

RESPIRATION RESPONSE OF EPIPELAGIC MARINE COPEPODS TO CHANGES IN WATER TEMPERATURE AND SALINITY

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Abstract. Copepods play a fundamental role in maintaining the health of both marine and freshwater ecosystems around the globe. Estuaries are particularly compelling environments to study the ecological function of copepods due to their significant abundance and productivity in an environment with dynamic temperature and salinity gradients. This study aims to better understand the respiratory physiology for two families of copepods occurring in an estuary on the island of Moorea, French Polynesia. This laboratory study measuring the respiration rate of copepods under changing variables of water temperature and salinity aims to provide useful information on the biological traits and performances of copepods by examining their respiratory physiology. Copepods for this study were collected in two locations with measured salinity differences and respirometry experiments were performed under conditions approximating those in the estuary of Cook's Bay. The results revealed that the two families of copepods do have a respiration response between a range of salinities from 10ppt to 40ppt. However, the copepods did not show a significant difference in respiration rate between the ambient temperature of 27.5°C and 30°C. There was no difference in respiration rates between families exposed to a certain salinity, suggesting that one family may not be more tolerant to certain environmental conditions than the other.

Key words: Zooplankton; Copepods; Clausocalanidae; Calanidae; Marine ecosystems; Moorea, French Polynesia; Tropical estuary; Salinity; Temperature; Respiratory Physiology; Metabolism; Tolerance; Performance

INTRODUCTION

Copepods are the dominant forms of the marine plankton and constitute the secondary producers in the marine environments that play a fundamental role in the trophodynamics of oceans (Smith and Johnson 1996). Phytoplankton support primary consumers such as zooplankton, which then support a host of zooplanktivorous organisms from fishes to whales.

The respiration of crustaceans, including copepods, is similar to that of other animals and is comprised of three main phases (Watermen 1960). The first is their requirement set by the metabolic need to eliminate carbon dioxide and the aerobic necessity to provide gaseous oxygen. The second is the problem of external and internal respiratory gas exchange between the animal and its environment, and third being the internal mechanism for transporting oxygen and carbon dioxide between the respiratory surface and the metabolizing protoplasm (Watermen 1960). Changes in environmental conditions (e.g.,

temperature) may lead to disruptions in any one of these pathways (Watermen 1960). Moreover, a copepod's respiration is significantly affected by dissolved oxygen saturation of water because copepods lack respiratory organs such as gills and their respiration is determined by the gradient of oxygen concentration through body integuments (Wolvekamp & Waterman 1960).

Estuaries, partially enclosed water systems with a river input and an open connection to the ocean (Pritchard 1967), are productive habitats that can support a large number of organisms. This is due mainly to high primary production, largely the production of phytoplankton (DeBoyd et al. 2013). Organisms in estuaries are subject to tremendous osmotic stresses ranging from regular tidal fluctuations to massive freshwater inputs during floods and an increase of salinity during a drought. In a tropical island estuary, the fluctuation of salinity as a result of freshwater from river run-off and rain activity is an important factor affecting zooplankton communities (Avois-Jacquet et al. 2000). In addition to

salinity, water temperature is another dynamic factor of a tropical estuary ecosystem. A study of a tropical estuary on the west coast of India found that water temperature variation from 30°C to 20°C in the winter was an important factor affecting the disappearance of microorganisms (Chandran and Hatha 2005). Seasonal changes in temperature and precipitation may result in cooler freshwater inputs into warmer marine environments. Preliminary measurements of water characteristics confirmed that there was salinity gradient in Cook's Bay as well as variation in water temperature. Temperature has profound effects on biological functions at levels of organization from molecules to ecosystems, and is thus thought to be one of the critical abiotic factors influencing the distribution and abundance of organisms (Schulte et al. 2011). The zone of tolerance for a given species is often correlated with aspects of the species' thermal environment in nature (Stillman 2002, Chown et al. 2004, 2010, Clusella-Trullas et al. 2011, Sunday et al. 2011). Indeed, temperature may be the principal factor in regulating metabolism for many marine invertebrates (Sumich 1988). As an example, a crustacean's locomotor activity, which includes swimming and feeding, has been demonstrated to have a direct relationship to temperature (Watermen 1960).

Osmoregulation and metabolism have a notable importance for being related to the distribution of crustaceans and zooplankton in different environments (Sumich 1988). Different species of marine copepods have been examined to have varying salinity tolerances, or abilities to withstand dilution (Lutz 1986). Respiratory metabolism for crustaceans has been found to adjust with changes in salinity (Lance 1964). Respiratory metabolism for copepods will be directly influenced by the amount of oxygen that can dissolve in water, and as salinity increases the amount of dissolved oxygen decreases. A study on zooplankton assemblage in Opunohu and Cook's Bay suggests that salinity is a major component influencing the abundance of copepods in estuarine systems (Mendez 2012).

Zooplankton can be good environmental indicators due to their short life cycles and rapid response to environmental changes and stresses (Attayde and Bozelli 1998). A study on copepod biodiversity in the California Current found

that the presence of certain copepod species was directly correlated with changes in water temperature and salinity (Hooff and Peterson 2006). In marine systems, temperature and salinity changes impact the population sizes of copepods and zooplankton, which in turn may lead to a suite of effects on an entire marine ecosystem (Pitermen 2012). Further scientific knowledge of environmental sensitivity of respiratory physiology for copepods will provide useful information for the organism's biological traits and performances under varying conditions of temperature and salinity and provide improved understanding of the conditions that individual families can tolerate. Much less is known about the respiration of consumers in the ocean than about the photosynthesizing producers (Pomeroy 1974).

The overall goal of this study was to explore how the respiratory physiology of copepods is influenced by temperature and salinity, using copepods collected along a longitudinal gradient of conditions in Cook's Bay (Moorea, French Polynesia), where water characteristics of salinity and temperature vary due to the extent of ocean and freshwater influences. Specifically, I will address the following questions using a laboratory study of copepod respiration rates: (1) Does temperature lead to a significant change in respiration rate for either of the two families? (2) How do the various treatments of salinities affect the respiration rate of copepods? (3) Does the interaction of temperature and salinity lead to a significant respiration response for either family of interest? (4) Will one family of copepod display a higher tolerance to changes in water temperature and salinity than the other? (5) Does the maximum performance, as determined in the laboratory, match the conditions where the organism was collected in nature? I hypothesized that (1) respiration rates will significantly differ between ambient ocean water temperature of 27.5°C and the warmer condition of 30°C for both families of copepod. (2) Respiration rate would increase in response to stressful saline conditions for both copepod families. (3) The interaction of temperature and salinity may result in an additive respiration response. (4) The family more adapted to freshwater or saline environments would have a lower respiration rate at their salinity of preference. (5) Respiration rates will determine copepods

to have maximum performance in a salinity and temperature closest to that of the environment they were collected.

METHODS

Copepod Collections

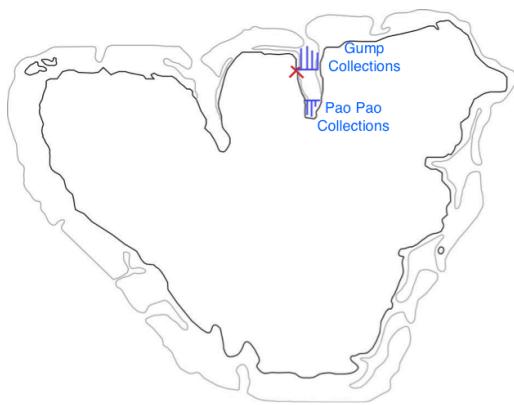


FIG. 1. Sites sampled in this study.

This study consisted of two collection sites, both of which were in Cook's Bay located on Moorea, French Polynesia. These sites were selected based on salinity gradients observed in preliminary water testing. The first collection of copepods used for respirometry took place October 12th, 2015, which was the first new moon. The last collection was performed on November 22nd, 2015. Based on salinity differences measured during a preliminary study, all collections in Cook's Bay would take place inshore of a buoy marker near the Pao Pao river mouth, and seaward of the Gump station.

Sampling

A variety of methods were used for copepod collection, the most successful and easily accessible of which was immediate off the dock at the Gump Station. These collections were performed using a dive light to attract copepods and plankton tow to collect between hours of 8 to 10 PM. A kayak was used for Plankton tows inshore of a buoy marker closest to Pao Pao, and seaward of the Farepotu at the Gump Station between the hours of 4:00-5:30 PM. Collection times remained consistent to account for the possibility of vertical migration on a daily cycle, which is a common occurrence in freshwater and marine zooplankton

(Hutchinson, 1967; Bainbridge, 1961). Each kayak collection included sampling of both locations. Once collected, the plankton in that sample would be transferred to a holding container. This holding container was aerated using an air stone, and consisted of the estuary water from the location of which the copepod was collected. Respiration measurements were not performed until 12 hours after collection and holding in aerated containers.

Fluorescence-based Oxygen Measurements

The Senor Dish Reader (SDR) non-invasively detects oxygen concentration through a sensor spot fixed at the bottom of each well. For each measurement of oxygen concentration the luminescent sensor spot is excited by light and the lifetime of the luminescence is dependent on the partial pressure of oxygen in the sealed well containing the copepod (Koster 2008). Oxygen concentration data was recorded on an interval of 15 seconds for 30 minutes. Respiration rate for each copepod in a well was calculated from the slope of the line created by the decrease in oxygen concentration over time. The measurement for respiration rate was then divided by the length of the copepod to control for size. After dividing by length, individual respiration rates of the copepods were determined by subtracting the average rates of the blanks from the individual respiration rates to eliminate net oxygen consumption/production by bacteria and microalgae (Koster 2008).

The SDR Plate has a total of 24 wells, and for each experiment with changing variables of temperature and salinity four blanks were used. Blanks were placed in wells A6, B6, C6, and D6. Control experiments had all wells at a constant salinity and temperature corresponding to the temperature and salinity at which the copepods were collected. For experiments manipulating the variable of salinity, each of the four blanks had different ratio of fresh to seawater. Each blank of varying salinities corresponds to a row, 1-5 of copepods, which are all held at the same salinity as the blank. For example, row A would consist of five copepods and a blank at measured salinity of 100% seawater. Row B would also hold five copepods and a blank at a measured salinity from a solution of 20% freshwater. Row C would consist of 40% freshwater, and Row D with 80%



FIG. 2. Sensor Dish Reader rows and columns.

freshwater. These solutions were based on salinity values recorded in Cook's Bay. Copepods were placed in petri dishes containing these four salinities where they were removed using a pipette and loaded into the wells just before running the experiment. A more accurate measurement for salinity was obtained by using a refractometer for each of the ratios of fresh to saltwater. Temperature was manipulated according to trial, but within each trial temperature remained constant at either 27.5°C or 30°C with the use of a water bath pump to keep water circulating around the sealed vessels containing the copepods. A thermometer placed in the water bath was used to measure temperature. Each well was loaded with one copepod and a total of 20 copepods could be loaded onto the plate. The rest of the wells in that row contained one copepod and 750 micro liters of the desired salinity. This would allow for a positive meniscus of solution and copepod in each well, and for an airtight seal of the lids. Each copepod used for respirometry was photographed for measurement and identification. Each one of these photographs would correspond to a well on the oxodish so the length and ID of the copepod could be matched up to its individual respiration rate.

Taxonomic Identification of Copepods

Copepods were identified to the family taxonomic level using an interactive key for

families of the order Calanoidea using DELTA system and INTKEY (Dallwitz 2000, Bradford 2002). Identification to the lowest taxonomic level was used to reduce the error of misidentification.

Data Analyses

A two-way ANOVA in combination with a Tukey-HSD was used to make multiple comparisons of means for respiration rates to the interactive variables of temperature and salinity. A one-way ANOVA was used to compare the averaged respiration rates between the ranges of salinities and two temperatures tested. Paired t-tests were used to determine if there was a significant difference in the averaged respiration rates between families at a certain salinity treatment (Ambrose, 2007) (R team 2015).

RESULTS

Higher salinities led to a significantly lower respiration rate for the Clausocalanidae (ANOVA, $F(12, 67) = 3.43, p < 0.001$). A post hoc test revealed significant difference ($p < 0.05$) for averaged respiration rates between the salinities 10-29, 10-34, 12-34, and 17-34 parts per thousand (Fig. 3). There was an 82% difference in respiration rate between salinities 10-29, 79% for 10-34, 79% for 12-34, and a 51% difference between salinities 34 and 17 (Table 1). The effect of salinity on respiration rate approached significance for the Clausocalanidae between salinities 10-39 (72% difference, $p=0.066$) and 12-29 (82% difference, $p=0.072$) (Fig. 3, Table 1).

Post hoc test on the Calanidae revealed a significant difference ($p < 0.05$) in respiration rate between the salinities of 17-34 parts per thousand (27% difference, $p < 0.01$) (Fig. 4, Table 2). A significant difference for respiration rate was recorded between high and low salinities for the Calanidae (ANOVA, $F(8, 30) = 2.54, p < 0.05$).

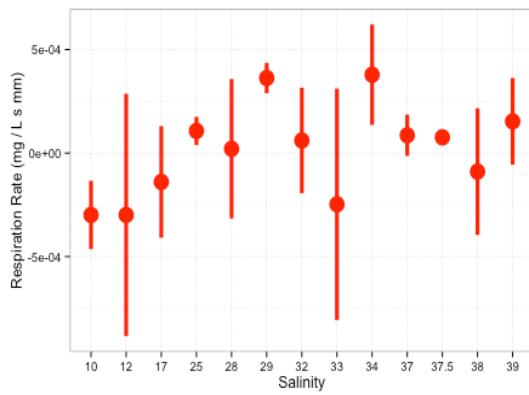


FIG. 3. Dots are the means of respiration rates measured at the range of salinities for the Copepod family Clausocalanidae. Error bars for all the following figures are +/- the standard deviation.

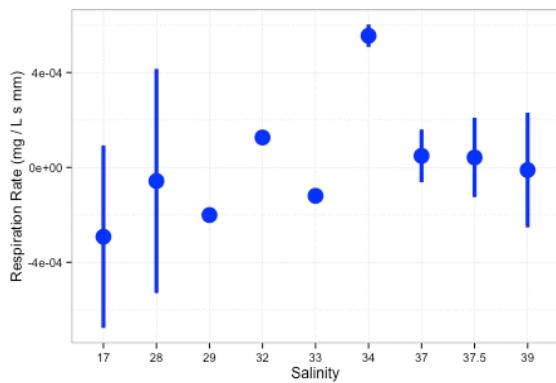


FIG. 4. Mean respiration rates at different treatments of salinity for the Calanidae.

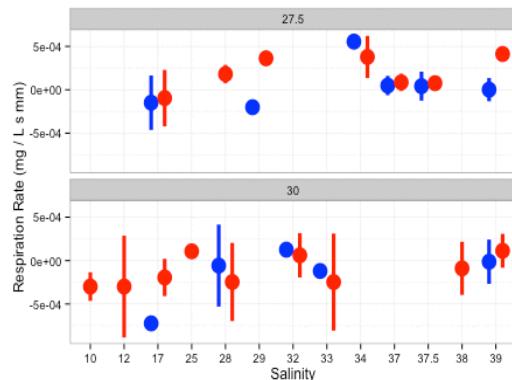


FIG. 5. Mean respiration rates with the interaction of salinity and temperature for both families of copepods (Red=Clausocalanidae) (Blue=Calanidae).

TABLE 1. Mean of respiration rates for the Clausocalanidae

Salinity	Temperature	Respiration
17	27.5	-9.55E-05
28	27.5	0.000180863
29	27.5	0.000362676
34	27.5	0.000378393
37	27.5	8.59E-05
37.5	27.5	7.60E-05
39	27.5	0.000412155
10	30	-0.000298918
12	30	-0.000298721
17	30	-0.000194225
25	30	0.000106962
28	30	-0.00024625
32	30	6.10E-05
33	30	-0.000247295
38	30	-8.95E-05
39	30	0.000113117

TABLE 2. Means of respiration rates for the Calanidae

Salinity	Temperature	Respiration
17	27.5	-0.000148583
29	27.5	-0.000200914
34	27.5	0.000554766
37	27.5	4.87E-05
37.5	27.5	4.19E-05
39	27.5	1.40E-06
17	30	-0.000723053
28	30	-5.73E-05
32	30	0.000126087
33	30	-0.000119757
39	30	-1.28E-05

Respiration rate for both families, Calanidae (ANOVA, $F(1,30) = 1.57$, $p > 0.05$) Clausocalanidae (ANOVA, $F(1,67) = 5.89$, $p > 0.05$) was insignificant when compared between the temperatures of 27.5 and 30 degrees Celsius (Fig. 5, Table 1 and 2).

There was no significant difference in respiration rate for the Clausocalanidae (ANOVA, $F(2,67) = 0.81$, $p > 0.05$) and the Calanidae (ANOVA, $F(1,30) = 3.17$, $p > 0.05$) between the interactions of salinity and temperature (Fig. 5). However, a post hoc found that at 30°C the respiration rate for the

Clausocalanidae treated at a salinity of 10ppt, significantly differed from its respiration rate at 27.5°C and salinity treatment of 34ppt (79% difference, $p < 0.05$). This significant occurrence was calculated again for the Clausocalanidae at 30°C with a salinity of 12ppt and 27.5°C with salinity 34ppt (79% difference, $p < 0.05$) (Fig. 5). For the Calanidae, a significant difference in respiration rate was calculated once for the temperature 30°C at salinity 17ppt and 27.5°C with salinity 34ppt (27% difference, $p < 0.01$) (Fig 5., Table 2).

There was no significant difference in respiration rates between the Calanidae and Clausocalanidae ($p > 0.05$) for each treatment of salinity when looking at copepods collected from the Pao Pao location (Fig.6,

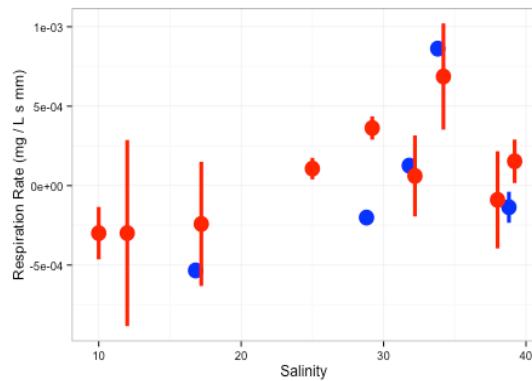


FIG. 6. Comparing respiration rates between families for copepods collected from Pao Pao.

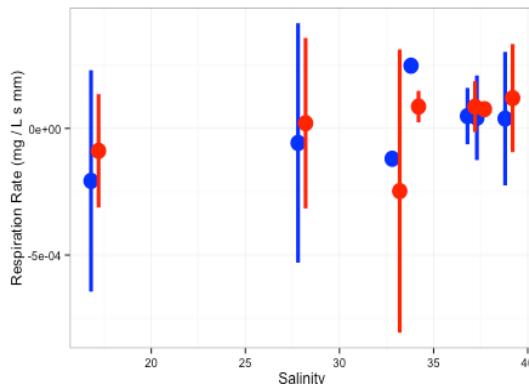


FIG. 7. Comparing respiration rates between families for copepods collected at the Gump Station.

Appendix B Table 4) and the Gump Station location (Fig.7, Appendix B Table 3).

DISCUSSION

Considering that water temperature has been recorded to effect the respiration response of crustaceans while changing the amount of dissolved oxygen available in the water (Watermen 1960), I hypothesized that a 2.5°C increase in water temperature from the ambient ocean temperature found at the Gump Station would result in a significant change in respiration rate for the copepods. Instead, the results from this laboratory experiment suggest that a 2.5°C increase in water temperature does not lead to a change in the mean respiration rate for either of the families studied. I believe that this result may have been obtained because the copepods were separated from the water bath by a sealed container that may have insulated the temperature within the well for the short period oxygen concentrations were measured. I believe that copepods directly exposed to a 2.5°C increase in water temperature in nature would have a much different respiratory response from the result obtained from the limitations of the laboratory set up. Instead of manipulating water temperature with the use of a water bath, more accurate results may have been obtained by raising the temperature of the water being placed directly in the wells. Conover (1961) has found that the copepod species *Calanus hyperboreus* almost perfectly acclimates its oxygen uptake over an experimental range commensurate with environmental temperatures. If this finding for a different species of Calanoida holds true for the two families studied in this experiment, then this may be a reasonable explanation for why there was no significant difference in respiration rates between the two temperatures tested. If oxygen consumption can be acclimated, then perhaps it is a physiological processes other than respiration that needs to be adjusted to acclimate to temperature change. Perhaps other forms of measuring the metabolic rate of copepods will reveal a physiological response to water temperature changes.

Salinity variation and the gradient created by the Pao Pao River mouth are very significant in the estuarine system of Cooks Bay. For example, on one occasion of heavy rain lasting for about four to five hours the

surface salinity in front of the Gump station was measured to be as low as 32ppt. Typically the salinity at this location ranged from 35-38ppt. Many small runoffs deposited freshwater around the bay as well as increased the inputs from the Pao Pao River. Plankton tows were not conducted on this day and were highly unsuccessful the following day with little to no copepods being caught. In my preliminary collections of copepods I found that the abundance of copepods of any species seemed to be concentrated in the bay as opposed to the passes or lagoon nearest the bay. Therefore the conditions within the bay seemed to be more conducive to epipelagic planktonic production and abundance similar to the findings presented by two former students of the class (Mendez 2012 and Piterman 2012).

For both families of copepods, respiration rate increased as salinity decreased supporting the original hypothesis. This finding suggests that the metabolic rate in terms of respiration for copepods may also increase when exposed to stressful salinities. It is also possible that an increase of respiration rate was observed at lower salinities because more dissolved oxygen was available for consumption than at higher salinities. With an increase of dissolved oxygen concentrations in the water, it is possible that copepods may increase their respiration rate at these low salinities to cope or tolerate the osmotic stresses. The mean respiration rate at the salinity of 34 for both families was measured to be a positive value, meaning that oxygen concentration did not decrease over time. If copepods are not consuming oxygen over time, then either the blank has a higher respiration rate than the copepod, or the copepod is producing oxygen. One explanation for this result is that the respiratory rate of the copepod is so low at that salinity that the microorganisms in the blank are consuming more oxygen. The total respiratory rate of copepods is so low that it is necessary to concentrate the organisms from a large volume of water in order to achieve enough sensitivity to measure changes in dissolved oxygen or any other parameter of respiration in a short time (Pomeroy 1974). Any concentration process of this sort has inevitable uncertainties and difficulties, which may have resulted in the positive respiration rate measured in this experiment that biologically does not make sense.

A salinity of 34 is a very common salinity for marine environments and close to the salinity of the water for copepods collected from the Gump station. The data suggest that respiration rate decreased and more commonly became positive with treatments of salinity that were closest to the salinity in which the copepods were collected.

Since temperature was calculated to have an insignificant effect on respiration rate, then salinity was the only variable contributing to the significant measurements of respiration between the interactive effects of salinity and temperature. These results also differed from the original hypothesis that the interaction of temperature and salinity would have an additive effect for respiration rate, meaning that the respiration rate measured at one salinity would increase between the two temperatures tested. Originally it was thought that looking at the interaction of salinity and temperature would simulate environmental conditions found in an estuary more accurately than looking at just one of the independent variables and its effect on respiration alone. The results from the interaction of the two independent variables suggest that temperature had a neutral effect on respiration rate across the range of salinities tested in the laboratory.

Lastly, this experiment compared the respiration rate of both the copepod families collected across the range of salinities tested. What I found was that neither of the families seemed to outperform one another in terms of respiration at either the low or high salinities tested. This result suggests that one of the families is not more tolerant to a certain salinity than the other. Although the copepods were collected in locations where salinity differed, both of the families could be collected in either location. Since both of the copepods could be collected in either location, it would make sense that their respiration rates did not differ in the laboratory because one did not display to be better adapted to more freshwater or saline conditions in the field than the other.

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APPENDIX A



- Rostral margin extends into 1 blunt protrusion; or extends into 2 blunt protrusions; or not extended (Grieve 2012)
- *Cephalosome and pedigerous somite 1 are separate*
- *Pedigerous somites 4 and 5 are fused or partly fused*
- *Posterior corners of prosome in lateral view are bluntly rounded*
- *Caudal rami is separate from the anal somite; or with one fused to anal somite*
- The surfaces of *Legs 2-4* are weakly spinulose or naked
- Depth distribution: epipelagic (0-500 m)



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- Rostral margin extends into 2 points or extends into 1 point (Grieve 2012)
- *Cephalosome and pedigerous somite 1* are separate
- *Pedigerous somites 4 and 5* are fused or partly fused
- *Leg 5* is present
- Depth distribution: epipelagic (0-500 m)

APPENDIX B

TABLE 4. Comparing Mean respiration rate between families according to salinity for copepods collected near Pao Pao.

Salinity	Family	N	Slope	sd
17	Calanidae	1	0.000534035	NA
17	Clausocalanidae	3	0.000241137	0.000390937
29	Calanidae	1	0.000200914	NA
29	Clausocalanidae	3	0.000362676	7.34E-05
32	Calanidae	1	0.000126087	NA
32	Clausocalanidae	8	6.10E-05	0.000254822
34	Calanidae	1	0.000862029	NA
34	Clausocalanidae	3	0.000686848	0.000334486
39	Calanidae	3	0.000135955	9.78E-05
39	Clausocalanidae	6	0.00015331	0.000136896

TABLE 3. Comparing Mean respiration rate between families according to salinity for copepods collected at the Gump Station.

Salinity	Family	N	Slope	sd
17	Calanidae	3	0.000207204	0.000437021
17	Clausocalanidae	6	-8.85E-05	0.000223726
28	Calanidae	2	-5.73E-05	0.000472597
28	Clausocalanidae	8	2.07E-05	0.000336638
33	Calanidae	1	0.000119757	NA
33	Clausocalanidae	4	0.000247295	0.000559156
34	Calanidae	1	0.000247503	NA
34	Clausocalanidae	2	8.62E-05	6.24E-05
37	Calanidae	9	4.87E-05	0.000111361
37	Clausocalanidae	8	8.59E-05	0.000100229
37.5	Calanidae	3	4.19E-05	0.000167114
37.5	Clausocalanidae	1	7.60E-05	NA
39	Calanidae	15	3.86E-05	0.000263633
39	Clausocalanidae	9	0.000119628	0.000213471