Letter of Response

Dear Editor

This is the letter of response to reviewers' comments accompanying a revised version of the MS.

We have fully revised the MS in according to comments from both reviewers and double checked all calculations. Tables and Figures have been changed and some Tables are now supplied as Supplemental Material, and some figures were removed as suggested. During the revision we have adjusted some calculations and estimates after issues raised from comments. The text has also been fully revised and edited.

Our responses to reviewers' comments are marked as blue text in italics, as follow:

Referee #1 Received and published: 29 April 2019

General comments: Tutasi & Escribano have collected a valuable dataset on zooplankton vertical distribution off Chile and have used it to estimate the zooplankton-mediated vertical carbon flux. As such, this is a valuable contribution to ongoing efforts to better constrain the different components of the biological carbon pump in the ocean. However, as is I cannot recommend publication in Biogeosciences because of several shortcomings in the analyses and presentation of the results.

We appreciate this general comment. However, we think that eventual shortcomings can be solved by providing some further support to our analyses and also adding some missing information to the MS that we recognize as important to sustain our findings and conclusions. From here and thereafter we have sorted the reviewer comments as to reply separately to each one of them

Most importantly, it is not stated in the paper how the major outcome of the study (the active carbon flux, with a mean of 678 mg C1 BGD Interactive comment Printer-friendly version Discussion paper C m-2 d-1) is calculated based on the biomass of the different functional groups. The authors claim that this term includes respiration, faecal pellet production, and mortality, but they never present how they estimated the different terms.

We estimated C flux based on previous works dealing with similar zooplankton groups. We agree with the reviewer that more detailed references should be provided to support the approaches and estimates. Therefore in our revised version we are including the following paragraph in the Methods section:

"To calculate the active C flux at each sampling station we used a daily respiration fraction of 0.12. This respiration rate was estimated by Hernández-León and Ikeda (2005) for total zooplankton biomass at temperatures ranging between 13°C and 18 1C for mid-latitude areas. We used this value considering a similar temperature range between surface water and within 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. The contribution of mortality to C flux was assumed to be 0.08 day^{-1} of migrant biomass as a conservative estimate suggested by Ohman and Wood (1996). We thus estimated total C flux as,

$$C\ Flux= (0.12*(MB) + 0.08*(MB)) / 2 + 0.09*(MB), \qquad (3)$$

where Rz, Mz, and Ez, are estimates of fractions of total migrant biomass (MB) for a 12-h period."

Were environmental data (temperature, depth, oxygen?) included in the scaling of metabolic rates? Up to now the presentation is only comprehensible in terms of abundance distribution.

Our estimates are based on parameters derived from ranges covering the temperature range observed in our sampling stations. We did not scale values for depth or oxygen concentration and the eventual effects of these environmental factors cannot be discarded, and so that we have included this as an important point for Discussion. For this, we raised the issue saying that further work (possibly modeling) is needed to asses as time-varying potential effect of an oxygen gradient on respiration, and physiological studies suggest a depressed metabolism upon low-oxygen, but ETS estimates (the suitable method to measure respiration at depth) do not account by such effects. With respect to oxygen or depth effects on egestion rates we have no available information and because animals may produce fecal pellets rapidly after feeding, but they can keep production at depth we reduced estimated rates in about 50% as suggested by Escribano et al, (2009). This information is now provided in Methods.

Even for biomass the "published regressions" that are used to convert from image-derived biovolume of the different taxonomic groups are mentioned, but not cited.

We agree that such information is important to be provided, but we actually did not use published regressions to estimate biomass, so this sentence has been removed in our revised version. Instead, we are now adding a Table (as Supplemental Material) with all the conversion factors between dry weight and C content.

To assume a density of 1 and a constant water content of 90% across taxa evokes a large error (and actually contradicts the results of the cited paper, Matsuno et al. 2009 who used this paper based upon the results by Yamaguchi et al. 2005 and found that it did not fit well).

The issue of converting body size (length, area, volume) into biomass and C content has received attention in several published works, and revising the literature does not lead readers to a unique Method or approach. We agree that different animals may exhibit different body densities and water content, and this variability can also occur with different life-stages. A body volume converted to wet body mass with density=1 has been widely assumed in many studies using taxa-specific masses (e.g. Yamaguchi et al. 2014 DSR-Part I, Sato et al. 2015 Zool. Studies, Donoso et al. 2018 JGR). This unique relationship is sustained by an early work of Wiebe (1975) who reported the relationship based on a large and varied zooplankton community. Also, the average water content for zooplankton as approximately 10% has been largely used in several published works (Yamaguchi et al. 2014, Sato al.,

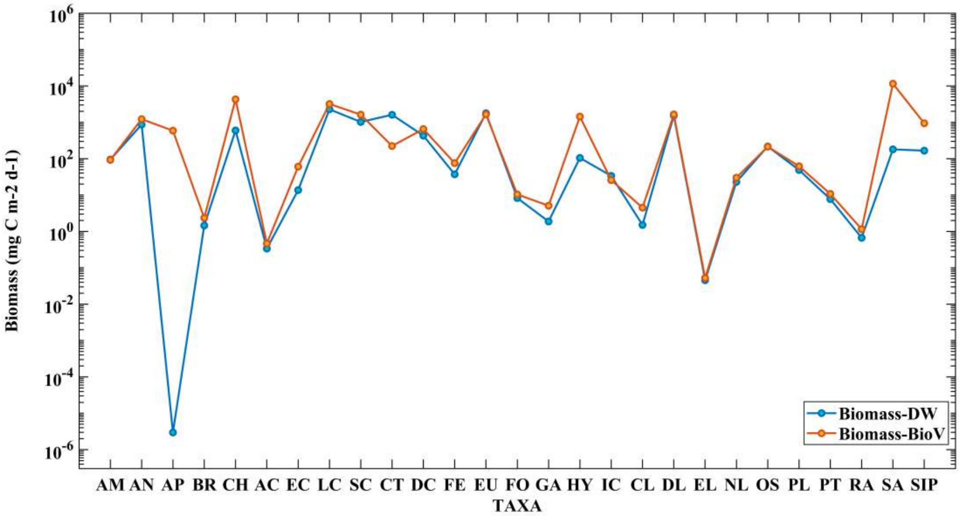
2015). It may be possible that some specific taxa may introduce underestimates or overestimates of body masses, but not exact conversion factors do exist for each taxonomic group, so average conversion rates appear as a conservative approach. The issue has received much discussion in several papers and no agreement or unique approach is currently adopted. In any case, we have now considered the issue to be part of the discussion

Why not use taxon-specific regressions for direct conversion from image area to carbon such as those published by Lehette and Hernandez-Leon 2009? I therefore recommend major revisions of the paper, where it is absolutely critical to resolve the abovementioned issues. Since this will involve generating new figures, tables, and rewrite the results section, it might be more practical for the authors to withdraw the contribution and resubmit as a new MS.

Lehette and Hernandez-Leon (2009) provide estimated regression equations for different zooplankton taxa between scanned area and biomass (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. We are now providing this information as Supplemental Material for readers to assure we are using correct factors.If we agree in any case that is maybe an important issue affecting the estimates of taxa-biomasses, so that we have added a paragraph in the Discussion regarding this issue and supporting our selected approaches. The new paragraph is:

"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 and C content. Various approaches have been adopted for converting sizes to body masses. For example, Lehette and Hernandez-Leon (2009) provided some general regression equations for subtropical and Antartic 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".

In any case, we tested and compare the use of both methods: Lehette & Hernández-León equations and the biovolume equation and C convertion ratio to dry weight. The following graph represents the comparison for all the taxonomic groups:



As we can see, there is no much difference for most taxa, except for Appendicularian where Lehette & Hernández –León equation results in much less C content. It is difficult to say which one represents better C content in this case, but clearly the Equation of Lehette & Hernandez-León appears well out of range for this taxonomic category.

I hope my suggestions help in the process. Specific comments The quality and conciseness of the text is very different between different parts of the paper.

We have fully revised the text to improve the manuscript

The introduction as well as the materials and methods section are reasonably well written (except that in the M&M the calculations for biomass and active flux are entirely missing).

We have greatly modified the M&M providing now the required and detailed information regarding the estimates of C contents by taxa and the estimates of C fluxes.

I have added some suggestions to a marked-up version of the pdf. Both the abstract and the discussion need some work, but the largest room for improvement is in the results section, and includes the quality of the text, figures, and tables.

We thank the reviewer by his(her) valuable comments and suggestion to improve the MS. We have considered all the comments and suggestions from the marked pdf file.

Please find some specific comments below. Throughout the results, the text needs to be shortened and rewritten. As a start, delete all meaningless filling words such as that some variable “showed to”, “appeared to”, etc. Also, the taxomomic group names are sometimes a bit awkward, e.g. for “Egg Fish” (I assume this is because in your sorting there is also Egg Other) fish eggs would C2 BGD Interactive comment Printer-friendly version.

We have now revised and re-written Results.

Discussion paper be more natural, for Nauplius Larvae simply nauplii would be shorter, and Ctenoforos and Ictioplankton in English would be Ctenophora and Ichthyoplankton , respectively.

Agreed now changed

I have not marked up the results text in the pdf because I feel they really should be rewritten, and also I recommend many changes of the tables and figures that will affect the text. All figures, tables, and text: I cannot follow the decision to define the “most important” zooplankton by number instead of biomass. Neither Acartia nor nauplii contribute substantially to total biomass, let alone migrant biomass. On the other hand, salps , chaetognaths, decapods and euphausiids do (Table 5).

We thank the reviewer for this comment. We have followed the suggestions and revise all graphs and tables. This has also implied recalculations of our estimates as it will be evident in the revised version of the MS.

It is unclear how the authors deal with uncertainty (i.e. variability between replicate net hauls) and spatial variability (differences between stations, which may be related to productivity differences and/or OMZ characteristics).

Our new Tables are now including standard deviations fro our estimates derived from the replicated samplings. In Methods we now explain how mean values and their associated errors are estimated when replicates measurements are available.

In table 6, a single estimate is presented with some error. There should be a table summarizing the results of the statistical comparison between stations.

A new Table is now presenting our estimates of migrant biomass with their associated standard errors, while statistical testing is described in the text.

Vertical zonation: the zonation as indicated in the hydrography plots (Fig. 2) does not match at all with the one indicated in figs 3 and 5, and is again different in figs 4, 6, 7 and 8. In fact, you call the 150-400m stratum “OMZ-LC” in the latter but according to Fig 2. this would be OMZ-UC. However, I think your Multinet depth intervals were well chosen for the given conditions. Why not just call the five depths Oxygenated Layer (0- 30m), Oxycline (30-90m), Upper OMZ (90-150), OMZ Core (150-400) and lower OMZ (400-600), then add a table with the mean and range in oxygen and temperature for the respective depth intervals at the three stations? From the plots it seems this should work.

We agreed with the reviewer and consider that is more clear using same pre-defined strata coinciding with sampled layers. Therefore, all the graphs have been redone in according to sampled strata.

Also please add the multinet depths to Fig.2 as horizontal lines. It makes little sense to use the variable definition according to Paulmier at al. if you cannot resolve it with the net anyway (because you never know where exactly in the depth layer all the specimens were caught within a given stratum).

Agreed, done

Hydrography of station T6: Initially I had assumed this nearshore station was only 350 m deep. The lack of CTD data needs to be noted somewhere (I assume gear failure), please clarify.

Agreed. We have clarified this in Methods and avoid referring to oxygen condition below 350 m

Also, it is unclear to me how the vertical zonation was done for this station (according to Figure 2, OMZ-LC is absent and OMZ-LW is present in the anoxic core). Because O2 data are lacking from the lower OMZ boundary (i.e. it is undefined where the water column begins to re-oxygenate), it is not valid to classify the two lower zones at all (unless you follow my recommendation above and assign them to the respective nets, arguing that the 400-600 m interval includes the OMZ base, which can be shown from other observations).

Agreed, as explained above

Table 1: As is, a lot of space in this table is taken up by redundant information (Lat, Lon, Sampling Depth). Since you made an effort to stay well out of the migration times at dusk at dawn, I also think the times are not of crucial importance. I recommend to move this table into a supplement and add to the methods text that you sampled four day/night pairs at T3 and T5 and two D/N pairs at T6. By the way, the nomenclature of the stations makes little sense to the reader, why not just call them either stations 1-3, or north inshore, north offshore and south inshore?

OK Table 1 I now supplemental material. We prefer to keep and T3, T5 and L6 because they are part of a Research Cruise from which other studies will refer to same stations.

Table 2: It makes little sense to use daily means (day- and nighttime data combined) for the vertical zonation data (because of DVM). Also, absolute integrated values would have been more meaningful to the reader than relative. Actually, I would have found it most informative to have a table with all taxa and total abundance (ind m-2) as well as biomass (mg C m-2) at the three stations. The vertical distribution can be shown in a figure (Fig 4).

We agree with this comment and now made all estimates with integrated values in the 0-90 m layer to estimate migrant biomass. We now do not combine day and night values. The suggested Table is also included in our revised version

Table 5: this table is informative and to me the key result of the paper. Error estimates should be added based upon the replicate sampling at each station.

We agree and now added standard errors

Table 7 (and related text): here you make an effort to relate zooplankton abundance/biomass as well as DVM-mediated flux to primary production, which is a nice idea, but the "10 000 mg C m-2 d-1" value (which seems to be taken from the Daneri paper, although I am not quite sure from where and why) seems a quite random choice and does not account for station differences. How about using satellite-derived PP instead (I know cloud cover is an issue in the region, but maybe an monthly mean for the respective station?), or was there a fluorometer mounted on the CTD to be able to compare integrated chl-a values between stations?

We agree with the comments and estimated net PP from satellite for the same sampling period and for stations. We used these satellite estimates of PP to assess the proportion being potentially exported by active transport.

Figure 4, 6, 7 and 8: To plot the different stations in one vertical distribution plot is visually misleading. First, the color codes are not well discernible (except Fig 8), but more importantly the depth distribution is not well represented. I suggest to use one plot per station, to make the y-axis (Depth) linear and to make the bars as wide as the depth layer. In this way, the area of the bar will represent the integrated biomass (or biomass difference) in the respective layer. Either simple bars with error bar can be used or stacked bars if several groups shall be represented.

We agree with this comments and we made new figures following these suggestions

Overall I recommend to show biomass, not abundance, and to focus on the groups that are important biomass wise (Fig.5), not abudance-wise. Figure 9: It is unclear to me what information this figure should convey. Caption says grey bars represent major zooplankton groups. There are no grey bars. Why do "non migrants" have a positive rate throughout? What is the red dashed line? Why are there no error bars? Also, it is virtually impossible to visually compare stations, because the shown taxonomic groups vary between panels.

We agree that this Figure was somehow confusing and decided to build a new Figure using only biomass and not abundance.

Technical corrections I have added some corrections to a marked-up version of the pdf. These are not comprehensive, because I think these type of corrections will be done in the second review stage after a substantial rewriting.

We have revised and considered all suggestions and corrections from the marked text.

Anonymous Referee #2

The manuscript (ms) entitled “Zooplankton diel vertical migration and downward C into the Oxygen Minimum Zone in the highly productive upwelling region off Northern Chile” by Tutasi and Escribano showed the results of day and night zooplankton vertical distribution at two oceanographic stations at 20oS and another at 29oS, in an area influenced by the coastal upwelling off Chile and the presence of a sharp oxygen minimum zone (OMZ). This is a quite interesting and valuable data set about the vertical distribution of the different groups and species of zooplankton in relation to the OMZ. They also showed the diel movements of the different zooplankton groups and species and their range of migration in relation to the OMZ. Moreover, they estimate migrant biomass and active flux by zooplankton. However, the ms has many problems related to presentation of results and estimation of migrant biomass and active flux. The authors showed migrant biomass in a rather peculiar way, as a rate, something introduced as a new concept. This reviewer (and therefore the future readers) was not able to understand the concept as biomass should be given as a weight per volume (or area). It is even more bizarre to give a value of active carbon flux (even in the abstract) without given any detail at all about how it was estimated. Moreover, the active flux value is one or two orders of magnitude higher than any other estimate in the literature. This reviewer and the future reader would be quite interested to know how active flux was assessed in order to compare with other procedures. Thus, I recommend major revision submitting a complete new version following the comments below.

Migrant biomass (mgC m-2) is the difference between day and night biomass in the upper layer affected by primary production and seasonal variability of the physical frame (to be defined for the specific region), or the same difference in the mesopelagic zone. Migrant biomass is normally estimated as the biomass difference in the defined upper layer. The mentioned boundary should be well defined as carbon exported downward towards the permanent thermocline should remain there for long period. In the oceanic warm waters this is known and normally the 150-200 m layer (below the seasonal thermocline) is considered the boundary layer. The biomass difference between day and night is the migrant biomass as stated above, but keep in mind to calculate this biomass as the integration of biomass in the different layers sampled during day and night. I suggest to revise the concept of rate of DVM. To me, and probably future readers, this concept is rather confusing. The authors could state the migrant biomass of each group or species and their proportion in relation to the total abundance or biomass. This could be, probably, more informative.

We appreciate these comments from the reviewer and agreed that our estimates and concepts should be presented more clearly. Therefore, attending these comments we have greatly modified the Methods as to better explain the calculations of migrant biomass and the concept of migration rate which is actually the proportion of biomass being transported daily downward as the reviewer suggested. For most conditions during the year cycle the upper boundary of the OMZ (1 mL O2 L-1) fluctuates between 30 and 90 m within the upwelling zone. Below this depth, oxygen concentration decreases abruptly and so representing the oxycline which coincides with the thermocline. These two upper layers (0-30 and 30-90 m) were sampled by our multinet and thus representing the zooplankton community potentially contributing to C downward flux below the oxycline (thermocline). Therefore, we used integrated biomass (day and night) in the upper 90 m to estimate DVM for each taxonomic

group and to obtain a total zooplankton migrant biomass. The contribution by each taxonomic group was so estimated as their proportion (%) of migrant biomass to total biomass as suggested by reviewer. We have thus re-estimated all values and better explained these calculation in Methods,

Active flux (mgC m-2 d-1) should be migrant biomass multiplied by the rates (respiration, excretion, mortality,. . .) estimated for these organisms at depth (the residence depth during the day). The most popular procedure is to use the equations of Ikeda (1985, 2014) using body weight and temperature to derive respiration (respiratory flux).Then, excretion, gut flux, and mortality could be estimated from equations relating respiration with the excretion,. . . rates. These physiological community rates will be estimated only for the residence time at depth (normally around 12 hours depending on season and latitude). In any case, the authors should give details of the procedure used to assess these rates.

We are now providing full references and explanations on how we estimated C flux from potential respiration, egestion and mortality, as shown above in the response for reviewer 1.

In order to present abundance and biomass data, I suggest to produce Figures showing the night (left, dark) and day (right, white) values in the five layers sampled but for each station (different Figures) and displaying average (and SD) values for each layer. Mean values of day and night biomass as displayed in Figures 6 and 7 are not informative. The authors should represent the real data.

Agree, we have now done so

Other comments:

Page 1, Line 15: Community structure is related to species abundance and biomass better than size composition.

Agree, modified now

Page 1, Line 21-22: Re-write this phrase as it is difficult to understand.

Done

Page 1, Line 26: Migrants biomass units cannot be as in the text. It should be mgC ˚um-2.

Agree. Corrected

Page 1, Line 27: This value of active flux is extraordinarily high. Please, revise your calculations.

Estimates have been fully revised

Page 2, Line 21: “in according” should be “according”.

Corrected

Page 4, Line 13: Later should Layer?

Corrected

Page 8, Figure legend: Describe in the legend what is OMZ-UB, OMZ-UC,. . . for better reading and understanding of Figure.

Agree, done

Page 9, Table legend: Define what is SC, LC, AC,. . . As in the above example it is defined in the text but the Table could be better explicative if it is stated in the legend or in the proper Table.

Agree, done

Page 12, Figure 4. This Figure is difficult to understand. Why not to display abundance during day and at night in the same level? This is the best way to compare the community structure during the diel cycle. Please, give details about units in the X- axis. Why there are no organisms in the mixed layer during night in T3?

This figure has been revised and a new figure is now provided considering these comments

Page 13, Line 1: had should be was.

Corrected

Page 14 Figure 5 (and also Figure 3): Better to show day values as white dots and night values as black dots.

Agree, done

Page 16, Line 1-2: Re-write the phrase. Perhaps, “were found” should be deleted.

Done

Page 19, Line 3: Biomass of these taxa was. . . Which taxa?

Corrected

Page 19, Figure 8: This Figure is difficult to understand as for instance in T6 small and large copepods are observed at depth during day but not at night at any level. Any explanation?

All the figures have been revised and corrected

Page 21, Figure 9: Define the values expressed in light and dark blue.

Done in new figures

Page 23, Line 9: Plan should be play?

Corrected

Page 26, Line8-9 and Table 7: It is not clear which is the primary production value as in line 9 is about 1 000 mgC m-2 d-1 and in Table 7 is 10 000 mgC m-2 d-1. Please estimate primary production for each station from remote sensing data.

We have now used satellite net PP for our estimates. Estimates of PP for same sampling period and the sampling stations

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~~ing~~ to the functioning of the biological pump. The magnitude and efficiency of this active transport of C may depend on the size and taxonomic structure of the migrant zooplankton. However, the impact that a variable community structure can have on zooplankton-mediated downward C 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, but comprised by a highly diverse ~~variable~~ community with variable DVM behavior~~structure (size-composition)~~. In these systems, presence of a subsurface oxygen minimum zone (OMZ) can impose an additional constraint to vertical migration and so influence~~ing~~ 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 2015. Automated analysis of zooplankton composition and taxa-structured biomass allowed us to estimate daily migrant biomass by taxa and their~~,~~ amplitude of migration~~and daily rate of migration, defined as the daily exchange of biomass between the upper mixed layer and below the thermocline~~. We found that a higher biomass aggregates above the oxycline, associated with more oxygenated surface waters and this ~~condition~~ was more evident upon a more intense OMZ. Some taxonomic groups~~a~~ however, were found closely associated with the OMZ. ~~We found that~~ M~~m~~ost taxa were able to perform DVM in the upwelling zone withstanding severe hypoxia. Also~~Even~~, ~~several~~ 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 showed that mean migrant biomass of 3.4 ~~(5099 ±2701~~ mg C m^{-2}d^{-1}~~)~~ may contribute with about 0.6~~78± 465 m~~g 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 by zooplankton is however strongly

dependent~~ing~~ on the taxonomic structure due to variable migration amplitude and DVM behavior~~ affecting the daily rate of diel vertical migration~~.

1 Introduction

The Oxygen Minimum Zone (OMZ) in the ~~eastern~~ Southeast Pacific Ocean, the fourth largest of the six permanent hypoxic regions in the world oceans (Paulmier *et al.,* 2006), is a key component of the water column and a permanent feature intruding the coastal zone of Ecuador, Peru and Chile (Fuenzalida *et al.,* 2009; Paulmier *et al.,* 2006). In the highly productive upwelling region of Northern Chile the OMZ is closely linked to wind-driven upwelling in the coastal area and associated to Equatorial Subsurface Water (ESSW), which is transported ~~from north to~~ southward along the continental slope by the Peru-Chile Undercurrent (PUC) as far south as 48°S(Fuenzalida et al., 2009; Morales et al., 1996; Silva and Neshyba, 1979). Off Iquique (20°S) the OMZ is characterized by being thick (500 m), very intense (< 20 µmol kg^{-1}) and O$_2$ concentrations in the core of OMZ at 21ºS are among the lowest found in the global ocean reaching the detection limit (<1 µM) (Ulloa and Pantoja, 2009), although it becomes thinner at about~~whereas that off Coquimbo at~~ 30ºS ~~becomes thinner~~ (Paulmier *et al.,* 2006).

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

The presence of oxygen-depleted water becomes a critical physiological constraint for pelagic and benthic organisms inhabiting the upwelling zone, impacting their biomass and productivity, the species diversity, distribution and behavior (Wishner *et al.,* 2018; Ekau *et al.,* 2010; Grantham *et al.,* 2004~~; Wishner *et al.,* 2018~~). 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 the ~~OMZ~~ intensity and distribution of the OMZ~~ and variation~~ (Escribano *et al.,* 2009; Hidalgo *et al.,* 2005; Judkins, 1980; Morales *et al.,* 1996; Wishner *et al.,* 2013). The OMZ can act as an ~~effective~~ ecological barrier for vertical distribution of many organisms, constraining ~~confining~~ most zooplankton to a narrow (50 m) upper layer, as shown in the coastal upwelling zone off Chile ~~in~~according to the works of Escribano (2006) and Donoso and Escribano (2014). Zooplankton also become limited to ~~,or by limiting them to~~ the upper 150 or 300 m ~~as found in copepods of~~ in 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 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~~ing~~ and~~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 D~~M~~VM behavior interacting with a shallow OMZ, and the implications this interaction can have o~~i~~n the magnitude of downward C flux in a highly productive coastal upwelling zone.

2 Methods

2.1 Study Area

The study area was located in the ~~eastern~~ 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 (20º S) and a coastal station (St. L6) off Coquimbo (29º S). The study was carried out during the Lowh~~P~~H~~h~~ox cruise conducted in November-December~~October~~ 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)

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and only 356 m (St. L6) using an oceanographic rosette ~~equipped~~ with a CTD SeaBird 911 (SBE 911 plus) equipped with a SeaBird SBE-43 oxygen sensor and Seatech Fluorometer. Discrete water samples were also obtained for chemical measurements of oxygen and Chlorophyll-*a* concentration.

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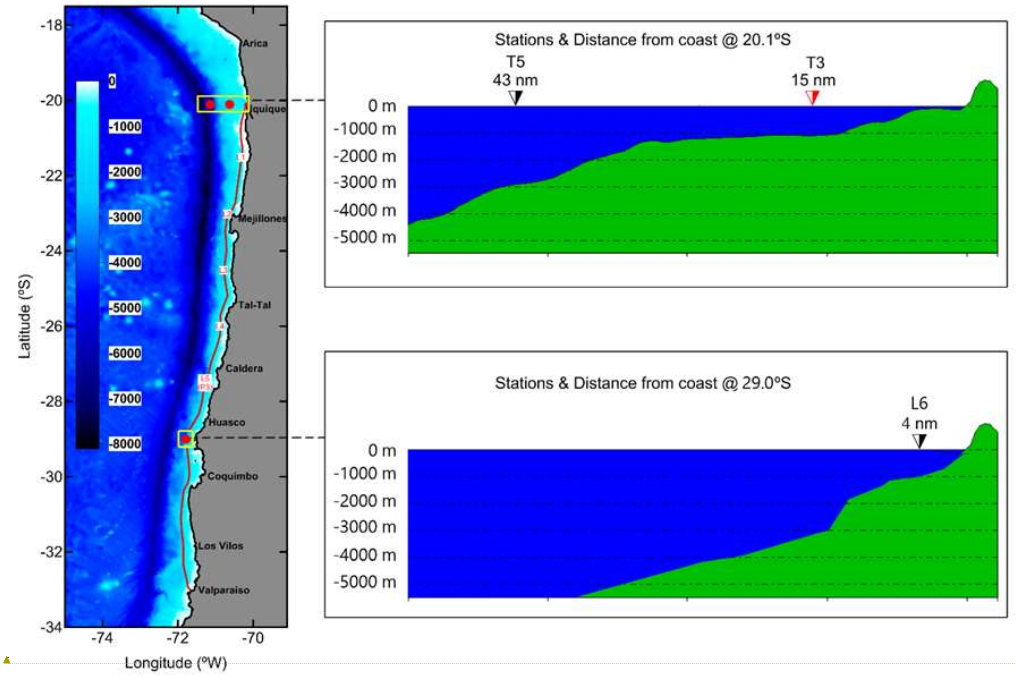

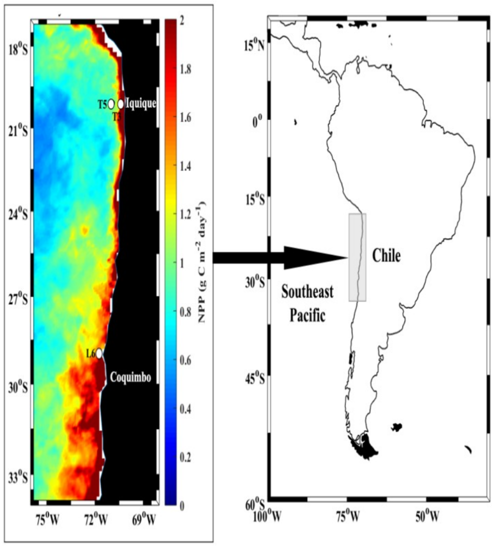

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Fig.1. Study area at the northern upwelling region of Chile, indicating sampling stations during the LowpHox cruise conducted in November-December 2015 onboard the R/V *Cabo de Hornos*. Satellite estimated Net Primary Production (NPP) averaged from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

2.2 Zooplankton sampling

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 ~~located~~ in the mouth of the MultiNet to estimate the volume of filtered water. At each station, 40 discrete samples were obtained from 600 to 0 m depth. Each sample corresponded to a different depth stratum (30-0, 90-30, 150-90, 400-150 and 600–400m). ~~The thickness of~~ T~~t~~hese strata were~~as~~ defined according to distribution of oxygen concentration and localization of the O~~Z~~MZ. Therefore they ~~These strata~~ were assumed as~~to~~ representing the near surface oxygenated later, the upper oxycline, the upper OMZ, the OMZ core and the lower boundary of~~below~~ the OMZ, as indicated in **Table S2 (Supplemental Material)**. Once onboard the collected zooplankton samples were preserved immediately in 5% buffered formalin-seawater solution.

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

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

2.3 Taxonomic and size measurements

Taxonomic identification and enumeration 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 subsample was fractionated again separately with a Motoda splitter until the zooplankton concentration was sufficiently diluted to avoid contact between organisms on the ZooScan scanning frame. Fractioning ~~Separation~~ into~~of the~~ small and large organisms ~~objects~~ and consequent separate image acquisition of the two size classes prevented underestimates of large-rare objects which may need less fractioning (Gorsky *et al.*, 2010). 179 subsamples were scanned and digitized at a resolution of 2400 dpi after manual separation of objects on the scanning tray. After processing the samples with ZooP~~p~~rocess 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 classi~~fi~~fied into 27 taxonomic groups, such as C~~c~~opepods, C~~c~~haetognaths, E~~e~~uphausiid, G~~g~~elatinous and other zooplankton (Table 2). 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. ~~Then~~ T~~t~~he 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):

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

where, the EBv corresponds to the biovolume of a prolate 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 ~~measured~~, 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 was in average 90% (DM = 0.1 × WW)), as suggested byYamaguchi *et al.* (2014) and Sato *et al.*(2015)~~, as shown by Matsuno *et al.*(2009)~~. Finally, Individual biomass was converted to carbon using a factor carbon for each taxonomic group from previous published data **Table S3 (Supplemental Material)**~~published regression equations relating organism size, area or volume to individual weight~~.

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 biomassin this layer to assess daily changes

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Con formato: Inglés (Estados Unidos) 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 the 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):

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

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,

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

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

2.5 Patterns of vertical distribution of migrating zooplankton

For the analysis of vertical distribution of organisms, the density estimates of the organisms were standardized to number of individuals per ~~1000~~ m^3 (for each stratum) or per m^2 (for integrated values~~the entire water column explored~~). In order to quantify the presence and extent of DVM of various taxa at each station, we calculated both night: day (N:D) ratios in each stratum and weighted mean depth (WMD) for zooplankton ~~biomass and for~~ abundance, as a measure of the center of gravity of a population's vertical distribution for each taxon and haul, in according to Andersen *et al*. (2004) following Eq. (5~~3~~):

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$$WMD = \frac{\Sigma(ni*zi*di)}{\Sigma(ni*zi)},$$ (5~~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~~*di* is the depth of a sample *i* (centre of the depth interval), *zi* the thickness of the stratum and *ni*the number of individuals per 1000 m^3 at that depth~~.

We calculated the amplitude of vertical migration (ΔDVM) as the difference between the WMD~~mean depth~~ of the organisms ~~*i*~~ during the day and the night and this ΔDVM was considered as the criterion to assess the DVM behaviour~~. To determine the DVM behavior, the difference of the average values of WMD between day and night~~ for each taxonomic group ~~was assessed~~. Positive values indicated normal DVM (pattern of nocturnal ascent by individuals that reside at depth by day) and negative values indicated reverse DVM (pattern of nocturnal descent by individuals that reside near the surface by day). The individuals that occupied the same depth stratum by day and by night, whether near the surface or at depth were considered as non migrant in according to Ohman (1990).

2.6 Multivariate analysis

For statistical analysis, as a criterion for determining if the DVM was significant, we tested for differences in the WMD mean between day and night using a two-tailed t test. We considered the occurrence of DVM when the difference in the WMD mean between day and night was significant ($p < 0.05$). In order to evaluate the similarity/dissimilarity in the abundance and biomass among station, strata, and day–night conditions, the multivariate grouping techniques were applied ("cluster analysis"), ANOSIM (Two-Way Crossed Analysis) tests and multidimensional scaling (MDS) with the data transformed in PRIMER v 6.1.16 (2013), prior to the application of the Bray-Curtis similarity index (Bray and Curtis, 1957). In general, WMD for taxonomic groups~~a~~ did not exhibit~~ing~~ a pronounced bimodal vertical distribution.

3 Results

3.1 Hydrographic conditions

Vertical profiles of temperature, DO, and sigma-t show general oceanographic conditions in all stations (**Fig. 2**), ~~as~~ such as~~,~~ the vertical distribution of oxygen and location of the OMZ ~~the structure of OMZ~~. From ~~By looking~~ the vertical profiles of oxygen and coinciding with the sampled layers of the Multinet different strata~~layers~~ were defined: A well oxygenated stratum with oxygen approaching air saturation (>250 µmol O_2 kg^{-1} ~~O_2~~) 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 ~~surface is intense~~ (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~~-1~~ µmol O_2 kg^{-1} ~~O_2~~) and a lower boundary (OMZ-LC) (1 to~~-<~~ <20 µmol kg^{-1} O_2), and finally a lower O_2 gradient

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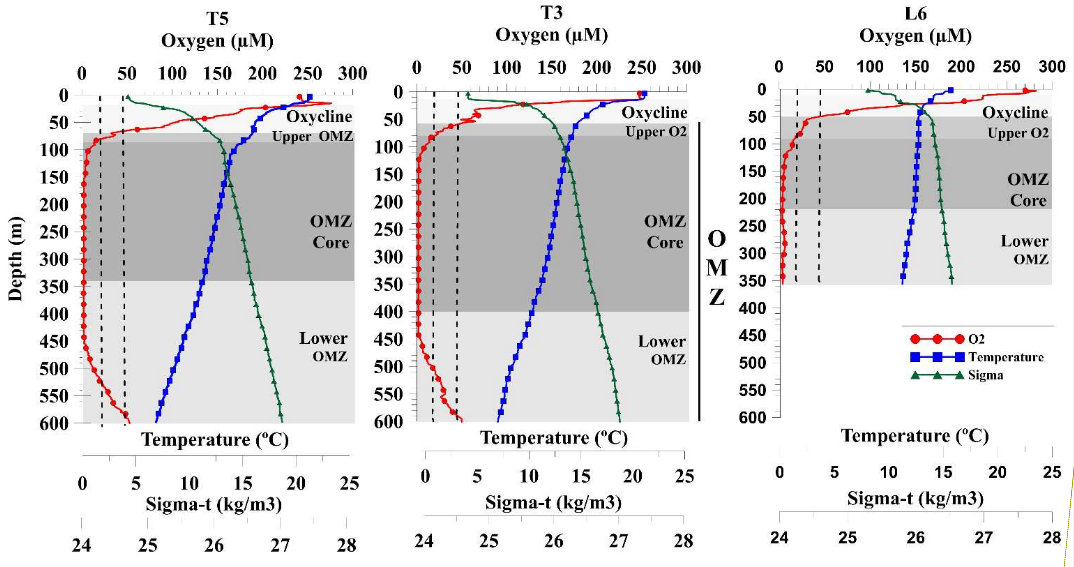
(OMZ-LW). ~~The thickness of each of these strata was variable among the stations and it was determined in according to described by Paulmier *et al.*(2006).~~

Across the zonal section off Iquique the offshore station (St. T5) and onshore station (St. T3) showed two contrasting hydrographic regimes ~~with~~ regarding ~~to~~ the OMZ. Station T5 ~~usually~~ had a less pronounced and thicker OMZ than station T3. At both stations of 5 strata were well defined in the water column (**Fig. 2**). The OX-ML (>250 µmol kg^{-1} O_2) was present at 18 m (St. T5) and- 15 m (St. T3) ~~of depth~~. The oxycline exhibited a gradual~~continuum~~ decrease from oxic (~250 µmol O_2 kg^{-1} ~~O_2~~) to suboxic (<20 µmol O_2 kg^{-1} ~~O^2~~) conditions associated with a strong stratification in the upper~~at about~~ 80 m depth ~~on average in both stations~~. The 45 µmol O_2 isoline (OMZ -UB) was present at the base of the oxycline at 70 m (St. T5) and 59 m (St. T3). The OMZ core (<20 O_2 µmol kg^{-1} ~~O^2~~) was located below the thermocline and below the 26.5 kg~~/~~ m^{-3} isopycnal following description of~~according to~~ Paulmier *et al.* (2006). In ~~in~~ the oceanic station (St. T5) the OMZ core~~it~~ was located between 80 to 341 m with 260 m thickness, while in the coastal station (St. T3) it was between 80 to 400 m ~~of depth~~ with 320 m thickness. The O_2 concentration~~s~~ in the core was ca. 1 µmol kg^{-1} O^2. The OMZ-LW at both station was delimited above the core and below the depth where the O_2 slope changed~~s~~ significantly (slope break >0.1 µmol /m) (**Fig. 2**).



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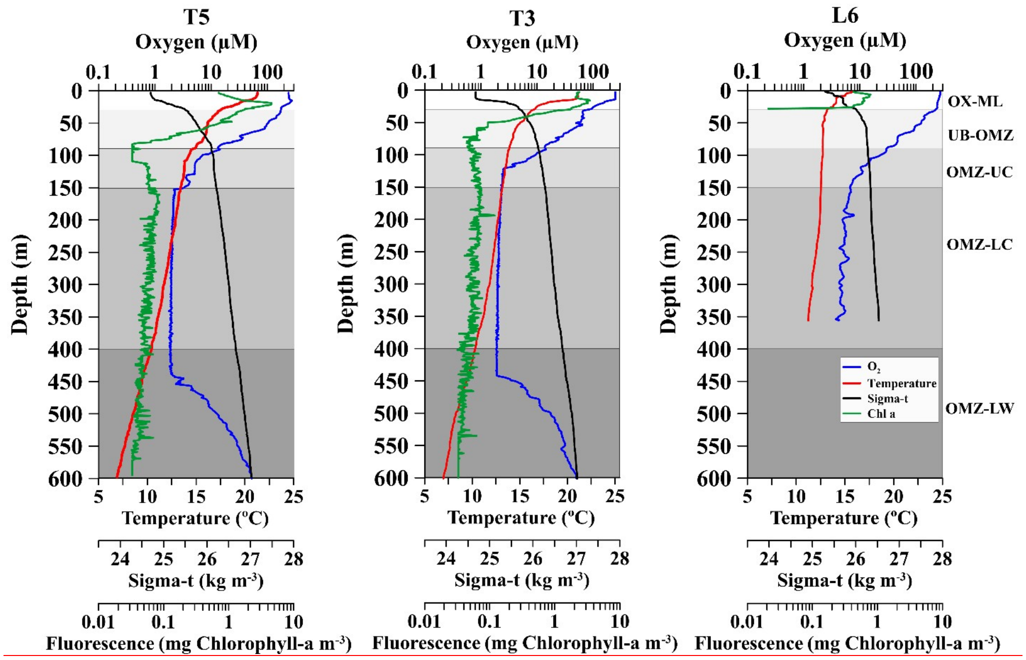

Fig.~~ure~~ 2. Vertical profiles of dissolved oxygen (O_2), temperature, Chlorophyll-a and water density (sigma-t), at 3 stations off northern Chile (see **Fig. 1**) during the LowpHox Cruise in the austral spring 2015. Shaded areas represent different layers defined according to oxygen concentration. 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.

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

The structure of OMZ at the coastal station (St. L6) off Coquimbo (29º S) (**Fig.1**), exhibited similar characteristics to St. T3 (21º S)~~ with 5 layers~~, but in this area the OMZ was deeper and thinner. The OX-ML was shallower~~present at 10 m~~. The OMZ -UP (45 µmol O2) in the base of oxycline was down to 65 m. The O_2 concentrations in the core were~~as~~ less intense than at 21º S (4 to 20 µmol O_2 kg^{-1} ~~O^2~~) and it was located below 90 m. The OMZ-LW could not be assessed because of lack of CTD data below 350 m.

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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**).

~~The OMZ-LW was delimited above the core and below the depth where the O2 slope changes significantly (>4 µmol /m) (Fig. 2).~~

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3.2 Zooplankton composition and abundance

A total of 27 zooplankton taxa were identified by the ZooScan and ZooProcess **(Table S4 Supplemental Material)**~~during the study period~~ ~~**(Table 2)**~~**.** The number of taxa varied among stations and strata ~~(Table 2)~~. Across the~~o~~ 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 ~~in each stations~~ 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). ~~Copepods (Small (SC.), Large (LC.), Eucalanidae (EC.) and Acartia (AC.)) constituting 86% (in St. T5), 80% (in St. T3) and 67% (in St. L6); Eggs Fish (EF.) constituting 2% (in St. T5), 5% (in St. T3) and 6% (in St. L6); Nauplius Larvae (NL) 1% (in St. T5), 1% (in St. T3) and 7% (in St. L6); Appendicularia (AP.)5% (in St. T5), 4% (in St. T3) and 3% (in St. L6). The remaining 19 groups only constituting 5% (in St. T5) 8% (in St. T3) and 12% (St. L6). (Fig. 3). Because these 7 taxonomic groups represented 91% of the average of the total abundance in the study area, we hereafter assumed that they represented the whole zooplankton community and therefore we used them for the vertical distribution analysis.The total integrated abundance of zooplankton in the study area ranged from 254,171 to 742,469 ind.~~ ~~m^{-2}~~ ~~(mean 480.037 ind.~~ ~~m^{-2}~~~~)~~. As based on a Two-Way Crossed Analysis ANOSIM test, this water-column integrated abundance did not show~~ed no~~ 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 29º S (St. L6) had a weaker and less extensive OMZ showing the highest zooplankton abundance (51% greater).

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

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

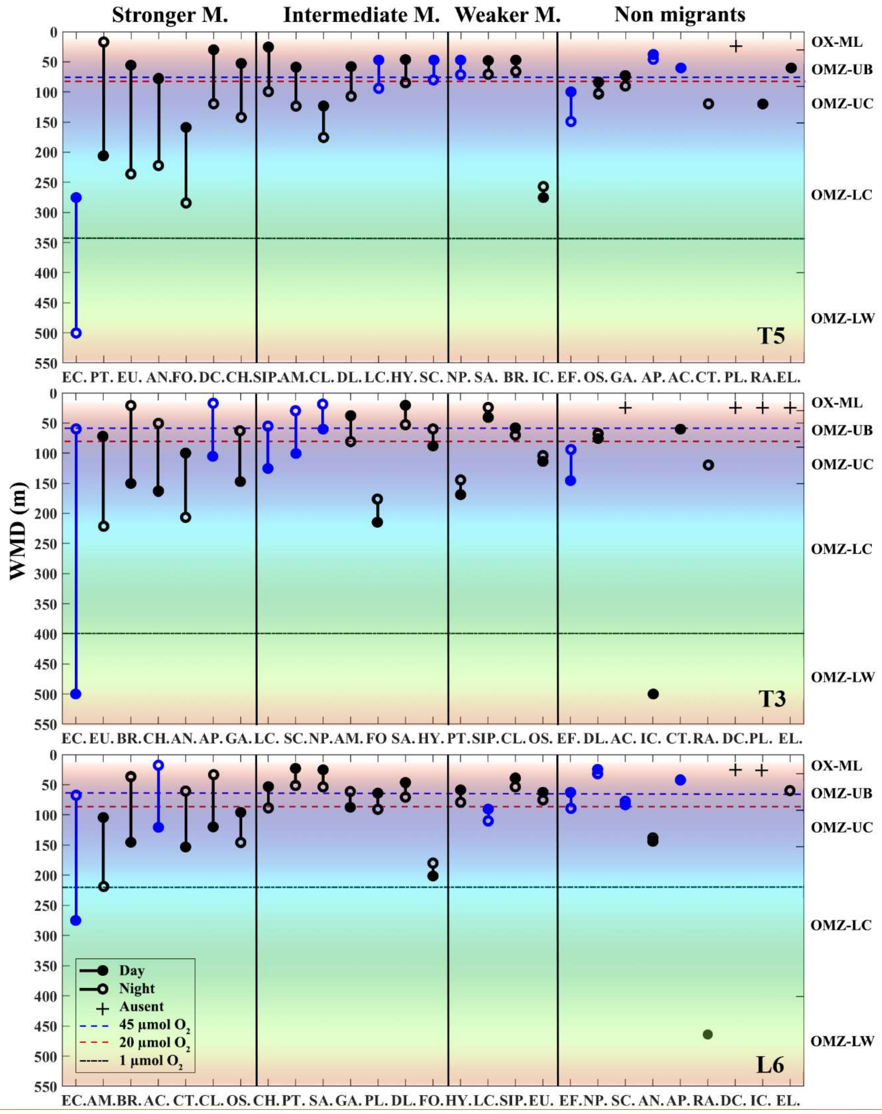
~~Regional difference among stations (Two Way Crossed Analysis ANOSIM p<0.05) were found, therefore, the different stations were treated independently. In general, across to zonal section off Iquique the abundance showed the lowest values at onshore station (St. T3 18%), which was characterized by the strongest and most extensive OMZ in the study area, these values increased at the offshore station (St. T5 31%), where the OMZ was less pronounced and thicker than in St. T3. Unlike the zonal section, the onshore station off 29ºS (St. L6) had a weaker and less extensive OMZ showing the highest abundance (51%) (Table 2).~~

3.3 Diel vertical migration (DVM) and v~~V~~ertical d~~D~~istribution

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.~~ure~~3**. These taxa were classified into four groups in according to their ΔDVM **(Table 1~~3~~)**: **1) Strong~~er~~ migrants**, represented by taxa that exhibited a strong DVM and showed a broad range of ΔDVM from 225 to 99 m~~225 -99 m~~ (in St.T5), 440 to ~~-~~84 m (in St. T3) and 208 to ~~-~~87 m (in St. L6). This group constituted~~ing~~ 70% of taxa with higher ΔDVM. The composition of taxa in this group was variable at each station **(Table 1~~3~~)**, but in general ~~it~~ was well represented by Eucalanidae Copepods (EC~~.~~), Euphausiids (EU~~.~~), *Acartia* Copepods (AC~~.~~), Ctenophores (CT~~.~~), Decapods~~a~~ (DC~~.~~), Annelidae (AN~~.~~), Bryozoan (BR~~.~~), Pteropods~~a~~ (PT~~.~~) and Chaetognaths~~a~~ (CH~~.~~). These taxa were mostly concentrated in the oxic surface stratum **(OX-ML)**, and **the OMZ core**

Con formato: Fuente: Sin Negrita, Cursiva showing a strong interaction both with the **OMZ-UC** and the **OMZ-LC** strata, an 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~~73–34 m~~ (in St. T5), 70 to ~~-~~27 m (in St. T3) and 49 to~~-~~ 22 m (in St. L6). This group constituted ~~ing~~23% of taxa with moderate ΔDVM. The composition of taxa in this group was also variable at each station **(Table 1~~3~~)**, but ~~in general~~ it was mostly represented by small (SC~~.~~) and large Copepods (LC~~.~~), Amphipods~~a~~ (AM~~.~~), Cirripedia Larvae (CL~~.~~), Gastropods~~a~~ (GA~~.~~), Siphonophores~~a~~ (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~~spatially changing from normoxia to hypoxia~~ condition, and vice versa between 0 to 200 m,~~.~~ **3) Weak~~er~~ 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)~~24-18 m (in St.T5),23-12 m (in St.T3) and 21-11 m (in St. L6)~~. This group constituted 5% of taxa of low range of ΔDVM. The composition of taxa in this group was also variable at each station **(Table 1~~3~~)**, but in general it was represented by Hydrozoa (HY~~.~~), Salps (SA~~.~~), Platyhelminthes (PT~~.~~), Decapoda Larvae (DL~~.~~), Ostracods~~a~~ (OS~~.~~), Naupli~~u~~i~~s Larvae~~ (NL~~.~~) and Ichthyoplankton (IC~~.~~). These taxa were concentrated mainly in the oxic surface strata (**OX-ML)** and in the **OMZ-UP,** but also in **OMZ-UC** at the onshore stations (Stations~~s.~~ T3 and Sation ~~-~~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~~that~~ did not exhibit a significant DVM and had ~~showed~~ a range of ΔDVM of 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~~ing~~ 1% of taxa with not significant ΔDVM. The composition of taxa in this group was also variable at each station **(Table 1~~3~~)**, but in general it was represented by fish eggs~~Egg Fish~~ (EF~~.~~), Radiolarians (RA~~.~~) and Echinoderm Larvae (EL~~.~~).



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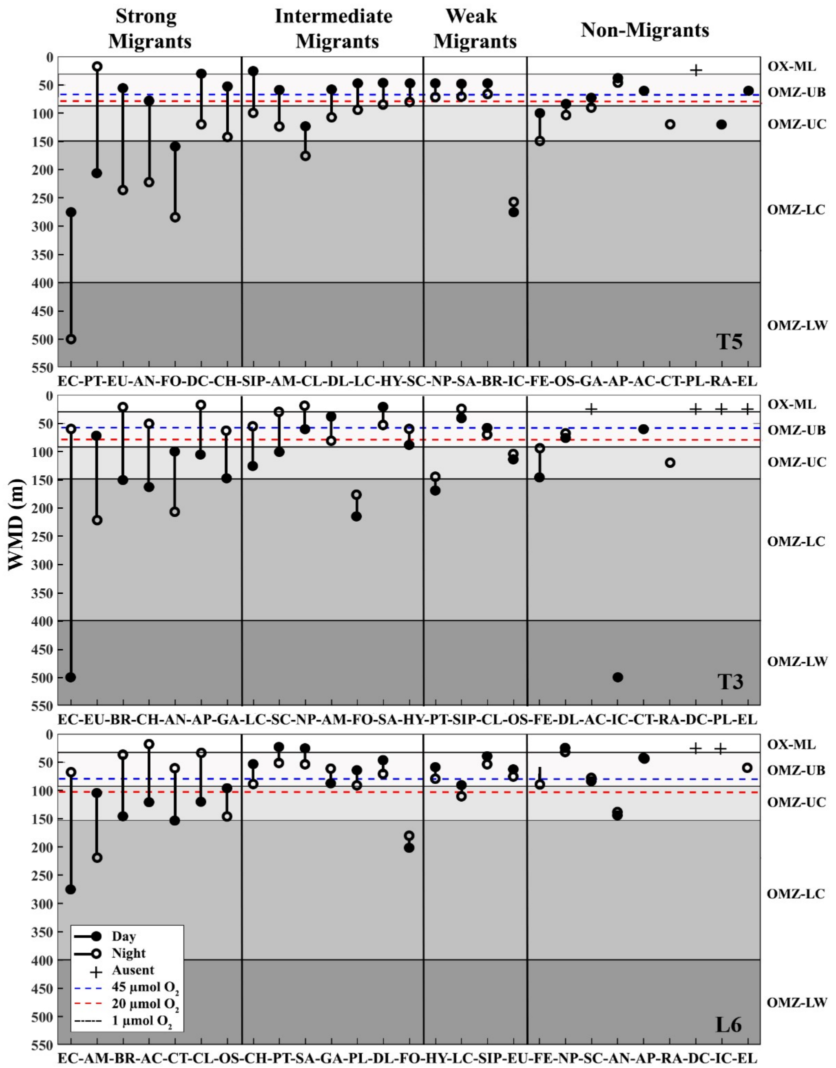

Fig.~~ure~~ 3. Weighed mean depth distribution (WMD) of the zooplankton community interacting with the OMZ off Iquique (Stations T5 and T3) and off Coquimbo (Station L6) at the northern upwelling area of Chile during the austral spring 2015. Shaded gray areas represent different layers defined by their oxygen levels (defined in Methods). The taxonomic groups were classified by automated analysis (ZooScan): EC= Eucalanidae copepods, AM= amphipods, BR=Bryozoan, AC= *Acartia*

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Copepods, CT= Ctenophores, CL=Cirripedia larvae, OS=Ostracods, CH=Chaetognaths, PT= Pteropods, SA=salps, GA= Gastropods, PL= Platyhelminthes, DL= Decapoda larvae, FO=Foraminiphera, 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.~~Weighed mean depth distribution (WMD) of zooplankton community within and outside to the OMZ off Iquique (Sts.T5-T3) and Coquimbo (St. L6) during 2015. The blue symbols represent major group of zooplankton. Background colour represents variable levels of oxygen as defined for each layer.~~

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	

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CT.	-	-	-	RA.	-	-	-	RA.	-	-	-	
PL.	-	-	-	DC.	-	-	-	DC.	-	-	-	
RA.	-	-	-	PL.	-	-	-	IC.	-	-	-	
EL.	-	-	-	*EL.*	-	-	-	*EL.*	-	-	-	

3.3.2 Vertical d~~D~~istribution and DVM of dominant ~~major~~ groups

Vertical distributions of zooplankton were assessed for 5~~the major~~ taxonomic groups~~ sampled: ~~, which represented 81% of total abundance: Salps (SA.); Copepods represented by small Copepods (SC.), Large Copepods (LC.), Eucalanidae Copepods (EC) and *Acartia* Copepods (AC); Chaetognaths(CH); Euphausiids (EU) and Decapoda Larvae (DL); as well as their patterns of strata–station–abundance relationships are illustrated in **Fig. 4**~~Copepods Small (SC.), Large (LC.), Eucalanidae (EC.) and Acartia (AC.), Eggs Fish (EF.), Nauplius Larvae (NL) and Appendicularia (AP.), as well as their patterns of strata station abundance relationships are illustrated in **Figure 4**~~**.** The abundance of these zooplankton groups regarding depth strata was significantly different ~~variable~~ (ANOSIM, p <0.05) at each station~~**(Table 2)**~~, and therefore representing~~ed~~ distinctive microhabitats characterized by specific depth and oxygen concentration~~ feature~~**.** In general, the higher abundance (>50%) was found in the shallower strata and well oxygenated layers **(OX-ML and- OMZ-UP)** ~~>50%)~~ (>250 µmol O_2 kg^{-1} ~~O_2~~), and then it decreased rapidly in the strata associated with the~~to~~ OMZ core (**OMZ-UC** and- **OMZ-LC**). Below this stratum a slight peak in abundance was present in the ~~at~~ **OMZ-LW** at all stations, occurring between 400-600 m, both daytime and night condition~~.~~ (**Fig. 4**).

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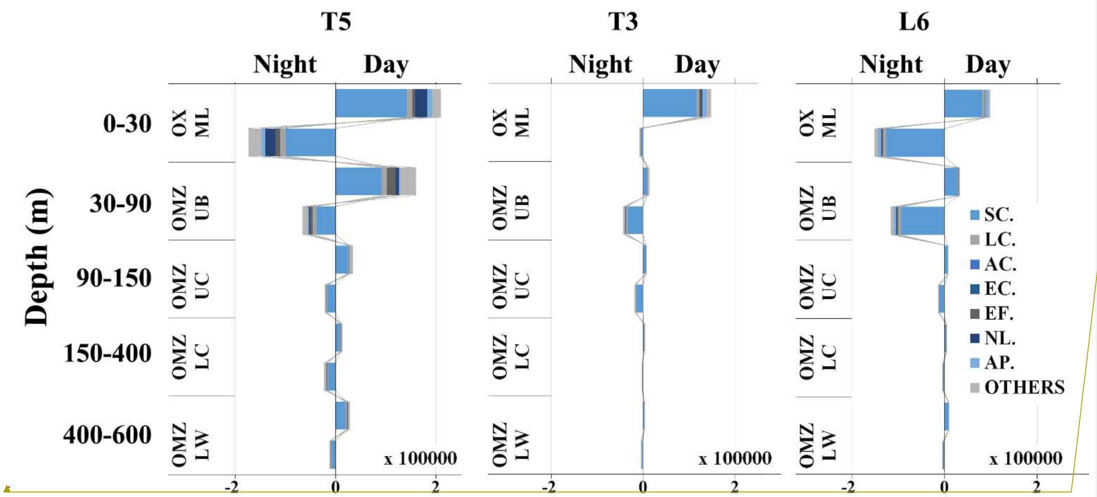

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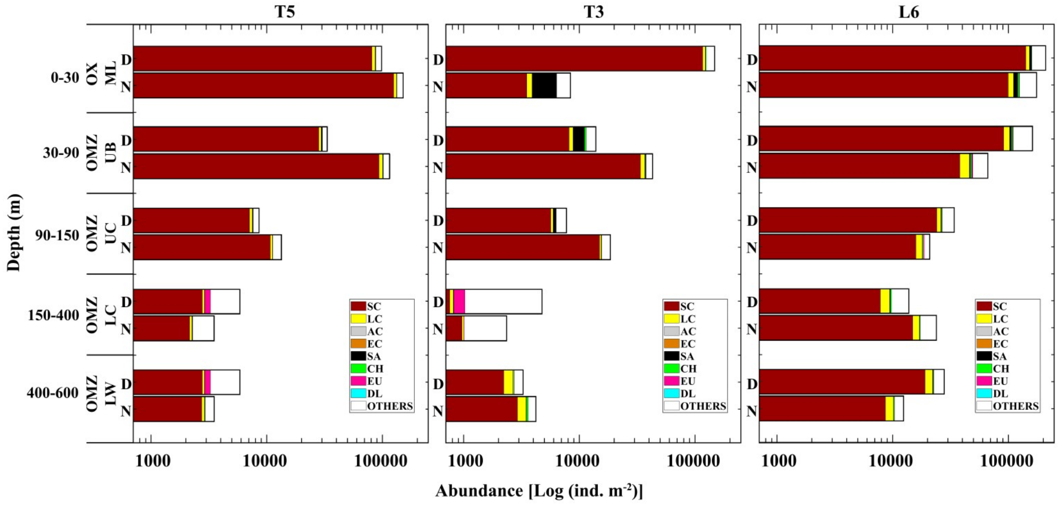

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Fig.~~ure~~ 4. Vertical distribution of dominant taxonomic groups of zooplankton sampled at 3 stations off northern Chile: off Iquique at 21° S (Stations T5 and T3) and off Coquimbo at 29° S (Station L6). Abundances are mean values from samples obtained 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.~~Vertical distributions of zooplankton for the major taxonomic groupoff Iquique (Sts. T5 and T3) and Coquimbo (St. L6) during consecutive days in spring 2015.~~

As expected, C~~c~~opepods dominated numerically the zooplankton community both within and outside ~~to~~ 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 SC.were the most abundant copepods, followed by LC.**(Table 2),** whereas AC. and EC. showed the lowest abundance~~. The largest aggregation Copepods (pooled data)~~of theses group~~ during the entire study period was observed at the offshore station St. T5 (86%), where abundances reached~~ing up to~~ 192088~~384,176~~ ind. m^{-2} ~~were found **(Fig. 4)**~~**.** ~~Across of zonal section~~ O~~o~~ff Iquique, the highest abundances and biomass were in the shallower strata **(OX-ML)** St.T5 (49%) and St. T3 (47%), and these values~~they~~ were reduced in the core of the OMZ at St. T5 (4 to 1%) and at T3 (8 to 1%)~~St. T5 (4-1%) and T3 (8-1%)~~ between 90-400 m, where oxygen had the lowest concentrations (< 20 µM to ~~-~~1 µM).~~The~~ A~~a~~bundances showed slight increases in the **OMZ-LW** stratum during daytime, where oxygen increased after the extremely low levels within the OMZ~~conditions started to restore again~~. At the onshore station off 29º S (Station~~.~~ L6), having a weaker and less extensive OMZ,~~with a weaker 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%. ~~(67%) in comparison with stations off Iquique.~~

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 (225 m). 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 (Stations T3 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

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

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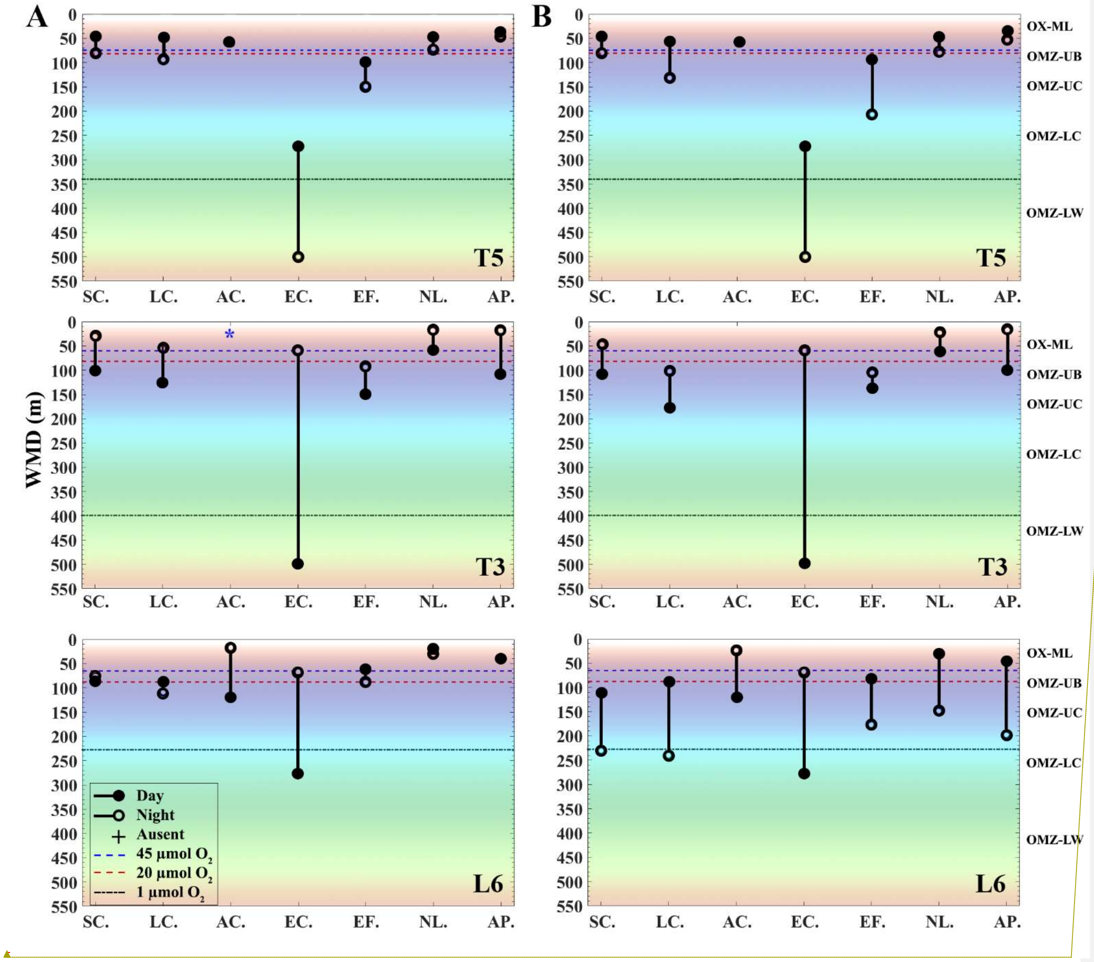
~~The second most abundant taxa of zooplankton, Egg fish showed the largest aggregation at the onshore station St. L6 (6%), with a weaker less extensive OMZ, where abundances made up to 41695 ind. m^{-2}**(Fig. 4)**. The WMD of Fish Eggs showed a range between 64 and 149 m depth **(Table 3)** and appeared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

~~Similarly, most of the individuals of Nauplius Larvae showed the largest aggregation at the onshore station St. L6 (7%), where abundances up to 41695 ind. m^{-2} were found **(Fig. 4)**. The abundance and biomass of this group increased in the oxic~~

~~surface strata **OX-ML** both by day and at night. No DVM was discernible in this station **(Fig. 4)**, because of the slight difference between their day- and night-time distributions. By contrast, at onshore station St.T3 they appeared to perform a weak DVM in the **OMZ-UB** stratum at night, as indicated by the overall N:D ratio (3.31) and by the migration indices (WMD ΔDVM) **(Table 3).**~~



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~~**Figure 5.** Dominant habitat and daily movements of zooplankton major taxa within and outside to the OMZ structure off Iquique (T5-T3) and Coquimbo (L6) during two consecutive days in 2015. **A** WMDof abundance of zooplankton community~~

~~and **B**WMDof biomass of zooplankton community. Background colour represents variable levels of oxygen as defined for each layer.~~

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

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

~~IC.~~	~~258~~	~~275~~	~~-18~~	-	~~OS.~~	~~105~~	~~114~~	~~-9~~	-	~~EU.~~	~~74~~	~~63~~	~~11~~	
~~EF~~	~~149~~	~~100~~	~~49~~		~~EF~~	~~94~~	~~146~~	~~-52~~		~~EF~~	~~89~~	~~64~~	~~25~~	
~~OS.~~	~~101~~	~~85~~	~~16~~		~~*DL.*~~	~~69~~	~~76~~	~~-7~~		~~NP.~~	~~31~~	~~25~~	~~6~~	
~~GA.~~	~~90~~	~~75~~	~~15~~		~~AC.~~	-	-	-		~~SC~~	~~78~~	~~82~~	~~-4~~	
~~AP.~~	~~46~~	~~39~~	~~7~~		~~IC.~~	-	~~500~~	-		~~AN.~~	~~138~~	~~143~~	~~-4~~	
~~AC.~~	-	~~60~~	-		~~CT.~~	-	~~60~~	-		~~AP.~~	~~43~~	~~41~~	~~2~~	~~Non Migrants<1 %~~
~~CT.~~	~~120~~	-	-		~~RA.~~	~~120~~	-	-		~~RA.~~	-	~~464~~	-	
~~PL.~~	-	-	-		~~DC.~~	-	-	-		~~DC.~~	-	-	-	
~~RA.~~	-	~~120~~	-		~~PL.~~	-	-	-		~~IC.~~	-	-	-	
~~*EL.*~~	-	~~60~~	-	-	~~*EL.*~~	-	-	-	-	~~*EL.*~~	~~60~~	-	-	

Similarly to Salps, most Chaetognaths showed the largest aggregation at the onshore station St. L6 (~2%), where their abundances reached up to 9510 ind. m^{-2}. 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

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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).~~The other main taxa, Appendicularia showed the largest aggregation at the onshore station T5 (5%), where abundances reached up to 21848 ind. m^{-2} were found **(Fig. 4)**. The abundance and biomass of this group were mainly concentrated in the oxic surface strata **OX-ML** atSt. T5 and St. L6both by day and at night. No DVM was attributed in these stations, judging by the small difference between their day- and night-time distributions,while at onshore station St. T3 appeared to perform a strong inverse DVM in **OMZ-UC** stratum at night, as indicated by the overall N:D ratio (5.91) and by the migration indices (WMD-ΔDVM) **(Table 3).** The WMD at this station showed a range between 18 and 106 m depth and ΔDVM of 88 m depth **(Fig. 4)**.~~

3.3.3 Others groups with vertical distribution associated to OMZ UC

The remaining 19 groups that only 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).**

~~The remaining 19 groups that only constituting 5% (in St.T5) 8% (in St.T3) and 12% (in St.L6) in abundance, they showed different behaviors at each station: Normal DVM (in St.T5) and inverse DVM (in Sts.T3-L6) **(Table 3).** These groups clearly exhibited different daytime and night depths associated to **OMZ core (OMZ UC-LC).**Overall they tended to live deeper by day and shallower by night at in St. T5 than at the other sites **(Fig.3).**~~

3.4 Vertical d~~D~~istribution of zooplankton biomass ~~and Migrant biomass~~

~~T~~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**).

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**

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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 Copepod	0.02	±	0.0	0.00	±	0.0	0.44	±	0.2
***Acartia* Copepod**	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
Appendicularia	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.

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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.

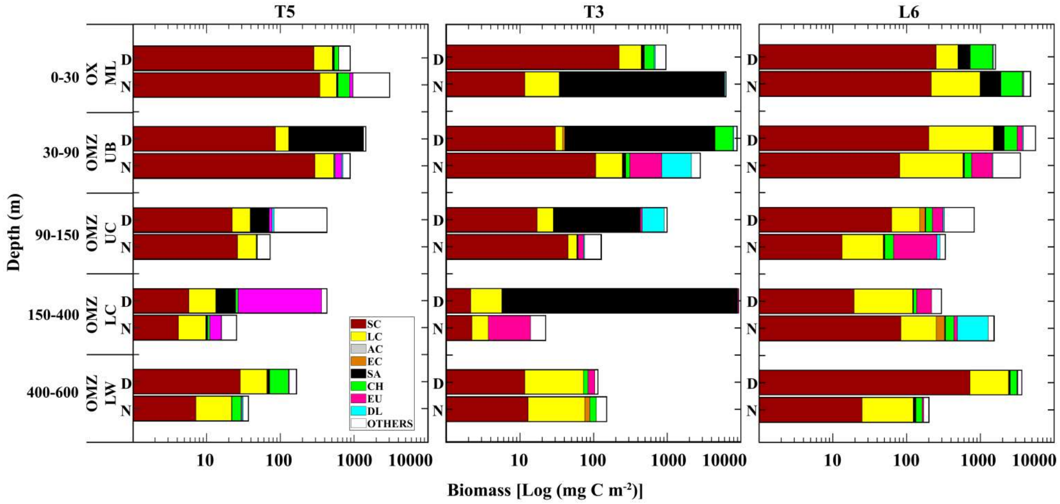

Fig.5. Daytime vs. Night-time vertical distribution of biomass of different taxonomic groups at 3 stations off northern Chile: off Iquique (StationsT5 and T3) and off Coquimbo (Station L6). Data are from night and day replicated samples during two consecutive days in the austral spring 2015. Values represent 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).

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~~he vertical distribution and daytime vs. Nighttimevariability of zooplankton biomassshowed distinctive features associated to OMZ structure, with significant difference ($p<0.05$) between strata in both daytime and nighttime sampling as based on the ANOSIM test. In the whole area most of the biomass was concentrated in a narrow band within the OX-ML and OMZ-UB strata, associated with more oxygenated surface waters, with reduced values in deeper waters associated with the OMZ core, in special at the onshore station off Iquique (St. T3) (Fig.6). Overall, we observed that highest values of biomass were present during the night, and they were concentrated above 150 m (negative values), .whereas in the deeper strata it was weakened, as expected from the effect of the DVM. Despite the fact that the zooplankton showed higher biomass during the night (**Fig.6**), the two-Way Crossed Analysis ANOSIM did not reveal a significant day-night difference ($p>0.05$).We observed a slight differences between day and night samples when comparing total biomass regardless the effects of strata suggesting that a small percentage of the zooplankton biomass migrated out of the upper 150 m during the day. However, these results can be underestimated due complex DVM behaviours (Normal-Inverse) (**Table 3**) that exhibit the taxa, depending on the species composition in each station.~~

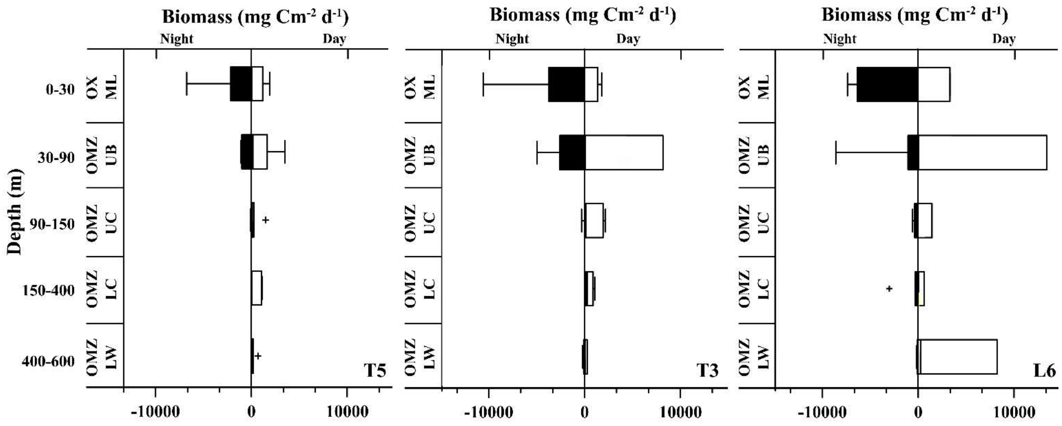

Fig. 6. Vertical distribution of total zooplankton biomass during daytime and night-time conditions at 3 stations off northern Chile: off Iquique (Stations T5 and T3) and off Coquimbo (Station L6) during two consecutive days in the austral spring 2015.Some outliers are plotted individually (+). Error 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).

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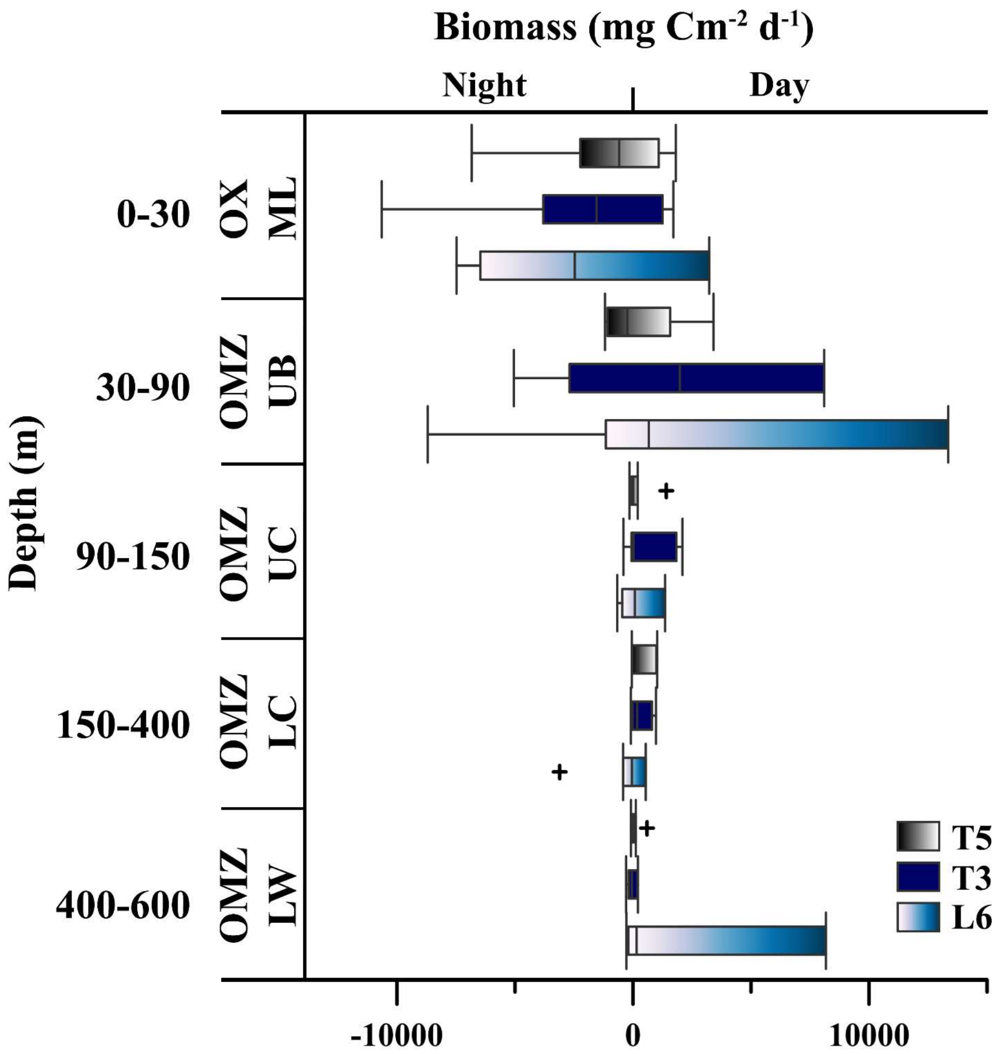

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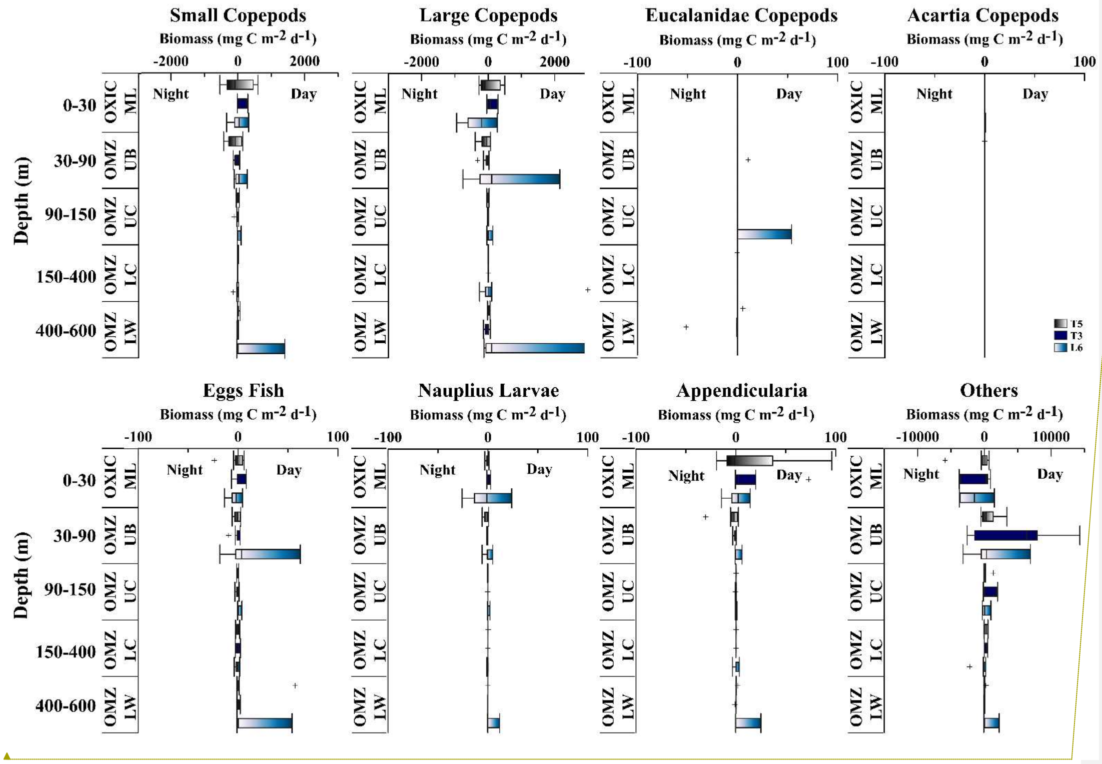
~~**Figure 6.** Differences in zooplankton biomass distribution between daytime and night in 3 station off Iquique (Sts.T5-T3) and Coquimbo (St. L6) during two consecutive days in 2015are averaged in a boxplot, with error bars indicating the range.~~

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

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



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

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3.4.1 Migrant biomass ~~spatial patchiness~~ of the ~~major~~ 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.

~~The migrant biomass and spatial patchiness of the zooplankton taxa was reflected in the day-minus-night biomass profiles **(Fig. 8)**.Biomass of these taxa was, in most situations, two orders of magnitude greater than the biomass of copepods. Biomass of Copepods was an order of magnitude more than other groups **(Fig. 8).** Some of these taxa, such as small and large copepods, exhibited very strong migration in special at the onshore station off Iquique (St. T3), showing the highest biomass in a narrow band within the oxyeline, but also in the OMZ-UB (St. T3).The magnitude of this migration also changed across of zonal section off Iquique (20ºS) speciallyat the offshore station (St. T5), which showed the lowest biomass in the whole study area. Subsurface mesopelagic peaks were present at onshore station off 29ºS(St. L6), occurring mainly between 400-600m, mirroring the mesopelagic peaks in total zooplankton biomass in this stratum **(Fig. 8).**~~

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

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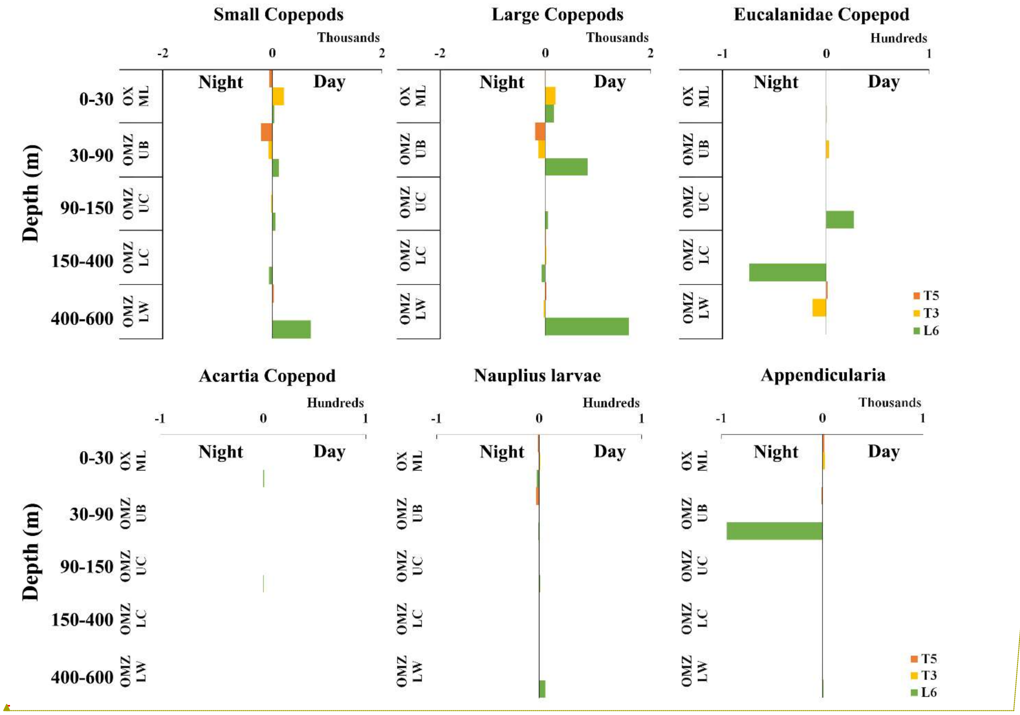

~~**Figure 8.**Migrant biomass (mg C m^{-2}): Day-minus-night profiles of average daily biomass in the water column off Iquique (Sts. T5-T3) and Coquimbo (St. L6) during two consecutive days in 2015.~~

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).

	ST-T5			**ST-T3**			**ST-L6**		
TAXA	**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

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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	

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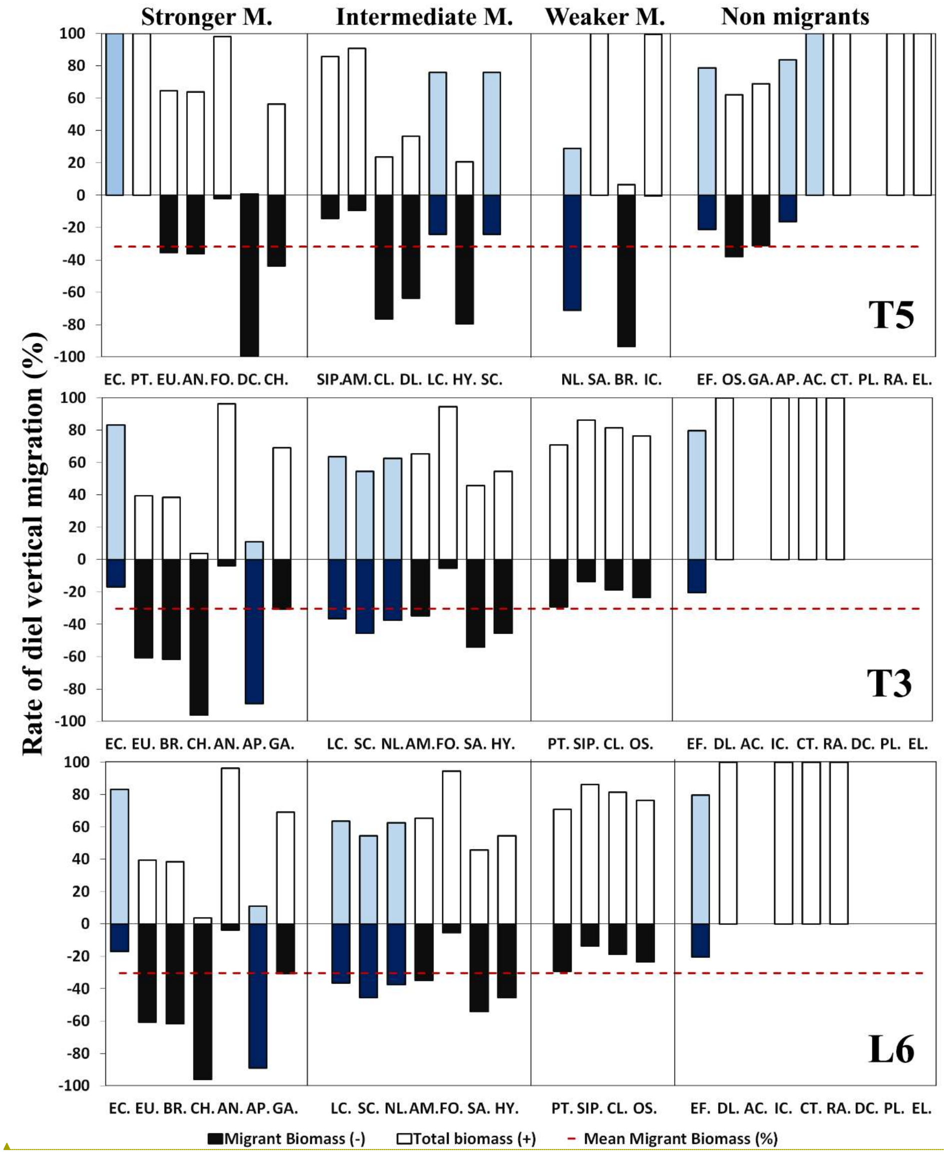
~~**Table 4-** Vertical distributions of mean biomass and migrant biomass (mg C m^{-3}) for the 27 zooplankton groups sorted by strata during daytime and night-time conditions.~~

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

~~600~~	~~400~~	~~0.75~~	~~0.19~~	~~0.56~~	~~0.57~~	~~0.73~~	~~-0.16~~	~~2.48~~	~~0.99~~	~~1.49~~

~~3.4.2 Rate of diel vertical migration~~

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



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

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

~~TAXA~~	**~~T5~~** -	**~~T3~~** -	**~~L6~~**	**~~RATE OF DVM (mg C m^{2} d^{-1})~~**
~~Salps~~	~~0.00~~	~~5851.57~~	~~675.60~~	~~2175.72~~
~~Chaetognatha~~	~~188.26~~	~~3462.59~~	~~1070.04~~	~~1573.63~~
~~Decapoda~~	~~1296.57~~	~~0.00~~	~~0.00~~	~~432.19~~
~~Appendicularia~~	~~9.96~~	~~26.30~~	~~1043.57~~	~~359.94~~
~~Euphausiids~~	~~209.63~~	~~531.44~~	~~212.29~~	~~317.79~~
~~Large Copepods~~	~~202.92~~	~~198.18~~	~~532.35~~	~~311.15~~
~~Hydrozoa~~	~~438.57~~	~~331.59~~	~~145.72~~	~~305.29~~
~~Small Copepods~~	~~266.81~~	~~210.54~~	~~155.92~~	~~211.09~~
~~Siphonophora~~	~~129.37~~	~~99.90~~	~~69.27~~	~~99.51~~
~~Annelida~~	~~51.36~~	~~8.28~~	~~145.27~~	~~68.30~~
~~Amphipoda~~	~~1.97~~	~~35.60~~	~~38.74~~	~~25.44~~
~~Decapoda Larvae~~	~~27.76~~	~~0.00~~	~~46.54~~	~~24.77~~
~~Ctenoforos~~	~~0.00~~	~~0.00~~	~~48.51~~	~~16.17~~
~~Ostracoda~~	~~9.07~~	~~7.76~~	~~28.57~~	~~15.13~~
~~Pteropoda~~	~~5.22~~	~~0.52~~	~~8.10~~	~~4.61~~
~~Nauplius Larvae~~	~~4.42~~	~~1.06~~	~~3.04~~	~~2.84~~
~~Cirripedia Larvae~~	~~0.38~~	~~0.05~~	~~2.97~~	~~1.13~~
~~Eucalanidae Copepod~~	~~0.00~~	~~2.65~~	~~0.03~~	~~0.89~~
~~Gastropoda~~	~~0.59~~	~~0.35~~	~~1.11~~	~~0.68~~
~~Foraminifera~~	~~0.05~~	~~0.01~~	~~1.73~~	~~0.60~~
~~Bryozoa~~	~~1.50~~	~~0.24~~	~~0.00~~	~~0.58~~
~~Acartia Copepod~~	~~0.00~~	~~0.00~~	~~0.81~~	~~0.27~~
~~Ictioplancton~~	~~0.06~~	~~0.00~~	~~0.00~~	~~0.02~~
~~Echinoderm Larvae~~	~~0.00~~	~~0.00~~	~~0.00~~	~~0.00~~
~~Platyhelminthes~~	~~0.00~~	~~0.00~~	~~0.00~~	~~0.00~~
~~Radiolario~~	~~0.00~~	~~0.00~~	~~0.00~~	~~0.00~~
~~TOTAL~~	~~2851.97~~	~~10772.97~~	~~4236.76~~	~~5946.86~~

4 Discussion

Studies on zooplankton DVM and active transport of C mediated by zooplankton have been documented previously for the Pacific Ocean and other areas of the world's ocean, as ~~we~~ summarized in **Table 4**~~6~~. 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~~associated with the 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 s~~S~~tudies 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~~Escribano, 1998~~), 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. ~~For instance, the extension and intensity of DVM, in terms of the total amount of zooplankton biomass which can daily be exchanged between the mixed layer and the subsurface stratum below the thermocline, could greatly affect the magnitude of the downward C being released at depth.~~

Our approach to assess downward C 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 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 and C content. Various approaches have been adopted

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Con formato: Fuente: Sin Negrita, Español (alfab. internacional) for converting sizes to body masses. For example, Lehette and Hernandez-Leon (2009) provided some general regression equations for subtropical and Antartic 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, a key migrant group is comprised by the copepods Eucalanidae which have been described as even being able to enter the core of the OMZ, and then migrate downward to the lower limit of the OMZ, which is slightly more oxygenated (Hidalgo *et al.,* 2005). In our study however, their contribution to total migrant biomass was 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, Decapoda, Annelidae, Bryozoan, Pteropods~~a~~ and Chaetognaths~~a~~ tended to concentrate~~d~~ 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 E~~e~~uphausiid in the coastal upwelling zone off Chile, is a well-adapted species to vertically migrate into the core of the OMZ. In fact, the E~~e~~uphausiids studied here showed a large DVM amplitude (~250 m), descending into the core of the OMZ and below 250 m each day. In general, all strong migrants taxa ~~seem to~~ showed a strong interaction with the core of OMZ, remaining there either temporarily or permanently during the day or night condition, contributing in~~in~~ this way to the release of C below the thermocline, despite presence of hypoxic conditions.

Our estimates of DVM-mediated fluxes showed that migrant biomass (3427±895~~5099 ±2701~~ mg C m^{-2} d^{-1}) and C flux estimates (678± 465mg 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 midwater depths (e.g. Kiko *et*

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Con formato: Sangría: Primera línea: 0" *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~~6~~**). High productivity and strong aggregation of zooplankton in coastal areas of this region (Escribano *et al.,* 2000; Escribano and Hidalgo, 2000) may promote~~favour~~ ~~a~~ greater amounts ~~availability~~ of migrant biomass. This requires however that DVM should not be majorly constrained by presence of the OMZ~~DMV~~ and that most migrant taxa are tolerant to low-oxygen. On the other hand, o~~O~~ur estimates of downward C flux were substantially lower than previous ones reported off northern Chile by Hidalgo *et al.* (2005) for *E. inermis* alone (14.1 mg C m-^{2} d^{-1}) and for copepods and euphausiids by Escribano *et al.* (2009) (7200 mg C m^{-2} d^{-1}) (**Table 4~~7~~**). 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~~exceed the level of primary production (~1000 mg C m^{-2} d^{-1})(Daneri *et al.,* 2000), suggesting that previous works may have overestimated active transport of C~~. Although t~~T~~he 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		154.8±		7.3± 1.4		5.4±1.	25.4	Zhang and Dam

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	zooplankton		32.4				1		(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	3427 ±895	674±292					This study

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

~~**Location**~~	~~**Taxa**~~	~~**PP**~~	~~**MB**~~	~~**AC**~~	~~**RF**~~	~~**EF**~~	~~**MF**~~	~~**% POC**~~	~~**References**~~
~~N. Hawaii ALOHA~~	~~DVM Zooplankton~~		~~108–216~~	~~7.1~~	~~2.6–4.8~~			~~12–18~~	~~Al-Mutairi and Landry (2001)~~
~~N. Hawaii ALOHA~~			~~157.9~~	~~3.2–13.6~~	~~3.7~~			~~18~~	~~Steinberg *et al.*(2008)~~
~~N.W. Pac.~~	~~DVM Metridia~~	~~**418**~~	~~144~~	~~**9**~~	~~**3**~~	~~**5**~~	~~1~~	~~23.1–61.8~~	~~Kobari *et al.* (2008)~~
~~N.W. Pac.~~	~~DVM copepods~~			~~8~~				~~22.3~~	~~Takahashi *et al.*(2009)~~
~~N.E. Pac.~~	~~Mesopelagic fishes~~	~~170~~			~~23.9~~				~~Davison *et al.*(2013)~~
~~Eastern Equator~~			~~96.0± 25.2~~		~~4.2± 1.2~~		~~2.9±0.8~~	~~18.4~~	~~Zhang and Dam (1997)~~

~~Eastern Equator~~	~~DVM zooplankton~~		~~154.8± 32.4~~		~~7.3± 1.4~~		~~5.4±1.1~~	~~25.4~~	~~Zhang and Dam (1997)~~
~~Central Equator (HNLC)~~			~~52.9~~		~~6~~		~~–~~	~~4~~	~~Rodier and Le Borgne (1997)~~
~~Western Equator~~			~~46.9~~		~~3~~		~~–~~	~~6~~	~~Rodier and Le Borgne (1997)~~
~~E. Eq. Pac.~~	~~DVM Zooplankton~~		~~**1214**~~	~~7.1~~	~~7.1~~			~~204~~	~~Rodier and Le Borgne (1997)~~
~~Western Equator~~	~~DVM Zooplankton~~		~~144–447~~	~~23.53-9.97~~	~~7.3–19.1~~		~~2.6–4.4~~	~~13–35~~	~~Hidaka *et al.*(2002)~~
~~Equator divergence~~			~~2.8–21.8~~		~~0.9–1.2~~			~~<1-2~~	~~Roman *et al.* (2002)~~
~~Oligotrophic area~~			~~30.2–33.8~~		~~1.3–1.7~~			~~4~~	~~Roman *et al.* (2002)~~
~~E.S.Pac. N.Chile~~		~~5503~~							~~Gonzalez *et al.*(1998)~~
~~E.S.Pac. N.Chile~~		~~10000~~							~~Daneri *et al.*(2000)~~
~~E.S.Pac. N.Chile~~	~~DVM Eucalanus~~		~~8.0–34~~	~~14.1~~					~~Hidalgo *et al.* (2005)~~
~~E.S.Pac. N.Chile~~	~~DVM zooplankton~~		~~37810~~	~~7200~~		~~6700~~			~~Escribano *et al.*(2009)~~
~~E.S.Pac. N.Chile~~	~~DVM zooplankton~~		~~5099 ±2701~~	~~678± 465~~					~~This study~~

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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.

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Even although the OMZ did not greatly prevent DVM migration, zooplankton behaviour appeared ~~as ~~disrupted~~,~~ or exhibited reversed patterns, depending on vertical distribution of the OMZ and on the taxonomic group being considered. This behaviour was more evident in the onshore stations (Stations~~s.~~ T3 and -L6), but in particular in the station off Iquique (St. T3) that also showed a higher migration rate (60%). ~~In ~~A~~a~~ccording 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~~amplitude~~ of the hypoxic events. This could explain why individuals within a single population can perform reverse, normal, or non DVM, apparently depending on the more important source of mortality: predation by nocturnal~~ly~~ 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 at~~off~~ northern Chile off Antofagasta (23° S) by Gonzalez *et al.* (1998) based on sediment traps (125 to 176 mg C m^{-2} d^{-1}).~~at 60 m depth 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 25 % 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.~~Our estimates represented 7±5 % of export of Carbon resulting from primary production in the upwelling region calculated as ~1000 mg C m^{-2} d^{-1}(Table 7). If we consider this is accounted only by mesozooplankton, then an important fraction of freshly produced C can be taken downward by zooplankton, and this zooplankton-mediated C flux ought to be taking into account when and analysing and modelling the C budget in the upwelling zone.~~

Table 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

~~**Table 7.**Mean primary production rate and estimates of daily downward C flux due to passive sinking and mediated by diel vertical migration of mesozooplankton at three stations in the coastal upwelling region off northern Chile during the spring 2015.~~

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

5 Conclusion

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 0.6 g 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.

~~The vertical distribution and diurnal variability of biomass of 27 taxonomic groups seem to be disturbed by the OMZ in the coastal zone off northern Chile, such that high biomass aggregates above the oxycline in a narrow band within the near-surface oxygenated layer, whereas much lower biomass resides in deeper waters, in particular within the OMZ. Many taxa, however, were found closely associated with the OMZ, and capable of performing DVM withstanding severe hypoxia. Even, several zooplankton groups are strong migrants, exhibiting a large DVM amplitude (~500 m). Among them, a key migrant group is comprised by the copepods Eucalanidae and euphausiids which can even enter the core of the OMZ, and then migrate downward to the lower limit of the OMZ, which is slightly more oxygenated. The variable behaviour among taxa reflected in different amplitudes of vertical migration can greatly affect the daily rate of migrant biomass, indicating that estimates of downward C must take into account taxonomic structure of the zooplankton community.~~

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References

Al-Mutairi, H. and Landry, M. R.: Active export of carbon and nitrogen at station ALOHA by diel migrant zooplankton, Deep. Res. Part II Top. Stud. Oceanogr., 48(8–9), 2083–2103, doi:10.1016/S0967-0645(00)00174-0, 2001.

Andersen, V., Devey, C., Gubanova, A., Picheral, M., Melnikov, V., Tsarin, S. and Prieur, L.: Vertical distributions of zooplankton across the Almeria-Oran frontal zone (Mediterranean Sea), J. Plankton Res., 26(3), 275–293, doi:10.1093/plankt/fbh036, 2004.

Antezana, T.: Vertical distribution and diel migration of Euphausia mucronata in the oxygen minimum layer of the Humboldt Current, Oceanogr. East. Pacific II, 13–28, 2002.

Antezana, T.: Species-specific patterns of diel migration into the Oxygen Minimum Zone by euphausiids in the Humboldt Current Ecosystem, Prog. Oceanogr., 83(1–4), 228–236, doi:10.1016/j.pocean.2009.07.039, 2009.

Antezana, T.: Euphausia mucronata: A keystone herbivore and prey of the Humboldt Current System, Deep. Res. Part II Top. Stud. Oceanogr., 57(7–8), 652–662, doi:10.1016/j.dsr2.2009.10.014, 2010.

Apablaza, P. and Palma, S.: Efecto de la zona de mínimo oxígeno sobre la migración vertical de zooplancton gelatinoso en la bahía de Mejillones, Investig. Mar., 34(2), 81–95, doi:10.4067/s0717-71782006000200009, 2006.

Bray, J. R. and Curtis, J. T.: An ordination of the upland forest communities of southern Wisconsin, Ecol. Monogr., 27(4),

Con formato: Fuente: Sin Negrita, Color de fuente: Automático, Español (alfab. internacional)

Con formato: Español (alfab. internacional)

Con formato: Fuente: Sin Negrita, Color de fuente: Automático, Español (alfab. internacional)

325–349, 1957.

Breitburg, D., A Levin, L., Oschlies, A., Grégoire, M., P Chavez, F., J Conley, D., Garcon, V., Gilbert, D., Gutiérrez, D., Isensee, K., S Jacinto, G., Limburg, K., Montes, I., Naqvi, S. W. A., Pitcher, G., Rabalais, N., R Roman, M., Rose, K., Seibel, B. and Zhang, J.: Declining oxygen in the global ocean and coastal waters, Science, 359(6371), doi:10.1126/science.aam7240, 2018.

Chang, C. Y., Ho, P. C., Sastri, A. R., Lee, Y. C., Gong, G. C. and Hsieh, C. hao: Methods of training set construction: Towards improving performance for automated mesozooplankton image classification systems, Cont. Shelf Res., 36, 19–28, doi:10.1016/j.csr.2012.01.005, 2012.

Dai, L., Li, C., Yang, G. and Sun, X.: Zooplankton abundance, biovolume and size spectra at western boundary currents in the subtropical North Pacific during winter 2012, J. Mar. Syst., 155, 73–83, doi:10.1016/j.jmarsys.2015.11.004, 2016.

Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P. and Ulloa, O.: Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas, Mar. Ecol. Prog. Ser., 197, 41–49, doi:10.3354/meps197041, 2000.

Davison, P. C., Checkley, D. M., Koslow, J. A. and Barlow, J.: Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean, Prog. Oceanogr., 116, 14–30, doi:10.1016/j.pocean.2013.05.013, 2013.

Donoso, K. and Escribano, R.: Mass-specific respiration of mesozooplankton and its role in the maintenance of an oxygen-deficient ecological barrier (BEDOX) in the upwelling zone off Chile upon presence of a shallow oxygen minimum zone, J. Mar. Syst., 129, 166–177, 2014.

Ducklow, H. W., Eborah, D., Steinberg, K. and Buesseler, K. O.: Upper ocean carbon export and the biological pump, Oceanography, 14(4), 50–58, doi:10.5670/oceanog.2001.06, 2001.

Ekau, W., Auel, H., P̈ortner, H. O. and Gilbert, D.: Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish), Biogeosciences, 7(5), 1669–1699, doi:10.5194/bg-7-1669-2010, 2010.

Escribano, R.: Population dynamics of Calanus chilensis in the Chilean Eastern Boundary Humboldt Current, Fish. Oceanogr., 7(3–4), 245–251, doi:10.1046/j.1365-2419.1998.00078.x, 1998.

Escribano, R.: Zooplankton interactions with the oxygen minimum zone in the eastern South Pacific, Supl. Gayana, 70, 19–21, 2006.

Escribano, R. and Hidalgo, P.: Spatial distribution of copepods in the north of the Humboldt Current region off Chile during coastal upwelling, J. Mar. Biol. Assoc. United Kingdom, 80(2), 283–290, 2000.

Escribano, R., Iribarren, C. and Marín, V.: Distribution of "Euphausia mucronata" at the upwelling area of Peninsula Mejillones, northern Chile: the influence of the oxygen minimum layer, Sci. Mar. ISSN 0214-8358, Vol. 64, N^{o}. 1, 2000, págs. 69-77, 64(1), 69–77, doi:10.3989/scimar.2000.64n169, 2000.

Escribano, R., Daneri, G., Farías, L., Gallardo, V. A., González, H. E., Gutiérrez, D., Lange, C. B., Morales, C. E., Pizarro, O., Ulloa, O. and Braun, M.: Biological and chemical consequences of the 1997-1998 El Niño in the Chilean coastal upwelling system: A synthesis, Deep. Res. Part II Top. Stud. Oceanogr., 51(20–21), 2389–2411, doi:10.1016/j.dsr2.2004.08.011, 2004.

Escribano, R., Hidalgo, P., González, H., Giesecke, R., Riquelme-Bugueño, R. and Manríquez, K.: Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile, Prog. Oceanogr., 75(3), 470–485, doi:10.1016/j.pocean.2007.08.027, 2007.

Escribano, R., Hidalgo, P. and Krautz, C.: Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000, Deep Sea Res. Part II Top. Stud. Oceanogr., 56(16), 1083–1094, 2009.

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

Fernández-Álamo, M. A. and Färber-Lorda, J.: Zooplankton and the oceanography of the eastern tropical Pacific: a review, Prog. Oceanogr., 69(2–4), 318–359, 2006.

Fuenzalida, R., Schneider, W., Garcés-Vargas, J., Bravo, L. and Lange, C. B.: Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean, Deep Sea Res. Part II Top. Stud. Oceanogr., 56(16), 992–1003, doi:10.1016/j.dsr2.2008.11.001, 2009.

García-Comas, C., Chang, C. Y., Ye, L., Sastri, A. R., Lee, Y. C., Gong, G. C. and Hsieh, C. hao: Mesozooplankton size structure in response to environmental conditions in the East China Sea: How much does size spectra theory fit empirical data of a dynamic coastal area?, Prog. Oceanogr., 121, 141–157, doi:10.1016/j.pocean.2013.10.010, 2014.

Gonzalez, H. E., Daneri, G., Figueroa, D., Iriarte, J. L., Lefevre, N., Pizarro, G. A., Quiñones, R., Sobarzo, M. and Troncoso, A.: Producción primaria y su destino en la trama trófica pelágica y océano-atmósfera de CO2 en la zona norte de la Corriente de Humboldt (23°S): Posibles efectos del evento El Niño, 1997-98 en Chile, Rev. Chil. Hist. Nat., 71, 429–458, 1998.

Gonzalez, R. R. and Quiñones, R. A.: Ldh activity in Euphausia mucronata and Calanus chilensis: Implications for vertical migration behaviour, J. Plankton Res., 24(12), 1349–1356, doi:10.1093/plankt/24.12.1349, 2002.

Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, Stephane Stemmann, L., Romagnan, Jean-Baptiste Cawood, A., Pesant, S., García-Comas, C. and Prejger, F.: Digital zooplankton image analysis using the ZooScan integrated system, J. Plankton Res., 32(3), 285–303, doi:10.1093/plankt/fbp124, 2010.

Grantham, B. A., Chan, F., Nielsen, K. J., Fox, D. S., Barth, J. A., Huyer, A., Lubchenco, J. and Menge, B. A.: Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific, Nature, 429(6993), 749–754, doi:10.1038/nature02605, 2004.

Herman, A. W. and Harvey, M.: Application of normalized biomass size spectra to laser optical plankton counter net intercomparisons of zooplankton distributions, J. Geophys. Res. Ocean., 111(5), 1–9, doi:10.1029/2005JC002948, 2006.

Hidaka, K., Kawaguchi, K., Murakami, M. and Takahashi, M.: Downward transport of organic carbon by diel migratory micronekton in the western equatorial Pacific:: its quantitative and qualitative importance, Deep Sea Res. Part I Oceanogr. Res. Pap., 48(8), 1923–1939, doi:10.1016/s0967-0637(01)00003-6, 2002.

Hidalgo, P., Escribano, R. and Morales, C. E.: Ontogenetic vertical distribution and diel migration of the copepod Eucalanus

Con formato: Fuente: Sin Negrita, Color de fuente: Automático, Español (alfab. internacional)

Con formato: Español (alfab. internacional)

Con formato: Fuente: Sin Negrita, Color de fuente: Automático, Español (alfab. internacional)

inermis in the oxygen minimum zone off northern Chile (20-21° S), J. Plankton Res., 27(6), 519–529, doi:10.1093/plankt/fbi025, 2005.

Judkins, D. C.: Vertical distribution of zooplankton in relation to the oxygen minimum off Peru, Deep Sea Res. Part A, Oceanogr. Res. Pap., 27(6), 475–487, doi:10.1016/0198-0149(80)90057-6, 1980.

Kiko, R., Hauss, H., Buchholz, F. and Melzner, F.: Ammonium excretion and oxygen respiration of tropical copepods and euphausiids exposed to oxygen minimum zone conditions, Biogeosciences (BG), 13(8), 2241–2255, 2016.

Kobari, T., Steinberg, D., Ueda, A., Tsuda, A., Silver, M. W. and Kitamura, M.: Impacts of ontogenetically migrating copepods on downward carbon flux in the western subarctic Pacific Ocean.pdf, Deep Sea Res. Part II Top. Stud. Oceanogr., 55, 1648–1660 [online] Available from: doi: 10.1016/j.dsr2.2008.04.016, 2008.

Lehette, P. and Hernández-León, S.: Zooplankton biomass estimation from digitized images: a comparison between subtropical and Antarctic organisms, Limnol. Oceanogr. Methods, 7(4), 304–308, doi:10.4319/lom.2009.7.304, 2009.

Longhurst, A. and Williams, R.: Carbon flux by seasonally migrating coepods is a small number, J. Plankton Res., 14(11), 1495–1509, 1992.

Longhurst, A. and Williams, R.: Carbon flux by seasonally migrating coepods is a small number, J. Plankton Res., 14(11), 1495–1509, 1992.

Matsuno, K., Kim, H. S. and Yamaguchi, A.: Causes of under- or overestimation of zooplankton biomass using Optical Plankton Counter (OPC): effect of size and taxa, Plankt. Benthos Res., 4(4), 154–159, doi:10.3800/pbr.4.154, 2009.

Morales, C. E., Braun, M., Reyes, H., Blanco, J. L. and Davies, A. G.: Anchovy larval distribution in the coastal zone off northern Chile: the effect of low dissolved oxygen concentrations and of a cold-warm sequence (1990-95), Invest. Mar., Valparaíso, 24, 77–96, doi:10.4067/s0717-71781996002400007, 1996.

Morales, C. E., Hormazábal, S. E. and Blanco, J. L. J.: Interannual variability in the mesoscale distribution of the depth of the upper boundary of the oxygen minimum layer off northern Chile (18–24S): Implications for the pelagic system and biogeochemical cycling, J. Mar. Res., 57(6), 909–932, 1999.

Ohman, M. D.: The demographic benefits of diel vertical migration by zooplankton, Ecol. Monogr., 60(3), 257–281, 1990.

Paulmier, A. and Ruiz-Pino, D.: Oxygen minimum zones (OMZs) in the modern ocean, Prog. Oceanogr., 80(3–4), 113–128, doi:10.1016/j.pocean.2008.08.001, 2009.

Paulmier, A., Ruiz-Pino, D., Garçon, V. and Farías, L.: Maintaining of the Eastern South Pacific Oxygen Minimum Zone (OMZ) off Chile, Geophys. Res. Lett., 33(20), 2–7, doi:10.1029/2006GL026801, 2006.

Putzeys, S., Yebra, L., Almeida, C., Bécognée, P. and Hernández-León, S.: Influence of the late winter bloom on migrant zooplankton metabolism and its implications on export fluxes, J. Mar. Syst., 88(4), 553–562, doi:10.1016/j.jmarsys.2011.07.005, 2011.

Rodier, M. and Le Borgne, R.: Export flux of particles at the equator in the western and central Pacific ocean, Deep. Res. Part II Top. Stud. Oceanogr., 44(9–10), 2085–2113, doi:10.1016/S0967-0645(97)00092-1, 1997.

Roman, M. R., Adolf, H. A., Landry, M. R., Madin, L. P., Steinberg, D. K. and Zhang, X.: Estimates of oceanic mesozooplankton production: A comparison using the Bermuda and Hawaii time-series data, Deep. Res. Part II Top. Stud. Oceanogr., 49(1–3), 175–192, doi:10.1016/S0967-0645(01)00099-6, 2002.

Sato, K., Matsuno, K., Arima, D., Abe, Y. and Yamaguchi, A.: Spatial and temporal changes in zooplankton abundance, biovolume, and size spectra in the neighboring waters of Japan: Analyses using an optical plankton counter, Zool. Stud., 54(JAN), doi:10.1186/s40555-014-0098-z, 2015.

Seibel, B. A.: Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones, J. Exp. Biol., 214(2), 326–336, doi:10.1242/jeb.049171, 2011.

Silva, N. and Neshyba, S.: On the southernmost extension of the Peru-Chile undercurrent, Deep Sea Res. Part A, Oceanogr. Res. Pap., 26(12), 1387–1393, doi:10.1016/0198-0149(79)90006-2, 1979.

Sprules, W. G., Jin, E. H., Herman, A. W. and Stockwell, J. D.: Calibration of an optical plankton counter for use in fresh water, Limnol. Oceanogr., 43(4), 726–733, doi:10.4319/lo.1998.43.4.0726, 1998.

Steinberg, D. K. and Landry, M. R.: Zooplankton and the Ocean Carbon Cycle, Ann. Rev. Mar. Sci., 9(1), 413–444, doi:10.1146/annurev-marine-010814-015924, 2017.

Steinberg, D. K., Cope, J. S., Wilson, S. E. and Kobari, T.: A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean, Deep. Res. Part II Top. Stud. Oceanogr., 55(14–15), 1615–1635, doi:10.1016/j.dsr2.2008.04.025, 2008.

Stramma, L., Johnson, G., Sprintall, J. and Mohrholz, V.: Expanding Oxygen-Minimum in the Tropical Oceans, Science (80-.)., 320, 655–658, 2008.

Takahashi, K., Kuwata, A., Sugisaki, H., Uchikawa, K. and Saito, H.: Downward carbon transport by diel vertical migration of the copepods Metridia pacifica and Metridia okhotensis in the Oyashio region of the western subarctic Pacific Ocean, Deep. Res. Part I Oceanogr. Res. Pap., 56(10), 1777–1791, doi:10.1016/j.dsr.2009.05.006, 2009.

Ulloa, O. and Pantoja, S.: The oxygen minimum zone of the eastern South Pacific, Deep. Res. Part II Top. Stud. Oceanogr., 56(16), 987–991, doi:10.1016/j.dsr2.2008.12.004, 2009.

Ulloa, O., Canfield, D. E., DeLong, E. F., Letelier, R. M. and Stewart, F. J.: Microbial oceanography of anoxic oxygen minimum zones, Proc. Natl. Acad. Sci., 109(40), 15996–16003, doi:10.1073/pnas.1205009109, 2012.

Wiebe, P. H., Boyd, S. and Cox, J. L.: Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon, Fish. Bull., 73(4), 777–786, 1975.

Wishner, K. F., Gelfman, C., Gowing, M. M., Outram, D. M., Rapien, M. and Williams, R. L.: Vertical zonation and distributions of calanoid copepods through the lower oxycline of the Arabian Sea oxygen minimum zone, Prog. Oceanogr., 78(2), 163–191, doi:10.1016/j.pocean.2008.03.001, 2008.

Wishner, K. F., Outram, D. M., Seibel, B. A., Daly, K. L. and Williams, R. L.: Zooplankton in the eastern tropical north Pacific: Boundary effects of oxygen minimum zone expansion, Deep. Res. Part I Oceanogr. Res. Pap., 79, 122–140, doi:10.1016/j.dsr.2013.05.012, 2013.

Wishner, K. F., Seibel, B. A., Roman, C., Deutsch, C., Outram, D., Shaw, C. T., Birk, M. A., Mislan, K. A. S., Adams, T. J., Moore, D. and Riley, S.: Ocean deoxygenation and zooplankton: Very small oxygen differences matter, Sci. Adv., 4(12), eaau5180, doi:10.1126/sciadv.aau5180, 2018.

Yamaguchi, A., Matsuno, K., Abe, Y., Arima, D. and Ohgi, K.: Seasonal changes in zooplankton abundance, biomass, size structure and dominant copepods in the Oyashio region analysed by an optical plankton counter, Deep Sea Res. Part I Oceanogr. Res. Pap., 91, 115–124, 2014.

Yebra, L., Almeida, C. and Hernández-León, S.: Vertical distribution of zooplankton and active flux across an anticyclonic eddy in the Canary Island waters, Deep. Res. Part I Oceanogr. Res. Pap., 52(1), 69–83, doi:10.1016/j.dsr.2004.08.010, 2005.

Zhang, X. and Dam, H. G.: Downward export of carbon by diel migrant mesozooplankton in the central equatorial Pacific, Deep Sea Res. Part II Top. Stud. Oceanogr., 44, 2191–2202 [online] Available from: https://ac.els-cdn.com/S096706459700060X/1-s2.0-S096706459700060X-main.pdf?_tid=d3d3eaed-5ca5-4ac5-ba8e-6e934a548139&acdnat=1535698698_4634563185704240d6eef101ba42f036, 1997.