Planktonic Communities and Trophic Interactions in the North Equatorial Pacific Ocean

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ABSTRACT

The complex relationships between marine planktonic trophic levels are not yet well understood, despite the importance of the plankton community in the global carbon cycle and its role as a food source for commercial fisheries. In this study, phytoplankton and zooplankton community samples were collected and identified along a transect from a Hawaiian cyclonic eddy, through the oligotrophic North Pacific gyre, to the high-nutrient equatorial ocean. Within the phytoplankton community, siliceous diatoms and dinoflagellates were found to respond differently to environmental fluctuations, with more significant correlations between nutrient availability and diatoms than dinoflagellates. Differential responses by different trophic communities were also found, with bottom-up forcings more important for phytoplankton communities and top-down influences primarily controlling zooplankton. Using the different productivities along this transect, planktonic biodiversity was correlated with resource availability. Phytoplankton, due to competitive exclusion, have higher diversity at lower productivities. Zooplankton, due to predation influences, have higher diversity at higher productivities. By tracking changes in planktonic biodiversity over time, both top-down effects from anthropogenic influences like overfishing and bottom-up forcings from nutrient runoff and ocean acidification may be revealed.

INTRODUCTION

While much scientific research in the Pacific Ocean has addressed the physical limitations of the environment on various taxonomic or functional groups in the marine ecosystem, there has been less of a focus on the interactions of multiple trophic levels in the complete ecological food web. In order to monitor the health of the entire marine system, it will be important to maintain a record of the species diversity that currently exists and begin to assess changes over time. While general classifications of primary productivity in the Pacific Ocean exist, specific records of community composition will give information about the taxonomic groups most affected by global change. Also, by comparing the differences between phytoplankton and zooplankton diversity in various ocean currents, links between trophic levels may be identified. If biodiversity is monitored at different trophic levels over time, a greater understanding of the vulnerabilities and potential trophic cascades of ocean ecosystems may be realized.

The regions to be studied in the Pacific Ocean include the oligotrophic Pacific Gyre, represented by the North Equatorial Current, and the High Nutrient Low Chlorophyll equatorial region, represented by the North Equatorial Countercurrent. The NEC composes the southern boundary of the gyre that covers most of the North Pacific. Studies have shown that phytoplankton in these waters are growing at less than their maximal rate because of a limitation by nitrogen (Blain 1997). The resulting phytoplankton community is composed mainly of micro- and pico-phytoplankton, which are less limited by nutrient limitations than large cells. The larger surface area to volume ratio allows small cells to absorb more nutrients through diffusion. Zooplankton play a very important role in the oligotrophic ocean, since they are responsible for recycling nitrogen and limit the growth rate of the phytoplankton (Banse 1995).

The HNLC equatorial Pacific ocean has a different physical composition than the gyre because of the upwelling along the NECC. It is characterized by high nutrient levels yet low chlorophyll due to a limitation by micronutrients like iron (Price 1994). The growth rate of phytoplankton is strongly controlled by zooplankton as micro-zooplankton eat pico-phytoplankton (Landry 1997) and larger zooplankton preferentially graze larger phytoplankton (Price 1994). The community is still dominated by pico-phytoplankton (Kaczamarska 1995) and maintains a relatively uniform composition across the equatorial Pacific (Boutellier 1991).

The relationship between specific taxa of phytoplankton and zooplankton has yet to be extensively explored. While size classes have been related to one another, preferential feeding by zooplankton may have a strong influence on certain geographical ranges.). A study on copepod diets gave evidence for a strong reliance on diatoms (Roman 1997), so there may exist a correlation between diatom and copepod densities, a relationship open to additional research. By relating the community composition of phytoplankton to zooplankton, it may be possible to correlate certain taxa with one another. Their influence in the entire ecosystem may be partially revealed when studied in conjunction with myctophids and other upper trophic levels. By relating plankton distribution with other than physical components in the ocean, important biological associations may be discovered.

Mixed results have been found on phytoplankton communities in different regions of the Pacific. In past studies, higher levels of siliceous diatoms were found in high nutrient waters, compared to cyanobacteria and dinoflagellates dominating in low nutrient waters (Gregg 2003). In low nutrient waters, diatoms only composed 5% of the biomass, while in higher nutrient seas, diatoms made up 10-35% of the carbon biomass. In past SEA, the ratio of diatoms to dinoflagellates was measured along a North-South transect along with zooplankton biomass and composition (MacLellan 2006). High levels of diatoms were found in both areas yet with a decreased ratio approaching the equator. The zooplankton was found to have higher diversity with lower biomass in the low nutrient area of the oligotrophic gyre compared to the equatorial HNLC. While these results are contrary, it was possible that micro- and picoplankton were not measured on the SEA voyage, making larger diatoms less prominent in the HNLC region.

On the S-211 voyage, the taxonomic composition and biomass of the phytoplankton and zooplankton communities were recorded across the North-South transect, covering a Hawaiian Eddy as well as the NEC and NECC. Similar results for zooplankton communities as MacLellan’s 2006 study were expected, with diversity inversely correlated to biomass. Large diatom dominance was also expected to decrease as micronutrient structural components for the cells became limiting along the equator and algae was able to better utilize the available nutrients for larger phytoplankton. Due to the copepod association with diatoms, copepod abundance was expected to be associated with diatom abundance. The physical factors of the ocean were expected to play the largest role in determining the community composition of the phytoplankton and zooplankton. Increases in biomass for both planktonic trophic levels was expected due to the increase in nutrients. Other links between phytoplankton and zooplankton were anticipated.

METHODS

Plankton samples were collected in ten locations along a southbound cruise track from Kealakekua Bay, Hawaii to Christmas Island, Kiribati at approximately 156°W. The first station was located in a cyclonic eddy off the Hawaiian Islands at 22°N. The next five stations were located in the North Equatorial Current between 15°N and 11°N. The four stations in the North Equatorial Counter Current were located between 9°N and 4°N. Seven stations included phytoplankton sampling, which were collected between the times of 1030 and 1330 (Table 1). The five stations with zooplankton sampling were collected primarily around midnight except for two samples taken at 1730 and 0500 (Table 2).

For phytoplankton sampling, a 63μm mesh net was used to collect phytoplankton samples. For each sample, the net was lowered to 125m below the surface, then immediately raised for a consistent volume of water sampled. The contents of the net were then rinsed into a bucket and concentrated into a vial with a 63μm filter. 10% formalyn was added to the the vial for preservation. For analysis, the samples were diluted with 60-120mL of filtered seawater, depending on the density of the sample, mixed, and pipeted into a 1mL counting chamber. Under a light microscope, 44% of the chamber was photographed, resulting in 30 photos available for phytoplankton identification. The phytoplankton were then counted and classified by family, genus and species to the utmost extent.

To determine the density of the phytoplankton, the dimensions of the counting chamber and photos were measured with a micrometer to determine the percentage of the phytoplankton identified and recorded. The fraction of the total sample was then calculated based on the diluted volume:

$$\frac{\text{44\% of 1mL}}{\text{mL of diluted sample}}$$

The inverse of this fraction was used to find the multiplication factor for the taxonomic groups identified in each sample. With this, the total number of each group was calculated for each sample. The ratio of cells:water volume was found using the length of the tow (125m down and 125m up) and net area (0.5m diameter). The density of the phytoplankton in cells per cubic meter was then graphed for the entire transect.

For zooplankton sampling, --µm Bongo net was towed for various time periods at depths close to 50m. The contents of the net were then collected and measured for volume of biomass present. A first hundred organisms were identified and counted for each sample to determine the community composition, and the relative ratios of each taxonomic group in the sample were graphed for the transect.

Other physical and biological samples were taken across the transect. Surface samples of water were collected to find nutrient and chlorophyll-a content. Phosphate and nitrate concentrations were measured from water samples. Chlorophyll-a was filtered from 250mL with a vacuum and also calculated. Temperature and salinity were recorded with a flow-through fluorometer and thermosalinograph.

RESULTS

Phytoplankton samples were analysed to find overall patterns of both the community and individual taxa across the currents of the transect. The stations were divided into currents, consisting of the Hawaiian Eddy, North Equatorial Current, and

North Equatorial Counter Current. The zooplankton samples were also analyzed, both in general and by individual taxa, for trends along the transect. Trends of the phytoplankton and zooplankton were then compared with each other for a larger community analysis.

Once the phytoplankton were quantified for each sample, their density was graphed along the southbound transect (Fig. 1). After a density of around 1500 cells/m^3 in the cyclonic Hawaiian Eddy, it decreases to around 500 cells/m^3 in the NEC, then increases to 3000 cells/m^3 in the NECC. These samples were then graphed by individual taxa, either by family or genera, across the same transect (Fig. 2). Due to the large differences in scale, these were graphed on a logarithmic scale so trends could be compared between taxa. Four families – Thalassiosiraceae, Rhizosoleniaceae, Thalassionemataceae, and Chaetocerotaceae – showed density decreases from the Hawaiian Eddy to the NEC, then density increases of over an order of magnitude from the NEC to the NECC.

The diatoms and dinoflagellates, both taxa within the phytoplankton community, were then compared to each other along the transect (Fig. 3). The four families that had shown such increase all fell into the diatom order. None of the dinoflagellate families were found to increase by such a degree. When compared to the original phytoplankton density graph, the diatom increase is most consistent with the overall increase in density. The dinoflagellate density is not consistent with the overall density.

Physical and biological measurements of the ocean from the same locations were then compared to the phytoplankton density (Fig. 4). Phosphate showed only a small increase in concentration over the transect. Chlorophyll-a and nitrate both showed a large increase in concentration from the NEC to the NECC, however, there was not a visible difference between the Hawaiian Eddy and the NEC. The phytoplankton density increase is similar to that of chlorophyll-a and nitrate.

Further analysis of the phytoplankton community was completed using PRIMER (Table 3). The taxonomic composition was compared to the Hawaiian Eddy(HE) and two currents, oligotrophic NEC (O) and equatorial NECC (E). Differences in the community due to the currents was calculated with statistical analysis. The Global R estimates how much of the difference can be accounted for by the currents as a factor. The overall phytoplankton community differences, with a Global R of 0.245 means that 24.5% of the composition difference is due to the change in currents. The significance is 0.001, showing over 99% confidence. Between individual currents, the Hawaiian Eddy and the NECC had the greatest R-value (0.436), showing that the currents played a stronger role in influencing community composition than between the NEC and NECC (0.193).

The diatom community was then analyzed to show a greater Global R of 0.307, indicating greater correlation of the community and current. Again, the differences between the Hawaiian Eddy and the NECC showed the greatest influence on community composition with an R-value of 0.459, compared to the 0.243 R-value of the NEC and NECC. Dinoflagellates, when analyzed, showed less correlation of composition differences and the current (insignificant Global R of 0.031). Almost all R-values for pairs of currents were insignificant as well, with low or negative values. This indicates that dinoflagellate community differences can not be explained by changes in the current, opposed to the diatom community.

The zooplankton community was analyzed in the same manner as the phytoplankton community, however, no taxa showed any relative trends related to the currents. While overall density of the zooplankton increased across the transect, individual group prominence could not be correlated with any other physical or biological factors. Zooplankton overall density showed similar trends to phytoplankton density, though, and shows a large increase from the NEC to the NECC (Fig 5). Zooplankton density decreases from the Hawaiian Eddy to the NEC, though, unlike the phytoplankton.

The diversity of the phytoplankton and zooplankton was calculated using the Shannon-Weiner Diversity Index. The two plankton groups were then compared to each other, showing opposite trends in diversity (Fig. 6). The phytoplankton diversity increased from the Hawaiian Eddy to the NEC, then decreased from the NEC to the NECC. Zooplankton diversity decreased from the Hawaiian Eddy to the NEC, then increased in the NECC.

DISCUSSION

Both the phytoplankton community itself and its relationship with the zooplankton community were the objects of this study. The physical environment was expected to play a large role in determining the community composition, but links between the two trophic levels were also anticipated. Results of the study indicated that physical factors of the ocean are very dominant in determining the community composition of phytoplankton, but little correlation of phytoplankton and zooplankton was evident.

The phytoplankton community seemed to be primarily controlled by the physical factors of the different oceanic regions. As Figure 1 shows, phytoplankton abundance appears to increase in the higher nutrient region closer to the equator from the oligotrophic gyre. This can be correlated with increases in nitrate (Fig. 4), the limiting factor in the gyre (Blain 1997). However, the elevated phytoplankton density in the Hawaiian cyclonic eddy can not be explained by nitrate increases, despite its potential role in upwelling nutrients. It is possible that most of the nutrients were consumed by the sampling time and the high phytoplankton resulted from an earlier time during the eddy's cycle. Neither of the nutrients, though, appears to be elevated in the eddy.

The disparity between diatom and dinoflagellate variability may help explain the dramatic increase in density in the higher nutrient waters. In a breakdown of the different taxonomic responses over the transect, a variety of phytoplankton families showed a very similar increase at lower latitudes. However, while they were not closely related, all of the families were members of the diatom order Biddulphiales. None of the dinoflagellate taxa responded similarly to the diatoms. Since diatoms are siliceous organisms, this increase may be associated mostly with the increased availability of SiO_2 in the HNLC. While this physical factor was not measured, other measured nutrients do increase in this region.

Dinoflagellate density remained relatively constant across the entire transect, perhaps indicating a different controlling factor on their populations besides nitrate and SiO_2. Past studies, like those by Blain (1997) and Price (1994), determined the limiting factor of the ocean as nitrogen by measuring the ratio of $Si[OH]_4$ to N. However, for primary producers that do not depend on silicates for growth, the limiting factor may be very different. The difference in growth rates between quickly-dividing diatoms and more heavily-armored dinoflagellates provides the background for one hypothesis. In the oligotrophic ocean with limited nutrients and zooplankton consumers, dinoflagellates with their protective plates are less vulnerable to consumers. Diatoms are then the favored food for zooplankton, supported by Roman's 1997 study of the copepod diatom diet. When diatoms are provided with higher nutrient levels, their fast growth rate allows them to overcome the high grazing rate and become relatively more dominant. Exploration of limiting factors on non-siliceous producers leaves much potential for future research.

The strong relationship between physical variables and diatoms was further supported by the PRIMER analysis. With the high Global R for diatoms, the factor of the current can account for a large amount of the community variability. The Hawaiian Eddy located in the middle of the oligotrophic gyre especially shows the influence of upwelled nutrients on the diatom populations. Since a large physical change is caused by an eddy, the diatom composition is strongly changed by its existence, even when it is formed within the low nutrient gyre. Although much of the phytoplankton community is composed of siliceous organisms, only the diatom taxa were responsible for the large Global R for variability correlation with the currents. Dinoflagellates, though, have an insignificant and sometimes negative variability that can be explained by the currents. Links to other biological or physical factors may exist instead.

The zooplankton analysis did not yield many correlations with physical or biological variables measured. The only positive trend identified was the biomass increase from the oligotrophic region to the HNLC region. Even with this correlation, the zooplankton density was very low in the Hawaiian Eddy, an opposite trend than that of phytoplankton. This may be due to interactions with higher trophic levels, such as the increased amount of planctivores predicted in eddies, since zooplankton are strongly controlled by top-down effects. This is very different than the bottom-up effects that control phytoplankton populations. Although these trophic levels have a high level of interaction, they seem to have little effect upon each other. This uncoupling may be attributed to a number of factors (Micheli 1999). Inter-species interactions of zooplankton and constant loss of nutrients and individuals from the system are both methods in which trophic interactions are dampened.

The differences in the diversity trends for phytoplankton and zooplankton support this disassociation with one another. Phytoplankton diversity peaks in the low-nutrient oligotrophic gyre, and decreases in the productive Hawaiian eddy and HNLC waters. The zooplankton instead peaks in the high-nutrient waters and decreases in the oligotrophic ocean. The two types of trophic interactions, top-down and bottom-up, are possibly responsible for these different reactions. A study on these varying types of control by Worm (2002) revealed that the different trophic levels react very differently to different levels of resource availability. In a typical curve of diversity vs. productivity, the peak in diversity occurs at an intermediate productivity, since greater resources result in competitive exclusion by few species and fewer resources result in little ability for many species to survive.

The diversity peaks can shift for different trophic levels, though, depending on the top-down or bottom-up control. For phytoplankton, at higher nutrient levels, a few species will dominate, such as certain diatoms, and the peak is shifted towards lower resource availability. This indicates bottom-up control, since the amount of nutrients controls the level of diversity. For zooplankton, higher level consumers provide the dominant controls on the community. While consumers seem to decrease diversity at low productivity levels, like the oligotrophic gyre, they tend to increase diversity at high productivity levels (Worm 2002). This top-down effect would explain the shift of peak diversity to the high-nutrient areas. While this trend has been consistent in past research, there is yet much to be understood, leaving much potential for future research on these trophic interactions with diversity.

While this research appeared to be relatively consistent with past research, not including MacLellan 2006, improvements in procedures may provide more concrete results. With the mesh size of the phytoplankton net, only large phytoplankton were able to be collected, leaving the majority of the phytoplankton community unsampled. By analyzing the micro- and picoplankton, a better estimate of density and community composition could be compiled. Higher resolution images of phytoplankton might make more specific identification possible, and more trends might be discovered within families and genera. For comparison with zooplankton samples, it would be preferable for zooplankton and phytoplankton samples to be taken at the exact same stations. The failure to do this for the entire transect may have made potential correlations between the trophic levels even more difficult to identify. Future research might address the limiting factors on non-siliceous primary producers or more possible links between phytoplankton and zooplankton populations.

While correlations between specific taxa of phytoplankton and zooplankton were not apparent with the data collected, different responses of the two trophic levels were evident with the trends in diversity. The bridge between bottom-up and top-down forcings appears to fall between these two levels. Abundance was not able to be correlated with diversity, though, and while phytoplankton and zooplankton biomasses respond relatively similarly to resource availability, these trends appear to be opposites in terms of diversity. Within the group of primary producers, there also appears to be a split between diatoms and dinoflagellates, the former group having a close tie with the physical environment, and the latter category having little correlation. With these conclusions, more research is desireable in the areas of non-siliceous producers and trophic interactions.

CONCLUSIONS

In studying the planktonic community of the Pacific Ocean, the primary objectives were to relate the phytoplankton community composition to the physical variables of the ocean, then explore potential links between the phytoplankton and zooplankton communities of each region. However, while both the phytoplankton and zooplankton communities appeared responsive to the physical environment, little correlation between the two trophic levels was evident. The phytoplankton community was distinctly divided into siliceous diatoms and algae dinoflagellates. While it seems possible to predict the responses of diatoms to changes in resource availability, less is known about algae producers. With primary production in the oceans such an important carbon sink, it is necessary to understand differential responses to predict bottom-up changes in the ecosystem. While phytoplankton may not be as affected by overfishing and disturbances to pelagic species, changes in the nutrient availability may cause wide changes in marine production.

The distinction between top-down and bottom-up influences is also important when considering the zooplankton community. While this is less affected by nutrient changes, decreases or changes in pelagic consumers may have a large impact on this trophic level. Because zooplankton are the primary food source for many marine organisms, the dynamics of trophic cascades should be understood to predict future responses to global change. With so many interacting variables on marine ecosystems, there is ample space for future research. A continued record of the planktonic community will provide evidence of both bottom-up and top-down changes in the environment, and may become invaluable in managing the marine ecosystem.

FIGURES

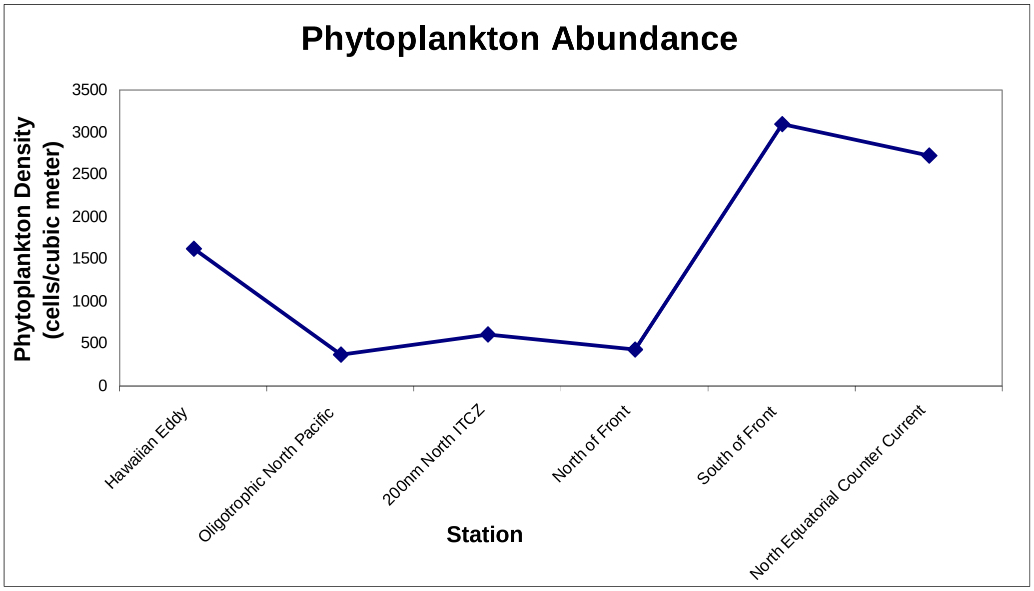

Figure 1: The phytoplankton density, measured in cells per cubic meter, is shown in six locations along the southbound cruise track of S211 from May 14-19, 2007. Three distinct areas are represented – the Hawaiian Eddy (1 station), the North Equatorial Current (3 stations), and the North Equatorial Counter Current (2 stations).

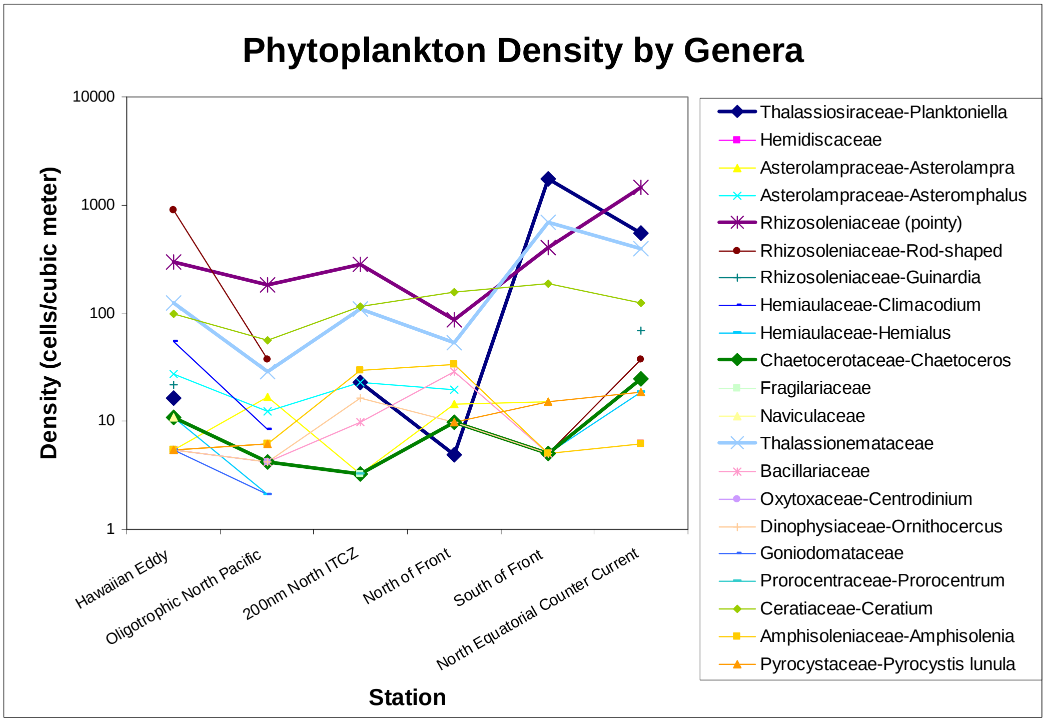

Figure 2: Phytoplankton density is divided into taxonomic groups by family and genera in six locations along the southbound cruise track of S211 from May 14-19, 2007. The series in bold (Thalassiosiraceae, Rhizosoleniaceae, Thalassionemataceae, and Chaetocerotaceae) are the groups that increased by an order of magnitude or more from the North Equatorial Current to the North Equatorial Counter Current.

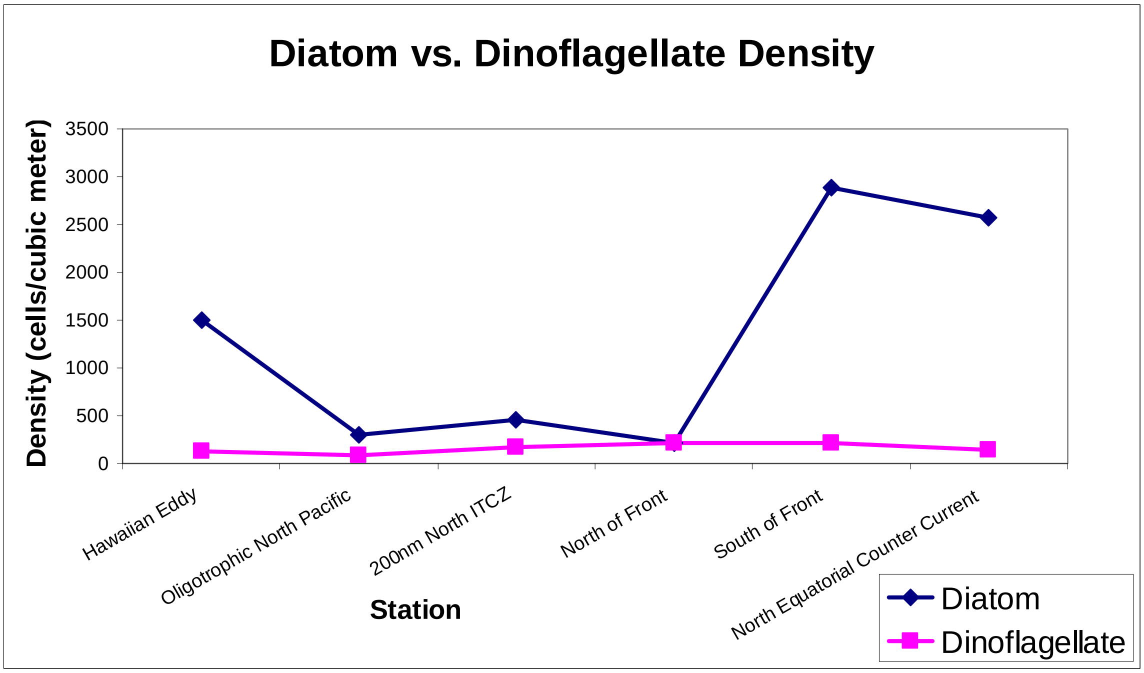

Figure 3: Phytoplankton density is divided into diatom and dinoflagellate genera in six locations along the southbound cruise track of S211 from May 14-19, 2007.

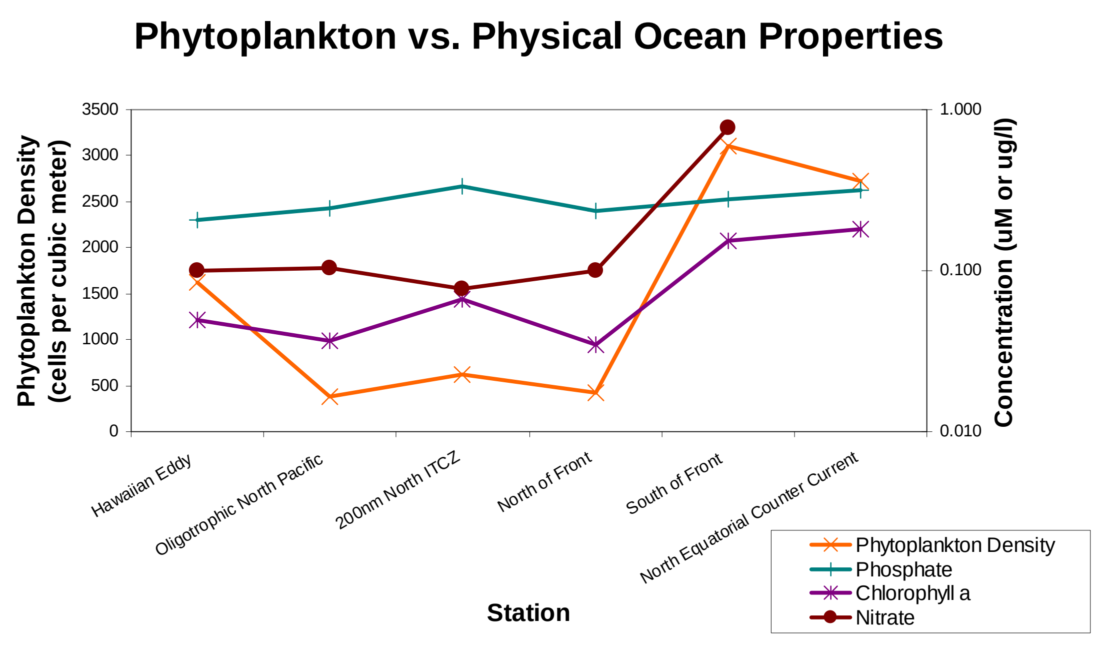

Figure 4: Phytoplankton density is compared to chlorophyll, nitrate, and phosphate concentrations measured in six locations along the southbound cruise track of S211 from May 14-19, 2007. The chlorophyll and nutrients are graphed on a log scale to highlight changes in concentration across the currents.

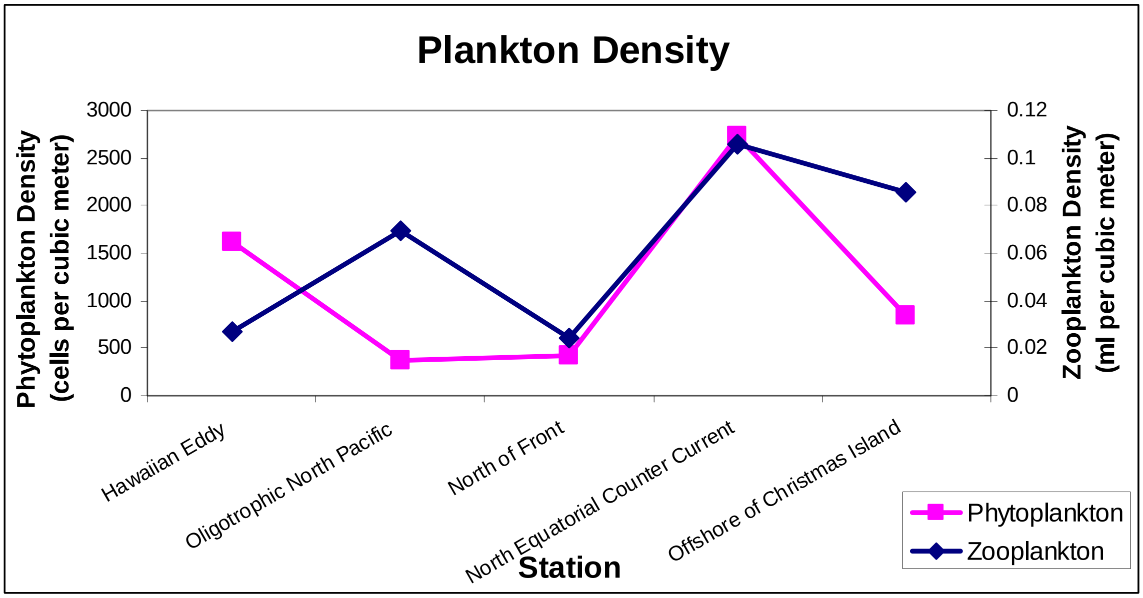

Figure 5: Phytoplankton and zooplankton densities are shown for five locations along the southbound cruise track of S211 from May 14-20, 2007. Phytoplankton are measured in cells per cubic meter, and zooplankton are measured in ml per cubic meter.

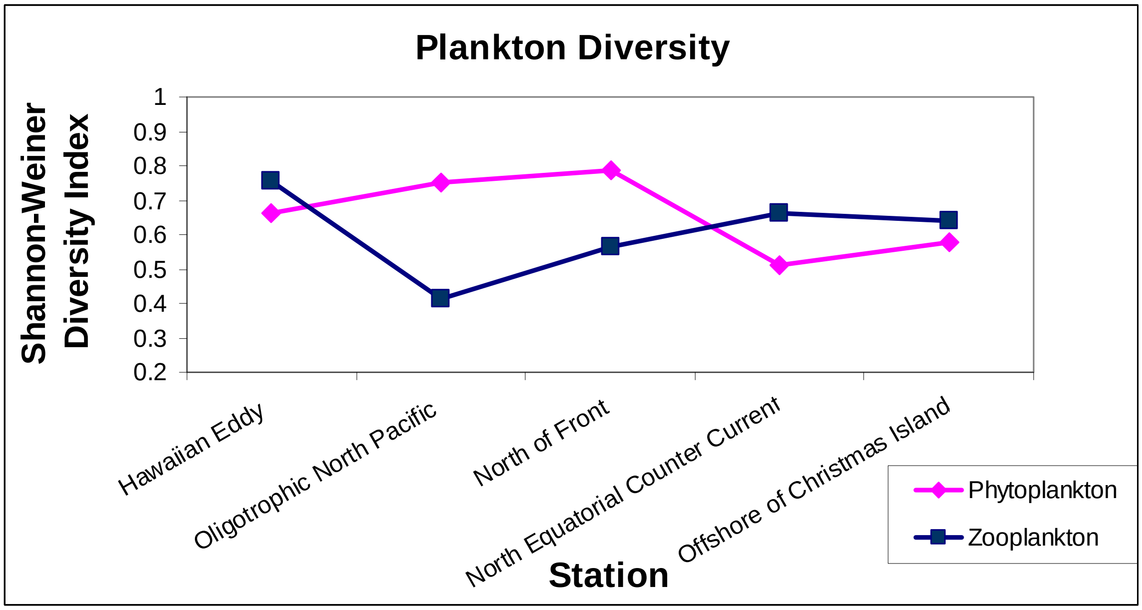

Figure 6: Phytoplankton and zooplankton diversity is represented by the Shannon-Weiner Diversity Index for five locations along the southbound cruise track of S211 from May 14-20, 2007.

TABLES

Station Location	Date	Time	Tow Depth	Latitude	Longitude
Hawaiian Eddy	14-May-07	1300	125	16°53.9' N	156°22.2' W
Oligotrophic North Pacific	15-May-07	1048	125	15°18.8' N	156°27.2' W
200nm North ITCZ	16-May-07	1219	125	13°21.0' N	156°31.7' W
North of Front	17-May-07	1238	125	11°40.6' N	156°37.0' W
South of Front	18-May-07	1236	125	9°30.9' N	156°32.3' W
North Equatorial Counter Current	19-May-07	1323	125	7°8.9' N	156°29.6' W

Table 1: Six phytoplankton samples were analysed along the southbound cruise track of S211 from May 14-19, 2007. The tow depth was uniform for all samples, and the tow took place near the same time of day for each sample.

Station Location	Date	Time	Tow Depth	Latitude	Longitude
Hawaiian Eddy	14-May-07	1720	50	16°44.7' N	156°26.9' W
Oligotrophic North Pacific	15-May-07	2332	58	14°28.3' N	156°30.5' W
North of Front	17-May-07	0518	44	12°17.4' N	156°33.3' W
North Equatorial Counter Current	19-May-07	2300	50	6°28.4' N	156°27.6' W
Offshore of Christmas Island	20-May-07	2352	79	4°58.8' N	156°29.3' W

Table 2: Five zooplankton samples were analysed along the southbound cruise track of S211 from May 14-20, 2007. Tow depths varied, but never exceeded the phytoplankton net tow depth. The sampling times were generally during the same time of day.

	Phytoplankton	Diatoms	Dinoflagellates
Global R	0.245 (Sig. = 0.001)	0.307 (Sig. = 0.001)	0.031 (Sig. = 0.062)
HE, O	0.230 (Sig. = 0.002)	0.358 (Sig. = 0.001)	-0.057 (Sig. =0.827)
HE, E	0.436 (Sig. = 0.001)	0.459 (Sig. = 0.001)	0.055 (Sig. = 0.132)
O, E	0.193 (Sig. = 0.001)	0.243 (Sig. = 0.001)	0.049 (Sig. = 0.001)

Table 3: PRIMER results for community composition relating to current are shown for overall phytoplankton, then for diatoms and dinoflagellates counted along the southbound cruise track of S211 from May 14-19, 2007. The global R represents the amount of community variation that can be accounted for by the different currents (Hawaiian Eddy, Oligotrophic, and Equatorial) and the significance of the association. The R-value of the community variation between individual currents and significance is also shown for each combination of currents.

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