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# Impact of hypoxia on the vertical distribution of jellyfish in the Eastern Tropical Northern Pacific

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## NONTECHNICAL SUMMARY

Baja Bay, located on the western coast of Mexico, is known for having water that has low levels of dissolved oxygen. While many organisms in the ocean cannot survive without oxygen, some jellyfish have the unique ability of being able to live in bodies of water that have low oxygen. However, the presence of jellyfish can be detrimental for marine habitats. Jellyfish tend to take over marine food webs and drive away most other marine organisms, which can also be detrimental to fishing industries and affect human businesses. In order to better understand how jellyfish react to low oxygen environments, I studied the abundance of jellyfish were at different depths in the Eastern Tropical North Pacific. I did this by collecting samples using a zooplankton net and counting them under a microscope. I then compared my results to oxygen levels from the different depths I sampled. I predicted that jellyfish would be more abundant at deeper depths where there were lower levels of oxygen, but found that they actually more abundant in the oxygen rich surface water. While my prediction was wrong, the numerous quantities of jellyfish in Baja Bay may be a sign that the health of the marine ecosystem in that area is deteriorating.

## ABSTRACT

Jellyfish are primarily carnivorous zooplankton and consist of many taxa that are known for their tolerance of hypoxic conditions – Siphonophora, Thaliacea, Ctenophora and Hydromedusae. In oxygen minimum zones (OMZs), jellyfish abundance has been observed to increase relative to oxic water (>1.1 mg O2 L-1) due to this ability to adapt to low oxygen stress. The presence of jellyfish, however, tends to disrupt the carbon transport between trophic levels, simplifying the marine food web in that area and causing larger predators to be driven out. Commercialized fishing industries are negatively impacted by this. Studying the vertical distributions of jellyfish in OMZs and how they interact with the oxygen minimum layer (OML) may help researchers get a better understanding of the carbon cycle and how it may change with future climate change. This research tract took place in late March between San Diego, CA and Manzanillo, Mexico. Depth stratified zooplankton samples were taken at stations of varying oxygen levels using bongo nets. Jellyfish abundances were then calculated at each depth. The average abundance of jellyfish decreased with depth from 8,430 (org.*1000 m-3) at the 0-50 m depth layer to 26 (org.*1000 m-3) in the OML (300-500 m). Feeding on anoxic intolerant prey and the inability tolerate hypoxia indefinitely may explain this avoidance of the OML. In order to assess the health of the Eastern Tropical Northern Pacific ecosystem, further jellyfish distribution studies will be needed to determine if their abundance is increasing.

Compared to other zooplankton species, jellyfish are a unique group of organisms. Not only are they primarily carnivorous, but several taxa, such as Siphonophora, Thalicea (Salps), Hydromedusae and planktonic members of Ctenophora, may be tolerant of hypoxic conditions (<1.1 mg O2 L-1) where other zooplankton would die (Mills 2001; Thuesen et al. 2005; Elliot et al. 2012). The mechanisms behind their low-oxygen tolerance are not well known, but some researchers believe it is due to a combination of reduced oxygen utilization when subjected to hypoxia and the ability of their gelatinous tissue to store oxygen.

Jellyfish also play a critical role in the transport of carbon throughout the ocean and the marine food web. Since they have very few predators and are not hindered by commercialized over-fishing, jellyfish are able to grow and expand with little restriction (Condon et al. 2010). In doing so, they take up a significant amount of carbon as biomass, the majority of which is consumed by bacterioplankton while only a small percentage of that carbon is transported to the higher trophic levels. In essence, jellyfish create a “dead end” in the marine food web and limit the amount of carbon available to higher trophic predators.

In the tropical regions of the ocean there are areas of hypoxic water are known as oxygen minimum zones (OMZs) (Stramma et al. 2008). These OMZs consist of a hypoxic layer of water located at intermediate depths in the water column known simply as the oxygen minimum layer (OML) (Childress and Seibel 1998). Very low biomass and animal diversity are found in OMLs and only organisms capable of efficiently utilizing low oxygen are able to survive (Childress and Seibel 1998). With the predicted rate of climate warming over the next hundred years, Breitburg et al. 2010 believe that the hypoxia in the worlds’ oceans will only worsen due to water-column stratification and reduced oxygen solubility, causing oxygen minimum zones to become more common and OMLs to expand in the water column. As a result of this future hypoxia, the diversity of the marine food webs may be reduced as jellyfish and other hypoxia tolerant organisms increase in abundance and dominance, driving out the bigger apex predators in regions of low oxygen due to a reduced food supply (Childress and Seibel 1998; Jackson 2008). This simplification of the food web will also cause major problems on human activities, such as fishing and tourism (Condon et al. 2010).

Many researchers believe that jellyfish have the potential to greatly impact the future of the world’s oceans because of their ability to tolerate hypoxic conditions and their effect on the distribution of carbon in the carbon cycle. Vinogradov et al. 1985 observed that ctenophores in the Black Sea were mainly concentrated between 50 to 150 m depth. However, there have been discrepancies among researchers about where jellyfish are most abundant in the water column. Vinogradov 2003found siphonophores and other jellyfish increase in abundance at mid and deep depths near 1000 m. The variation in jellyfish distribution between the two studies is heavily influenced by dissolved oxygen levels in the water column.

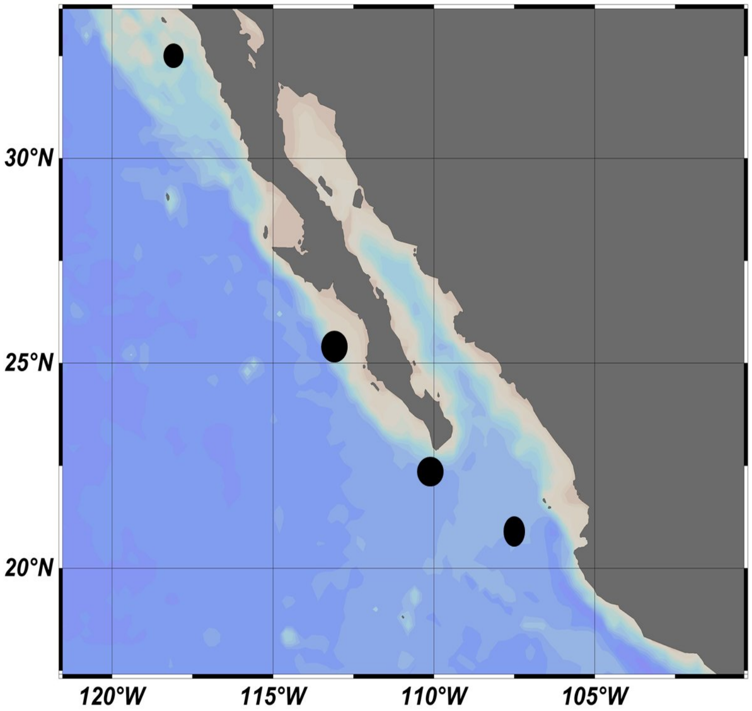

Fig. 1. Map of study area. Black dots indicate study sites. Stations go in order from Station 1 in the north to Station 4 in the furthest south.

Table 1. The dates, locations and depth ranges of the four survey sites on the transect from San Diego, CA to Manzanillo, Mexico.

| Station | Date | Location | Depth Ranges |
|---|---|---|---|
| 1 | 17-Mar | 32° 36.2 N, 117° 28.5 W | 0-50, 50-150, 150-300 m |
| 2 | 19-Mar | 25˚ 11.9 N, 113˚ 06.02 W | 0-50, 50-150, 150-300, 300-500 m |
| 3 | 23-Mar | 21˚ 44.3 N, 108˚ 26.7 W | 0-50, 50-150, 150-300, 300-500 m |
| 4 | 24-Mar | 21˚ 11.5 N, 107˚ 7.3 W | 0-50, 50-150, 150-300, 300-500 m |

In the waters of the Eastern Tropical Northern Pacific (ETNP) there is a well-documented OMZ with an OML that expands nearly1000 m in depth (Cartapanis et al. 2011). Dense populations of jellyfish have been recorded in the ETNP near Manzanillo, Mexico (Segura-Puertas et al. 2010). To determine how the vertical distribution of jellyfish is affected by hypoxia, an experiment was conducted to explore whether they are consistently more abundant in OMLs than normoxic water on the western coast of Mexico. Since jellyfish have the ability to adapt to low oxygen environments, the prediction was made that their abundance would increase in the OML where they could avoid predators and prey upon smaller zooplankton. Siphonophora, Thaliacea (Salps), Ctenophora and Hydromedusae were the main focus of the study as they are common in OMZs (Mills 2001, Elliot et al. 2012). Studying how jellyfish respond to low oxygen environments may give researchers a better understanding of how jellyfish populations might change in the future and possible impacts that will have on marine ecosystems and the carbon cycle.

## METHODS

Zooplankton samples were taken March 17-25, 2012 aboard the R/V Thompson. The cruise took place on a transect between 32.7 N, 117.3 W and 18.9 N, 104.4 W, including Baja Bay and the coast of Manzanillo, Mexico. An opening-closing Bongo net (0.6 m net diameter, 335 μm mesh) was hauled obliquely at a ship speed of 1 knot at four survey sites across four separate depth ranges (Table 1). A flowmeter was attached inside of one of the nets to measure the volume of water filtered. Prior to dropping the Bongo nets, the depth of the oxygen minimum layer was calculated using a Seabird conductivity temperature and density (CTD) to determine the depth ranges that were sampled. Samples were only taken during the daytime to negate the effect of diel-vertical migration.

On board the ship, zooplankton samples were sieved with a 335 μm mesh and preserved in 5% buffered formalin. Jellyfish were separated from the other zooplankton and counted using a dissecting scope. For a majority of the jellyfish counted, genus and/or species was determined and recorded with the aid of the World Register of Marine Species and Marine Species Identification Portal databases. Using volume data from the flowmeter, the counting results were converted into # of organisms*1000 m-3.

Diversity and evenness was measured using the Shannon-Wiener Diversity Index:

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

$p_i$ is the proportion of individuals of species to the total. The Shannon index is a measure of diversity that takes into account species richness and proportion of species. Species evenness is a measure of how well abundance is distributed among species within a community (Wilsey and Potvin 2000).

In order to determine if the trends found in the jellyfish were unique among the zooplankton in that region, the vertical distribution of jellyfish were compared to that of zooplankton in the region collected by Martha James.

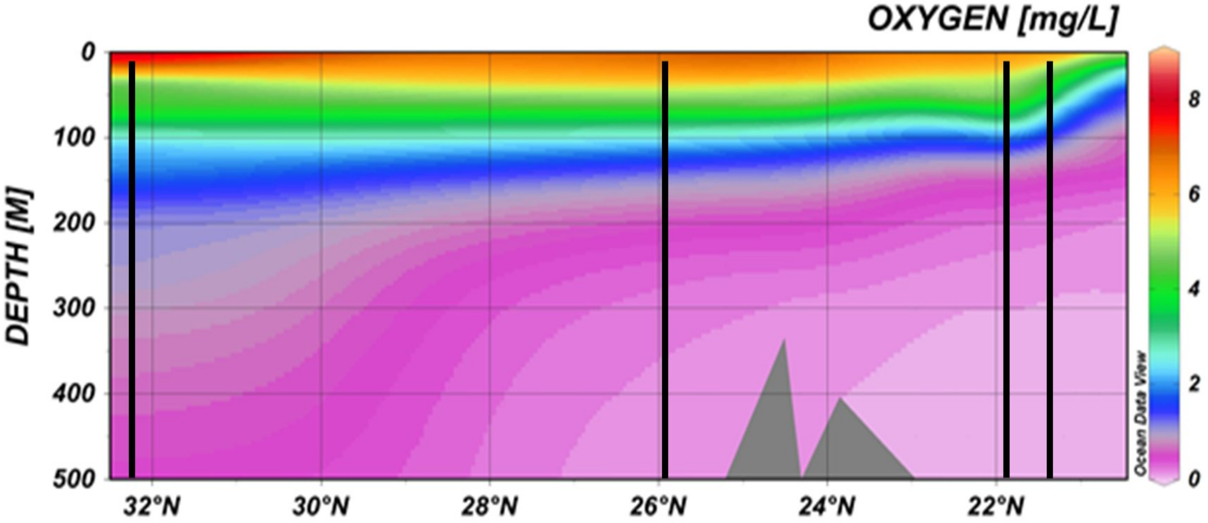

Fig. 2. Vertical profile of dissolved oxygen along the cruise tract and a map of the cruise transect. The vertical black lines on oxygen profile indicate the locations of the four sample sites.

## RESULTS

### *Oxygen*

From 32˚N to 20˚N the dissolved oxygen (DO) data shows that the depth at which the water column became hypoxic shoaled towards the south of the transect (Fig. 1). At Station 1, off the coast of San Diego, DO reached 1.1 mg O2 L-1 around at a depth 243 m. Station 1 had the deepest layered of oxygenated water (<1.1 mg O2 L-1). DO at Station 4 reached the hypoxic level at 45 m, a shoaling of nearly 200 m between Stations 1 and 4. The hypoxia depth for Stations 2 and 3 were similar. The surface DO also showed variability, ranging from a maximum of 8.3 mg O2 L-1 at Station 1 to minimum of 6.5 mg O2 L-1 at Station 3.

### *Abundance*

The jellyfish taxa that were collected consisted of Siphonophora, Thaliacea (Salp), Hydromedusae and Ctenophora. Siphonophora were the most commonly collected taxa, being found at every depth range at every station recorded (Fig.3). Ctenophora were only found at three stations and limited to the 50-150 m depth range and 0-50 m at Station 1. Thaliacea showed the widest abundance range. The lowest Thalicea abundance was recorded between 300-500 m at Station 4 (86 org.*1000 m-3), whereas the highest (29, 900 org.*1000 m-3) occurred between 0-50 at Station 2 (Fig. 3). Hydromedusae and Ctenophora displayed the lowest abundance range with only a 1,310 (org.*1000 m-3) difference between the highest and lowest measured. They also had the lowest total abundances in this region with 10,760 (org.*1000 m-3) and 2,090 (org.*1000 m-3) respectively.

Generally, the abundance of each taxa decreased with depth (Fig.3). The average combined abundance of jellyfish in the surface (0-50 m) layer for all the sample sites was 8,430 (org.*1000 m-3) while the average abundance for the deepest (300-500 m) layer sampled was 26 (org.*1000 m-3). The only exceptions to this observation were Thaliacea and Siphonophora at Station 1, which increased in abundance from the 50-150 m to 150-300 m depth.

Additionally, the jellyfish abundance was severally reduced at Station 1 compared to the other stations (Fig. 3). The total jellyfish abundance at Station 1 for 0-300 m depth reached only 2,460 (org.*1000 m-3). The overall abundance of jellyfish at Station 2 for the same depth range was 73,900 (org.*1000 m-3), more than 30 times greater. The count data also revealed that several species/geneses were particularly abundant in the ETNP.

Lensia, Doliolum, Thalia democratica, and Muggiaea made up for 73.3% of the total

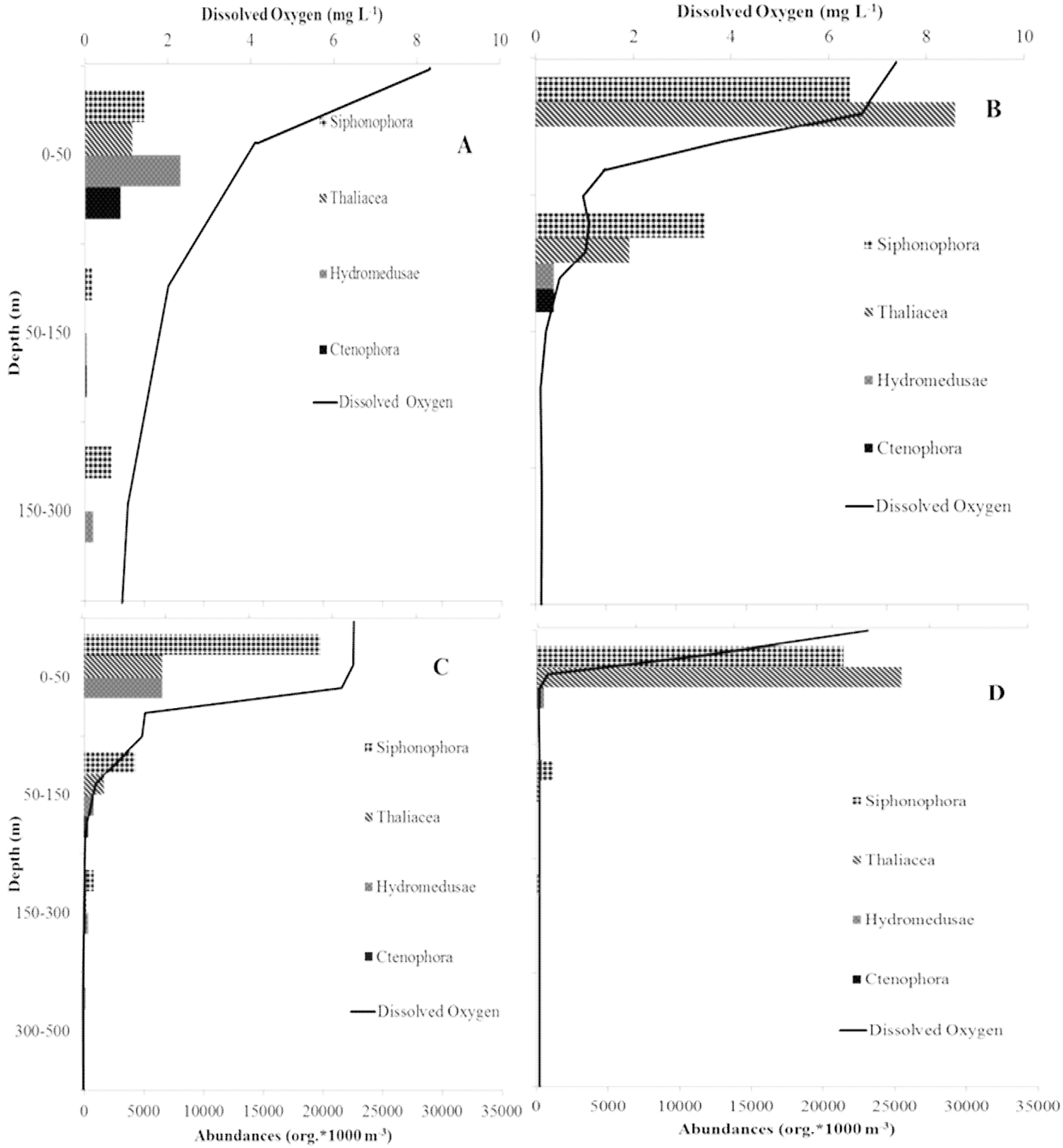

Fig. 3. The vertical distribution of jellyfish abundance plotted against the oxygen profile at A) Station 1 off the coast of San Diego. The scale for abundance at this station was amplified 10x B) Station 2 at 26° N near Soledad Basin C) Station 3 near the tip of Baja peninsula D) Station 4 in the middle of Baja Bay.

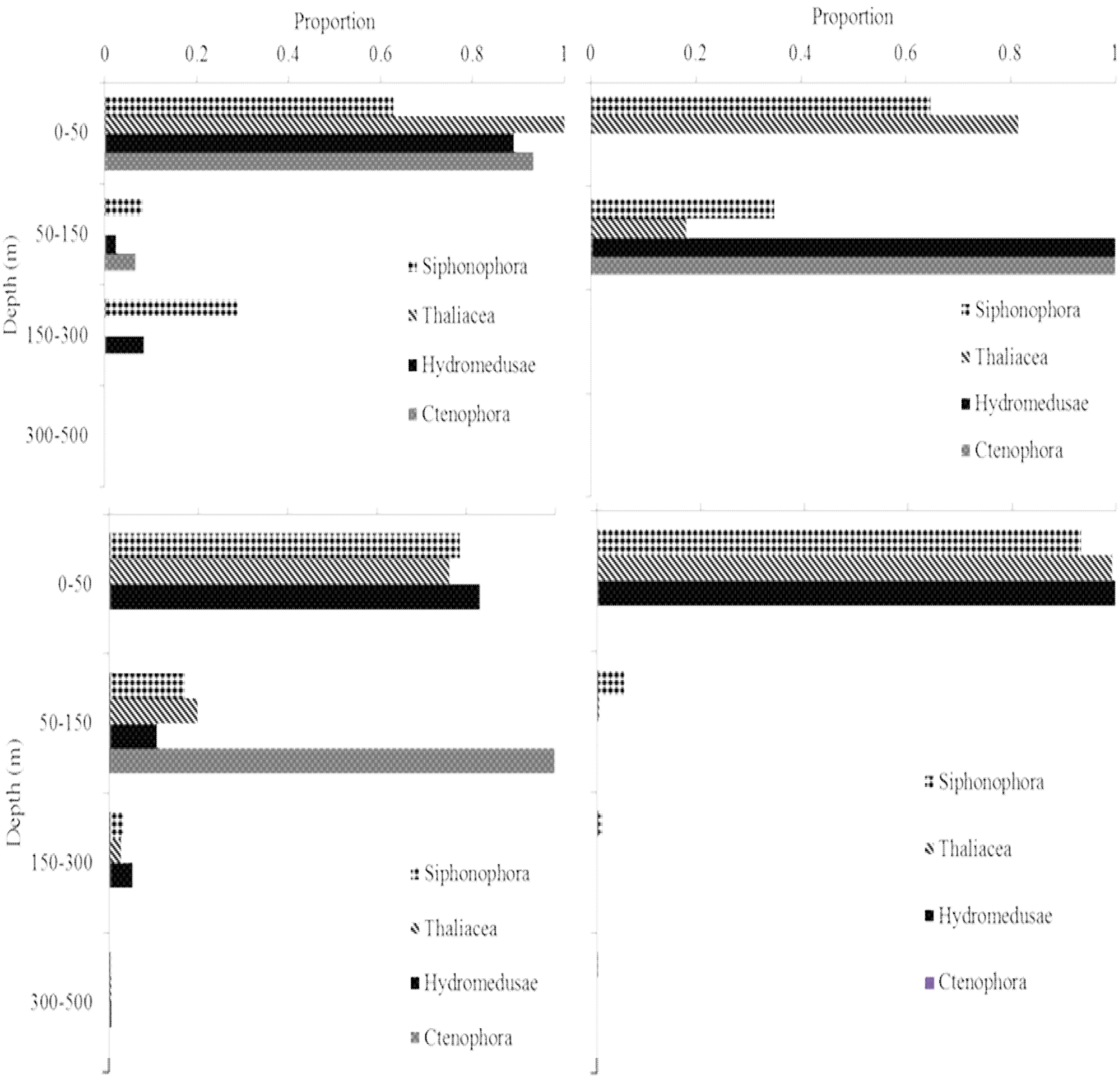

Fig. 4.The proportion of jellyfish taxa abundance at each depth layer relative to the entire water column at each station.

abundance for all stations (Table 2). These species/geneses were also found at at least three of the four sample sites and were most abundant in the 0-50 m. In fact, the majority of the species/geneses sampled were abundant in the 0-50 m depth layer. L. tetraphylla, Beroë, and S. bitentaulata were the only exceptions (Table 2). L. tetraphylla and Beroë were most abundant in the 50-150 m depth layer while S. bitentaulata was only found at 300-500 m depth.

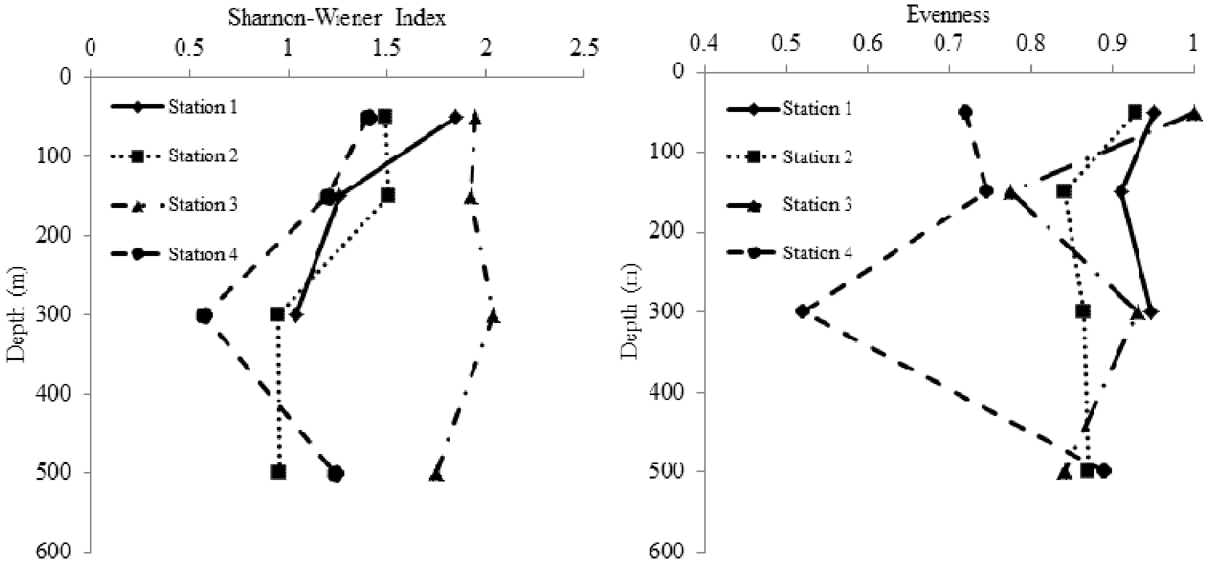

Fig. 5. Shannon diversity index (left) and Evenness (right) for all stations plotted against depth.

The proportion of Siphonophora in the 0-50 m depth layer increased in the later stations (Fig. 4). At Station 1 the proportion of Siphonophora in the surface layer was 0.628 and increased to 0.932 at Station 4. No other taxa displayed this similar trend. However, at Station 4, the proportion of Siphonophora, Thaliacea and Hydromedusae were largest in the surface layer. This result differs from every other station sampled.

*Diversity*

At most stations, diversity decreased with

Table 2. List of genus/species name, taxonomic group, stations found at, average abundance each genus/species for all stations, min and max abundance, percent of total jellyfish abundance and depth layer of greatest abundance for the most common jellyfish collected at sample sites.

| Genus/Species | Common Name | Station | Avg. Abundance (org./1000 m$^3$) | Min-Max Abundance | % Total Jellyfish Abundance | Most abundant depth layer |
|---|---|---|---|---|---|---|
| Lensia | Siphonophore | 1, 2, 3, 4 | 10,550 | 13.1 - 11,194 | 25.2 | 0-50 m |
| Doliolum | Doliolid | 1, 2, 3, 4 | 7,175 | 0 - 18,657 | 17.1 | 0-50 m |
| Thalia democratica | Salp | 2, 3, 4 | 7,100 | 0 - 23,200 | 16.9 | 0-50 m |
| Muggiaea | Siphonophore | 1, 2, 3, 4 | 5,925 | 0 - 7,540 | 14.1 | 0-50 m |
| Dioletta gegenbauri | Doliolid | 2 | 2,800 | 0 - 11,194 | 6.67 | 0-50 m |
| Geryonia | Hydromedusa | 3 | 1,703 | 0 - 6,600 | 4.1 | 0-50 m |
| Liriope tetraphylla | Hydromedusa | 1, 2, 3 | 670 | 0 - 1,343 | 1.6 | 50-150 m |
| Beroë | Ctenophore | 1, 2, 3 | 329 | 0 - 1,343 | 0.78 | 50-150 m |
| Solmundella bitentaulata | Hydromedusa | 3 | 136 | 0 - 546 | 0.32 | 300-500 m |

depth (Fig. 5). The diversity at Station 4, however, increased dramatically from 0.57 at 150-300 m to 1.23 at 300-500 m depth. The highest index value, 2.04, was found at Station 3 at the 150-300 m depth layer while a minimum of 0.57 occurred at Station 4 at the same depth.

Although there was no visible trend in the diversity index from north to south, there was an apparent decrease from Station 3 to Station 4 (Fig. 5). Station 3 had the highest overall diversity index of 2.3. The lowest calculated Shannon-Wiener index was seen at Station 4 with 1.5, a decline of 0.8 from the previous station. The increase in the diversity index seen at Station 4 was the result of a small sample size and is misleading. A similar decreasing pattern with depth was found in the evenness data as well (Fig. 5). Stations 1, 2 and 3 each displayed an overall decrease in evenness with depth. However, like the diversity index, there was an increase of 0.52 to 0.89 for Station 4 at the 150-300 m to 300-500 m depth layers, respectively.

## DISCUSSION

The prediction that greater jellyfish abundance would be recorded in the OML was bit substantiated by the dissolved oxygen and count data. As the sample sites progressed south and came closer to the OMZ in Baja Bay, the shallower the hypoxic (<1.1 mg $O_2$ $L^{-1}$) depth became in the water column (Fig. 2 and 3). From this trend, the OML expanded within the water column in the more southern stations. In addition, jellyfish became less prevalent at those stations (Fig. 3). The overall abundances of jellyfish were mainly concentrated to the top 50 m of the water column. By Station 4, where the OML began at 50 m depth the abundance of jellyfish in the 50-150 layer (mid layer) was 15 times lower than the abundance of that same depth layer at Station 2. The top of the OML at Station 2 only reached up to a depth of 110 m. The jellyfish in the ETNP, particularly among Siphonophora and Thaliacea, avoided the hypoxic water, despite their reported hypoxia tolerance (Theusen et al. 2005).

It is important to note that jellyfish abundances have been found to fluctuate with climatic cycles and jellyfish blooms tend to occur in late spring and early summer (Purcell et al. 2007). This cruise took place in late March, so it is possible that a jellyfish bloom had not taken place yet. A bloom may have resulted in more anoxic tolerant jellyfish species being present in the region and affecting the overall vertical distribution.

Station 1 had originally been intended to serve as a control site for vertical distributions of jellyfish in oxygenated water because the OML is thinner there (Fig. 3a). Upon review of the data, however, some anomalies became apparent at this site. The gross jellyfish abundance was 30 times smaller than that found at Station 2, which had the largest total abundance (Fig. 3b). Station 1 was also located off the coast of San Diego, CA. The California Current is strong on the coast and the jellyfish at this station may have been subject to different oceanographic stresses, affecting their vertical distribution. Sampling in international waters north of 26˚N was prohibited, but sampling in those waters may have given more coherent results.

Previous studies have also observed that jellyfish tend to limit their migration to oxygenated surface water. Vinogradov 2004 studied the vertical distribution of jellyfish in North Atlantic oxygenated water columns and found that Siphonophora abundance peaked at 650 m depth and inhabited depths as deep as 2000 m. This trend was partly due to an insurgence of oxygenated water from the Labrador Sea. In Norway where the water is oxygen rich, Periphylla periphylla abundance reached a maximum at 300 m depth (Bamstedt et al. 2003). In regions of the ocean where the DO levels remain relatively high, jellyfish are able survive at deeper depths. However, in the ETNP where DO reaches nearly zero mg $O_2$ $L^{-1}$ with depth, jellyfish were concentrated in the surface waters.

Causes for the concentrated abundance of jellyfish in the surface 50 m include predatorial habits. Jellyfish feed primarily on small zooplankton, such as copepods (Peng and Dabiri 2009). On this same research cruise, another researcher (Martha James) found that the copepods in the ETNP were most abundant in the top 50 m of the water column – mirroring the jellyfish. Several species of copepod cannot cope with low oxygen stress and remain only in the surface 0-50 m depth layer where DO remains above hypoxic conditions. This similarity in vertical distribution between predator and prey suggests that jellyfish distribute themselves in the water column where it is most beneficial for them to feed.

In addition, on further inspection of the oxygen storage capacities of gelatinous bodies, it would appear that while jellyfish are tolerant of low oxygen water, they are not immune to it. Even jellyfish that are tolerant of anoxic water, if they are subject to hypoxia for long enough, can die from oxygen depletion in their body (Thuesen et al. 2005). Even though jellyfish can migrate through and hunt for prey in even severely hypoxic water for several hours, they would not be able to live in those conditions indefinitely.

The proportion data also supports these feeding habit and hypoxia theories. Siphonophora abundance became more concentrated in the surface layer in the areas where the OML was largest (Fig. 4). Additionally, the overall jellyfish abundance at Station 4, where the OML was the largest, was limited to the surface layer. Jellyfish following their hypoxia intolerant prey could explain this shift in abundance towards the surface. Their inability to live in anoxic water permanently would also explain the shift. Of all the jellyfish taxa, Siphonophora are the least suited to survive in the OML.

On the other hand, certain jellyfish species collected were better adapted to the anoxic conditions of the OMZ than others. Every genus/species collected within the Siphonophora and Thaliacea taxa were most abundant in the surface layer (Table 2). However, L. tetraphyla (Hydromedusae), Beroë (Ctenophora), and S. titantaulata (Hydromedusae) were three of the most common jellyfish species collected but they were mainly found in the mid and deep layers. These distributions, which differed from those of Siphonophora and Thaliacea, could be related to their feeding habits. Migrating into the OML allows those species to avoid predators, while moving up the water column into oxygenated water permits them to find prey. Further study of the diel-vertical migration patterns of jellyfish in the ETNP will be needed to test this hypothesis.

The diversity profiles also support the idea that there is variability in hypoxia tolerance among jellyfish. At nearly every station, the Shannon-Wiener diversity index and evenness decreased with depth (Fig. 3). This decreasing trend shows that as the DO decreased, there was a decrease in the jellyfish diversity. Only the jellyfish capable of handling such low oxygen levels inhabited the lower depth layers, such as Ctenophora who can regulate their oxygen utilization (Childress and Seibel 1998).

While the vertical distribution of jellyfish in the ETNP did not follow the predicted model, some researchers suggest that it is not the distribution but the excessive abundance of jellyfish that is most important in assessing ecosystem health. Areas in the ocean where the environment has been damaged by processes such as hypoxia, warming, acidification and/or overfishing are commonly referred to "dead zones" (Jackson 2008). These dead zones are marked by an increasing abundance of jellyfish and other diverse microbes as they are the only organism able to endure such harsh circumstances. Since an increase of jellyfish abundance over time is an indicator of marine food web and ecosystem health decline, more observational research tracts through the ETNP will be needed to measure the temporal change in abundance. The impacts climate change has had on the biological habitat in this region can be better gauged at that time.

## CONCLUSIONS

- From 32°N to 21°N, oxygen decreased and the OML expanded vertically, resulting in a shoaling of hypoxic water from 250 m to 50 m.

- On average, highest jellyfish abundances were not associated with hypoxic water; abundances averaged 400x higher in the surface layer than in the deep, hypoxic layer. Feeding habits and inability to survive in severe hypoxic water could be explanations.

- The proportion of Siphonophora in the surface layer increased where the OML was the widest, suggesting an inability to thrive in hypoxic water.

- Siphonophora and Thaliacea are the most abundant jellyfish in the ETNP; they made up for the majority of jellyfish collected.

- The large abundance of jellyfish may indicate deterioration of ETNP ecosystem. Future cruises are needed to measure temporal change of jellyfish.

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