night conditions.

As expected, Copepods dominated numerically the zooplankton community both within and outside the OMZ **.** Small Copepods (SC) were the most abundant (70%), followed by large Copepods (LC) (6%)**,** whereas the Copepods *Acartia* (AC) and Eucalanidae (EC) showed the lowest abundances among Copepods. The largest aggregation of Copepods (pooled data) altogether during the entire study period was at the offshore station St. T5 (87%), where abundances reached 192088 ind. m^{-2}. At the onshore station (St. T3) the percentage of contribution of copepods was 79% and 69% at the St L6 **(Table S5 Supplemental Material).** Off Iquique, the highest abundances were in the shallower strata **(OX-ML) at** St.T5 (46%) and at St. T3 (47%), and reduced in the core of the OMZ at St. T5 (4 to 1%) and at T3 (8 to 1%) between 90-400 m, where oxygen had the lowest concentrations (< 20 μM to 1μM). At the St. T5 the second peak of abundances was in the **OMZ-LW** stratum during daytime condition, where oxygen levels increased after the extremely low levels within the OMZ, while at the onshore station St T3 it was much dimmer and during nigh condition. At the onshore station off 29º S (St. L6), having a weaker and less extensive OMZ, the vertical distribution of abundance was similar. However, the abundance of copepods was lowest in this station (in about 69%) in comparison with stations off Iquique, in the core of the OMZ the percentage was between 5 to 3%.

DVM of Copepods was pronounced at onshore stations (StationsT3 and L6), but the strength of migration was higher overall at St. T3 off Iquique, as reflected by the migration indices (WMD and ΔDVM) **(Table 1).**The WMD of these taxa had a broad range (17–500 m), which varied significantly among copepods groups and stations, both in day and night samples ($p<0.05$) **(Fig. 3)**. During the night, at the offshore station (St. T5) most Copepods exhibited normal DVM and they were concentrated mainly in the oxic surface strata (**OX-M)** and **OMZ-UB** (40-60 m) without interacting with the OMZ; except for Eucalanidae which concentrated deeper in the **OMZ-LC** stratum, associated with the lower core of the OMZ and showing a high ΔDVM (225m).During the day these four groups of Copepods tended to remain deeper in the stratum associated with the lower core of the OMZ (**OMZ-UC**) and lower O_2 gradient (**OMZ-LW**), except for small Copepods that remained at the **OMZ-UB** stratum with a smaller ΔWMD (34 m). At the offshore stations (StationsT3 and L6) the DVM was reverse in most Copepods, except for large Copepods (LC) which showed slightly normal DVM at St. L6 off 29ºS. At night Copepods were concentrated deeper in the stratum associated with the lower core of OMZ (**OMZ-UC**) and lower O_2 gradient **(OMZ-LW),** particularly Eucalanidae with a strong DVM and high ΔWMD of 440 m (St. T3) and 208 m (St. L6) and *Acartia* Copepods with 103 m (St. L6) **(Table 1)**, whereas at St. L6 small Copepods (SC) were caught in abundance at the **OMZ-UB** stratum down to 82–90 m depth, respectively **(Fig. 3).** During the day, Copepods remained shallower than at night, although they concentrated at different depths. Small Copepods were in the oxic surface strata **OX-ML** (St. T3) and remained in the upper boundary of the OMZ (St. L6) without detectable DVM, as judging by the small difference between their day- and night-time distributions (ADVM ca. 4 m). Large Copepods (LC), as expected, showed a normal migration and stayed inside the OMZ, concentrated in the **OMZ-UC** stratum (St. L6) and **OMZ-UB** (St. T3). Finally, Eucalanidae, with a strong DVM tended to distribute in the **OMZ-UC (**St. T3**)** and the **OMZ UB** (St. L6) **(Fig. 3).**

Unlike copepods, the Euphausiids were more abundant at the onshore station L6 (<1%), where they reached up to 1683±473ind. m^{-2} d^{-1}. The OMZ-UB stratum was the most abundant in this station, with a peak of abundance during the daytime, however no DVM was detectable, judging by the small difference between their day- and night-time distributions **(Fig. 3)**. Off Iquique, also the highest abundance was in OMZ-UB stratum at night, butwith a second peak in OMZ-LC stratum during daytime in both station (Sts. T3 and T5) **(Table S4 Supplemental Material).** The euphausiids appeared to perform a strong DVM in these stations **(Fig. 3)**, with a vertical range between 236 and 56 m and a mean ΔDVM of 181 m at T5 and at St. T3 between 222 and 73 m with a mean ΔDVM of 149 m **(Table 1)**.

Decapods larvae were more abundant at StT5 (428±132 ind. m^{-2} d^{-1}) and were associated with the **OMZ-UB** stratum, where they performed a strong normal DVM with a vertical range between 120 and 30 m and a mean ΔDVM of 90 m **(Table 1)**. At the offshore station (St.T3), the surface peak of abundance was in the **OX-ML** stratum during the day and in the**OMZ-UB** layer at night , where they reached up to 292±62 ind. m^{-2} d^{-1}, with a weak reverse DVM (ΔDVM-7 m). Off Coquimbo (St. L6) they reached up to 400±88 ind. m^{-2} d^{-1}, the **OMZ-UB** stratum was the most abundant, with a slight second peak in the OMZ-LW stratum during daytime, at this station the vertical range was between 70 and 48 m with a mean ΔDVM of 22 m **(Fig. 3).**

The largest aggregation of Chaetognaths was at the onshore station St. L6 (~2%), where their abundances reached up to 4755±1038 ind. m^{-2} d^{-1}. The abundance and biomass of this group increased in the upper boundary of the OMZ (**OMZ-UB)** during day and night. No DVM was discernible for this group in this station, because of the slight difference between their day- and night-time distributions. By contrast, off Iquique they appeared to perform a strong DVM between the **OMZ-UB** and the **OMZ-UC** strata, as indicated by the migration indices (WMD-ΔDVM) **(Table 1).** However, at the onshore station (St. T3) they showed a reverse DVM.

The other main taxon, Annelida was more abundant at the onshore station St. L6, where their abundances reached up to 7395±847ind. m^{-2} d^{-1} **(Table S4 Supplemental Material)**. In the whole area, the highest of abundance was in the OMZ-UB, however a second peak of abundance was in the OMZ-LC during daytime at St T5 and T3 and during the night at St. L6. The

DVM of this group was high off Iquique with ΔDVM of 145 m (St. T5) and 105 m (St. T3), while at St. L6 off Coquimbo no DVM was discernible for this group.

3.3.3 Others groups with vertical distribution associated to OMZ UC

The remaining 19 groups constituted 11% (in St. T5) 17% (in St. T3) and 27% (in St. L6) in abundance. The DVM behaviour was variable at each station, but in general it was Normal at St. T5 and reverse at Sts.T3-L6 **(Table 1).** These groups clearly exhibited different daytime and night depths associated with the **OMZ core (OMZ UC-LC).** Overall, they tended to reside deeper by day and shallower by night in St. T5 than at the other sites **(Fig.3).**

3.4 Vertical distribution of zooplankton biomass

Estimates (mean ± SD) of biomasses of the taxonomic groups integrated by depth strata are summarized in **Table 2**. These data, averaged from day and night measurements, contrast with the numerical abundances, which were dominated by copepods. In this case, the bulk of zooplankton biomass was dominated by different groups depending on Stations. In terms of biomass, Copepods, Euphausiids, Decapods L. Chaetognaths, and Annelids accounted, more or less equally, for >84% in the whole area (**Table 2**). At the stations less affected by the effect of OMZ the bulk of biomass was dominated by copepods ~50% at St. T5 and ~40% at St. L6, while Decapods largely dominated the bulk of biomass at Station T3 (~40%), followed by Copepods(19%) and Euphausiids (16 %). (**Table 2**).

Table2. Mean and Standard Deviation (±) of integrated biomass (mg C m-^{2}) by taxonomic groups identified and sorted by ZooScan during daytime/ night-time conditions at three stations (T5, T3 and L6) sampled off northern Chile, during the austral spring 2015. Mean ± SD are from n=**8**for Stations T5 and T3, and n=4 for Station L6.

	T5			**T3**			**L6**		
TAXA	**Integrated Biomass**			**Integrated Biomass**			**Integrated Biomass**		
Copepods									
Large C	383.73	±	89.3	286.75	±	50.6	1727.49	±	340.8
Small C	467.55	±	115.9	194.51	±	41.4	416.14	±	66.6
Eucalanidae C	0.22	±	0.1	2.42	±	0.8	11.78	±	4.1
***Acartia* C**	0.02	±	0.0	0.00	±	0.0	0.34	±	0.1
Euphausiids	349.48	±	77.6	412.38	±	103.0	1060.58	±	305.8
Decapoda L	20.04	±	4.7	1015.61	±	294.6	537.17	±	176.8
Chaetognaths	63.97	±	15.7	215.20	±	79.3	641.85	±	172.9
Annelida	50.76	±	7.4	79.59	±	11.8	734.67	±	196.4
Decapods	442.38	±	187.4	0.00	±	0.0	0.00	±	0.0
Ostracods	20.83	±	2.9	25.14	±	1.9	171.01	±	15.2
Ctenophores	0.45	±	0.2	101.44	±	45.4	100.01	±	29.9

Hydrozoan	31.48	±	9.9	28.39	±	8.3	132.34	±	39.0
Salps	15.96	±	6.0	129.33	±	33.5	35.14	±	9.9
Siphonophores	71.53	±	25.4	55.30	±	16.3	39.17	±	9.8
Amphipods	8.78	±	1.7	43.32	±	13.2	28.34	±	5.3
Platyhelminthes	0.00	±	0.0	0.00	±	0.0	48.83	±	21.0
Ichthyoplankton	7.62	±	2.2	28.64	±	12.8	0.00	±	0.0
Nauplius L	2.15	±	0.6	1.02	±	0.3	19.78	±	5.6
Pteropods	4.20	±	1.8	0.62	±	0.2	5.02	±	2.2
Foraminiphers	0.45	±	0.1	0.27	±	0.1	7.55	±	0.9
Gastropods	0.35	±	0.1	0.21	±	0.0	1.32	±	0.2
Cirripedia L	0.17	±	0.0	0.09	±	0.0	1.25	±	0.4
Bryozoa L	0.59	±	0.2	0.16	±	0.0	0.70	±	0.3
Radiolarian	0.02	±	0.0	0.05	±	0.0	0.60	±	0.2
Echinoderm L	0.01	±	0.0	0.00	±	0.0	0.04	±	0.0
Appendicularian	0.00	±	0.0	0.00	±	0.0	0.00	±	0.0
Fish Egg	0.00	±	0.0	0.00	±	0.0	0.00	±	0.0
Total	1943	±	435	2620	±	572	5721	±	1019

When assessing the day vs. night vertical distribution of taxonomic groups in terms of their contribution to biomass, different patterns arise compared to numerical abundance. In this case, we used 9 taxonomic categories to examine vertical distribution and DVM in terms of biomass: small Copepods (SC), large Copepods (LC), *Acartia* Copepods (AC), Eucalanidae Copepods (EC), , Euphausiids (EU), Decapod larve (DL), Chaetognaths (CH), Annelids and all the other taxa (**Fig. 4**). Contrasting with numerical abundance, the vertical distribution of biomass was more heterogeneously divided among taxonomic groups and DVM patterns vary strongly between stations. Small Copepods continue to dominate at the St. T5 (24%), with two peaks of biomass, a surface peak associated to the upper oxic layer (**OX-ML**) and OMZ-UB stratum during night condition, and a second peak associated to deeper stratum (OMZ-LW) during daytime. At the onshore Stations T3 and L6 the biomass had a similar vertical distribution but lower (~7%), at the Station T3 the peak of biomass was in the upper oxic layer (**OX-ML**) during daytime condition and then it decreases sharply within the **OMZ-UB** and within the OMZ core (**OMZ-UC** and **OMZ-LC**). This abrupt decrease in biomass coincides with the intense OMZ present at this station T3. The second peak of biomass during daytime was in deeper stratum (OMZ-LW), where oxygen conditions seem to be restored. Large Copepods dominate at the onshore St L6(30 %) where their biomass reached up to 1727.49±340.8mg C. m^{-2} d^{-1} **(Table 2).** A surface peak of biomass was associated to OMZ-UB stratum during daytime condition, and a second peak associated to deeper stratum (OMZ-LW) also during daytime. Off Iquique they were the second dominant group, with a surface peak in OX-ML stratum during night at St. T5 and daytime at St. T3, and a second peak in deeper stratum (OMZ-LW), during daytime in both stations (**Fig. 4**).The biomass of Eucalanidae and Acartia copepods were lower than the other copepods in the whole area, but in general Eucalanidae was associated to the deeper stratum.

Following Copepods, Euphausiids were the second dominant group in term of biomass in the whole area. In general, their ascent from deep layers to the upper ones at night was also evidenced by increasing proportions of these group in the OMZ-UB stratum at night. The highest biomass was in St L6(19%) where reached up to 1060.58±305.8 mg C. m^{-2} d^{-1}**(Table 2).** A surface peak of biomass was associated to OMZ-UB stratum during night condition, decreasing in the deep strata (**Fig. 4**). Across of the zonal section off Iquique two peak of biomass was in both stations. A surface peak was in OMZ-UB stratum during night condition followed by lower biomass within the OMZ core, then a second peak was in the OMZ-LC during daytime.

Decapod Larvae clearly dominated over copepods in the St. T3 (39%). The high biomass was in OMZ-UB stratum during night condition followed by lower biomass within the OMZ Core. At the St L6 also was a second peak of biomass in the OMZ-LC during night. Chaetognaths and Annelids were other groups with an important vertical movement of biomass between day and night across strata, and like other groups with two peaks of biomass. The high biomass was at St. L6 in both groups (**Fig. 4**).

Total added biomass of zooplankton revealed more clearly DVM behaviour of the whole zooplankton community (**Fig. 5**). The vertical distribution and daytime vs. Night-time variability of zooplankton biomass showed distinctive features associated with the OMZ structure, with significant differences ($p<0.05$) between strata for both daytime and night-time samplings, as based on the ANOSIM test ($p<0.05$). 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.5). Overall, we observed that highest values of biomass were during the night at the shallower sampling stratum (Ox-ML) and in the subsurface during the day. There was also an important increase in biomass at the deepest stratum (OMZ-LW) during the daytime and night condition.

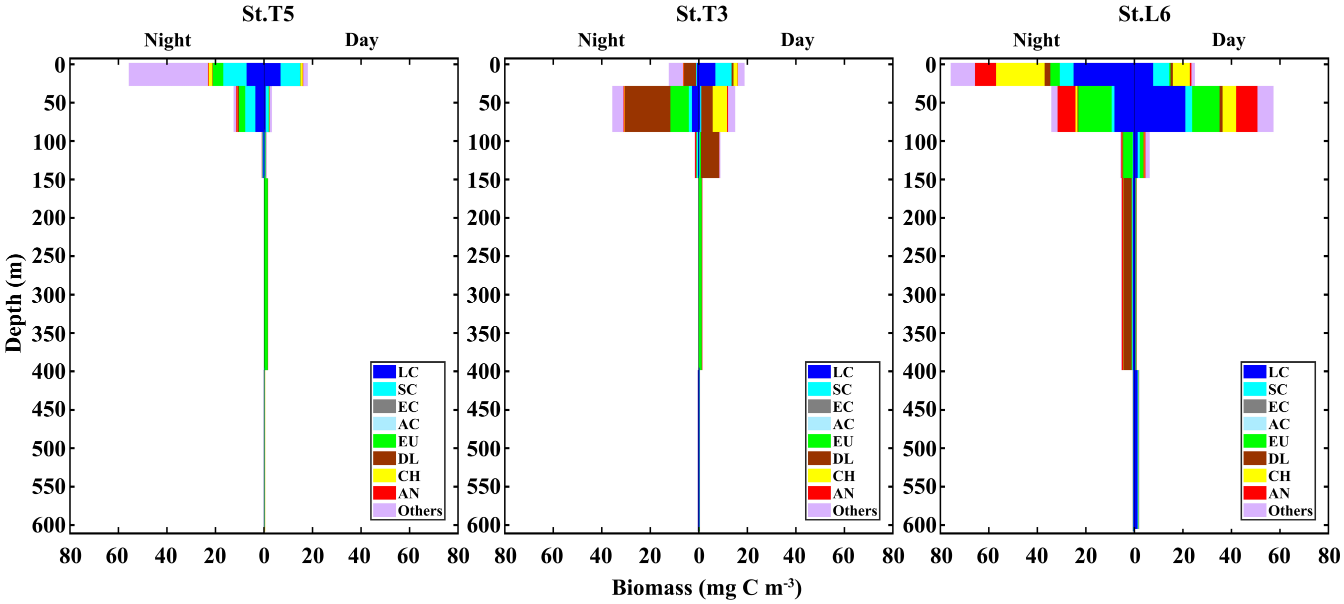

Fig.4. Daytime vs. Night-time vertical distribution of biomass of dominant taxonomic groups at 3 stations off northern Chile: off Iquique (StationsT5 and T3) and off Coquimbo (StationL6). Data are from night and day replicated samples during two consecutive days in the austral spring 2015. Values represent means from sampling size n=4 for St.T5 and St. T3, and n=2 for St. L6.

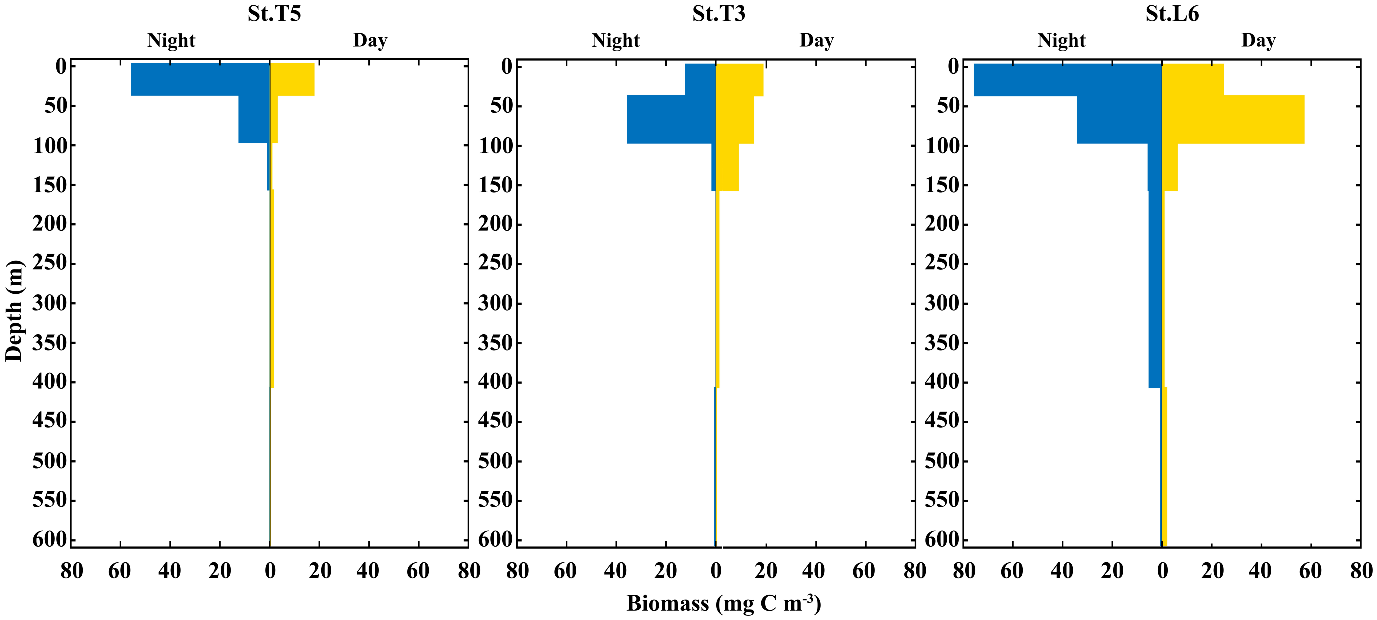

Fig. 5. Vertical distribution of total zooplankton biomass during daytime and night-time conditions at 3 stations off northern Chile: off Iquique (StationsT5 and T3) and off Coquimbo (StationL6) during two consecutive days in the austral spring 2015.).

3.4.1 Migrant biomass of the zooplankton taxa

The migrant biomass of the zooplankton taxa and the rate of migration (RM), represented by the proportion of biomass (%) being vertically moved daily from the upper 90 m are shown in **Table 3**. Most dominant groups showed a high rate of migration as reflected in the RM. In terms of migrant biomass, Decapod larvae, Euphausiids, Decapods, Copepods and Chaetognaths accounted for a large proportion of total migrant biomass (81%), although high estimates of migrant biomasses were also associated with high standard deviations, indicating a strong variation among replicated samples (**Table 3**). Presence of zero values in **Table 3** represents absence of a given taxonomic group in the upper 90 m layer or extremely low values of biomass under both conditions' day and night, so that such groups did not contribute, or they had a non-significant contribution to total migrant biomass.

Table3. Migrant biomass (mg C m^{-2}) and rate of migration (RM) (%) for taxonomic groups of zooplankton sampled at northern Chile at 3 stations: off Iquique (Stations T5 and T3) and off Coquimbo (Station L6) during the austral spring 2015. RM represents the proportion (%) of migrant biomass with respect to total biomass found at night in the 0-90 m for a given taxonomic group.SD= Standard deviation of the migrant biomass estimated from n=4 (St. T5 and St. T3) and n=2 (St. L6).

	ST-T5			**ST-T3**			**ST-L6**		
TAXA	**MB**	**SD**	**RM %**	**MB**	**SD**	**RM %**	**MB**	**SD**	**RM %**
Decapoda L	24.50	17.32	**1**	968.95	685.15	**40**	**12.19**	8.62	**1**
Euphausiids	269.50	190.56	**11**	455.14	321.83	**19**	**247.96**	175.34	**10**
Decapods	876.93	620.08	**36**	0.00	0.00	**0**	**0.00**	0.00	**0**
Chaetognaths	20.31	14.36	**1**	390.72	276.28	**16**	**105.39**	74.52	**4**
Copepods									
Small C.	223.31	157.90	**9**	139.02	98.30	**6**	**128.19**	90.64	**5**
Large C.	183.07	129.45	**8**	43.78	30.96	**2**	**245.28**	173.44	**10**
***Eucalanidae* C.**	0.00	0.00	**0**	1.10	0.78	**0**	**0.12**	0.09	**0**
***Acartia* C.**	0.04	0.03	**0**	0.00	0.00	**0**	**0.62**	0.44	**0**
Ctenophores	0.00	0.00	**0**	202.89	143.46	**8**	**81.61**	57.71	**3**
Annelids	32.50	22.98	**1**	4.03	2.85	**0**	**156.14**	110.41	**6**
Hydrozaa	35.83	25.34	**1**	7.80	5.52	**0**	**79.04**	55.89	**3**
Siphonophores	34.89	24.67	**1**	58.18	41.14	**2**	**0.33**	0.23	**0**
Amphipods	5.62	3.98	**0**	32.50	22.98	**1**	**32.93**	23.29	**1**
Salps	27.36	19.34	**1**	38.56	27.27	**2**	**4.57**	3.23	**0**
Ostracods	17.80	12.59	**1**	12.92	9.14	**1**	**36.37**	25.72	**2**
Platyhelminthes	0.00	0.00	**0**	0.00	0.00	**0**	**63.08**	44.61	**3**
Pteropods	3.97	2.81	**0**	0.07	0.05	**0**	**9.85**	6.96	**0**
NaupliusL	3.06	2.17	**0**	0.36	0.25	**0**	**2.84**	2.01	**0**

Foraminiphers	0.09	0.07	**0**	0.03	0.02	**0**	**3.11**	2.20	**0**
Cirripedia L	0.26	0.18	**0**	0.01	0.01	**0**	**1.87**	1.32	**0**
Bryozoa L	1.06	0.75	**0**	0.18	0.13	**0**	**0.83**	0.59	**0**
Gastropods	0.22	0.16	**0**	0.12	0.09	**0**	**0.11**	0.08	**0**
Echinoderm larvae	0.02	0.01	**0**	0.00	0.00	**0**	**0.07**	0.05	**0**
Ichthyoplankton	0.06	0.04	**0**	0.00	0.00	**0**	**0.00**	0.00	**0**
Appendicularia	0.00	0.00	**0**	0.00	0.00	**0**	**0.00**	0.00	**0**
Fish Eggs	0.00	0.00	**0**	0.00	0.00	**0**	**0.00**	0.00	**0**
Radiolarian	0.00	0.00	**0**	0.00	0.00	**0**	**0.00**	0.00	**0**

4 Discussion

Studies on zooplankton DVM and the active transport of C mediated by zooplankton have been documented previously for the Pacific Ocean and for other areas of the world's ocean, as summarized in **Table 4.** However, downward C flux due to DVM in highly productive upwelling regions, such as northern Chile, which is also characterized by severe subsurface hypoxic conditions upon presence of a shallow OMZ, is 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). These studies have shown 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 and McLaren, 1999). Therefore, it seems that the OMZ can plan a very significant role influencing vertical distribution, DVM and ultimately the downward C flux mediated by zooplankton.

Our approach to assess downward C flux 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 different zooplankton can have for vertical flux of C and hence 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 *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 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).

Regarding the estimates of biomass for each of the taxonomic groups, our approaches can certainly introduce variation, depending on selected regressions and conversion factors from highly diverse body shapes and body densities of the zooplankton taxa affecting the estimates of body area and volume, dry weight and C content. Various approaches have been adopted for converting sizes to body masses. For example, Lehette and Hernández-León (2009) provided some general regression equations for subtropical and Antarctic zooplankton describing the relationship between scanned area and body mass (C content). These authors also proposed two separate regressions for crustacean and gelatinous zooplankton, because of different body densities. In our study, we adopted more direct estimates of body masses by converting individual areas or volumes (from ZooScan) using published regressions for separate taxonomic groups. Also, in our samples there was a high diversity of taxonomic groups as identified by ZooScan, such that unique regressions for crustacean and gelatinous organisms may lead to strong biases in body mass estimates, because of high variability in C content, which is the key component of body mass needed to estimate C flux. Therefore, the use of taxa-specific conversion factors, as those detailed in our Table S3 (Supplemental Material) is strongly recommended.

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, an important 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 too small (ca. 0.4 mg C m-^{2} d^{-1}), as compared to the estimate made by Hidalgo *et al.*(2005). In fact, the migrant biomass and rate of migration of this group was non-significant when considering DVM between the upper 90 m and below, suggesting a little or no contribution to downward flux of C for this group of copepods. However it seems that Eucalanidae remain below the oxycline or nearby the base of the oxycline day and night, as shown by their weighted mean depth (WMD) and therefore suggesting that they may still contribute to vertical flux by feeding at the base of the oxycline at night and then migrating into the OMZ during the day.

Other taxa, such as Euphausiids, *Acartia* spp., other copepods, Ctenophores, Decapods, Annelidae, Bryozoa L, Pteropods and Chaetognaths tended to concentrate their populations inside the OMZ core showing a strong link to the OMZ with important movement throughout the water column. 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 showed 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.

Our estimates of DVM-mediated C flux showed that migrant biomass (958±778 mg C m^{-2} d^{-1}) and C flux estimates (71±64mg 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 however have not been done in regions with severe hypoxia or anoxia at mid water depths (e.g. Kiko *et al.,* 2016), such as the highly 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 4**). High productivity and strong aggregation of zooplankton in coastal areas of this region (Escribano *et al.,* 2000; Escribano and Hidalgo, 2000) may promote greater amounts of migrant biomass. This requires however that DVM should not be majorly constrained by presence of the OMZ and that most migrant taxa are tolerant to low-oxygen. On the other hand, our estimates of downward C flux were substantially lower than previous ones reported off northern Chile by Hidalgo *et al.* (2005) for *Eucalanus inermis* alone (14.1 mg C m-^{2} d^{-1}) and for copepods and euphausiids by Escribano *et al.* (2009) (7200 mg C m^{-2} d^{-1}) **(Table 4).** Although, such previous estimates may be too high, considering the level of primary production in the upwelling zone of Chile (~10000 mg C m^{-2} d^{-1}, the maximum estimated value) (Daneri *et al.,* 2000), suggesting that previous works may have overestimated active transport of C. Although 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 (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 some macrozooplankton, and therefore such values may be greater.

Table 4. Comparison of active transport of carbon (AC) (mg C m^{-2} d^{-1}) by vertically migratory taxa in Pacific Ocean. Diel vertically migratory taxa (DVM), productivity primary (PP) (mg C m^{-2} d^{-1}), migrant biomass (MB) (mg C m^{-2}), respiratory loss (R) (mg C m^{-2} d^{-1}), faecal pellets production (F) (mg C m^{-2} d^{-1}) and mortality (M) (mg C m^{-2} d^{-1}). Where provided by authors, estimated passive export (POC) is listed. Fluxes refer 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	R	F	M	% 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	2833±1155	958 ±778	71±64					This study

Differences of our estimates with previous works may also be accounted by strong variability of zooplankton abundance in the upwelling zone. In fact, our estimates of migrant biomasses of the different taxonomic groups based on 2 days of sampling and two replicates for each condition (day and night) are strongly variables, as shown by the standard errors in **Table 3** which can be as much as 100% from the mean value. Therefore, comparisons must take caution upon strong time-space variation when assessing zooplankton abundance. Nevertheless, a strong spatial variation in migrant biomass was also evident when comparing the three sampling stations. For instance, St. L6 had more biomass than the other stations, but much less migrant biomass, and thus a very low contribution to vertical flux of C by DVM. At station L6, large copepods, Euphausiids, Annelids and Chaetognaths largely contributed to biomass, although they did not show significant DVM. Therefore, species composition and their DVM behaviour appear as a key factor to determine the downward flux of C mediated by active transport.

Even although the OMZ did not greatly prevent DVM migration, zooplankton behaviour appeared 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 (StationsT3 and L6), but in particular in the station off Iquique (St. T3) that also showed a higher migration rate (60%). 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 intensity of the hypoxic events. This could explain why individuals with in a single population can perform reverse, normal, or non DVM, apparently depending on the more important source of mortality: predation by nocturnal feeding, normally migrating carnivorous zooplankton, or visually hunting planktivorous fish (Ohman, 1990). These kind of DVM behaviors can only be better assessed and understood when looking at the population level, although again time-space variation in zooplankton abundance in a highly heterogeneus upwelling zone should be kept in mind.

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 off Antofagasta (23°S) by Gonzalez *et al.*(1998)based on sediment traps (125 to 176mg C m^{-2} d^{-1}). Regarding the question on how efficient is active C transport mediated by DVM, we obtained satellite-based (http://science.oregonstate.edu.ocean.productivity) estimates of net primary production (monthly means for November-December 2015) for the coastal area (Stations T3 and L6) and the coastal transition zone (Station T5), averaged for the months of November and December 2015. Our estimates of downward C flux represented a mean of ca. 4 % of export of Carbon resulting from net primary production in the upwelling region, estimated in the range of 1500-3500 mg C m^{-2} d^{-1} **(Table 5).** If we consider this is accounted only by mesozooplankton, then an important fraction of freshly produced C might be taken downward by zooplankton, and this DVM-mediated C flux ought to be taking into account when and analysing and modelling the C budget in the upwelling zone.

Table5. Mean net primary production rate and estimates of daily downward C flux due to passive sinking and mediated by diel vertical migration (DVM) of mesozooplankton at three stations (T5, T3 and L6) in the coastal upwelling region off northern Chile during the austral spring 2015. Primary production represents satellite-based estimates of monthly mean (November-December 2015) at the 3 sampling stations. Passive C flux is a mean value estimated from sediment traps by González et al. (2000) off Antofagasta (northern Chile, 23 °S) for January 1997. Total biomass and epipelagic biomass are mean observed values from day-night conditions after 2 consecutive days of sampling.

Station	**T5**	**T3**	**L6**	**Mean ± SD**		
Primary Production mg C m^{-2} d^{-1}	1500	3500	3500	2833	±	1155
Passive Carbon Flux mg C m^{-2} d^{-1}				151	±	36
Integrated Abundance ind. m^{-2} (0–600 m)	221735	127085	371235	240018	±	123097
Total biomass mg C m^{-2} d^{-1} (0–600m)	1943	2620	5721	3428	±	2015
Epipelagic biomass (mg C m^{-2}) (0–90m)	1581	1988	4259	2609	±	1443
Migrant biomass (mg C m^{-2} d^{-1})	1686	1048	139	958	±	778
Rate of Biomass migration (%)	70	42	3	38	±	34
Active Carbon Flux (mg C m^{-2} d^{-1})	139	63	11	71	±	64
Total Active Carbon exported (%)	9.3	1.8	0.3	3.8	±	4.8

5. Conclusions

In the coastal upwelling zone off northern Chile the presence of a subsurface oxygen minimum zone (OMZ) can impose an important constraint for diel vertical migration of zooplankton and so influencing the downward C export mediated by zooplankton. We found that most of the zooplankton biomass aggregates above the oxycline, associated with more oxygenated surface waters and this was evident upon presence of a more intense OMZ. Some taxonomic groups however, were found closely associated with the OMZ and several taxa were able to perform DVM in the upwelling zone withstanding severe hypoxia. Also strong migrants, such as large sized copepods and copepod of the group Eucalanidae and Euphausiids, can exhibit a large migration amplitude (~500 m), remaining either temporarily or permanently during the day or night condition within the core of the OMZ, and so contributing to the release of C below the oxycline (and thermocline). Our estimates of DVM-mediated C flux suggested that a mean migrant biomass of 957.7 mg C m^{-2} d^{-1} may contribute with about 71.1 mg C m^{-2} d^{-1} to the OMZ system through respiration, mortality, and C excretion a at depth, accounting for ca, 4% of the net primary production, and so implying the existence of a efficient mechanism to incorporate freshly produced C into the OMZ. This downward C flux mediated by zooplankton DVM is however strongly depending on the taxonomic structure due to variable migration amplitude and DVM behavior. These estimates should also consider the strong temporal-spatial variation in zooplankton abundance in the upwelling zone for comparison purposes.

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