The impacts of ocean acidification on the geographic distribution, abundance, species composition and species diversity of oceanic thecosome pteropods in the southeast Pacific

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Abstract

Thecosome pteropods are shell-forming planktonic gastropods, which are sensitive to ocean acidification due to their aragonite shells. This study investigated how continued ocean acidification will impact the geographic distribution, total abundance, species composition and species diversity of oceanic thecosome pteropods in the southeast Pacific. Pteropods were collected at nine stations along the cruise track with a 333 µm-mesh meter net. At the same locations, hydrographic measurements and seawater samples were collected with a CTD and Niskin bottles, respectively. Pteropods were counted and speciated using a dissecting microscope. Total abundance, species composition and species diversity were compared with latitude, pH, total carbonate alkalinity (TCA), sea surface temperature (SST), dissolved inorganic carbon (DIC), and aragonite saturation state ($\Omega_{aragonite}$). Total abundance, species composition and species diversity were not significantly associated with SST, pH, TCA, DIC or $\Omega_{aragonite}$. Species composition in the same general locale tended to be similar, however was primarily determined by the dominating species. *Limacina spp.* were the most common pteropods present along the cruise track and often dominated the species composition. Pteropod communities with low abundances typically had high species diversities, and no dominating species. The results of this experiment suggest that although ocean acidification is increasingly becoming a threat to pteropods, it is not currently affecting these organisms in their natural environment.

Introduction

A key problem facing ocean scientists and managers concerns the impacts on marine ecosystems of changing seawater chemistry associated with continued increases in atmospheric carbon dioxide. Ocean acidification is the process by which the concentration of carbonate ion (CO_3^{2-}) and the pH of seawater have decreased due to the absorption of anthropogenic carbon dioxide (CO_2) from the atmosphere by the oceans (Doney et al., 2009). This process has resulted in a decrease in surface water pH by approximately 0.1 units, from approximately 8.16 to 8.05, since pre-industrial times (Figure 1; Caldeira and Wickett, 2003; Rost et al., 2008). Continued CO_2 emissions are predicted to cause a further decrease in pH to 7.80 by 2100 (Caldeira and Wickett, 2003).

Ocean acidification will likely affect biological processes at all levels. Particularly, it is likely that the decrease in CO_3^{2-} concentration will have important implications to marine organisms that secrete calcium carbonate ($CaCO_3$) shells or skeletons (Fabry et al., 2008; Reid et al., 2009). Not only is it expected that the calcification rate of these organisms will slow (e.g., Riebesell et al., 2000; Comeau et al., 2009), but it is also expected that there will be increased dissolution of their shells in response to ocean acidification (e.g. Orr et al., 2005). Further, planktonic shell-forming organisms are key prey for a variety of higher predators including commercially valuable fishes, seabirds and whales. Changes in the distribution, abundance, and species composition of these organisms could have profound ramifications to coastal and open ocean pelagic ecosystem function as well as marine fisheries. Few studies have investigated

the effects of ocean acidification on thecosome pteropods, even though they are important ecosystems members (Fabry et al., 2008).

Prediction of ecosystem changes due to ocean acidification is presently hampered by a lack of knowledge on the baseline vertical and horizontal distribution, and abundance of aragonite secreting-organisms. A key question is whether these organisms can adapt or whether their horizontal range will contract as surface waters become undersaturated relative to aragonite (Orr et al., 2005). Field studies addressing these questions are particularly lacking (Fabry et al., 2008). This work directly addresses the need for observational networks to quantify and track ocean acidification and its effects, focusing on an aragonite-shelled holoplankton, the thecosome pteropod.

Ocean Carbonate System

The inorganic carbon system is one of the most important chemical equilibria in the ocean. Dissolved inorganic carbon (DIC) exists in seawater in three major forms: aqueous carbon dioxide ($CO_{2\,(aq)}$), bicarbonate ion (HCO_3^-), and carbonate ion (CO_3^{2-}). When CO_2 dissolves in seawater, it reacts with water to form carbonic acid (H_2CO_3). Most of the H_2CO_3 dissociates by losing hydrogen ions to form HCO_3^- and CO_3^{2-}. The net effect of adding CO_2 is to increase the concentrations of H_2CO_3, HCO_3^-, and hydrogen ion (H^+) in seawater, and decrease the concentration of CO_3^{2-}. It also lowers the pH of seawater ($pH = -\log[H^+]$). Thus, increased carbon in the system can lead to ocean acidification.

The reaction of CO_2 with seawater reduces the availability of CO_3^{2-}, which is necessary for marine calcifying organisms to produce their $CaCO_3$ shells and

skeletons (Fabry et al., 2008). The extent to which such organisms are affected depends largely upon the $CaCO_3$ saturation state (Ω):

$$\Omega = [Ca^{2+}][CO_3^{2-}]/K^*_{sp},$$

where K^*_{sp} is the apparent stoichiometric solubility product for either aragonite or calcite, two types of $CaCO_3$ commonly secreted by marine organisms. Shell formation generally occurs where $\Omega > 1.0$ whereas dissolution occurs when $\Omega < 1.0$ (Doney et al., 2009). Saturation states are generally highest in the tropics and lowest in the high latitudes (Fabry et al., 2008). Consequently, there is significant shoaling of saturation horizons from south to north in the Pacific (Figure 2). Moving north, the aragonite saturation depth shoals from approximately 1000 m near 30°S to 300 m at the equator (Feely et al., 2012). The aragonite saturation horizon is currently experiencing an upward migration, averaging 1 to 2 m per year, due to the uptake of anthropogenic CO_2 by the oceans (Feely et al., 2012). Most of the change is occurring in the upper 600 m of the water column.

Seawater has the natural ability to neutralize acids with weak bases in order to stabilize its pH. This is known as total alkalinity:

$$A_T \approx [HCO_3^-] + [CO_3^{2-}] + [CO2_2^-].$$

Ocean acidification is expected to decrease $CaCO_3$ saturation states and increase dissolution rates (Doney et al., 2009). Thus, ocean alkalinity and the ocean's capacity to take up more CO_2 from the atmosphere will presumably increase. However, the rate of anthropogenic CO_2 input to the atmosphere will likely overwhelm the natural buffering capacity of the ocean. Therefore, the

ocean's efficiency for taking up carbon will probably decline with time over the next two centuries (Doney et al., 2009).

Oceanic Thecosome Pteropods

Thecosome pteropods are a group of calcareous planktonic gastropod mollusks widely distributed and abundant in coastal and open ocean pelagic ecosystems of the world's oceans (Lalli and Gilmer, 1989). Commonly referred to as 'pelagic snails' or 'sea butterflies,' they secrete an aragonite shell and are generally smaller than 2 mm. Thecosome pteropods are important ecosystem members as abundant herbivores and/or detritivores (Bernard and Froneman, 2009). They are key prey for a number of higher predators, including commercially exploited fishes including pollock (Brodeur et al., 2000) and juvenile pink salmon (Armstrong et al., 2005) and seabirds (Karnovsky et al., 2008).

Most information on thecosome pteropods concerns their biogeography (Be and Gilmer, 1977; Lalli and Gilmer, 1989; Bednarŝek et al., 2012b). Their biogeographic distribution is thought to relate to water mass distributions (van der Spoel, 1967; Be and Gilmer, 1977). Specifically, pteropods are abundant in active current systems in upwelling regions such as the California Current, but are sparser in the oligotrophic central water masses. Further, pteropod distribution patterns can be separated into three major zoogeographic regions: northern cold-water region, circumglobal warm-water region, and southern cold-water region (Be and Gilmer, 1977). These regions can be further separated into provinces. The expected species composition for the three provinces of the circumglobal warm-water region is listed in Table 1. Species in the "Warm-water

Cosmopolitan Province" have the ability to adapt to a wider range of environmental conditions because the majority live in both tropical and subtropical waters (Be and Gilmer, 1977).

Species composition is relatively similar between oceanic regions at the same latitude, although faunal variations do exist (Be and Gilmer, 1977). Horizontal distributions are greatly influenced by variations in abundance due to patchiness, diel vertical migration and seasonal abundance (Be and Gilmer, 1977). Overall, there is a higher abundance of pteropods at higher latitudes (Be and Gilmer, 1977; Lalli and Gilmer, 1989). However, there is a higher diversity of pteropods at lower latitudes (Be and Gilmer, 1977; Lalli and Gilmer, 1989; Fabry et al., 2008).

Thecosome pteropods are typically only a minor contributor to abundance and biomass in plankton net samples relative to more common taxa, such as copepods (Lalli and Gilmer, 1989). However, thecosome pteropods play an important role in the marine carbon and aragonite cycles, and are the only major planktonic aragonite producers (Hood et al., 2006; Fabry et al., 2008; Doney et al., 2009). Thus, future changes in ocean carbonate chemistry are expected to strongly impact their calcification rates and susceptibility to dissolution (Orr et al., 2005; Comeau et al., 2009). When exposed experimentally to decreasing pH and CO_3^{2-} concentration, thecosome pteropods have shown reduced calcification rates and increased dissolution of their aragonite shells (Feely et al., 2004; Orr et al., 2005; Fabry et al., 2008; Comeau et al., 2009; Bednarŝek et al., 2012a).

Additionally, pteropod shells have smaller volumes at higher temperatures (Schalk, 1990; Sato-Okoshi et al., 2010).

Less is known about the potential changes in horizontal and vertical distribution, abundance, and species composition of thecosome pteropds that may accompany ocean acidification. Many thecosome pteropods are known to undergo extensive diel vertical migrations (Be and Gilmer, 1977; Wormuth, 1981, 1985; Nigro and Seapy, 2008), in which animals migrate to shallow depths during the night to feed and return to deeper depths by day to avoid visual predators (Frost and Bollens, 1992; Bollens et al., 1994; Hays, 2003). Factors such as light intensity (Andersen et al., 1997), and temperature (Lischka et al., 2011) greatly influence the diel vertical migrations patterns of these organisms. Light intensity is defined by the moon phase and the amount of cloud cover. Most pteropods are primarily found in surface layers, down to approximately 200 m (van der Spoel, 1967; Wormuth, 1981, 1985). *Limacina helicina*, for example, migrates to a depth of 150 m during the day (Falk-Petersen et al., 2008). As the water column in some regions continues to become undersaturated with respect to aragonite, thecosome pteropods may disappear from portions of their current vertical and horizontal ranges (Orr et al., 2005). However, a long-term study of variability in abundance of pteropods by Ohman et al. (2009) in the California Current did not show any decline associated with changes of aragonite saturation state of about 0.2 units. Overall, *in situ* studies of the response of thecosome pteropods to shoaling aragonite saturation states are mostly lacking.

Previous studies on the impacts of ocean acidification on pteropods have primarily been conducted in polar regions (e.g. Gilmer and Harbison, 1991; Gannefors et al., 2005; Comeau et al., 2009, 2010; Bernard and Froneman, 2009). Although pteropod observations are available for all ocean basins, there is a clear bias of the data towards observations in the Northern Hemisphere (NH) and within the latitudinal band of 10-60° N (Figure 3; Bednarŝek et al., 2012b). To date few pteropod observations are available for the South Pacific marine ecosystem. This investigation will conduct baseline surveys of the horizontal distribution of these organisms that will capitalize on a unique cruise track from San Diego to Tahiti.

The overall goal of this work is to understand the impacts of continued ocean acidification on the ecology and role within the pelagic ecosystem of thecosome pteropods. The primary objective in this study is to quantify the geographic distribution, numerical abundance, species composition and species diversity of oceanic thecosome pteropods in the southeast Pacific, and correlate these quantities to latitude, temperature and measurements of carbonate chemistry, including vertical and horizontal distributions of aragonite saturation levels.

It is hypothesized that:

H1. Species composition will vary with latitude, similarly to the latitudinal patterns described by Be and Gilmer (1977). It will not be dependent on temperature, and concurrent measurements of carbonate chemistry.

H2. Total pteropod abundance will decrease with lower latitudes and thus, higher sea surface temperatures as previous studies have found the highest abundances of pteropods at high latitudes (Be and Gilmer, 1977). Additionally, total pteropod abundance will decrease with decreasing surface pH, total carbonate alkalinity and aragonite saturation state, and increasing DIC as increased rates of mortality are expected with increasing ocean acidification (Lischka et al., 2011).

H3. Pteropod species diversity will increase with lower latitudes, and thus, higher sea surface temperatures as previous studies have found the highest diversity of pteropods at lower latitudes (Be and Gilmer, 1977). Additionally, pteropod species diversity will increase with decreasing surface pH, total carbonate alkalinity and aragonite saturation state, and increasing DIC as these are the oceanographic conditions expected at lower latitudes (Fabry et al., 2008; Feely et al., 2012).

Methods

Study Area and Data Collection

We conducted a 46-day cruise to the southeast Pacific from November 5 to December 20, 2013 on the SVV *Robert C. Seamans* sailing out of San Diego, CA and into Papeete, Tahiti (Figure 4).

Surveying along the study transect from San Diego, CA to Nuku Hiva, French Polynesia involved sampling stations at approximately 2200 (LAT) every three to four days (Table 2). At these stations, we collected pteropods using a 333µm-mesh meter net towed obliquely at 2 knots to sample the top 50 m of the water column. We typically towed the meter net for a total tow time of approximately 30 minutes: down to approximately 50 meters in 15 minutes, and returned to the surface in 15 minutes. We used a flow meter to measure the volume of water that flowed through the meter net. This allowed us to normalize abundance, species composition, and species diversity values for tow volume. We deployed a total of nine meter nets along our cruise track (Figure 4). We only conducted night tows to minimize the effects of the diel vertical migratory behavior of pteropods on the data collected.

At these stations, we also deployed vertical hydrocasts to 550 m. We collected seawater samples using Niskin bottles at 5, 50 and 150 m and measured temperature, salinity and pressure throughout the water column using a SeaBird Model 19Plus Conductivity, Temperature, Depth sensor (CTD). These depths correspond to: (1) where the highest abundance of pteropods was expected (Bednarŝek et al., 2012b), (2) the deepest depth at which we towed the

net, and (3) the deepest depth at which we expected to find pteropods (van der Spoel, 1967; Wormuth, 1981, 1985).

Sample Processing

We collected pteropods from each net tow using the “swirling” method. We vigorously swirled the biomass collected to allow for heavier organisms, such as pteropods, to fall to the bottom of a bucket. Using a turkey baster, we extracted these heavier organisms from the bottom of the bucket as the swirling continued and placed them in a pint jar. We repeated this process 3 to 4 times, which allowed us to recover most of the pteropods collected. Using a pipette, we repeated the method described above in the pint jar. This removed additional small biomass that was likely not calcareous organisms. We preserved the final fraction, composing predominantly of shelled organisms, in a scint vial with ethanol. Swirling occurred after we removed a 100-count sample, and determined the total volume of all organisms collected in the net sample.

We counted and speciated all the pteropods collected for each meter net tow using a compound microscope, and a key to pteropods in the tropical Pacific provided by Amy Maas (personal communication). We supplemented this key with general keys by Van der Spoel (1967) and Bé and Gilmer (1977). Abundance values were normalized to account for different tow volumes by dividing abundance by tow volume.

We measured the pH of collected seawater samples using a spectrophotometer and the protocol outlined by Clayton and Byrne (1993). We titrated 100 mL of seawater with a 10% HCl solution to measure both the total carbonate alkalinity (TCA) of the seawater samples using the protocol outlined by

Dickson et al. (2003). Using temperature, salinity, pressure, pH, and total carbonate alkalinity as inputs, we calculated DIC and aragonite saturation state using the CO2SYS program from the Carbon Dioxide Information Analysis Center developed by Lewis and Wallace (1998). We left phosphate and silicate values blank in the program as there were no readily available values at desired depths. Both of these values are very small in shallow water oceanic environments and thus, omitting this information should not significantly affect the results.

Statistical Analysis

I used the Shannon-Wiener diversity index to quantify the diversity of species observed at different locations and under different environmental conditions. The Shannon-Wiener diversity index is defined as:

$$H' = -\sum_{i=1}^{OS} p_i \ln p_i ,$$

where *OS* = observed number of species, and p_i = proportional abundance of species *i* (Omori and Ikeda, 1991). Normalized abundance values were used to compute the Shannon-Wiener diversity index.

I compared latitude, sea surface temperature, and pH, total carbonate alkalinity, DIC, and aragonite saturation state at 5, 50 and 150 m, respectively (independent variables) to normalized numerical abundance, and the Shannon-Wiener diversity index (dependent variables), respectively. I used Pearson's product-moment correlation coefficient to determine the amount of association between each independent variable and the two dependent variables. Pearson's product-moment correlation coefficient is defined as:

$$r_{Y_1Y_2} = \frac{\sum y_1 y_2}{(n-1)s_{Y_1}s_{Y_2}},$$

where $r_{Y_1Y_2}$ is the product-moment correlation coefficient between variables y_1 and y_2. I determined significance by comparing computed Pearson's product moment correlation coefficient to values of Table VIII in Sokal and Rohlf (1987). This table has tabulated significance tests following:

$$t_S = r\sqrt{\frac{n-2}{1-r^2}}.$$

This allowed direct inspection of the computer correlation coefficient for significance without further computation. If the computed Pearson's product-moment correlation coefficient is greater than the value at the appropriate number of degrees of freedom (df = n – 2) and at the significance level of $p < 0.01$, it was assumed that the association was significant (Sokal and Rohlf, 1987). I used Excel to plot and calculate all statistics.

I also plotted general locale on a histogram against species composition, normalized numerical abundance, and the Shannon-Wiener diversity index, respectively. I used Pearson's product-moment correlation coefficient to determine how similar the species composition is at each station and determined significance using the same method described above.

Results

Oceanographic Variables

Five oceanographic variables were sampled for comparison with pteropod species composition, total abundance and species diversity. pH measurements were collected from analyses of water collected in Niskin bottles at 5, 50 and 150 m from 8 hydrocasts. pH measurements generally decreased with depth in the water column. pH measurements at 5 m water depth ranged between 8.029 and 8.543. pH measurements at 50 m water depth ranged between 7.859 and 8.427. pH measurements at 150 m water depth ranged between 7.633 and 8.129. Mean pH measurements and their associated standard deviations at the 3 sampled depths are shown in Figure 5A.

Total carbonate alkalinity (TCA) measurements were collected from analyses of water collected in Niskin bottles at 5, 50 and 150 m from 9 hydrocasts. TCA measurements at 5 m water depth ranged between 1511.615 and 2480.205 µmol/kg. TCA measurements at 50 m water depth ranged between 978.625 and 2383.405 µmol/kg. TCA measurements at 150 m water depth ranged between 1309.161 and 2587.040 µmol/kg. Mean TCA measurements and their associated standard deviations at the 3 sampled depths are shown in Figure 5B.

Sea surface temperature measurements ranged between 18.5 and 28.0 °C at stations where pteropods were collected. Mean SST and associated standard deviation was 24.4 ± 3.8 °C.

Dissolved inorganic carbon measurements were computed from the addition of HCO_3, CO_3, and CO_2 values generated by CO2SYS at 5, 50 and 150 m, respectively. DIC measurements at 50 m water depth ranged between 773.8 and 2094.4 µmol/kg. DIC measurements at 150 m water depth ranged between 1188.3 to 2308.6 µmol/kg. Mean DIC measurements and their associated standard deviations at the 3 sampled depths are shown in Figure 5C.

Aragonite saturation state measurements were computed by CO2SYS at 5, 50 and 150 m. Aragonite saturation state measurements generally decreased with depth in the water column. Aragonite saturation state measurements at 5 m water depth ranged between 2.35 and 5.84. Aragonite saturation state measurements at 50 m water depth ranged between 1.52 and 5.32. Aragonite saturation state measurements at 150 m water depth ranged between 1.06 and 2.20. Mean aragonite saturation state measurements and their associated standard deviations at the 3 sampled depths are shown in Figure 5D.

Pteropods

The pteropods collected in nine meter nets were counted and identified. A total of fifteen different species of thecosome pteropods were identified: *Limacina inflata*, *Limacina bulimoides*, *Limacina lesueuri*, *Limacina trochiformis*, *Styliola subula*, *Cuvierina columnella*, *Clio pyramidata*, *Clio polida*, *Creseis virgula*, *Creseis acicula*, *Diacavolinia longirastris*, *Diacria quadridenta*, *Diacria tripspinosa*, *Cavolinia inflexa*, and *Cavolinia unccinata* (Figure 6). However, only *L. inflata*, *L. bulimoides*, and *L. trochiformis* were present in all meter net sample. Thecosome pteropods from the genus *Limacina* dominated (i.e. over 50% of the composition) each meter net sample. *L. inflata* dominated five meter net samples

collected at stations 003, 007, 034, 045, and 051. The meter net sample from station 028 was dominated by *L. trochiformis*. No species dominated meter net samples from stations 011, 015, and 022. Pearson's product-moment correlation coefficients were computed to compare the species composition between stations (Table 3).

The total abundance of thecosome pteropods in each meter net sample was determined (Figure 7). The lowest total abundance was 13 thecosome pteropods in the meter net sample collected at station 015, while the highest total abundance was 1635 thecosome pteropods in the meter net sample collected at station 051. The total abundance at each station was compared to the pH of the seawater at 5, 50 and 150 m, the sea surface temperature, the total carbonate alkalinity at 5, 50 and 150 m, the dissolved inorganic carbon at 5, 50 and 150 m, the aragonite saturation state at 5, 50 and 150 m, and the latitude using the product-moment correlation coefficient (Table 4).

The species diversity of thecosome pteropods in each meter net sample was quantified using the Shannon-Wiener Diversity Index (Figure 8). The lowest species diversity was 0.371 in the meter net sample collected at station 003, while the highest species diversity was 1.839 in the meter net sample collected at station 011. The Shannon-Wiener Diversity Index at each station was compared to the pH of the seawater at 5, 50 and 150 m, the sea surface temperature, the total carbonate alkalinity at 5, 50 and 150 m, the dissolved inorganic carbon at 5, 50 and 150 m, the aragonite saturation state at 5, 50 and 150 m, and the latitude (Table 4).

Discussion

In a situation where pteropods are affected by ocean acidification, one would expected that pteropod abundance would decrease and that species diversity would increase with lower latitudes, higher sea surface temperatures (SST), lower pH, lower total carbonate alkalinity (TCA), higher dissolved inorganic carbon (DIC), and lower aragonite saturation state. Species composition should only vary with latitude. Contrary to expectations, neither species composition, normalized total abundance nor species diversity are significantly associated with any of the measured oceanographic variables (Figures 15-20). Thus, the impacts of continued ocean acidification on the ecology and role of thecosome pteropods within the pelagic ecosystem could not be observed. Previous studies that have shown the effects of changing oceanographic conditions on these organisms have primarily been laboratory experiments that have used extreme environmental values currently not present in the natural environment of pteropods. For example, a study by Lischka et al. (2011) only demonstrated the impacts of ocean acidification on pteropods at pHs less than 7.5 and aragonite saturation states less than 1.0. Oceanographic conditions varied minimally along the study transect and did not exhibit any of these experimental extremes (Figures 9-12). Thus, it is possible that pteropod species composition, normalized total abundance and species diversity do vary as hypothesized, but at more extreme environmental conditions.

Furthermore, species encountered along the study transect are classified as part of the warm-water cosmopolitan province, which tend to have the ability

to adapt to a wider range of environmental conditions (Be and Gilmer, 1977). For example, *L. inflata* has been found to inhabit waters with a temperature range of 14 to 28 °C (Be and Gilmer, 1977), which is well within the range of sea surface temperatures observed along the study transect. Due to the lack of *in situ* observations of pteropods in the southeast Pacific, the observations from this study could not be compared to previous studies. Thus, these observations can now be used as a baseline for future pteropod and ocean acidification studies.

The species composition of the pteropod communities studied along the study transect were dominated (> 50%) by pteropods from the genus *Limacina* (Figure 13). Pteropods of this genus are the most abundant type of pteropods worldwide (Be and Gilmer, 1977). *L. inflata*, *L. bulimoides* and *L. trochiformis* are very abundant subtropical and tropical species (Be and Gilmer, 1977), and were found at every location sampled (Figure 13). Additionally, the species composition of pteropod communities in the same general locale tended to have significantly similar species composition (Table 3). For example, the two stations in the California Current were almost identical (r = 1.000) in species composition. These stations only differed largely in normalized total abundance, which cannot be explained by other factors, including moon phase and cloud cover. Published pteropod distribution patterns correspond closely with ocean circulation patterns of the upper water masses of the oceans and can extend over 40° of latitude (Be and Gilmer, 1977). Thus, the similarity between stations in the same general locale is a reasonable observation as stations were no more than approximately 7° of latitude apart.

Nevertheless, the species composition of pteropod communities appears to be primarily influenced by the dominating species. Species composition was similar if the same species dominated, regardless of latitudinal separation and different oceanographic conditions. For example, although separated geographically, stations 003, 007, 034, 045 and 051 have significantly similar species compositions. At all of these stations, *L. inflata* was the dominant species. Further, station 028 was dissimilar from all stations, including station 034, which occurred in the same general local. The only difference between this station and others is that *L. trochiformis* is the dominating species at this station. This further propels the idea that species composition is determined by the dominating species, and not by the environmental conditions. It is unclear based on the measured oceanographic conditions why *L. inflata* or *L. trochiformis* were able to dominate in these particular locations. However, *L. inflata's* ability to protect its brood in its mantle cavities before the brood attains a size of about 67 µm in shell diameter may provide a key advantage in offspring survival (Be and Gilmer, 1977). Previous studies have reported a peak abundance of *L. trochiformis* in tropical regions (Be and Gilmer, 1977).

Pteropod communities with low abundances typically had high species diversities and no dominating (> 50%) species (Figures 13, 14 and 21). For example, station 011 displayed the highest diversity of species and had a low normalized total abundance. The station had no dominating species. Station 015 had the lowest normalized total abundance and high diversity. There was no dominating species here as well. The inverse relationship between low abundances and high diversities was expected based on the global diversity and

abundance patterns of pteropods described by many previous studies (e.g. Be and Gilmer, 1977; Lalli and Gilmer, 1989). However, the global trend of lower abundances at lower latitudes was not observed. Only the trend of higher diversity at lower latitudes was observed. It is unclear why only the diversity trend was observed, however it may likely be due to the dependence of abundance upon other factors such as light intensity.

There are multiple limitations in this study which may have weakened the results. First, the inherent patchiness of zooplankton distribution and diel vertical migratory behavior of pteropods may have increased or decreased the number and types of pteropods collected. The patchiness was not accounted for during analyses. Sampling only occurred at night and extended to approximately 50 m depth to eliminate the effect of the migratory behavior. Second, only nine meter net samples were collected, processed and used for the analyses presented. The small data set made it difficult to identify meaningful trends. Sampling on a finer scale with replicates would allow the investigator to further statistically nullify the effects of all of these factors. Finally, multiple individuals were involved in the collection and processing of the pteropods. Pteropod species were independently verified to reduce error associated with species misidentification. Reducing the number of individuals ‘swirling’ for pteropods may have produced a cleaner data set.

Future studies should focus on investigating the impacts of ocean acidification on pteropod shell size and shell condition rather than abundance and diversity. Using these factors instead of abundance and diversity may directly show the impacts of ocean acidification, as it is the shell of a pteropod

that makes it sensitive to ocean acidification. Future investigations should continue recording the species composition of pteropod communities to further investigate the dominance trends observed in this study.

This study investigated how continued ocean acidification would impact the ecology and role of oceanic thecosome pteropods within the pelagic ecosystem. Results showed that ocean acidification, as expressed in SST, pH, TCA, DIC and aragonite saturation state, is currently not affecting the distribution, abundance, species composition and species diversity of thecosome pteropods in their natural environment. However, pteropod communities with high species diversity tend to have low abundance. Species composition of pteropod communities in the same general locales tend to be similar, however species composition is largely determined by the dominating species. Pteropods of the genus *Limacina* are extremely abundant in the southeast Pacific and tend to dominate pteropod communities.

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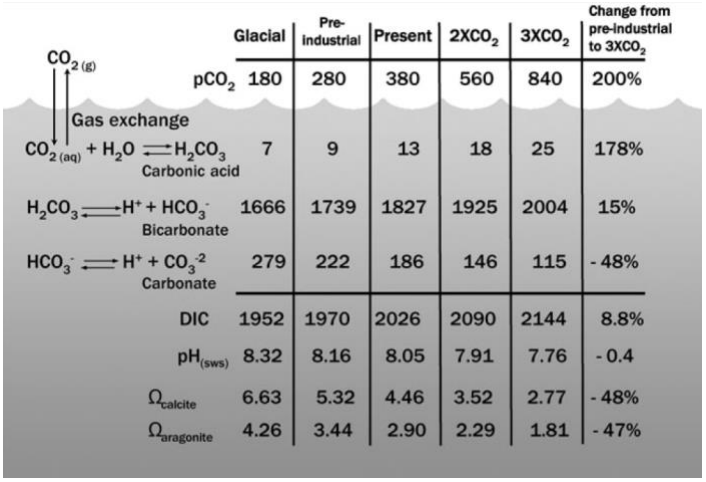
Figures



	Glacial	Pre-industrial	Present	$2XCO_2$	$3XCO_2$	Change from pre-industrial to $3XCO_2$
pCO_2	180	280	380	560	840	200%
Carbonic acid	7	9	13	18	25	178%
Bicarbonate	1666	1739	1827	1925	2004	15%
Carbonate	279	222	186	146	115	- 48%
DIC	1952	1970	2026	2090	2144	8.8%
$pH_{(sws)}$	8.32	8.16	8.05	7.91	7.76	- 0.4
$\Omega_{calcite}$	6.63	5.32	4.46	3.52	2.77	- 48%
$\Omega_{aragonite}$	4.26	3.44	2.90	2.29	1.81	- 47%

Figure 1. Concentrations of carbon species (in units of μmol kg^{-1}), pH values, and aragonite and calcite saturation states of average surface seawater for pCO_2 concentrations (ppmv) during glacial, preindustrial, present day, two times pre-industrial CO_2, and three times pre-industrial CO_2 (from Fabry et al., 2008).

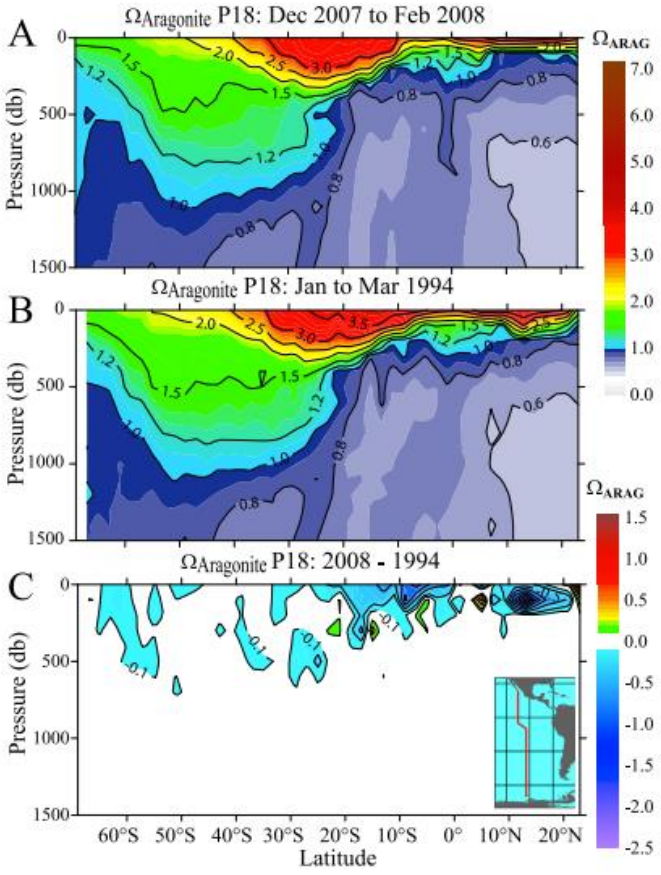


Figure 2. Aragonite saturation state for (a) $\Omega_{aragonite}$ for 2008, (b) 1994, and (c) $\Omega_{aragonite}$ difference (2008-1994) along the P18 section from Antarctica to Mexico (from Feely et al., 2012).

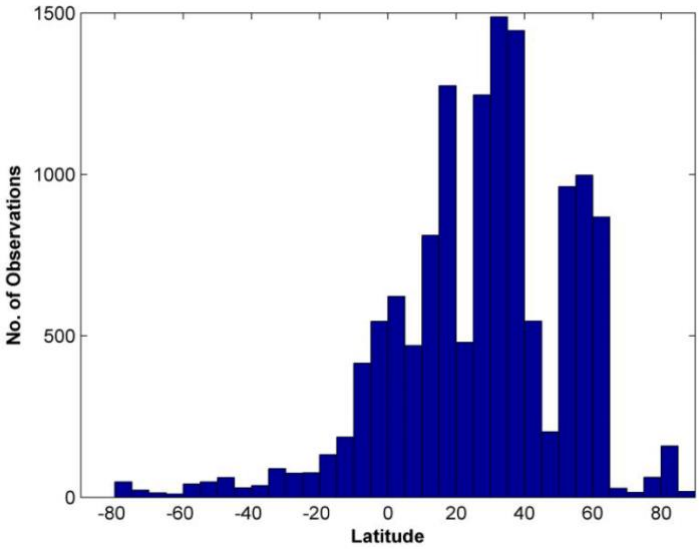


Figure 3. Number of pteropod observations as a function of latitude for the period of 1950-2010 (from Bednarŝek et al., 2012b). Negative latitude values represent Southern latitudes; positive latitude values represent Northern latitudes.

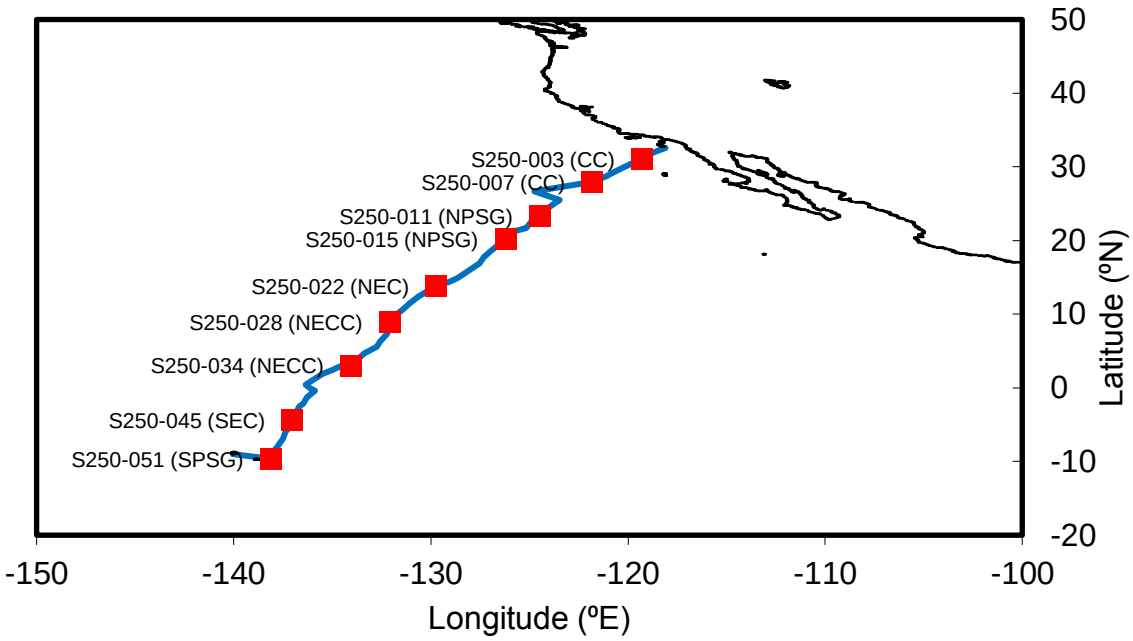


Figure 4. Location of meter net deployments along the study transect (blue line) from San Diego, CA to Nuku Hiva, French Polynesia (red squares). Cruise S250 continued to Tahiti, but that portion of the cruise track is not shown as no meter net samples were collected during that leg of the cruise.

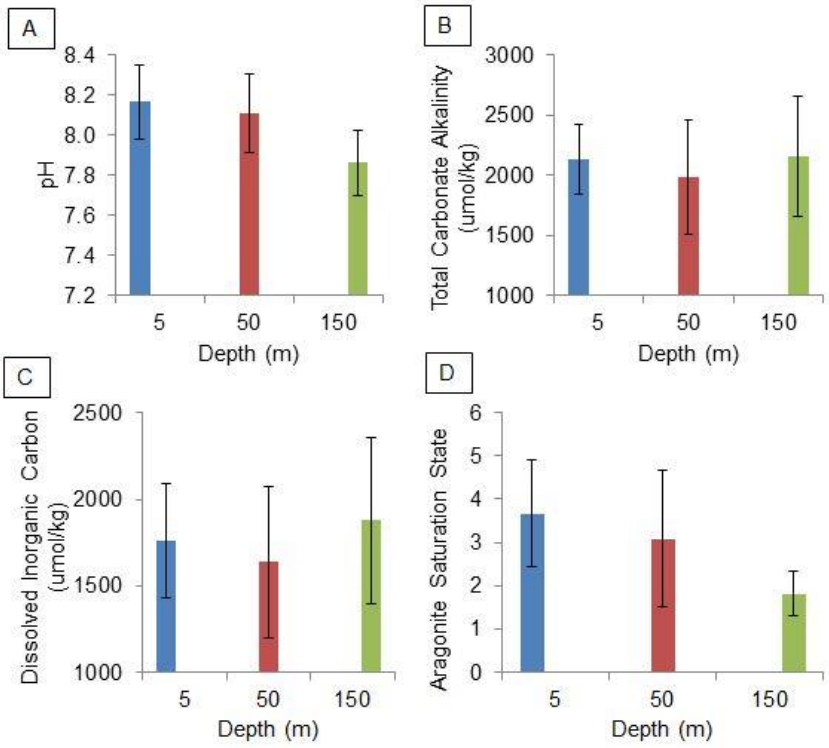


Figure 5. Mean (±SD) (a) pH, (b) total carbonate alkalinity (µmol/kg), (c) dissolved inorganic carbon (µmol/kg), and (d) aragonite saturation state at 3 sampled depths: 5, 50 and 150 m.

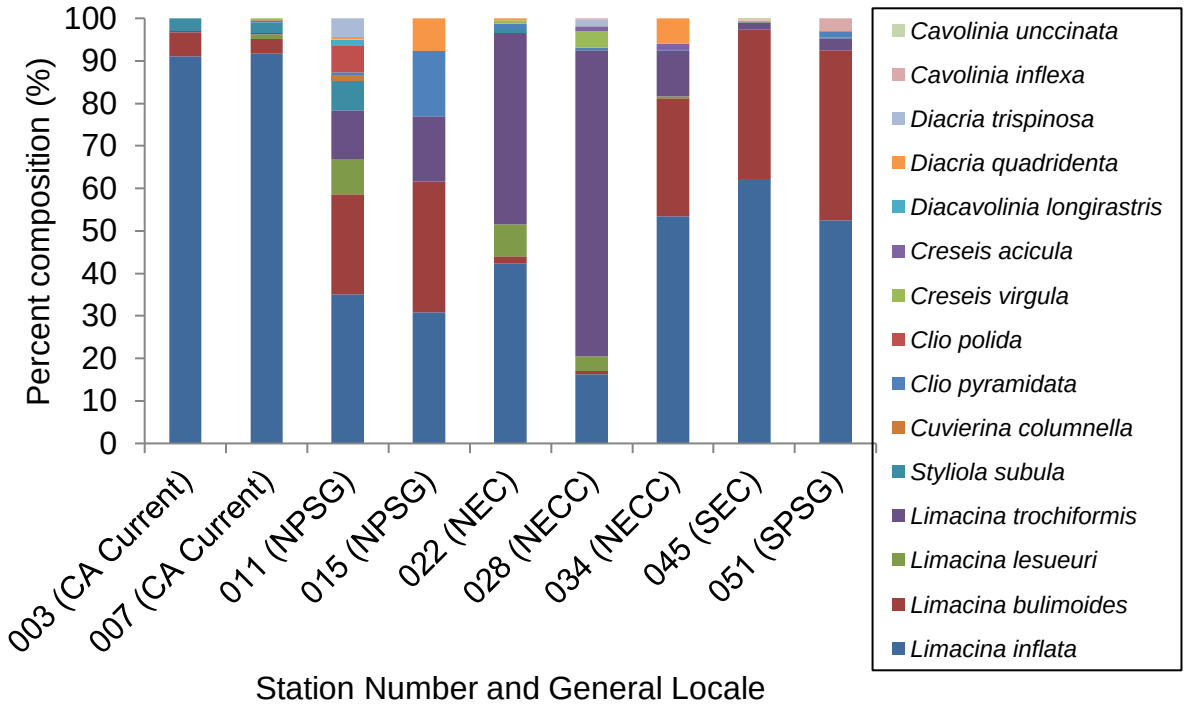


Figure 6. The percent composition of thecosome pteropods in meter net samples collected at various stations and general locales from San Diego, CA to Nuku Hiva, FP during SEA Semester Cruise S-250.

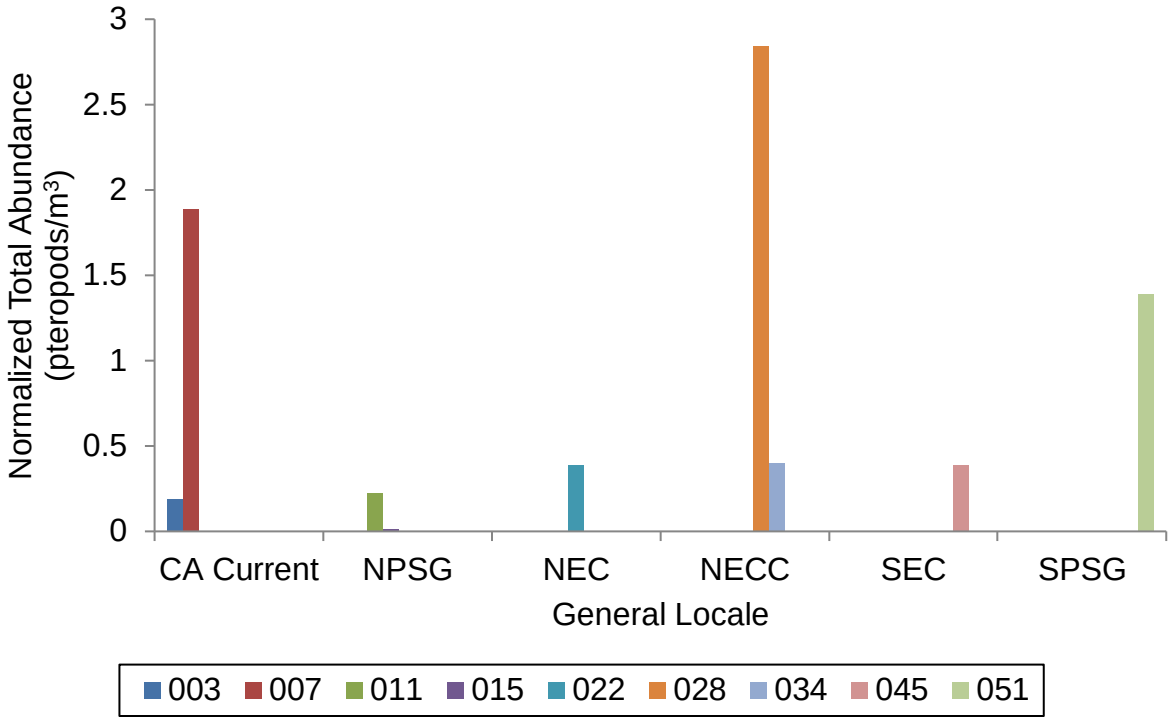


Figure 7. Normalized total abundance (pteropods/m^3) of thecosome pteropods in meter net samples collected at various stations and general locales from San Diego, CA to Nuku Hiva, FP.

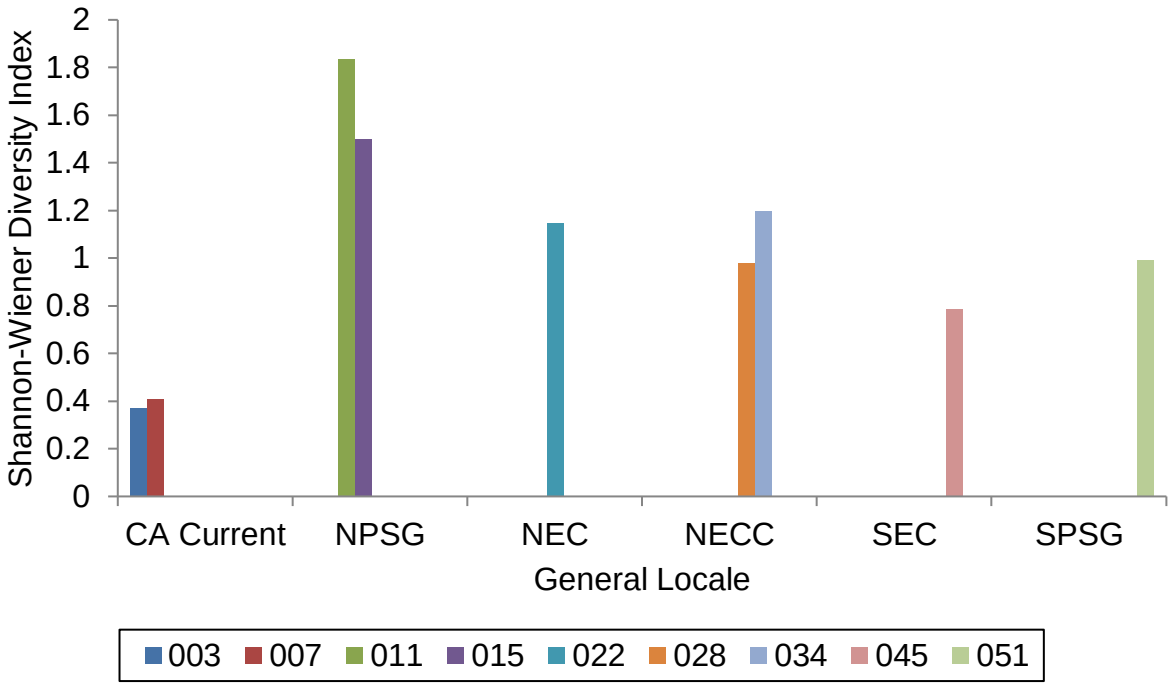


Figure 8. Shannon-Wiener diversity index for meter net samples collected at various stations and general locales from San Diego, CA to Nuku Hiva, FP.

Tables

Table 1. Species composition of pteropods in the circumglobal warm-water region (adapted from Be and Gilmer, 1977).

Subtropical Provinces (20° N/S – 40° N/S)	Tropical Province (20° N - 20° S)	Warm-water Cosmopolitan Province (40° N - 40° S)
Limacina lesueuri	*Limacina trochiformis*	*Limacina inflata*
Limacina bulimoides	*Hyalocylis striata*	*Creseis virgula virgula*
Creseis virgula constricta (North Atlantic)	*Cavolinia uncinata*	*Creseis virgula conica*
Styliola subulua	*Clio convexa* (Indo-Pacific only)	*Creseis acicula*
Clio pyramidata	*Cavolinia globulosa* (Indo-Pacific only)	*Cuvierina columnella*
Cavolinia gibbosa		*Clio euspidata*
Cavolinia inflexa		*Clio balantium*
		Cavolinia longirostris
		Cavolinia tridentata
		Diacria trispinosa
		Diacria quadridentata

Table 2. Station number, date (DD-MMM-YY), start time (Local Apparent Time), tow volume (m^3), general locale, latitude, and longitude for each station.

Station Number	Date	Start Time (LAT)	Tow Volume (m^3)	General Locale	Latitude	Longitude
S250-003	8-Nov-13	2101	1434.12	CA Current	31°6.0'N	119°18.7'W
S250-007	10-Nov-13	2125	753.41	CA Current	27°56.3'N	121°49.7'W
S250-011	12-Nov-13	2124	694.92	NPSG	23°22.6'N	124°29.5'W
S250-015	14-Nov-13	2111	731.42	NPSG	20°16.7'N	126°13.1'W
S250-022	18-Nov-13	2121	1047.14	NEC	13°54.5'N	129°44.6'W
S250-028	21-Nov-13	2221	414.39	NECC	9°0.2'N	132°5.6'W
S250-034	24-Nov-13	2237	1119.03	NECC	3°5.5'N	134°3.1'W
S250-045	29-Nov-13	2128	1119.38	SEC	4°22.6'S	137°3.0'W
S250-051	2-Dec-13	2129	1177.53	SPSG	9°37.2'S	138°8.3'W

Table 3. Pearson's product-moment correlation coefficients comparing species composition between stations. Values whose cells are highlighted red are significant at the 0.01 level.

	3	*7*	*11*	*15*	*22*	*28*	*34*	*45*	*51*
3	1.000								
7	1.000	1.000							
11	0.810	0.797	1.000						
15	0.630	0.614	0.837	1.000					
22	0.648	0.651	0.673	0.590	1.000				
28	0.139	0.140	0.299	0.333	0.837	1.000			
34	0.891	0.880	0.944	0.877	0.673	0.258	1.000		
45	0.891	0.878	0.937	0.843	0.558	0.109	0.983	1.000	
51	0.813	0.798	0.933	0.878	0.506	0.098	0.966	0.988	1.000

Table 4 Product-moment correlation coefficient between fourteen oceanographic variables, and normalized total abundance and Shannon-Wiener diversity index, respectively. n is the number of measurements of the oceanographic variable. df is the degrees of freedom used to determine significance at the 0.01 level (n – 2 = df).

Oceanographic Variables	**n**	**df**	**Normalized Total Abundance (pteropods/m^3)**	**Shannon-Wiener Diversity Index**
pH at 5 m	8	6	-0.199	0.478
pH at 50 m	8	6	-0.522	0.536
pH at 150 m	6	4	0.757	0.450
Sea Surface Temperature	9	7	0.216	0.255
Total Carbonate Alkalinity at 5 m	9	7	0.234	-0.279
Total Carbonate Alkalinity at 50 m	9	7	0.012	0.247
Total Carbonate Alkalinity at 150 m	5	3	0.566	0.021
Dissolved Inorganic Carbon at 5 m	8	6	0.223	-0.437
Dissolved Inorganic Carbon at 50 m	8	6	0.063	0.098
Dissolved Inorganic Carbon at 150 m	4	2	0.488	-0.022
Aragonite Saturation State at 5 m	8	6	-0.091	0.448
Aragonite Saturation State at 50 m	8	6	-0.356	0.608
Aragonite Saturation State at 150 m	4	2	0.191	0.250
Latitude	7	5	-0.155	-0.106

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