To start, I can tell that the authors have made an effort to address my and the other reviewer's comments. The paper also has improved in terms of readability, and figures 1, 2 and 3 are much better now.

But there remain a few issues that prevent publication, and therefore I again need to ask for a thorough revision. I still consider this an interesting dataset, and I know how much work went into the image analysis.

The first point is again the biomass estimation. While the figure the authors provided in response to my previous comment looks convincing (then again, it is a log scale), the way they got to their values is absolutely NOT correct, and since a paper like this will be read a lot and table S3 will be used by others, I absolutely insist that this is corrected. I still think it would be easiest to ditch all the four steps of ellipsoid biovolume calculation, wet weight and dry weight assumptions, and finally carbon conversions, and simply use the image area to carbon conversion regressions (sources for which are already halfway compiled in their own table S3).

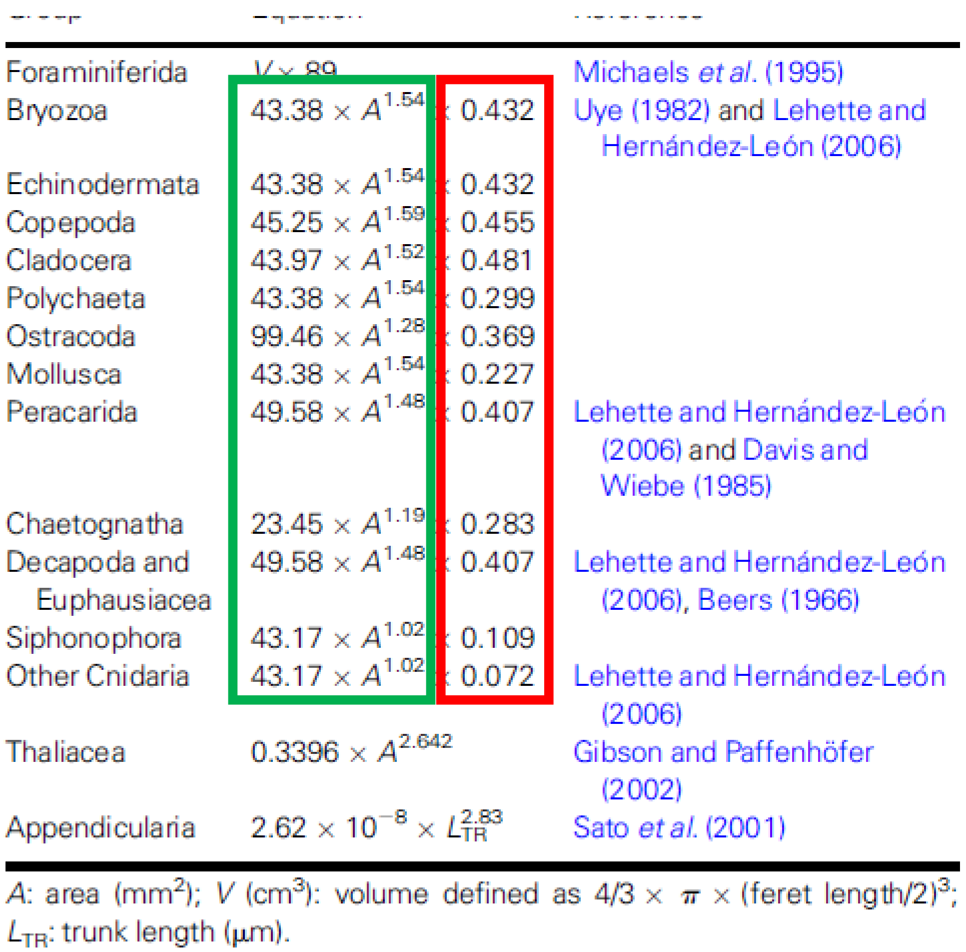
In table S3, conversion factors from dry weight to carbon are listed. There are several errors in this table. First, citing is sloppy, making it quite difficult to track down the errors (apart from the fact that the full references are missing). For example. Marcolin et al. (2015) is cited a lot, but their values mostly originate from Lehette & Hernandez-Leon 2009.

More importantly, THESE VALUES ARE NOT THE FRACTION OF DRY WEIGHT THAT IS MADE UP OF CARBON!!!

Instead, these values are the parameter a (intercept) from the regression DW = a * Image Area^b.

I suspect this mistake somehow happened because many values are near 0.4. However, one could have noted that a 99% carbon content in ostracods would mean they are basically charcoal.

Table 1 from Marcolin et al. 2015. Regression equations used to estimate carbon from size (image area). Red box marks the dry weight to carbon conversion factors. Green box marks the regression parameters from Lehette & Hernandez-Leon 2006.



Foraminiferida	$V \times 89$	Michaels *et al.* (1995)
Bryozoa	$43.38 \times A^{1.54} \times 0.432$	Uye (1982) and Lehette and Hernández-León (2006)
Echinodermata	$43.38 \times A^{1.54} \times 0.432$	
Copepoda	$45.25 \times A^{1.59} \times 0.455$	
Cladocera	$43.97 \times A^{1.52} \times 0.481$	
Polychaeta	$43.38 \times A^{1.54} \times 0.299$	
Ostracoda	$99.46 \times A^{1.28} \times 0.369$	
Mollusca	$43.38 \times A^{1.54} \times 0.227$	
Peracarida	$49.58 \times A^{1.48} \times 0.407$	Lehette and Hernández-León (2006) and Davis and Wiebe (1985)
Chaetognatha	$23.45 \times A^{1.19} \times 0.283$	
Decapoda and Euphausiacea	$49.58 \times A^{1.48} \times 0.407$	Lehette and Hernández-León (2006), Beers (1966)
Siphonophora	$43.17 \times A^{1.02} \times 0.109$	
Other Cnidaria	$43.17 \times A^{1.02} \times 0.072$	Lehette and Hernández-León (2006)
Thaliacea	$0.3396 \times A^{2.642}$	Gibson and Paffenhöfer (2002)
Appendicularia	$2.62 \times 10^{-8} \times L_{TR}^{2.83}$	Sato *et al.* (2001)

A: area (mm^2); V (cm^3): volume defined as $4/3 \times \pi \times (\text{feret length}/2)^3$; L_{TR}: trunk length (μm).

To recapitulate: in the first round of review (where the calculation methods were not described yet, so I could not find the error), I suggested to do this:

Use regression $DW(\mu g) = a*A^b$

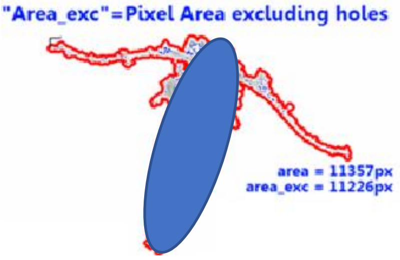
Where A is image area (mm^2)

And a and b are regression parameters from published literature (mainly L&H 2009)

Use published conversion factors for dry weight to carbon (mainly Kiorboe 2013)

Instead, the authors insisted that "Lehette and Hernandez-Leon (2009) provide estimated regression equations for different zooplankton taxa between scanned area and biomass (C content)((COMMENT: THIS IS INCORRECT,THEY PROVIDE DW FROM SCANNED AREA, NOT C CONTENT)). This is a direct relationship between size and C content which is actually the key parameter needed for estimates of migrant biomass and flux of C. We do not question such relationships by Lahette and Hernandez-Leon, but they are not suitable for our taxonomic composition and do not account for variable C-specific contents (which are independent of size). Instead, we used taxa-specific size and C content conversion factors previous published works which are suitable for our taxonomic groups and for the study region."

And they did this:



Calculate volume of rotating ellipsoid (blue)

Assume density of 1

($1mm^3$

= 1mgWW)

Assume water content of 90%

1mg WW

=0.1mg DW

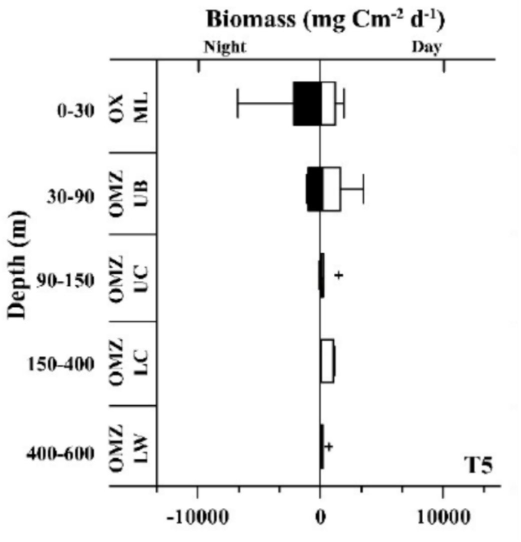
Use completely random numbers for carbon conversion

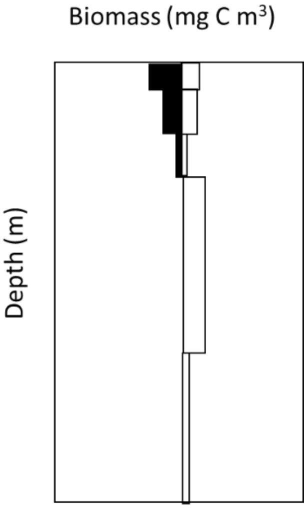
mgDW->mgC

This needs to be corrected.

Second, the use of a log-axis on a stacked bar chart (figs 4 and 5) is not possible. Please use a linear axis. Actually I don't think the stacked bar chart are really necessary, the taxon-specific values are listed in the tables.

Third, visualizing the total distribution of biomass (Fig 6) should be kept, but this figure has some issues – first, the x-axis lable is a rate. This also does not fit to the figure caption. I still think the most logical way to plot biomass distribution is as bar chart with variable widths on a linear depth axis. This way, you can plot biomass concentration (mg C m-3) as the height of the bars, and the bar area gives a good idea on the integral, which makes it nicer to compare depth strata with different thickness (and also relate to the hydrography in fig 2). I made a sketch to illustrate what I mean (it is just a sketch, so it lacks axis tick marks, error bars, and layer names). Left: one panel of Fig 6 now, right: suggestion.





Lastly, the results are still quite lengthly. The words “show” and “exhibit” are used both about fifteen times each. Try to streamline the writing a bit, using mostly active voice ("Copepod abundance was higher here than there" rather than "Copepods exhibited higher abundances here than there").

I do look forward to the final version of the paper.

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 zooplankton biomass becomes aggregated in the coastal zone and composed by a highly 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 3.4 g C m^{-2} d^{-1} may contribute with about 0.6g C m^{-2} d^{-1} to the OMZ system through respiration, mortality, and production of fecal pellets at depth, accounting for ca. 25% of the net primary production, and so implying the existence of a very efficient mechanism to incorporate freshly produced C into the OMZ. This downward C flux mediated by zooplankton is however strongly 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 and behaviour (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 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 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).

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

2 Methods

2.1 Study 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 Sea tech Fluorometer. Discrete water samples were also obtained for chemical measurements of oxygen.

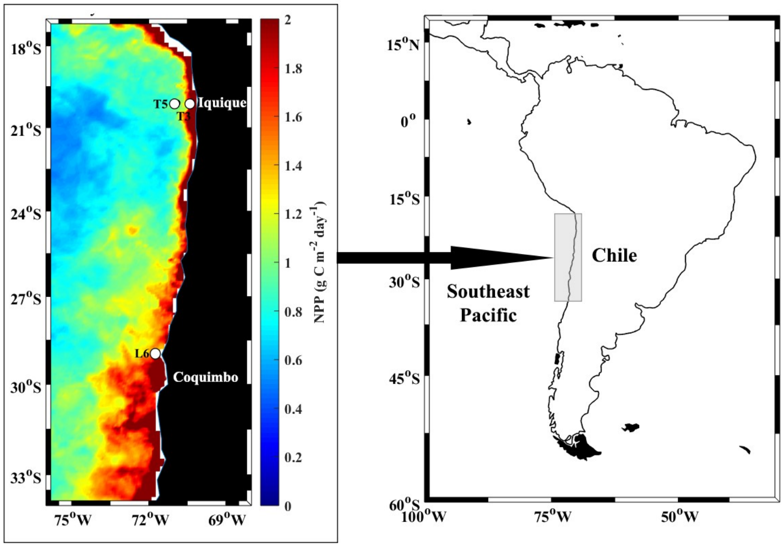

Fig. 1. Study area at the northern upwelling region of Chile, indicating sampling stations during the LowpHox cruise conducted in November-December 2015 onboard the R/V *Cabo de Hornos*. Satellite estimated Net Primary Production (NPP), averaged for November-December 2015 is shown. NPP was obtained from 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).** Zooplankton hauls 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. 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. Therefore, they were assumed as representing the near surface oxygenated layer, the upper oxycline, the upper OMZ, the OMZ core and the lower boundary of the OMZ indicated in **Table S2 (Supplemental Material)**. Once onboard the collected zooplankton samples were preserved immediately in 5% buffered formalin-seawater solution.

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}) and stratum-integrated abundance (ind. m^{-2}) of total zooplankton or of each taxonomic group was calculated following Eq. (1):

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

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 net tows in a 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 for each organism. The ellipsoidal biovolume (EBv) was computed instead of equivalent spherical diameter (ESD). Biovolume was used because most of the zooplankton shapes were elongated, 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):

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

where, the EBv corresponds to the biovolume of an ellipsoid, Major is the longest axis of the object and Minor is the minor axis of a perfect ellipse of the same area of the measured object, both axes are in mm and were provided by ZooScan. We used EBv (mm^3) for estimating biomass (mg C) for all taxonomic groups. Conversions 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 in average was 90% (DM = 0.1 × WW), as suggested by Yamaguchi *et al*. (2014) and Sato *et al.*(2015). Finally, individual biomass was converted to carbon using a factor carbon for each taxonomic group from previous published data **Table S3 (Supplemental Material).**

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 used a daily respiration fraction of 0.12. This proportion of biomass being respired was estimated by Hernández-León and Ikeda (2005) for total zooplankton biomass at a temperature ranging between 13°C and 18 1C for mid-latitude areas. We used this value considering a similar temperature range between surface water and the core of the OMZ (**Fig. 2**). The daily contribution of egestion rate to C flux was assumed to be 0.09 of migrant biomass, as suggested by Escribano *et al.* (2009). This estimate was derived from a combined biomass of large-sized copepods and euphausiids which are the major groups contributing to migrant biomass in this upwelling area. This value also considers that most egested faecal pellets may be produced rapidly in the upper layer upon feeding (Escribano *et al.,* 2009). The contribution of mortality to C flux was assumed to be 0.08 d^{-1} of migrant biomass, as a conservative estimate suggested by Ohman and Wood (1996). We thus estimated total C flux following Eq. (3):

$$\text{C Flux} = \left(\frac{\text{RZ} + \text{MZ})}{2}\right) + EZ \qquad (3)$$

where Rz, Mz, and Ez, are Respiration, Mortality and Egestion estimates of fractions of total migrant biomass (MB) for a 12-h period. We thus estimated total flux as,

$$\text{C Flux} = (0.12*(\text{MB}) + 0.08*(\text{MB})) / 2 + 0.09*(\text{MB}) \qquad (4)$$

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 both night: day (N:D) ratios in each stratum and 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, in according to Andersen *et al.* (2004) following Eq. (5):

$$WMD = \frac{\Sigma(ni*zi*di)}{\Sigma(ni*zi)}, \quad (5)$$

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

Vertical profiles of temperature, DO, and sigma-t show general oceanographic conditions in all stations (**Fig. 2**), such as the vertical distribution of oxygen and location of the OMZ. From the vertical profiles of oxygen and coinciding with the sampled layers of the Multinet different strata were defined: A well oxygenated stratum with oxygen approaching air saturation (>250 µmol O_2 kg^{-1}) defined as 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).

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 exhibited a gradual decrease 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 present 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 located 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 located 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 core was ca. 1 µmol O_2kg^{-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**).

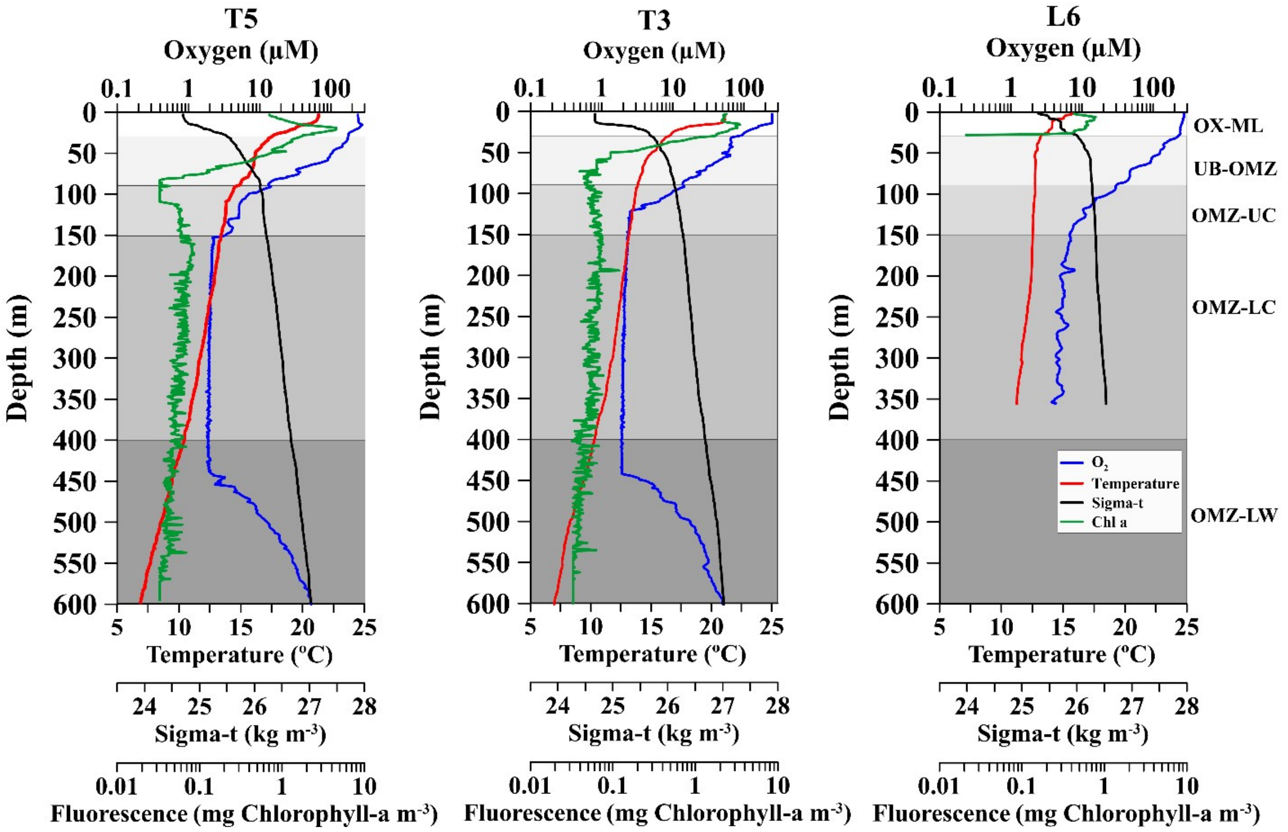

Fig. 2. Vertical profiles of dissolved oxygen (O_2), temperature, Chlorophyll-a and water density (sigma-t), at 3 stations off northern Chile (see **Fig. 1**) during the LowpHox Cruise in the austral spring 2015. Shaded areas represent different layers defined according to oxygen concentration. OX-M=Oxic 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 (29º S) (**Fig.1**), exhibited similar characteristics to St. T3 (21º S), 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 oxycline was down to 80 m. The low O_2 concentrations in the core were less intense than at 21ºS (4 to 20 µmol $O_2 kg^{-1}$) 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 located 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 present off 29º S (St. L6). The most dominant taxa both daytime and night conditions, were: Copepods 87% (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); Appendicularian 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 shown 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). Significant differences among stations (Two-Way Crossed Analysis ANOSIM p<0.05) were found, so that the stations were treated independently. Off Iquique the abundance showed the lowest values 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 shown 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 that exhibited a strong DVM and showed 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), Annelidae (AN), Bryozoan (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 that exhibited a moderate DVM and showed 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 Appendicularian (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 exhibited a weak DVM and showed 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)** and in the **OMZ-UP,** but also in the **OMZ-UC** at the onshore stations (StationT3 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).

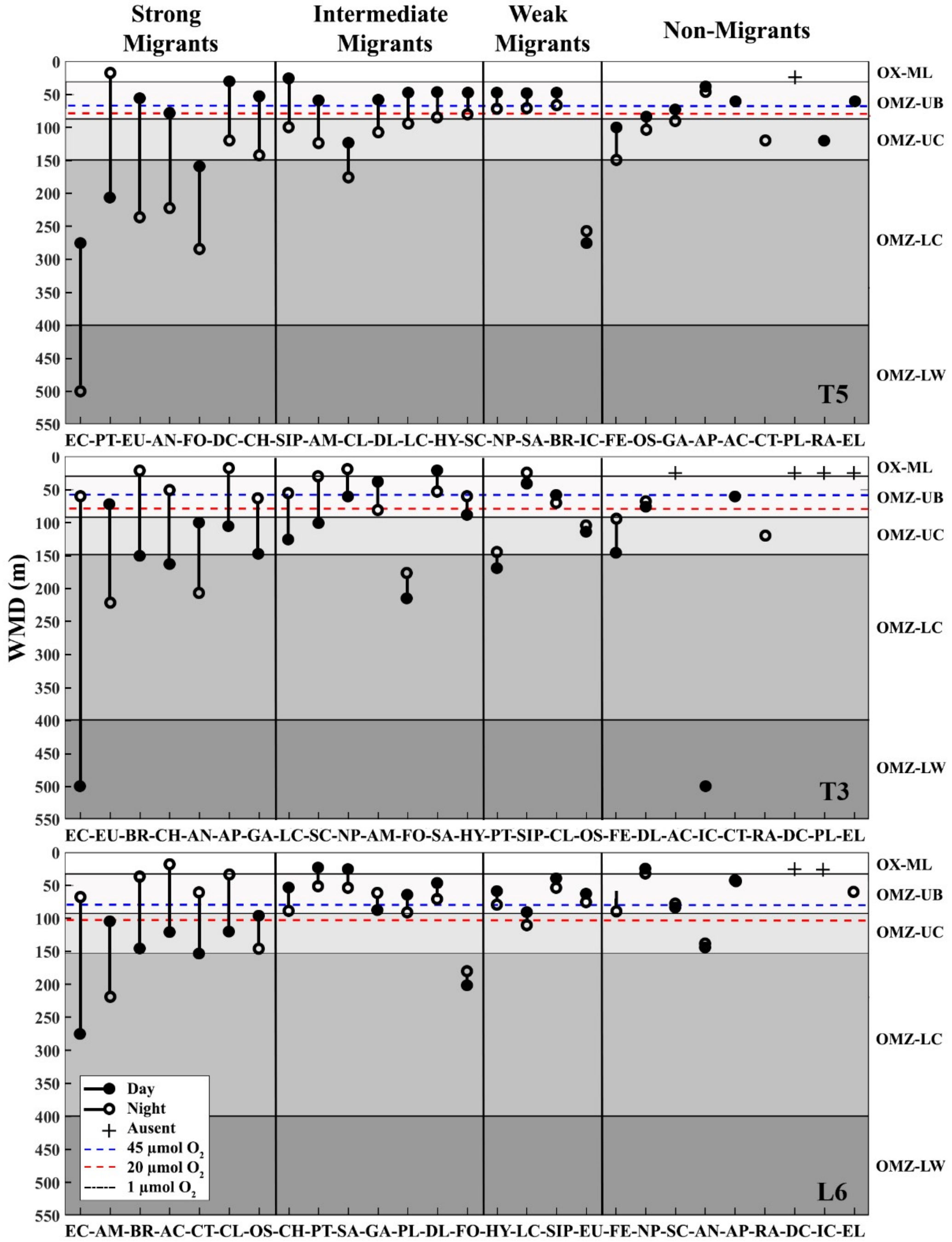

Fig. 3. Weighed mean depth distribution (WMD) of the zooplankton community interacting with the OMZ off Iquique (Stations T5 and T3) and off Coquimbo (Station L6) at the northern upwelling area of Chile during the austral spring 2015. Shaded gray areas represent different layers defined by their oxygen levels (defined in Methods). The taxonomic groups

were classified by automated analysis (ZooScan): EC= Eucalanidae Copepods, AM= amphipods, BR=Bryzoan, 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= Annelidae, AP=Appendicularian, 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). N: D is Night: day ratio of abundance. Four groups are defined in according to DVM behaviour. Relative abundances are shown in %.

	T5				**T3**				**L6**			
TAXA	**ΔDVM**	**N:D**	**%**	**TAXA**	**ΔDVM**	**N:D**	**%**	**TAXA**	**ΔDVM**	**N:D**	**%**	**MIGRANTS**
EC.	225	0.6	14	**EC.**	-440	8.3	28	**EC.**	-208	4.1	20	**STRONG MIGRANTS > 5%**
PT.	-188	12.4	12	**EU.**	149	0.3	10	**AM.**	115	0.5	11	
EU.	181	0.2	11	**BR.**	-129	7.0	8	**BR.**	-107	3.8	10	
AN.	145	0.3	9	**CH.**	-114	3.2	7	**AC.**	-103	7.0	10	
FO	126	0.6	8	**AN.**	105	0.5	7	**CT.**	-94	2.6	9	
DC.	90	0.3	6	**AP.**	-88	5.9	6	**CL.**	-87	3.6	8	
CH.	88	0.4	6	**GA.**	-84	2.3	5	**OS.**	49	0.7	5	
SIP.	73	0.3	5	**LC.**	-70	2.3	5	**CH.**	35	0.6	3	**INTERMEDIATE MIGRANTS > 2%**
AM.	64	0.5	4	**SC**	-70	3.3	5	**PT.**	29	0.4	3	
CL.	51	0.7	3	**NP.**	-42	1.6	3	**SA.**	29	0.5	3	
DL.	50	0.5	3	**AM.**	42	3.3	3	**GA.**	-27	1.4	3	
LC.	47	0.7	3	**FO**	-38	0.5	2	**PL.**	26	0.7	2	
HY.	39	0.5	2	**SA.**	32	1.2	2	**DL.**	22	0.7	2	
SC	34	0.5	2	**HY.**	-27	0.4	2	***FO***	-22	0.7	2	
NP.	24	0.6	2	**PT.**	-23	1.5	1	**HY.**	21	1.1	2	**WEAK MIGRANTS > 1%**
SA.	23	0.7	1	**SIP.**	-15	1.2	1	**LC.**	19	0.7	2	
BR.	18	0.7	1	**CL.**	12	1.6	1	**SIP.**	15	0.8	1	
IC.	-18	0.7	1	**OS.**	-9	0.8	1	**EU.**	11	0.7	1	
FE	49	1.1	3	**FE**	-52	1.1	3	**FE**	25	0.9	2	**NON-MIGRANTS <1%**
OS.	16	0.8	1	***DL.***	-7	1.1	0	**NP.**	6	0.8	1	
GA.	15	0.8	1	**AC.**	-	-	-	**SC**	-4	1.1	0	
AP.	7	0.8	0	**IC.**	-	-	-	**AN.**	-4	1.0	0	
AC.	-	-	-	**CT.**	-	-	-	**AP.**	2	1.0	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 82% of total abundance in average: Salps (SA.); Copepods represented by small Copepods (SC.), Large Copepods (LC.), Eucalanidae Copepods (EC) and *Acartia* Copepods (AC); Chaetognaths (CH); Euphausiids (EU) and Decapods Larvae (DL); as well as their patterns of strata–station–abundance relationships are illustrated in **Fig. 4.** 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 (>50%) was found in the shallower strata and well oxygenated layers **(OX-ML and OMZ UP)** (>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 slight peak in abundance was present in the **OMZ-LW** at all stations, occurring between 400-600 m, both daytime and night conditions (**Fig. 4**).

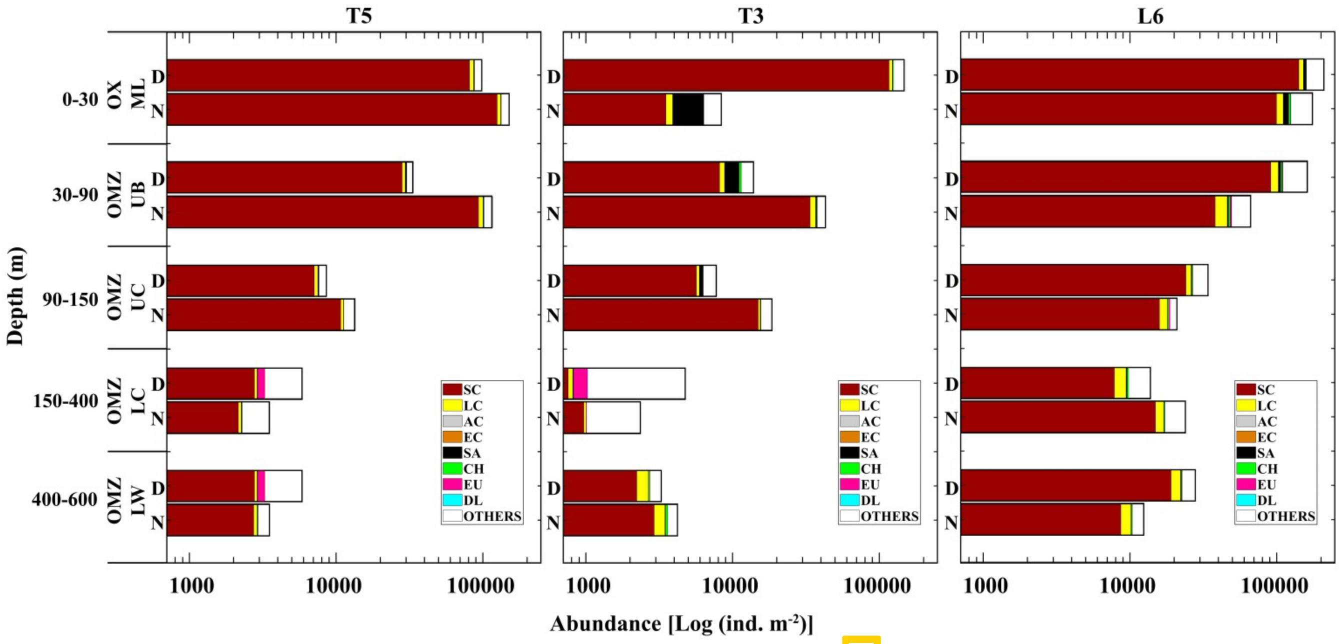

Fig. 4. Vertical distribution of dominant taxonomic groups of zooplankton sampled at 3 stations off northern Chile: off Iquique at 21° S (Stations T5 and T3) and off Coquimbo at 29° S (Station L6). Abundances are mean values from samples obtained during 2 consecutive days under night and day conditions in the austral spring 2015. Sampled layers represent

different conditions in terms of oxygen levels (see Methods) and the taxonomic groups and their acronyms are detailed in Supplemental Material **Table S3**.

As expected, Copepods dominated numerically the zooplankton community both within and outside the OMZ **(Fig. 4).** Small Copepods (SC) were the most abundant, followed by large Copepods (LC)**,** 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 observed at the offshore station St. T5 (87%), where abundances reached 192088 ind. m^{-2}. At onshore station St. T3 percentage of contribution of copepods was 79% and 69% at the St L6 **(Table S5 Supplemental Material).** Off Iquique, the highest abundance and biomass were in the shallower strata **(OX-ML) at** St.T5 (46%) and at St. T3 (47%), and these values were 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). Abundances showed slight increases in the **OMZ-LW** stratum during daytime, where oxygen levels increased after the extremely low levels within the OMZ. At the onshore station off 29ºS (St. L6), having a weaker and less extensive OMZ, the abundance showed similar vertical distribution. 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 (Stations T3 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 showed 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 and showed a smaller ΔWMD (34 m). At the offshore stations (StationsT3 and L6) most Copepods exhibited reverse DVM, except for large Copepods (LC) which showed slightly normal DVM at St. L6 off 29º S. At night Copepods tended to concentrate deeper in the stratum associated with the lower core of OMZ (**OMZ-UC**) and lower O_2 gradient **(OMZ-LW),** particularly Eucalanidae which exhibited a strong DVM with 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 tended to concentrate 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 tended to stay inside the OMZ and concentrated in the **OMZ-UC** stratum (St. L6) and **OMZ-UB** (St.T3). Finally, Eucalanidae, which exhibited a strong DVM tended to distribute in the **OMZ-UC (**St.T3**)** and the **OMZ UB** (St. L6) **(Fig. 3).**

Following Copepods, Salps were the second most abundant taxa of zooplankton, showing the largest aggregation at the onshore station St. L6 (~3%), where abundances made up to 10347±219 ind. m^{-2} d^{-1}. The WMD of Salps showed a range between 54 and 25 m depth **(Table 1)** and appeared to aggregate deeper at all stations, also present in the OMZ **(Fig. 3).** Similarly to Salps, most Chaetognaths showed the largest aggregation 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 **(Fig. 4)**. 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.

Euphausiids exhibited greater abundances at the onshore station L6 (<1%), where they reached up to 4755±1038 ind. m^{-2} d^{-1}, although regarding vertical distribution they were mainly concentrated in the **OMZ-UB** and **OMZ-LC** in St. T5 and St. T3 at day and at night, respectively. No DVM was detectable in the onshore station (St. L6), judging by the small difference between their day- and night-time distributions **(Fig. 4)**. However, at the offshore station St. T5 they appeared to perform a strong DVM with a vertical range between 236 and 56 m and a mean ΔDVM of 181 m **(Table 1)**. Decapods larvae were abundant at the **OMZ-UB** stratum during the day and at the **OMZ-UC** at layer at night in the offshore station (St.T3), where they reached up to 292±62 ind. m^{-2} d^{-1}, with a weak reverse DVM. However, at the offshore station St. T5 they appeared to perform a strong normal DVM with a vertical range between 120 and 30 m and a mean ΔDVM of 90 m **(Table 1)**.

The other main taxa, Appendicularian, showed the largest aggregation at the onshore station T5 (5%), where abundances reached up to 21848 ind. m^{-2}. The abundance and biomass of this group were mainly found in the oxic surface strata OX-ML at St. T5 and St. L6 both at day and at night. No DVM was detected in these stations, judging by the small difference between their day- and night-time distributions, while at the onshore station (St. T3) they appeared to have a strong reverse DVM into the OMZ-UC stratum at night as indicated by the migration indices (WMD-ΔDVM) (Table 1). The WMD at this station T3 showed a range between 18 and 106 m depth and ΔDVM of 88 m depth (**Table 1**).

3.3.3Others groups with vertical distribution associated to OMZ UC

The remaining 19 groups that only constituted 12% (in St.T5) 17% (in St.T3) and 26% (in St.L6) in abundance, showed variable DVM behaviours at each station: Normal DVM (in St.T5) and reverse DVM (in 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, Salps, Copepods, Chaetognaths, Euphausiids and Decapods accounted, more or less equally, for >70% in the whole area (**Table 2**). The bulk of biomass at Station T5 was dominated by Decapods, Salps, Copepods and Siphonophores >70% in this station, while Salps largely dominated the bulk of biomass at Station T3 (>60%) followed by Chaetognaths (12%). At the onshore Station L6, Copepods and Chaetognaths accounted for about 40% of total biomass (**Table 2**).

Table 2. 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**
Salps	652.37 ± 262.0	9904.93 ± 1906.6	963.60 ± 245.6
Copepods			
Large Copepods	552.91 ± 137.4	231.05 ± 46.9	838.28 ± 139.6
Small Copepods	419.12 ± 96.9	271.77 ± 48.4	2500.51 ± 400.3
Eucalanidae Copepods	0.02 ± 0.0	0.00 ± 0.0	0.44 ± 0.2
***Acartia* Copepods**	0.71 ± 0.3	8.75 ± 3.2	50.89 ± 16.3
Chaetognaths	215.71 ± 72.1	1800.82 ± 744.1	2261.81 ± 510.6
Euphausiids	296.39 ± 69.0	436.24 ± 115.4	919.43 ± 250.6
Decapoda Larvae	21.83 ± 5.4	1074.62 ± 321.2	549.82 ± 160.0
Hydrozoa	275.97 ± 106.9	363.61 ± 128.2	796.03 ± 182.7
Annelidae	71.17 ± 9.8	105.60 ± 15.4	1044.62 ± 268.9
Siphonophores	452.64 ± 106.5	363.37 ± 103.3	124.70 ± 29.9
Decapods	652.79 ± 279.4	0.00 ± 0.0	0.00 ± 0.0
Appendicularian	30.30 ± 10.1	14.79 ± 5.9	543.98 ± 232.7
Ctenophores	0.62 ± 0.3	119.55 ± 53.5	102.50 ± 31.7
Ostracods	11.92 ± 1.3	16.51 ± 1.1	185.56 ± 35.4
Amphipods	10.62 ± 2.2	51.17 ± 15.8	30.73 ± 6.4
Fish Eggs	17.64 ± 3.0	10.64 ± 1.4	47.24 ± 9.1
Platyhelminthes	0.00 ± 0.0	0.00 ± 0.0	62.04 ± 26.7
Nauplii	3.11 ± 0.8	1.41 ± 0.4	25.53 ± 7.6
Ichthyoplankton	6.98 ± 2.1	18.83 ± 8.4	0.00 ± 0.0
Pteropods	5.58 ± 2.4	0.89 ± 0.2	4.27 ± 1.8
Foraminifera	1.14 ± 0.4	0.14 ± 0.0	9.13 ± 2.5
Gastropods	0.94 ± 0.2	0.56 ± 0.1	3.59 ± 0.4
Cirripedia Larvae	0.25 ± 0.1	0.14 ± 0.0	4.10 ± 1.1
Bryozoan	0.80 ± 0.2	0.20 ± 0.0	1.35 ± 0.4
Radiolarian	0.04 ± 0.0	0.08 ± 0.0	1.03 ± 0.4
Echinoderm Larvae	0.01 ± 0.0	0.00 ± 0.0	0.04 ± 0.0

Total	3702	±	805	14796	±	2512	11071	±	1635

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), Salps (SA), Chaetognaths (CH), Euphausiids (EU), Decapod larve (DL), and all the other taxa (**Fig. 5**). Contrasting with numerical abundance (**Fig. 4**), the vertical distribution of biomass was more heterogeneously divided among taxonomic groups and DVM patterns vary strongly between stations. Small Copepods continue to dominate in the upper oxic layer (**OX-ML**), but at the Station T3 their biomass decreases sharply within the **OMZ-UB** and within the OMZ (**OMZ-UC** and **OMZ-LC**). This abrupt decrease in biomass coincides with the intense OMZ present at this station T3. Large Copepods tended to distribute more homogeneously in the water column, although they also tend to diminish their biomass during the day in the upper layers, while Euphausiids showed their ascent from deep layers to the upper ones at Station T5, but with lower biomass within the OMZ at the onshore stations T3 and L6. Chaetognaths were another group exhibiting important vertical movements of biomass between day and night across strata, although with not clear night ascent (**Fig. 5**).

Total added biomass of zooplankton revealed more clearly DVM behaviour of the whole zooplankton community (**Fig. 6**). 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. 6). Overall, we observed that highest values of biomass were present 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 day.

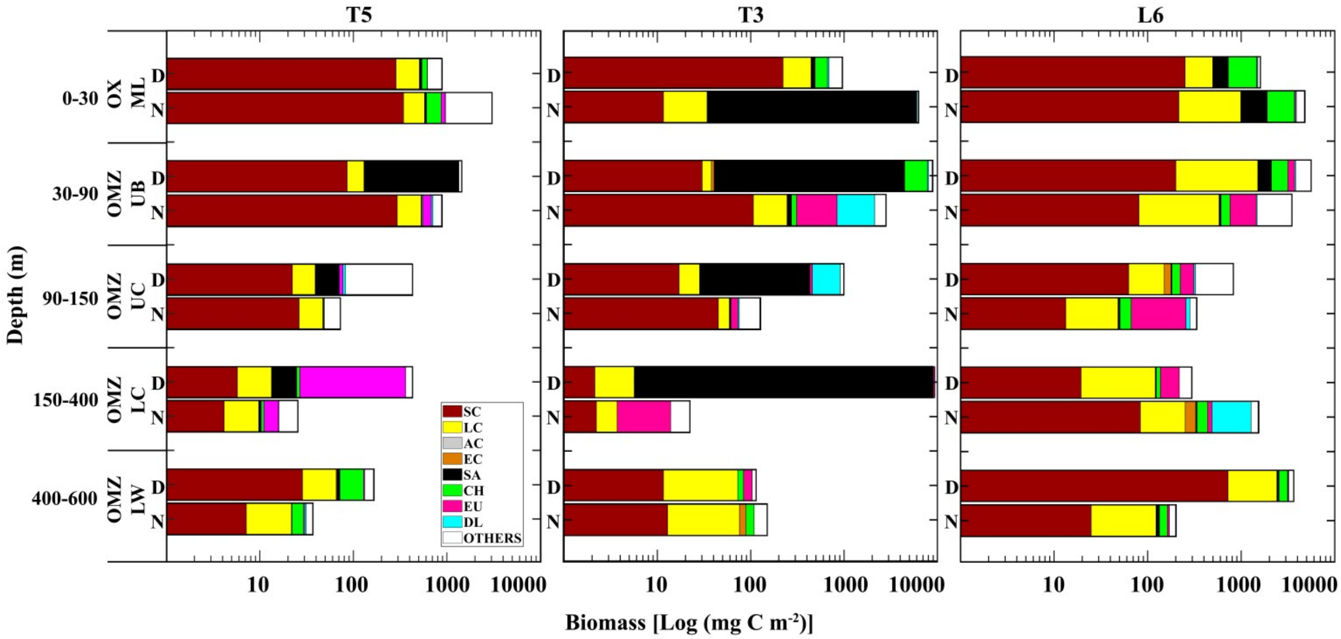

Fig. 5. Daytime vs. Night-time vertical distribution of biomass of different taxonomic groups at 3 stations off northern Chile: off Iquique (StationsT5 and T3) and off Coquimbo (Station L6). Data are from night and day replicated samples during two consecutive days in the austral spring 2015. Values represent means from sampling size n=4 for St.T5 and St. T3, and n=2 for St. L6. Layers were defined from variable levels of oxygen concentration (see Methods).

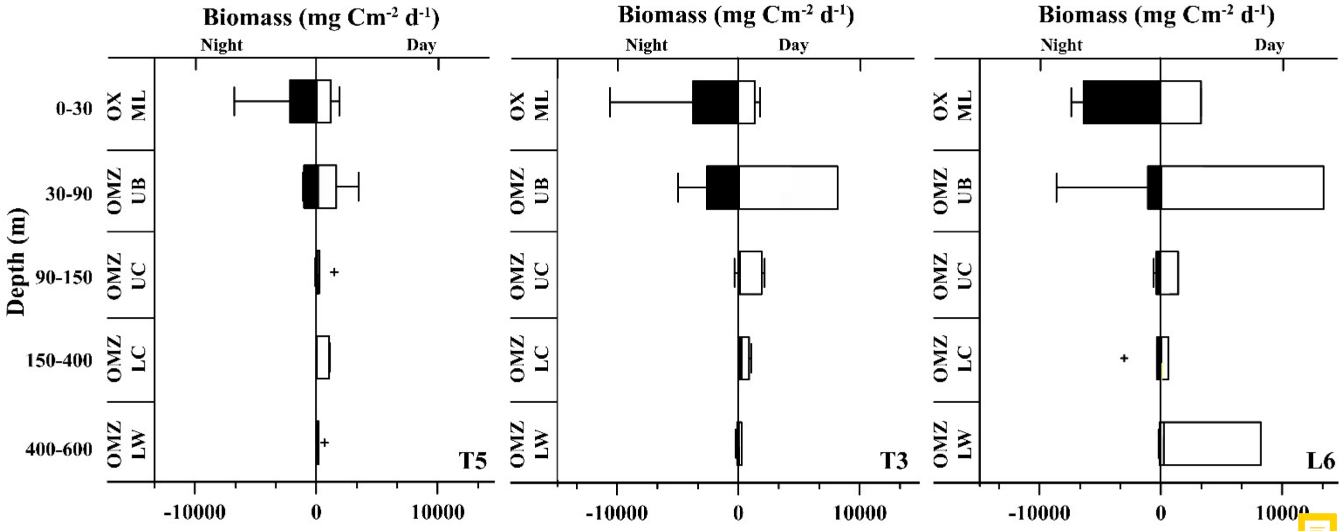

Fig. 6. Vertical distribution of total zooplankton biomass during daytime and night-time conditions at 3 stations off northern Chile: off Iquique (Stations T5 and T3) and off Coquimbo (Station L6) during two consecutive days in the austral spring

2015. Some outliers are plotted individually (+). Error bars are standard deviations from sampling size (n=4 for St. T5 and St. T3 and n=2 for St. L6). Layers were defined from variable levels of oxygen concentration (see Methods).

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 groups showed a high rate of migration as reflected in the RM. In terms of migrant biomass, Copepods, Chaetognaths, Euphausiids, Hydrozoa and Decapod larvae accounted for a large proportion of total migrant biomass (>80%), although high estimates of migrant biomasses were also associated with high standard deviations, indicating s 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.

Table 3. 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).

TAXA	**ST-T5**			**ST-T3**			**ST-L6**		
	Migrant Biomass	**SD**	**RM %**	**Migrant Biomass**	**SD**	**RM %**	**Migrant Biomass**	**SD**	**RM %**
Salps	0.00	0.00	0	2296.90	3248.31	54	314.46	444.71	60
Copepods									
Large Copepods	202.92	143.03	41	0.00	0.00	0	261.35	369.61	44
Small Copepods	266.81	67.20	41	0.00	0.00	0	0.00	0.00	0
Eucalanidae Copepod	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Acartia Copepod	0.04	0.06	100	0.00	0.00	0	0.00	0.00	0
Chaetognaths	243.92	344.96	93	0.00	0.00	0	651.37	921.18	59
Euphausiids	209.63	288.02	58	530.47	616.61	99	212.29	67.48	48
Decapoda Larvae	27.76	21.73	79	1261.69	1784.30	100	6.54	9.25	14
Hydrozoa	427.18	603.78	48	0.00	0.00	0	41.90	59.25	77
Annelidae	51.36	31.95	72	20.92	29.59	80	182.49	57.38	36
Siphonophores	113.28	140.89	34	71.80	101.55	27	32.45	45.89	46
Decapods	1296.57	1833.63	100	0.00	0.00	0	0.00	0.00	0
Appendicularia	0.00	0.00	0	0.00	0.00	0	1041.36	1471.54	52
Ctenophores	0.00	0.00	0	239.10	338.14	100	149.20	211.01	50
Ostracods	9.07	5.29	81	0.06	0.09	2	28.57	8.78	50

Amphipods	0.12	0.18	9	35.60	20.17	56	38.74	54.78	98
Fish Eggs	7.50	4.07	61	0.00	0.00	0	1.11	1.56	14
Platyhelminthes	0.00	0.00	0	0.00	0.00	0	2.12	2.99	100
Nauplii	4.42	2.75	84	0.00	0.00	0	4.05	5.73	42
Ichthyoplankton	0.06	0.08	0	0.00	0.00	0	0.00	0.00	0
Pteropods	0.00	0.00	0	0.91	1.29	100	8.10	2.57	99
Foraminifera	0.05	0.05	80	0.00	0.00	0	0.00	0.00	0
Gastropods	0.76	1.07	87	0.00	0.00	0	0.12	0.17	31
Cirripedia Larvae	0.38	0.26	97	0.06	0.08	100	0.00	0.00	0
Bryozoan	1.50	1.13	99	0.00	0.00	0	1.10	1.55	82
Radiolarian	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Echinoderm Larvae	0.03	0.04	100	0.00	0.00	0	0.00	0.00	0
Total	2863	1177.94		4457	4227.70		2977	116.66	

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 biovolume, 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 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, following Yamaguchi *et al*. (2014) and Sato *et al.* (2015), we converted biovolumes into dry weights using a mean body density and mean water content of zooplankton, estimated across taxa by Wiebe (1975), but then taxa-specific Carbon: dry weight ratios collected from published works. In any case, the use of single conversion factors between body volume and mass and wet weight and dry weight among taxa must be considered as source of variability in the estimates of taxonomic biomasses.

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. 2.6 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 remains 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, Bryozoan, 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 (3433±889 mg C m^{-2} d^{-1}) and C flux estimates (674±291mg 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	3433 ±889	674±291					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.

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 (Stations T3 and L6), but in particular in the station off Iquique (St. T3) that also showed a higher migration rates (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 within 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 176 mg 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 of25 % 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.

Table 5. 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)	3702	14796	11071	9856 ± 5646
Epipelagic biomass (mg C m^{-2}) (0–90m)	3126	*9391*	7679	6732 ± 3238
Migrant biomass (mg C m^{-2} d^{-1})	2863	4457	2977	3433 ± 889
Rate of Biomass migration (%)	51	26	37	38 ± 12
Active Carbon Flux (mg C m^{-2} d^{-1})	428	996	598	674 ± 291
Total Active Carbon exported (%)	29	28	17	25 ± 7

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 3.4 g C m^{-2} d^{-1} may contribute with about 0.6g C m^{-2} d^{-1} to the OMZ system through respiration, mortality, and production of fecal pellets at depth, accounting for ca, 25% of the net primary production, and so implying the existence of a very 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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