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Undergraduate

THE EFFECTS OF A FRESHWATER GRADIENT ON ZOOPLANKTON DISTRIBUTION AND COPEPOD RESPONSE TO SALINITY SHOCKS

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Abstract. Estuaries are some of the most productive ecosystems in the world; though human development and global warming are threatening them. Zooplankton communities can serve as biological indicators of stresses due to their short lifecycles and sensitivity to environmental shocks, such as salinity changes. Studies have looked at the effects of freshwater shocks in the lab outnumber those that surveyed natural zooplankton distributions change along the freshwater gradient created by outflow from rivers. This study surveys the distribution of various taxa and examines the relationship this has with salinity by sampling zooplankton in Pao Pao River and Opunohu River on the island of Moorea in French Polynesia. In addition, this study tests the ability of copepods native to brackish water in Pao Pao to survive various shocks of increasing or decreasing salinity over time, as well as their response to bright light. Significant differences were found in overall community composition between bays and along the freshwater gradient. Most taxa exhibited strong correlations to salinity levels; some positive, some negative and some parabolic. Sharp rises in salinity appear not to affect copepod survival rates significantly, but abrupt drops do have significant effects. Light seems to repel copepods significantly as well.

Key words: zooplankton; veligers; copepods; hydrozoan; foraminifera; phytoplankton; larvae; community structure; Moorea, French Polynesia

INTRODUCTION

Estuaries are important sites of biodiversity and often provide many ecological services such as nutrient cycling and removal of contaminants (Schallenberg *et al.* 2003). These environments provide safe habitats for many organisms, such as fish, crustaceans and shellfish to grow and mature, transporting 5-10% of the total primary production out into the open ocean as juveniles migrate to adult habitats (Gillanders 2003). These nurseries therefore have commercial importance, acting as spawning grounds for many economically valuable vertebrates and invertebrates (Gillanders 2003). However, climate change and human development are endangering these fragile ecosystems. Aquaculture, even on a small commercial level such as the shrimp farm in Opunohu Bay on Moorea, has also been shown to significantly increase algal growth over short periods (Lin and Fong 2008). Understanding how these systems function will be crucial for addressing problems and making policy decisions, but to do so one must look at microscopic organisms in addition to the macroscopic ones.

Zooplankton communities are a key component of aquatic ecosystems, being comprised of many macroscopic benthic and pelagic organisms' larval phases and form important links in food webs, transferring energy and nutrients from phytoplankton producers and larger consumers. For example, planktonic copepods may be the most abundant animals on earth and are part of most open ocean food webs, transferring vast amounts of energy and nutrients up the food chain from the primary producers to fish (Ohman 2001). Planktonic protozoans make up a substantial portion of deep-sea biomass and are very involved in the turn over of organic material in the water column (Gross 2000). They also can help mitigate or prevent the occurrence of toxic phytoplankton blooms. Observations have shown that copepods ingest toxic phytoplankton and may be responsible for retarding initial development of blooms while polychaete larvae can remove 100% of blooming phytoplankton daily (Turner and Tester 1997). In addition, many important macroscopic organisms including fish, crustaceans, mollusks and cnidarians spend some part of their cycle as free-floating zooplankton. This planktonic larval phase is crucial in the dispersal of species into new

areas, especially for species where the adult forms are unable to swim great distances or are incapable of displacement altogether (Olson 1985). The survivorship and recruitment of these planktonic larvae often is the determining factor in adult benthic distribution (Metaxas 2000).

Greenhouse gas emissions are projected to rise uniformly over the next century, but sea surface temperatures and rainfall changes are expected to have regional variations (Xie *et al.* 2010). There is a positive correlation between these temperature increases and rainfall (Xie *et al.* 2010) and observations have shown that in the South Pacific is expected to receive a greater amount of it. French Polynesia, in particular, has seen total average annual rainfall increase of over 50% between 1976 and 1998 (Manton *et al.* 2001). Runoff from the extra rain increases the amount of nutrients, pollutants, and sediments present in estuaries and bays, with greater impact in more urbanized areas (Morrisey *et al.* 2002). Surpluses of nutrients from agricultural runoff have been known to cause eutrophication events that are harmful to marine life (Nixon 1995).

Zooplankton can be good environmental indicators due to their short life cycles and since their response to stresses can be very rapid and will be evident in changes community structure (Attayde and Bozelli 1998). Foraminifera, for instance, show rapid microhabitat preference and can actively seek out more suitable locations based on environmental gradients of biotic factors such as food, or abiotic factors such as temperature and oxygen concentration (Gross 2000). Species composition usually remains constant in lakes for extended periods once established and the organisms have adapted to the local conditions, but may shift in favor of one group or another upon environmental disturbances (Gannon 1978). In addition, plumes resulting from freshwater runoff due to intense rains exhibit sharp drops in surface salinities and, at least in the short-term, have shown to lower numbers of zooplankton (Canepa 1996), while lab experiments have shown up to 100% mortality of copepods from 50% salinity drops (Harris 2007). Intense rains would also mean stronger current flows in rivers, which has been correlated with lower zooplankton numbers (Basu 1996). Zooplankton are also logistically easier to manage than phytoplankton and respond more quickly to changes than fish do (Gannon 1978).

This study surveys the distributions of several taxa of zooplankton along Pao Pao River and Opunohu River, on the island of Moorea in French Polynesia. The objective was to determine how taxa abundance and species composition varied along a freshwater gradient and if there were any differences in species composition or taxa abundance between both rivers. I wanted to determine if there were any natural distributions that correlated with salinity, as these distributions would likely be affected by increases in freshwater outflow due to rainfall. In addition, by running several tests in the laboratory on copepods found at a brackish water site in Pao Pao River, I wanted to determine how tolerant these copepods were to abrupt changes in salinity, how they responded to intense light stimulus and to see if they could survive long term exposure to freshwater environments in the lab. This was intended to simulate conditions they might experience from intense rains or environmental blocks to sunlight, such as cloud cover, sedimentation or obstructions.

I hypothesized that there would be significant differences observed along the freshwater gradient because of different species' ability to deal with osmotic stress. I also hypothesized that Pao Pao and Opunohu would be similar in community structure and composition since both are physically comparable. I hypothesized that fast shocks of increasing or decreasing salinity would have negative impact copepod survival, and they would be unable to survive in freshwater because of a previous study's findings (Harris 2007). In addition, I hypothesized that the copepods would be repelled by intense light.

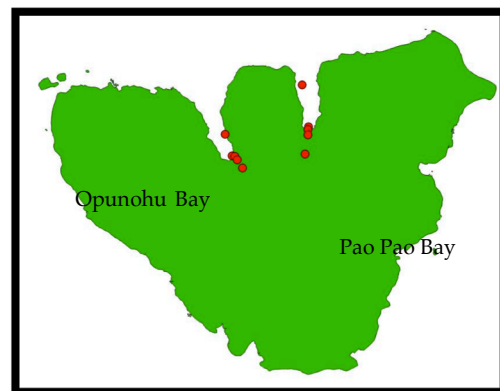


FIG. 1. Sampling sites on Moorea in this study: 5 in Pao Pao River and 5 in Opunohu.

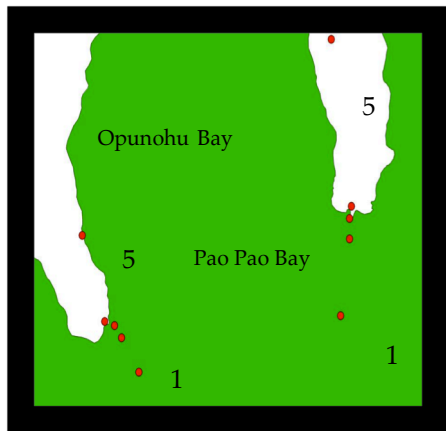


FIG. 2. Close up of sampling sites in this study.

METHODS

Study sites

Moorea is a volcanic island in French Polynesia with a subtropical climate, located in the South Pacific (17.533°S 149.833°W). Figures 1 and 2 are maps of the island with points at my study sites.

In order to study the distribution of zooplankton along a freshwater gradient, I sampled Pao Pao River and Opunohu River because they were the two largest rivers on Moorea by volume and shared many characteristics. Both rivers have agricultural development upstream and carry more water during the rainy season. Several key differences include Pao Pao having greater urban development, especially surrounding the river mouth, and the presence of a shrimp farm at the river mouth at Opunohu that drains the ponds every several months, releasing nitrogenous waste into the bay.

Sampling

In order to collect zooplankton samples, I chose 10 sites to conduct plankton tows in. Five were in Pao Pao, and five were in Opunohu. They were chosen to be comparable between bays and to represent a range of salinities. The sites were numbered one through five corresponding to relative salinity levels of the sites. The first site in each bay was meant to represent a purely freshwater stream with no saltwater inflow from tides. Sites two,

three and four contained brackish water, with variable salinities, and generally with salinity being higher at site four than site two. Site five was chosen to be a pure saltwater site, to compare other sites against.

Measuring Abiotic Factors

To measure abiotic factors at each site, I took salinity readings with an Instant Ocean Hydrometer (Marineland Labs) that measured salinity based on density, temperature readings with a thermometer, depth readings with a 1m PVC pipe with 5cm marks on it, and current-speed readings by measuring the time it took a leaf to travel 1m with a stopwatch.

Plankton Tows

To sample plankton numbers I took 20 one meter tows with a 64 micron plankton mesh net by hand. The contents of the tows were collected in a 50 mL plastic bottle that could be screwed and unscrewed at the bottom of the plankton net. The contents of the bottle would then be emptied into a larger 100 mL bottle that was labeled with a number (1-5) corresponding to the site it was collected. I would always begin by sampling farthest up the river first at site one (pure freshwater site), and then work my way down, as the tide receded.

I sampled twice a week on average for a total of 10 samplings on random days of the week, between October 9th and November 10th. The first five were done in Pao Pao in early and mid-October, and the other five were done in Opunohu in late October and early November. I controlled for the time of day and tide by sampling between 12:00 and 15:00 hours, which coincided approximately with high tide (according to NOAA data for Fare Ute Point on Tahiti). The greatest difference between high tide and low tide between that time was only approximately one foot, but may have been as little as 0.1 feet. Sampling was done regardless of weather conditions. After the samples were collected, they were placed in the refrigerator to kill or slow down the specimens for a period of at least 24 hours.

Study Organisms

The main groups of organisms found in the tows were copepods and their eggs, hydrozoan larvae, bivalve and gastropod

veligers, ostracods, platyhelminthes, nematodes, polychaetes and foraminifera.

To identify the different taxa observed in the tows I used the pictures found in "A Guide to Marine Coastal Zooplankton and Marine Invertebrate Larvae" as well as "Guide to the Common Inshore Plankton of Southern California" (UCLA Marine Science Center, 2003). Pictures were taken of different taxa using a microscope camera kit. I also consulted Professor Scott Fay about the identification of some unknown Foraminifera.

To count the zooplankton, 0.5 mL subsamples from the large samples were collected, after mixing and homogenizing the large samples thoroughly. Each 0.5 mL was spread over 5 microscope slides and analyzed under an Olympus compound microscope with 4x, 10x and 40x magnification. This was chosen over the use of a dissecting microscope and petri dishes for several reasons. The first was because the slides fixed any specimens that had survived refrigeration and allowed for easier counting and identification. The second was that some samples were so dense that 0.5 mL was more than enough to obtain a large number of organisms. The third reason was that moving petri dishes disturbed the water and mixed specimens around, making it difficult to keep track of where one was on the dish and what had been counted. The slides were easier to methodically search through. Finally, the slides prevented dense samples from stacking specimens on top of one another, allowing for more effective counting.

Lab experiments

Copepod samples were taken from the third site in Pao Pao Bay, which contained brackish water. This site was sampled three times and the three experiments were run on each of these different samples.

Salinity shock experiment

To test Copepod tolerance to abrupt salinity changes, I exposed the Copepods to different salinity levels. The first experiment consisted of 4 subsamples being subjected to an abrupt salinity drop, with 1 control. I took five 5mL subsamples and placed them into separate vials. Each vial received 5 mL of homogenized sample water with Copepods in it and 5mL of water with different salinities. For the control I used filtered water taken from the sample site, which had a consistent salinity of approximately 20ppt. For the four

treatments I added 0.5, 1.5, 2.5 and 5mL of freshwater, and then added the corresponding amount of control water to make 5mL: 4.5, 3.5, 2.5 and 0mL. I took 0.5mL subsamples at different times: 0, 15, 30, 45 and 60 min from the initial addition of treatment water. Each subsample had approximately 20-40 Copepods. I counted the total number present, and then the number that were not moving, which were considered dead. I repeated this experiment 3 times. I also performed a salinity rise experiment with the same methods, but instead of freshwater from the tap I used filtered seawater from off the Gump Station dock, which had a consistent salinity of 35.

Light reaction experiment

To test how copepods reacted to an intense light source I used a 40W, 220V fluorescent lamp 20 centimeters from top end of a petri dish with a subsample of around 50 copepods. This was compared to a control treatment where the light was off. After adding the Copepods I waited 5 minutes and then observed the sample under a dissecting microscope to see if the copepods were randomly distributed, or clustered around half of the dish nearer, or further from the light. This was repeated five times per sample, and three replicates with Copepods sampled on different days were performed.

Long term salinity drop experiment

To test if Copepods taken from brackish water were capable of surviving in pure freshwater for an extended period, I placed around 40 Copepods into a petri dish with pure freshwater taken from the tap, and around 40 into a petri dish with filtered control water. This was merely a qualitative pilot study for future research. I checked the copepods after 3, 6, 12 and 24 hours and simply looked for movement. This was replicated 3 times with Copepods taken on different days.

Statistical tests

To compare the overall community differences between bays, community differences among sites within each bay, and individual site community differences between bays I used a Discriminant Multivariate Analysis.

I used ANOVA tests to compare differences between average number of

individual taxa at each site, and Tukey-Kramer HSD tests to test for significant differences between individual means. I also used ANOVA and Tukey-Kramer HSD tests to test for significant differences between salinity treatments.

To test for correlations between salinity and taxa distribution, I ran a regression analysis for each taxon and tested for a linear or second-degree polynomial fit.

I performed a t-test to compare the difference between the ratio of copepods located on the top half of the petri dish (near the light source) in the control and in the experimental groups.

All the statistical analysis was done with the software JMP, Version 10. SAS Institute Inc., Cary, NC, 1989-2012.

RESULTS

Figure 3 shows the total number of plankton 12 different varieties of zooplankton caught at each site. A multivariate discriminant analysis of community structure by bay showed that the differences between the two bays were highly significant (Wilks' Lambda Value=0.34, F=6.01, P<0.0001).

A multivariate discriminant analysis of communities by field site in each individual bay also yielded significant results. Pao Pao had sites with community differences that

were highly significant (Wilks' Lambda Value=0.004, F=2.38, P=0.0038) and Opunohu showed similar results (Wilks' Lambda Value=0.004, F=2.38, P=0.0038).

When I analyzed the sites from both bays together with a multivariate discriminant analysis, they were found to be significantly different from one another (Wilks' Lambda=0.004, PF= 2.3, P<0.0001). Figure 4 shows that when plotted on two canonical axes that best showed the differences in community structure between sites, I found that some sites had a large amount of overlap, such as site 1 and 2 in Opunohu, while site 4 in Pao Pao shared no overlap with other sites.

I ran ANOVAs of taxa number versus sample sites in order to determine if any sites had significant differences in taxa, and then Tukey-Kramer HSD tests to determine specifically which sites were significantly different. I found that Spiny Foraminifera, gastropod veligers and Nematodes had no significant differences between sites. I also found that sit 4 in Pao Pao had significantly greater numbers of polychaetes (P= between 0.0001 and 0.025), significantly greater numbers of ostracods (P= between 0.0016 and 0.018) and significantly greater numbers of Miliolida foraminifera (P=between 0.0002 and 0.0223) except compared to site 5 in Opunohu.

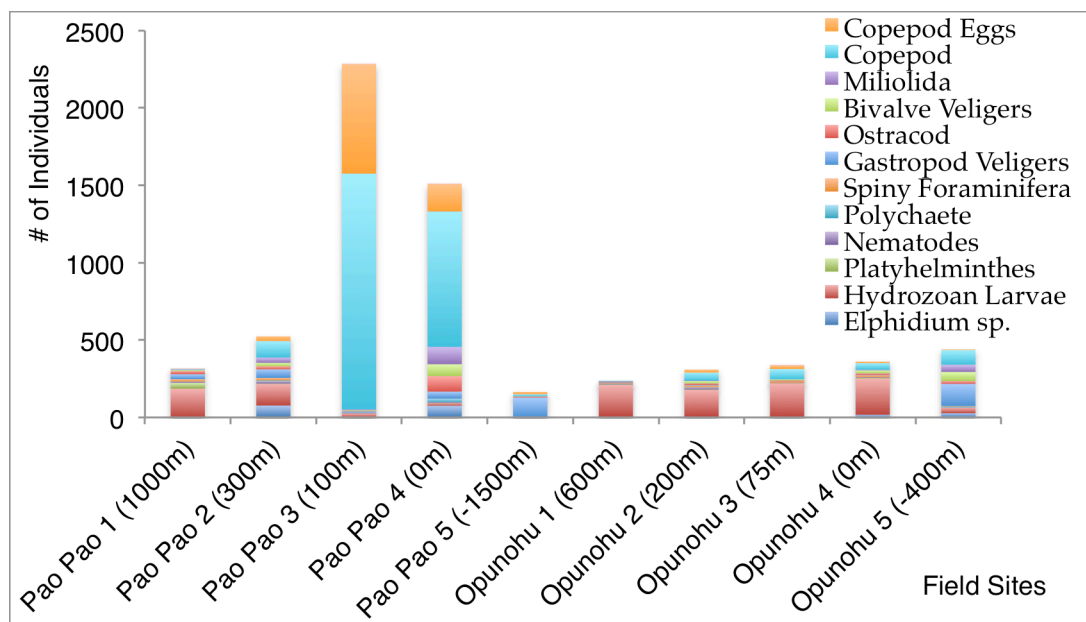


FIG. 3. This graph shows the total number of different organisms counted in the plankton tows on the Y-axis, and field site with its distance upstream from the river mouth on the X-axis. Negative values represent distance into the bay.

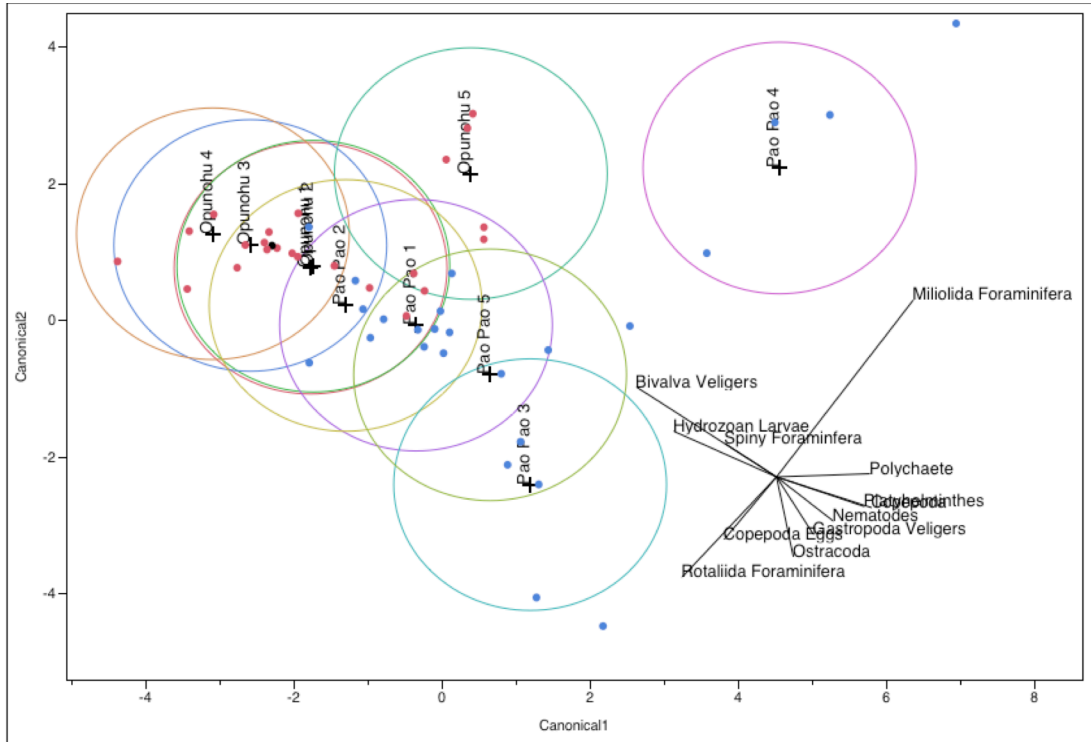


FIG. 4. This figure shows the overlap in community structure of different sites between bays. Each axis is a canonical axis, meaning it was created based on Y-axis data I input to show the maximum differences between sites. Each point represents a different community. the biplot in the lower right corner shows which variables (taxa) are important for discriminating sites. If two sites are along the same line then that taxon is important for discriminating between the two. If the line is perpendicular, then it isn't very important. The length of the line determines the magnitude of the contribution of that taxon to the discrimination.

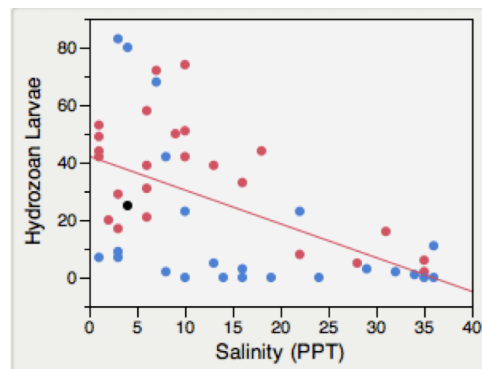
The Tukey-Kramer HSD test also showed that there was a significantly greater amount of copepods in site 3 of Pao Pao, compared to all other sites, except for site 4 of Pao Pao ($P=$ between 0.0089 and 0.019). Copepod eggs shared a similar distribution, begin significantly more abundant at site 3 in Pao Pao than anywhere else ($P=$ between 0.0005 and 0.018).

The ANOVA showed that there were significant differences in the distribution of Hydrozoan larvae ($P=0.0002$, F Ratio=4.79). Tukey-Kramer HSD tests showed that sites 3 and 4 in Opunohu had significantly more Hydrozoans than sites 4 and 5 in Pao Pao.

To determine if there was significant correlation between individual taxa and salinity levels measured at each site, a regression analysis was run for each taxonomic group. Hydrozoan larvae and spiny agglutinated foraminifera showed strong negative correlations with salinity

($P<0.0001$, $R^2=0.33$ and $P=0.011$, $R^2=0.13$ respectively). Four taxa exhibited significant positive correlations with salinity: Polychaetes ($P=0.006$, $R^2=0.15$), Gastropod Veligers

FIG. 5. This graph shows the linear correlation between hydrozoan larvae (Y-axis) and salinity (X-axis).



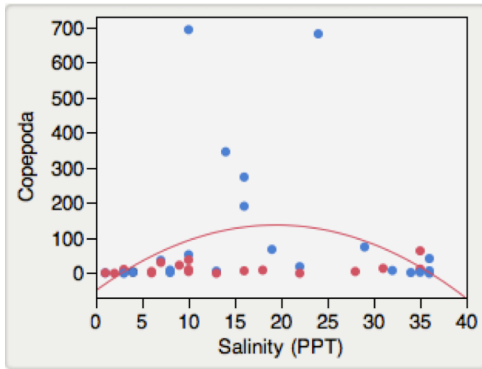


FIG. 6. This graph shows the relationship between copepods on the Y-axis and salinity levels on the X-axis.

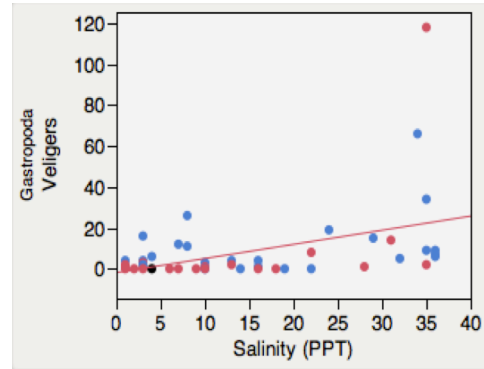


FIG. 7. This graph shows the relationship between gastropod veligers on the Y-axis and salinity levels on the X-axis.

($P=0.002$, $R^2=0.19$), bivalve veligers ($P=0.02$, $R^2=0.11$) and Miliolida foraminifera ($P=0.006$, $R^2=0.15$). Copepods and copepod eggs showed a significant second degree polynomial fit ($P=0.03$, $R^2=0.14$ and $P=0.04$, $R^2=0.13$ respectively). Figures 5, 6 and 7 show organisms with strong correlations to salinity, positive, parabolic and negative respectively.

Figures 9 and 10 show the survival rate of copepods subjected to different decreases or increases in salinity respectively. To compare the effects of different salinity shocks on copepods survival during the salinity experiment, I ran ANOVAs on the proportion of surviving copepods after 60 minutes. I then compared the different treatments with Tukey-Kramer HSD tests. The results for the salinity increase experiment showed no significant difference in the proportion of surviving copepods at different

increases in salinities after an hour ($P=0.46$, F Ratio=0.99). The results for the salinity drop experiment, however, showed highly significant differences in copepod survival between different treatments after an hour ($P=0.0003$, F Ratio=14.8). In particular the treatments with 1.5mL, 2.5mL and 5mL of freshwater added were significantly different from the control ($P=0.04$, $P=0.0003$, $P=0.002$ respectively).

Results for the light experiment are shown in figure 11 and had significant differences between the petri dishes exposed to light when compared to the control. The average ratio of copepods near the top of the petri dish (near the light source) to those on the bottom in the experimental treatment was significantly lower than that same ratio in the control treatment, which was closer to a 1:1 ratio. $P<0.0001$, DF=25.4, $t=-10.7$.

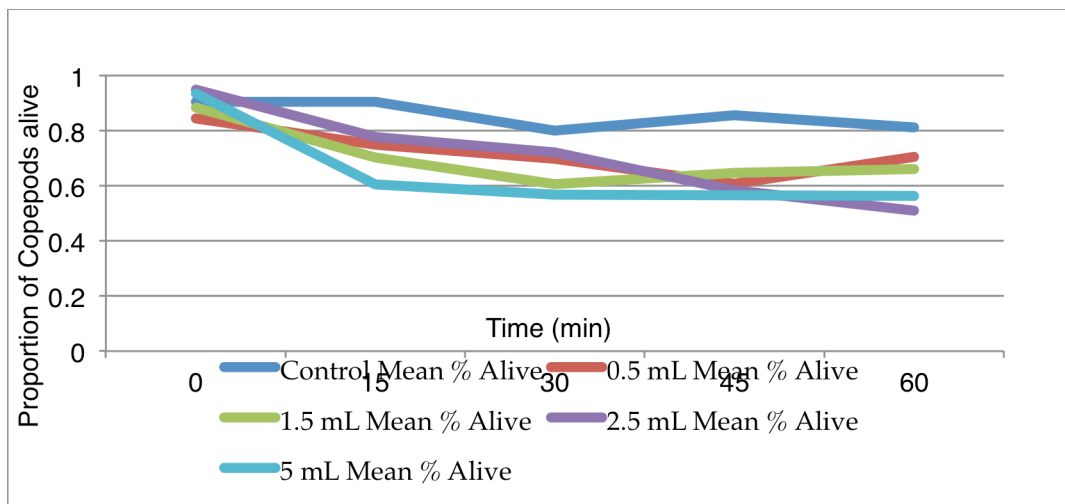


FIG. 9. This graph shows the proportion of copepods alive over time for different amounts of freshwater added.

differences between the two. This is

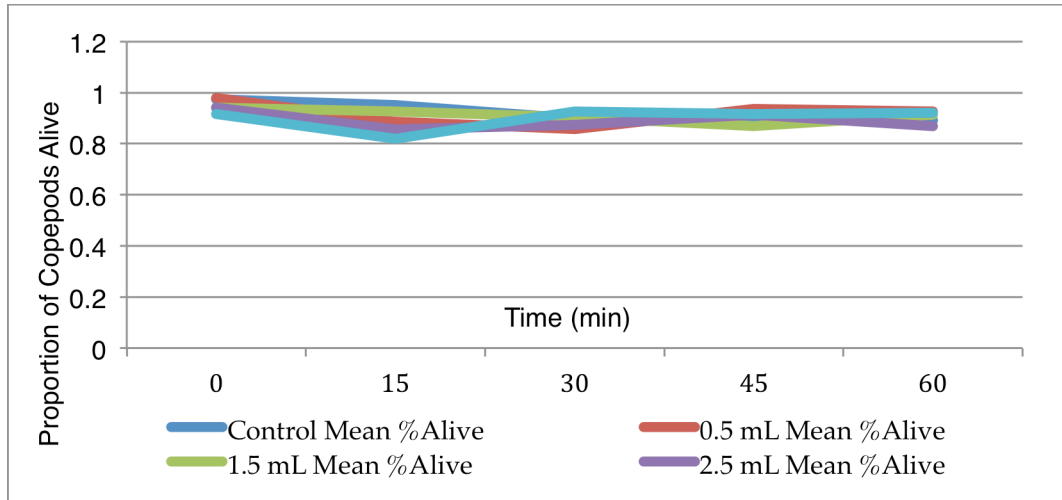


FIG. 10. This graph shows the proportion of copepods alive over time for different amounts saltwater added.

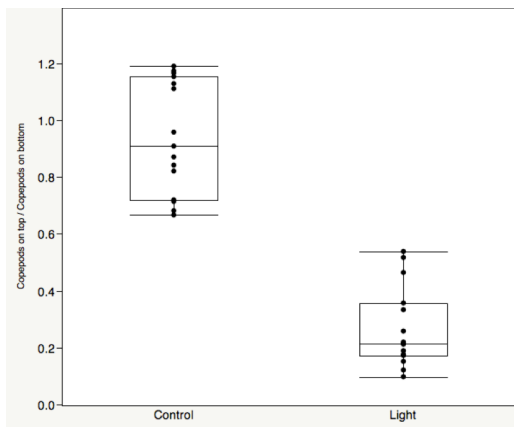


FIG. 11. This graph shows the results for the light experiment. The ratio of copepods on the top half of the petri dish to copepods on the bottom half is on the Y-axis and the different treatment categories are on the X-axis, those being the no light control and the light experiment.

DISCUSSION

The results from this study match the initial hypotheses fairly well, though there were some interesting and surprising results. Comparing the two rivers' overall communities showed that there were large

immediately obvious when the total numbers of each different variety of organisms is seen for the first time and is confirmed by the multivariate analysis. The most striking of these differences is that Pao Pao has far more copepods and copepod eggs and these are found in brackish water, not ocean water. A slightly more subtle difference is the predominance of hydrozoan larvae in the first four sites in Opunohu, making up a large part of these very similar communities. These resemble the pure freshwater site in Pao Pao in terms of community structure, except they are found further downstream. One possibility for this could be due to Opunohu River carrying more water, which might be pushing freshwater organisms downstream. Another possibility is competition or predation in Pao Pao isn't allowing as many of these hydrozoans to survive.

Individual taxon distribution proved to be somewhat of a trickier subject. Though ANOVA confirmed that there were in fact taxa differences between sites, Tukey-Kramer HSD tests showed that often that was due to one or two sites and that the rest had no significant difference. For example, site 4 in Pao Pao had significantly greater levels of polychaetes, Miliolida foraminifera and ostracods as well as copepods, with the exception of site 3 in Pao Pao. This is consistent with the findings of the multivariate analysis that show this site as

being the most different from all the rest. Hydrozoans seemed to have a greater occurrence in freshwater sites and in Opunohu, and these ANOVAs confirm this.

To get a better idea about distribution, looking at the individual correlations is also helpful. Most taxa had some significant correlation with salinity that was either positive, negative or, in the case of copepods, parabolic. This suggests that salinity is one of the major determining factors for community structure, which is consistent with the hypothesis about osmotic stress causing this distribution. However, salinity is likely not the only factor involved in how taxa and communities are distributed. Temperature, pH, nitrates and turbidity are a few among many other factors that may also play important roles.

The results of the salinity experiments were quite surprising. In a previous study, 100% of copepods tested were found to have died within 15 minutes of a 50% salinity drop. In my experiment, only around 50% died over the course of the hour of testing, and I consistently found that they were capable of surviving in freshwater for up to 12 hours. This may be due to testing different varieties of copepods, since mine were collected at an already brackish water site while the previous study used copepods from a pure saltwater environment. It seems that the term copepod is too broad to immediately make inferences about salinity tolerances, even on a small island. Interestingly though, the copepods I tested did not respond adversely to abrupt increases in salinity, which may occur in nature if they are swept out into the ocean during a storm, in the short term. These copepods seemed better adapted to salinity changes than the ones studied previously on Moorea.

The copepods also avoided bright light, which is not surprising given what is known on diel migration and lunar cycling. However, this could be important for understanding why so many copepods are found at site 3 in Pao Pao. There is a large bridge there that casts a shadow all day on a small section of the river, providing shade that the copepods may be attracted to, and it was merely a coincidence or small sample size that I found so many where I did. However, site 3 in Opunohu had a similar bridge and did not show nearly as many copepods and site 4 in Pao Pao did not have a significantly different number from site 3, so it is likely that there is

some other difference between the rivers or the bays.

Understanding zooplankton distributions and how different groups respond to changes can be important because of their bioindicator capabilities since these changes can be subtle. For example, the ratio of nematodes to copepods has been shown to be higher when pollution levels are higher (Raffaelli, 1981). This could mean that Opunohu, though less developed, may have more polluted water flowing out of the river and that Pao Pao is relatively clean because of the high number of copepods. One study showed a significant correlation between freshwater hydrozoan larvae density and percent cloud cover, suggesting a response to decreasing light conditions (Harrel, 2002). It could be that parts of Opunohu simply receives less sunlight because of mountains, such as Rotui, are blocking the sun for much of the day and this manifests itself as different biological communities.

Conclusion

I found that Pao Pao and Opunohu have significantly different zooplankton communities along their freshwater gradients and these communities generally correlate quite strongly with salinity levels. This difference suggests to me that there are other important variables that explain the observed differences. In addition, at least one variety of copepod on Moorea can tolerate brackish or even freshwater for extended periods and they show active light evasion supporting the theory that diel migration occurs due to light cues.

A topic for future study could be size comparisons of Copepods found in brackish water and those found in saltwater. I noticed that the copepods captured in brackish water might have been smaller than the oceanic ones on average. It could be that adaptations to variable environments have high metabolic costs, which would explain size variations, and in a changing world this may have drastic impacts. Certain varieties of copepods deal with osmotic stress by regulating free amino acid levels in their cells, but this is energetically costly, consisting of up to 11% of daily energy use (Goolish and Burton, 1989). Phylogenies showing how freshwater tolerant copepods arrived on a volcanic island thousands of miles from the mainland could also be interesting.

It is difficult to fully appreciate the complexity of zooplankton communities. They are very small, very diverse and very

dynamic, responding to stresses and stimuli very quickly. This means that not only are the effects from large storms or algal blooms easily observed, but also even more subtle daily cycles, lunar cycles and seasonal cycles based on predictable conditions can be witnessed. It would be possible to study a very small area over a long period and still find surprising results. Because only five samplings were made in each bay, the high variances in my results are not too surprising. To achieve a fuller understanding of zooplankton community dynamics, more samples over a longer period would be needed. However, given their importance in ecosystems, their usefulness as bioindicators and their diversity as a whole, I believe further study is warranted with much left to be discovered about the inner working of this ecosystem.

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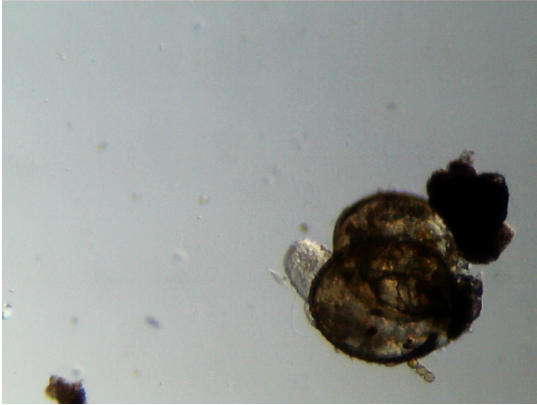
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APPENDIX A

Below are photos of the different organisms I found during my plankton tows with their taxonomic names in alphabetical order.



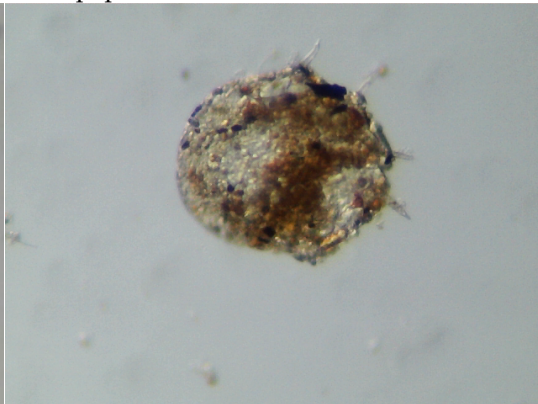
Bivalvia (veliger) (indet.)



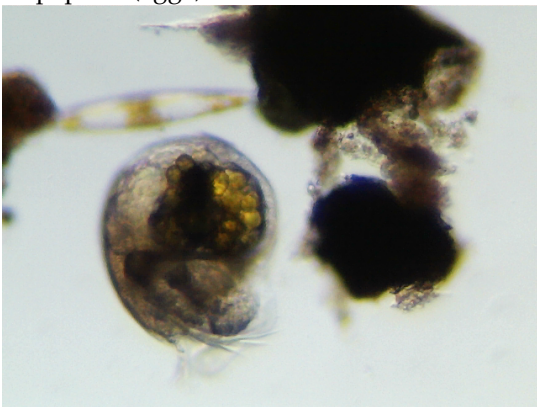
Copepoda



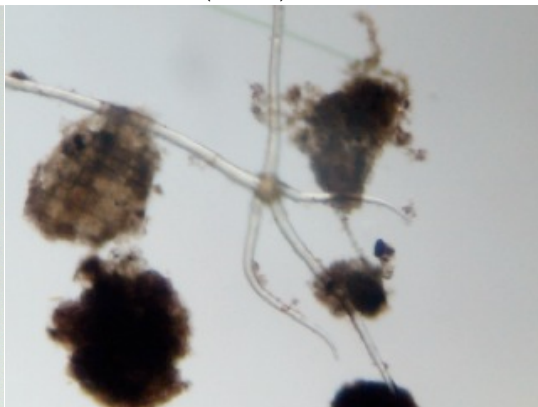
Copepoda (eggs)



Foraminifera (indet.)



Gastropoda (veliger) (indet.)



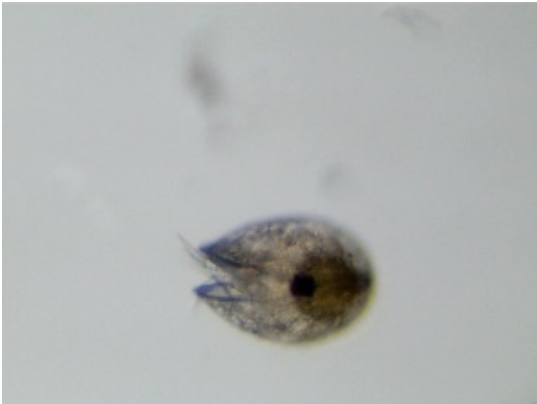
Hydrozoa (larvae) (indet.)



Miliolida (indet.)



Nematoda (indet.)



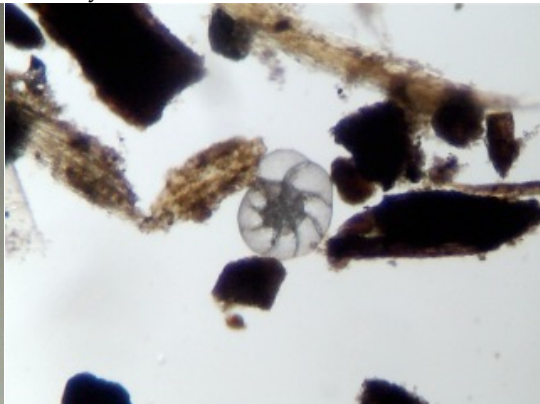
Ostracoda (indet.)



Platyhelminthes (indet.)



Polychaeta (larvae) (indet.)



Rotaliida (indet.)

APPENDIX B

TABLE 1. Coordinate information for each site sampled at is located in Table 1

Site	Approximate Distance Upstream	Coordinates
Pao Pao 1	1000 m	-17.515541, -149.82193
Pao Pao 2	300 m	-17.509023, -149.821898
Pao Pao 3	100 m	-17.507187, -149.82186
Pao Pao 4	0 m	-17.506501, -149.821726
Pao Pao 5	-1500 m	-17.49168, -149.823518
Opunohu 1	600 m	-17.520275, -149.846144
Opunohu 2	200 m	-17.516992, -149.848286
Opunohu 3	75 m	-17.516258, -149.849003
Opunohu 4	0 m	-17.515802, -149.849668
Opunohu 5	-400 m	-17.511542, -149.850062