



Expanse of the oxygen minimum zone and denitrification in the eastern tropical North Pacific

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NONTECHNICAL SUMMARY

The oxygen concentrations in the eastern tropical North Pacific (ETNP) are quite anomalous; waters ranging from approximately 300 to 1000 meters have very low amounts of oxygen, some even having no oxygen at all. This zone, defined as the oxygen minimum zone or OMZ, has a large impact on the distribution of macro- and microscopic organisms which makes it quite important to define the extent of this water mass in the water column. In order to determine the OMZ's location in the water column, water samples were collected using a CTD which obtained sealed water containers at various depths for subsequent analysis on the vessel. At very low oxygen concentrations, nitrite concentrations greatly increase, signaling the presence of denitrification. However, the exact oxygen concentration is controversial and has yet to be widely agreed upon. With data from the cruise and the World Ocean Atlas collectively, a value was obtained for the denitrification boundary in the OMZ. The OMZ's in the ocean are quite small in size, composing only ~1% of the total ocean volume; they are, however, major contributors for oceanic nitrogen loss which makes OMZs highly important to observe and correctly define.

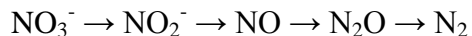
ABSTRACT

The OMZ in the eastern tropical north Pacific is a unique environment; profiles of dissolved oxygen and nitrite concentrations are anomalous compared to the vast majority of the world's oceans. In this region, measurements of dissolved oxygen were taken in addition to nitrite concentrations in order to determine the threshold at which denitrification occurs as nitrite and nitrate take over the role as the primary hydrogen acceptor (Cline et al. 1970). The oxygen profiles show a large OMZ ranging between ~200-800m in the northern stations, and ~50-1000m in the southern stations. It has been found that the current threshold of denitrification is at ~1 μM dissolved oxygen which agrees with previous studies by Cline and Richards, (1970), Morrison et al., (1999), and Devol, (1975).

INTRODUCTION

Oxygen minimum zones play a vital role in the biogeochemical processes taking place in the world's oceans (Stramma 2008; Ulloa et al. 2008). The oxygen levels in the water column can control the distribution of macroorganisms, as well as microorganisms, due to oxygen sensitivity ranges in different species (Matear et al. 2003). Another process it regulates is the denitrification, namely whether or not it can take place (Cline and Richards 1972; Stramma 2008).

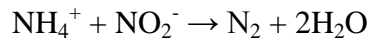
Denitrification literally means the loss of nitrogen from a system regardless of the exact path (Lam et al. 2011). In the oceanographic sense, however, denitrification refers to the following sequential reduction of nitrate to gaseous N_2 products:



(Lam et al. 2011).

Since organic matter is respired in this process, it is more formally known as heterotrophic denitrification (Lam et al. 2011). Another process that is prevalent in the conversion of ammonium and nitrite to N_2 is the anaerobic ammonium oxidation (anammox) reaction, which involves the direct autotrophic conversion of ammonium and nitrite into N_2 when anoxic conditions are present (Devol et al. 2006; Jensen et al. 2011).

The simplified reaction for anammox is as follows:



(Jensen et al. 2011).

When oxygen concentrations are low, nitrate and nitrite turn into the main hydrogen acceptors which allow molecular nitrogen to be produced (Cline et al. 1970; Devol 1978; Wright et al. 2012). The co-occurrence of suboxic conditions as well as nitrite maxima signify that denitrification is the main respiratory pathway taking place, utilizing fixed nitrogen and reducing it to free nitrogen gas (Devol 1978; Morrison 1995). When values for the denitrification intermediate NO_2^- were plotted against dissolved oxygen in prior studies, it was found that NO_2^- does not appear until values of oxygen are below 2 μM (Capone et al. 2008).

The question under investigation is “at what concentrations of oxygen in the OMZ does denitrification begin to take place at in the ETNP”. There have been many studies of the concentrations of oxygen at which denitrification can take place. However to further complicate the decision, no consensus has yet been reached concerning the concentration of oxygen that defines an OMZ and the extent of OMZ's are typically evaluated by the denitrification criteria which

are oxygen-dependent (Paulmier 2009). A loose adaptation has been conceived stating that O_2 levels less than or equal to $20 \mu M$ is the maximal O_2 level in which use of an alternative electron acceptor has been reported (Ulloa et al. 2008; Lam et al. 2011). Thus in this study, the OMZ will be defined as a body of water that has less than or equal to $20 \mu M$ of dissolved oxygen present.

While denitrification only occurs in approximately $< 1\%$ of the earth's oceans, as defined by the OMZ parameters from above, it has been estimated that these OMZ waters are responsible for 30-50% of nitrogen loss in the world's oceans (Codispoti et al. 2001; Galán et al. 2008; Lam et al. 2011; Ulloa et al. 2008). This relatively insignificant quantity of the world's oceans has quite an important role in the biogeochemical processes taking place in our oceans, and OMZs appear to be increasing in size. Recent analyses of current and historical data sets have shown a global expansion of the OMZs, deoxygenating at a rate of $0.09-0.34 \mu mol kg^{-1} yr^{-1}$, which would in theory further exacerbate the nitrogen loss due to denitrification in the OMZs (Lam et al. 2009; Stramma et al. 2008; Stramma et al. 2009; Lam et al. 2011).

More specifically, this increasing deoxygenation of the world's oceans has crucial implications on the cycling of the macronutrients nitrogen and phosphorus (Jayakumar et al. 2009; Franz et al. 2012). As organic matter from the surface sinks through the water column, it begins with a relatively fixed ratio of nitrogen to phosphorus, its stoichiometric 16:1 N:P ratio, referred to as the Redfield ratio (Redfield 1934; Redfield et al. 1963; Ulloa et al. 2008). As the organic matter sinks, organisms uptake fixed nitrogen and phosphate in this static stoichiometric ratio of 16:1; when denitrification is taking place, organic nitrogen as well as nitrate is processed which further decreases the bioavailability of nitrogen in the water

(Jayakumar et al. 2009; Koeve et al. 2010; Franz et al. 2012). Due to this, nitrogen in OMZs is lost primarily as N_2 through denitrification and anammox. Denitrification and anammox represent large sinks of inorganic nitrogen in these suboxic to anoxic waters; this will eventually lower the N:P stoichiometry of the water column driving the system into a state of nitrogen limitation (Ulloa et al. 2008; Jayakumar et al. 2009; Koeve et al. 2010; Franz et al. 2012).

With more data and information from the different OMZs around the world, nutrient profiles can be extrapolated into the future in hopes of determining how global climate change and deoxygenation of the ocean waters will affect our oceans biological and chemical distributions.

METHODS

The research vessel used to perform this research was the *Thomas G. Thompson*, on a cruise from San Diego, California, to Manzanillo, Mexico. The majority of data collection took place in March, 2012, with subsequent data being collected from a following cruise that took place through March and April, in the same region. On the first leg of the cruise which I was a part of, 44 stations were sampled ranging from $26^\circ N$ down to $18.9^\circ N$, Manzanillo Mexico. On the second leg, researchers sampled 145 stations, again off of the *Thomas G. Thompson*, and compiled the data from the second leg with that of the first. In figure 1, the transects skirting the coast of the Baja Peninsula and crossing the opening of the Gulf of California to mainland Mexico are stations sampled during the first leg of the cruise, while the stations lower than $20^\circ N$ as well as the vertical line of stations following $110^\circ W$ are all stations sampled during the second leg.

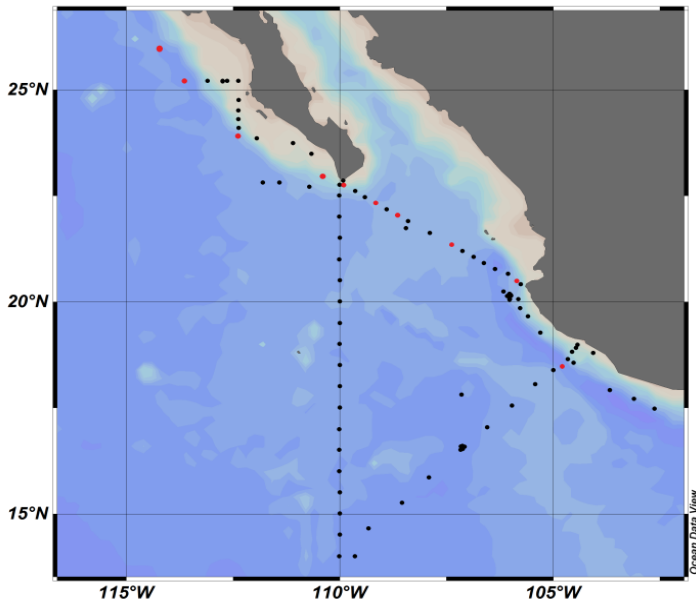


Figure 1. Study region in the eastern tropical north Pacific. Black dots indicate stations sampled solely via CTD sensor readings, while red dots are stations where CTD readings were used in tandem with Winkler titration samples.

Oxygen samples were collected via both the attached SBE 43 oxygen sensor (SeaBird Electronics, Bellevue, USA) as well as through 24- 10L niskin bottles which were both attached to a rosette. Niskins were closed at differing depths depending on the SBE 43 oxygen profile displayed in the control room during the descent of the CTD package. Samples were taken from three major features in the water column: below, in, and above the OMZ.

Samples were drawn from the niskins and flushed thoroughly through the Erlenmeyer flasks to be used, ensuring no bubbles were present to contaminate the sample. Further, duplicate and triplicate samples were collected to ensure accurate titration readings. Oxygen concentrations were later determined by Winkler titration using a dosimat titrator (Carpenter 1966). In order to determine the levels at which denitrification began to occur, oxygen sensor recordings throughout the water column were necessary but needed to be moderately accurate in order to ensure placement of denitrification with an oxygen level was precise. Titration values

were used to calibrate the SBE oxygen sensor readings. Oxygen concentrations falling below 5 $\mu\text{mol/kg}$ ended up being problematic to accurately sample as the oxygen sensor was precise yet inaccurate, and the titration data was quite accurate yet less precise. Correlating the two allowed us to determine the slope and obtain a proper correction value for our data.

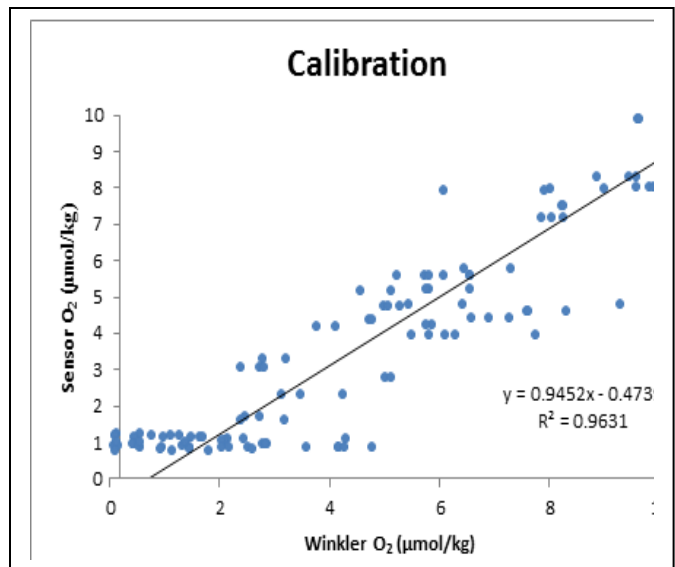


Figure 2. Calibration curve, plotting SBE 43 sensor O_2 values on the Y axis, Winkler O_2 values on the X axis. O_2 concentrations measured in $\mu\text{mol/kg}$.

The value of the slope that was determined through the calibration graph above was used to correct for the inaccuracy of the CTD mounted oxygen sensor. It was found that the sensor readings from the CTD were erroneous, measuring approximately 10% lower than the titration values. This was apparent when surface measurements were made and the O_2 saturation resulted in something less than the expected 100% O_2 saturation that surface water should be. It also flat lines in the above calibration graph to a point of approximately 1 $\mu\text{mol/kg}$, never able to reach a lower value. After the slope was determined, the sensor O_2 readings were divided by the slope in order to give the corrected O_2 values.

RESULTS

The oxygen profile of the ETNP appeared to follow the expected trend for the region; oxygen concentrations declined at a slower rate in the northernmost stations, and declined rapidly to 0 $\mu\text{mol/kg}$ in the southern stations as shallow as 50 meters. In Figure 3, station 4, which is one of the northernmost stations, possesses surface waters that start with very high O_2 concentrations of approximately 235 $\mu\text{mol/kg}$, and then declines to a minimum of about 10 $\mu\text{mol/kg}$ at 200 meters. Opposite of this trend, station 37 starts at the same surface O_2 levels, but decreases almost immediately to approximately 0 $\mu\text{mol/kg}$ at 50 meters.

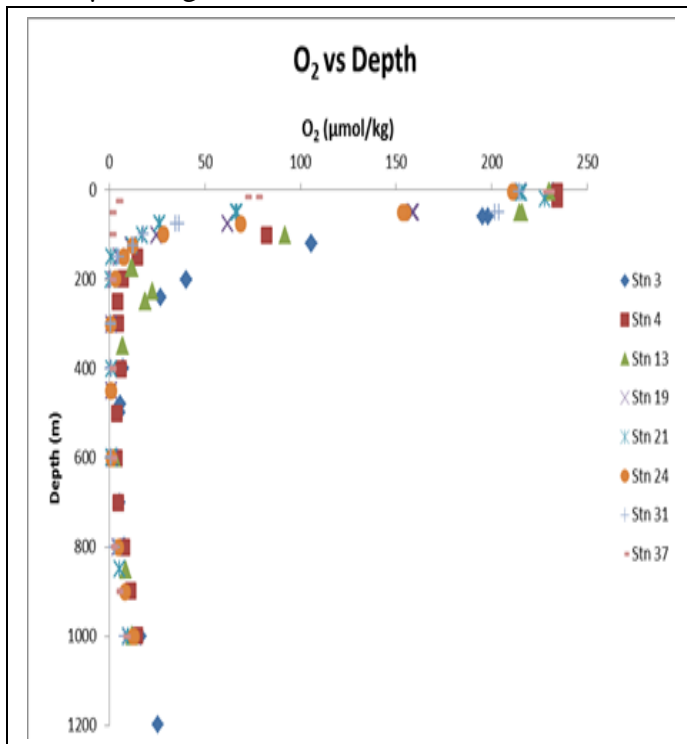
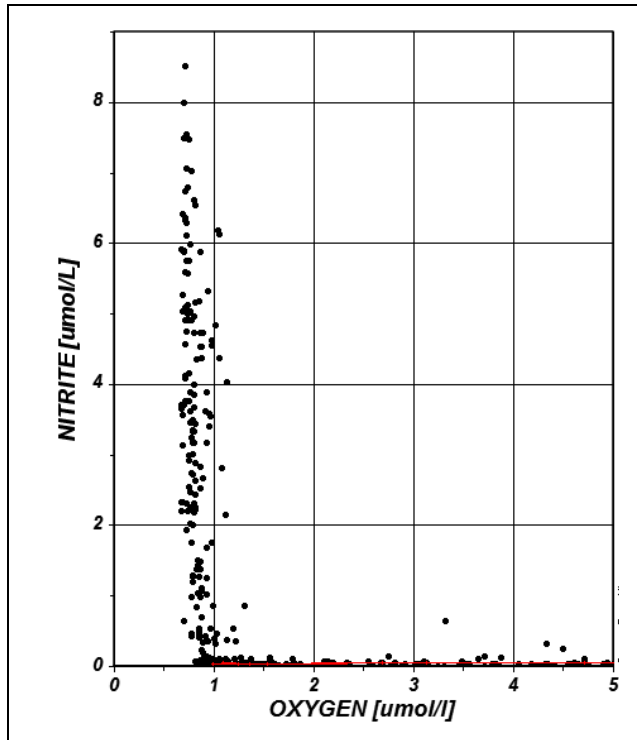


Figure 3. Oxygen vs. depth graph. Stations coordinated by color and symbols, key on the right. Station 3 is the northernmost red dot appearing on Figure 1, with subsequent red dots represented by the increasing stations.

The relationship between nitrite and dissolved oxygen were plotted in Figure 4, with the graph focusing on the low oxygen concentrations, ranging from 0 to 1 $\mu\text{mol/l}$.

The NO_2^- curve appears to be spiking at a value just below 1 $\mu\text{mol/kg}$. The O_2 levels appear to be unchanging past approximately 0.8 $\mu\text{mol/l}$.

Figure 4. Dissolved oxygen versus nitrite concentrations, in the OMZ layer (defined at $<20 \mu\text{mol/kg}$) of the ETNP. Both axes in $\mu\text{mol/l}$. Vertical line signifies the possible threshold at which denitrification can occur at.



Oxygen levels show wide variance along the transect with highly saturated surface waters becoming deoxygenated very quickly by the OMZ water mass. As stated earlier, the OMZ is a body of water containing less than or equal to 20 $\mu\text{mol/kg}$ O_2 . This appears on the color scale of figure 5 as anything in the purple to light purple region. In the northern stations this would indicate an OMZ from ~200m-800m. Towards the latter end of the transect, between 1000-1200 km on the x axis of figure 5, the OMZ expands into shallower as well as deeper waters, ranging from ~50m-1000m.

In conjunction with these dissolved oxygen values, the nitrite shows an abundance in the water column between 900 km and 1300 km at the southern end of the section. This region of elevated nitrite extends from surface waters down to approximately 500 meters in depth. There is a notable lack of nitrite in the water column prior to this spike in the southern stations, remaining between 0 and 0.5 $\mu\text{mol/l}$.

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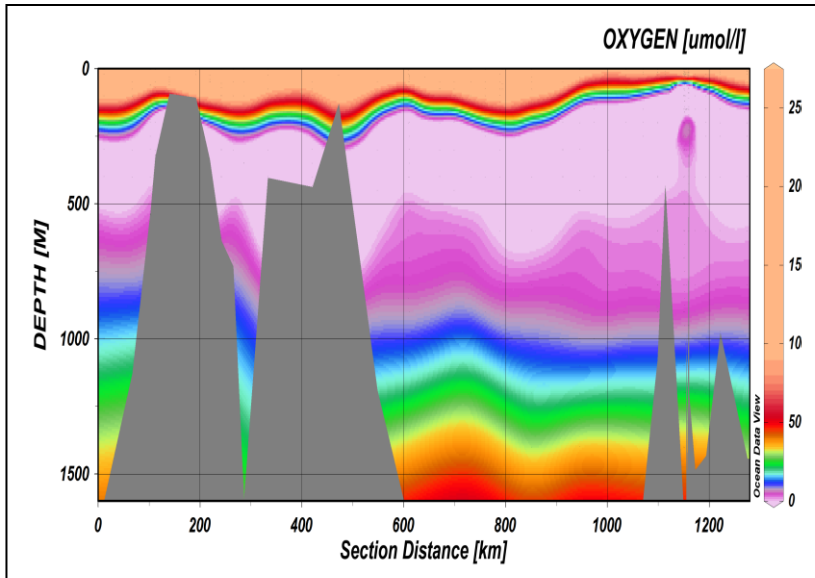


Figure 5. Dissolved oxygen plotted in ODV versus depth and distance from start and end of transect, from left to right respectively. Oxygen units are $\mu\text{mol/l}$, color bar depicting oxygen concentrations on right.

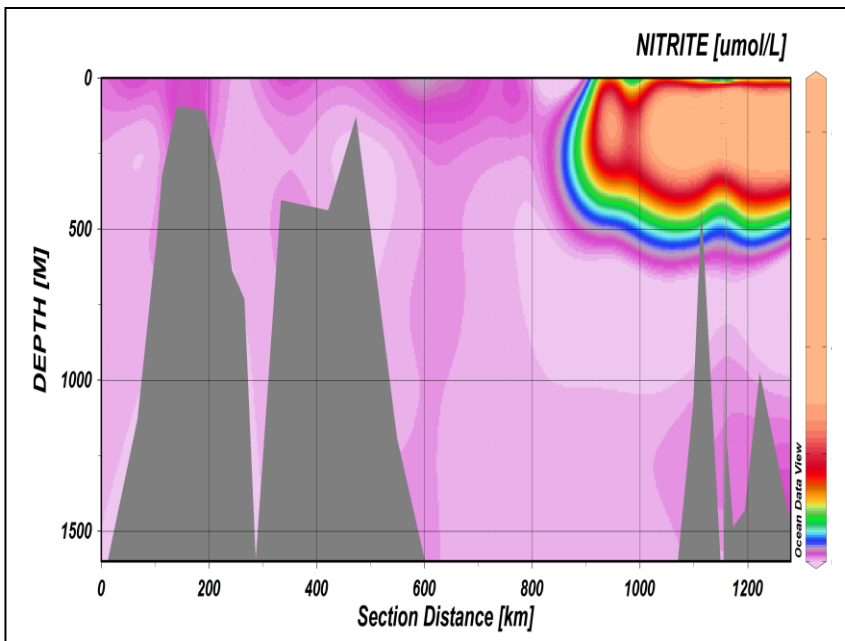


Figure 6. Nitrite levels in the water column, plotted in ODV versus depth and distance on transect. Beginning of transect on the left, end of the transect on the right. Nitrite concentrations depicted by color bar to the right.

The dissolved oxygen concentrations observed in the ETNP are minute, with an OMZ ranging from 300-1000 meters and oxygen concentrations ranging from 0-10 $\mu\text{mol/l}$; the measured oxygen concentrations also correlate with nitrite quite strongly indicating that denitrification is indeed taking place in this region. The dissolved oxygen to nitrite plot shows nitrite peaking at 1 $\mu\text{mol/l}$ O_2 with almost no nitrite being found in waters with oxygen concentrations higher than that. My results in Figure 4 show a strong relationship with Figure 7 (Devol 2008), with nitrite levels greatly increasing below 1.5 μM of dissolved oxygen. The lower plot in Figure 7, the Saanich Inlet, clearly differs from the two plots above as well as from Figure 4. This elevated threshold for denitrification in Saanich Inlet was attributed to a response by the microbial community to the transient nature of the suboxic environment in this fjord (Devol 2008).

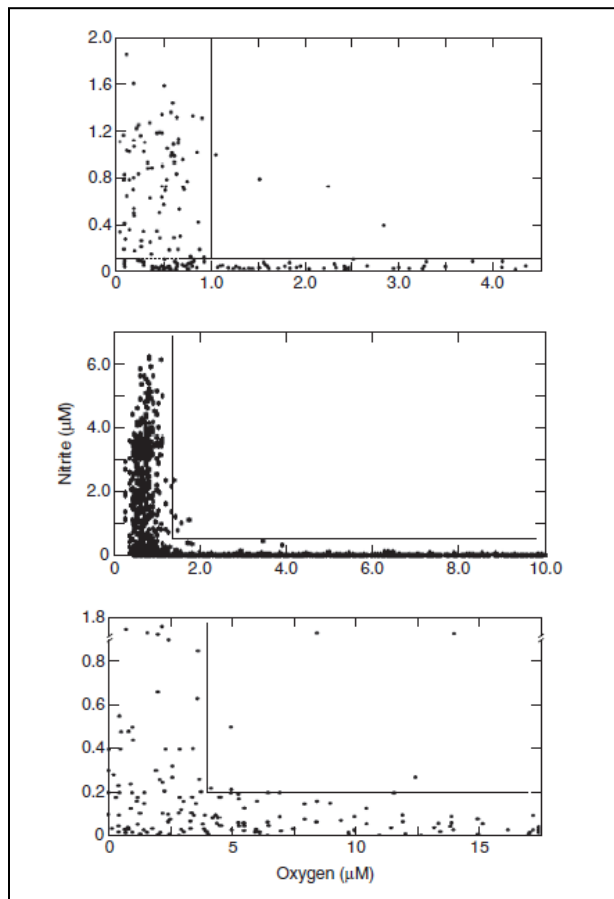


Figure 7. Located on bottom left of the page. Figure from Allan Devol, from Capone et al, Nitrogen in the marine environment, 2nd ed. Academic. Dissolved oxygen versus nitrite concentrations, for waters of the OMZ ($<20 \mu\text{M}$) in the ETNP. Note that the axes are different for the three plots, and the vertical lines denote possible threshold for denitrification. Upper plot is from Cline and Richards, 1972 of ETNP; middle plot is of the Arabian Sea by Morrison et al. 1999; bottom plot is the Saanich Inlet by Devol, 1975.

The similarity between Figure 7 and Figure 4 leads me to believe the nitrite threshold in the ETNP is at or around a value of approximately 0.8 $\mu\text{mol/kg}$ of dissolved oxygen. The upper plot in Figure 7 is also of the ETNP, however the oxygen values their threshold was produced on ranged between 1 and 0 μM . The difference between this plot and Figure 4 is likely that the oxygen measurements from Cline and Richards were much more accurate, detecting oxygen concentrations as low as nearly 0 μM .

In a normalized water column containing Redfield composition, $(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4)_1$, oxidation will take place favoring the oxidant yielding the greatest change in free energy per mol of organic carbon that is oxidized (Froelich et al. 1979; Wright et al. 2012). When the most favorable oxidant is depleted, oxidation will then proceed to utilize the next most energetically efficient oxidant, continuing on in this trend until all oxidants are consumed or organic matter is depleted (Froelich et al. 1979; Wright et al. 2012). When oxygen is present, oxidation will favor aerobic respiration, using up the oxygen and yielding a Gibbs free energy of $\Delta G^{\circ} = -3190 \text{ kJ/mol}$; on the other hand, in regions where oxygen is no longer present such as OMZs, the next most favorable reaction would be denitrification and anammox, which use nitrate in place of oxygen as a hydrogen acceptor. This reaction, being less energetically favorable, only yields

a free energy of $\Delta G^\circ = -2750$ kJ/mol (Devol 1978; Froelich et al. 1979; Wright et al. 2012).

The differences in energy yields of aerobic respiration and denitrification/anammox, as well as the diffusion rates of oxygen and nitrate into bacterial cells, are the primary factors causing denitrification thresholds to appear as they do in Figures 4 and 7. When oxygen concentrations are greater than or equal to approximately $1.5 \mu\text{M}$, there is sufficient oxygen present in the water for the organism to still harness the most energetically favorable of the free energies. This point is known as the critical oxygen concentration, or COC, essentially the lowest oxygen level that the oxygen supply is sufficient to meet the energetic requirements of the organism. Once the oxygen concentrations drop below $1.5 \mu\text{M}$, there is no longer a sufficient supply of oxygen to maintain aerobic respiration and still oxidize the maximum amount of energy possible. At this point, denitrification and anammox become the more energetically efficient pathways of oxidation due to high levels of nitrate present in the water column. More nitrate will be able to diffuse into the cell than oxygen, and while the nitrate oxidation yields a smaller free energy, the significantly greater amount of nitrate present allows more oxidation to take place overall producing a total energy yield much higher than if the bacterial cell were to continue to attempt to oxidize low concentrations of oxygen.

The point at which the shift from oxidizing oxygen to oxidizing nitrate takes place is typically found through a kinetic approach using Michaelis-Menten kinetics to determine the half saturation constant. Determining the half saturation constant (K_s), however, depends on a multitude of oceanic environmental features such as temperature, size of the organism, and even the specific bacterial flora present (Devol 1978). Due to

these factors, determining an absolute concentration of oxygen at which denitrification begins is essentially impossible (Devol 1978). However, using prior data collected in the ETNP by Cline and Richards, 1972, Allan Devol was able to determine a close approximation for the average COC and K_s of the open tropical Pacific bacteria. A value of $1.95 \mu\text{M/l}$ and $0.62 \mu\text{M/l}$ were determined for the COC and K_s , respectively. This value of K_s is comparable to the denitrification threshold determined in this study, depicted in Figure 4. Recalling back to Figure 4, the threshold was located at approximately $0.8 \mu\text{M/l}$, which is quite similar to the K_s value determined by Devol. In spite of this it is important to note that my threshold value might possibly be too large due to difficulties obtaining measurements of oxygen lower than this value of $0.8 \mu\text{M l}^{-1}$; this would account for the difference between the K_s value and my threshold value.

Furthermore, the ETNP OMZ possesses a significant possibility in the future for a shift towards a greater abundance of deoxygenated water in the water column which would likely result in an increase in denitrification, and consequently a sink of oceanic nitrogen (Galán et al. 2008; Lam et al. 2009; Stramma et al. 2008; Ulloa et al. 2008; Lam et al. 2011).

With this possible shift in the amount of nitrogen in the water column, the stoichiometric ratios crucial for maintenance and productivity of microbial primary production in the ocean will be challenged, possibly with adverse consequences. There is a possibility of a shift towards 'Non-Redfieldian' primary production, in that coastal diatoms that generally require low N:P ratios, <16:1, would partake in an exponential bloom (Ulloa et al. 2008; Jayakumar et al. 2009; Koeve et al. 2010; Franz 2012). This would leave very little reduced phosphorus for the diazotrophic phytoplankton and could shift

the phytoplankton community towards a few dominant species (Franz 2012).

If more precise oxygen concentrations could be collected in future experiments, a more precise threshold could be determined. Additionally, if a new COC and K_s were to be ascertained for the current environment and bacterial flora present in the ETNP, a highly accurate interpretation would be possible for the denitrification threshold. It will be interesting to observe this region for the years to come to monitor future changes in the chemistry as well as biology of the region, and to see how scientific technology will progress to enhance the ability of scientists to obtain essential, highly precise data.

CONCLUSIONS

While a definitive nitrite to dissolved oxygen profile was attained during this cruise, a longer period of time for research, as well as more stations to sample, would have helped to solidify the findings of this study. The denitrification threshold found from the nitrite to oxygen profile is located at an oxygen concentration of approximately $0.8 \mu\text{M l}^{-1}$, which is in agreeance with the half saturation constant determined by Allan Devol (1978) to be approximately $0.62 \mu\text{M l}^{-1}$ in the open tropical Pacific bacterial. Further investigation is necessary to validate the conclusions of this study and corroborate the current understanding of denitrification in the OMZ of the ETNP. With additional data collection from the different OMZs around the world, the current OMZ features could be juxtaposed with historical data; this would allow for nutrient profiles to be extrapolated into the future in hopes of determining how global climate change and deoxygenation of the ocean waters will affect the oceans biological and chemical distributions.

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REFERENCE LIST

- Carpenter J. H. 1966. New measurements of oxygen solubility in pure and natural water. *Limnology and Oceanography*. **11**: 264–277
- Cline, J. D. and Goering, J. J. 1970. A note on denitrification in seawater. *Limnology and Oceanography*. **15**: 306-309.
- Cline, J. D. and Richards, F. A. 1972. Oxygen deficient conditions and nitrate reduction in the eastern tropical north Pacific ocean. *Limnology and Oceanography*. **17**: 885-900.

- Codispoti, L. A. et al. 2001. The oceanic fixed nitrogen and nitrous oxide budgets: Moving targets as we enter the anthropocene? *Scientia Marina*. **65**: 85-105.
- Devol, A. H. 1978. Bacterial oxygen uptake kinetics as related to biological processes in oxygen deficient zones of the oceans. *Deep-Sea Research*. **25**: 137-146.
- Devol, A. H. et al. 2006. Molecular evidence for the broad distribution of anaerobic ammonium-oxidizing bacteria in freshwater and marine sediments. *Applied and Environmental Microbiology*. **72**: 6829-6832.
- Devol, A. H. 2008. Denitrification including anammox, p. 263-301. In D. G. Capone et al, Nitrogen in the marine environment, 2nd ed. Academic.
- Franz, J. et al. 2012. Dynamics and stoichiometry of nutrients and phytoplankton in waters influenced by the oxygen minimum zone in the eastern tropical Pacific. *Progress in Oceanography*. **62**: 20-31.
- Galán, A. et al. 2009. Anammox bacteria and the anaerobic oxidation of ammonium in the oxygen minimum zone off northern Chile. *Progress in Oceanography*. **56**: 1021-1031.
- Jayakumar, A. et al. 2009. Denitrifying bacterial community composition changes association with stages of denitrification in oxygen minimum zones. *Microbiology of Aquatic Systems*. **58**: 350-362.
- Jensen, M. M. et al. 2011. Intensive nitrogen loss over the Omani shelf due to anammox coupled with dissimilatory nitrite reduction to ammonium. *The International Society for Microbial Ecology*. 1-11.
- Koeve, W. and Kähler, P. 2010. Heterotrophic denitrification vs. autotrophic anammox – quantifying collateral effects on the oceanic carbon cycle. *Biogeosciences Discussions*. **7**: 1813-1837.
- Lam, P. et al. 2009. Revising the nitrogen cycle in the Peruvian oxygen minimum zone. *Proceedings of the National Academy of Sciences of the United States of America*. **106**: 4752-4757.
- Lam, P. and Kuypers, M. M. 2011. Processes in oxygen minimum zones. *Annual Review of Marine Science*. **3**: 317-345.
- Matear, R. J. 2003. Long-term changes in dissolved oxygen concentrations in the ocean caused by protracted global warming. *Global Biogeochemical Cycles*. **17**, 35 (1-20).
- Morrison, J. M. et al. 1999. The oxygen minimum zone in the Arabian Sea during 1995. *Deep-Sea Research II*: **46**: 1903-1931.
- Paulmier, A. and Ruiz-Pino, D. 2009. Oxygen minimum zones (OMZs) in the modern ocean. *Progress in Oceanography*. **80**: 113-128.
- Redfield, A. C. 1934. On the proportions of organic derivatives in seawater and their relation to the composition of plankton. *James Johnstone Memorial Volume*. 177-192.
- Redfield, A. C. et al. 1963. The influence of organisms on the composition of seawater. *The sea: ideas and observations on progress in the study of the seas*, **2**: 26-77.
- Stramma, L. 2008. Expanding oxygen-minimum zones in the tropical oceans. *Science*. **350**, 655-658

Stramma, L. et al. 2009. Deoxygenation in the oxygen minimum zone of the eastern tropical North Atlantic. *Geophysical Research Letters*. **36**: 1-5.

Ulloa, O. and Pantoja, S. 2009. The oxygen minimum zone of the eastern south Pacific. *Progress in Oceanography*. **56**: 987-991.

Wright, J. J., et al. 2012. Microbial ecology of expanding oxygen minimum zones. *Nature*.**10**: 381-394.