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**TROPHIC ECOLOGY OF OXYGEN MINIMUM ZONE ZOOPLANKTON
REVEALED BY CARBON AND NITROGEN STABLE ISOTOPES**

BY

REBECCA WILLIAMS

**A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF**

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OF
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UNIVERSITY OF RHODE ISLAND

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ABSTRACT

Oxygen minimum zones (OMZs) are areas in which midwater oxygen concentration can be significantly lower than in non OMZ areas at comparable depths. OMZs are of great interest because of the limits oxygen availability places on life. The potential for OMZ expansion with warming of the oceans has refocused attention on the importance of these areas and their potential impacts on the global carbon cycle. The large open ocean OMZs of the Eastern Tropical Pacific and Arabian Sea are notable for their size, thickness, and the intensity of oxygen depletion ($<1\mu\text{M}$) in their cores. Zooplankton play a major role in the global carbon cycle via their role in the transfer of carbon to the deep sea as part of the biological pump. While several studies have described zooplankton abundance and distribution in OMZs, little is known about how zooplankton diets and feeding are affected in the presence of OMZs.

Here, I use measurements of natural abundance carbon and nitrogen stable isotopes (as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) to investigate zooplankton diets within the Eastern Tropical Pacific OMZ. The use of stable isotopes rests on the premise that the $\delta^{13}\text{C}$ values of consumers are similar to their ultimate organic carbon source, primary producers, while the $\delta^{15}\text{N}$ values reflect more proximal sources of organic matter and can be used to evaluate trophic position. To examine the energy sources and trophic interactions of zooplankton in the Eastern Tropical North Pacific OMZ, samples were collected in 2007 and 2008 at two stations, the Tehuantepec Bowl (TB) and Costa Rica Dome (CRD), using vertically stratified MOCNESS net tows between 0-1200 m. Environmental data were collected concurrently with zooplankton samples and particulate organic matter (POM) was collected with McLane large volume *in situ*

pumps. Zooplankton samples were separated into four size fractions and processed at sea to select aliquots for bulk (mixed zooplankton) analysis and individual taxa samples were analyzed for stable carbon and nitrogen isotopes.

Bulk zooplankton and POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values revealed strong depth gradients associated with oxyclines (oxygen gradients) at the upper and lower OMZ boundaries. While the source of low $\delta^{13}\text{C}$ values at the upper oxycline could not be determined, the sharp gradient in $\delta^{15}\text{N}$ values at the lower oxycline indicated a depth zone of increased trophic progression. Furthermore, $\delta^{15}\text{N}$ values were significantly lower at CRD than at TB, suggesting that nitrogen fixation may have been present at CRD. Low $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations in all zones at CRD suggested that the products of nitrogen fixation were transferred to zooplankton food webs throughout the sampled water column.

Stable isotope values of individual zooplankton taxa also suggested that zooplankton collected within and above the OMZ core likely fed on material from the upper 110m of the water column, while lower oxycline zooplankton likely consumed deep POM exiting the OMZ. There were significant differences in the isotope values of zooplankton taxa with different trophic strategies (particle feeders, omnivores, carnivores) in the OMZ core and lower oxycline community, but not for those living in the mixed layer and upper oxycline. Furthermore, calculated trophic levels for lower oxycline taxa were much higher than expected based on *a priori* trophic level designations. The copepod *Eucalanus inermis* is thought to diapause in the lower oxycline, but low C:N ratios and $\delta^{15}\text{N}$ values measured were not consistent with expectations for a diapausing population. However, storage of ammonium by *E.*

inermis for buoyancy regulation could have resulted in the observed C:N ratios and $\delta^{15}\text{N}$ values. In the lower oxycline, the trophic isolation of particle feeders the sharp $\delta^{15}\text{N}$ gradients at that depth, and the large proportion of carnivorous taxa supported the idea that this is a zone of vigorous trophic processing

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PREFACE

This dissertation is presented in manuscript format. The first chapter is an introduction to the formation and ecological significance of oxygen minimum zones (OMZs) and the mechanism for and uses of stable carbon and nitrogen isotope analysis in ecological studies. Chapters 2 and 3 examine zooplankton food sources and trophic interactions throughout the Eastern Tropical North Pacific (ETNP) OMZ. Chapter 2 is in review for publication with Deep-Sea Research Part I. Chapter 3 is in preparation for publication in Progress in Oceanography. Chapter 4 summarizes the findings of the preceding chapters and suggests future studies. Appendix A lists $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all individual zooplankton taxa. Appendix B shows $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all size fractionated bulk zooplankton, and Appendix C shows means of %C and %N and C:N values calculated from 2008 data.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS.....	v
PREFACE	vi
TABLE OF CONTENTS.....	vii
LIST OF TABLES	x
LIST OF FIGURES	xii
CHAPTER 1: OXYGEN MINIMUM ZONES AND STABLE ISOTOPE ECOLOGY	1
1.1 Physical and Chemical Characteristics of Oxygen Minimum Zones.....	1
1.2 Potential Impacts of OMZs on Marine Communities.....	4
1.3 Stable Isotope Ecology in Marine Environments	7
CHAPTER 2: TROPHIC ECOLOGY AND VERTICAL TRENDS OF CARBON AND NITROGEN STABLE ISOTOPES IN OXYGEN MINIMUM ZONE ZOOPLANKTON.....	13
2.1 Abstract	14
2.2 Introduction	16
2.3 Methods.....	18
2.3.2 Vertical Zonation of the OMZ.....	20
2.3.3 Data analysis.....	21
2.4 Results	22
2.4.1 Hydrographic data	23
2.4.2 Stable isotopes and environmental variables.....	23
2.4.3 Contribution from lipids	24

2.4.4	Stable isotope vertical profiles	24
2.4.5	Zooplankton trophic interactions.....	25
2.5	Discussion	26
2.5.1	General trends.....	26
2.5.2	Comparisons to other regions	27
2.5.3	Influence of the physical environment	29
2.5.4	Trophic structure of OMZ zooplankton community	30
2.6	Conclusions	33
2.7	Acknowledgements	34
2.8	References	36
CHAPTER 3: TROPHIC INTERACTIONS OF ZOOPLANKTON TAXA IN AN OXYGEN MINIMUM ZONE.....		54
3.1	Abstract	55
3.2	Introduction	57
3.3	Methods.....	62
3.3.1	Sample collection and processing.....	62
3.3.2	Vertical Zonation of the OMZ.....	65
3.3.3	Data analysis.....	66
3.4	Results	69
3.4.1	Vertical and Temporal Trends.....	69
3.4.2	Zooplankton Food Sources	70
3.4.3	Trophic Interactions Between Zooplankton Taxa	70

3.4.4	Diets and Trophic Interactions of Key Taxa	71
3.5	Discussion	72
3.5.1	General Trends	72
3.5.2	Carbon and Nitrogen Sources Entering Zooplankton Trophic Webs.	72
3.5.3	Trophic Interactions of the Zooplankton Community	75
3.5.4	Key Taxa.....	77
3.6	Conclusions	84
3.7	Acknowledgements	84
3.8	References	86
CHAPTER 4: CONCLUSIONS		110
APPENDIX A: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all individual zooplankton taxa.		113
APPENDIX B: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of size fractionated bulk zooplankton for each MOCNESS net in each tow.		130
APPENDIX C: Net average %C, %N with standard deviations and C:N ratios of 2008 individual zooplankton taxa.....		135
APPENDIX D: Literature cited		138

LIST OF TABLES

Table 2.1: Tows and depth ranges for MOCNESS tows and pump casts. TB is the Tehuantepec Bowl and CRD is the Costa Rica Dome.....	42
Table 2.2: Table of statistical tests used in this study. Permutational Analysis of Variance (PERMANOVA), Distance Based Linear Model (DISTLIM), and Distance Based Redundancy Analysis (dbRDA) were calculated using PRIMER v6 +PERMANOVA (Clarke & Gorley, 2001; Anderson et al., 2008)	43
Table 2.3: Results from 2-way PERMANOVA comparing zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes between stations and ecological zones. ML is the mixed layer, UO is the upper oxycline, OMZ is the OMZ core, and LO is the lower oxycline. Only data from 2008 were used in these comparisons. * indicates significant results.	44
Table 2.4: Relationship between environmental variables and Eastern Tropical North Pacific OMZ zooplankton isotope data based on a forward selected R^2 DISTLIM test (Table 3). Marginal tests consider the importance of each variable in the absence of the other variables. Sequential tests consider the importance of variables in conjunction with the other variables starting with the variable explaining the greatest variance. * indicates significant results	45
Table 2.5: Ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for POM and zooplankton from this and other studies.	46
Table 3.1: Tow information and depth ranges for MOCNESS samples for individual zooplankton taxa used in stable isotope analysis. TB is the Tehuantepec Bowl and CRD is the Costa Rica Dome.	96
Table 3.2: Means, standard, deviations ($\pm$), number of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ samples run (n) and estimated number of individuals collected (ni) for zooplankton taxa collected at each station, combined for 2007 and 2008.	97
Table 3.3: Table of statistical tests used in this study. Linear regressions were calculated using SigmaPlot 8.0 while Permutational Analysis of Variance (PERMANOVA), MDS plots, cluster analyses, and Similarity Profile (SIMPROF) routines were calculated using PRIMER 6 + PERMANOVA. All multivariate methods are described in Clark & Gorley (2001) and Anderson et al. (2008).....	98
Table 3.4: <i>a-priori</i> and calculated trophic levels for zooplankton taxa. TL = trophic level, PF= particle feeder, O = omnivore, and C = Carnivore	99

Table 3.5: Results of a) 3-way PERMANOVA on all individual taxa from both years and stations comparing station, ecological zone, and time of day (i.e. day or night) b) 3-way PERMANOVA pair-wise test results c) 2-way PERMANOVA on <i>E. inermis</i> and biomass weighted mean zooplankton at Tehuantepec Bowl and d) Costa Rica Dome ; and e) DISTLIM marginal tests of the contribution of physical properties to variation in isotope data. * indicates significant results.	100
Table 3.6: Results of 1-way ANOVAs with associated significant pairwise (Tukey) tests and Student's t-tests on key zooplankton taxa. $\bar{X}_a - \bar{X}_b$ is the difference in sample means. Cycloth = <i>Cyclothone</i> spp. ; H. long = <i>H. longicornis</i> ; E. inerm = <i>E. inermis</i> ; and L. huls = <i>L. hulsemannae</i>	101
Table 3.7: Elemental composition and molar C:N ratios of 2008 zooplankton taxa at both stations ($\pm$) indicates standard deviation.	102

LIST OF FIGURES

Fig. 1.1: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of polar marine taxa from Figure 1 in Hobson et al (2002). Primary producers are pelagic POM and ice algae, both of which are located to the lower left of consumers.	12
Fig. 2.1: Station map	47
Fig. 2.2: Hydrographic profiles of a) TB in 2007, b) CRD in 2007, c) TB in 2008, and d) CRD in 2008. Profiles are truncated to the depth where isotopic data were obtained. Shaded areas represent the oxygen minimum zone core Graph d) has all five ecological zones delineated by dotted lines and labeled to the right. ML= mixed layer, UO= upper oxycline, OM= oxygen minimum zone core, LO= lower oxycline, and SO= suboxycline. Data are from MOCNESS tows 605, 618, 626, 629, 631, 635, 636, and 637. More extensive hydrographic analyses are found in Wishner et. al. (2013).	48
Fig. 2.3 dbRDA plot of zooplankton stable isotope values from all stations and years. The length and direction of each vector relates to its partial correlation with the dbRDA axes. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with arrow symbols represent the direction of association of each isotope with the plotted data. See Table 2.2 for statistical parameters.....	49
Fig. 2.4: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vertical profiles of the biomass weighted means of zooplankton size classes, POM and oxygen. Shaded areas represent the extent of the OMZ core. The red asterisk represents the depth of the secondary zooplankton biomass peak.....	50
Fig. 2.5: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vertical profiles of separate zooplankton size fractions for rows a) 2007 TB, b) 2007 CRD, c) 2008 TB, and d) 2008 CRD. Open symbols are $\delta^{13}\text{C}$ values and filled symbols are $\delta^{15}\text{N}$ values. Depths where no data were available for a given size fraction are represented by broken lines. Only samples between 0- 250m were collected in 2007.	51
Fig. 2.6: 2007 and 2008 zooplankton biomass weighted means for TB and CRD. Green consumer polygons represent the likely range zooplankton feeding primarily on shallow (0-110m) POM and blue consumer polygons represent the range for zooplankton feeding on deep (110-1000m) POM. Light blue triangles represent zooplankton from the LO biomass peak.	52
Fig. 2.7: $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ of all zooplankton size classes at TB and CRD in both years for each ecological zone. Closed symbols represent zooplankton samples and open symbols represent POM values. Triangles represent data from 2007 and circles represent 2008 data. Regression lines and equations were calculated using zooplankton values only.	53
Fig. 3.1: Station Map.....	103

- Fig. 3.2: Hydrographic profiles of stations TB and CRD in 2007 and 2008. The data shown are is for Tows 609, 614, 632, and 636. Right side plots are biomass weighted mean bulk zooplankton $\delta^{13}\text{C}$ (circles) and $\delta^{15}\text{N}$ (triangles) at each station in 2008 from Williams et al (submitted). Grey boxes represent the extent of the OMZ core. 104
- Fig. 3.3: Vertical profiles of zooplankton individual taxa $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from both years, and C:N data for 2008 at TB (top row), and at CRD (bottom row). All points represent average $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for each taxon in a single net. Starred data represents biomass weighted mean $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for bulk zooplankton (chapter 2). Grey boxes denote range of C:N ratios indicating taxa with tissues dominated by lipids 105
- Fig. 3.4: Average $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ for zooplankton taxa in each ecological zone at TB and CRD. Consumer polygons representing the likely range of consumers feeding on shallow (0-110m) POM are indicated by green dotted lines, while likely ranges of consumers feeding on deep POM (110-1000m) are represented by blue dotted lines. Equations and black lines represent linear regressions. Error bars denote standard deviations. 106
- Fig. 3.5: MDS plots showing zooplankton trophic levels for each ecological zone at both stations combined. Trophic levels were assigned for each species based on values reported in the literature (left column), and calculated for each species using $\delta^{15}\text{N}$ values (right column). MDS plots and group average cluster analyses were calculated from Euclidean distance resemblance matrices. Circles represent significant ($p \leq 0.05$) clusters identified by SIMPROF routines. All points represent average $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for each taxon in a single net. 107
- Fig. 3.6: Trophic Level box plot of zooplankton taxa from both years and stations combined. The upper and lower boundaries of the box represent the 25th (bottom) and 75th (top) percentiles, the line inside each box is the median, error bars represent the 10th (bottom) and 90th (top) percentiles, and black circles represent outliers. 108
- Fig. 3.7: Vertical profiles of zooplankton individual taxa $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from both years, and C:N data from 2008 at a) TB and b) CRD including values for *Eucalanus inermis* (red circles), *Subeucalanus subtenius* (blue squares), and *Lucicutia hulsemannae* (green triangles). All points represent average $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for each taxon in a single net. Starred data represents biomass weighted mean $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for bulk zooplankton data. Grey boxes denote range of C:N ranges indicating taxa with tissues dominated by lipids 109

CHAPTER 1:

OXYGEN MINIMUM ZONES AND STABLE ISOTOPE ECOLOGY

Oxygen minimum zones (OMZs) are naturally occurring midwater areas of low oxygen concentrations found in the Atlantic, Pacific, and Indian oceans (Benstead et al., 2006; Karstensen et al., 2008; Ito & Deutsch, 2013). Although oxygen concentrations decrease at intermediate depths in all oceans, they can be fifty times lower in the OMZs (Paulmier & Ruiz-Piño, 2009). The extent, thickness, and degree of hypoxia within OMZs are driven by a combination of physical, geographical, biochemical, and biological properties (Hidalgo et al., 2005a; Fiedler & Talley, 2006; Karstensen et al., 2008; Pantoja et al., 2009; Cartapanis et al., 2013). Today, the intense open ocean OMZs are located in upwelling regions where circulation and biological productivity work together to deplete subsurface oxygen concentrations to near zero. Renewed interest in OMZs in recent years stems from the theoretical suggestion that the OMZs may either expand or intensify (i.e. develop lower oxygen concentrations) as the ocean warms. (Stramma et al., 2008b; Deutsch et al., 2011; Stramma et al., 2011)

1.1 Physical and Chemical Characteristics of Oxygen Minimum Zones

The primary factors influencing the formation and intensity of OMZs are high biological productivity in the mixed layer and the presence of sluggish, poorly oxygenated water masses at intermediate depths (Fiedler & Talley, 2006; Paulmier & Ruiz-Piño, 2009; Cartapanis et al., 2013). High surface productivity results in greater export of organic material to intermediate depths, relative to areas of lower productivity. This exported organic carbon is a source of energy to both zooplankton

and heterotrophic bacteria during respiration. The regionally high rates of respiration consume oxygen in the water column more rapidly than it is resupplied (Karstensen et al., 2008; Paulmier & Ruiz-Piño, 2009; Deutsch et al., 2011; Ito & Deutsch, 2013). Surface production can be influenced by changes in atmospheric circulation affecting the strength, duration, or frequency of upwelling events (Cartapanis et al., 2013; Ito & Deutsch, 2013). Changes in surface productivity can occur on interannual, decadal, or geological timescales and can be driven by climate cycles (Cartapanis et al., 2013; Ito & Deutsch, 2013). For example, changes in the El Niño Southern Oscillation (ENSO) can depress the thermocline, reduce the nutrient availability in the mixed layer, and lower primary productivity (Ito & Deutsch, 2013). Less productivity results in lower export of organic carbon and a smaller OMZ (Ito & Deutsch, 2013).

Although changing surface productivity is probably the most important factor affecting OMZs, changes in the rate of intermediate water mass formation or advection, can also affect the concentration of oxygen within intermediate water masses flowing into OMZ areas. Oxygen concentrations in intermediate water masses can be influenced by changes in upwelling and primary production in adjacent areas upstream of the OMZ, and such changes are often related to phase changes of climate cycles such as El Niño or the Pacific Decadal Oscillation (Robinson et al., 2009; Cartapanis et al., 2013). Phase changes in climate cycles can also alter the rate of source water formation and subsequent advection rates (Cartapanis et al., 2013). Lastly, oxygen concentrations of subsurface water masses can change if the productivity of the overlying water mass in another area changes. For example, changes in productivity in the equatorial upwelling system can decrease the oxygen

concentration in intermediate source water to the ETP OMZs (Robinson et al., 2009; Ito & Deutsch, 2013).

In addition to the very low oxygen concentrations which are the defining characteristic of OMZs, many components of the nitrogen cycle occur in OMZs that are otherwise found only in sediments or anoxic basins. One of the most important of these processes is denitrification, the process by which biologically available forms of nitrogen are converted into a form of nitrogen that cannot be utilized by most autotrophs (Lam et al., 2009; Lam & Kuypers, 2011; Zehr & Kudela, 2011). There are two varieties of denitrification in OMZs. Heterotrophic denitrification is the process by which nitrate is converted to N_2 in several steps ($NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$) under anoxic conditions by a number of different bacterial groups and was long believed to be the only mechanism for nitrogen loss in OMZs (Altabet, 1996; Ward et al., 2008; Bulow et al., 2010; Lam & Kuypers, 2011). Nitrate and nitrite are the only bioavailable forms of nitrogen for most phytoplankton taxa; thus nitrogen converted from one of these compounds to NO, N_2O or N_2 , by this process is said to be “lost” (Miller, 2004). Nitrogen is the limiting nutrient controlling phytoplankton productivity in most marine systems and 30-50% of nitrogen loss in marine systems occurs in OMZs (Lam & Kuypers, 2011). Furthermore N_2O , a greenhouse gas, is one product of denitrification and may significantly contribute to global warming if OMZs expand (Codispoti et al., 2001; De Pol-Holz et al., 2009).

In recent years, another form of denitrification known as anaerobic ammonia oxidation (anammox) has also been found in OMZs (Murray et al., 2005; Lam et al.,

2009; Bulow et al., 2010; Pitcher et al., 2011). Anammox ($\text{NH}_4^+ + \text{NO}_2 \rightarrow \text{N}_2 + 2 \text{H}_2\text{O}$) is a chemoautotrophic process carried out by bacteria under anoxic conditions.

1.2 Potential Impacts of OMZs on Marine Communities

Recent concerns relating to OMZ expansion in response to climate change have led to more urgent efforts to understand the physical, chemical, and biological features and processes of OMZs (Stramma et al., 2008b; Deutsch et al., 2011; Stramma et al., 2011). Warmer temperatures reduce the amount of gas that can be held in solution; thus warmer oceans may cause a decline in total oceanic dissolved oxygen concentrations (Stramma et al., 2008b). Additionally, climate change related reductions in thermohaline circulation could reduce the exchange of oxygen between water masses at depth (Stramma et al., 2011), although, a recent study argued that warmer temperatures may result in reduced upwelling, lower surface productivity, and smaller OMZs (Ito & Deutsch, 2013). It is important to understand how OMZs affect various processes in order to predict how they may be impacted by climate change.

One important impact of expanding OMZs involves potential changes to the carbon cycle. The biological pump is an important mechanism by which carbon is transported from the mixed layer to the deep sea. Zooplankton undergoing diel vertical migration (DVM) feed in the mixed layer at night and swim to deeper waters during the day (Longhurst, 1991). While at depth, these zooplankton continue to respire and egest waste and are thus responsible for actively transporting carbon from the mixed layer to the deep sea (Longhurst & Harrison, 1989; Longhurst, 1991). Because of the extremely low ($<1 \mu\text{M}$) oxygen concentrations in OMZs, such as those in the Arabian Sea and ETP, all animals living in these areas must employ behavioral

and physiological adaptations to survive. Specifically, many animals avoid the most oxygen depleted regions of OMZs, resulting in vertical patterns of zooplankton biomass and abundance unique to OMZ areas (Saltzman & Wishner, 1997b; a; Wishner et al., 2008; Wishner et al., 2013). Reduced movements of zooplankton biomass into midwater depths may impact the carbon cycle, but much greater understanding of the biological and physiological adaptations and consequences of living in OMZ areas is required in order to fully understand how. It is, therefore, important that we improve our understanding of these processes to understand the full implications of how climate change will affect the carbon cycle in OMZs.

Nearly all organisms living in or near OMZs have physiological adaptations for life at low oxygen concentrations (Flint et al., 1991; Childress & Seibel, 1998; Seibel, 2011). Most OMZ taxa are able to remove oxygen from the water more efficiently than non OMZ taxa (Childress & Seibel, 1998; Seibel, 2011), and the efficiency of any particular animal greatly depends on the lowest oxygen concentration that individual is likely to encounter (Childress & Seibel, 1998; Seibel, 2011). However, when oxygen partial pressures fall below 0.8kPa, adaptations for increasing the efficiency of oxygen removal are no longer sufficient to support aerobic metabolism (Seibel, 2011). Energetic organisms such as pelagic fish may also suffer detrimental effects from OMZ expansion, and some pelagic fish already show signs of reduced diving depths in areas with strong OMZs (Stramma et al., 2010; Stramma et al., 2011). The reduced ranges of these taxa may be the result of the relatively low pH of water within OMZs, which can reduce the efficiency with which animals are able to remove oxygen from the surrounding water (Stramma et al., 2010; Stramma et al.,

2011). However, the majority of zooplankton biomass is often constrained to the upper 100-200m of the water column, so it is also possible that fish migrate to shallower depths because that is where most of their food can be found (Wishner et al., 2013).

In vertical profiles, zooplankton biomass peaks near the thermocline and is lowest within areas of lowest oxygen concentrations (Saltzman & Wishner, 1997b; a; Wishner et al., 2008; Wishner et al., 2013). However, a secondary peak in zooplankton biomass in the lower oxycline suggests that OMZs may impact the efficiency of the biological pump (Saltzman & Wishner, 1997b; a; Wishner et al., 2008; Wishner et al., 2013). In non-OMZ areas, the consumption of organic matter is so efficient that roughly 99% of the organic carbon fixed in the mixed layer is remineralized within the upper water column (Wakeham et al., 1997). Material which is transported to intermediate depths is consumed and subsequently broken up into smaller particles by zooplankton (Van Mooy et al., 2002; Steinberg et al., 2008). Though there is no conclusive evidence that greater particle concentrations are present below OMZs than in non-OMZ areas (e.g. (Lee et al., 1998), low midwater zooplankton abundance in OMZs suggests that less particulate material may be consumed and broken up by zooplankton in OMZs than in comparable non-OMZ areas. It is also unclear what effect the lower oxycline zooplankton community has on carbon transport. This zooplankton community may feed on particles exiting the OMZ core, but gut contents of some zooplankton taxa suggest a potential reliance on microbial food sources as well (Gowing & Wishner, 1992; Wishner et al., 2000). OMZs support large and active microbial communities which thrive on the chemical

gradients present in OMZs and it is possible that some of these microbes may be an important food source for deep zooplankton. Regardless of food sources for these zooplankton, it is vital to understand the trophic strategies of OMZ zooplankton in order to understand the carbon cycle in OMZs.

1.3 Stable Isotope Ecology in Marine Environments

The diets of animals can be examined using several methods including gut content studies, gut fluorescence, examination of fecal pellet contents, and various biomarker studies, including stable isotope analysis. Analysis of stable carbon and nitrogen isotopes can also provide information about food sources and trophic positions of consumers. Carbon and nitrogen isotopes, vital elements found in all living things, can be used together for these purposes. The C and N isotopic compositions of organisms reflect the isotopic composition of the sources of these nutrients as well as any fractionating processes associated with the uptake and incorporation of these elements into their biomass (Fry, 2006; Michener & Lajtha, 2007). In turn, the isotopic compositions of the nutrient source are also a reflection of fractionating processes associated with the biogeochemical cycling of these elements. Observed fractionations in OMZs primarily reflect kinetic isotope effects, driven by the fact that atoms of the heavier isotope make stronger molecular bonds than those of the lighter isotope (Fry, 2006; Michener & Lajtha, 2007). These stronger bonds require more energy to break, resulting in a slower reaction rate for heavier isotopes.

Kinetic isotope effects are also the most common cause for isotope fractionation in biological systems, but the overall difference between the isotope value of the substrate and that of the product is affected by the amount of available

substrate (Fry, 2006; Michener & Lajtha, 2007). For example, phytoplankton in tropical areas have a kinetic fractionation factor of 3-5‰ during the uptake of nitrate (Altabet & Francois, 1994). Because of this, phytoplankton will utilize the available $^{14}\text{NO}_3^-$ molecules before $^{15}\text{NO}_3^-$ are utilized. However, when the water column is stratified, this can be considered a “closed system” because nitrate concentrations are low, and all of the available nitrate is consumed. Therefore, the biomass of phytoplankton in a closed system will have roughly the same $\delta^{15}\text{N}$ value as that of the substrate $\delta^{15}\text{NO}_3^-$ in the surrounding water (Fry, 2006; Michener & Lajtha, 2007). Conversely, in open systems, such as times of upwelling, the amount of available nitrate is practically unlimited. As in the closed system, phytoplankton will utilize $^{14}\text{NO}_3^-$ first, but the nearly unlimited quantity (Fry, 2006; Michener & Lajtha, 2007) is an example of an “open system”. Phytoplankton in open systems have much lower $\delta^{15}\text{N}$ values than those in closed systems because they never run out of $^{14}\text{NO}_3^-$ (Fry, 2006; Michener & Lajtha, 2007). Therefore the difference between the $\delta^{15}\text{N}$ of phytoplankton and $\delta^{15}\text{N}$ of nitrate depends largely on how much nitrate is available.

Food sources and trophic positions are often examined using stable carbon and nitrogen isotopes. $\delta^{13}\text{C}$ values of consumers are mostly dictated by the carbon fixation pathway of primary producers at the base of the food web. In upwelling systems, marine phytoplankton are the primary source of organic matter sinking out of the euphotic zone. Most marine phytoplankton utilize the C3 carbon fixation pathway (Michener & Lajtha, 2007), resulting in a mean $\delta^{13}\text{C}$ value of -22‰, with a range from -30 to -18‰ (Altabet, 1996; Michener & Lajtha, 2007). In addition to photosynthetic carbon fixation pathways, there are a number of chemoautotrophic carbon fixation

pathways which can alter $\delta^{13}\text{C}$ values in different ways. Chemosynthetic carbon fixation is of particular importance in cold seep and hydrothermal vent communities, where many animals rely on symbiotic relationships with chemoautotrophic microbes, or consume free living bacteria directly (Van Dover & Fry, 1989; Burd et al., 2002; Sansone et al., 2004; Bergquist et al., 2007; Macavoy et al., 2008; De Busserolles et al., 2009). In hydrothermal vent communities, animals with chemosynthetic endosymbionts usually have very low $\delta^{13}\text{C}$ values (-35 to -27‰), while organisms feeding on free living bacterial mats often have higher $\delta^{13}\text{C}$ values (-15 to -10‰) relative to average marine phytoplankton (Van Dover & Fry, 1989). Many endosymbionts and free living bacteria in hydrothermal vent communities utilize a form of sulfur oxidation, but different fixation pathways are present (De Busserolles et al., 2009). Cold seep microbes, on the other hand, generally use some form of methane oxidation for chemosynthesis. Methane oxidation produces biomass with $\delta^{13}\text{C}$ values of -65 to -45‰ (Levin et al., 2000; Macavoy et al., 2008). There are a number of other chemoautotrophic processes in marine systems, but their fractionation factors and trophic pathways are not well known and are thus difficult to trace in food webs

. The most important source of nitrogen isotope variation in most ecosystem studies of consensus is trophic enrichment. $\delta^{15}\text{N}$ values of consumers are higher than their food source $\delta^{15}\text{N}$, because urea production favors excretion of $\delta^{15}\text{N}$ (Montoya, 2008b). The amount of fractionation occurring between trophic levels varies by organism, and much recent debate has revolved around this topic. However, there is a consistent change of 1-4‰ between trophic levels for most organisms (Post, 2002;

McCutchan et al., 2003; Hannides et al., 2009; Aita et al., 2011). Because there is also a small (0.5-1‰) enrichment of $\delta^{13}\text{C}$ values with each trophic level, the relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for different animals in a community is very informative about the food sources consumed at the base of the food web and the trophic interactions between zooplankton taxa.

The model presented in Hobson et al (2002) illustrates this relationship very clearly (Fig. 1.1). Although the model outlines a polar food web, it clearly shows the relationship between different consumers and primary producers and how multiple carbon sources can affect the resulting isotope values of consumers. There are two carbon sources, pelagic POM and ice algae, in Hobson's figure, and the consumers reliant upon the two sources are clearly distinguishable. Furthermore, there is a clear trophic progression showing increases in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from primary consumers to polar bears for the pelagic POM-based community. This illustrates the potential power and usefulness of stable isotope analysis for describing trophic interactions in marine systems.

In addition, underlying trophic enrichment, $\delta^{15}\text{N}$ values of consumers also reflect the $\delta^{15}\text{N}$ values of nutrients utilized by the phytoplankton community. The three main processes affecting $\delta^{15}\text{N}$ values of nutrients in marine systems are fractionation of nitrate during uptake and assimilation of nutrients, denitrification, and nitrogen fixation. When nitrate is limiting, phytoplankton $\delta^{15}\text{N}$ values are similar to $\delta^{15}\text{N}$ of nitrate in the water column. However during upwelling or other times of high nitrate abundance, selection for ^{14}N causes phytoplankton $\delta^{15}\text{N}$ to decrease by as much as 2-10‰ (Montoya, 2008b). Denitrification, in contrast, results in the production of a

residual nitrate pool in the OMZ, causing the residual nitrate to have $\delta^{15}\text{NO}_3^-$ values of 15-20‰, as opposed to the 4-5‰ value for mean ocean $\delta^{15}\text{NO}_3^-$ (Montoya, 2008b). Lastly, $\delta^{15}\text{N}$ values of nitrogen fixing phytoplankton have $\delta^{15}\text{N}$ values of -2 to 1‰, because the process of nitrogen fixation does not fractionate atmospheric nitrogen ($\delta^{15}\text{N}=0$) (Montoya et al., 2002; Montoya et al., 2004; Montoya, 2008a). Nitrogen fixation is most prevalent in subtropical gyres. Nitrogen fixation can be carried out only by cyanobacteria, most commonly those of the genus *Trichodesmium* sp. and *Richelia*. However, recent discoveries of picoplanktonic nitrogen fixers have highlighted the potential importance of nitrogen fixers in the marine environment (Montoya et al., 2004; Zehr, 2011).

The goal of this dissertation is to assess the impact of the OMZ environment on the diets and trophic interactions of zooplankton living in different depths. Chapter 2 focuses on the broad impacts of zooplankton community by examining isotope patterns in size fractionated bulk zooplankton and POM. It has been submitted to Deep Sea Research part I. Chapter 3 examines the trophic interactions between different taxa and the trophic structure of the zooplankton community, and has been prepared for submission to Progress in Oceanography. Chapter 4 presents a summary of the major conclusions and suggestions for further research.

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Fig. 1.1: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of polar marine taxa from Figure 1 in Hobson et al (2002). Primary producers are pelagic POM and ice algae, both of which are located to the lower left of consumers.

CHAPTER 2:
TROPHIC ECOLOGY AND VERTICAL TRENDS OF CARBON AND NITROGEN
STABLE ISOTOPES IN OXYGEN MINIMUM ZONE ZOOPLANKTON

By

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Submitted to Deep Sea Research Part I

2.1 Abstract

The unique physical and biogeochemical characteristics of oxygen minimum zones (OMZs) influence plankton ecology, including zooplankton trophic webs. While material produced in the mixed layer is likely an important dietary component for OMZ zooplankton, species living near the upper and lower OMZ oxyclines may utilize novel food resources, such as chemoautotrophic microbes, living at these interfaces. Using carbon and nitrogen stable isotopes, this study examined the importance of potential food sources for the zooplankton community in the Eastern Tropical North Pacific (ETNP) OMZ. $\delta^{13}\text{C}$ values were used to indicate zooplankton food sources, and $\delta^{15}\text{N}$ values were used to indicate zooplankton trophic position and nitrogen cycle pathways. Vertically stratified MOCNESS net tows collected zooplankton from 0-1000 m at two stations along a north-south transect in the ETNP during 2007 and 2008, the Tehuantepec Bowl (TB) and the Costa Rica Dome (CRD). Zooplankton samples were separated into four size fractions for stable isotope analyses. Particulate organic matter (POM) was collected with McLane large volume *in situ* pumps. Zooplankton and POM vertical profiles of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showed strong isotope gradients associated with oxyclines at the upper and lower OMZ boundaries and with particle peaks. Different $\delta^{15}\text{N}$ values for zooplankton at the two stations suggested the presence of different nitrogen cycle processes, such as denitrification, incomplete nitrate utilization, or nitrogen fixation. Shallow POM was likely the primary food source for mixed layer and upper oxycline zooplankton, and multiple carbon sources may have been incorporated into zooplankton diets in that zone. Zooplankton collected in the OMZ core fed primarily on shallow POM,

whereas zooplankton from the lower oxycline likely relied more on deep POM. Strong zooplankton $\delta^{15}\text{N}$ gradients and zooplankton biomass peaks at the lower oxycline also suggested progression up the trophic web (feeding) within this layer.

2.2 Introduction

Oxygen minimum zones (OMZs) are areas of increasing interest because it is believed they will expand in response to warming ocean temperatures associated with climate change (Stramma et al., 2008a). Previous studies have examined how OMZs influence zooplankton abundance and distributions (Saltzman & Wishner, 1997b; a; Madhupratap et al., 2001; Koppelman et al., 2005; Fernández-Álamo & Färber-Lorda, 2006; Escribano et al., 2007; Wishner et al., 2008; Escribano et al., 2009), but effects on zooplankton diets and feeding are uncertain. Because of the potential expansion of OMZs and the importance of zooplankton in the biological pump, it is essential to understand zooplankton diets and feeding in OMZs to fully understand the carbon cycle in these areas.

Extremely low oxygen concentrations in some OMZs affect zooplankton distributions and may influence zooplankton diets in a number of ways. The OMZ may represent a physical barrier for some species which may influence the type or amount of available food as compared to non-OMZ areas. A secondary peak in zooplankton biomass and abundance is often present at depth just below the lowest oxygen concentrations (Saltzman & Wishner, 1997b; a; Wishner et al., 1998; 2008; 2013), and zooplankton congregating to feed on particles or other zooplankton is one explanation for the existence of this peak. Additionally, the biogeochemical gradients bordering OMZs may support midwater microbial processes (Galán et al., 2009; Lam & Kuypers, 2011; Pitcher et al., 2011; Podlaska et al., 2012; Rush et al., 2012) not found in non-OMZ areas. The potential importance of microbial aggregates in the diets of OMZ zooplankton was suggested by Gowing and Wishner (1992; 1998) who

examined zooplankton gut contents in the lower oxycline and OMZ of the Arabian Sea and Eastern Tropical Pacific. Though most species were omnivorous, individual guts of several species contained large amounts of bacteria-like bodies, probably consumed as microbial aggregates (Gowing & Wishner, 1992; 1998). This process may be an important contribution to zooplankton diets at one or both oxyclines.

Stable carbon and nitrogen isotope values were used to investigate the trophic interactions of the OMZ zooplankton community, especially relationships to POM (the assumed food source of zooplankton). Stable isotope values of consumers reflect the average diet and, through analysis of bulk samples, can provide information about zooplankton species that are too small or rare to analyze individually. Carbon stable isotopes ($\delta^{13}\text{C}$) are useful for examining the relative importance of different carbon sources because there is only a small (~ 0.1 - 1‰) increase in $\delta^{13}\text{C}$ with each increase in trophic level (Minagawa & Wada, 1986; McCutchan et al., 2003; Aita et al., 2011). Nitrogen stable isotopes ($\delta^{15}\text{N}$) are commonly used to track trophic positions among taxa because nitrogen values increase by 1.5 - 4‰ with each trophic level (Minagawa & Wada, 1984; Post, 2002; McCutchan et al., 2003; Aita et al., 2011). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can indicate the presence of unique biogeochemical processes that may be reflected in the POM and zooplankton. For example, significant sources of chemoautotrophic carbon fixation should produce material with $\delta^{13}\text{C}$ values different from phytoplankton, and some microbially mediated processes of the nitrogen cycle should produce material with different $\delta^{15}\text{N}$ values.

The aims of this study were to: 1) obtain vertical profiles of carbon and nitrogen stable isotope values for the zooplankton community and its potential food

sources throughout an OMZ, 2) assess relationships between the zooplankton community and potential food sources, 3) examine the potential contribution of selected biogeochemical pathways in zooplankton diets, 4) investigate relationships between the physical environment and zooplankton stable isotope values. This study was carried out in the Eastern Tropical North Pacific (ETNP) a region with a large OMZ and very low oxygen concentrations, ($<2 \mu\text{M}$).

2.3 Methods

2.3.1 *Sample collection and processing*

Zooplankton samples were collected during two cruises. These occurred on the *R.V. Seward Johnson* from 18 October- 6 November 2007 and *R.V. Knorr* from 7 December 2008- 6 January 2009 in the Pacific Ocean west of Central America. Vertically stratified zooplankton samples were collected at two stations: the Costa Rica Dome (CRD) (9°N , 90°W), a site with reported upwelling (although not during our sampling) and high productivity, and the Tehuantepec Bowl (TB) (13°N , 105°W), a site with relatively low productivity (Fiedler & Talley, 2006; Pennington et al., 2006) (Fig. 2.1). Zooplankton samples were collected between 0-1200m using a MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) with $153 \mu\text{m}$ mesh nets (Wiebe et al., 1976). Shallow, mid, and deep tows were used for isotope analysis of zooplankton size fractions in 2008, but only shallow tows were used for that purpose in 2007 (Table 2.1). Environmental data, including temperature, salinity, depth, oxygen concentration, fluorescence, and light transmission (a proxy for particulate concentration), were recorded during all tows. Zooplankton sampling

details and MOCNESS environmental data processing are described in Wishner et al. (2013).

Quarter splits of fresh samples from selected nets (Table 2.1) were refrigerated immediately after collection. To obtain zooplankton samples representative of different trophic levels, each split was poured through a series of sieves to obtain four size classes: 0.2 - 0.5 mm, 0.5 - 1 mm, 1 - 2 mm, and 2 - 5 mm. Material was scooped out of each sieve, stored in a pre-labeled aluminum or glass container, and frozen at -20°C. In the lab, samples were thawed and dried at 70°C for at least 48 hours, then homogenized by grinding to a fine powder using a mortar and pestle (Levin, 2010). All $\delta^{13}\text{C}$ samples were acid fumigated to remove CaCO_3 exoskeletons according to the method in Harris et al. (2001). Stable isotope values were determined using a Carlo-Erba NA 1500 Series II Elemental Analyzer interfaced to a Micromass Optima Isotope Ratio Mass Spectrometer in the Environmental Protection Agency Atlantic Ecology Division, Narragansett, RI. Sample material reanalyzed periodically over a several month period exhibited a precision of ± 0.30 ‰, calculated as a single sigma standard deviation of all replicate values. This latter estimate of precision applies to both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values determined in this study.

A total of 317 zooplankton samples were processed for 2007 and 1033 for 2008, representing material from 59 nets (Table 2.1). Typically, four subsamples of each of the four size classes from each net were analyzed for each isotope; carbon and nitrogen isotopes were obtained from different subsamples. The value for each size class is the mean of its subsamples. The value for each net is the biomass weighted mean of the four size classes from that net.

POM samples were collected *in situ* at each station using McLane WTS-LV large volume *in situ* filtration systems deployed with a CTD cable. Approximately 2000L of water were filtered at each depth. Water was filtered first through a 53µm nitex mesh prefilter, and particles between 0.7-53µm were captured on a 142mm GF/F filter. Material on the filters was assumed to represent zooplankton food sources, and 14mm plugs were removed from each filter for isotope analysis. Filter plugs intended for $\delta^{13}\text{C}$ analysis were acidified. All POM samples were analyzed with a Thermo Scientific Flash EA Series 1112 coupled with a Finnigan Conflow interfaced to a Thermo Delta V isotope ratio mass spectrometer. Biomass weighted means of the two POM size classes were used for all graphs and analyses. Sample stable isotope % C and % N values were calibrated against internal laboratory chitin powder standards, which in turn had previously been cross-calibrated against USGS 40 and 41 international isotope standards

Lipids can have $\delta^{13}\text{C}$ values 6 - 9‰ lower than carbohydrates and proteins, and the amount of lipid may vary significantly from one individual to the next. Therefore, many researchers either chemically extract lipids prior to analysis or use a lipid normalization model afterwards (DeNiro & Epstein, 1977; McConnaughey & McRoy, 1979; Post et al., 2007). To determine whether a lipid normalization model should be used to correct zooplankton $\delta^{13}\text{C}$ values in this study, molar C: N values were calculated and plotted against $\delta^{13}\text{C}$ values in each size class, year, station, and ecological zone.

2.3.2 *Vertical Zonation of the OMZ*

To examine vertical patterns of zooplankton isotope values, five ecological zones were defined using the profile shape and range of oxygen concentrations encountered by each net. Ecological zones were the mixed layer (ML), upper oxycline (UO), oxygen minimum zone core (OM), lower oxycline (LO), and suboxycline (SO) (Fig. 2.2). The conceptual framework for these divisions was derived from the Arabian Sea OMZ (Wishner et al., 2008) and defined for the ETNP in Wishner et al., (2013). Ecological zone divisions for the ETNP were defined as follows: the ML was between the surface and thermocline, the UO extended from the thermocline through the region where oxygen concentrations decreased or were variable, the OM had the lowest oxygen concentrations ($<1.8\mu\text{M}$), the LO was the area below the OM where oxygen concentrations began to increase, and the SO was arbitrarily defined as the area below the LO where oxygen concentrations were $>9\mu\text{M}$.

2.3.3 Data analysis

Correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated possible contributions of multiple carbon or nitrogen sources to zooplankton diets in each ecological zone. To determine whether there were significant differences between zooplankton living in each ecological zone, a 2-factor Permutational Analysis of Variation (PERMANOVA) with a significance level of 0.05 was used. All multivariate procedures followed the methods of Anderson et al. (2008). Relationships between environmental properties and zooplankton isotope values were examined using a Distance-based Linear Model (DISTLIM). DISTLIM results (Table 2.2) were used to select the most appropriate environmental variables for inclusion in a Distance-based Redundancy Analysis (dbRDA) plot. Variation in zooplankton isotope values was tested in relation to four of

the six environmental variables (temperature, salinity, oxygen, and light transmission). Density was not included in the dbRDA model because it was colinear with temperature and salinity. Depth was not included because it strongly influenced nitrogen values and masked the importance of other variables. Finally, because the models require equal sample sizes for all comparisons, only zooplankton samples were included. All multivariate procedures followed the methods of Anderson et al. (2008) and used PRIMER v.6 +PERMANOVA software.

To investigate whether zooplankton ate material from their depth zone or elsewhere, POM values were separated into shallow (0-110m) or deep (110-1000m) groups for each station. Deep suspended POM is characterized by having higher $\delta^{15}\text{N}$ values than shallow suspended POM (Altabet, 1996), and the increase in POM $\delta^{15}\text{N}$ values always occurred below 110m. The fractionation factor associated with an increase of one trophic level was then added to each value. Fractionation occurring with each increase in trophic level is not the same for all organisms, and bulk zooplankton samples contain many different species with different feeding strategies. Therefore, we selected a range of likely trophic fractionation factors ($\Delta^{13}\text{C} = 0.1\text{-}1\text{‰}$; $\Delta^{15}\text{N} = 1\text{-}3.4\text{‰}$) from the literature (Post, 2002; McCutchan et al., 2003; Hannides et al., 2009; Aita et al., 2011) and added the highest and lowest value of that range to each POM value. Consumer polygons were then drawn around the outermost points to enclose the entire calculated range. When compared with zooplankton stable isotope values, these consumer polygons should encompass samples of zooplankton likely to have consumed POM from that depth range.

2.4 Results

2.4.1 *Hydrographic data*

The depth and thickness (vertical extent) of each ecological zone varied between stations and years (2.2). The ML was never more than 40m thick, but UO thickness varied from 40 to 350m. Similarly, the thickness of the OM varied from 200 to 620m. The only SO sample was collected at CRD in 2008. Both sites were strongly stratified with no upwelling during the cruises.

The thermocline marked the upper boundary of the UO (Fig. 2.2). Temperature ranged from a high of 28.4° C in the ML to a low of 4.5° C at 1000m at CRD in 2008. There were primary and secondary peaks in fluorescence at TB in both years, but only a single fluorescence peak at CRD in 2008 (no fluorescence data were available for CRD 2007). Primary fluorescence peaks were coincident with the UO and thermocline in all years. Secondary fluorescence peaks at TB (Tows 605 and 629) occurred at 55m and 107m in 2007 and 2008, respectively. The secondary fluorescence peak at TB in 2007 was also associated with a layer of diatoms (mostly *Rhizosolenia*) that was not observed at other times (Olson & Daly, 2013). Particle peaks in the upper water column generally co-occurred with fluorescence peaks, but those deeper than 200m occurred independently of fluorescence peaks. Deep particle peaks were largest near the LO in TB (Tow 631), and within the OM at CRD in 2008 (Tow 636).

2.4.2 *Stable isotopes and environmental variables*

A total of 43.5% of the variation in the zooplankton stable isotope dataset was associated with temperature, salinity, oxygen, and light transmission, and all four of these variables were statistically significant in sequential tests (Table 2.4). Light

transmission and salinity were associated with the largest variability, followed by oxygen and temperature. Depth also accounted for significant variability in marginal tests but was not considered in the sequential testing, as noted in the methods. In the resulting dbRDA plot (Fig. 2.3), the first axis distinguished between UO, OM, and LO samples. The data described a rough “v” shape, which corresponded horizontally with increasing $\delta^{15}\text{N}$ values (left to right) and vertically with increasing $\delta^{13}\text{C}$ values (bottom to top). On the left side of the “v”, vertical variation corresponded mostly with oxygen, and horizontal variability corresponded with light transmission. The left side of the graph also showed the variability of zooplankton isotope values within the UO. Samples in the right arm of the “v” were associated with salinity and temperature and largely distinguished between OM and LO samples.

2.4.3 Contribution from lipids

There was no apparent effect of lipids on the total $\delta^{13}\text{C}$ value of zooplankton samples, as determined by lack of correlations between $\delta^{13}\text{C}$ and mean molar C: N. Lipids have very low $\delta^{13}\text{C}$ values relative to other biochemical compounds (DeNiro & Epstein, 1977) and have very little nitrogen, so samples containing high concentrations of lipids should have low $\delta^{13}\text{C}$ values and a negative correlation between $\delta^{13}\text{C}$ and C:N (Fanelli et al., 2009; Richoux & Froneman, 2009). However, there was no significant relationship of this type for either POM ($R^2 < 0.25$) or zooplankton ($R^2 < 0.25$). Furthermore, C:N values in this study were < 3.5 , the value below which Post et al. (2007) suggested that lipid concentrations are low enough that lipid normalization is not necessary.

2.4.4 Stable isotope vertical profiles

Zooplankton and POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied between stations and years. The largest isotope gradients occurred at the oxyclines (Fig. 2.4). $\delta^{13}\text{C}$ values of POM and zooplankton followed the same basic patterns with depth through the water column. $\delta^{13}\text{C}$ values of all POM samples decreased by an average of 5.3‰ (± 2.7) between the ML and UO at all stations except CRD in 2008. Zooplankton $\delta^{13}\text{C}$ values also decreased by 1.6-5.7‰ between the ML and UO for most zooplankton size classes at all stations (Fig. 2.5). Deep ($> 110\text{m}$) POM $\delta^{13}\text{C}$ values increased slightly and then gradually decreased with depth through the remainder of the sampled water column (Fig. 2.4).

The most prominent features of $\delta^{15}\text{N}$ vertical profiles were the large between station differences in the upper water column and the large increase in zooplankton $\delta^{15}\text{N}$ values in the LO compared to the OM at both stations in 2008 (Fig. 2.4). POM and zooplankton $\delta^{15}\text{N}$ values in the upper 50m at CRD were, respectively, 5-7‰ and 4-10‰ lower than at TB. Between the OM and LO, zooplankton $\delta^{15}\text{N}$ values increased by an average of 6‰ at both stations. This isotope gradient, which began at the top of the LO, was almost 200m deeper at TB compared to CRD, but occurred at the same oxygen concentration. There was also greater differentiation between zooplankton size classes in the LO than in the OM (Fig. 2.5).

2.4.5 *Zooplankton trophic interactions*

Consumer polygons showed a likely dietary separation between zooplankton from the upper three zones (ML, UO, and OM) compared to the LO zooplankton community at both stations (Fig. 2.6). $\delta^{13}\text{C}$ values of ML zooplankton were significantly higher than those of most UO zooplankton (Fig. 2.6), (PERMANOVA

$p < 0.005$) (Table 2.3). Consumer polygons (Fig. 2.6) and vertical profiles (Fig. 2.4) showed that $\delta^{15}\text{N}$ values of ML, UO, and OM zooplankton were similar, and PERMANOVA results showed there were no significant differences between OM and ML or UO zooplankton (Table 2.3). Nearly all ML, UO, and OM zooplankton at TB fell within or near the shallow consumer polygons (Fig. 2.6), while at CRD, about half of the zooplankton samples from these zones were located within the shallow consumer polygon while the rest fell between the shallow and deep consumer polygons. Some LO zooplankton from both stations fell within or near deep consumer polygons, and LO zooplankton almost always had higher $\delta^{15}\text{N}$ values than zooplankton from other zones. LO zooplankton were also significantly different from UO zooplankton. Unlike most LO zooplankton, samples collected at the depths of peak LO biomass (Wishner et al., 2013) were sometimes different from other LO zooplankton at both stations (Figs. 4 & 6) and had isotopic characteristics more similar to UO or ML zooplankton.

2.5 Discussion

2.5.1 *General trends*

The isotopic composition and trophic ecology of the ETNP zooplankton community had unique spatial and vertical characteristics, which were clearly influenced by the OMZ. Between-station differences in $\delta^{15}\text{N}$ values suggested that different nitrogen cycle processes were present at the two locations. The largest vertical isotope gradients were in the UO and LO. Material with lower $\delta^{13}\text{C}$ values was apparently produced in the UO and was subsequently consumed by zooplankton. Shallow POM (0-110m) was likely the most important food source for ML, UO, and

OM zooplankton. LO zooplankton were more closely associated with deep POM, and vertical gradients in zooplankton $\delta^{15}\text{N}$ values suggested that this community utilized different food sources or trophic strategies than OM zooplankton.

2.5.2 *Comparisons to other regions*

POM and zooplankton $\delta^{13}\text{C}$ values in this study were similar to those reported in previous ETNP studies (Table 2.5). The relatively low POM $\delta^{13}\text{C}$ values measured in the UO at both stations were within the range of values reported at two anoxic basins (the Black Sea and Cariaco Basin) (Table 2.5), but were also similar to those reported near the thermocline in non-OMZ areas (Eadie & Jeffrey, 1973; Jeffrey et al., 1983). Anammox is a chemosynthetic process which has been reported in the ETNP OMZ and both anoxic basins (Francis et al., 2007; Fuchsman et al., 2008; Pitcher et al., 2011; Podlaska et al., 2012; Rush et al., 2012; Wakeham et al., 2012) and produces material with relatively low $\delta^{13}\text{C}$ values (Schouten et al., 2004). It is possible that the presence of chemoautotrophy contributed to the low subsurface $\delta^{13}\text{C}$ values between these locations (Podlaska et al., 2012). However, there are other possible explanations for low $\delta^{13}\text{C}$ values in the upper water column in non-OMZ areas discussed below.

Zooplankton and POM $\delta^{15}\text{N}$ values were markedly different between the two stations, indicating that different nitrogen cycle processes occurred at the two stations. Denitrification occurs in OMZs and results in the formation of $\delta^{15}\text{NO}_3^-$ values up to 6‰ higher than in non-OMZ areas (Altabet, 1996). This nitrate is taken up by phytoplankton in areas where denitrification occurs, producing POM with $\delta^{15}\text{N}$ values 2-4‰ higher than POM in non-OMZ areas (Altabet, 1996; Montoya, 2008b). The comparatively high $\delta^{15}\text{N}$ values of TB zooplankton and POM were similar to those

previously reported in OMZs and likely reflected the presence of denitrification at that station (Table 2.5). In contrast, the comparatively low POM $\delta^{15}\text{N}$ values in the upper 50m of CRD were intermediate to values in the equatorial upwelling region and those in subtropical gyres (Table 2.5).

There are two processes which could have contributed to these relatively low $\delta^{15}\text{N}$ values at CRD. First, incomplete nitrate utilization has been shown to create POM with $\delta^{15}\text{N}$ values as low as 2-3‰ in tropical upwelling zones because $^{14}\text{NO}_3^-$ is abundant and is preferentially taken up by phytoplankton (Altabet, 1996; Montoya, 2008b). Upwelling was not present at CRD in either year but surface nitrate concentrations were 5-11 μM (Daly, unpublished data). Using the method outlined in Lourey et al (2003), theoretical accumulated $\delta^{15}\text{N}$ values of POM ($\delta^{15}\text{N}_{\text{acc}}$) were calculated for the range of nitrate concentrations measured between 0-200m at CRD in both years. Subsurface $\delta^{15}\text{NO}_3^-$ values were assumed to be between 8-11‰ based on $\delta^{15}\text{N}$ values of subsurface POM and tropical Pacific $\delta^{15}\text{NO}_3^-$ values in Rafter (2012). The fractionation factor (ϵ) was assumed to be 5‰ (Altabet, 2001). Though the lowest POM $\delta^{15}\text{N}$ value measured at CRD was -1.8‰ in 2007 and 1.4‰ in 2008, the lowest possible POM value attributable to incomplete nitrate utilization ($\delta^{15}\text{N}_{\text{acc}}$) was 3.1‰. Therefore, another source of low $\delta^{15}\text{N}$ must have contributed to the POM $\delta^{15}\text{N}$ values measured at CRD,

Nitrogen fixing phytoplankton are periodically abundant in subtropical gyres and can produce material with $\delta^{15}\text{N}$ values of -2-1‰ (Montoya, 2008a). The importance of nitrogen fixation in OMZs and anoxic basins has gained recognition in recent years (Fernandez et al., 2011; White et al., 2013), and POM $\delta^{15}\text{N}$ values at CRD

in 2007 were very similar to those recorded for nitrogen fixing organisms (Montoya, 2008b). The following mass balance equation modified from Lourey et al. (2003) was used to determine the fraction of POM contributed by nitrogen fixation (f) in each year: $\delta^{15}\text{N-POM} = \delta^{15}\text{N}_{\text{fix}} * f + \delta^{15}\text{N}_{\text{acc}} * (1-f)$ where $\delta^{15}\text{N-POM}$ is the lowest POM $\delta^{15}\text{N}$ value observed in each year at CRD, $\delta^{15}\text{N}_{\text{fix}}$ is the $\delta^{15}\text{N}$ value of nitrogen fixers (-2‰), and $\delta^{15}\text{N}_{\text{acc}} = 3.1\text{‰}$ (calculated in preceding paragraph). Results showed that 96% and 33% of POM was attributable to nitrogen fixation at CRD in 2007 and 2008, respectively. While an estimated 96% contribution of nitrogen fixation may be unrealistic, fractionation processes occurring during nitrogen fixation have been studied only with respect to *Trichodesmium* spp. and *Richellia* spp. However, other types of nitrogen fixing organisms have been recently identified (Zehr, 2011), and these may produce material with $\delta^{15}\text{N}$ values $<-2\text{‰}$. Therefore, while it is apparent that the two stations were influenced by different processes, further studies are required to isolate which process most influenced CRD $\delta^{15}\text{N}$ values.

2.5.3 Influence of the physical environment

There were clear vertical and spatial trends and interannual differences in zooplankton and POM carbon and nitrogen isotope values at both stations, with the most pronounced gradients occurring near the upper and lower oxyclines. Light transmission and depth were associated with the largest portion of variability in the zooplankton dataset. The association of OM and LO zooplankton isotopic variability with salinity and temperature was likely related to the strong vertical hydrographic gradients. Light transmission is inversely related to particle concentration and is a good indicator of particle layers in the water column. Particle layers were likely

associated with zooplankton isotopic variability because particles, whether composed of microbes, marine snow, phytoplankton, or fecal pellets, make up the base of zooplankton food webs. Thus, particle layers should be locations of feeding in the water column. Zooplankton and POM $\delta^{15}\text{N}$ values at depth may have been influenced by trophic cycling of sinking organic matter through ingestion and fecal pellet production, resulting in higher $\delta^{15}\text{N}$ values of particles in the deeper samples at the LO. Both the consumption of particles with higher $\delta^{15}\text{N}$ values and the higher proportion of carnivorous zooplankton living at depth would cause $\delta^{15}\text{N}$ values to be higher for deep sea zooplankton (Altabet, 1996; Mintenbeck et al., 2007).

2.5.4 Trophic structure of OMZ zooplankton community

Shallow POM was the preferred food source for UO and ML zooplankton at both stations, as evidenced by consumer polygon plots. There was also a consistent pattern of low $\delta^{13}\text{C}$ values for both zooplankton and POM in the UO at both stations in both years. A trophic link between zooplankton and microbial communities at oxygen interfaces was suggested by Gowing and Wishner, (1992; 1998), who found bacteria-like bodies inside guts of ETNP OMZ zooplankton and hypothesized that zooplankton consumed microbial aggregates at the lower oxycline. Biogeochemical gradients at the oxyclines also support populations of chemoautotrophic microbes, including nitrifiers and anammox bacteria. Indicators of these microbes or processes associated with them have been identified in several OMZs (Jaeschke et al., 2007; Galán et al., 2009; Lam et al., 2009; Pitcher et al., 2011) and were sometimes present in the UO during both cruises of this study (Podlaska et al., 2012; Rush et al., 2012). Although processes such as bacterial or archaeal ammonia oxidation may produce POM with

$\delta^{13}\text{C}$ values higher than phytoplankton, anammox produces material with relatively low $\delta^{13}\text{C}$ values (Schouten et al., 2004). Biogeochemical indicators of anammox bacteria coincided with low POC $\delta^{13}\text{C}$ values during the 2007 cruise (Podlaska et al., 2012), suggesting this process may have produced material with low $\delta^{13}\text{C}$ values. Correlations between zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at the UO of TB suggested that only one carbon source contributed to the low $\delta^{13}\text{C}$ values at that station. Zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were not correlated in the UO at CRD, suggesting that more than one carbon source was present at this station.

Two additional causes of low $\delta^{13}\text{C}$ values in the upper 50m are refractory lipids and carbon fractionation by growth limited phytoplankton. Refractory lipids (left by decaying organic material) may collect at the pycnocline and can be consumed by zooplankton (Eadie & Jeffrey, 1973; Jeffrey et al., 1983; Altabet, 1996). Lipids often remain intact long after other compounds have been remineralized, and $\delta^{13}\text{C}$ values are 6-9‰ lower than those of proteins or carbohydrates (DeNiro & Epstein, 1977; Post et al., 2007; Smyntek et al., 2007). Because trophic fractionation of carbon is <1‰, zooplankton consuming refractory lipids would also have lower $\delta^{13}\text{C}$ values. However, high lipid concentrations result in strong negative correlations between $\delta^{13}\text{C}$ and C: N values of zooplankton and POM (Romanuk & Levings, 2005; Fanelli et al., 2009; 2011), yet this did not occur. Therefore, refractory lipids were likely not the cause of the low zooplankton and POM $\delta^{13}\text{C}$ values in the UO. Another possible source of these low values is related to carbon fractionation by some phytoplankton under low growth rates (Laws et al., 1995; Burkhardt et al., 1999). Not all phytoplankton species fractionate carbon at low growth rates, but this varies with

species, and growth parameters of the phytoplankton community during these cruises are not known. Therefore, the question of which process was responsible for low $\delta^{13}\text{C}$ values could not be resolved with the available data.

In the OM, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicated that zooplankton primarily consumed food from shallow water. OM zooplankton fell entirely within shallow consumer polygons, and zooplankton $\delta^{15}\text{N}$ values were either lower than or equal to the nearest measured POM $\delta^{15}\text{N}$ values. Even the most conservative estimates of trophic fractionation require that zooplankton $\delta^{15}\text{N}$ values be higher than their primary food source (McCutchan et al., 2003), which indicates that OM POM was likely not a major food source for OM zooplankton. The association between OM zooplankton and shallow consumer polygons suggests that zooplankton either migrated to shallower depths to feed or fed at depth on large, rapidly sinking material that retained the isotopic properties of shallow POM. Feeding at depth may be unlikely because metabolic suppression was observed for some OM zooplankton species at low oxygen concentrations (Cass, 2011; Maas et al., 2012).

Zooplankton $\delta^{15}\text{N}$ values increased in the LO at both stations, indicating that there was a change in either diet or trophic activity between the OM and LO. This occurred at similar oxygen levels but different depths at the two stations (Wishner et al., 2013). Zooplankton gut contents from an earlier study indicated most animals had omnivorous diets, including detrital material originating in the ML, remains of other zooplankton, and bacteria-like bodies, (Gowing & Wishner, 1992; 1998). In this study, LO zooplankton fell within or near deep consumer polygons suggesting they had a greater reliance on deep POM than zooplankton from shallower zones.

However, the overlap between deep and shallow polygons and intermediate positioning of most LO zooplankton samples suggest that shallow POM was also a component of LO zooplankton diets. Furthermore, differentiation between $\delta^{15}\text{N}$ values of zooplankton size classes in the LO also suggested an increase in the proportion of carnivorous species in this zone compared to the OM.

Although the LO was notable both for the secondary zooplankton biomass peak (Wishner et al., 2013) and strong gradients of zooplankton $\delta^{15}\text{N}$ values, these features did not always occur at the same depth. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of zooplankton samples collected at the LO biomass peak in 2008 were lower than those of the LO zooplankton community peak (Wishner et al., 2013) and were isotopically more similar to zooplankton from the ML and UO. The most abundant species from this biomass peak in 2008 was a seasonal resting population of the copepod *Eucalanus inermis* (Wishner et al., 2013), and the isotopic composition of this species may have dominated the analysis. Like the shallower population of *E. inermis* examined by Cass (2011), the LO population may have fed near the surface at an earlier point in its life history before migrating into the LO .

2.6 Conclusions

The ETNP OMZ zooplankton community likely consumed food with a variety of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Differences between $\delta^{15}\text{N}$ values at the two stations suggested that different processes such as denitrification, incomplete nitrate utilization, or nitrogen fixation were present at the two stations. In the UO of both stations, POM and zooplankton $\delta^{13}\text{C}$ values indicated that a source of low $\delta^{13}\text{C}$

material, possibly representing chemoautotrophic carbon fixation, entered zooplankton food webs, but other processes causing similar values could not be ruled out.

The majority of the OM community did not feed on deep POM, suggesting either that they fed only in shallow water during vertical migrations or on large, rapidly sinking surface derived particles at depth. The LO zooplankton community was also notable for the strong depth gradient of $\delta^{15}\text{N}$, indicating a change in diet or overall trophic activity. Low $\delta^{15}\text{N}$ values associated with the secondary zooplankton biomass peak in the LO in 2008 may represent a resting stage population of *E. inermis*, a common copepod species (Wishner et al., 2013). The variable trophic strategies of zooplankton in different zones of the OMZ likely play an important role in carbon export because of the influence of zooplankton in repackaging particles at depth (Steinberg et al., 2008; Wilson et al., 2008; Escribano et al., 2009).

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Table 2.1: Tows and depth ranges for MOCNESS tows and pump casts. TB is the Tehuantepec Bowl and CRD is the Costa Rica Dome.

MOCNESS Tows								
Year	Station	Date (GMT)	Time (local)		Tow #	Depth	Depth Intervals of Samples Used in Stable Isotope Analysis	# of nets
			Start	End				
2007	TB	Oct-27	10:10	11:50	605	0-250	0-35-40-60-80-100-150-190-250	8
	CRD	Nov-9	10:44	12:36	618	0-150	0-20-30-40-50-60-80-100-150	8
2008	TB	Dec-15	13:20	14:55	626	0-150	40-50-60-80	3
		Dec-20	01:20	02:52	633	0-150	0-20-30-40-50-60-80-100-150	8
		Dec-17	20:37	00:54	629	150-550	150-200-250-300-350-400	5
		Dec-18	11:59	18:12	631	550-1000	550-700-775-800-825-850-875-900-1000	8
	CRD	Dec-28	09:53	11:16	635	0-150	0-20-30-40-50-60-80-100-150	8
		Dec-29	09:59	13:55	637	150-550	150-200-250-300-350-400-450; 500-550	7
		Dec-29	21:53	03:35	636	525-1000	525-550; 575-600; 625-650; 900-1000	4
		Total # of Nets Sampled						
Pump Casts								
Year	Station	Date (GMT)	Time (local)	CTD Cast #	Sample Depths	# of Samples		
2007	TB	Oct-29	17:25	SJ07.042	3, 25, 35, 75, 120	5		
		Oct-31	06:20	SJ07.058	200	1		
	CRD	Nov-10	19:24	SJ07.124	3, 10, 25, 50, 125,	5		
		Nov-11	16:31	SJ07.133	200	1		
		Dec-20	17:00	KN08-15	3	1		
2008	TB	Dec-17	09:20	KN08-08 & 09	50, 110, 500, 750	4		
		Dec-19	23:55	KN08-12 & 13	326	1		
		Dec-31	05:32	KN08-35	28, 156	2		
	CRD	Jan-2	12:39	KN08-40	264, 409	2		
		Dec-31	23:11	KN08-37	540, 690	2		
		Total # of POM Samples						24

Table 2.2: Table of statistical tests used in this study. Permutational Analysis of Variance (PERMANOVA), Distance Based Linear Model (DISTLIM), and Distance Based Redundancy Analysis (dbRDA) were calculated using PRIMER v6 +PERMANOVA (Clarke & Gorley, 2001; Anderson et al., 2008)

Test	Purpose	Preliminary Tests/ Transformations	Factors	Data Used
2- way PERMANOVA	Examines differences between isotope values in different ecological zones	Normalized data; Euclidean distance similarity matrix, PERMDISP	Station Ecological Zone	2008 zooplankton
DISTLIM	Determines which environmental factors are significantly related to isotopic variability	Euclidean distance similarity matrix	N/A	All zooplankton
dbRDA	Plots the combination determined by DISTLIM in a principle component ordination with vector overlay of environmental covariates	See above for DISTLIM	N/A	See above for DISTLIM

Table 2.3: Results from 2-way PERMANOVA comparing zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes between stations and ecological zones. ML is the mixed layer, UO is the upper oxycline, OMZ is the OMZ core, and LO is the lower oxycline. Only data from 2008 were used in these comparisons. * indicates significant results.

2-way PERMANOVA	df	SS	MS	Pseudo-F	p
Station	1	20.49	20.49	14.69	0.0001*
Ecological Zones	3	13.12	4.37	1.13	0.0204*
Station x Ecological Zone	3	3.70	1.23	0.88	0.4717
Pair-wise Tests for Ecological Zones				t	P
ML, UO				2.18	0.043*
UO, LO				2.35	0.012*
UO, OM				1.64	0.105
OM, LO				1.65	0.103
OM, ML				1.32	0.186
LO, ML				0.99	0.356

Table 2.4: Relationship between environmental variables and Eastern Tropical North Pacific OMZ zooplankton isotope data based on a forward selected R^2 DISTLIM test (Table 3). Marginal tests consider the importance of each variable in the absence of the other variables. Sequential tests consider the importance of variables in conjunction with the other variables starting with the variable explaining the greatest variance. * indicates significant results

<i>DISTLIM Test Results</i>			
Environmental Parameter	Pseudo-F	p	% Explained Variance
Marginal Tests			
Light Transmission	16.40	0.0001*	20.65
Salinity	2.65	0.0687	4.51
Oxygen	5.30	0.0101*	8.65
Temperature	5.11	0.0095*	8.37
Depth	14.56	0.0001*	20.64
Sequential Tests			
Light Transmission	16.40	0.0001*	20.66
Salinity	8.46	0.0002*	10.32
Oxygen	6.51	0.0018*	7.21
Temperature	3.11	0.0320*	3.31
<i>Total Variance Explained</i>			<i>43.49%</i>

Table 2.5: Ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for POM and zooplankton from this and other studies.

Location	POM				Zooplankton				Depth (m)
	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		
<i>Pacific Ocean</i>									
W. Australia	-23.5	-19.7 ^a	4.9	7.3 ^a	-23.4	-19.7 ^a	5.4	6.9 ^a	0-150
Station ALOHA	-26.5	-23.1 ^b					1.2	11.5 ^{c,d*}	1- 1000
California Bight							8.1	12.3 ^{d*}	euphotic
California Current							9.3	14.3 ^{e*}	
Juan de Fuca Ridge					-26.9	-17.6 ^f	5.8	17.1 ^f	epibenthic
Alaska					-23.0	-19.4 ^g	8.3	12.0 ^g	0- 50
9°S 140°W	-21.0 ^h		8.4 ^h						euphotic
5°S 140°W	-21.9	-20.9 ^h	2.1	3.1 ^h					euphotic
0° 140°W	-22.4	-21.7 ^h	3.0	3.3 ^h					euphotic
5°N 140°W	-22.1	-21.6 ^h	7.4	7.5 ^h					euphotic
9°N 140°W	-22.5	-20.6 ^h	4.6	7.3 ^h					euphotic
<i>Atlantic Ocean</i>									
Gulf of Maine					-23.1	-22.0 ⁱ	5.5	9.2 ⁱ	euphotic
Georges Bank					-22.8	-18.6 ⁱ	6.3	8.6 ⁱ	euphotic
Sargasso Sea			-1.0	8.2 ^{ij}	-21.2	-19.0 ^j	0.6	6.9 ^k	0- 300
South Atlantic					-28.4	-21.3 ^l	3.0	9.9 ^l	5- 1600
<i>Other</i>									
Baltic Sea					-26.2	-21.9 ^m	3.7	10.6 ^m	5- 10
Gulf of California	-23.4	-19.5 ⁿ	7.0	11.3 ⁿ					360
Mediterranean	-23.8	-18.5 ^{o,p}	1.4	7.5 ^{o,p}	-22.4	-17.1 ^p	1.5	11.4 ^p	0- 1000
Southern Ocean	-24.9	-22.5 ^{q,r}	2.5	5.5 ^q	-27.0	-17.5 ^{q,r}	-1.6	10.3 ^{q,r}	140- 300
<i>OMZs and Anoxic Basins</i>									
Black Sea	-26.3	-21.6 ^{o,†}	-8.1	14.8 ^{o,s,†}					0- 280
Cariaco Basin	-27.5	-17.7 ^{t,u,v}	2.5	6.1 ^w					290- 1000
Arabian Sea							4.4	14.2 ^x	0- 1000
ETNP (Other Studies)	-28.2	-21.4 ^{y,z}	0.8	13.4 ^z	-20.6	-19.9 ^{aa,§}			0-1000
TB 2007 (This Study)	-26.2	-22.4	5.3	10.7	-27.5	-19.6	4.9	10.7	0- 225
TB 2008	-23.9	-20.9	5.6	11.9	-23.7	-17.9	6.1	15.7	0- 1000
CRD 2007	-26.9	-22.4	-1.9	9.6	-22.6	-19.8	3.3	9.2	0- 225
CRD 2008	-23.3	-21.4	1.4	11.2	-23.3	-18.7	2.2	12.6	0- 1000

*a. Waite et al., 2007; b. Sannigrahi et al., 2005; c. Hannides et al., 2009; d. Mullin et al., 1984; e. Ohman et al., 2012; f. Burd et al., 2002; g. Kline, 1999; h. Altabet, 2001; i. Fry and Quinones, 1994; j. Montoya et al., 2002; k. Mintenbeck et al., 2007; l. Laakmann and Auel, 2007; m. Rolff et al., 2000; n. Aquina et al., 2010; o. Coban – Yildiz et al., 2006; p. Kopplemann et al. 2009; q. Kahler et al., 2000; r. Richoux and Froneman, 2009; s. Fuchsman et al. 2008; ; t. Thunell et al., 2000; u. Woodworth et al., 2004; v. Wakeham et al. submitted; w. Thunell, 2004; x. Kopplemann and Wiekert, 2000; y. Jeffrey et al., 1983; z. Voss et al., 2001; aa.. Rau et al., 1983; * samples collected in euphotic zone; † only samples collected above the anoxic zone were included; ^z samples collected at 0-400m; [§] samples collected at 0- 15m.*

Fig. 2.1: Station map

Fig. 2.2: Hydrographic profiles of a) TB in 2007, b) CRD in 2007, c) TB in 2008, and d) CRD in 2008. Profiles are truncated to the depth where isotopic data were obtained. Shaded areas represent the oxygen minimum zone core. Graph d) has all five ecological zones delineated by dotted lines and labeled to the right. ML= mixed layer, UO= upper oxycline, OM= oxygen minimum zone core, LO= lower oxycline, and SO= suboxycline. Data are from MOCNESS tows 605, 618, 626, 629, 631, 635, 636, and 637. More extensive hydrographic analyses are found in Wishner et. al. (2013).

Fig. 2.3 dbRDA plot of zooplankton stable isotope values from all stations and years. The length and direction of each vector relates to its partial correlation with the dbRDA axes. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with arrow symbols represent the direction of association of each isotope with the plotted data. See Table 2.2 for statistical parameters

Fig. 2.4: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vertical profiles of the biomass weighted means of zooplankton size classes, POM and oxygen. Shaded areas represent the extent of the OMZ core. The red asterisk represents the depth of the secondary zooplankton biomass peak

Fig. 2.5: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vertical profiles of separate zooplankton size fractions for rows a) 2007 TB, b) 2007 CRD, c) 2008 TB, and d) 2008 CRD. Open symbols are $\delta^{13}\text{C}$ values and filled symbols are $\delta^{15}\text{N}$ values. Depths where no data were available for a given size fraction are represented by broken lines. Only samples between 0- 250m were collected in 2007.

Fig. 2.6: 2007 and 2008 zooplankton biomass weighted means for TB and CRD. Green consumer polygons represent the likely range zooplankton feeding primarily on shallow (0-110m) POM and blue consumer polygons represent the range for zooplankton feeding on deep (110-1000m) POM. Light blue triangles represent zooplankton from the LO biomass peak.

Fig. 2.7: $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ of all zooplankton size classes at TB and CRD in both years for each ecological zone. Closed symbols represent zooplankton samples and open symbols represent POM values. Triangles represent data from 2007 and circles represent 2008 data. Regression lines and equations were calculated using zooplankton values only.

CHAPTER 3:
TROPHIC INTERACTIONS OF ZOOPLANKTON TAXA IN AN OXYGEN
MINIMUM ZONE

By

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This paper is written for submission to Progress in Oceanography

3.1 Abstract

Physical and chemical characteristics of oxygen minimum zones (OMZs) affect zooplankton distributions, but their effect on zooplankton diets is not well understood. This study examined diets and trophic interactions of zooplankton taxa in an OMZ using stable carbon and nitrogen isotopes. $\delta^{13}\text{C}$ values were used to track zooplankton food sources, and $\delta^{15}\text{N}$ values indicated zooplankton trophic position and nitrogen sources. Vertically-stratified MOCNESS tows collected environmental data and zooplankton from 0-1000 m at two stations, the Tehuantepec Bowl (TB) and Costa Rica Dome (CRD), along a north-south transect in the Eastern Tropical North Pacific during 2007 and 2008 as part of the Eastern Tropical Pacific Project. Individual taxa were analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C:N ratios. Vertical profiles of particulate organic matter (POM), a likely food source for zooplankton, were also collected using McLane large volume *in situ* pumps. Results showed significant differences between stable isotope values of deep and shallow zooplankton. Individuals collected within or above the OMZ core were mostly associated with shallow (0-110m) POM food sources. Zooplankton collected below the OMZ core had higher $\delta^{15}\text{N}$ values than those from within or above the OMZ core and were associated with deep (110-1000m) POM food sources. Zooplankton at CRD showed indications of multiple carbon or nitrogen sources entering the trophic web, while TB zooplankton appeared to have only a single carbon and nitrogen food source. OMZ zooplankton had different trophic strategies, indicated by isotopic differences among taxonomic groups and trophic level calculations. There were significant differences in stable isotope values between zooplankton identified *a priori* (from the literature) as particle feeders versus those identified as carnivores or omnivores. Independent trophic

level calculations based on measured $\delta^{15}\text{N}$ values confirmed the presence of different trophic strategies. Several key taxa, including the copepods *Eucalanus inermis*, *Pleuromamma johnsoni*, and *Lucicutia hulsemannae*, had distinct isotope signatures relative either to other taxa collected at the same depth or to expectations based on previous studies.

3.2 Introduction

Oxygen Minimum Zones (OMZs) are found in most oceans, but the largest and most hypoxic are located in the Arabian Sea and Eastern Tropical Pacific (e.g. Fiedler & Talley, 2006; Paulmier & Ruiz-Pino, 2009; Ito & Deutsch, 2013). As global average temperatures increase, OMZs are predicted to expand in size, become thicker, and become more hypoxic (Stramma et al., 2008b; Stramma et al., 2010; Stramma et al., 2011). Marine zooplankton in these OMZs play a fundamental role in the biological pump and global carbon cycle by repackaging small particles into rapidly sinking fecal pellets, and by feeding at the surface and then vertically migrating to depth where carbon is released via respiration, excretion, and egestion (Longhurst & Harrison, 1989; Longhurst, 1991; Ducklow et al., 2001). To understand the functioning of the carbon cycle in OMZs, it is important to identify how different zooplankton taxa are influenced by the structure and processes of OMZs. While several studies have examined the impacts of OMZs on zooplankton distribution and abundance, the influence of these OMZ's on zooplankton diets and, thus, their role in the global carbon cycle is currently not as well understood.

OMZs are characterized by midwater areas with very low oxygen concentrations (Karstensen et al., 2008; Paulmier & Ruiz-Piño, 2009) that can sometimes approach 0 μM (Thamdrup et al., 2012). Although oxygen concentrations are often lower in the mesopelagic zone relative to the mixed layer or deep sea, oxygen concentrations in OMZs can be 50 times lower than at comparable depths in non-OMZ areas (Wishner et al., 1990; Childress & Seibel, 1998; Wishner et al., 2008; Paulmier & Ruiz-Piño, 2009). Within the regions of lowest oxygen concentrations inside an OMZ, zooplankton

abundance and biomass are much lower when compared to similar depths in non-OMZ areas, and many species have reduced vertical ranges. Zooplankton communities living in near-surface waters in areas with or without an OMZ are dominated by herbivorous species and employ similar trophic strategies (Longhurst & Harrison, 1989; Saltzman & Wishner, 1997b; a; Escibano et al., 2007; Escibano et al., 2009; Williams et al., submitted). Some species undergo diel vertical migration between deeper water and the upper water column, typically feeding at shallower depths (Miller, 2004). Species living within OMZs have a number of adaptations to aid survival at very low oxygen concentrations. Adaptations include the ability to efficiently remove oxygen from the water, reduced metabolic rates, or anaerobic respiration (Ellington, 1983; Flint et al., 1991; Childress & Seibel, 1998; Cass, 2011; Seibel, 2011). The trophic structure of zooplankton communities inside OMZs is not well understood, but the need to conserve energy at such low oxygen concentrations may favor less active trophic strategies (e.g. suspension feeders) than would be found in communities from the same depths in non-OMZ areas. Conversely, some taxa found in the OMZ core may feed only in the oxygenated surface waters during diel vertical migration.

One method of examining the impact of OMZs on the carbon cycle has been to study how zooplankton abundance and distribution change with depth through an OMZ (Saltzman & Wishner, 1997b; a; Wishner et al., 2008; Wishner et al., 2013). In OMZs, zooplankton biomass and abundance is highest near the surface and lowest in the region of lowest oxygen concentrations. There is also a secondary zooplankton biomass peak located in the lower oxycline, just below the area of lowest oxygen concentrations, a feature not found in non-OMZ areas (Wishner et al., 1995; Saltzman & Wishner, 1997b;

a; Gowing et al., 2003; Wishner et al., 2008; Wishner et al., 2013). The lower oxycline zooplankton community has been a subject of interest for some time because of its proximity to potential food sources such as particles exiting the OMZ, and to redox transition zones which support a variety of microbial processes (Wishner et al., 1995; Gowing et al., 2003; Ward et al., 2009; Lam & Kuypers, 2011; Pitcher et al., 2011). If the lower oxycline zooplankton community has access to significant quantities of particulate or microbial food sources, it may contain a much greater number of particle feeders than deep sea zooplankton communities in non OMZ areas, which are dominated by carnivorous and omnivorous taxa (Yamaguchi et al., 2002; Hannides et al., 2009; Wilson & Steinberg, 2010). Studies of zooplankton gut contents from the lower oxycline have found a variety of trophic strategies among taxa associated with this community, including omnivory, detritivory, and carnivory, and showed no clear dominance by any trophic guild (Gowing & Wishner, 1992; 1998). Additionally, large amounts of material resembling bacteria were found in zooplankton guts examined in studies of lower oxycline zooplankton diets in the ETNP and Arabian Sea OMZs (Gowing & Wishner, 1998; Wishner et al., 2000). The quantity and ubiquity of this material suggested a trophic link between zooplankton and the microbial community, but it was not known if these microbes originated *in situ* or were attached to sinking material, or if they were assimilated by zooplankton versus remaining intact and bound inside fecal pellets (Gowing & Wishner, 1992; 1998).

In the past, analysis of zooplankton gut contents was a common method for obtaining information about consumer diets, but this method is very labor intensive and may under or over value the contributions of certain prey types because of net feeding

and unequal rates of digestion for different taxa (Harris et al., 2000). Analysis of stable carbon and nitrogen isotopes provides information about diets over longer timescales than gut content analysis and is therefore less susceptible to confounding factors such as net feeding (Michener & Kaufman, 2007; Michener & Lajtha, 2007). Stable isotope analysis is also less labor intensive than gut content studies, allowing for the analysis of a greater number of samples. Zooplankton $\delta^{13}\text{C}$ values are related to carbon sources and increase by a small amount (~ 0.1 - 1‰) with increasing trophic level (Minagawa & Wada, 1986; McCutchan et al., 2003; Aita et al., 2011). $\delta^{15}\text{N}$ values increase by 1.5 - 4‰ with each trophic level (Minagawa & Wada, 1984; Post, 2002; McCutchan et al., 2003; Aita et al., 2011). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are thus able to provide information relating to trophic position. $\delta^{15}\text{N}$ values can also indicate the presence of multiple nitrogen sources such as products of upwelling and nitrogen fixation.

Elemental ratios of carbon and nitrogen are related to zooplankton body composition, and C: N ratios can be calculated using data collected during stable isotope analysis (see methods). For marine zooplankton, C:N ratios provide information about relative amounts of lipid and protein in body tissues (Ventura & Catalan, 2008; Ikeda, 2012). Correlations between C: N and $\delta^{13}\text{C}$ values are also often used to examine the impact of lipid concentration on the interpretation of $\delta^{13}\text{C}$ data (McConnaughey & McRoy, 1979; Post et al., 2007). Also, because both C: N ratios and $\delta^{15}\text{N}$ ratios can change during periods of diapause, the relationship between them can provide information about the life history strategies of some taxa (Adams & Sterner, 2000; Forest et al., 2011).

The purpose of this study, a part of the Eastern Tropical Pacific (ETP) project, was to examine trophic interactions and food sources of ETNP zooplankton taxa throughout the OMZ using stable carbon and nitrogen isotope analysis of the bulk tissues of individual taxa. We hypothesized that the elemental and isotopic compositions of taxa collected within the OMZ differed from those in the mixed layer and in mesopelagic non-OMZ regions. We further expected that zooplankton trophic webs in the mixed layer above the OMZ were similar to those in other tropical areas without OMZs. Zooplankton trophic strategies were also expected to be influenced by depth and oxygen gradients. Finally, we hypothesized that some zooplankton taxa would have isotope values indicating trophic links between zooplankton and chemoautotrophic microbes.

A previous manuscript (Chapter 2 of this thesis) presented stable C and N isotope values of bulk mixed zooplankton obtained from the same samples as individual taxa reported here. POM data from in situ pump casts were also described. Zooplankton collected within or above the OMZ core (the zone of lowest oxygen concentrations) were associated with shallow food sources (POM from 0-110m), while those below the OMZ core were associated with deep food sources (POM from 110-1000m). This suggested that species living in the OMZ core either migrated to the surface to feed or consumed large, rapidly sinking particles *in situ*. No evidence of a trophic link between the chemoautotrophic microbial community and bulk zooplankton was found, but this did not rule out the potential importance of chemoautotrophic microbes as a food source for some taxa. Furthermore, there was a large difference in both zooplankton and POM $\delta^{15}\text{N}$ values between stations, likely related to the presence of episodic nitrogen fixation at the Costa Rica Dome.

3.3 Methods

3.3.1 *Sample collection and processing*

Zooplankton samples were collected in the Pacific Ocean west of Central America on the *R.V. Seward Johnson* from 18 October- 6 November 2007 and on the *R.V. Knorr* from 7 December 2008- 6 January 2009 as part of the ETP project (Wishner et al., 2013). MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) tows using 153 μm mesh nets were used during day and night to collect vertically stratified zooplankton samples between 0-1200m at two stations: the Costa Rica Dome (CRD) (9° N, 90°W) and the Tehuantepec Bowl (TB) (13°N, 105°W) (Wiebe et al., 1976) (Fig. 3.1). During both cruises, zooplankton taxa were selected from shallow, mid, and deep tows, and samples were also selected from standard tows (extending from 0-1200m) in 2007 (Table 3.1). However, it was not possible to obtain day and night isotope samples from the same depths at both stations in both years. Temperature, salinity, depth, oxygen concentration, fluorescence, and light transmission were recorded during all tows. Zooplankton sampling details and MOCNESS environmental data processing are described in Wishner et al. (2013).

Quarter splits of fresh samples from selected nets (Table 3.1) were refrigerated immediately after collection. All samples were examined at sea under a dissecting microscope, and zooplankton individual taxa were removed using forceps. The criteria for selecting zooplankton taxa for stable isotope analysis were designed to maximize the variety of taxa collected while minimizing sample processing time. Therefore, only taxa that were >2mm in length, easily identifiable under a dissecting microscope, and relatively abundant were selected for analysis. Copepods collected during this study

were identified to species when possible, and were otherwise grouped by genus, while non-copepod taxa were identified to broad groups. Neither gender nor life stages were identified for any taxon. Reference samples were collected and preserved in 4% borate buffered formalin for most species. Taxa were identified using a set of digital photographs of tropical zooplankton species, on a 5th generation iPod with a screen resolution of 162 dpi. Zooplankton depicted in identification photographs were collected in the Cariaco Basin and identified by graduate students in the Daly Lab at the University of South Florida (Owre & Foyo, 1967; Boltovskoy, 1999). For species from the ETNP not found in the Cariaco Basin, zooplankton identification photographs were created by photographing reference samples from a previous study of ETNP zooplankton (Fleminger, 1973; Saltzman & Wishner, 1997b; a; Ferrari & Saltzman, 1998; Markhaseva & Ferrari, 2005). Identifications were confirmed microscopically by an experienced zooplankton technician (Outram).

Taxa were analyzed according to the relevant methods outlined for infauna and fish in Levin and Currin (2012). However, samples were not incubated for evacuation of gut contents because many of the deeper zooplankton were likely not alive by the time of processing, although samples were typically refrigerated for several hours before processing. Additionally, taxa 2-4mm in length were rinsed in deionized (DI) water, placed in pre-weighed tin capsules, and dried at 65°C at sea. Multiple individuals of the same species were put in each capsule. In the lab, each tin capsule was weighed using a Cahn ATI microbalance, and the mass of the tin capsule (measured prior to the cruise) was subtracted from the result to determine the sample mass. When sample masses exceeded 0.5mg for $\delta^{13}\text{C}$ or 1.2mg for $\delta^{15}\text{N}$ (the respective mass limits of the mass

spectrometer), a clean forceps was used to remove some material from the capsule into a separate pre-weighed capsule. Typically, 4 $\delta^{13}\text{C}$ and 4 $\delta^{15}\text{N}$ samples were created for each taxon sampled in each net, and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of both capsules were averaged to estimate a composite $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value for each sample. Means and standard deviations of all samples of a taxon from a single net (using composite values when appropriate) were calculated to obtain a single “net average” $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for that taxon. A list of taxa can be found in Table 3.2.

For taxa in the >4 mm size range, the mass of a single individual would have exceeded the carbon mass limit of the mass spectrometer. Therefore, while nitrogen samples were collected in the same manner described above for smaller taxa, carbon samples were collected as follows. For a particular taxon in a single net, four sample vials were filled with filtered seawater, 3-6 individuals were placed in each vial, and the vials were frozen at -20°C. Onshore, vials were thawed and the zooplankton in each vial were rinsed in DI, placed in an aluminum weigh boat, and dried for at least 24hrs at 65°C. The material in each weigh boat was ground using a mortar and pestle, and the resulting powder was transferred to a pre-combusted glass vial. 2-4 replicates of material from each sample vial were analyzed, and the resulting $\delta^{13}\text{C}$ values were averaged to obtain a mean (composite) value for each of the four carbon samples collected. “Net averages” for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were then calculated as described above for smaller taxa. Taxa >1 cm in length were dissected to remove digestive organs, scales, and exoskeletons prior to grinding, and a portion of the ground material was analyzed.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured using a Carlo-Erba NA 1500 Series II Elemental Analyzer interfaced to a Micromass Optima Isotope Ratio Mass Spectrometer

in the Environmental Protection Agency Atlantic Ecology Division, Narragansett, RI. The instrument precision was ± 0.30 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and all runs were corrected for linearity. The order of samples was randomized prior to analysis to spread samples of each species and tow across multiple runs. A total of 674 zooplankton samples were processed for individual taxa in 2007 and 816 in 2008, representing material from 25 taxa in 83 nets (Tables 1 and 2).

Elemental compositions of zooplankton were calculated using data from the elemental analyzer attached to the mass spectrometer. Several different masses of a standard (urea) with a known elemental composition were weighed out and analyzed during each sample run. The mass of each standard was plotted against the beam area (measured by the elemental analyzer) and the slope of the resulting line was determined. The mass of C or N in each sample was determined by dividing the beam area measured for that sample by the slope of the regression line mentioned above. %C or %N values were then determined by dividing the calculated C or N mass of each sample by the total mass of that sample and multiplying by 100. To simplify the description of how C: N ratios were calculated, we will explain the process for a single taxon in one net; these calculations were repeated for each taxon in each net. First, all %C samples were averaged to obtain the net mean %C value, and the process was repeated for %N values and for all sample masses of a particular taxon. %C and %N values were then multiplied by the average sample mass to determine the mass of carbon and nitrogen for all samples of a particular taxon measured in the net. The molar C: N ratios were then calculated by the following formula: $\text{C: N} = (\text{Mass C} / 12.01) / (\text{Mass N} / 14.0)$.

3.3.2 *Vertical Zonation of the OMZ*

Five ecological zones, the mixed layer (ML), upper oxycline (UO), oxygen minimum zone core (OM), lower oxycline (LO), and suboxycline (SO) were defined using the profile shape and range of oxygen concentrations measured during each tow (Fig. 3.2). A detailed explanation of the criteria for these divisions is outlined in Wishner et al., (2013) but they are broadly defined as follows: the ML was between the surface and thermocline, the UO extended from the thermocline through the region of decreasing or variable oxygen concentrations, the OM was the region with the lowest oxygen concentrations ($<1.8\mu\text{M}$), the area below the OM where oxygen concentrations began to increase was the LO, and the SO began at the depth below the LO where oxygen concentrations were $>9\mu\text{M}$, which was an arbitrary boundary definition.

3.3.3 *Data analysis*

Zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were analyzed to examine relationships between stations, ecological zones, and collection time (i.e. day or night) using a 3-way Permutational Multivariate Analysis of Variance (PERMANOVA). The contribution of temperature, oxygen concentration, and % light transmission to variability in individual zooplankton taxa stable isotope values was investigated using a distance based linear model (DISTLIM). Depth was not included in this model because it is strongly correlated with temperature and the combined influence of both factors would obscure the contribution of other factors to zooplankton isotopic variability. All multivariate procedures used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individual zooplankton taxa averaged for each net. The methods of Anderson et al. (2008), using PRIMER v.6 +PERMANOVA software, were followed. A summary of statistical procedures is in Table 3.3.

To investigate the contribution of POM from different depths to zooplankton diets, POM values were separated into shallow (0-110m) or deep (110-1000m) groups for each station (see Williams et al., submitted for the rationale behind this grouping). $\delta^{15}\text{N}$ values of deep suspended POM are usually higher than $\delta^{15}\text{N}$ values of shallow suspended POM (Altabet, 1996), and this difference should be retained as isotopic differences in zooplankton primary consumers feeding on material from different depths. The increase in POM $\delta^{15}\text{N}$ values occurred below 110m at both stations in both years (Williams et al submitted). “Consumer polygons” were calculated to investigate the contribution of deep and shallow POM to zooplankton diets by adding the fractionation factor associated with an increase of one trophic level to each POM value. Because trophic fractionation factors are not the same for all organisms, a range of likely trophic fractionation factors ($\Delta^{13}\text{C} = 0.1\text{-}1\text{‰}$; $\Delta^{15}\text{N} = 1\text{-}3.4\text{‰}$) was selected from the literature (Post, 2002; McCutchan et al., 2003; Hannides et al., 2009; Aita et al., 2011). The highest and lowest fractionation factors were added to each measured POM value. The resulting $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were plotted and lines drawn around the outermost points to produce the resulting consumer polygons. When plotted with measured zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, these polygons should encompass zooplankton species likely to have consumed POM from that depth range. Consumer polygons were constructed separately for the combined ML+UO, the OM, and the combined LO+SO at each station. ML+UO samples were combined because of the small number of samples collected within the narrow ML (Fig. 3.2), and LO+SO samples were combined because the SO was not sampled at every station.

Trophic positions of zooplankton taxa were examined in three ways. First, trophic levels from the literature were assigned *a-priori* to zooplankton taxa (Table 3.4). Trophic level data for the same species were used whenever possible. When no exact species match could be made, trophic levels from animals in the same major taxonomic group from similar areas were used. Second, multidimensional scaling (MDS) plots, group average cluster analyses, and similarity profile (SIMPROF) routines were constructed using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individual zooplankton taxa to identify statistically significant groups of zooplankton. Third, trophic levels were calculated for all taxonomic groups using the equation from Vander Zanden and Rasmussen (1999) $\text{TL}_c = ((\delta^{15}\text{N}_c - \delta^{15}\text{N}_b) / \Delta^{15}\text{N}) + \text{TL}_b$, where TL_c is the trophic level of the consumer, $\delta^{15}\text{N}_c$ is the $\delta^{15}\text{N}$ value of the consumer, $\delta^{15}\text{N}_b$ is the $\delta^{15}\text{N}$ value of a “baseline” food item, $\Delta^{15}\text{N}$ is the trophic fractionation factor, and TL_b is the assumed trophic level of the baseline food item. A trophic fractionation factor of 2.5‰ was selected for this study as it has previously been used for trophic calculations of deep sea zooplankton (Caut et al., 2009; Fanelli et al., 2009; Fanelli et al., 2011).

Zooplankton in the 0.2-0.5mm size fraction from bulk size fractionated zooplankton analysis discussed in Chapter 2 were chosen as the baseline food item (Table 3.4) and were assumed to have a trophic level of 2 (TL_b). Trophic levels for zooplankton taxa collected above 110m were calculated using mean $\delta^{15}\text{N}$ values for all 0.2-0.5mm bulk size-fractionated samples collected between 0-110m at each station. With the exception of the copepod *Eucalanus inermis*, mean 0.2-0.5mm zooplankton $\delta^{15}\text{N}$ values for bulk size-fractionated samples from 110-1000m were used in TL calculations for taxa collected below 110m at each station. *E. inermis* at depth are believed to be in a resting

stage and likely do not feed. Therefore, only shallow (0-110m) 0.2-0.5mm zooplankton values were used as the baseline for trophic level calculations for this species.

3.4 Results

3.4.1 *Vertical and Temporal Trends*

A detailed description of hydrographic features and vertical patterns of bulk size fractionated zooplankton isotope values were reported in Chapter 2 and Wishner et al (2013). In short, an OMZ was present at both stations in both years but its thickness and depth varied (Fig. 3.2). TB in 2008 had the thickest OMZ core (620m) extending from 80 to 700m, and the thinnest ML+ UO zones measured during this study. The OMZ core was 200 m thick at all other stations and started at 350m at CRD in 2007, 355m at TB in 2007, and 300m at CRD in 2008.

There were clear trends in zooplankton isotope values with depth. There was insufficient replication of day and night samples collected at similar depths to test the effect of time on the isotope values of any single taxon. However, a 3-way PERMANOVA on combined zooplankton taxa showed no differences between isotope values collected at different stations or times of day, though there were significant differences between zooplankton collected in different ecological zones (Table 3.5). Isotope values of zooplankton taxa collected in the LO+SO were significantly different from those in the ML+UO and the OM. Temperature was the only environmental variable (not including depth) that was significantly associated with the isotope variability of zooplankton taxa (Table 3.5). Finally, while there were no overall trends in the $\delta^{13}\text{C}$ or C: N values of zooplankton taxa with depth, there was a significant increase in $\delta^{15}\text{N}$ values of zooplankton between the OM and the LO (Fig. 3.3; Table 3.6).

3.4.2 *Zooplankton Food Sources*

Though the individual taxa represented in Fig 3.4 likely occupied a variety of trophic levels, most taxa collected in the ML+UO and OM were more closely associated with shallow consumer polygons, while zooplankton from the LO+SO mostly fell within deep consumer polygons. The association of zooplankton in the ML+UO and OM with shallow consumer polygons was most clear at TB. However, many ML+UO taxa at CRD were also near or within the shallow POM polygon, but the large difference between $\delta^{15}\text{N}$ values of shallow and deep consumer polygons caused many taxa for that station to plot somewhere between the two polygons. Zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the OM were similar to those in the ML+UO at both stations, with most taxa at TB falling within the shallow polygon. Many CRD taxa were intermediate to the two food types. LO+SO zooplankton were associated mostly with the deep consumer polygons, suggesting they had different POM food sources than taxa in other zones.

Linear regressions of zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig 3.4) are related to the number of carbon and nitrogen sources contributing to the food web at each station (Fry, 2006; Michener & Kaufman, 2007). Zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at TB were positively correlated in all zones; correlations were highest in the ML+UO and the OM. At CRD, zooplankton isotope values were highly correlated in the OM but there was no correlation in either the ML+UO or the LO+SO.

3.4.3 *Trophic Interactions Between Zooplankton Taxa*

There were three *a-priori* trophic levels identified for the selected zooplankton taxa. These included particle feeders (PF) (TL= 2-2.4), which consumed phytoplankton, heterotrophic microbes, and marine snow; omnivores (O) (TL= 2.5-2.9) that fed on

particles and other zooplankton, and carnivores (C) (TL >3) that fed exclusively on zooplankton (Table 3.4). Two significantly different groups of zooplankton taxa were identified by cluster analyses and similarity profiles in the OM and LO+SO zones (Fig 3.5). Most carnivorous and omnivorous species were contained in the first group, while the majority of particle feeders were contained in the second. Trophic levels calculated from $\delta^{15}\text{N}$ values measured in this study largely agreed with *a-priori* trophic level designations, though calculated trophic levels were higher than predicted for species in the LO+SO (Fig 3.6, Table 3.4). For example, the copepod *Lucicutia hulsemannae* was designated as an omnivore in previous literature, but its calculated TL was 4.4, suggesting it is a carnivorous species.

3.4.4 Diets and Trophic Interactions of Key Taxa

The copepod *Pleuromamma johnsoni* was collected in the UO, OM, and LO at both stations, but was more abundant at TB, with an abundance peak at 80-150m, and a second at 750-900m (Wishner unpublished data). Though this species was assigned the *a-priori* trophic level of “carnivore”, its mean trophic level was 2.4 (± 0.57) based on calculations from $\delta^{15}\text{N}$ values (Table 3.4), suggesting it is a particle feeder. At TB, there was a large shift upward in $\delta^{15}\text{N}$ values of *P. johnsoni* individuals collected in the LO+SO compared to those in the ML+UO and OM, but there were insufficient data points to determine the significance of this trend (Fig. 3.3). *P. johnsoni* was associated with shallow polygons in all zones at both stations (Fig. 3.4).

The Eucalanid copepod *Eucalanus inermis* was present in all zones at both stations and had significantly different isotope values from other zooplankton (Table 3.5, 3.6; Fig. 3.7). *E. inermis* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly lower than bulk values

in all zones at both stations (Table 3.5). Although *E. inermis* was identified *a-priori* as a particle feeder and had an average calculated trophic level of 2.0 (Table 3.4), $\delta^{13}\text{C}$ values of *E. inermis* in the ML+UO were significantly lower than those of *Subcalanus subtenuis*, another particle feeding Eucalanid copepod in the ML+UO (Table 3.6).

Average $\delta^{15}\text{N}$ values of all other taxa (excluding *E. inermis*) were significantly higher in the LO+SO than in the other two zones (Table 3.6). There was no difference between *E. inermis* $\delta^{15}\text{N}$ values in the ML+UO and those in the LO+SO (Table 3.6). Because there was no change in *E. inermis* isotope values with depth, this species was associated with shallow consumer polygons in all three zones at both stations (Fig. 3.4). *E. inermis* $\delta^{15}\text{N}$ values were also significantly different from 3 abundant taxa in the LO community, the copepods *H. longicornis* and *L. hulsemannae*, and the fish *Cyclothone* spp. (Table 3.6).

3.5 Discussion

3.5.1 General Trends

Zooplankton in the ML+UO and the OM primarily fed on shallow (0-110m) POM as a primary food source, while LO+SO zooplankton relied on deep (110-1000m) POM at both stations. Furthermore, while zooplankton at TB appeared to incorporate carbon and nitrogen from a single source, evidence of multiple carbon or nitrogen sources was present at CRD.

3.5.2 Carbon and Nitrogen Sources Entering Zooplankton Trophic Webs

Zooplankton at the two stations in the ETNP OMZ likely consumed material originating from different carbon or nitrogen sources. The correlation between zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values is affected by the addition of material arising from

different carbon fixation pathways or from changes in nitrogen sources. Because both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values increase with trophic level, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the entire zooplankton community will be positively correlated ($R^2 > 0.5$) if the primary producers forming the base of the food web utilize only one carbon and one nitrogen source (Polunin et al., 2001; Fanelli et al., 2009). The relatively high correlations between zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in all zones at TB suggest a single carbon and nitrogen source at that station (Fig 3.4). However, the lack of a strong correlation between zooplankton carbon and nitrogen isotopes in the ML+UO and LO+SO at CRD suggest either that more than one type of carbon fixation occurred at the site or that phytoplankton at CRD had access to more than one source of new nitrogen.

The correlation between consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values is most commonly used to detect the incorporation of multiple carbon sources, such as terrestrial plant matter or chemoautotrophic carbon fixation, to zooplankton food webs (Burd et al., 2002; Bergquist et al., 2007; Macavoy et al., 2008). Both stations examined in this study were too far from land to see appreciable inputs of terrestrial carbon to zooplankton food webs but OMZs do support many microbial processes. These include anaerobic ammonia oxidation (anammox), a chemoautotrophic process which is an important part of OMZ nitrogen cycles (Jaeschke et al., 2007; Galán et al., 2009; Rush et al., 2012). Additionally, most forms of chemoautotrophic carbon fixation result in the production of material with significantly lower $\delta^{13}\text{C}$ values than marine phytoplankton (Michener & Kaufman, 2007), which is also true for anammox bacteria (Schouten et al., 2004). Low POM $\delta^{13}\text{C}$ values were associated with the presence of anammox microbes in the TB OMZ in 2007 (Podlaska et al., 2012). Significant ingestion of chemoautotrophically

fixed carbon would likely decrease the $\delta^{13}\text{C}$ values of zooplankton consumers, but $\delta^{13}\text{C}$ values at CRD and TB were similar at all depths. However, because mixing models require knowledge of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ inputs, we cannot use them to ascertain the contribution of additional carbon fixation pathways to food webs until data pertaining to the natural $\delta^{15}\text{N}$ values of chemoautotrophic microbes associated with processes such as anammox become available,. However, $\delta^{13}\text{C}$ data for the zooplankton were not unusually low and thus did not suggest the input of chemoautotrophically derived carbon in the OMZ.

Correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can also be influenced by multiple nitrogen sources, and was likely the cause of the non-significant regression for CRD zooplankton (Fig. 3.4). Nitrogen fixation was previously suggested as the source of significantly low $\delta^{15}\text{N}$ values for POM and size fractionated bulk zooplankton samples (Williams et al., submitted) at CRD. $\delta^{15}\text{N}$ values at CRD were similar to those of zooplankton collected in subtropical gyres, which are known to support nitrogen fixation (Montoya et al., 2002; Montoya et al., 2004), and to $\delta^{15}\text{N}$ in the Equatorial Pacific upwelling regions (Altabet, 2001).

The low correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the LO+SO community at CRD also suggests that the nitrogen fixed in the surface layer has been either directly or indirectly transported to depth and incorporated by the zooplankton community. Aggregations of phytoplankton or marine snow can entangle algal cells, cyanobacteria, and other small particles in the mixed layer and transport them rapidly to depth where they may be consumed by zooplankton (Silver et al., 1998). Marine snow is an important food source for zooplankton in some areas (Wilson et al., 2008; Wilson & Steinberg,

2010). Because $\delta^{15}\text{N}$ values in the ML+UO at CRD were significantly lower than at TB ($t=3.65$; $p<0.001$), the LO+SO communities at the two stations should also have significantly different $\delta^{15}\text{N}$ values if zooplankton directly consumed nitrogen fixing cyanobacteria rapidly transported from the surface layer. Fixed nitrogen may have also been remineralized by microbes, which were then consumed by zooplankton. However, $\delta^{15}\text{N}$ values in the LO+SO were not significantly different between the two stations ($t=0.96$; $p=0.344$). At CRD, the higher $\delta^{15}\text{N}$ values of LO+SO zooplankton compared to ML+UO zooplankton suggests that the food items consumed by the deep zooplankton were more degraded or processed (e.g. fecal pellets) relative to food sources consumed by shallow zooplankton.

3.5.3 Trophic Interactions of the Zooplankton Community

Zooplankton taxa designated *a-priori* as particle feeders, including *E. inermis*, *S. subtenuis*, ostracods, and amphipods, fell within shallow polygons in both the ML+UO and the OM, suggesting food webs within and above the OM relied primarily on POM from the upper water column. Similar associations between bulk zooplankton and POM were described in Williams et al. (submitted) where it was hypothesized that zooplankton in the OM zone fed either at the surface during migrations or at depth on fresh sinking material. Although no significant isotope differences were detected between particle feeders and carnivores or omnivores in the ML+UO (Fig. 3.5), species designated *a-priori* as carnivores or omnivores in that zone and in the OM plotted near the border between polygons at TB or in the space between polygons at CRD (Fig. 3.4). This probably occurred because of the increase in $\delta^{15}\text{N}$ values associated with increasing trophic levels.

Two copepods, *Pleuromamma johnsoni* and *Rhincalanus rostrifrons*, produced unexpected results with respect to their calculated trophic levels. Neither species was associated with either deep or shallow consumer polygons, instead having isotope values falling somewhere between the two food types. Calculated trophic levels for *R. rostrifrons* and *P. johnsoni* were 2.4 and 3.0, respectively indicating that these species were either omnivorous, or fed on a mixture of shallow and deep particles. Lipid biomarkers examined by Cass (2011) as a part of the ETP project indicated that *R. rostrifrons* collected within the upper 300m fed primarily on particles below the thermocline. If *R. rostrifrons* fed on deep particles, it would likely have higher $\delta^{15}\text{N}$ values than material from shallower waters. Additionally, the higher baseline $\delta^{15}\text{N}$ value of particles below 110m could potentially give consumers such as *R. rostrifrons* a $\delta^{15}\text{N}$ value similar to that of secondary consumers in the mixed layer. In contrast, *P. johnsoni*, which also plotted in the transitional areas between consumer polygons in all zones at both stations, was previously identified as a carnivore (TL >3) (Gowing & Wishner, 1992). It had a calculated trophic level of an omnivore (2.5-3) or particle feeder (2-2.5) in this study, rather than an obligate carnivore.

In contrast to the ML+UO, *a-priori* defined zooplankton particle feeders in the LO+SO were closely associated with deep polygons, suggesting that these species fed on deep POM. The majority of zooplankton taxa within deep consumer polygons were species associated with the LO zooplankton community. Many species living in this area do not undergo diel vertical migration (DVM) (Saltzman & Wishner, 1997b; a; Wishner et al., 2008; Wishner et al., 2013) and likely have access to deep particles. Therefore, deep POM was likely the major dietary component for primary consumers below the

OM. *A-priori* defined carnivorous and omnivorous taxa at the LO+SO also fell within or near deep consumer polygons but had higher $\delta^{15}\text{N}$ values than particle feeders in that zone. There were no differences between carnivorous and omnivorous species, using either *a-priori* or calculated trophic levels in any zone (Fig 3.5). Omnivores, by definition, have mixed diets so it is likely that this method was not sufficiently sensitive to statistically differentiate the two feeding strategies.

3.5.4 Key Taxa

The copepods *E. inermis* and *L. hulsemannae* are closely tied to the OMZ in both the north and south Eastern Tropical Pacific (Saltzman & Wishner, 1997b; a; Hidalgo et al., 2005b; Escribano et al., 2007; Wishner et al., 2013). *E. inermis* is highly tolerant of low oxygen concentrations within the OMZ core (Flint et al., 1991; Cass, 2011), but is most abundant at the oxyclines and in the mixed layer (Wishner et al., 2013). *L. hulsemannae*, and its Arabian Sea counterpart *L. grandis*, occur below the deep *E. inermis* community at the lower oxycline, and both are considered to be indicator species for their respective lower oxycline communities (Saltzman & Wishner, 1997b; a; Gowing & Wishner, 1998; Wishner et al., 2008; Wishner et al., 2013). Although the feeding ecology of both species was previously studied with gut content analysis, isotope analysis revealed unexpected patterns discussed below.

Among the individual taxa examined in this study, the copepod *E. inermis* was unique, both for the depth range in which it was present and for the relative stability of isotope values measured at all depths. *E. inermis* had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that were significantly different from bulk zooplankton isotope values at both sites and in all zones (Table 3.2). Furthermore, $\delta^{13}\text{C}$ values of *E. inermis* in the ML+UO were significantly

different from those of another Eucalanid copepod, *Subeucalanus subtenius*, thought to have a diet similar to that of *E. inermis* (Cass, 2011). High lipid concentrations can contribute to low $\delta^{13}\text{C}$ values (DeNiro & Epstein, 1977; Post et al., 2007; Smyntek et al., 2007), but because lipids contain almost no nitrogen, there will be a negative correlation between $\delta^{13}\text{C}$ values and C: N ratios if lipid content has influenced $\delta^{13}\text{C}$ values. (Murry et al., 2006; Post et al., 2007; Smyntek et al., 2007). Although lipid sacs were identified inside many individuals of *E. inermis* collected during this cruise (Cass, 2011; Wishner et al., 2013), *E. inermis* $\delta^{13}\text{C}$ and C: N values were not correlated at either station ($R^2 < 0.125$), suggesting that lipids did not affect $\delta^{13}\text{C}$ values of *E. inermis*. Furthermore, when $\delta^{13}\text{C}$ values of both *E. inermis* and *S. subtenius* were corrected for lipids using the normalization model in Smyntek (2007), there was still a significant difference between the two species ($t = -2.30$; $p = 0.041$). It is possible that low $\delta^{13}\text{C}$ values for *E. inermis* at TB were the result of consumption of a novel carbon source by this species. Low POM $\delta^{13}\text{C}$ values in the water column were observed in conjunction with anammox biomarker lipids in 2007, but peak anammox biomarker concentration abundance occurred in the center of the OM where *E. inermis* populations were low (Podlaska et al., 2012; Rush et al., 2012; Wishner et al., 2013). Thus, these microbes were not a likely food source for *E. inermis*. Furthermore, although *E. inermis* $\delta^{13}\text{C}$ values were low at both stations, the zooplankton community at TB showed no signs of having incorporated more than one source of carbon into the trophic web. Also, because no studies have determined the fractionation of nitrogen for anammox bacterial biomass, it is not possible to determine if they were a significant proportion of zooplankton diets at that depth. While it is not clear at present what caused the differences in $\delta^{13}\text{C}$ values between *E. inermis* and *S. subtenius*,

it may be a function of the unique metabolism or body chemistry of *E. inermis*, discussed below.

In the ETNP OMZ, some individuals of *E. inermis* were often present at the LO, possibly in a dormant stage (Hidalgo et al., 2005b; Wishner et al., 2013). Most diapausing copepods are large, lipid rich species, living in areas where food becomes scarce on a seasonal cycle (Forest et al., 2011; Perrin et al., 2012; Maps et al., 2013). Many of these species, such as *Calanus finmarchicus* and *Calanus helgolandicus* live at temperate latitudes (Miller, 2004; Perrin et al., 2012; Maps et al., 2013), while others, such as *C. pacificus* are found in coastal upwelling zones (Osgood & Checkley, 1997; Johnson & Checkley Jr, 2004; Ohman et al., 2012) or in tropical and subtropical areas, such as *Calanoides carinatus* (Arashkevich et al., 1996; Idrisi et al., 2004; Irigoien et al., 2005; Verheye et al., 2005; Wishner et al., 2008). In the OMZ of the ETSP, *E. inermis* reproduces in near surface water for most of the year, but is presumed to undergo diapause at depth during the cooler and less productive winter months (Hidalgo et al., 2005b; a; Escibano et al., 2007; Escibano et al., 2009; Manriquez et al., 2009). While there are no similar studies of the annual life history of *E. inermis* in the ETNP OMZ, zooplankton abundance and distribution data from the ETP Project found secondary *E. inermis* abundance peaks in the LO at both stations in 2008, but not in 2007 when the cruise occurred several weeks earlier in the year. This suggested the presence of a seasonal diapausing population at some times (Wishner et al., 2013).

Diapausing copepods are expected to have body compositions that are distinctly different from non-diapausing individuals (Adams & Sterner, 2000; Ikeda et al., 2006; Forest et al., 2011). Most notably, diapausing copepods require significant lipid stores to

survive for long periods of time at depth, which is reflected by the high C: N ratios (>8), (Ikeda et al., 2006; Forest et al., 2011; Ikeda, 2012). Though metabolism of diapausing individuals is significantly lower than that of active individuals, diapausing animals must utilize lipid stores, potentially resulting in a decrease in C: N over time (Adams & Sterner, 2000; Forest et al., 2011). $\delta^{15}\text{N}$ values of diapausing individuals may also increase over time because the breakdown of amino acids and excretion favor the removal of ^{14}N , (Adams & Sterner, 2000; Forest et al., 2011). However, there was no significant difference between deep and shallow *E. inermis* C:N values, and C:N ratios of *E. inermis* values were well below 8.3, the value indicating a balance between lipid and protein (Ventura & Catalan, 2008; Ikeda, 2012). This suggests that *E. inermis* body tissues may not have contained sufficient lipid concentrations to support a long duration diapause. $\delta^{15}\text{N}$ values of the deep and shallow *E. inermis* populations were also not significantly different, suggesting that the low *E. inermis* C: N ratios likely did not result from utilization of lipid stores during diapause, as this would have also caused an increase in $\delta^{15}\text{N}$ values.

Although the biochemical indicators of deep *E. inermis* were not representative of expectations for a diapausing population of copepods, one potential explanation for these values may be that *E. inermis* stores ammonium, possibly as a means of regulating buoyancy. $\delta^{15}\text{N}$ values of animals retaining ammonium rather than expelling it would not increase in $\delta^{15}\text{N}$ values during diapause because ^{14}N would be retained inside the body. The retention of nitrogenous wastes may also result in lower C: N ratios. A recent study by Schröder et al (2013) found that some species of diapausing Antarctic copepods were able to store significant amounts of NH_4^+ in their hemolymph. While there are

methodological questions associated with this method, Schröder et al (2013) asserts that NH_4^+ storage may be a superior method of maintaining buoyancy in diapausing taxa compared to lipid storage, because lipids are utilized over time. Changes in C: N ratios can significantly affect buoyancy control. NH_4^+ is a waste product and is metabolically “cheap” to produce, whereas lipids are needed to supply energy during diapause and cannot be replaced while an individual is at depth (Schröder et al., 2013). However, further testing is needed to determine if the deep *E. inermis* population stored ammonium.

While it is not clear how $\delta^{15}\text{N}$ and C: N values of LO *E. inermis* relate to the life history, evidence suggests the LO population may be aggregated in that area because it provides a refuge from predation by both diel vertical migrators from above and the LO zooplankton community below. *E. inermis* in the LO at both stations in 2008 were located just above the LO zooplankton community, where oxygen concentrations were lower. *E. inermis* probably did not feed at depth, as there were no significant differences between $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or C: N values for shallow and deep *E. inermis* populations at both sites. *E. inermis* was also the only taxon collected within the LO that plotted within shallow consumer polygons at both stations, suggesting. Deep *E. inermis* $\delta^{15}\text{N}$ values in the LO were 8‰ lower than $\delta^{15}\text{N}$ values of other taxa, suggesting it is not a common food source for LO community. Therefore, *E. inermis* may aggregate in the lower oxycline, not to take advantage of higher quality or more abundant food, but to avoid predation. The depth of the LO *E. inermis* biomass peak is well below the maximum depth for most diel vertically migrating zooplankton and they may provide a refuge in part of the OMZ that few other animals can tolerate.

It has been hypothesized that the zooplankton community associated with the LO takes advantage of particle food sources at the base of the OMZ core. Particulate matter originating from the ML may be an important food source for LO zooplankton, but previous studies of LO zooplankton diets have also suggested that microbes may be an important source of food (Gowing & Wishner, 1992; Wishner et al., 2000). Large numbers of bacteria-like bodies were found in the guts of *L. hulsemannae* and *H. longicornis* (Gowing & Wishner, 1998), and in *L. grandis*, a comparable LO species in the Arabian Sea OMZ (Wishner et al., 2000). Bacteria are often associated with larger particles and aggregates and may have been consumed by deep sea zooplankton feeding on particles (Steinberg et al., 2008; Wilson et al., 2008; Wilson et al., 2010). Because redox transition zones in OMZs support vigorous biogeochemical cycling, the bacteria-like bodies found in zooplankton guts may be the result of consumption of deep sea chemoautotrophic microbes in these transition zones (Gowing & Wishner, 1992; Wishner et al., 2008). However, $\delta^{13}\text{C}$ values of LO taxa were not significantly different from zooplankton in other zones, as would be expected for species feeding on significant quantities of chemoautotrophic microbes. If chemoautotrophic organisms contributed to the high $\delta^{15}\text{N}$ values in the LO+SO, it would have resulted in poor $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations for the zooplankton community at both stations, yet zooplankton only at CRD had low $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations. This suggests that primary producers in the upper water column were the primary food source for zooplankton grazers in the LO+SO.

Among the zooplankton taxa examined in this study, both *a-priori* defined trophic levels and trophic level calculations based on measured $\delta^{15}\text{N}$ values suggest that the relative abundance of carnivorous species increased in the LO+SO. Higher relative

abundance of carnivorous species at depth is commonly described in studies of deep sea zooplankton in non-OMZ areas (e.g. (Yamaguchi et al., 2002; Koppelmann & Frost, 2008; Wilson et al., 2010)). There may be sampling bias in this study, because only larger taxa were selected for analysis. However, the same size ranges of individuals were selected for all ecological zones. Trophic levels calculated for some LO+SO taxa were much higher than expected. For example, trophic levels of 4.1 and 4.7 were calculated for the copepods *Heterostylites longicornis* and *L. hulsemannae* respectively, but both taxa were previously described as omnivores by Gowing and Wishner (1992). These trophic levels are unusually high for copepods and suggest that the two species prey on other carnivorous zooplankton. By comparison, deep sea copepods in the Mediterranean Sea had trophic levels of 3-3.9 (Fanelli et al., 2009; Koppelmann et al., 2009; Fanelli et al., 2011), almost a full trophic level less than LO+SO copepods in this study. However, zooplankton in the Benguela upwelling also found high trophic levels for copepods collected below 700m (TL= 3.2- 4.5) which were comparable to those reported here (Schukat et al., in press). Deep sea copepods in this and the Benguela upwelling study had $\delta^{15}\text{N}$ values equal to or greater than those of fish or shrimp collected at the same depths. The high trophic level of copepods and larger taxa suggests the LO+SO is an area of vigorous trophic processing with smaller organisms feeding on particles or microbes from the OM and larger taxa feeding on the smaller taxa. The gradient in $\delta^{15}\text{N}$ of bulk stable isotopes analysis(Chapter 2) also suggested a zone of trophic progression (Wishner et al., 2013)It is not clear if the LO community is likely to facilitate carbon sequestration by repackaging smaller particles exiting the OMZ into larger fecal pellets, or if the sinking carbon is almost entirely consumed by the LO community.

3.6 Conclusions

The trophic web of the ETNP OMZ zooplankton community varied with depth and station. The contribution of nitrogen fixation in the ML+UO of CRD could be seen throughout the water column. Species living within and above the OM appeared to rely on shallow particles as a food source, while LO taxa relied only on deep particles. Furthermore, there was no indication that chemoautotrophic microbes were a significant part of the diet of any zooplankton taxon in this study.

Among key zooplankton taxa, *E. inermis* fed only on shallow POM, regardless of the zone it was collected in, but its $\delta^{13}\text{C}$ values were significantly different from other copepods with a similar diet which fed in a similar depth range. Furthermore, the deep *E. inermis* population did not have several biochemical and isotopic characteristics of a diapausing population although many individuals had stored oil and developing eggs. These may be individuals newly arrived from the surface, or alternatively, this copepod may store ammonium for buoyancy regulation. This would both increase C: N ratios of diapausing individuals and result in no change in $\delta^{15}\text{N}$ values, since ^{14}N would be retained in the body. Finally, though the LO zooplankton community may have deep POM as its initial source of carbon, nearly all of the LO+SO taxa examined in this study were carnivores as indicated by their high trophic levels, although gut contents from prior work showed more omnivory (Gowing & Wishner, 1992). This suggests vigorous trophic processing at the LO, but it is unclear what effect this trophic activity may have on carbon transport to depth.

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Table 3.1: Tow information and depth ranges for MOCNESS samples for individual zooplankton taxa used in stable isotope analysis. TB is the Tehuantepec Bowl and CRD is the Costa Rica Dome.

MOCNESS Tows									
Year	Stn	Date (GMT)	Time (local)		Tow	Tow Depth	Depth Intervals of Samples Used in Stable Isotope Analysis	# of nets	
2007	TB	Oct-27	14:15	16:00	606	0-200	0-20; 50-60; 80-100	3	
		Oct-31	22:20	00:00	612	0-150	30-41; 51-61-80	3	
		Oct-26	22:41	00:41	604	0-360	0-80; 100-150; 250-360	3	
		Oct-30	13:12	15:50	611	100-500	200-250; 350-401; 450-500	3	
		Oct-28	10:12	15:00	607	0-1200	550-750; 750-900-1200	3	
		Oct-29	22:30	03:15	609	0-1200	500-750-900-1200	3	
		Oct-29	23:33	04:52	610	700-1200	950-1000	1	
		Nov-1	10:13	16:19	613	700-1200	750-800	1	
		CRD	Nov-9	10:44	12:36	618	0-150	20-30; 40-50; 60-80	3
			Nov-11	00:10	03:10	621	0-150	20-30; 100-150	2
			Nov-7	08:40	18:24	614	0-1200	80-150-350-550-750-900-1200	6
			Nov-9	21:53	06:59	617	350-1200	350-550-750-900-1200	4
2008	TB	Dec-15	13:20	14:55	626	0-150	40-50-60-80; 100-150	4	
		Dec-20	01:20	02:52	633	0-150	20-30-40-50-60-80-100-150	7	
		Dec-17	20:37	00:54	629	150-550	150-200-250-300-350-400-450-500-550	8	
		Dec-18	11:59	18:12	631	550-1000	700-775-800-825-850-875-900-1000	7	
	CRD	Dec-28	09:53	11:16	635	0-150	20-30; 40-50; 60-80-100-150	5	
		Dec-29	09:59	13:55	637	150-550	200-250-300-350-400-450; 500-550	6	
		Jan-01	00:31	04:22	641	200-550	200-250; 300-350; 400-450; 500-550	4	
		Dec-29	21:53	03:35	636	525-1000	525-550-575-600-625-650-750- 900	7	
Total # of Nets Sampled								83	

Table 3.2: Means, standard, deviations ($\pm$), number of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ samples run (n) and estimated number of individuals collected (ni) for zooplankton taxa collected at each station, combined for 2007 and 2008.

Species	Depth (m)	Tehuantepec Bowl						Costa Rica Dome					
		$\delta^{13}\text{C}$	n	n _i	$\delta^{15}\text{N}$	n	n _i	$\delta^{13}\text{C}$	n	n _i	$\delta^{15}\text{N}$	n	n _i
<i>Eucalanus inermis</i>	20-850	-24.89 $\pm$ 3.49	61	51	6.59 $\pm$ 2.36	50	114	-22.06 $\pm$ 2.29	82	73	5.24 $\pm$ 1.99	77	180
<i>Euchaeta</i> spp.	0-900	-20.96 $\pm$ 1.35	13	13	11.57 $\pm$ 2.28	12	39	-21.95 $\pm$ 1.75	8	8	7.54 $\pm$ 4.57	13	39
<i>Gaetanus</i> spp.	100-1200	-20.05 $\pm$ 0.48	3	5	15.99 $\pm$ 3.68	6	24	-19.78 $\pm$ 1.36	11	12	12.29 $\pm$ 1.23	8	44
<i>Heterostylites longicornis</i>	350-775	-20.82 $\pm$ 0.89	5	7	13.45 $\pm$ 2.22	5	19	-19.73 $\pm$ 1.11	42	44	13.45 $\pm$ 1.26	20	78
<i>Haloptilus</i> spp.	60-900	-20.05 $\pm$ 1.60	5	3	14.89 $\pm$ 3.56	2	4	-19.72 $\pm$ 1.19	20	13	13.35 $\pm$ 3.19	17	34
<i>Lucicutia hulsemannae</i>	500-850	-20.86 $\pm$ 1.20	26	193	16.51 $\pm$ 1.74	36	49	-21.12 $\pm$ 1.44	39	286	13.89 $\pm$ 0.59	53	72
Megacalanidae	625-750			No Data				-22.39 $\pm$ 0.05	2	2	14.47 $\pm$ 0.05	2	2
<i>Pleuromamma abdominalis abyssalis</i>	250-300			No Data				-22.84 $\pm$ 0.25	6	7	5.97 $\pm$ 0.03	3	21
<i>Pleuromamma johnsoni</i>	30-900	-22.42 $\pm$ 0.63	24	41	10.49 $\pm$ 1.52	33	130	-21.54 $\pm$ 0.76	3	3	7.84 $\pm$ 1.37	7	28
<i>Rhincalanus rostrifrons</i>	80-350	-17.87	1	1	No Data			-21.91 $\pm$ 1.52	6	10	9.49 $\pm$ 1.52	11	44
<i>Subeucalanus subtenis</i>	20-100	-21.12 $\pm$ 1.24	19	30	8.67 $\pm$ 1.15	12	52	-19.39 $\pm$ 1.24	28	40	5.78 $\pm$ 0.62	28	104
Scolecitrichidae	550-1200			No Data				-20.97 $\pm$ 1.78	5	5	11.78 $\pm$ 0.52	5	10
Amphipods- Gammarid	200-900	-21.60 $\pm$ 0.91	5	46	9.36 $\pm$ 1.15	5	63	-21.09 $\pm$ 1.74	6	52	6.54 $\pm$ 1.95	7	63
Amphipods- <i>Phronima</i>	325-325			No Data				-20.94 $\pm$ 0.76	2	5	7.50 $\pm$ 0.67	2	4
Chaetognaths	0-1200	-19.60 $\pm$ 2.47	3	8	12.61 $\pm$ 1.44	5	31	-19.87 $\pm$ 1.30	28	104	10.95 $\pm$ 3.70	20	123
Euphausiids	30-400	-20.61 $\pm$ 1.51	6	20	11.80 $\pm$ 0.96	6	20	-20.81 $\pm$ 2.00	15	60	8.46 $\pm$ 1.11	14	14
Fish	450-900	-20.98 $\pm$ 0.84	2	5	16.46 $\pm$ 1.51	2	5	-24.50	1	3	6.51	1	3
Fish- <i>Cyclothone</i> spp.	350-1200	-20.08 $\pm$ 1.38	15	153	14.38 $\pm$ 0.73	17	108	-18.75 $\pm$ 1.11	17	146	13.81 $\pm$ 1.22	12	88
Fish- Myctophid	50-500	-19.99 $\pm$ 0.55	3	10	12.00 $\pm$ 0.05	2	9	-22.03 $\pm$ 0.07	2	5	9.58 $\pm$ 0.03	2	5
Ostracods	60-1199	-20.86 $\pm$ 1.05	10	29	10.42 $\pm$ 1.77	10	36	-20.44 $\pm$ 2.21	12	22	8.12 $\pm$ 1.56	16	9
Polychaetes	550-1199	-21.32 $\pm$ 1.11	9	9	12.36 $\pm$ 1.03	9	9	-19.95 $\pm$ 1.53	3	3	11.12 $\pm$ 1.14	19	19
Shrimp	250-1200	No Data			12.81	1	3	-22.17 $\pm$ 1.71	2	8	12.80 $\pm$ 1.57	2	8
Shrimp- Caridean	900-1201	-20.31	1	1	16.35	1	1	No Data					
Shrimp- <i>Gennades</i>	550-574			No Data				-20.48	1	1	12.86	1	1
Shrimp- Sergestid	200-900			No Data				-20.60 $\pm$ 1.29	2	4	11.13 $\pm$ 6.31	2	38
Total # Samples Run= 1107								Total # Individuals Analyzed = 3127					

Table 3.3: Table of statistical tests used in this study. Linear regressions were calculated using SigmaPlot 8.0 while Permutational Analysis of Variance (PERMANOVA), MDS plots, cluster analyses, and Similarity Profile (SIMPROF) routines were calculated using PRIMER 6 + PERMANOVA. All multivariate methods are described in Clark & Gorley (2001) and Anderson et al. (2008)

Test	Purpose	Preliminary Tests/ Transformations	Factors	Data Used
Linear Regression	Elucidate potential carbon and nitrogen sources entering the zooplankton trophic web	N/A	N/A	Zooplankton taxa appearing in multiple nets at TB & CRD
2-way ANOVA	Examine differences between <i>E. inermis</i> and bulk zooplankton in different zones	Equal variance and normality	Ecological zone, species	2007 & 2008 <i>E. inermis</i> and biomass weighted mean bulk zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data
Student's t-test	Identify differences between isotope and C:N values of key zooplankton taxa collected at similar depths	Equal variance and normality	N/A	2008 <i>E. inermis</i> , <i>S. subtenuis</i> , and <i>L. hulsemannae</i> from TB and CRD combined
3- way PERMANOVA	Examine differences between zooplankton taxa by station, ecological zone, and time of day	Normalized data; Euclidean distance similarity matrix,	Station, ecological zone, day night	2007 & 2008 zooplankton taxa
DISTLIM	Determine which environmental factors are significantly related to isotopic variability	Euclidean distance similarity matrix	Depth, temperature, oxygen, % transmission	2007 & 2008 zooplankton taxa and tow environmental data
Multidimensional Scaling (MDS) plots	Identify relationships between zooplankton taxa, trophic levels, and ecological zones	Euclidean distance similarity matrix	Species, trophic level, zone	2007 & 2008 zooplankton taxa
Group average cluster analysis	Examine relationships between zooplankton taxa, trophic levels, and ecological zones	Euclidean distance similarity matrix	Species, trophic level, zone	2007 & 2008 zooplankton taxa
SIMPROF	Determine significance of cluster analysis dendrogram divisions compared to predicted outcomes calculated from randomized data.	Euclidean distance similarity matrix	Species, trophic level, zone	2007 & 2008 zooplankton taxa

Table 3.4: *a-priori* and calculated trophic levels for zooplankton taxa. TL = trophic level, PF= particle feeder, O = omnivore, and C = Carnivore

Species	TL from $\delta^{15}\text{N}$	TL <i>a-priori</i>	Reference
Phylum Arthropoda			
Order Copepoda			
<i>Eucalanus inermis</i>	2.0 ± 0.67	PF	Cass, (2011)
<i>Euchaeta</i> spp.	3.4 ± 1.33	C	Hannides et al (2009)
<i>Gaetanus</i> spp.	3.9 ± 0.46	O	Gowing & Wishner, (1992)
<i>Heterostylites longicornis</i>	4.1 ± 0.53	O	Gowing & Wishner, (1992)
<i>Haloptilus</i> spp.	4.5 ± 1.07	C	Longhurst, (1985)
<i>Lucicutia hulsemannae</i>	4.4 ± 0.20	O	Gowing & Wishner, (1992)
Megacalanidae	4.7 ± 0.02	C	Schukat et al, (2013)
<i>Pleuromamma johnsonii</i>	2.4 ± 0.57	C	Gowing & Wishner, (1992)
<i>Rhincalanus rostrifrons</i>	3.0 ± 0.42	PF	Cass et al, (2011)
<i>Subeucalanus subtenuis</i>	2.4 ± 0.28	PF	Cass, (2011)
Scolecitrichidae	3.7 ± 0.12	O	Longhurst, (1985)
Order Amphipoda			
Gammarid	1.7 ± 0.44	PF	Gowing & Wishner, (1992)
<i>Phronima</i> spp.	2.2	C	Fanelli et al, (2009)
Order Euphausiacea	2.8 ± 0.59	C	Kinsey & Hopkins, (1994)
Order Decapoda			
Caridean	4.4	C	Hopkins et al, (1994)
<i>Gennades</i> spp.	4.1	C	Hopkins et al, (1994)
Sergestid	3.5 ± 2.30	C	Hopkins et al, (1994)
Misc. Unidentified	3.8 ± 0.70	-	-
Order Ostracoda	2.5 ± 0.65	PF	Gowing & Wishner, (1992)
Phylum Annelida			
Class Polychaeta	3.1 ± 0.08	C	Fauchauld & Jumars (1979)
Phylum Chaetognatha	3.7 ± 1.22	C	Feigenbaum & Maris (1984)
Phylum Chordata			
Class Osteichthyes			
<i>Cyclothone</i> spp.	4.1 ± 0.44	C	Gordon et al, (1985)
Myctophids	3.1 ± 0.31	C	Cherel et al (2010)
Misc. Unidentified	3.3 ± 2.13	-	-
0.2-0.5 mm Bulk Zooplankton $\delta^{15}\text{N}$ values			
TB Shallow	8.09 ± 0.93	Williams et al, submitted	
TB Deep	9.77 ± 2.01	Williams et al, submitted	
CRD Shallow	4.48 ± 1.39	Williams et al, submitted	
CRD Deep	7.04 ± 1.10	Williams et al, submitted	

Table 3.5: Results of a) 3-way PERMANOVA on all individual taxa from both years and stations comparing station, ecological zone, and time of day (i.e. day or night) b) 3-way PERMANOVA pairwise test results c) 2-way PERMANOVA on *E. inermis* and biomass weighted mean zooplankton at Tehuantepec Bowl and d) Costa Rica Dome ; and e) DISTLIM marginal tests of the contribution of physical properties to variation in isotope data. * indicates significant results.

3-way PERMANOVA on All Taxa in Both Years					
Source	df	SS	MS	Pseudo-F	p
Station	1	24.2	24.2	1.79	0.1750
Zone	2	301.9	150.9	11.17	0.0001*
Time	1	8.6	8.6	0.64	0.4903
Station x Zone	2	13.66	6.8	0.51	0.6911
Station x Time	1	2.24	2.2	0.17	0.8210
Zone x Time	2	13.13	6.6	0.49	0.7085
Station x Zone x Time	2	60.6	30.3	2.24	0.0840
Residual	108	1459.8	13.5		
Total	119	2109.4			
Pair-Wise for Ecological Zones				t	p
ML+UO, OM				0.680	0.6217
ML+UO, LO+SO				4.140	0.0001*
OM, LO+SO				3.218	0.0007*
2-way PERMANOVA on <i>E. inermis</i> vs. Bulk Zooplankton					
Tehuantepec Bowl	df	SS	MS	Pseudo-F	p
<i>E.inermis</i> vs. Bulk	2	199.78	99.89	17.913	0.0001*
Ecological Zone	2	1.70	0.85	0.153	0.9464
Species x Zone	2	24.26	12.13	2.175	0.0966
Residual	38	211.91	5.58		
Total	44	444.18			
Costa Rica Dome					
<i>E.inermis</i> vs. Bulk	1	42.21	42.21	10.693	0.0006*
Ecological Zone	2	11.38	5.69	1.442	0.2258
Species x Zone	2	15.46	7.73	1.959	0.1119
Residual	39	153.96	3.95		
Total	44	221.52			
Results of DISTLIM Marginal Tests					
Variable	SS(trace)	Pseudo-F	P	% Var	
Oxygen	37.28	2.20	0.115	1.38%	
Temperature	316.9	20.94	0.0001*	11.77%	
% Transmission	9.76	0.571	0.5901	0.36%	

Table 3.6: Results of 1-way ANOVAs with associated significant pairwise (Tukey) tests and Student's t-tests on key zooplankton taxa. $\bar{X}_a - \bar{X}_b$ is the difference in sample means. Cycloth = *Cyclothone* spp. ; H. long = *H. longicornis*; E. inerm = *E. inermis*; and L. huls = *L. hulsemannae*

1-way ANOVA Main Test Results						Significant Pairwise Tests (Tukey) Results			
Source	DF	SS	MS	F	P	Comparison	$\bar{X}_a - \bar{X}_b$	q	P
<i>E. inermis</i> vs. Lower Oxycline Community Taxa									
C:N									
Species	3	16.53	5.51	3.58	0.033*	L. huls vs. Cycloth.	2.41	4.53	0.022*
Residual	19	29.27	1.54						
Total	22	45.80							
$\delta^{13}\text{C}$									
Species	3	23.88	7.96	5.21	0.009*	Cycloth. vs. E. inerm	2.42	5.13	0.009*
Residual	19	29.02	1.53						
Total	22	52.90							
$\delta^{15}\text{N}$									
Species	3	364.28	121.43	150.17	<0.001*	L. huls vs. E. inerm	8.93	24.64	<0.001*
Residual	19	15.36	0.81			H. long vs. E. inerm	8.12	20.85	<0.001*
Total	22	379.64				Cycloth vs. E. inerm	7.95	23.16	<0.001*
<i>E. inermis</i> vs. Bulk Zooplankton									
C:N									
Species	2	7.63	3.81	1.44	0.245	Main test was NS. No pairwise tests were run			
Residual	64	169.65	2.65						
Total	66	177.28							
$\delta^{13}\text{C}$									
Species	2	1.44	0.72	0.63	0.534	Main test was NS. No pairwise tests were run			
Residual	65	73.83	1.14						
Total	67	75.27							
$\delta^{15}\text{N}$									
Species	2	278.35	139.18	25.82	<0.001*	LO+SO vs. OM	4.25	7.41	<0.001*
Residual	65	350.36	5.39			LO+SO vs. ML+UO	4.13	9.39	<0.001*
Total	67	628.72							
Ecological Zones for all taxa									
Zones	2	409.00	204.50	20.02	<0.001*	LO+SO vs. ML+UO	3.68	8.38	<0.001*
Residual	135	1378.98	10.22			LO+SO vs OM	3.27	6.46	<0.001*
Total	137	1787.98							
Students t-test Results							df	t	P
ML+UO <i>E. inermis</i> vs <i>S. subtenuis</i>									
$\delta^{13}\text{C}$							10	-5.03	<0.001*
$\delta^{15}\text{N}$							10	-0.77	0.464
C:N							9	0.47	0.648
ML+UO vs SO+LO <i>E. inermis</i>									
$\delta^{13}\text{C}$							10	-1.14	0.278
$\delta^{15}\text{N}$							10	1.74	0.110
C:N							11	-0.77	0.458

Table 3.7: Elemental composition and molar C:N ratios of 2008 zooplankton taxa at both stations (±) indicates standard deviation.

Species	Tehuantepec Bowl				Costa Rica Dome			
	C	N	C:N	n	C	N	C:N	n
Phylum Arthropoda								
Order Copepoda								
<i>Eucalanus inermis</i>	21.46 ± 3.05	5.38 ± 1.04	4.84 ± 1.37	12	23.34 ± 3.42	6.04 ± 1.52	4.66 ± 0.85	11
<i>Euchaeta</i> spp.	27.82 ± 7.44	6.15 ± 0.44	5.34 ± 1.79	2	37.45 ± 16.33	7.35 ± 1.38	5.80 ± 1.50	2
<i>Gaetanus miles</i>		No Data			27.70 ± 3.74	7.32 ± 0.59	4.45 ± 0.96	2
<i>Heterostylites longicornis</i>	20.65	2.95	8.17	1	13.26 ± 1.72	3.73 ± 0.41	4.21 ± 0.99	3
<i>Lucicutia hulsemannae</i>	30.41 ± 0.93	5.15 ± 0.51	6.93 ± 0.89	2	31.92 ± 4.89	5.63 ± 1.10	6.06 ± 1.58	3
Megacalanidae		No Data			36.27 ± 2.87	5.45 ± 0.38	7.80 ± 1.16	2
<i>Pleuromamma johnsoni</i>	31.64 ± 4.18	8.00 ± 1.86	4.76 ± 0.86	5	22.33	5.94	4.38	1
<i>Rhincalanus rostrifrons</i>		No Data			35.65 ± 10.02	5.19 ± 0.07	8.02 ± 2.33	3
<i>Subeucalanus subtenuis</i>	24.18 ± 5.05	6.28 ± 0.93	4.53 ± 0.93	5	16.73 ± 0.96	6.07 ± 0.18	3.22 ± 0.28	2
Order Amphipoda								
Gammarid	34.84 ± 12.55	6.47 ± 0.38	6.36 ± 2.64	2	25.42 ± 2.28	4.41 ± 2.02	7.66 ± 4.11	2
<i>Phronima</i> spp.		No Data			17.69	3.42	6.03	1
Order Euphausiacea	29.78 ± 2.14	7.14 ± 1.61	4.98 ± 0.73	4	33.28 ± 1.75	6.66 ± 0.46	5.83 ± 0.17	4
Order Decapoda								
Shrimp	34.86	6.63	6.13	1	33.55 ± 1.45	7.31 ± 1.87	5.58 ± 1.33	3
Order Ostracoda	35.11	7.59	5.39	1	33.52 ± 6.94	6.21 ± 3.60	7.11 ± 2.82	2
Phylum Annelida								
Class Polychaeta	30.75 ± 2.63	6.31 ± 0.41	5.68 ± 0.11	2		No Data		
Phylum Chaetognatha								
	26.17	7.15	4.27	1	24.96 ± 3.41	6.76 ± 0.47	4.34 ± 0.89	2
Phylum Chordata								
Class Osteichthyes								
<i>Cyclothone</i> spp.	38.51 ± 1.83	10.55 ± 0.62	4.26 ± 0.05	2	38.96 ± 0.78	11.81 ± 1.15	3.88 ± 0.49	4
Myctophids	44.34	11.98	4.32	1	38.45	8.75	5.13	1
Misc. Un-id Fish	34.69	8.98	4.51	1	38.75	10.03	4.51	1

Fig. 3.1: Station Map.

Fig. 3.2: Hydrographic profiles of stations TB and CRD in 2007 and 2008. The data shown are for Tows 609, 614, 632, and 636. Right side plots are biomass weighted mean bulk zooplankton $\delta^{13}\text{C}$ (circles) and $\delta^{15}\text{N}$ (triangles) at each station in 2008 from Williams et al (submitted). Grey boxes represent the extent of the OMZ core.

Fig. 3.3: Vertical profiles of zooplankton individual taxa $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from both years, and C:N data for 2008 at TB (top row), and at CRD (bottom row). All points represent average $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for each taxon in a single net. Starred data represents biomass weighted mean $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for bulk zooplankton (chapter 2). Grey boxes denote range of C:N ratios indicating taxa with tissues dominated by lipids

Fig. 3.4: Average $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ for zooplankton taxa in each ecological zone at TB and CRD. Consumer polygons representing the likely range of consumers feeding on shallow (0-110m) POM are indicated by green dotted lines, while likely ranges of consumers feeding on deep POM (110-1000m) are represented by blue dotted lines. Equations and black lines represent linear regressions. Error bars denote standard deviations.

Fig. 3.5: MDS plots showing zooplankton trophic levels for each ecological zone at both stations combined. Trophic levels were assigned for each species based on values reported in the literature (left column), and calculated for each species using $\delta^{15}\text{N}$ values (right column). MDS plots and group average cluster analyses were calculated from Euclidean distance resemblance matrices. Circles represent significant ($p \leq 0.05$) clusters identified by SIMPROF routines. All points represent average $\delta^{13}\text{C}$ of $\delta^{15}\text{N}$ values for each taxon in a single net.

Fig. 3.6: Trophic Level box plot of zooplankton taxa from both years and stations combined. The upper and lower boundaries of the box represent the 25th (bottom) and 75th (top) percentiles, the line inside each box is the median, error bars represent the 10th (bottom) and 90th (top) percentiles, and black circles represent outliers.

Fig. 3.7: Vertical profiles of zooplankton individual taxa $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from both years, and C:N data from 2008 at a) TB and b) CRD including values for *Eucalanus inermis* (red circles), *Subeucalanus subtenius* (blue squares), and *Lucicutia hulsemannae* (green triangles). All points represent average $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for each taxon in a single net. Starred data represents biomass weighted mean $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for bulk zooplankton data. Grey boxes denote range of C:N ranges indicating taxa with tissues dominated by lipids

CHAPTER 4: CONCLUSIONS

The research presented in this manuscript examined the food sources and trophic interactions of the ENTP OMZ zooplankton community using carbon and nitrogen stable isotopes of bulk zooplankton, individual zooplankton taxa, and POM, as well as C: N ratios of zooplankton individual taxa.

POM $\delta^{15}\text{N}$ values consistently increased at depths below 110m, but there was no comparable increase in $\delta^{15}\text{N}$ of bulk zooplankton at the same depth. Bulk zooplankton and individual taxa $\delta^{15}\text{N}$ values remained relatively constant with depth until the lower oxycline, where there was a sharp increase in $\delta^{15}\text{N}$ over a short depth interval. Bulk zooplankton and individual taxa collected within and above the OMZ core had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values similar to shallow POM (<110m) and were associated with shallow POM consumer polygons. Although shallow POM was the expected food source for mixed layer and upper oxycline zooplankton, the finding that shallow POM was also the primary food source for zooplankton within the OMZ core suggests that these zooplankton do not feed *in situ* on suspended POM. Instead, zooplankton in the OMZ core either consume large aggregates of fresh material at depth, or feed at shallower depths during vertical migrations. Oxygen concentrations within the OMZ core were <2 μM which may have been low enough to necessitate regular migrations to shallower depths to “burn off” their oxygen debt” (Childress & Seibel, 1998; Seibel, 2011) and feed.

In contrast to OMZ core zooplankton, lower oxycline bulk zooplankton and individual taxa had much higher $\delta^{15}\text{N}$ values and were associated with deep POM

consumer polygons. This suggests that the lower oxycline zooplankton community may be physically and trophically isolated from the food and animals in the overlying water column. Furthermore, trophic level calculations for many lower oxycline zooplankton taxa were much higher than expected based on *a priori* trophic level designations. OMZs have large and active microbial communities, and it is possible that isotope fractionation occurring within the microbial loop inflated the calculated trophic levels of the lower oxycline zooplankton community. The lower oxycline is an area of vigorous trophic processing as indicated by strong isotope gradients. The lower oxycline zooplankton community may also be a food source for larger midwater pelagic taxa, a subject for future studies.

In addition to the large changes in isotope values with depth, there were significant differences between zooplankton and POM $\delta^{15}\text{N}$ values at the two stations. $\delta^{15}\text{N}$ values at TB were high compared to those of average marine phytoplankton but similar to those in other regions with OMZs. Therefore, TB $\delta^{15}\text{N}$ values were most likely influenced by the high $\delta^{15}\text{NO}_3^-$ values produced by heterotrophic denitrifiers in the OMZ core. CRD, in contrast, had much lower $\delta^{15}\text{N}$ values, suggesting that nitrogen fixation may be a significant source of new nitrogen at that station. Furthermore, the relationship between zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at CRD indicated that nitrogen fixation had occurred for long enough or occurred frequently enough for even the deepest zooplankton community to show signs of multiple nitrogen inputs. However, nitrogen fixation has not previously been noted in this area, and the available data cannot rule out other potential sources of low $\delta^{15}\text{N}$ values at CRD. Future studies should focus on examining the significance of nitrogen fixation

in this area and how it may impact zooplankton productivity as compared to areas such as TB, which did not show signs of significant nitrogen fixation.

The abundance, distribution, and life history of the copepod *E. inermis* have been extensively studied previously, but few earlier studies have examined populations below 300m or its diet at any depth. Results of this study suggested that *E. inermis* fed only on shallow POM, even when collected below the lower oxycline. Additionally, the population of *E. inermis* associated with the lower oxycline is thought to be composed of diapausing individuals, but the $\delta^{15}\text{N}$ and C: N values of lower oxycline *E. inermis* were far lower than expected for diapausing individuals. One potential explanation for these unexpectedly low $\delta^{15}\text{N}$ values and C:N ratios is that *E. inermis* may store ammonium as a means of buoyancy regulation (Schröder et al., 2013). This is a commonly used strategy for cephalopods, but recent work has shown that some diapausing copepods are capable of ammonium storage as well (Schröder et al., 2013). Storing ammonium would maintain higher nitrogen content in the body tissues relative to carbon, which would reduce C:N ratios. It would also prevent enrichment of $\delta^{15}\text{N}$ by retaining ^{14}N that would otherwise be excreted. However, further study of the behavior and body chemistry of deep *E. inermis* populations are needed to determine the cause of the isotope and body chemistry patterns observed in this study.

APPENDIX A: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all individual zooplankton taxa. Values represent single samples. The values of larger taxa that required homogenization or otherwise dividing into two more than a single measurement are shown as averages of the subsamples. $\pm$ represents standard deviations. requiring homogenization or which needed to be split prior to running a sample.

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
Phylum Arthropoda									
Order Copepoda									
<i>E. attenuatus</i>	2007	1	604	5	90	-19.42	1		
<i>E. inermis</i> -		8	614	6	114	-19.32	1	9.33	1
								2.89	1
		8	614	5	250			4.48	1
								4.83	1
								4.77	1
		8	622	7	260			5.02	± 3.44 2
								5.16	1
								6.32	1
<i>E. inermis</i> F		1	607	3	650	-22.34	1	2.49	1
						-22.17	1	3.24	1
						-36.44	1		
						-33.72	1		
		1	611	1	476	-21.21	1		
						-24.42	1		
		1	612	6	35	-31.56	1	5.88	1
						-30.27	1	6.57	1
						-24.38	1	4.42	1
								16.33	1
								5.68	1
								4.64	1
		8	614	6	114	-20.78	1		
						-20.93	1		
						-20.57	1		
						-19.27	1		
		8	614	5	250	-21.27	1		
						-21.25	1		
		8	614	4	450	-20.36	1	8.90	1
						-18.25	1	4.27	1
								8.05	1
								2.42	1
		8	614	3	650			4.46	1
								2.94	1
								2.74	1
								2.87	1
		8	617	4	450	-20.85	1	1.03	1
						-21.92	1	1.70	1
						-23.68	1	4.57	1
		8	617	3	650	-21.38	1	3.29	1
						-19.42	1	3.65	1
								5.56	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
								4.29	1
		8	618	5	45			4.48	1
								2.47	1
								5.79	1
		8	622	2	250	-19.55	1		
						-22.35	1		
						-22.85	1		
	2008	1	631	6	789	-2.89	1	6.23	1
								5.15	1
								9.28	1
								7.85	1
								6.70	1
		1	631	5	814	-22.98	1	8.06	1
						-25.04	1	2.26	1
						-24.74	1	5.06	1
						-20.33	1	5.27	1
						-23.90	1		
						-22.45	1		
		1	631	4	839	-24.24	1	7.69	1
						-25.03 ± 0.20	2	7.20	1
						-22.73 ± 0.95	2		
		8	635	8	13			7.51	1
								4.97	1
		8	635	3	71	-23.05	1	4.97 ± 0.21	2
								5.42	1
		8	635	2	91	-21.54 ± 1.25	2	5.13	1
						-25.12 ± 0.03	2	7.15	1
						-21.39	1	5.18	1
								5.81	1
		8	636	8	538			2.86	1
						-24.43 ± 0.60	2	5.58	1
						-24.08 ± 1.22	3	8.78	1
								7.05	1
								3.96	1
		8	637	5	325	-24.15	1	5.25	1
						-24.84	1	4.90	1
						-23.61 ± 0.52	2	5.20	1
						-25.14	1		
		8	637	3	426	-23.65 ± 0.79	2	4.21	1
						-23.44 ± 0.26	2	3.96	1
						-23.20	1	4.23	1
						-22.28	1		
		8	637	1	526	-21.14 ± 1.46	2	5.75	1
						-22.77 ± 0.78	2	3.88	1
						-24.23	1		
		8	641	8	226	-23.59 ± 0.01	2	10.95	1
						-25.30 ± 0.85	2	8.71	1
						-24.07	1	8.75	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
<i>E. inermis</i> I	2007	8	641	6	325	-23.80	1	3.62	1
						-24.92	1	4.83	1
						-25.13	1	4.60	1
						-23.11	1	4.78	1
		8	641	6	325	-23.67	1		
						-24.12	1		
		8	641	4	426	-19.94	1	12.65	1
						-29.47 $\pm$ 7.91	2	5.58	1
						-23.78	1		
		8	641	1	506	-22.67	1	5.13	1
						-22.17	1	5.03	1
						-20.26	1		
						-24.07	1		
		2007	1	612	6	35	-31.66	1	
							-29.78	1	
		8	614	5	250	-22.82	1		
		8	614	4	450	-22.47	1	10.39	1
						-20.54	1		
						-21.03	1		
		8	617	4	450	-19.84	1	8.20	1
						-21.90	1		
						-22.14	1		
		8	617	3	650			5.12	1
		8	618	5	45	-23.77	1	2.98	1
						-23.79	1		
						-23.60	1		
						-24.44	1		
		8	618	3	70	-21.34	1	4.25	1
						-22.28	1		
	2008	1	626	3	71	-22.18	1	8.10	1
						-22.34	1	8.56	1
						-22.41	1	9.47	1
						-21.61	1		
		1	626	1	127	-24.84	1		
						-24.30	1	8.18	1
						-25.60	1	7.00	1
						-23.00	1	8.78	1
		1	629	8	175	-23.17	1	7.67	1
						-25.46	1	7.53	1
								6.31	1
		1	629	7	226	-25.15	1	6.60	1
						-25.02	1	7.71	1
						-20.19 $\pm$ 0.57	2		
						-20.33	1		
		1	629	2	477	-21.84	1	9.30	1
		1	629	1	526	-20.60	1	7.35	1
						-20.60	1	6.07	1
						-21.29	1		

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
<i>E. inermis</i> M						-21.67 $\pm$ 0.45	2		
						-24.32	1	6.28	1
						-27.33	1	5.76	1
						-25.40 $\pm$ 0.21	2	5.84	1
						-22.98	1	6.76	1
						-25.14	1	6.64	1
						-22.28	1	7.06	1
						-19.11	1	5.18	1
						-23.88	1		
						-20.87	1		
						-17.40	1	6.10	1
						-24.97	1	8.19	1
						-25.34	1		
						-29.74	1		
						-21.40 $\pm$ 0.90	2		
						-21.32	1		
						-22.62	1	8.65	1
						-25.23	1		
						-19.96	1	3.99	1
						-22.43	1	5.17	1
						-16.26	1	4.75	1
						-19.20	1	5.15	1
						-17.18	1		
						-25.53	1	4.78	1
						-21.86	1	6.72	1
						-20.96	1	4.64	1
						-22.33	1	7.45	1
								5.73	1
								4.00	1
								4.99	1
						-30.63 $\pm$ 0.42	2	4.40	1
								2.86	1
								4.30	1
						-26.65	1	4.55	1
						-30.76	1	3.23	1
						-28.90 $\pm$ 3.62	2	4.53	1
						-22.24	1		
						-22.15	1		
						-22.07	1		
						-18.02	1		
						-22.21	1		
						-19.21	1		
						-15.18	1		
						-19.77	1		
						-18.86	1		
						-21.72	1	5.84	1
								6.17	1
								4.79	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
								6.36	1
<i>Euchaeta</i> (dreamcicle)	2007	8	617	2	860	-18.56	1	16.98	1
<i>Euchaeta</i> spp.		1	609	3	650	-22.34	1		
<i>Euchaeta</i> sp.2		1	607	1	1050			18.26	1
		1	609	1	1050	-20.45	1	9.82	1
<i>Euchaeta</i> sp.4		1	606	8	150	-21.62	1	9.67	1
								11.74	1
								12.02	1
								12.17	1
<i>Euchaeta</i> sp.8		1	609	2	825	-17.85	1		
<i>Euchaeta</i> spp.	2008	1	633	5	46	-27.10	1	10.88	1
						-22.65	1	10.80	1
						-22.11	1	11.27	1
		1	633	3	71	-24.89	1		
<i>Euchaeta</i> sp.20		1	626	5	45	-23.04	1	11.73 ± 0.82	2
						-22.58	1		
						-23.92	1		
		1	633	4	55			10.62	1
								9.87	1
		8	635	7	25	-23.02	1	4.31	1
						-20.98	1	4.54	1
						-20.61	1	5.03	1
								4.53	1
								4.67	1
								4.84	1
								4.40	1
		8	635	5	46			6.34	1
								6.84	1
								6.39	1
<i>Euchaeta</i> sp.21		1	633	3	71	-25.75	1		
<i>Euchaeta</i> sp.22 F		8	641	8	226	-23.55 ± 0.10	2	14.52	1
						-22.52	1	14.56	1
<i>Euchaeta</i> sp.22 M		1	629	8	175	-20.20	1		
		8	641	8	226	-23.41	1		
						-22.93	1		
<i>Gaetanus</i> sp.1	2007					-20.17	1		
		1	609	1	1050	-20.45	1		
		1	611	6	225	-19.52	1	19.37	1
								13.67	1
								15.14	1
								17.98	1
								19.58	1
								10.22	1
		8	614	5	250	-18.51	1	10.57	1
								10.41	1
		8	614	2	825	-18.52	1	12.41	1
						-18.87	1		
		8	614	1	1050	-18.57	1	13.58	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
<i>Gaetanus</i> sp.8	2008	8	617	2	860	-19.42	1	13.50	1
						-19.24	1	12.12	1
		8	617	1	1050	-20.14	1	12.51	1
						-19.48	1	13.24	1
		8	635	1	127	-20.96	1	11.92	1
						-20.97	1		
<i>H. longicornis</i>	2007	8	641	8	226	-22.85	1	10.17	1
								10.03	1
		1	607	3	650	-20.84	1	15.27	1
						-19.89	1	9.77	1
		8	614	4	450	-19.51	1		
						-19.71	1		
		8	614	3	650	-21.16	1	12.15	1
						-18.64	1	12.05	1
		8	617	4	450	-18.47	1		
						-18.47	1		
						-19.64	1	12.64	1
						-19.23	1		
						-19.51	1		
						-19.22	1		
		8	617	3	650	-20.29	1		
		8	617	2	860	-19.96	1		
						-18.82	1		
						-19.36	1		
<i>H. longicornis</i> F	2008	8	614	4	450	-19.46	1	13.77	1
						-20.25	1	14.72	1
		8	617	3	650	-19.24	1		
						-19.75	1	15.93	1
						-20.37	1	13.20	1
						-20.53	1	14.28	1
<i>H. longicornis</i> F	2008	8	617	3	650	-19.22	1	11.01	1
						-18.74	1		
						-18.76	1		
		1	631	7	738	-20.61 $\pm$ 0.71	3	14.79	1
								13.02	1
						-21.67	1	13.60	1
						-21.45	1	13.33	1
		8	636	6	588	-20.56	1	14.90	1
						-20.90	1	14.03	1
<i>H. longicornis</i> M	2007	8	641	1	506	-20.89	1	13.23	1
						-21.95	1	14.26	1
		8	614	4	450	-21.75	1		
						-22.02	1		
						-19.52	1	10.82	1
						-19.32	1	13.80	1
								13.99	1
		8	617	3	650	-19.18	1		
						-17.85	1		

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
						-19.53	1		
						-18.64	1		
						-18.58	1		
						-19.64	1		
<i>H. longicornis</i> M	2008	1	631	7	738	-20.49	1	14.38	1
						-22.29	1		
		8	636	8	538	-18.69	1	13.03	1
						-20.94	1	14.18	1
		8	636	6	588	-17.44	1		
<i>Haloptilus</i> sp.1	2007	1	607	3	650	-19.05	1		
						-18.04	1		
						-19.96	1		
		1	609	2	825			17.41	1
		1	612	1	125			12.37	1
		8	614	3	650	-18.43	1	15.99	1
						-18.89	1	15.93	1
						-19.28	1	17.11	1
						-18.37	1	16.28	1
		8	614	2	825	-19.26	1	17.12	1
						-18.98	1	16.14	1
						-19.10	1	10.95	1
						-18.69	1		
						-18.59	1		
		8	614	1	1050	-19.86	1		
		8	617	3	650	-18.59 ± 0.28	2	16.69	1
		8	618	3	70	-21.00	1	14.26	1
						-21.35	1	10.58	1
		8	621	1	125	-18.36	1	11.66	1
						-20.21	1	6.10	1
								9.45	1
<i>Haloptilus</i> sp.6		8	614	5	250			11.74	1
<i>Haloptilus</i> sp.7		8	614	6	114	-20.10	1		
		8	614	2	825			13.61	1
<i>Haloptilus</i> sp.1 F		1	604	5	90	-21.15	1		
<i>Haloptilus</i> sp.1 I						-22.06	1		
<i>Haloptilus</i> sp.21 F	2008	8	641	8	226	-20.86	1	12.26	1
						-22.04 ± 0.03	2	11.14	1
						-21.56	1		
						-20.87	1		
		8	618	3	70	-22.06	1		
<i>L. hulsemannae</i> F	2007	1	607	2	825	-19.51 ± 0.44	2	16.07	1
						-19.83 ± 0.27	2	15.39	1
						-20.09 ± 0.14	2	15.64	1
		1	609	2	825	-19.24	1	16.46 ± 0.58	2
						-19.41 ± 0.02	2	14.20	1
						-19.10 ± 0.51	2		
		1	613	7	775	-20.47	1	16.13 ± 0.19	4
						-21.00 ± 0.85	2	15.92	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
<i>L. hulsemannae</i> F	2008	8	614	3	650	-20.12 $\pm$ 0.17	3	15.28	1
						-19.59 $\pm$ 0.01	2	14.63	1
						-20.26 $\pm$ 0.17	2	14.01	1
						-19.16 $\pm$ 1.43	2	14.49	1
								15.01	1
						-19.50	1	13.77	1
						-19.99	1	14.83	1
						-18.00	1	14.93	1
						-20.84	1	13.50	1
						-19.83 $\pm$ 0.46	2	14.11	1
		1	607	3	650			14.02	1
								20.77	1
								17.84	1
								16.42	1
								16.84	1
								19.70	1
								21.36	1
								21.02	1
						-22.63 $\pm$ 0.20	3	15.65	1
						-21.83 $\pm$ 0.33	3	15.41	1
						-21.75 $\pm$ 0.86	3	16.13	1
						-22.69 $\pm$ 0.21	3	15.72	1
		8	636	7	563	-22.61 $\pm$ 0.30	3		
						-23.39 $\pm$ 0.81	2		
						-23.24	1	13.62	1
								14.40	1
								12.84	1
								13.37	1
								14.38	1
								14.39	1
						-20.66 $\pm$ 0.62	4	14.84 $\pm$ 0.47	2
						-20.95 $\pm$ 0.74	2	13.63 $\pm$ 1.32	2
						-22.19 $\pm$ 0.08	3	14.08 $\pm$ 1.40	2
						-22.13	1	14.81	1
		8	636	3	700	-21.37	1		
						-20.16 $\pm$ 0.49	2		
						-22.84 $\pm$ 0.16	2	14.25 $\pm$ 0.25	3
						-22.04	1	13.82	1
						-18.16	1	13.88	1
								13.32	1
								13.56	1
								14.19	1
						-19.18 $\pm$ 1.02	4	13.94	1
								13.88	1
								13.87	1
								13.75	1
<i>L. hulsemannae</i> I	2007	8	614	3	650				
<i>L. hulsemannae</i> I	2008	1	631	5	814	-21.85 $\pm$ 0.73	2	17.24	1
						-21.62	1	15.57	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
						-21.89	1	15.05	1
								16.49	1
								17.44	1
								14.98	1
<i>L. hulsemannae</i> I		8	636	8	538			12.76	1
		8	636	6	588	-20.90 $\pm$ 0.38	2	13.25	1
						-23.25 $\pm$ 1.40	3	13.92 $\pm$ 0.46	2
						-21.61 $\pm$ 0.87	2	13.27	1
						-22.99	1	13.95	1
						-22.16 $\pm$ 0.66	2	12.51	1
<i>L. hulsemannae</i> M	2007	1	607	2	825	-21.10	1	16.98	1
						-21.14	1	17.25	1
								16.27	1
						-18.36 $\pm$ 0.05	2	16.03	1
						-19.38 $\pm$ 0.16	2	14.24	1
		1	613	7	775	-21.48	1	15.52 $\pm$ 0.76	2
						-20.41 $\pm$ 0.56	2	15.64	1
						-21.85 $\pm$ 0.29	2		
		8	614	3	650			12.83	1
								13.56	1
								13.56	1
								14.15	1
		8	614	2	825	-20.16	1	14.13	1
						-19.83	1	14.14	1
						-20.91 $\pm$ 0.90	2		
		8	617	3	650	-20.61	1	14.52	1
						-20.29 $\pm$ 0.19	2	12.96	1
						-21.03 $\pm$ 0.39	3	13.48	1
<i>L. hulsemannae</i> M	2008	1	631	4	839	-22.28 $\pm$ 0.26	2	15.01	1
					839	-21.50 $\pm$ 0.63	3	17.21	1
					839	-21.70 $\pm$ 0.62	3	15.28	1
								16.14	1
		8	636	7	563	-22.81	1		
		8	636	6	588	-23.00 $\pm$ 0.14	2	14.36	1
								13.87	1
								13.30	1
								13.36	1
		8	636	5	613	-22.10 $\pm$ 0.55	4	14.02 $\pm$ 1.03	2
						-21.72 $\pm$ 0.66	5	14.74	1
						-19.84 $\pm$ 1.39	3	13.78	1
						-21.65 $\pm$ 0.60	2	13.49	1
		8	636	4	638	-22.61	1		
<i>Lucicutia</i> sp.1	2007	1	604	4	125			15.24	1
<i>Lucicutia</i> sp.2		8	617	1	1050			16.29	1
<i>Megacalanidae</i>	2008	8	636	4	638	-22.36	1	14.50 $\pm$ 0.08	3
		8	636	3	700	-22.43	1	14.43 $\pm$ 0.15	3
<i>P. abdominalis abyssalis</i>		8	637	6	276	-23.20	1	5.94	1
						-22.77	1	6.01	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
<i>P. johnsonii</i>	2007	1	606	2	150	-22.55	1	5.96	1
						-22.62	1		
						-23.07	1		
						-22.83	1		
						-23.70	1		
						-23.37	1		
			607	2	825	-22.22	1	12.21	1
						-22.07	1	12.31	1
						-22.62	1	13.39	1
			609	2	825	-22.31	1	13.43	1
						-22.19	1		
		1	611	3	375			11.04	1
								10.64	1
								14.35	1
		1	611	1	475			11.46	1
								13.59	1
								10.32	1
								10.45	1
								10.49	1
								10.38	1
		8	614	5	250			9.71	1
								10.25	1
						-21.26	1	7.81	1
						-20.96	1	7.37	1
								7.58	1
								8.02	1
		8	614	4	450			8.67	1
						-22.39	1	9.96	1
								5.45	1
<i>P. johnsonii</i>	2008	1	631	2	889	-22.99	1	10.47	1
						-22.98	1	10.35	1
<i>P. johnsonii</i> F		1	629	5	326	-22.64	1	8.06	1
						-22.08 $\pm$ 1.38	2	9.12	1
		1	629	5	326	-22.23 $\pm$ 1.59	2	9.40	1
						-20.42	1	9.40	1
		1	629	4	376	-21.23	1	9.15	1
						-22.90	1	8.79	1
						-19.41	1	9.50	1
						-20.39	1	9.27	1
						-20.36	1		
		1	629	3	426	-21.95	1	9.37	1
						-21.15	1	9.51	1
						-21.19	1	10.55	1
								9.81	1
								8.53	1
		1	631	2	889	-21.45 $\pm$ 2.68	2		
		1	633	4	55	-25.57	1	10.45	1
						-23.51	1	10.46	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
<i>R. rostrifrons</i>	2007	1	604	1	305	-17.87	1	10.06	1
								11.40	1
								10.87	1
		8	614	5	250	-20.66	1	10.98	1
								11.87	1
<i>R. rostrifrons</i>	2008	8	635	2	91	-21.61	1	7.46	1
								8.12	1
		8	635	1	127	-21.49	1	9.47	1
		8	641	8	226	-23.53 $\pm$ 0.98	2	8.16	1
		8	641	8	226	-23.94 $\pm$ 1.63	2	8.54	1
<i>S. subtenuis</i>	2007	8	621	7	25	-18.71	1	8.83	1
								8.73	1
								6.07	1
								5.47	1
								6.15	1
								5.34	1
								5.23	1
								4.43	1
								4.32	1
								5.61	1
								5.66	1
								5.65	1
								5.33	1
								6.06	1
								5.50	1
								5.34	1
<i>S. subtenuis</i> F	2007	8	618	7	25	-18.76	1		
								6.21	1
								6.52	1
								6.57	1
								6.53	1
<i>S. Subtenuis</i> F	2008	1	626	5	45	-22.40 $\pm$ 1.57	2	9.84 $\pm$ 0.40	3
		1	626	4	55	-23.19 $\pm$ 0.10	2	8.87	1
								8.83	1
								8.39	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
						-22.06 $\pm$ 1.30	2		
						-20.83 $\pm$ 0.87	2		
		1	633	4	55	-22.27 $\pm$ 0.90	3	9.59	1
						-22.01	1	9.10	1
		8	635	7	25	-21.93	1	6.52	1
						-20.15	1	6.32	1
						-20.84	1	5.68	1
								5.17	1
		8	635	5	46	-19.85	1	6.74	1
						-18.59	1	5.50	1
<i>S. subtenuis</i> I	2007	8	618	7	25			5.80	1
								6.60	1
								5.69	1
								5.94	1
<i>S. subtenuis</i> I	2008	1	626	4	55	-22.43	1		
						-21.12	1		
						-20.52	1		
		1	633	5	46			8.44	1
		1	633	3	71	-22.41 $\pm$ 0.18	4	5.35	1
						-21.65	1	9.46	1
						-21.44 $\pm$ 0.04	2		
						-21.10 $\pm$ 0.01	2		
		1	633	2	91	-23.48	1	8.85	1
						-23.21	1	8.28	1
								9.04	1
<i>Scolecitrichidae</i>	2007	8	617	3	650	-20.32	1	12.52	1
						-19.91	1	11.50	1
								11.32	1
		8	617	2	860	-24.10	1	12.12	1
		8	617	1	1050	-20.66	1	11.45	1
						-19.86	1		
OrderAmphipoda									
Gammarid (deep sea)	2007	1	609	2	825			$\pm$ 11.36	1
		8	614	4	450	-20.71	1		
		8	614	2	825	-19.30	1	8.05 $\pm$ 0.10	2
Amphipod sp.5		1	611	3	376	-21.05	1		
						-20.38	1		
		8	614	5	250	-18.96	1	6.81 $\pm$ 5.51	2
		8	614	1	1050			9.98	1
Amphipod sp.20	2008	1	629	5	326	-20.21	1	8.40 $\pm$ 1.51	3
						-19.44	1		
		1	629	4	376			9.01 $\pm$ 1.93	3
		1	629	3	426	9.09 $\pm$ 0.10	2	9.09 $\pm$ 0.10	2
		1	631	2	889	-22.53	1	$\pm$ 8.95	1
		8	637	7	226	-22.44 $\pm$ 0.10	2	4.59	1
		8	641	6	325	-23.34	1	5.30	1
						-21.77 $\pm$ 1.30	3	6.28 $\pm$ 1.01	2
								4.74	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
Amphipod- <i>Phronima</i> spp.		8	637	5	325	-21.48 $\pm$ 0.26	2	7.03 $\pm$ 0.07	2
						-20.41 $\pm$ 0.40	3	7.98 $\pm$ 0.01	2
Order Euphausiacea									
<i>E. khroni</i>	2007	8	614	5	250	-19.78	1	8.49	1
		8	621	1	125	-19.76	1	7.18 $\pm$ 0.94	3
								7.02 $\pm$ 0.60	4
<i>E. khroni</i> I		8	614	5	250			6.88	1
<i>E. khroni</i> F		1	611	6	225			11.15	1
<i>E. khroni</i> M		8	614	4	450	-18.51	1		
		8	614	3	650			9.26	1
Euphausiid sp.7 F		8	621	1	125	-24.75	1	9.41	0.30
						-19.01	1		
Euphausiid sp.7 M						-19.52	1	9.52	
						-19.27	1		
Euphausiid sp.8		1	611	6	225	-18.70	1		
						-18.68	1		
		8	614	5	250	-18.58	1	8.94	1
						-19.03	1		
bi-lobed eyes	2008	1	633	4	55	-19.89	1	11.59 $\pm$ 0.83	3
		8	635	3	71	-24.05	1	10.14	1
		8	637	6	276	-21.73	1	9.77	1
		8	637	4	375	-22.46 $\pm$ 0.03	2	7.69 $\pm$ 0.21	2
<i>E. sibogae</i>		1	629	6	276	-21.84 $\pm$ 0.75	2	10.46 0.00	2
Round eyes		1	629	7	226	-19.80	1	12.88	1
								12.89	1
		1	633	6	36	-20.04	1	11.85 $\pm$ 0.18	2
		8	637	7	226	-22.16 $\pm$ 0.13	3	7.39 0.40	3
		8	637	6	276	-22.00	1	7.82	1
		8	637	4	375	-21.57	1	8.87	1
Order Decapoda									
Misc. Un-id	2007	8	614	1	1050	-20.96	3	13.91	3
Misc. Un-id	2008	1	631	2	889	-23.04 $\pm$ 0.03	2	12.81 $\pm$ 0.02	2
		8	637	6	276	-23.38 $\pm$ 0.09	2	11.69 $\pm$ 0.27	2
Caridean		1	607	1	1050	-20.31	2	16.35	2
<i>Gennades</i> spp.		8	636	7	563	-20.48 $\pm$ 0.12	3	12.86 $\pm$ 0.31	3
Sergestid			614	2	825	-19.69	2	15.59	2
		8	637	7	226	-21.52 $\pm$ 0.38	2	6.66 $\pm$ 0.07	2
Order Ostracoda									
Ostracod (deep sea)	2007	1	607	2	825			14.25	1
		1	610	3	475	-18.64	1	12.14	2
		8	614	1	1050	-19.52	1		
						-18.88	1		
		8	617	1	1050	-18.26	1	10.64	1
						-18.71	1		
		8	636	2	826	-22.62 $\pm$ 1.12	2	9.36 $\pm$ 0.86	4

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
						-25.15	1		
Ostracod sp.1	2007	1	611	6	225			10.92	1
Ostracod sp.2		1	604	5	90	-21.73	1		
		1	604	4	125			10.07	1
		1	606	2	150	-21.83	1		
		8	614	6	114	-20.08	1	9.66	1
						-19.97	1	9.29	1
								10.24	1
		8	614	2	825			8.66	1
		8	618	3	70	7.23	1	7.23	1
						7.95	1	7.95	1
						7.79	1	7.79	1
		8	621	1	125	-17.62	1	7.80	1
						-19.95	1	9.57	1
								6.66	1
Ostracod sp.3	2007	1	604	4	125			10.48	1
								9.50	1
								10.64	1
Ostracod sp.20	2008	1	629	8	175	-22.47	1	8.59	1
						-20.11 $\pm$ 0.37	2	8.28	1
						-22.36	1	9.31	1
						-22.04 $\pm$ 0.38	3		
						-21.66 $\pm$ 0.01	2		
						-20.07 $\pm$ 1.16	2		
						-20.49 $\pm$ 0.49	2		
		8	635	1	127	-22.71	1	6.87 $\pm$ 0.22	2
						-21.85	1	6.50 $\pm$ 0.81	2
								5.26	1
								6.49	1
Phylum Annelida									
Class Polychaeta									
	2007	8	614	3	650			11.21	1
								11.84	1
								10.60	1
		8	614	2	825	-18.74	1	10.23	1
						-19.44	1	8.86	1
						-21.67	1	11.08	1
		8	617	3	650			10.65	1
								13.57	1
								11.11	1
								12.84	1
					650			10.60	1
					650			11.02	1
		8	617	2	861			10.72	1
					861			12.20	1
		8	617	1	1050			9.56	1
					1050			12.18	1
					1050			10.27	1

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
		8	617	1	1050			12.29	1
					1050			10.55	1
	2008	1	631	4	838			10.46	1
		1	631	3	864	-22.41	1	12.65	1
						-21.59 $\pm$ 1.11	2	13.25	1
						-21.50	1	13.93	1
								12.07	1
		1	631	2	889	-19.87 $\pm$ 0.42	2	13.21	1
						-21.87	1	11.89	1
						-21.28	1		
						-19.63	1		
						-20.68	1		
		1	631	1	951			11.69	1
								12.04	1
Phylum Chaetognatha									
Chaetognath sp.1	2007	1	606	8	10			14.85 $\pm$ 2.86	2
		8	614	1	1050	-19.03	1	15.98 $\pm$ 0.20	2
						-18.72	1	16.42	1
						-19.22	1		
Chaetognath sp.2		1	609	1	1050	-18.86	1		
		8	614	2	825	-18.64	1		
						-18.42	1		
		8	614	1	1050	-19.33	1	16.27 $\pm$ 0.25	2
						-19.68	1	16.36	1
						-18.81	1	16.25	1
Chaetognath sp.3		1	611	1	476	-17.59	1	13.01	1
								11.92	1
Chaetognath sp.4		8	617	6	450	-18.29 $\pm$ 0.21	2		
		8	617	3	650	-18.42	1		
		8	617	2	860	-18.81	1		
		8	617	1	1050	-20.30	1		
		8	617	2	861			16.44	1
Chaetognath sp.7						-19.33	1		
		8	617	1	1050	-18.22	1		
Chaetognath sp.9		8	618	7	25	-21.84	1	7.51 $\pm$ 2.32	2
						-19.34	1		
		8	621	7	25	-19.12	1	5.94	1
						-19.82 $\pm$ 1.26	2		
		8	621	1	125	-20.65	1		
Chaetognath sp.10		8	618	5	45			9.36	1
								9.76	1
		8	617	4	450	-19.67	1		
Chaetognath sp.20	2008	1	633	4	55	-21.64 $\pm$ 1.00	2	11.02	1
		8	635	3	72			10.11	1
								9.61	1
		8	635	2	91	-21.90	1	8.10 $\pm$ 0.69	3
						-21.53	1		

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
		8	635	1	127	-20.36 $\pm$ 0.55	5	9.14 $\pm$ 0.82	2
		8	635	1	127	-20.62 $\pm$ 0.88	3	9.25 $\pm$ 0.62	5
		8				-22.98 $\pm$ 0.82	2	8.75 $\pm$ 0.80	3
						-21.72	1		
Chaetognath sp.21		1	626	5	46			12.23 $\pm$ 0.28	4
Chaetognath sp.25		8	635	7	25			7.66 $\pm$ 0.78	4
		8	635	2	91	-20.05 $\pm$ 1.43	2	8.94	1
		8	635	1	127	-21.67 $\pm$ 0.10	2	8.83 $\pm$ 0.35	2
Chaetognath sp.26		8	635	3	72			8.27	1
Phylum Chordata									2
Class Osteichthyes									1
Misc. Un-id	2007	1	611	1	476	-21.58 $\pm$ 0.02	2	15.39 $\pm$ 0.38	2
	2008	1	631	2	889	-20.39 $\pm$ 0.08	3	17.53 $\pm$ 0.20	3
		8	636	2	826			6.51 $\pm$ 1.01	3
Cyclothone spp.		1	607	1	1050	-19.99	1	14.64 $\pm$ 0.14	3
						-20.82	1	14.70 $\pm$ 0.11	3
						-19.71 $\pm$ 0.21	3	14.10	1
						-18.01 $\pm$ 0.30	3	12.97	1
		1	609	2	825	-19.41	1	13.96 $\pm$ 0.25	3
						-19.26 $\pm$ 0.20	4	14.33	1
		1	609	1	1050	-19.35	1	14.87	1
						-18.46	1	15.20	1
						-17.95	1	14.01	1
		8	614	4	450	-18.03 $\pm$ 0.15	3	13.15 $\pm$ 0.32	2
						-17.41 $\pm$ 0.23	3	15.81 $\pm$ 0.22	3
		8	614	3	650	-17.89 $\pm$ 0.04	2	14.16 $\pm$ 0.32	3
						-17.46 $\pm$ 0.08	2	11.29 $\pm$ 0.56	2
						-18.36 $\pm$ 0.17	3	14.53 $\pm$ 1.70	2
						-17.75 $\pm$ 0.20	3	15.53 $\pm$ 0.00	2
		8	614	2	825	-18.17 $\pm$ 0.15	2	14.06 $\pm$ 0.08	2
						-18.05 $\pm$ 0.19	4	13.10 $\pm$ 0.17	3
		8	617	2	860	-17.72	1		
						-18.12	1		
	2008	1	631	3	864	-20.34 $\pm$ 0.79	6	13.83 $\pm$ 0.50	2
						-21.74 $\pm$ 0.56	3	13.98 $\pm$ 3.22	4
						-22.27 $\pm$ 1.05	5		
		1	631	2	889	-22.03 $\pm$ 0.22	3	13.92	1
						-20.73 $\pm$ 0.22	4	14.25 $\pm$ 0.13	2
						-21.16 $\pm$ 0.14	3	14.02 $\pm$ 0.15	4
								15.75 $\pm$ 0.17	3
		1	631	1	951			14.10	1
								15.89	1
		8	636	7	563	-19.44 $\pm$ 1.48	2	14.31 $\pm$ 0.91	3
		8	636	6	588	-20.22	1	12.88 $\pm$ 0.05	2
						-20.25 $\pm$ 0.09	3		
						-19.81	1		
		8	636	5	613	-19.95 $\pm$ 0.09	2	13.23	1
		8	636	3	700	-20.55 $\pm$ 0.10	3		

Species-Stage	Year	Stn	Tow	Net	Mid Depth	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n
		8	636	2	826	-19.63 $\pm$ 0.46	2	13.70 $\pm$ 0.07	2
Myctophid sp.1	2007	1	611	3	376	-19.40 $\pm$ 2.65	6	12.03 $\pm$ 0.17	5
	2008	1	633	4	55	-20.56	1	11.96 $\pm$ 0.32	4
Myctophid sp.2						-21.57	1		
Myctophid sp.3		8	637	2	426	-21.98 $\pm$ 0.08	2	9.60 $\pm$ 0.19	2
						-22.08 $\pm$ 0.13	3	9.56 $\pm$ 0.14	3

APPENDIX B: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of size fractionated bulk zooplankton for each MOCNESS net in each tow.

Year	Stn	Tow	Net	Depth	Size	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	n		
2007	1	605	8	10	202	-20.74	0.01	2	8.51	1.13	3
					505	-20.49	0.63	2	9.21	0.69	3
					1000	-20.48	0.23	2	9.43	0.15	3
					2000	-20.73		1	10.42	1.35	3
			7	25	202	-22.25	0.66	2	7.75	1.34	3
					505	-21.56	0.05	2	8.20	0.46	3
					1000	-21.66	0.55	2	7.87	0.59	3
					2000	-21.87	0.61	2	8.04	0.66	3
			6	35	202	-25.94	0.15	2	5.61	0.40	3
					505	-23.46	1.96	2	6.43	0.60	3
					1000	-27.53	0.22	2	4.92	0.48	3
					2000	-26.85	0.10	2	5.70	1.18	3
			5	45	202	-25.77	0.13	2	7.86	0.80	3
					505	-24.11	0.15	2	8.15	0.39	3
					1000	-25.27	0.07	2	6.98	0.75	3
					2000	-25.57	0.01	2	5.74	3.06	3
			4	55	202	-22.01	0.08	2	10.22	1.36	3
					505	-21.50	0.22	2	10.36	1.30	3
					1000	No Data			10.08		1
					2000	-22.21	0.24	2	9.59	0.07	3
			3	70	202	-22.24	0.06	2	8.72	0.82	3
					505	-21.84	0.21	2	9.35	0.47	3
					1000	-23.14	1.23	2	8.56	1.20	3
					2000	-22.40	0.43	2	7.95	1.32	2
			2	90	202	-21.87	0.55	2	9.48	1.10	3
					505	-20.38	0.00	2	9.56	0.46	3
					1000	-20.20	0.10	2	9.53	0.51	3
					2000	-19.62	0.00	2	9.34	1.11	3
			1	150	202	-21.64	0.09	2	10.73	0.70	3
					505	-21.69	0.43	2	10.20	0.60	3
					1000	-22.23	0.41	2	9.47	1.29	3
	8	618	8	10	202	-20.36	0.13	2	3.46	0.26	3
					505	-20.34	0.10	2	3.31	1.05	3
					1000	-19.83	0.01	2	4.60	0.45	3
					2000	-20.06	0.01	2	4.74	0.57	3
			7	25	202	-21.63	0.04	2	4.14	1.03	4
					505	-20.52	0.17	2	4.89	1.12	4
					1000	-19.77	0.01	2	5.75	0.09	3
					2000	-20.27	0.37	2	6.01	0.17	3
			6	35	202	-22.41	0.10	2	3.91	0.62	4
					505	-21.63	0.00	2	5.95	0.44	3
					1000	-20.33	0.06	2	6.26	0.09	3
					2000	-21.72	0.32	2	6.98	1.50	4
			5	45	202	-22.54	0.03	2	5.10	0.27	3
					505	-22.08	0.11	2	6.19	1.05	5
					1000	-21.16		1	6.83	0.23	3
					2000	-21.29	0.09	2	6.73	0.58	3

Year	Stn	Tow	Net	Depth	Size	$\delta^{13}\text{C}$		n	$\delta^{15}\text{N}$		n
2007	8	618	4	55	202	-22.64	0.13	2	5.78	0.24	3
					505	-21.26	0.31	2	6.41	1.51	4
					1000	-20.95	0.33	2	6.80	0.36	3
					2000	-21.31	0.09	2	6.56	0.31	3
			3	70	202	-22.43	0.03	2	5.76	1.16	4
					505	-21.61	0.20	2	8.13	0.40	3
					1000	-21.00	0.23	2	7.26	0.91	3
					2000	-21.19	0.09	2	6.72	0.15	3
			2	90	202	-21.99	0.35	2	6.04	0.77	3
					505	-21.95	0.55	2	7.63	0.44	3
					1000	-20.73	0.00	2	9.15	0.17	3
					2000	No Data			6.52	0.80	3
			1	125	202	-21.63	0.05	3	7.07	0.10	3
					505	-20.88	0.67	3	8.67	0.15	3
					1000	-20.53	0.15	3	8.00	0.09	2
					2000	-20.50	0.22	3	8.22	0.35	3
2008	1	626	3	70	202	-22.36	0.30	4	8.27	0.24	3
					505	-22.39	0.28	4	8.49	0.36	3
					1000	-22.96	0.11	3	7.82	0.18	3
					2000	-21.03	0.27	5	11.06	0.08	3
			4	55	202	-21.88	0.35	5	8.53	0.13	3
					505	-21.55	0.23	5	9.09	0.02	2
					1000	-19.84	0.26	3	9.09		1
					2000	-18.40	1.80	5	10.87	0.13	3
					5000	No Data			11.43	0.07	3
			5	45	202	-21.38	0.18	4	8.59	0.07	3
					505	-21.77	0.19	4	9.25	0.02	3
					1000	-21.12	0.40	5	9.96	0.09	3
					2000	-19.96	1.19	4	11.13	0.05	2
		629	4	375	202	-21.00	0.31	5	8.13	0.28	3
					505	-20.14	0.39	4	9.40	0.12	3
					1000	-20.38	0.32	5	9.44	0.14	3
					2000	-19.59	0.07	5	9.81	0.24	3
			5	325	202	-21.13	0.12	4	8.05	0.42	3
					505	-20.97	0.17	4	9.21	0.10	3
					1000	-21.18	0.04	4	9.30	0.08	3
					2000	-20.47	0.24	5	9.26	0.03	2
			6	275	202	-21.47	0.19	5	9.85	1.26	3
					505	-21.13	0.15	5	9.61	1.43	3
					1000	-19.38	0.19	5	9.70	1.06	3
					2000	-20.83	0.16	3	7.86	3.34	3
			7	225	202	-21.49	0.25	3	12.24	1.38	3
					505	-20.92	0.23	5	11.88	2.59	3
					1000	-19.82	0.07	5	14.68	2.21	3
					2000	-19.27	0.06	5	12.54	0.32	3
			8	175	202	-21.27	0.46	4	9.68	0.69	3
					505	-21.79	0.38	5	9.58	1.00	3
					1000	-22.23	0.08	4	10.02	0.79	3
		631	1	950	202	-20.09	0.29	3	12.57	0.28	3

Year	Stn	Tow	Net	Depth	Size	$\delta^{13}\text{C}$		n	$\delta^{15}\text{N}$		n
2008	1	631	1	950	505	-19.70	0.38	3	12.28	1.33	3
					1000	-19.32	0.25	5	11.27	2.28	3
					2000	-19.10	0.33	3	15.67	1.93	2
			2	888	202	-20.65	0.12	3	10.32	0.67	3
					505	-20.28	0.56	3	8.95	0.31	3
					1000	-20.92	0.47	3	10.41	2.03	3
			3	864	2000	-19.83	0.26	3	10.08	0.80	3
					202	-20.52	0.13	3	13.05	0.87	3
					505	-20.92	0.17	3	11.88	0.95	3
			4	838	1000	-20.59	0.29	3	13.22	0.95	3
					2000	-17.93	0.00	2	12.75		1
					202	-20.15	0.42	3	11.29	0.34	3
			5	813	505	-20.64	0.09	3	12.58	0.30	3
					1000	-20.70	0.10	5	12.44	0.10	3
					2000	-19.76	0.15	4	13.75	0.09	3
			6	790	202	-20.40	0.22	3	10.40	0.28	3
					505	-20.26	0.12	3	15.62	0.19	3
					1000	-22.21	0.16	3	9.38	0.27	3
			7	722	2000	-21.10	0.18	4	10.43	0.20	2
					202	-20.27	0.32	4	9.47	0.28	3
					505	-19.96	0.52	3	13.48	0.24	3
			8	610	1000	-21.58	0.15	3	6.75	0.18	3
					2000	-21.21	0.26	3	7.36	0.18	3
					202	-20.61	0.06	3	6.12	1.42	3
			1	125	505	-23.08	1.82	3	8.96		1
					1000	-23.67	1.12	3	6.93	0.17	3
					202	-20.33	0.28	3	6.31	1.54	3
			2	90	505	-20.02	0.28	3	9.18	0.28	3
					1000	-23.15	0.09	3	7.30	0.06	3
					2000	-21.02	0.50	2	9.18	1.28	3
			3	70	2000	-22.28	0.33	3	8.71	0.22	3
					505	-21.74	0.14	3	8.95	0.17	3
					1000	-22.94	0.26	4	8.04	0.12	3
			4	55	2000	-20.99	0.48	3	8.99	0.27	3
					202	-23.05	0.41	4	7.64	0.23	3
					505	-22.52	0.63	3	8.38	0.08	3
			5	45	1000	-22.48	0.17	4	8.14	0.14	3
					2000	-20.24	0.22	3	10.25	0.30	3
					202	-23.24	0.10	3	7.75	0.65	3
			6	40	505	-21.06	0.10	3	8.88	0.12	3
					1000	-20.98	0.28	3	9.18	0.15	3
					2000	-19.95	0.27	3	10.65	0.20	3
			7	30	202	-21.92	0.19	3	8.02	0.12	3
					505	-21.34	0.43	4	9.04	0.11	3
					1000	-20.89	0.29	4	9.60	0.17	3
			8	20	2000	-19.35	0.46	4	10.72	0.01	3
					202	-21.45	0.25	3	8.11	0.20	3
					505	-20.90	0.22	3	8.93	0.01	3
			9	10	1000	-20.60	0.26	3	9.68	0.11	3

Year	Stn	Tow	Net	Depth	Size	$\delta^{13}\text{C}$		n	$\delta^{15}\text{N}$		n		
2008	1	633	5	45	2000	-19.31	0.31	3	10.48	0.04	3		
					6	35	202	-20.87	0.29	3	7.86	0.38	3
					505		-20.12	0.35	3	8.90	0.32	3	
					1000		-20.06	0.18	3	10.11	0.14	3	
			7	25	2000		-19.44	0.37	3	10.38	0.02	3	
					202	-20.61	0.22	3	8.05	0.18	3		
					505	-20.21	0.35	3	9.62	0.11	3		
					1000	-19.57	0.13	3	10.19	0.15	3		
			8	10	2000	-20.03	0.23	3	10.67	0.05	3		
					202	-20.34	0.10	3	8.56	0.09	3		
					505	-19.94	0.26	3	9.34	0.16	3		
					1000	-19.82	0.32	3	10.21	0.12	3		
			8	635	1	125	2000	-20.26	0.15	3	10.64	0.06	3
							202	-22.16	0.58	2	6.02	0.11	3
							505	-21.33	0.70	3	7.06	1.14	3
							1000	-21.25	0.12	2	7.01	0.13	3
			2	90	2000	-21.08	0.59	2	6.86	0.39	3		
					202	-22.98	0.15	3	5.83	0.58	3		
					505	-21.57	0.12	2	7.84	0.59	3		
					1000	-21.81	0.15	2	7.34	0.30	3		
			3	70	2000	-22.08	0.64	3	6.81	0.34	3		
					202	-23.33	0.31	3	4.67	0.38	3		
					505	-23.10	0.62	3	5.94	0.58	3		
					1000	-22.02	0.85	3	6.57	0.25	3		
	4	55	2000	-22.00	0.79	2	5.76	0.47	3				
			202	-23.32		1	3.64	0.30	3				
			1000	-21.64	0.04	2	6.18	0.20	3				
			2000	-21.89	0.20	2	6.22	0.10	3				
	5	45	202	-22.65	0.37	3	5.48	0.19	3				
			505	-22.25		1	3.41	0.22	3				
			1000	-21.34	0.97	3	4.93	0.03	3				
			2000	-21.24	0.33	3	5.34	0.05	3				
	6	35	202	-20.61	0.01	2	6.18	0.41	3				
			505	-20.59	0.91	3	2.91	0.21	3				
			1000	-20.67	0.23	3	3.92	0.10	3				
			2000	-20.37	0.57	3	5.29	0.06	3				
	7	25	202	-20.97	0.32	3	5.27	0.07	3				
			505	-19.77	0.15	3	3.27	0.23	3				
			1000	-19.63	0.38	3	3.66	0.30	3				
			2000	-19.31	0.33	3	4.80	0.11	3				
	8	10	202	-20.81	0.23	3	4.68	0.02	2				
			505	-20.07	0.33	3	2.20	0.91	3				
			1000	-20.24	0.20	2	3.96	0.11	3				
			2000	-20.52	0.39	3	4.29	0.14	3				
	8	636	1	950	202	-20.30	0.41	3	10.83	0.12	3		
					505	-19.21	0.33	3	8.05	0.11	3		
					1000	-20.39	1.29	3	3.50	0.23	3		
					2000	-20.05	0.05	3	10.50	0.19	3		
			4	640	202	-20.45	0.14	3	12.58	0.40	3		

Year	Stn	Tow	Net	Depth	Size	$\delta^{13}\text{C}$		n	$\delta^{15}\text{N}$		n
2008	8	636	4	640	505	-19.44	0.39	3	8.32	1.01	3
					1000	-19.47	0.36	3	9.57	0.29	3
					2000	-19.50	0.17	3	12.55	0.20	2
				587	202	-20.45	0.09	3	8.86	0.17	3
					505	-19.68	0.25	3	7.77	1.55	3
					1000	-20.58	0.12	3	11.85	0.51	3
					2000	-19.91	0.11	3	8.80	0.32	3
			8	540	505	-19.03		1	4.83	0.29	3
					1000	-21.15	0.17	3	11.99	0.17	3
					2000	-20.90	0.19	3	4.66	0.86	3
			1	525	202	-20.70	0.21	3	5.89	0.32	2
					505	-19.97	0.36	2	9.10		1
					1000	-20.92	0.19	3	4.76	0.14	3
					2000	-20.92	0.19	3	5.20	0.07	3
				425	202	-20.48	0.62	3	6.66	0.35	2
					505	-18.60	0.58	3	7.60	0.07	3
					1000	-20.15	0.21	3	6.84	0.11	3
					2000	-20.14	0.16	3	7.91	0.18	3
			4	375	202	-21.10	1.47	3	7.83	0.11	3
					505	-21.15	0.56	3	5.99	0.18	2
					1000	-20.64	0.28	3	6.98	0.14	3
					2000	-20.76	0.25	3	5.79	0.07	3
			5	325	202	-20.37	0.19	3	6.01	0.42	3
					505	-19.89	0.27	3	7.20	0.09	3
					1000	-20.19	0.25	3	6.58	0.10	3
					2000	-19.93	0.24	3	6.93	0.09	3
			6	275	202	-19.56	0.04	3	8.72	0.69	3
					505	-20.28	0.19	3	10.15	0.01	3
					1000	-20.92	0.22	3	5.92	0.18	3
					2000	-21.33	0.29	3	5.58	0.23	3
			7	225	202	-21.46	0.28	3	6.30	0.38	3
					505	-20.83	0.27	3	6.50	0.09	3
					1000	-20.69	0.06	3	5.88	0.26	3
					2000	-19.89	0.27	3	8.08	0.14	3
			8	175	202	-22.50	0.31	3	5.87	0.13	3
					505	-21.84	0.12	3	6.77	0.31	3
					1000	-20.55	0.30	3	5.30	0.22	3
					2000	-20.24	0.35	3	6.49	0.15	3

APPENDIX C: Net average %C, %N with standard deviations and C:N ratios of 2008 individual zooplankton taxa

Species	Stn	Tow	Net	Depth	%C	SD	n	%N	SD	n	C:N
Phylum Arthropoda											
Order Copepoda											
<i>E. inermis</i> F	1	631	6	790	25.3%		1	4.6%	0.51%	4	6.48
	1	631	5	814	19.8%	5.03%	5	6.0%	1.00%	4	3.84
	1	631	4	840	20.2%	3.41%	3	6.1%		1	3.89
	8	635	3	71	28.2%		1	6.0%	0.44%	2	5.50
	8	635	2	91	25.8%	1.81%	2	5.7%	1.35%	4	5.32
	8	636	6	590	21.6%	4.52%	3	5.9%	1.40%	4	4.28
	8	637	5	325	19.8%	2.71%	4	5.9%	1.13%	3	3.93
	8	637	3	426	20.5%	7.94%	4	6.5%		1	3.66
	8	637	1	526	24.6%	9.67%	3	5.6%	0.67%	2	5.11
	8	641	8	226	24.3%	3.61%	3	7.3%	1.07%	3	3.87
	8	641	6	325	25.6%	4.62%	6	6.5%	1.21%	4	4.58
	8	641	4	426	22.5%	2.25%	3	4.5%	0.20%	2	5.82
	8	641	1	506	27.9%	4.29%	4	9.4%		1	3.47
<i>E. inermis</i> I	1	626	1	127	25.0%	3.27%	3	3.6%		1	8.04
	1	629	8	175	19.4%	3.08%	2	4.9%	0.70%	3	4.64
	1	629	7	226	23.2%	2.31%	4	5.1%		1	5.30
	1	629	2	476	21.7%		1	6.5%	2.34%	2	3.89
	1	629	1	526	18.6%	4.51%	4	5.9%	0.65%	2	3.69
	1	631	7	740	18.4%	3.64%	3	4.0%	0.27%	3	5.42
	1	631	6	790	25.8%	1.52%	2	4.7%	0.70%	3	6.43
	1	631	5	814	20.2%	2.42%	3	5.2%		1	4.56
	1	633	3	71	16.7%	4.58%	4	4.7%	1.20%	2	4.12
	1	633	1	127	25.8%		1	6.6%	0.69%	3	4.55
	8	636	8	538	18.9%	4.42%	4	4.2%	0.72%	4	5.23
	8	637	3	426	18.4%	3.42%	3	3.4%	0.39%	3	6.34
	8	637	1	526	20.5%		1	5.0%	0.51%	4	4.76
<i>E. inermis</i> M	8	635	2	91	27.4%		1	6.4%	0.55%	3	5.02
<i>Euchaeta</i> sp.20	1	626	5	46	33.1%	2.14%	3	5.8%	1.28%	2	6.61
	8	635	7	25	25.9%	0.93%	3	6.4%	0.85%	7	4.74
<i>Euchaeta</i> sp.22 F	8	641	8	226	32.9%		1	7.4%		1	5.20
<i>Euchaeta</i> sp.22 M	8	641	8	226	44.6%		1	9.3%		1	5.61
<i>Euchaeta</i> spp.	1	633	5	46	48.3%	3.18%	2	6.5%	0.32%	3	8.71
<i>G. miles</i>	8	635	1	127	30.8%		1	6.9%		1	5.21
	8	641	8	226	30.3%	4.02%	2	7.7%	0.17%	2	4.58
<i>H. longicornis</i> F	1	631	7	740	25.1%		1	3.0%	1.15%	2	9.79
	8	636	8	538	11.4%	5.25%	4	4.0%	0.40%	2	3.34
	8	636	6	590	13.3%	2.18%	2	3.3%	0.08%	2	4.65
	8	641	1	506	17.3%		1	4.2%		1	4.86
<i>H. longicornis</i> M	1	631	7	740	13.7%		1	2.9%		1	5.57
	8	636	8	538	22.3%	0.26%	2	3.4%	0.37%	2	7.55
<i>L. hulsemannae</i> F	1	631	4	840	23.5%	3.44%	4	5.9%	0.63%	4	4.66
	8	636	6	590	32.2%	8.54%	2	5.7%	0.85%	6	6.57

Species	Stn	Tow	Net	Depth	%C	SD	n	%N	SD	n	C:N
	8	636	5	613	38.6%		1	7.0%	0.69%	4	6.43
	8	641	1	506	29.1%	3.81%	4	4.5%	1.79%	3	7.47
<i>L. hulsemannae</i> I	1	631	5	814	24.8%		1	4.8%	0.70%	6	6.04
	8	636	6	590	31.1%	3.58%	2	6.4%	0.38%	5	5.63
<i>L. hulsemannae</i> M	1	631	4	840	21.2%		1	5.2%	0.42%	4	4.79
	8	636	6	590	38.5%		1	5.4%	0.91%	4	8.30
	8	636	5	613	37.8%	7.42%	2	7.3%	0.61%	4	6.08
Megacalanidae	8	636	4	638	39.1%		1	5.2%		1	8.81
	8	636	3	700	38.3%		1	5.7%		1	7.81
<i>P. abdominalis abyssalis</i>	8	637	6	276	34.2%		1	5.9%	0.52%	3	6.72
<i>P. johnsoni</i>	1	631	2	890	22.3%	4.74%	5	5.0%	0.41%	3	5.23
<i>P. johnsoni</i> F	1	629	5	325	32.6%	0.60%	2	9.5%	1.98%	3	3.99
	1	629	4	376	30.7%	4.35%	3	8.9%	1.60%	4	4.01
	1	629	3	426	35.1%	3.56%	5	7.5%	0.79%	5	5.48
	1	633	4	55	22.9%	3.30%	3	9.1%	0.22%	3	2.94
<i>R. rostrifrons</i>	8	635	1	127	30.9%		1	5.2%		1	6.89
	8	637	4	136	24.5%		1	5.2%		1	5.47
	8	641	8	226	38.5%	0.56%	3	5.1%	0.47%	3	8.77
<i>S. subtenuis</i>	1	626	5	46	49.4%		1	6.8%	0.17%	3	8.53
	1	626	4	55	20.6%	5.91%	3	6.7%	0.56%	3	3.58
<i>S. subtenuis</i> F	1	633	4	55	27.0%	2.39%	5	7.2%	0.19%	2	4.38
	8	635	7	25	31.7%	3.09%	2	6.2%	0.56%	4	5.97
	8	635	5	46	16.1%	1.54%	3	5.9%	0.02%	2	3.15
<i>S. subtenuis</i> I	1	633	3	71	24.8%	5.40%	2	4.8%	0.49%	2	5.99
	1	633	2	91	23.2%	1.33%	3	5.9%	0.30%	3	4.60
Order Amphipoda											
Gammarid	1	629	5	325	26.0%		1	6.7%	3.39%	3	4.49
	1	631	2	890	43.7%		1	6.2%		1	8.22
	8	637	7	225	27.0%		1	3.0%		1	10.56
	8	641	6	325	23.8%	0.18%	2	5.8%	0.66%	3	4.75
<i>Phronima</i> spp.	8	637	5	325	17.7%	6.21%	2	3.4%		1	6.03
Order Decapoda											
Shrimp	1	631	2	890	34.9%		1	6.6%		1	6.13
	8	636	7	560	35.2%		1	6.3%		1	6.54
	8	637	7	225	32.9%		1	9.5%		1	4.06
	8	637	6	275	32.5%		1	6.2%		1	6.14
Order Euphausiacea	1	629	7	230	30.6%		1	7.2%		1	4.96
	1	629	6	230	32.0%		1	9.4%		1	3.97
	1	633	6	35	26.9%		1	5.8%	0.37%	2	5.40
	1	633	4	55	29.7%		1	6.2%		1	5.60
	8	635	3	70	32.6%		1	6.3%		1	6.07
	8	637	7	225	31.2%		1	6.3%		1	5.81
	8	637	6	275	34.2%	0.65%	2	7.0%	0.01%	2	5.67
	8	637	4	375	35.1%	2.40%	2	7.1%	1.29%	2	5.78
Order Ostracoda	1	629	8	175	35.1%	4.63%	8	7.6%	0.76%	3	5.39
	8	635	1	125	38.4%	1.45%	2	8.8%	0.74%	4	5.11

Species	Stn	Tow	Net	Depth	%C	SD	n	%N	SD	n	C:N
	8	636	2	825	28.6%	6.85%	2	3.7%	0.97%	4	9.10
Phylum Anelida											
Order Polychaeta	1	631	3	865	32.6%	9.42%	3	6.6%	1.19%	4	5.76
	1	631	2	890	28.9%	1.96%	3	6.0%	0.04%	2	5.60
Phylum Chaetognatha	1	633	4	55	26.2%		1	7.2%		1	4.27
	8	635	2	90	22.6%	4.59%	4	7.1%	0.54%	2	3.71
	8	635	1	125	27.4%	2.76%	6	6.4%	0.99%	4	4.96
Phylum Chordata											
Order Osteichthyes											
<i>Cyclothone</i> spp.	1	631	3	865	37.2%	3.69%	5	10.1%	0.96%	2	4.29
	1	631	2	890	39.8%	1.65%	3	11.0%	0.61%	3	4.22
	8	636	7	560	40.1%		1	10.2%		1	4.58
	8	636	6	590	38.5%	1.65%	3	12.3%	0.83%	2	3.63
	8	636	5	610	38.5%	0.96%	2	12.9%		1	3.49
	8	636	2	825	38.7%	1.43%	2	11.8%		1	3.82
Misc. Un-id	1	631	2	890	34.7%		1	9.0%		1	4.51
	8	636	2	825	38.5%		1	8.7%	1.51%	2	5.13
Myctophid	1	633	4	55	44.3%	0.32%	2	12.0%		1	4.32
	8	637	2	475	38.8%	1.67%	2	10.0%	0.24%	2	4.51

APPENDIX D: Literature cited

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