Zooplankton diversity, abundance, and species composition across an oxygen gradient in the Eastern Tropical North Pacific

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NONTECHNICAL SUMMARY

Dissolved oxygen is necessary for aerobic respiration, and therefore can influence zooplankton communities. I examined how an oxygen gradient in the Eastern Tropical North Pacific impacted zooplankton diversity, abundance, and species composition. Predominately, low levels of oxygen decreased total biomass of zooplankton, which has larger implications for food webs and carbon transport. Additionally, it is evident that some species of zooplankton can thrive in low levels of oxygen while others avoid it completely.

ABSTRACT

Horizontal and vertical distribution of zooplankton across an oxygen gradient was investigated by examining diversity, abundance, and species composition in the Eastern Tropical North Pacific (ETNP) on the senior thesis cruise 16–27 March 2012 aboard the R/V *Thomas G. Thompson*. Overall, abundances were represented by 70% copepods, 7% chaetognaths, and 3% various stages of euphausiids, in addition to various larval stages, ostracods, larvaceans, amphipods and radiolarians. No relationship between diversity and oxygen was observed. Linearly, abundance increased with increased dissolved oxygen; likewise, a similar linear relationship existed between abundance and depth. Two abundant copepod species, *Plueromamma* spp. and *Oithona* sp., demonstrated a contrasting linear trend between abundance and oxygen; both were observed at high abundances in very low dissolved oxygen. Zooplankton biomass decreased with decreasing oxygen—an observation that may have implications for food webs and carbon transport within oxygen minimum zones.

INTRODUCTION

Oxygen is a key component to geochemical cycling and biological processes, and plays an important role in zooplankton distribution and behavior (Auel and Verheye 2007; Ulloa and Pantoja 2009). Approximately 1.0 mg O_2 L^{-1} is commonly defined in mesocosm and laboratory experiments as a hypoxic condition for zooplankton, although zooplankton species require varying levels of dissolved oxygen to thrive (Breitburg et al. 1997, Auel and Verheye 2007, Larsson and Lampert 2011). The gradient from unlivable conditions to acceptable conditions can be small; a laboratory experiment indicated that copepodids could survive at 1.5 mg O_2 L^{-1}, but could not tolerate an oxygen concentration of less than 1.1 mg O_2 L^{-1} (Auel and Verheye 2007).

Oxygen minimum zones (OMZs) can uniquely affect different species of zooplankton. Some organisms avoid OMZs; an area of low dissolved oxygen in the northern Benguela Current showed a

severe reduction of both the abundance of calanoid copepods and the biomass of mesozooplankton within the oxygen minimum layer (Auel and Verheye 2007). Despite the negative physiological impact hypoxia has on some species (Auel and Verheye 2007), there is evidence of daily migrations of copepods and euphausiids through the OMZ in the Eastern Tropical North Pacific (ETNP) (Escribano et al. 2009). It is evident the OMZ significantly influences the vertical distribution of zooplankton—some may avoid it for physiological reasons, while others may benefit from the lack of predation in areas of low dissolved oxygen (Larsson and Lampert 2011).

The presence of an OMZ may alter the typical trophic dynamics observed in a marine environment, resulting in a shift in community vertical distribution. In a study off northern Chile, an OMZ of 1.0 mL O_2 L^{-1} restricted the vertical distribution of chaetognaths, a voracious zooplankton predator, to above or below the OMZ, indicating no movement across the OMZ (Giesecke and Gonzalez 2004). Known to be a significant predator on copepod communities, a lack of chaetognaths in the OMZ could make a substantial impact on the vertical distribution of those copepods resilient to the low dissolved oxygen levels. Likewise, energy flow pathways have been observed to change (Breitburg et al. 1997; Larsson and Lampert 2011); trophic systems can become dependent on predation rates and distribution influenced by oxygen susceptibilities of species.

Oxygen is a clear influence on the trophic interactions, behavior, and vertical distribution of zooplankton species. Species composition can determine the contribution of exported carbon from zooplankton (Al-Mutairi and Landry 2001)—for example, a study in Norway showed that when the zooplankton biomass was dominated by krill, more than 90% of particulate organic carbon was attributable to zooplankton, whereas when smaller zooplankton like copepods dominated, less than 20% of the particulate organic carbon came from zooplankton (Riser et al. 2010).

Zooplankton species composition in OMZs can be extrapolated to include the future biological implications of decreased oxygen in coastal waters (Doney et al. 2010). Zooplankton taxonomic composition and vertical location in the water column can significantly impact ocean carbon transport, thus biomass calculations are significant in understanding how an OMZ is influencing zooplankton's role in ocean carbon transport.
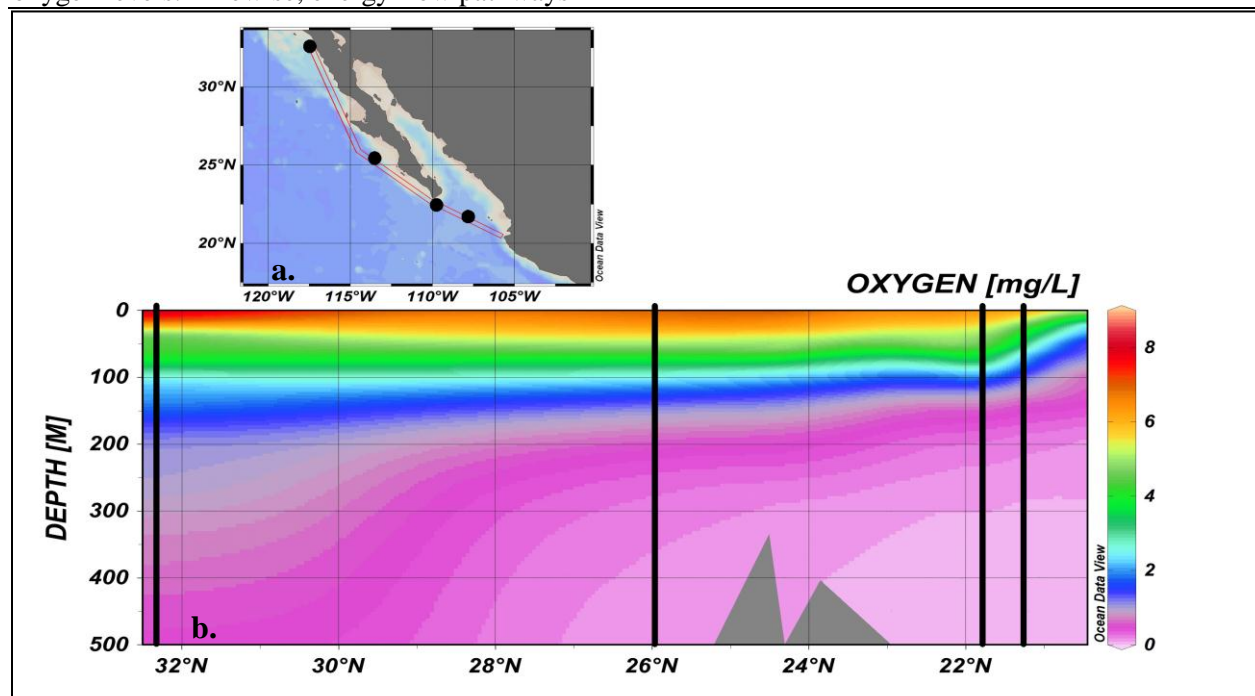

Fig. 1. Map of cruise transect (a) and vertical profile of dissolved oxygen (mg L^{-1}) (b). Vertical black lines and black dots represent zooplankton sampling sites: 2, 5, 26, 32 between San Diego, California and Manzanillo, Mexico.

METHODS

A CTD cast and three to four zooplankton net tows were taken at four locations aboard the R/V *Thomas G. Thompson* between San Diego, California, and Manzanillo, Mexico from 16–27 March 2012 (Fig. 1). A General Oceanics open-closing bongo zooplankton net with a diameter of 60 cm was towed obliquely over depth ranges of 0–50m, 50–150m, 150–300m, and 300–500m. While the net was deployed and retrieved at 30m/min, the R/V *Thomas G. Thompson* moved at ~1 knot to maintain a line angle of ~45°. All samples were taken in the early afternoon to avoid variation caused by diel vertical migration (Escribano et al. 2009). The samples were collected from the nets and preserved in 4–5% formalin solution. Subsamples were then counted and identified, and multiplied by the dilution factor of the subsample to assume a representation of abundance and diversity of each sample. Diversity was measured using the Shannon-Wiener Diversity Index (H) where p_i is the proportion of individuals of species to the total:

$$H = -\sum p_i ln(p_i)$$

Biomass calculations included measuring individual species' prosome length (L) to use in species-specific dry weight (DW) and carbon content (C) equations from previous literature (Table 1). Only the biomass of the most abundant species was calculated (Table 1). It was assumed *Calanus* sp., *Pseudocalanus* sp., *Pleuromamma* spp., and *Rhincalanus* sp. have the same carbon fraction of 44% carbon to dry weight (McCauley 1984).

Table 1. Dry weight and carbon calculations used for individual copepods and chaetognaths.

Organism	Length (μm) (L)	Dry Weight (DW) (μg)	Carbon (C) (μg)
Calanus sp.	3000	$DW = 2 * L^{3.92}$ (J. Keister per. com. from Peterson 1980 PhD thesis)	$C = DW * 0.44$ (McCauley 1984)
Pseudocalanus sp.	2000	$DW = 0.01816 * L^{2.39}$ (J. Keister per. com. from Robertson 1968)	$C = DW * 0.44$ (McCauley 1984)
Pleuromamma spp.	2500	$DW = 18.91 * L^{3.016}$ (J. Keister per. com. from Yamaguchi and Ikeda 2000)	$C = DW * 0.44$ (McCauley 1984)
Oithona sp.	400	--	$C = 10^{(1.45*Log(L)-4.25)}$ (J. Keister per. com. from Uye 1982)
Rhincalanus sp.	6000	$DW = e^{3.061*\ln(L)+2.1224}$	$C = DW * 0.44$ (McCauley 1984)
Chaetognath	6000	--	$C = 10^{3.16*Log(L)-1.29}$ (J. Keister per. com. from Uye 1982)

RESULTS

Starting with Station 2 and moving south towards Station 32, the region of low dissolved oxygen became both shallower and more severe (Fig. 1). Normal oxygen conditions were observed at Station 2 for our 150-300m net tow, however ending with Station 32 only our 0-50m net tow was normoxic.

There was no pattern observed between Shannon Wiener Diversity Index and average oxygen values for each net tow (Fig. 2a). Twelve out of 15 net tows were within one standard deviation, and 14 out of 15 were within two standard deviations for the Shannon Wiener Diversity Index. The primary outlier was the 50 m sample at Station 2—the area with the highest oxygen had the lowest diversity (Fig. 2b).

There was a linear relationship between oxygen and abundance, as well as between oxygen and depth (Fig. 3).

A linear decrease was observed in the combined carbon values of most abundant zooplankton for each station with movement south into the OMZ (Fig 4). This decrease was similarly observed in the average dissolved oxygen for each station from 0-500 m.
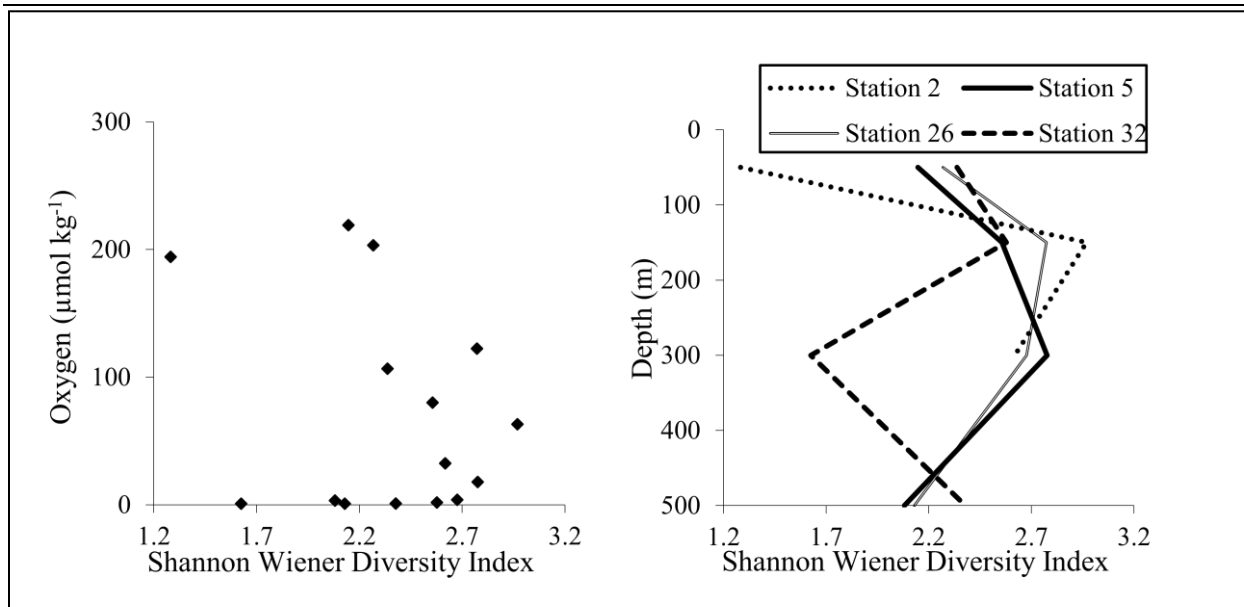

Fig. 2a. Shannon Wiener Diversity Index and average oxygen values (µmol kg^{-1}) for separate net tows.

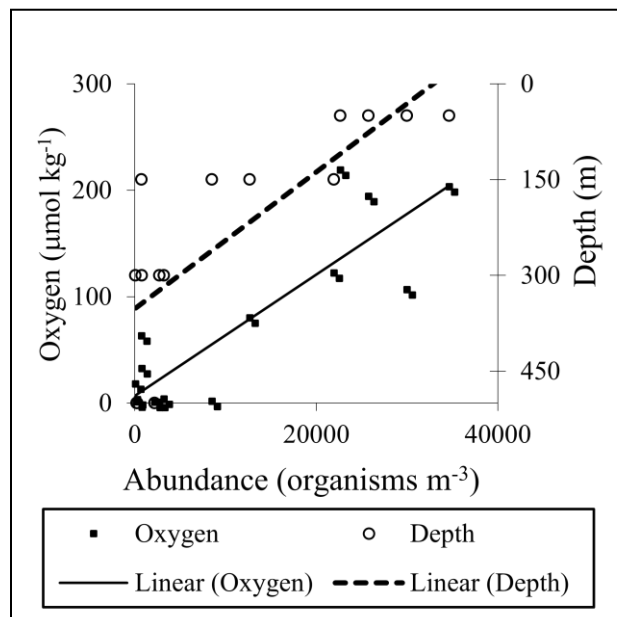Fig. 2b. Depth profile of Shannon Wiener Diversity Index for each station.

Fig. 3. Average oxygen (µmol kg^{-1}), maximum depth (m) per net tow and abundance (organism m^{-3}). Lines represent linear relationships. R^2 values are 0.7689 and 0.6316 for oxygen and depth, respectively.
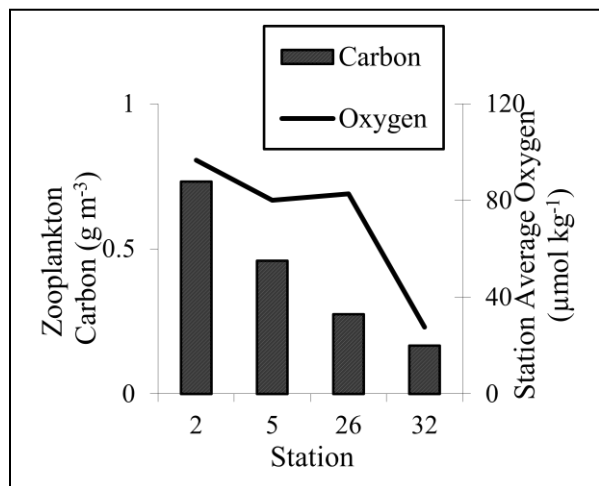

Fig. 4. Carbon from zooplankton (g m^{-3}) and average oxygen per station (µmol kg^{-1}).

The majority of zooplankton identified showed increasing abundance with increasing dissolved oxygen (Fig. 5). However, *Pleuromamma* spp. and *Oithona* sp. show anomalously high abundances at very low oxygen values. *Pleuromamma* spp.'s peak abundance of
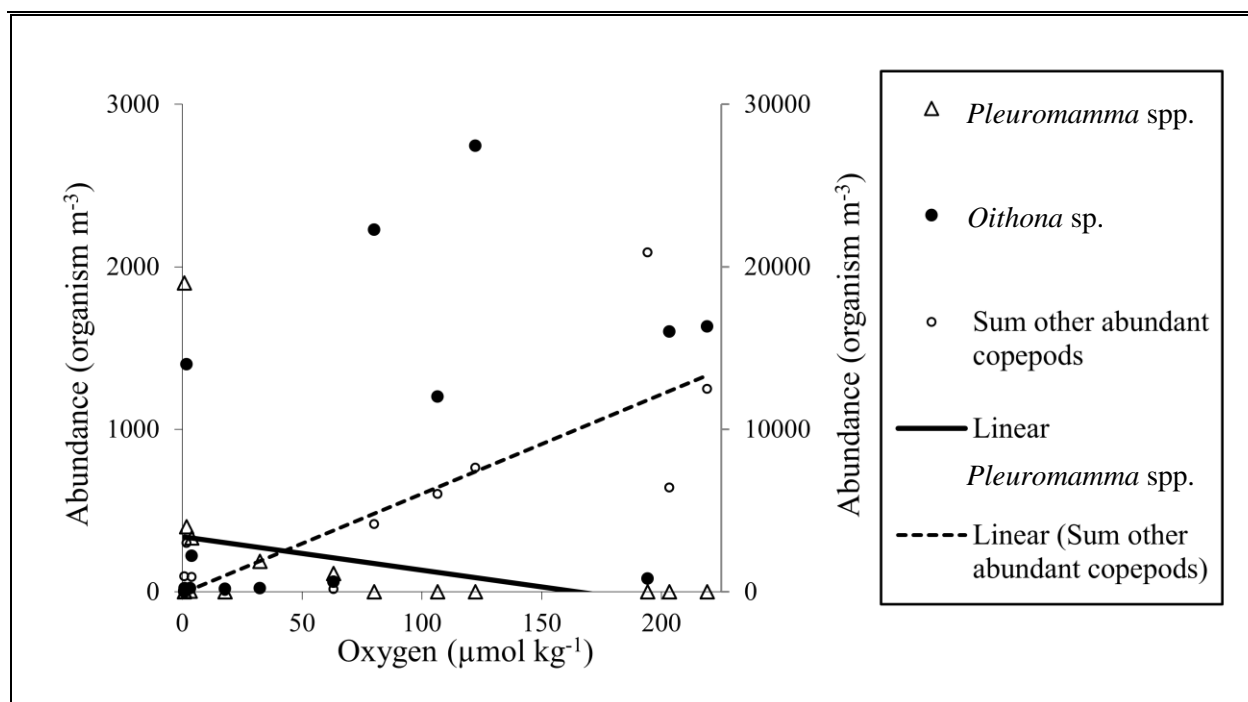
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Fig 5. Abundance of individual organisms vs. oxygen. Both *Oithona* sp. and *Pleuromamma* spp. were observed at high abundances at very low levels of oxygen

1900 organisms/m^3 was observed at 0.92 μmol O$_2$ kg^{-1}; it was not present at any normoxic conditions. *Oithona* sp. and *Rhincalanus* sp. were present in samples of both low and high oxygen; however, *Rhincalanus* sp. numbers were very low in comparison to surface samples.

It should be noted that particularly high levels of lipids within *Calanus pacificus* were observed at Station 2 from 50-300m, while these high levels of lipids were not seen in *Calanus pacificus* at other locations.

DISCUSSION

Diversity

No correlation was observed between diversity and oxygen (Fig. 2a); thus, there was no indication that oxygen played a prominent role in determining the diversity distribution of zooplankton communities. However, the lowest diversity, by a substantial margin, was observed at the surface at Station 2 (Fig. 2b), indicating that higher oxygen levels throughout the water column may decrease diversity. Fewer species in greater

abundance dominated in these areas, while more species at lower abundances dominated in the deeper, less oxygenated waters. The lower oxygen levels may be decreasing predation, and those species that can survive in hypoxic conditions may be utilizing it as a protection from predators that must avoid hypoxic waters for their own fitness (Larsson and Lampert 2011; Breitburg et al. 1997).

Abundance

Abundance showed linear relationships with both depth and dissolved oxygen—however, because the R^2 value relating oxygen and abundance (0.7689) was higher than that of depth (0.6316), we might infer that oxygen influenced abundance, and possibly influenced it more than depth (Fig. 3). If zooplankton distribution is determined by oxygen there are implications for the horizontal distribution of zooplankton, diel vertical migration (DVM), carbon transport, diapause, and predation patterns.

Oithona sp. and *Pleuromamma* spp. displayed exceptions to the general trends of abundance versus oxygen; both were abundant at

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very low levels of oxygen (Fig. 5). *Pleuromamma* spp. demonstrated a linear trend negative to that of other abundant zooplankton. Similarly, *Oithona* sp. was abundant at low oxygen levels despite documented reduced survival and fecundity in hypoxic conditions (Roman et al. 1993). *Oithona* sp. has lower metabolism than calanoid copepods (Almeda et al. 2011); a higher tolerance to low oxygen conditions explains the ability of *Oithona* sp. to live in a range of dissolved oxygen concentrations (Fig. 5). Potential benefits to living at depths, such as predator or UV radiation avoidance, or reduced metabolism in colder temperatures, must have been greater for *Pleuromamma* spp. and *Oithona* sp. than any adverse effects experienced from low dissolved oxygen concentrations.

Zooplankton abundance was highest near the surface during the day, which may signify suppressed DVM due to the OMZ. The consistent day sampling of my study does not allow for DVM analysis; however, because previous studies have shown that low oxygen can inhibit DVM, this process or lack thereof must be considered as an ecological impact of low oxygen (Auel and Verheye 2007). *Pleuromamma* spp., abundant at depths during the day, was likely participating in DVM (Buskey et al. 1989). DVM can be extremely important for zooplankton success, and has subsequent impacts on marine ecosystems and carbon cycling (Berge et al. 2008). In fact the largest coordinated movement of biomass on the planet is attributed to DVM; an OMZ inhibiting this vital process due to zooplankton physiological intolerances may be incredibly influential on ecosystem dynamics and transportation of carbon from surface waters to the deep. Furthermore, *Oithona* sp. and *Pleuromamma* spp., abundant in the OMZ, were relatively small in comparison to larger species such as *Rhincalanus* sp., other *Calanus* spp., or chateognaths. When studying carbon cycling, it is significant to consider the patterns of those organisms with the largest amount of biomass—very small organisms such as *Oithona* sp. may prove to be insignificant carbon transporters both due to their small carbon content and their relatively short DVM (*Oithona* sp. length was 6-20% of other abundant copepods observed (Table 1)).

While no explicit lipid analyses were conducted, lipid-rich *Calanus pacificus* were abundant between 50-300m at Station 2. Diapause, a form of overwintering that is commonly associated with high lipid content for energy storage in copepods, has been observed in this species (Alldredge et al. 1984). Diapause commonly occurs at colder deeper locations in the water column as the temperature can allow for reduced metabolic maintenance (their lipid stores can last longer), and predators are fewer in deeper waters (Alldredge et al. 1984). In the Santa Barbara Basin, these diapausing copepods were observed in abundance at low levels of oxygen (0.2 ml O_2 L^{-1}), but ceased to occur in regions where the water became nearly anoxic (Alldredge et al. 1984). Comparatively, I observed these lipid-rich copepods before the oxygen levels at depth became close to anoxic. It can hesitantly be concluded from the absence in hypoxic samples that the extremely low levels of oxygen hinder or even prevent the over-wintering process of this copepod species, a serious implication for the life cycle of *Calanus pacificus*. However, it should be noted that groups of diapausing copepods also exhibit patchiness (Alldredge et al. 1984); our nets could have easily missed diapausing copepods in anoxic regions.

Chateognaths in the ETNP have been documented to remove as much as 6% of the copepod stock in the spring, focusing on and removing 20% of such copepod species as *Centropages* sp. and *Corycaeus* sp. (Giesecke and Gonzalez 2004). Chaetognaths, *Centropages* spp. and *Corycaeus* sp. were all observed to increase in abundance with increasing oxygen concentrations in my study; likewise, Giesecke and Gonzalez (2004) found particular species of chaetognath to be found exclusively above or below the OMZ. My study did not sample below the OMZ due to time constraints, but based off of this previous study, which found chaetognaths at depth, it can be concluded that their vertical distribution was attributed to oxygen values rather than simply depth. Acting as considerable predators for copepods, it is possible that species such as *Oithona* sp. and *Pleuromamma* spp. chose to live in the low oxygen areas to avoid predation from chaetognaths.

Carbon

There was a distinct correlation between carbon content of zooplankton at each station and average dissolved oxygen at each station (Fig. 4). This decline in carbon within the OMZ has implications for the carbon cycle, the food web, and future oceans. As previously discussed, abundant, active (participating in DVM) zooplankton are key contributors to carbon transport—the clear decrease in zooplankton carbon observed in the OMZ indicates how OMZs are decreasing zooplankton involvement in carbon transport.

With most species of zooplankton avoiding OMZs, the base level of the food chain is depleted. Essentially, there is less carbon available within the OMZ for uptake by small fish or other zooplankton. Furthermore, many fish that are intolerant to hypoxic conditions also avoid OMZs (Breitburg et al. 1997). With such physiological intolerances common in these marine ecosystems, OMZs can create huge dead-zones of reduced habitat where very little phytoplankton energy is transferred trophically. OMZs are predicted to increase in size and severity from anthropogenic impacts (Doney 2010); less zooplankton biomass in these regions may become more of a severe issue in the future as OMZs expand.

While my study was widespread in its analysis of oxygen's influence on zooplankton communities, further studies could supplement this topic. Sampling on a temporal scale (both day/night and seasonal) could provide insights into DVM and diapause. Additionally, towing the zooplankton net at different speeds may allow for reduced avoidance from faster organisms and better sampling of gelatinous organisms.

CONCLUSIONS

- Oxygen appeared to have little effect on zooplankton diversity; however a decreased diversity seen in regions of high dissolved oxygen may indicate OMZs were used by zooplankton as refuges from predators.
- Abundance was linearly related to both dissolved oxygen and depth.
- *Pleuromamma* spp. displayed negative abundance trends to other abundant species.

This is likely due to a persistent DVM despite possible physiological adversities experiences from low oxygen concentrations.
- *Oithona* sp. was observed at high abundances in anoxic conditions, which is likely attributed to a particularly low metabolism that allows for success in OMZs.
- DVM may be inhibited by the OMZ.
- Diapause may have been restricted in the anoxic regions of the OMZ, based on abundant lipid-rich copepods found at depth at Station 2 but not elsewhere.
- Lack of chaetognaths in the OMZ may decrease predation on copepods, and therefore make the OMZ a superior habitat for copepods able to withstand low levels of oxygen.
- Zooplankton carbon is reduced with movement south into the OMZ. A decrease in carbon content has significant implications on the food web and carbon cycling.
- OMZs are predicted to increase in future oceans, making my zooplankton study a model for potential zooplankton communities in the future.

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