AN ANALYSIS OF MARINE PRIMARY PRODUCTION: 
CHARACTERIZING SPATIAL VARIATION OF BENTHIC 
AND PLANKTONIC MICROBIAL ACTIVITY ALONG 
MARGINS OF PAO PAO BAY, MOOREA, FRENCH 
POLYNESIA

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Abstract: Acting as the direct interface between the organic and inorganic world, photosynthetic microbes are major drivers for energy production and transfer into food webs of all major marine ecosystems. Being a major pillar for stability of marine life, the productivity of microbial communities is of great interest across spatial and temporal contexts. At present, many marine systems are generally understood through broad application of dynamics observed in areas which have been heavily investigated. These current understandings, however significant in quantifying and analyzing trophic dynamics and biogeochemical cycling, carry certain assumptions of uniformity across the regions that resulting global models describe. Such uniformity across regions, generally classified by factors such as temperature and nutrient availability, is not the case, as systems such as lagoons and estuaries carry nuanced features which provide variability in the many factors which drive them. Thus, a certain level of error is intrinsic to current models of global and region-specific primary productivity, in particular. Furthermore, these models of present day microbial production of are tools for predicting how projected shifts in global temperature, ocean acidity, etc. will impact the systems in place, and provide means for understanding how these systems will react to climate change. In particular need of more thorough investigation are systems in tropical regions, wherein consensus of unproductive microbial communities has left a whole in the primary literature. Overlooked by most considerations of tropical microbial activity is the benthic contribution to system-wide production. Studies conducted in better understood systems have found significant contributions of benthic photosynthesis to systems driven by microbial activity. Thus, in order to fine-tune understanding of microbial activity in a lesser studied system, a study of benthic and pelagic photosynthetic activity was conducted in Pao Pao Bay, Moorea, French Polynesia. Within Pao Pao Bay, strong gradients exist along the margins of an estuary fed by a mountainous tropical stream. Said gradient was exploited to investigate spatial variation in microbial photosynthetic activity among benthic and pelagic communities. It was found that both communities vary in productivity with respect to these gradients and their geospatial distribution. Most interestingly, it was found that benthic communities contribute largely to primary production throughout the entire bay, especially in more classically tropical waters relatively nutrient deplete. With these findings, further research is of interest to expand global understandings of primary productivity beneath the water column and into lesser studied tropical microbial communities.

Key words: photosynthesis, algae, primary production, microbes, French Polynesia, estuary

INTRODUCTION

At the foundation of all food webs is the primary production of organic carbon by plants, algae and cyanobacteria. Photosynthetic organisms, terrestrial and aquatic, are the primary energy input which drives trophic ecosystem dynamics across all scales (Hoegh-Guldberg 2010). Therefore, driven by concerns about anthropogenic disruption to biogeochemical cycling, much research into dynamics of carbon processing has been conducted (Clausing 2016, Bellinger, et al. 2006, MacIntyre, et al. 1996, Fielding, 1988,
Wilkins-Smith & Piedrahita 1988, Azov 1981). Though a significant proportion of primary production is conducted in terrestrial plant communities, an equally significant proportion of productivity exists within marine ecosystems (F.P. Chavez, 2011). Given the importance of the ocean’s role in carbon dynamics and understanding of global climate change trends, it is surprising to note a disproportionately small amount of published research concerning marine environments (~5%), when compared to research in terrestrial systems (Hoegh-Guldberg 2010). Furthermore, the majority of marine productivity research involves nutrient-rich environments, e.g. the coasts of California and South Africa, in relation to understanding atmospheric-photosynthetic interactions (Clausing 2016, Bellinger, et al. 2006, Maclntyre, et al. 1996, Fielding, 1988, Wilkins-Smith & Piedrahita 1988, Azov 1981). With global trend toward increased ocean temperatures, however, an expanded understanding of microalgal communities in warmer, less nutrient-rich waters, is necessary for predicting implications of global climate change. Nutrient-deplete water systems need to be studied with respect to projected climate change conditions in order to have a rounder understanding of the future of our oceans.

Furthermore, a small subset of research concerning marine productivity extends beneath the water column into the upper centimeters of shallow water sediments (Garrigue 1998, Underwood & Paterson 1993, Fielding 1988). One of the first studies done with this perspective, done in Langebaan Lagoon, on the west coast of South Africa, found nearly a fourth of the production in the lagoon to be contributed by benthic algae (Fielding, 1988). That study, and others, points to benthic microalgal communities as an important contributor to processing of carbon in marine environments, typically attributed mostly to planktonic activity (Garrigue 1998, Fielding 1988). Therefore, an increased understanding of the role of benthic microalgae in more systems would be of great interest. Spatial variability in benthic production across Langebaan Lagoon observed by Fielding (1988) was correlated strongly with sediment type (i.e. size).

Benthic communities, and their pelagic counterparts, are strong reflections of trophic status and overall stability of a marine system, needing more quantitative study (Sany 2013). When the intertwined effects of predicted environmental shifts across the marine environment (i.e. high pCO2, rising ocean temperatures, ocean acidification, enhanced stratification, increased light intensity, etc.) are considered, the need to study benthic communities is accentuated (Gao, et al. 2012, *Gao, et al. 2012*).

The present study aimed understand the role of benthic photosynthetic communities play in overall primary production of tropical waters within Pao Pao Bay, Moorea, French Polynesia. Furthermore, this study aimed to characterize variability in microbial production in the benthos and the water column, correlated with gradients of three abiotic factors presumed under observation. Two of these gradients were substantiated by a tangentially related study conducted by Harbaugh (2000), wherein several inputs to Pao Pao bay, namely nutrient concentrations and sediments, were quantified and observed. These gradients were then considered qualitatively, along with quantitative consideration of sediment variability along the bay, in selection of site selection and design of this study. The secondary goal of this study was to explore the synergistic effect of light intensity and projected pCO2 concentrations on the productivity and respiration dynamics of microalgae living in the column of Cook’s Bay. The following specific questions were addressed:

1) In light of a relatively nutrient deplete water column surrounding Moorea, how might the benthic photosynthetic community differ in its rate of primary production when compared to the water column above? It was hypothesized that significantly higher rates of production will be found within the top 2 cm of the benthic community, as sediment deposition from streams will likely concentrate nutrients in the benthos.

2) Does this productivity (benthic & planktonic) vary across the length of Cook’s Bay? It was hypothesized that a higher ratio of benthic ; overall production will be found at sites more distant from the Pao Pao river output.

3) How does the mean ratio of net benthic productivity compare to those documented in more productive regions of the ocean? It was hypothesized that there will be higher a mean benthic productivity ratio in this tropical system than reported in temperate South Africa.

4) Is there a relationship between sediment type and productivity? It was hypothesized that sediments with greater
surface area (smaller particulate size) will be more productive.

(5) How might the community productivity change when exposed to predicted high pCO2 concentrations and various light exposure regimes? It was hypothesized that there will be a decrease in productivity of communities incubated in high pCO2 water under intense light, as compared to those in ambient water with lower light availability.

METHODS

Study sites

This study was conducted along the western margin of Cook’s Bay, Moorea, French Polynesia. Three study sites were selected in locations along Cook’s Bay, dependent primarily upon documented and expected abiotic gradients (nutrient concentrations, turbidity, and sediment size). Both gradients of nutrient concentrations and turbidity of the water column were presumed based upon prior observations, however, a gradient in sediment size was observed and quantified in this study.

FIG. 1. Map of three field sites located along Pao Pao Bay, Moorea, French Polynesia. Note orientation along Western margin of the bay and unequal distance from river outlet at head of bay, due to limited access to waterfront.

Field study to assess benthic productivity and spatial variation

At each of these sites, four jars (~1.2L) were filled at two locations in the water column; two were filled with seawater collected at 0.5 m below the surface, and two were filled with 50 mL of sediment (scraped into a falcon tube) with water collected as close to the benthos as possible (1.0 m). Prior to deploying the containers, all samples were quickly tested for dissolved oxygen concentrations via a Milwaukee Instruments dissolved oxygen (DO) probe, through small holes bored into jar caps. Each sample was then closed and sealed with a water-tight tape, and left in their respective collection locations for two hours. Water column samples collected at 0.5 meters were suspended at a uniform depth via a buoy-anchor system. After two hours the samples were retrieved and DO measurements were again recorded to establish the change in dissolved oxygen concentration. Benthic and pelagic samples were run through these trials simultaneously to control for temporal abiotic variability (e.g. light availability, temperature). Furthermore, corresponding pairs of both pelagic and benthic samples were sealed in containers wrapped in black electrical tape, and deployed along with unwrapped samples, to eliminate light penetration into the water/sediment. These dark run values were subtracted from light run values to estimate photosynthetic activity within the closed systems. Measurements of DO (mg of dissolved oxygen) were recorded at the start and end of each incubation, then subtracted from one another to establish a change in DO. These value were then normalized by time to account for variations in deployment times. Normalized values from corresponding light and dark chambers were then subtracted from one another in order to isolate positive changes in dissolved oxygen, a proxy for photosynthetic activity.

Due to a lack of equipment to assess light availability beneath the surface, lux measurements at the surface were taken as a proxy. On the shore adjacent to each trial site, an average representation of the two hour incubations was obtained across a 5-minute interval, wherein an average lux measurement was taken every 60 seconds, and the 5 values were then averaged.

Sediment size analysis

Sediment samples were collected at each of the three field sites by scraping of the top ~2 cm of sediments into Falcon 50mL Conical Centrifuge Tubes. All three samplings were done at ~1 m of depth, where field deployments were also conducted. Samplings were conducted within 30 minutes of each other to account for any potential changes in composition in response to tidal currents.
In the lab, samples were shaken and allowed to settle before forceps were used to transfer a small amount of sediment onto three slides corresponding to each site. Slides were photographed under a compound light microscope at 40X magnification and analyzed via ImageJ. Twelve grains of sediment were randomly selected from one representative image for each site, measured using a pixel-to-mm scale ratio, and averaged to reach a mean value at each site.

Lab experiment to assess activity of Pao Pao communities under climate change conditions

A separate lab component was designed with intentions of comparing similar microbial communities to field sites, wherein samples of ambient and carbon-acidified water (400ppm pCO2 and 1000ppm pCO2, respectively) were exposed to two light levels simulating low and high light availability. High light levels were implemented to simulate increased light availability associated with greater stratification of the ocean associated with increased global temperatures. Measurements identical to field trials were taken: DO measurement at the beginning and end of a four-hour time trial. Water utilized in these trials was acquired via experimental flume affluent, sand-filtered and collected via a pump at 60ft. depth. Light level was controlled through the use of sunlight (weather permitting) and the variation in availability was obtained via utilization of mesh with 50% light penetration. The ‘high’ exposure treatment had no mesh covering while ‘low’ exposure treatment had a layer of mesh filtering sunlight. Water samples were collected via flume outflow tubes in large bins to then be distributed across incubation chambers in order to control for dissolved oxygen variability between jars. Incubation chambers were then submerged to be filled and sealed without air pockets. Incubations were run in jars (~0.6L), similar to those employed in the field. A separate jar was filled with those used in the experiments and a DO measurement was taken as the overall initial measurement for all those jars utilizing water from the collection bin.

Statistical Analyses

Statistical analysis to substantiate difference between benthic and pelagic productivity across field sites was achieved via a one-way ANOVA. One-way ANOVA analysis was also conducted to confirm a gradient in sediment size across sites. Similar one-way ANOVA analysis was employed in discerning a statistical difference between productivity under prescribed conditions for the lab component.

RESULTS

Study sites

Three sites were ultimately selected per accessibility to the public, as much of the land along Pao Pao Bay is privately owned and fenced. These sites were along the western portion of the bay in order to control for variability of abiotic factors on either side of the bay.

Field study

Over the course of the field study, twelve total incubations were ultimately conducted, with four at each of the three sites. Net water column (pelagic) and sediment (benthic) productivity across sites exhibited downward and upward trends, respectively, across sites (Fig. 2). While a one-way ANOVA run with respect to variation across discrete sites, depicted in this plot, does not conclude significance (p>0.05, F,.=1.0867), a visual trend is apparent.

FIG. 2. Boxplots representing mean productivity (mg O2/L) of benthic and pelagic communities at each of the three field sites.

Benthic and pelagic production was also analyzed for variance (one-way ANOVA) across field sites. Benthic production exhibited a statistically significant upward trend in production, with respect to distance from Pao Pao River outlet (R=0.4972, F,.=6.4384, p<0.05;
Pelagic production exhibited a weak negative trend in production, with respect to distance from Pao Pao River outlet ($R^2 = -0.0732$, $F_{1,10} = 0.2497$, $P>0.05$; Fig. 4). Table 1 tabulates average values of productivity (change in DO).

A one-way ANOVA run for these calculated values proved to be statistically significant in its difference across sites, with respect to distance from the Pao Pao river outlet ($F_{6} = 6.4601$, $p<0.05$). A scatter plot was generated with a regression line which illustrated a positive trend of benthic contribution with respect to distance from the Pao Pao river outlet ($R=0.3317$; Fig. 5).

**TABLE 1.** Tabulated average productivity values for each field site, and within each experimental depth, or zone.

<table>
<thead>
<tr>
<th>Distance from river outlet</th>
<th>Site</th>
<th>Zone</th>
<th>Average change in DO (mg O2/L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Pao Pao</td>
<td>Benthic</td>
<td>0.111</td>
</tr>
<tr>
<td>0</td>
<td>Pao Pao</td>
<td>Pelagic</td>
<td>0.195</td>
</tr>
<tr>
<td>500</td>
<td>Churches</td>
<td>Benthic</td>
<td>0.251</td>
</tr>
<tr>
<td>500</td>
<td>Churches</td>
<td>Pelagic</td>
<td>0.227</td>
</tr>
<tr>
<td>1900</td>
<td>Gump</td>
<td>Benthic</td>
<td>0.698</td>
</tr>
<tr>
<td>1900</td>
<td>Gump</td>
<td>Pelagic</td>
<td>0.097</td>
</tr>
</tbody>
</table>

Contribution of benthic sediments to the overall production of the system was calculated by first adding the net values of each light/dark pelagic and benthic pair to establish a system-wide net activity during each given incubation trial. This addition was then used to divide the corresponding benthic net activity values to reach a proportional contribution of benthic-to-overall activity, or production. A one-way ANOVA run for these calculated values proved to be statistically significant in its difference across sites, with respect to distance from the Pao Pao river outlet ($R^2 = 0.5113$) (Fig. 6).

**Sediment size analysis**

Analysis (via one-way ANOVA) of sediment photographs in ImageJ confirmed a strong and statistically significant gradient of sediment size, with respect to distance from the Pao Pao river outlet ($F_{6} = 37.616$, $p<0.01$), and is plotted with regression [$R=0.5113$] (Fig. 6).
FIG. 6. Scatterplot fitted with regression line regarding average sediment size across field sites, with respect to distance from Pao Pao River outlet.

**Lab experiment**

Data plotted and analyzed (nested ANOVA) concerning the net change in DO under light intensity and pCO2 treatments did not illustrate significant variation among treatment groups ($F_1,1=1.44$, $p>0.05$), nor was any visual trend apparent, aside from a slight increase in net DO values recorded in the high light intensity OA treatment (Fig. 7).

**DISCUSSION**

These findings support the notion of strong spatial variation in primary productivity along Pao Pao Bay. However, data collected does not follow the trends expected, with respect to presumed effects of gradients associated with the Pao Pao river output. With large deposition of fine sediment (Fig. 5) from the mouth of the Pao Pao river outlet, it was expected that benthic productivity would be higher in response. This was not the case; as benthic production was lowest at this point along the gradient. With this, alternative hypothesis (4) cannot be supported, wherein sediments with greater surface area (smaller grain size) will have higher levels of production. Interestingly, however, when sediment size data is considered alongside proportional benthic contribution to overall production (Fig. 4), both statistically significant trends seem to follow a general geospatial proportionality as sampling moved continuously away from the Pao Pao output. This statistical significance does not hold true when pelagic productivity is considered alongside these two trends, suggesting varied affects of the abiotic gradients upon benthic and pelagic producers.

With lesser primary production recorded at the head of the bay, the interaction of the other two gradients, nutrient concentrations and turbidity of water, are likely to have strong affects upon productivity in the benthos, and the water column. The latter of these gradients seems most likely to be the driver for this depression in benthic activity in the benthos. Data recorded by Harbaugh (2000), notes a substantial murkiness of the water feeding into the bay towards Pao Pao, especially when compared to water in more distil areas of the bay. This increased turbidity, or murkiness of the water column above the Pao Pao benthos results in an obvious reduction in light able to reach 1.0 m depth, therefore inhibiting the activity of photosynthetic microbes. A gradual decrease in the turbidity of water, observed by Harbaugh, and a statistically significant increase in benthic production across sites moving away from Pao Pao supports this notion of light availability being a dominant driver for photosynthetic activity in the benthos, despite other notable gradients.

Quantification and analysis of nutrient concentrations across sites was not feasible over the course of this study, however, data recorded by Harbaugh (2000) provides a general understanding of nutrient availability along the western margin of Pao Pao Bay, where this study was conducted. Despite the measurements and scope of Harbaugh’s study being specific to eutrophication in stream outflows along the bay, these streams are major...
inputs to the areas along the margin of Pao Pao Bay, making these data sufficient for discussion of conclusions drawn from this study. While benthic productivity seems to relate most closely to light availability, pelagic production seems to be most reasonably related to nutrient concentrations in the water column. With highest production in the water column at the mouth of the Pao Pao River outlet, and the highest recorded nitrate levels at Harbough’s field site closest to Pao Pao, this presumption is supported. Interestingly, benthic production was lowest at this site with the highest concentration of nutrients, thus failing to support hypothesis (1). Despite the likelihood that nutrient levels in the sediments are similarly elevated at this location, it seems that light availability is the stronger limiting factor in benthic production, thus opposing likely drivers for pelagic production.

Greater activity in the water column surrounding the river outlet begs further questioning as to how much of a role the microbes present in the freshwater inputs may play in the net productivity. Nutrient availability is a reasonable assumed driver for productivity in the column, but freshwater microbes may well be contributing to the dissolved oxygen production measured here. Analysis of these community compositions and interactions is of great interest for future research.

Lux measurements collected for a subset of the reported data were intended to be related to productivity across benthos and the water column, however, were excluded from any analysis due to insignificance. These data are plotted and associated statistical values are recorded in the appendix (Fig. 9).

Overall, a strong proportional contribution of benthic to overall productivity, across all sites, supports hypothesis (2), as well as hypothesis (3). With lower nutrient concentrations in the clearer water column above more classically marine sediments (those less saturated with fine river sediment) generally depressed, it fits that benthic microbes would then have a larger contribution to the areas total production (Fig. 4). Proportional contributions of benthic to overall community production exceeds that found in the S. African temperate system which sparked the majority of this study; these values were calculated as follows: 32% at Pao Pao (0m from river outlet), 48% at Churches (500m from river outlet), 100% at Gump (1900m from river outlet). This was to be expected, given the nutrient deplete characteristic of tropical systems, but is nevertheless interesting to document and confirm.

Lab experiments seeking to elucidate productivity under future conditions were unsuccessful, as data collected an analyzed was inconclusive (Fig. 6). These data are likely inconclusive for several reasons. Water sampled was collected from 18 m depth and sand-filtered before reaching experimental chambers. This sampling depth may have such low abundance of primary producers that no photosynthesis occurred, or these microbes could have been filtered from the samples entirely; a community analysis was not conducted due to time constraint. Furthermore, a low abundance of producers could have made a four-hour incubation simply too short to have captured a signal. In the future, equipment to isolate and inoculate treated and thoroughly filtered water would provide potential for more successful experimentation.

Studies like this conducted in the field and considered in conjunction with lab studies designed with projected climate change conditions (i.e. pCO2 levels, light availability, etc.), are those which provide framework for navigating a changing planet. Current models of global carbon processing in the ocean are often based upon general trends observed in systems representative of entire latitudes, therefore are lacking in resolution. Studies geared towards better understanding of individual, and often nuanced, systems can be incorporated into these global models to strengthen current datasets, which in turn can be utilized in modeling exercises predictive of future dynamics, namely carbon processing by primary producers inhabiting the largest habitats on Earth.

ACKNOWLEDGEMENTS

First, I’d like to acknowledge the University of California, Berkeley and the department of Environmental Science, Policy, and Management for providing this opportunity to conduct research at Gump Field Station, Moorea, French Polynesia. Next I’d like to acknowledge the course facilitators: Stephanie Carlson, Brent Mishler, Vince Resh, and Jonathon Stillman, as well as the graduate student instructors: Caleb Caswell-Levy, Audrey Haynes, and Suzanne Kelson, for providing insight and assistance of all kinds during over the course of developing and conducting this study. I’d also like to thank all my colleagues for their encouragement and regular assistance throughout the project,
especially Charlotte Jamar, for hours of brainstorming and deployment assistance. Finally, I'd like to thank the Gump Station staff, namely Hinano Murphy, and members of the Long Term Ecological Research Project (LTER).

LITERATURE CITED


FIG. 8. Scatterplot showing statistically insignificant positive relationship between lux measurement at the surface and net change in dissolved oxygen in both pelagic and benthic incubations ($R^2 = 0.02342$, $F_{1,14} = 1.3597$, $p > 0.05$).

FIG. 9. Boxplot paired with sediment photos illustrating variance in mean size across field sites.
FIG. 10. Microscope photo taken at 100X magnification, depicting an unidentified microbe among detritus and, presumably, bacterial clusters.

FIG. 11. Microscope photo taken at 100X magnification, depicting what is likely a *Volvox* colony.
## Table 2

Table containing a subset of raw data to illustrate the processing of collected dissolved oxygen values in order to reach proportional values used in addressing the leading hypothesis.

<table>
<thead>
<tr>
<th>Date</th>
<th>Distance</th>
<th>Site</th>
<th>Zone</th>
<th>Net (Light)</th>
<th>Net (Dark)</th>
<th>Net Normalized</th>
<th>Net System (Pelagic + Benthic)</th>
<th>Net Benthic / Net System</th>
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