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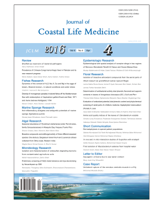

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Seasonal abundance of *Pyrodinium bahamense* (order Peridiniales, family Gonyaulacaceae) in Mosquito Bay, Vieques, Puerto Rico

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ABSTRACT

Objective: To determine the presence of consistent spatial or temporal patterns to the abundance of *Pyrodinium bahamense* (*P. bahamense*) in Mosquito Bay, Vieques, Puerto Rico.
Methods: Measurements of dissolved oxygen, pH, salinity, water temperature, tide level, wind speed, and density counts of *P. bahamense* were taken at six sites in the bay over approximately one year. The data were analyzed statistically to determine if spatial or temporal patterns were present.
Results: There were statistically significant patterns of *P. bahamense* seasonally, which was similar to other studies done in other subtropical locations with phytoplankton. Also, trends were seen that rain events caused short-term increases in abundance and shallow areas of the bay had lower abundance than that of deeper areas. The average number of organisms from 736 samples was 26.8 per mL. The average water temperature was 29.0 °C, the average salinity was 36.8 ppt, the average pH was 8.11, and the average dissolved oxygen level was 4.27 mg/L.
Conclusions: The abundance of *P. bahamense* varies seasonally over shorter time periods. The abundance also varies over a few meters in small coastal bays. This information indicates that economically important bioluminescent bays are vulnerable to changes in freshwater input, water temperature, water circulation patterns and possibly the nutrient inputs from the land surrounding such bays.

1. Introduction

Bioluminescent dinoflagellates are common in most marine waters. While the mechanisms of their light production are understood, its function is still debated[1]. The factors affecting its distribution may be of interest for both ecotourism and ecosystem health. The production of light by *Pyrodinium bahamense* var. *bahamense* (*P. bahamense* var. *bahamense*) (Plate, 1906) is an ecotourism attraction on several islands in the Caribbean. In the last five years, *Pyrodinium bahamense* var. *compressum* (*P. bahamense* var. *compressum*) (Böhm, 1931) has been responsible for neurotoxic red tides worldwide, including the Caribbean. On the Puerto Rican island of Vieques, Mosquito Bay is one of the brightest bioluminescent bays in the world, because of the high concentration of *P. bahamense* var. *bahamense*[2]. Understanding the conditions that lead to high concentrations of *P. bahamense* is an important step to conserve this natural phenomenon and its use in ecotourism on the island. It is also possible that factors which affect *P. bahamense* var. *bahamense* population numbers may also impact *P. bahamense* var. *compressum*.

The importance of bioluminescent bays as a source of eco-tourism revenue is clear on Vieques; a number of businesses on this island of approximately 9 000 people depend on it, and we (Grasso and Bras) are or have been part of businesses taking tourists to Mosquito Bay. However, such bays are vulnerable to changes in nutrients, or water flows that change the density of the bioluminescent organisms present[3,4] have compared sites containing *P. bahamense* in the Caribbean such as the Virgin

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Islands, Puerto Rico and Vieques in terms of geomorphology and substrate composition. Their findings indicate that shallow bays with limited water flows and high nutrient levels are important to high *P. bahamense* numbers. The goals of this study were to investigate if certain abiotic conditions correlate with high levels of *P. bahamense* var. *bahamense* and determine if spatial or seasonal patterns exist in its abundance within Mosquito Bay, Vieques.

2. Materials and methods

The study was done on Vieques Island, a small island off the east coast of Puerto Rico. The study location on Vieques was Mosquito Bay. This is a small bottle-necked bay from approximately 1.15 km east-west to 1.66 km north-south from opening to back of the bay (Figure 1). The bay is approximately 4 m deep at its deepest point, with the majority less than 1 m in depth. The bay is surrounded by healthy red mangrove (*Rhizophora mangle*).

Water samples were taken for a period of approximately one year (April 25, 2002 to March 3, 2003) every three to ten days at six locations throughout the bay (Figure 1). Water samples were taken at 1 m and 2 m depths at each site on each day of sampling. This was done by lowering an approximately 200 mL bottle to the desired depth on a pole and pulling a line attached to a lid temporarily affixed to the neck of the bottle. Testing was done between local time 10:00 and 02:00 pm. The following parameters were measured by YSI water meter: water temperature (°C), salinity (ppt), total dissolved solids (g/L), pH, conductivity (μS/cm) and dissolved oxygen concentration (mg/L). For each sample date, moon phase and tide level (in cm from mean lower low water) were recorded by the United States National Oceanic and Atmospheric Administration at a monitoring station on Vieques approximately 1 km west of Mosquito Bay. The wind speed and direction were recorded either by a handheld anemometer while sampling on the bay or from a mounted weather station approximately 2 km west of the bay.

P. bahamense counts were obtained by using two 1 mL Sedgewick-Rafter slides. From each sample (200 mL bottle), an approximately 50 mL aliquot was taken, agitated, and 21 mL subsamples were placed on the Sedewick-Rafter counting slides. Both slides were counted entirely. The two counts were averaged together and recorded.

The data were analyzed by using JMP version 8.0.1 using the distribution function and the non-parametric multivariate platform, and Analyse-it version 2.21 for the Kruskal-Wallis tests[5,6].

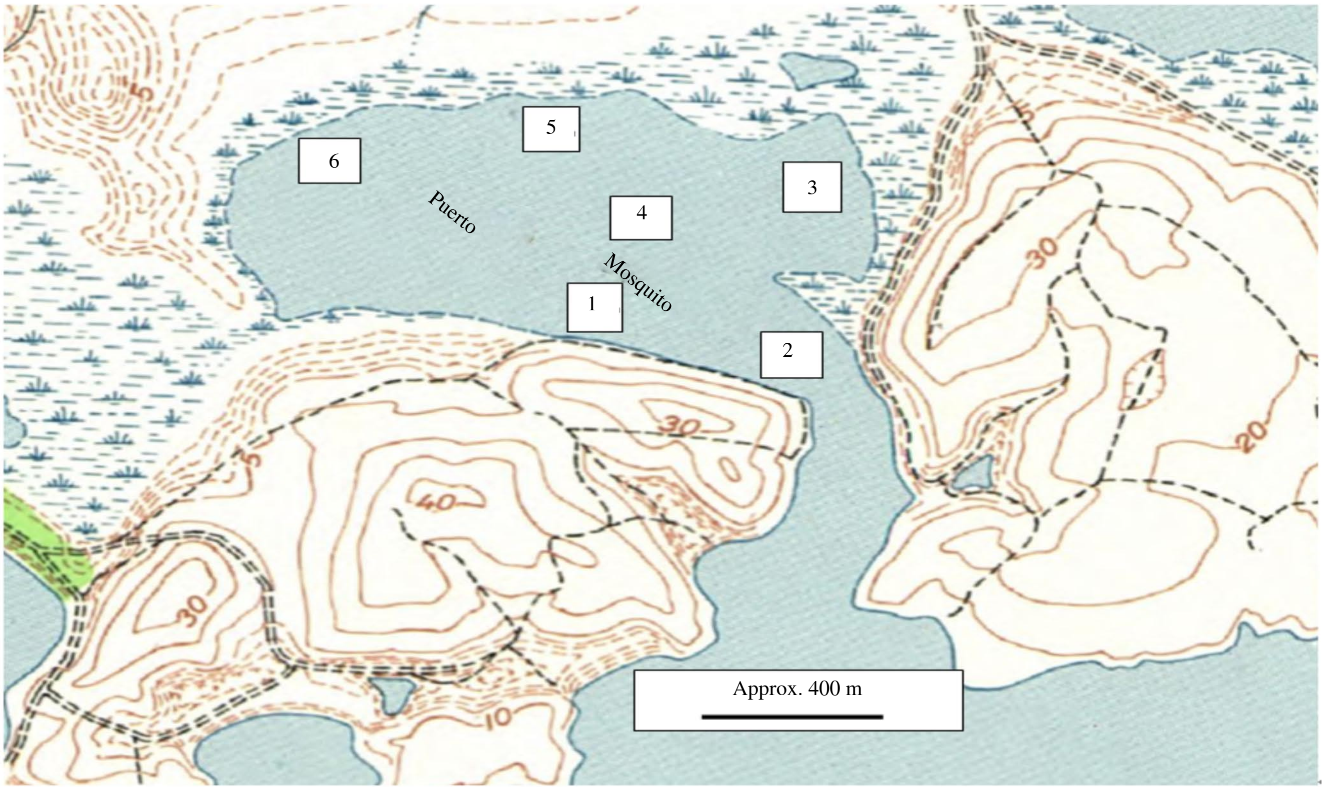

Figure 1. Section of the USGS 1:24 000 map of Mosquito Bay, Vieques, Puerto Rico.
Sample sites are numbered. Note that sample site 2 is in the mouth of the bay, sample site 4 is in the middle and deepest part of the bay, and sample site 6 is located where tour operators launch and recover kayaks and boat trips. Red mangrove is shown by marsh symbols in this image.

3. Results

3.1. The distribution of *P. bahamense*

There were 736 data points from 122 sample dates, 2 sample depths and 6 sample sites. The abundance of *P. bahamense* in the samples varied from 0 to 244 organisms/mL. This range of abundance is similar to those found by other studies in Mosquito Bay[7-9]. *P. bahamense* counts of up to 273 organisms/mL were reported in Oyster Bay, Jamaica[3]. In our study, spanning a similar time period, the mean dinoflagellate count was 26.8 organisms/mL[3]. The count values were not normally (Shapiro-Wilk W-test, W value = 0.757, $P < 0.0001$), or symmetrically distributed (Figure 2). Counts over 150 dinoflagellates/mL were rare, making up only 6 of the 736 values recorded, in contrast to 57 values between 0 and 5. Descriptive statistics of *P. bahamense* counts indicated that site 4 appeared to have more dinoflagellates than other sites (Table 1), followed by sites 1 and 3. Kruskal-Wallis analysis of the data with Bonferroni tests indicated that only sites 1, 2, 3 and 6 had similar count data ($n = 736$, K-W statistic 236.55, $df = 5$). All other sites pair tests were significantly different from each other at $P < 0.0001$. Site 5 *vs* site 6 and site 2 *vs* site 5 comparisons were also significantly different but at different P values ($P = 0.0015$ and $P = 0.0024$, respectively).

The abiotic variables measured were tested for normality and descriptive statistics calculated (Table 2). All of the abiotic variables tested were non-normally distributed. The abiotic data were then tested for correlations between each other and *P. bahamense* counts by Spearman's rho nonparametric pairwise tests (Table 3). With this, many comparisons reducing alpha by Bonferroni correction could be done, but to keep the analysis more clear, and because the calculated *P*-values were so low generally, the correction was not done. Conductivity, total dissolved solids, and salinity measured similar abiotic properties and were almost perfectly correlated with each other at 99.3%. Therefore, only salinity was reported and used for the rest of the analysis.

Table 1
Results of Kruskal-Wallis test on count data of *P. bahamense* density (organisms/mL) over the entire study period.

Site	*N*	Mean *P. bahamense* count	SD	Group
1	125	31.2	20.9	B
2	122	15.4	14.6	D
3	123	28.6	24.6	B
4	124	46.7	28.1	A
5	124	22.1	20.7	C
6	118	16.1	19.3	D

Sites that have statistically similar count data have the same letter grouping.

Table 2
Mean, interquartile range, and normality test for the abiotic variables measured in the study.

Variable	Median	Interquartile range	Shapiro-Wilk W normality test
Water temperature (°C)	29.50	3.46	0.94***
Salinity (ppt)	37.00	1.50	0.51***
Dissolved oxygen (mg/L)	3.94	1.12	0.76***
pH	8.14	0.14	0.54***
Tide level (cm)	15.00	13.00	0.97***

***: $P < 0.0001$. These values indicate the variance and lack of normality in the data.

3.2. Temporal variation

The method of data collection allows the ability to examine the counts of *P. bahamense* for both temporal and spatial variation at Mosquito Bay. Plotting the data chronologically allows visualization of the relationships between measured variables (Figure 3). Most of the year during which samples were taken for the *P. bahamense* counts

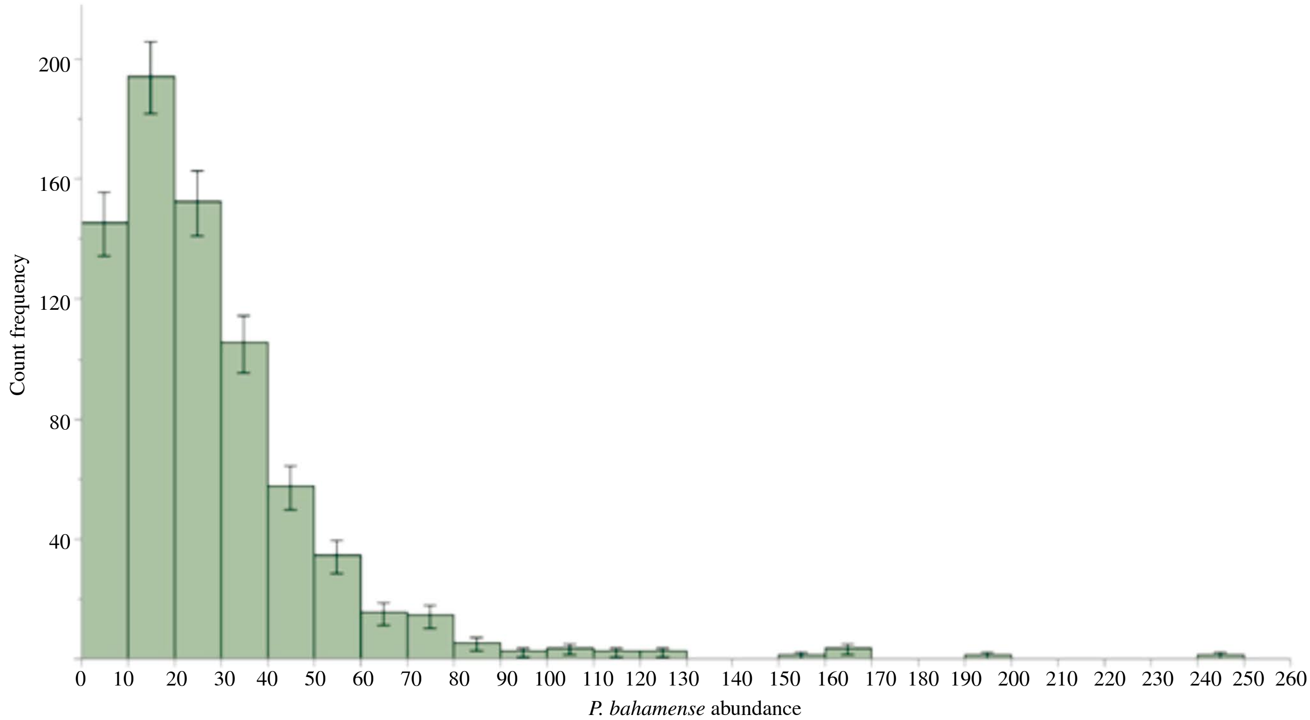

Figure 2. Distribution of *P. bahamense* count data from Mosquito Bay, Vieques.
The histogram shows the distribution of counts from all samples with standard error bars. The distribution is non-normal and strongly skewed with a long tail of rare, high values.

were relatively consistent when the counts between sampling sites were averaged together. Much larger counts were seen during the month of October. This time of year is the beginning of the rainy season in Puerto Rico and the water chemistry did appear to change in late September and October. Specifically there was a decrease in salinity, which in this bay is due to freshwater runoff from the surrounding hills. It is likely that this runoff also caused the drop in water temperature and pH that was seen in most sample sites at this time as well. Vieques, Puerto Rico, is a subtropical island and the average daily temperature changes < 5 °C over the course of the year.

Table 3

Significant correlations are shown between abiotic variables and *P. bahamense* counts using non-parametric Spearman's ρ (rho) pairwise test.

Variable 1	Variable 2	Spearman ρ	Probability
Dissolved oxygen	Depth	-0.1894	< 0.0001
pH	Water temperature	0.4238	< 0.0001
pH	Dissolved oxygen	0.2005	< 0.0001
pH	Salinity	0.3510	< 0.0001
P. bahamense	pH	0.1678	< 0.0001
P. bahamense	Salinity	-0.1415	0.0001
P. bahamense	Tide level	0.1719	< 0.0001
P. bahamense	Date	0.1574	< 0.0001
P. bahamense	Water temperature	-0.1134	0.0021
Tide level	Dissolved oxygen	-0.0871	0.0259
Tide level	pH	-0.0882	0.0242
Tide level	Salinity	-0.4620	< 0.0001
Tide level	Date	0.4667	< 0.0001
Tide level	Water temperature	-0.2529	< 0.0001
Tide level	Wind speed	-0.2168	< 0.0001
Time	Dissolved oxygen	-0.1819	< 0.0001
Time	Salinity	-0.5216	< 0.0001
Time	Water temperature	-0.6618	< 0.0001
Time	pH	-0.1559	< 0.0001
Water temperature	Salinity	0.2804	< 0.0001
Wind speed	pH	0.1328	0.0008
Wind speed	Salinity	0.3217	< 0.0001
Wind speed	Date	-0.3438	< 0.0001
Wind speed	Water temperature	0.2345	< 0.0001

All relationships here are significant at a level of $P < 0.0001$ unless otherwise stated. Non-significant results were not presented here for the sake of clarity. Water samples were taken only at 1 m and 2 m depths.

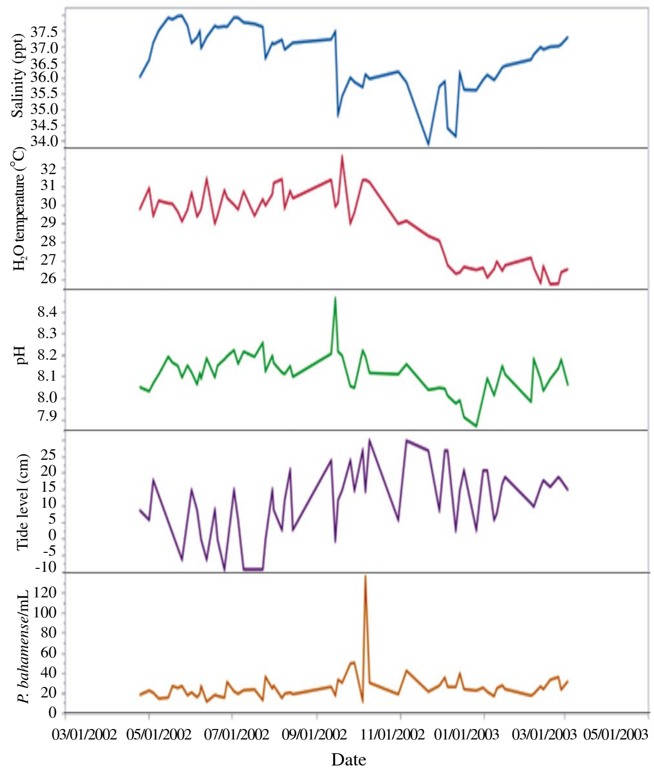

Figure 3. The relationship of 5 abiotic variables to *P. bahamense* counts for all data.

These are average values across all sample sites in Mosquito Bay. The X-axis shows the dates during the experiment, starting form April 24th of 2002, ending on March 3rd, 2003. The Y-axis shows the dinoflagellate *P. bahamense* count with the bottom line, then water level (tidal change) above that (cm), the middle line is pH, above that is water temperature (°C), and the top line is salinity (ppt). Note the spike in *P. bahamense* on early October. This correlates with a seasonal drop in salinity, pH, and water temperature that indicate the arrival of the fall rainy season in Puerto Rico.

3.3. Spatial variation

Table 4 shows pairwise correlations of variables measured within sites for the entire study period. Table 5 uses the Wilcoxon nonparametric test to determine if measured variables had different

Table 4

The pairwise correlations of data within all the sites of the study (direction of the correlations and statistical significance values are given).

Variables	Direction	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Overall
Salinity *vs* temperature	+	0.0091	< 0.0001***	0.0063**	0.0218*	0.0058	0.0003***	< 0.0001***
Dissolved oxygen *vs* temperature	+	0.4007	0.0005***	0.5846	0.8486	0.6424	0.2063	0.1034
P. bahamense vs temperature	-	0.4699	0.0319*	0.0598	0.1441	0.0096**	< 0.0001***	0.0021**
P. bahamense vs salinity	-	0.2241	0.3725	0.1245	0.6655	0.0007***	0.0001***	0.0001***
P. bahamense vs dissolved oxygen	+	0.2223	0.5576	0.0824	< 0.0001***	0.0031**	0.4455	0.4551
pH *vs* temperature	+	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	0.0003***	< 0.0001***	< 0.0001***
pH *vs* salinity	+	< 0.0001***	< 0.0001***	< 0.0001***	0.0026**	< 0.0001***	< 0.0001***	< 0.0001***
pH *vs* dissolved oxygen	+	0.2735	0.0016**	0.4505	0.2169	0.2326	0.0653	< 0.0001***
pH *vs P. bahamense*	+	0.5470	0.9086	0.8933	0.6425	0.8597	0.4181	< 0.0001***
Day *vs* temperature	-	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***
Day *vs* salinity	-	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***
Day *vs* dissolved oxygen	-	0.0559	< 0.0001***	0.1426	0.0317*	0.0449*	0.4685	< 0.0001***
Day *vs P. bahamense*	+	0.9179	0.0406*	0.0018**	0.0260*	< 0.0001***	< 0.0001***	< 0.0001***
pH *vs* day	-	0.0413*	< 0.0001***	0.1413	0.6772	0.8307	0.0037**	< 0.0001***
Tide *vs* temperature	-	0.0305	0.0051**	0.0250*	0.0109*	0.0026**	0.0059**	< 0.0001***
Tide *vs* salinity	-	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	0.0001***	< 0.0001***
Tide *vs* dissolved oxygen	-	0.4913	0.1423	0.6658	0.0387*	0.8141	0.3573	0.0259*
Tide *vs P. bahamense*	+	0.7390	0.9879	0.1514	0.0229*	< 0.0001***	< 0.0001***	< 0.0001***
Tide *vs* pH	-	0.3187	0.0140*	0.4088	0.0555	0.2602	0.2956	0.0242*
Tide *vs* day	+	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***	< 0.0001***

*: P value < 0.05; **: P value < 0.01; ***: P value < 0.001.

values across all the sites. The statistical power is shown here to indicate the confidence in the test results. Site 2 had the lowest salinity, while site 6 had the highest. Site 1 had the highest dissolved oxygen, while site 2 had the lowest. Site 1 had the highest pH, while site 2 had the lowest. Site 4 had the highest *P. bahamense* counts, while site 6 had the lowest.

Table 5

Wilcoxon analysis of variables across sample sites.

Variable	*Chi*-square value	*P*-value	Power
Water temperature	4.41	0.4920	0.2035
Salinity	19.15	0.0018	0.4550
Dissolved oxygen	63.95	< 0.0001	0.9991
pH	144.00	< 0.0001	0.9990
P. bahamense count	236.60	< 0.0001	1.0000

Significant values indicate differences in recorded values between sample locations.

The different relationships between sites can also been seen graphically. Figure 4 shows the sample data from the study at Site 2. Site 2 was located at the constricted mouth of Mosquito Bay. This is a shallow site, but is where the most water movement occurs into and out of the bay. Figure 5 shows the sample data for Sites 4 and 6. These sites are more similar to each other than Site 2, but together with Figure 4 form a transect from the mouth of the bay to the back. These sites are similar to each other in that they are in parts of the bay that may see the most water turnover. The sites that are not shown in these figures are located more peripherally and may therefore experience different water chemistry. It is useful to refer to Figure 3 for comparison to the combined sample data.

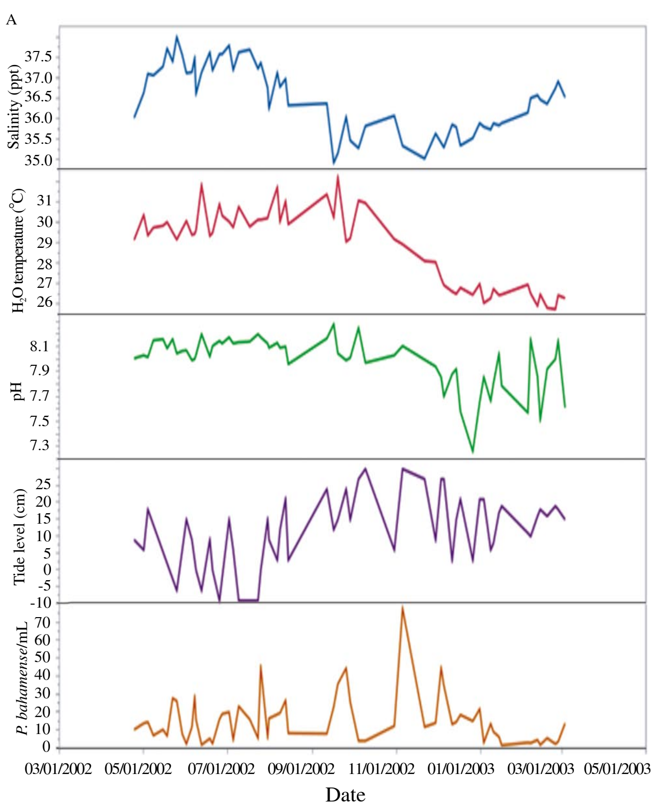

Figure 4. Comparison of *P. bahamense* and 5 abiotic variables for Site 2 during the study.

The pattern is similar in the values of the variables measured, but differ between sites. The X-axis shows the dates during the experiment, starting April 24th of 2002, ending March 3, 2003. The Y-axis shows the dinoflagellate P. bahamense count with the bottom line, then water level (tidal change) above that in cm, the middle line is pH, above that is water temperature in C, and the top line is salinity in ppt.

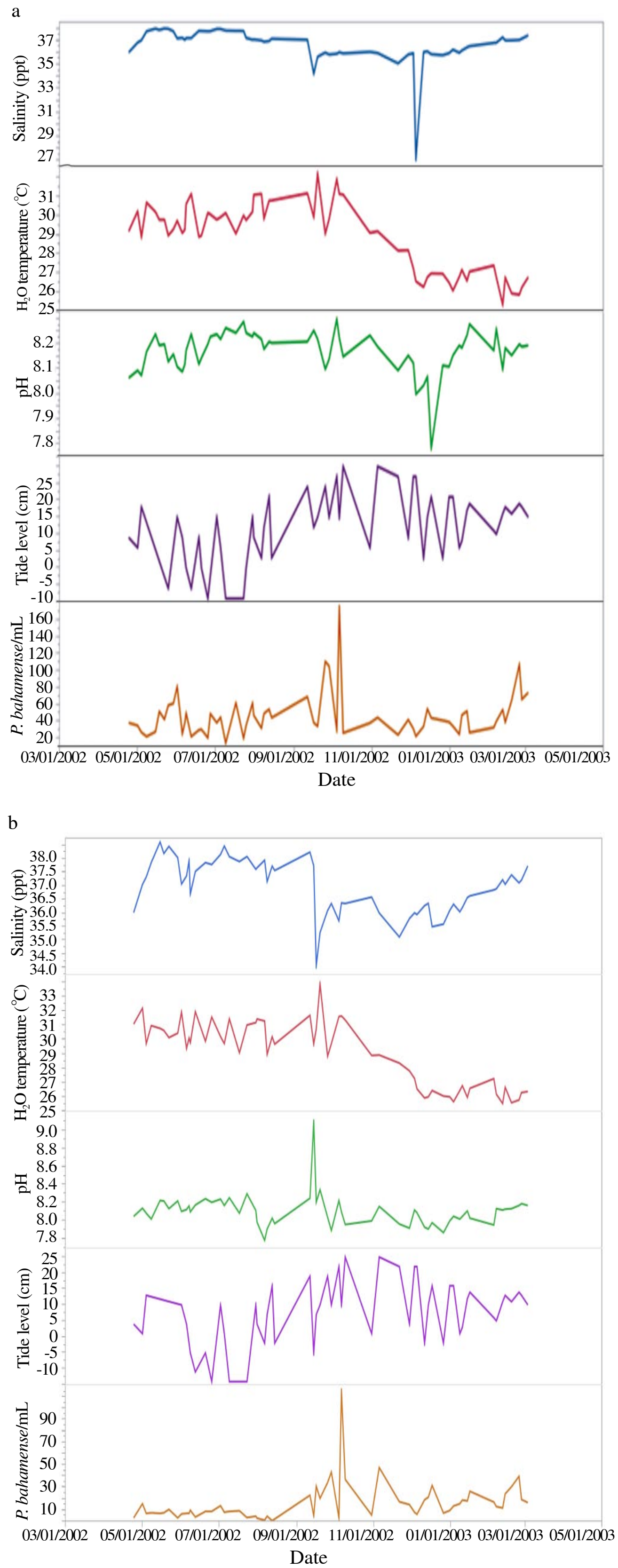

Figure 5. Comparison of *P. bahamense* and 5 abiotic variables for Sites 4 (a) and 6 (b) during the study.

The patterns are similar in the values of the variables measured, but differ between sites. The X-axis shows the dates during the experiment, starting from April 24th, 2002, ending on March 3, 2003. The Y-axis shows the dinoflagellate *P. bahamense* count with the bottom line, then water level (tidal change) above that (cm), the middle line is pH, above that is water temperature in °C, and the top line is salinity (ppt).

4. Discussion

Studies indicate that the phytoplankton abundance is affected by hydraulic flow, sunlight availability in the water column, and levels of phosphorus and nitrogen[3,10,11]. The studies showed that greater water flow reduced *P. bahamense* numbers, while greater levels of sunlight, phosphorus, and nitrogen rose the number. High numbers of *P. bahamense* are also caused by high levels of available organic nutrients, a lack of phytoplankton species that shade the water and sufficient water mixing in a bay by wind[10,11]. In this study, *P. bahamense* counts were significantly negatively correlated with salinity and water temperature. Conversely, pH, higher tide level and time of year correlated positively with *P. bahamense* counts.

The results suggest that water that is isotonic, or slightly hypertonic and relatively warm is not favorable conditions for *P. bahamense*. While lower salinity and higher tide level are correlated with high *P. bahamense* abundance. This may be a result of these physical events such as rain or as a result of nutrients transported into the bay, which may also be increased during rain events[12].

The levels of dissolved oxygen and the pH, even though significantly correlated with *P. bahamense* abundance, do not appear to have a direct impact on the abundance. Both of these variables had large changes around September 15th, 2002 that may indicate a biological or biochemical process at work in Mosquito Bay at this time. Dissolved oxygen levels were significantly negatively associated with higher tide level for the study as a whole as most variables. Dissolved oxygen was positively associated with pH levels and may also indicate metabolic or chemical processes occurring in the bay during spring.

The clearest change in the data through time is the water temperature. The water temperature peaks in the bay in late August or early September. The temperature then drops about 5 °C over the next 3 months. During the same period of the year, the salinity decreases as tide level increases. The salinity decrease was due to either tidal washing of the bay or increased rainfall or both. Fall and early winter is the rain and hurricane season in Vieques. At the peak level of *P. bahamense*, the dissolved oxygen drops in Mosquito Bay. Mosquito Bay may have had a phytoplankton bloom at this time that caused dissolved oxygen to drop.

P. bahamense count numbers, pH, and salinity ended the study period of approximately one year at values close to those seen at the beginning of the study. Studies have reported low populations of *P. bahamense* in April and December[10,13,14]. In this study, the early dip was unexplained, but the December drop was attributed to lack of wind to mix the waters of the bay in the study[10,14]. These times were also times of low abundance in this study, though the drops in population were less severe.

The data fit the pattern of a seasonal temperature cycle in the water of Mosquito Bay as well as cycling of other abiotic factors including pH, dissolved oxygen, and salinity. It appears that *P. bahamense* achieves the highest density in Mosquito Bay when tide levels increase, pH is above 8.1, salinity falls below 36 ppt, and the water temperature is above 30 °C.

Population counts of *P. bahamense* varied broadly, increasing almost 300% from September 1st to October 5th. Similar patterns in *P. bahamense* abundance have been seen in *Gymnodinium splendens* and *Ceratium furca* var. *hircus*. These patterns are thought to be caused by competition for resources[14]. The authors also point out that *P. bahamense* is positively phototactic even in full tropical sunlight, and requires sunlight every day to survive[10]. The abundance of *P. bahamense* may be influenced by rainfall and the availability of nitrogen and phosphorus in the bays[15].

The analysis indicates *P. bahamense* may undergo a seasonal cycle of abundance peaking in late summer. At least in the year of this study, the increase of the temperature corresponded with an increase in water level and a decrease in salinity from the upper range of ocean salinity towards a typical value (38 ppt to 35 ppt).

The shape and depth of Mosquito Bay, as in other bays on Vieques, contribute to the abundance of *P. bahamense*[4]. The passage to Mosquito Bay is narrow and crooked. It is shallow, and surrounded on all sides by healthy mangrove forest. The mangrove-surrounding Mosquito Bay may contribute to the nutrients needed by *P. bahamense* as first described by McLaughlin and Zahl[16]. These include B_{12}, thiamine, biotin, and bay-mud acid hydrolysate. These factors plus prevailing and daily winds blowing into the bay are the four requirements for a bioluminescent bay suggested[4,10]. These factors allow *P. bahamense* to reproduce into numbers large enough to yield the bioluminescent phenomena appreciated by tourists. Bioluminescence itself may be a relatively short term phenomena geologically as sedimentation records show that high dinoflagellate density in bays such as Mosquito Bay may be only approximately two hundred years old[17].

The 6 sampling sites in Mosquito Bay are approximately 50 m from each. This is a small sampling area, but given the shape of the bay, particularly its outlet to the ocean, it is likely that there is relatively little mixing of water as compared to more open bays. Furthermore, there are typically only a few small boats a day that enter and leave this bay. The passage to the ocean is approximately 60 cm at its shallowest (Albrecht, unpublished data).

While the sites are close to each other in absolute terms and part of the same bay, the differences in *P. bahamense* counts between sites indicate fine spatial scale differences. Site 2 is located at the mouth of the bay, while the passage to the ocean is shallow (60 cm or less). This is where the bay and ocean communicate. Site 4 is in the deepest part of the bay (approximately 4.5 m) and has the highest *P. bahamense* counts in most samples. Site 6 is the site the farthest from the mouth. It also has the most potential disturbance as this is close to where tour operators launch and recover boats from a small parking area.

Comparing sites 2, 4, and 6 visually shows the degree of similarity and differences in both *P. bahamense* counts and several abiotic variables. Specifically, *P. bahamense*, dissolved oxygen, and pH have different values at the different sites. Tide levels were recorded from the National Oceanic and Atmospheric Administration equipment offsite and are therefore not spatial component to these values, but water temperature was recorded at each site and was similar among all sites even though they have different depths and proximity to the channel. This supports the view that differences in water chemistry impact *P. bahamense* population levels (and those of other phytoplankton) on the spatial scale of tens of meters[9].

Tables 4 and 5 can be used to see the dynamics of the bay more clearly. Table 4 shows that correlations, significant or not, tend to follow the same pattern across the different sites. Table 5 shows that the values of the variables are different between sites for most variables measured.

Therefore, in Mosquito Bay similar relationships are occurring between measured variables though the absolute values of the parameters are different at the various sample sites. This is true even though the sites are only about 50 m apart. The differences between sites are also enough to cause *P. bahamense* to be present at greater numbers at some sample locations areas consistently.

This study did not elucidate the biological interactions occurring, but recorded the numbers of *P. bahamense* present. Studies show that biotic, abiotic, hydrological and meteorological factors underlie the occurrence of high density populations of *P. bahamense*[4,10,11]. The loss or change of any of the factors included in the bioluminescent bay model would likely negatively impact *P. bahamense* populations[10]. The small scale variation in *P. bahamense* abundance indicates that human modifications to natural bays may have long-term impacts on the population of these dinoflagellates. The populations of *P. bahamense* do not flow around the bay or occur homogenously throughout the bay. Locations of high abundance at one time for *P. bahamense* appear to be locations of high abundance in the following week, four weeks, or 12 weeks. The absolute numbers may increase or decrease but the relative rank of a location appears to be relatively stable. Changes to a bioluminescent bay such as channel dredging, mangrove clearing or changed wind patterns are likely to decrease the number of bioluminescent organisms in Mosquito Bay.

This information may be useful for monitoring and controlling *P. bahamense* var. *compressum*. Perhaps monitoring should be at specific locations and interventions such as changing water salinity could reduce the occurrence of damaging dinoflagellate blooms.

Conflict of interest statement

We declare that we have no conflict of interest.

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