Water Temperature Variation and the Meteorological and Hydrographic Environment of Bocas del Toro, Panama

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ABSTRACT.—Bahía Almirante is a shallow lagoon on the Caribbean coast of western Panama almost entirely surrounded by land. Rainfall is most intense during the night and least intense in the late afternoon, a pattern common in tropical coastal areas. Water temperatures are often elevated in the inshore waters relative to surface temperatures immediately offshore, at times exceeding 30°C. Analysis of solar radiation, wind speed, humidity and air temperature indicate that variations in solar radiation and wind speed were responsible for much of the observed excursions from the offshore temperatures. Environmentally stressful temperatures can result from a month or two of clear skies, and an equal period of cloudy skies can bring the temperatures down again rapidly. Shallow water has the most extreme daily and annual ranges in temperature, but water up to 20 m shows a similar range in temperatures over periods of several years. Salinity at the surface is usually 30 to 34 ppt, but can drop to as low as 20 ppt after heavy rain. Historical records of monthly rainfall explain only 9.6% of the variation in monthly water temperature changes. There appears to be a thermal gradient in the bay and adjacent areas across three sites with for which we have 4 to 6 years of hourly temperature data. The innermost site, closest to the mainland, had the highest mean temperature and the highest range in temperature. The two sites on the seaward side of the bay had less extreme temperatures.

KEYWORDS.—rainfall, water temperature, solar radiation, wind speed, Central America, temperature stress, coral bleaching

INTRODUCTION

Bahía Almirante is a shallow lagoon about 20 by 30 km bounded by a large coastal swamp and mangrove forest to the northwest, the archipelago of Bocas del Toro to the north and southeast, and the mainland to the southwest. There are no large marine passages to the Caribbean on the north or to the Laguna de Chiriquí to the southeast. The mountains of the central cordillera to the south and east are the highest in Panama, but a low ridge about 5 km from the southwestern coast diverts runoff from the mountains to either the Laguna de Chiriquí or to the Caribbean. Accordingly, the watershed of the bay is very restricted, approximately the same size as the bay and about half of that consists of coastal wetlands. Chiriquí Lagoon to the southeast is similarly isolated from oceanic influences, but has several major rivers with sources in the central cordillera draining into it. Both lagoons have significantly higher concentrations of nutrients, chlorophyll, and zooplankton biomass than the open ocean, but Bahía Almirante has substantially less (D'Croz et al. 2004) and in addition has a thriving coral reef fauna not found in much of the more turbid Chiriquí Lagoon (Guzmán and Guevara 1998).

Offshore sea surface temperatures (SSTs) in the Caribbean are affected by the annual movements of the Intertropical Convergence Zone (ITCZ) and on an intraseasonal time scale, by the movement of tropical waves westward across the Atlantic. Variations in insolation and other weather related phenomena result in offshore SST anomalies, and ultimately, offshore temperatures are a major determinate of inshore temperatures. However, local weather conditions varies in a complex way in Central America, as evidenced by the great variation in rainfall patterns, and the resulting differences in weather can be expected to affect local water temperatures.

The Environmental Sciences Program (ESP) at the Smithsonian Tropical Research Institute (STRI) laboratory in Bocas del

Toro has been collecting meteorological and oceanographic data since 1999 and other historical rainfall records are available going back to 1926. Our objective is to describe the physical conditions affecting the local fauna and flora, particularly those related to temperature stress, and to develop baseline values so that episodes of extreme conditions will be recognized. We describe the interannual to diurnal patterns of change in meteorological parameters and how they affect water temperatures in Bahía Almirante and nearby waters.

MATERIALS AND METHODS

Laboratory and instrument locations

The laboratory at Bocas del Toro is located on a narrow land peninsula connecting the town of Bocas del Toro with the remainder of Isla Colón, a low lying island that forms part of the archipelago of Bocas del Toro (Fig. 1). On the northwest side of this neck of land is a bay opening to the Caribbean Sea. On the southeast side is a shallow bay, surrounded by mangroves, opening to the Bahía Almirante. Three permanent biological monitoring sites are located near the laboratory (Guzmán et al. 2005). A mangrove and a grassbed site are several hundred meters northwest of the pier used by the laboratory. A coral reef site is about 500 m east just outside the bay. A meteorological tower on a platform about 100 m east of the pier is used to collect meteorological and oceanographic parameters.

Water temperature

This is recorded hourly with individual underwater temperature loggers (Hobo StowAway TidbiT and Hobo Water Temp Pro, Onset Computer Corp., Bourne, Mass.) attached to the bottom at four sites, Colón Coral Reef, Colón Grassbed, Cayo Roldán, and Cayo Agua (Fig. 1). Each logger is calibrated annually for several days in a water bath at about 21°C against a glass NBS traceable thermometer and all measurements are adjusted by the calibration. The accuracy of the data can be considered to be at least ± 0.25°C. Data collection started

at the Colón Coral Reef in March, 1999 at 1 m, 4 m, 10 m, and 20 m depth and at 2 m the Colón Grassbed. The 1 m site was discontinued in 2000. Water temperature data has also been collected from 4 meters at Cayo Agua and Cayo Roldán starting in December, 2000 and March, 1999, respectively. Temperatures from March 25, 1999 to September 11, 2000 were also collected at 1 m, 10 m, and 20 m at Cayo Roldán. Cayo Agua is an island separating the Chiriquí Lagoon from the open ocean and the water temperature site there is in a coral reef on the south side of the island. Cayo Roldán is a mangrove island that forms part of a barrier enclosing a smaller bay (9 km by 5 km) on the south side of Bahía Almirante and bounded on its southwest side by the mainland. Offshore water temperatures are weekly means of a one degree quadrat centered at 81.5 W, 9.5 N. (IGOSS 2004). A small part of the southwest corner of this quadrat intersects the mouth of the Chiriquí Lagoon near the Cayo Agua site.

Rainfall

We have four sources of rainfall data. The longest is a record of monthly rainfall from January 1926 to October, 2004, collected by the Chiriquí Land Company in Changuinola (Finca 8), R.P., about 33 km northwest of Bocas del Toro (here identified as the Changuinola data). Changuinola is 8 km from the coast at an elevation of 20 m and surrounded by banana plantations. These data were collected daily by the overseer of the plantation in a collector similar to that used by the U.S. Forest Service and phoned in to the main office every day. The data were considered very important since they were used to predict the size of the banana crop, and it is likely that care was taken in their collection (Clyde Stephens pers. comm.). No extreme values or other inconsistencies were found in the data.

Starting in 1972, rainfall data were collected at the airport in Bocas del Toro (here identified as the Airport data) by the Instituto de Recursos Hidraulicos y Electrificación, the state owned electric company. Monthly and annual summaries were pub-

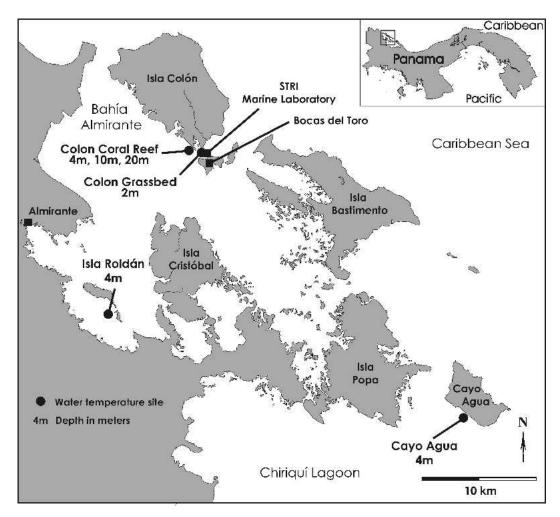


FIG. 1. Smithsonian Tropical Research Institute laboratory at Bocas del Toro, Panama and surrounding area.

lished in Estadística Panameña (1973-1994). In 1998, after the company was privatized, data collection and distribution were taken over by Empresa de Transmisión Electrica S. A. We have daily airport rainfall data supplied by them from 1989 to 2000 and monthly data for 2001 to 2003. The airport is less than 2 km from the STRI station.

The STRI ESP started collecting daily rainfall data in a US Forest Service type rain gauge on July 1, 2000 at the site of the main laboratory in Bocas del Toro (here called the Daily ESP data). Rainfall is recorded each morning at about 8 AM to the nearest 0.2 mm. On May 16, 2002, the ESP started collecting hourly data with a Vitel VRG-TB3 Tipping bucket (here called the Tip-

ping Bucket data). Rainfall is recorded in increments of 2.54 mm. The tipping bucket is attached to the ESP meteorological tower near the STRI pier.

In order to confirm the accuracy of the various rainfall records, annual and monthly totals were compared with linear regressions where overlapping data exists. The monthly total of the Daily ESP data was very similar to the monthly total of the Tipping Bucket data (N = 30, $\rm r^2 = 0.980$, slope = 1.124, intercept set to 0, P < 0.0005). That the Daily ESP data records about 12% more rain than the Tipping Bucket data is not unexpected since tipping buckets tend to underestimate during periods of heavy rainfall. The monthly totals for the Airport

data matched the Daily ESP data well (N = 45, $r^2 = 0.92$, intercept = 1.7, slope = 0.881). The monthly totals for the Changuinola data also matched the monthly Airport data from 1989 to June, 1998 well (N = 113, $r^2 = 0.71$, intercept = 10.5, slope = 0.813). Two months from the Airport data and one from the Daily ESP data were excluded from the analysis based on the large residuals in the Airport/Daily ESP regression and the lack of concordance with the Changuinola data. Estimates for the two missing Airport months were calculated from the regression on the Daily ESP data and substituted before proceeding with further analysis. A reduced major axis regression on the yearly totals from Changuinola and the Airport data (1973-2003, N = 28, r^2 = 0.762, intercept = 943, slope = 0.835) showed that the Airport station averaged about 300 to 600 mm more than the Changuinola station, with the largest differences during drier years.

Air temperature and relative humidity

These were recorded hourly between Jan 1 and Dec 31, 2003 with a Viasala HMP45 relative humidity and temperature sensor attached to the ESP meteorological tower about 3 m above the water. Air temperatures were compared to weekly measurements taken with a digital thermometer at the rainfall station and to hourly measurements recorded in a nearby mangrove forest.

Wind speed and direction

These were recorded with an R. M. Young Model 05103 anemometer (R. M. Young Co., Traverse City, Michigan) attached to the top of the ESP tower 7 m above the water. Each hour, the scalar mean wind speed and the wind direction at that time were recorded. Data collection started on August 20, 2002. Wind direction and speed are checked on the ground several times a year and compared to the instantaneous reading from the anemometer and the direction on a hand held compass. This is to ensure that there hasn't been any

major drift from the calibration at installation.

The anemometer is not sufficiently elevated to remove the interference from trees around the lab or from the hills on Isla Colón from the NE to the NW quadrats. Strong trade winds from the NE develop further east along the coast from January to March (Robertson et al. 1999) and are evident at Bocas del Toro on trips to more open areas, but these winds are not well recorded at the laboratory site. The data are probably representative of wind conditions on the lee side of the island, but not the large scale wind pattern.

Solar radiation

This is recorded using a Licor LI-200 pyranometer (LI-COR, Inc., Lincoln, Nebraska). Data were recorded as the total radiation for each hour in W/m² based on samples every 5 seconds. Two pyranometers attached to arms sticking out from the north and south sides of the tower are used. To avoid shadows from the tower, data from the south side are used from March to September, and from the north side for the remainder of the year, with the opposite side then serving as a backup. The pyranometer on the south side was not installed until Jan 30, 2003. To ensure consistency and to check against degradation of the sensors, these pyranometers are calibrated once a year against a set of Licor pyranometers that we keep in the laboratory for the purpose. All data are corrected for deviation from the standards.

Salinity

It is measured every Wednesday between 1000 and 1200 EST at 0.5 m depth at the grassbed adjacent to the laboratory and at a nearby coral reef. Measurements are either taken with an A & O Model 10419 temperature compensated hand held refractometer or using a YSI Model 85 handheld sensor (YSI Inc., Yellow Springs, Ohio). Both the refractometer and the YSI were calibrated at least annually with distilled water and Copenhagen water or its

equivalent. The refractometer is accurate to ± 1 ppt, the YSI to ± 0.3 ppt.

Secchi disk

These readings were taken at the same location and time as the salinity readings. At the grassbed site, they are taken horizontally at 0.5 m depth and the disk extinction distance is read in meters with a dive mask. At the coral reef site, the measurement is taken vertically and the extinction is read in meters from above the water surface.

Statistical Analyses

Analysis and statistics were done with Microsoft Visual Foxpro 8.0 and Systat 9.0.

RESULTS

Interannual and regional patterns for rainfall and water temperature

Annual total rainfall for the four data sources is shown in Figure 2. The data show maxima and minima during the same years, but the Bocas del Toro totals are consistently higher than Changuinola, demonstrated above. The annual mean at Changuinola is 2615 mm (N = 78, SD = 550 mm) while that at Bocas del Toro is 3277 mm (N = 28, SD = 461 mm).

Rainfall at Changuinola for 2002 was

4024 mm, the highest in 78 years. This value is matched by a total of 4255 mm for the Airport data, also the highest of the 28 years for which we have annual totals, and 4979 mm for the Daily ESP data.

Water temperatures at the three sites were monitored from 1999 to 2004. Temperatures at Isla Colón, Cayo Roldán, and Cayo Agua, rose and fell together, even when examined on a scale of a week or less (Fig. 3A). Temperatures varied from an hourly low of 26.2°C at Isla Colón to a high of 32.1°C at Cayo Roldán. At the end of each year, temperatures at all sites fell from 2 to as much as 5 degrees from what was often the annual high in September or October to the annual low in December or the first two months of the next year. In most years, there was also a peak in May or June followed by lows in July and August (Fig. 4). The offshore IGOSS temperatures followed a pattern similar to the three sites we monitored, but the inshore waters often had higher highs and less commonly, lower lows. The largest changes in mean daily temperature at 4 m at Isla Colón over approximately a month's time were a drop of 2.8°C in 2001 over 30 days starting on November 5 and a rise of 2.8°C in 2002 over 27 days starting on May 8.

The mean temperatures from 1999 to 2004 at all sites and depths (Table 1) were very similar, ranging from 28.5°C at the Colón Coral reef 10 m and 20 m sites to

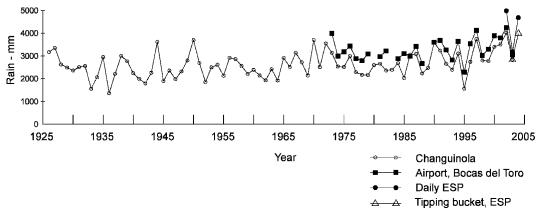


FIG. 2. Annual rainfall records from Changuinola and Bocas del Toro. Annual total rainfall from four data sources. Missing connectors between data points indicate missing data for a year. For description of data sources, see methods section.

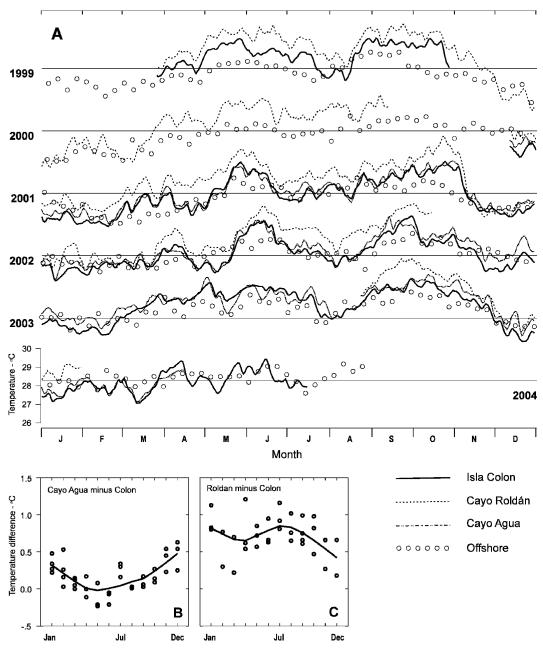


Fig. 3. Regional water temperatures: Three sites and offshore, 1999 to 2004. A: Daily mean water temperatures at 4 meters combined with 1 week smoothed offshore water temperatures (circles) from IGOSS database (81.5 W, 9.5 N). The horizontal line indicates the mean offshore temperature for 1999-2003 28.3°C. B. Difference in mean monthly water temperature at Cayo Agua and Colón for each month, 1999 to 2004. C. Same, for Roldán and Colón. Line in B and C is LOWESS smoother.

29.1°C at the Roldán 4 m site. The means of the coldest two months of the year, January and February, were all within 0.5°C of each other (27.3°C to 27.9°C). For the warmest

two months of the year (September and October), the mean for Cayo Roldán at 4 m (30.5°C) was 0.9°C higher than that for Isla Colón at 4 m (29.6°C), not a great amount

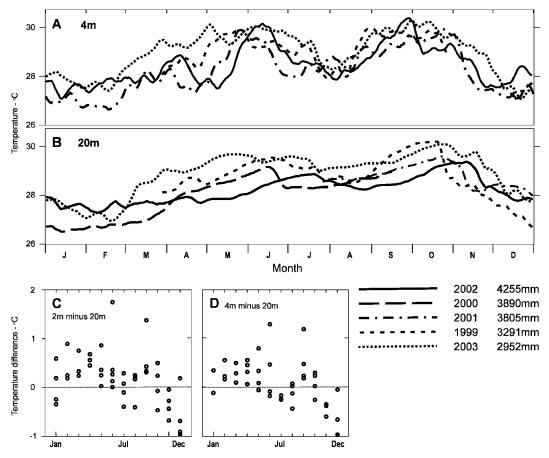


FIG. 4. Water temperatures at different depths: Isla Colón, 1999 to 2004. A: Running one week mean water temperatures at 4 m from Isla Colón. B. Same, for 20 m depth. In the legend, the column to the right is the total rain during the year from the Airport data. Heavier lines correspond to larger annual totals. C. Difference in mean monthly water temperature between 2 m (grassbed) and 20 m (coral reef) depths at Isla Colón. D. Same, for 4 m minus 20 m differences. Line in C and D is LOWESS smoother (Systat 9.0 SPSS, Inc., Chicago)

but significant in view of the temperature differences known to damage corals (below). The mean for Cayo Agua (29.7°C) was similar to Isla Colón. The mean temperature offshore was slightly colder (0.2 to 0.8°C) than all of the other sites. In the 23 year IGOSS record, the months with the lowest and highest mean temperatures were February (27.8°C) and September (28.9°C), respectively; thus the two-month means for the IGOSS data in Table 1 are a good representation of the coldest and warmest periods offshore. The January-February IGOSS mean matches that of Cayo Agua and is slightly warmer than the remaining sites. The September-October

offshore temperature however, is just 1.1°C warmer than the coldest months, while all of the inshore means are over 2°C warmer than their coldest months.

To determine whether water temperatures among the three sites were more different at some times of the year than others, we calculated the mean temperature for each month and examined the differences among them. (Fig. 3B, C) .The monthly differences between Cayo Agua and Isla Colón (Fig. 3B) were greatest during the beginning and end of the year, when Cayo Agua was as much as 0.5°C warmer. The monthly differences between Cayo Roldán and Colón were higher for the first 10

TABLE 1. Water temperature means, maxima, and minima for each site and depth. The inshore data is for all months for which we have at least 15 days of complete data, the IGOSS offshore data includes all data from April 7, 1999 to March 31, 2004 from quadrat noted in Fig. 3. Mean: Mean of 12 monthly means. Each of the 12 monthly means was based on 4 to 6 means for a given month from 1999 to 2004, but different months were missing in different years. Max, Min: The maximum and minimum of daily means found for each site. IGOSS offshore data are smoothed over 2 weeks so Max and Min are not tabulated. Jan-Feb Mean: Same as Mean but only January and February monthly means are used. Sept-Oct Mean: Same as Mean but only September and October means are used. Temperatures are °C.

	Depth	Mean	Max	Min	Jan- Feb Mean	Sept- Oct Mean
Cayo Agua	4 m	28.7	30.8	26.5	27.8	29.7
Cayo Roldán	4 m	29.1	31.6	25.8	27.9	30.5
Isla Colón Grassbed	2 m	28.6	31.4	25.6	27.5	29.7
Isla Colón Coral Reef	4 m	28.6	30.5	26.6	27.5	29.6
	10 m	28.5	30.8	25.9	27.3	29.7
	20 m	28.5	30.3	26.5	27.3	29.3
IGOSS offshore	0 m	28.3	_	_	27.8	28.9

months of the year and lower for November and December, but the ANOVA was not significant (Cayo Agua minus Colón, N=38, $r^2=0.723$, P<0.001, Roldán minus Colón, N=33, $r^2=0.416$, N.S.).

For all months combined, the mean difference in monthly means between Cayo Agua and Isla Colón was 0.16° C and the maximum difference was 0.63° C in December, 2002 (t-test Cayo Agua minus Colón, N = 38, P < 0.0001). The mean difference between Cayo Roldán and Isla Colón was 0.72° C and the maximum was 1.21° C in May, 2001 (Roldán minus Colón t-test, N = 33, P < 0.0001).

To contrast interannual differences in temperatures at different depths and relate them to annual rainfall, 7 day smoothed temperatures at 4 m and 20 m at Isla Colón were plotted on the same set of axes for each depth (Fig. 4A, B). Temperatures at 20 m did not vary over a period of weeks or even months as much as those at 4 m at Isla Colón, but over a period of several years, sometimes reached the same highs and lows (Table 1, Fig. 4). Years with high rainfall, 2002 and 2000, had generally lower temperatures than those years with lesser rainfall, 1999 and 2003, but there were numerous exceptions. This pattern is more distinct at 20 m. Note that four out of the five years for which we have water temperature data were years of above average rainfall (Fig. 4).

Intraseasonal patterns

In 15 years of monthly Airport data (1989-2004, Fig 5A), the month with the least median monthly total rainfall was September with less than half the rain of the greatest month in December. The other minimum and maximum of the year was February and June, respectively. The monthly pattern for 72 years of Changuinola data (not shown) was similar. The September to October minimum in rainfall is very regular. In the Changuinola data, it appears in box plots for every decade.

Water temperatures at the 2 m Isla Colón grassbed site (1999 to 2004 with some gaps, Fig. 5B) can be characterized as a period of rising temperatures from February to June, followed by a dip from July to September or October, and then a decrease reaching annual lows in December and extending to the following January and February.

As might be expected, the solar radiation data (Fig. 5C) shows maxima where rainfall is minimal and minima where rainfall is maximal, but the pattern is not as distinct. Wind speed (Fig. 5D) was less variable but because of the anemometer's sheltered location, the data do not show the strong NE trade winds that are present from mid-December to March each year. Air temperature (Fig. 5E) shows a pattern similar to that of the water temperature, although we only have one year of data. Relative humid-

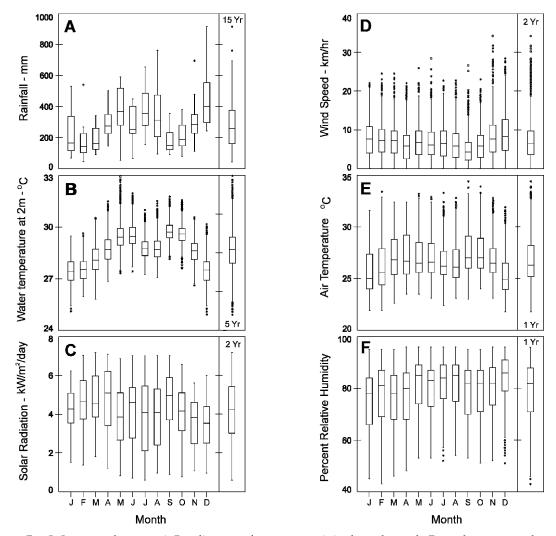


FIG. 5. Intraannual patterns 1. Box diagrams of summary statistics for each month. For each parameter, the box diagrams show the median (horizontal line) and the upper and lower quartiles enclosing 50% of the data (rectangle). The two lines above and below the rectangle extend to furthest points that are within a distance of 1.5 times the height of the rectangle. If there are any points outside of these boundaries, either above or below, they are each marked on the diagram with a symbol. (Systat 9.0, SPSS, Inc., Chicago).

To the right of each set of monthly diagrams is a box diagram showing the summary for the entire period that each monthly diagram covers. The length of the period is given at the top or bottom. A. Rainfall: Data are monthly totals from Airport data from January, 1989 to August, 2004. B. Water temperature: Data are sample water temperature for each hour from the Grassbed site (2m) from 4/25/99 to 4/24/04. C. Solar radiation: Data are daily totals from 8/17/02 to 8/16/04. D. Wind speed: data are mean scalar wind speed for each hour from 8/17/02 to 8/16/04. E. Air temperature: Data are sample air temperature for each hour from 1/1/03 to 12/31/03. F. Relative humidity: Data are sample relative humidity for each hour from 1/1/03 to 12/31/03.

ity (Fig. 5F) is strongly affected by temperature and is higher during months with higher temperatures and vice versa.

Generally, during periods of rising water temperatures, the 2 m site rose the most rapidly and peaked earlier and at the highest temperature (Fig. 4). The temperatures at the 4 m, 10 m and 20 m sites (not all shown) rose at successively lower rates and had lower and later peaks. In periods of temperature decline, usually during the peak rainfall months of August and De-

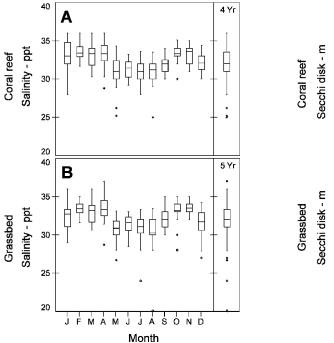
cember, the 2 m and 4 m sites dropped much faster and to a lower level than the 20 m site. The 10 m site usually followed the two shallower sites but sometimes maintained a higher temperature similar to the 20 m site. Sometimes, 20 m temperatures would continue to rise slowly for several weeks after the shallower water started dropping.

After periods of temperature decline at 10 m depth and above, temperatures at 20 m were often warmer. Presumably the water remained stratified because the colder surface water was less saline than the 20 m water and still less dense despite the temperature difference. This suggests that vertical mixing was not occurring at these times. Similar temperature reversals (not shown) were observed at Cayo Roldán, and these periods of temperature reversals would sometimes last for a month or more. These episodes occurred most often from June to August and October to January.

Salinities at both the Colón coral reef and the Colón grassbed sites (Fig. 6A, B) were high, around 34 ppt, during months of less rain and lower, 30 to 31 ppt, during the rainy months. At times the salinity fell to around 25 ppt, and once, associated with heavy rainfall, fell to 20 ppt in the grassbed site. The secchi disk readings (Fig. 6C, D) gradually decrease from high levels in February until July and August and then increase through October when there is reduced rainfall and higher salinity. The horizontal readings in the grassbed were generally lower than those at the coral reef, taken vertically.

Daily patterns

More rain falls at night than during the day, and the number of hours with measurable rain was greater at night than during the day (Fig. 7A). The least rainy part of the day was the late afternoon, from 1400 to 1700 h. To examine the amount of rain falling as part of heavy downpours rather than as light rain, the proportion of rain falling during hours categorized by amount of



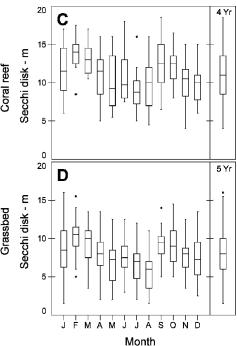


FIG. 6. Intraannual patterns 2. A, B. Salinity measured at 30 cm. at the coral and grassbed sites at Isla Colon. C, D. Secchi disk readings at same sites. The coral reef data is from vertical readings, the grassbed data from horizontal readings underwater near the surface. See Fig. 5 for explanation of box diagrams.

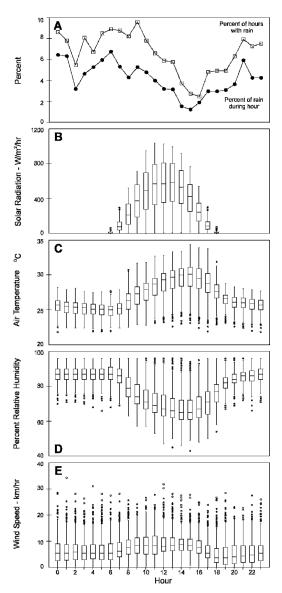


FIG. 7. Daily patterns. Box diagrams of summary statistics for each hour of the day. Each figure has the hour labeled as the time at the beginning of the hour. A. Tipping bucket data from August 17, 2002 to August 16, 2004. Upper line: Percent of hours with any amount of rain for each hour of the day. Lower line: Percent of total rain for the 2 years that fell in the designated hour. B. Solar radiation C. Air temperature D. Relative Humidity E. Wind speed. Sites, starting and ending dates, and summary statistics for B to D are the same as corresponding figure in Fig. 5. See Fig. 5 for explanation of box diagrams.

rain was tabulated (Table 2). Over 93% of the hours had no measurable rain, and 48% of the rain fell during 1% of the hours. Rainfall is infrequent and very patchy.

The amount of solar radiation for a mostly cloud free noon hour should be between 900 and 1040 W/m², depending on the time of year, (unpublished ESP data for STRI Galeta station near Colón). At the Bocas station, 75% of the hours had less than 800 W/m² of solar radiation for the noon hour and 50% of those hours had less than 600 W/m^2 , which is a bit over half that of a cloud free noon hour. This demonstrates that it is frequently cloudy, in sharp contrast to the small amount of time that rain is falling. The daily pattern (Fig. 7B) shows more light at noon, but, in the absence of clouds, the hours on either side of the noon hour should have a symmetrical pattern, since the local noon at the laboratory is 1230. However, the distribution of solar radiation is slightly skewed to the right, which is consistent with the number of hours with rain being less in the afternoon than in the morning. Air temperature peaks, and humidity reaches a minimum (Fig. 7C and D), at hour 15, about the same time as the rainfall reaches its low. Wind speed however (Fig. 7D), doesn't reach a minimum until hour 18, a time when the rainfall has already started increasing. Maximum wind speed during a typical hour (Fig. 7E) is less than 18 km/hr 50% of the time, but at times reaches 60km/hr.

The effect of weather on water temperature

Here, we analyzed the effect of solar radiation, rain, wind, humidity, and air temperature on water temperature at different depths and the periods of time over which high or low temperatures persisted.

Water temperature often fluctuates daily in response to radiant solar heating, as well as to other factors, with relative maxima around noon and minima at night (Table 3). At the 1 m site at Isla Colón, the diurnal fluctuations averaged 1.15°C but, the greatest one day temperature change was over 3°C. In the grassbed at 2 m, the greatest fluctuation was still 2.55°C. At 10 m and 20 m, there was often a daily signal

TABLE 2. Frequency distribution of rainfall. The amount of rain during each hour, in mm, is categorized by exponentially increasing size classes (Rainfall Category) from August 17, 2002 to August 16, 2004. The total rain that fell in hours belonging to each size class (Total Rain), the percent of the hours with rainfall amounts in each size class (Percent of Hours), and the percent of all of the rain falling in the two year period in each size class (Percent of Rain) are tabulated. The first size class, 0-2, has an upper bound just below the minimum amount recorded by the tipping bucket, 2.54 mm and so probably includes trace amounts of rain, but has 0 mm of rain tabulated in column 2.

Rainfall	Total	Number	Percent	Percent
Category	Rain	of	of	of
(mm)	(mm)	Hours	Hours	Rain
0-2	0	16381	93.4	0
2-4	1781	701	4.0	26.5
4-8	1694	285	1.6	25.2
8-16	1288	104	.59	19.1
16-32	1331	59	.34	19.8
32-64	536	13	.074	8.0
64	81	1	.006	1.2

TABLE 3. Daily temperature fluctuations. The mean and maximum of the daily temperature ranges in °C. Isla Colón 1 m 3/99-8/01, 2 m, 4 m, 10 m, 20 m 3/99-7/04. Cayo Roldán 1 m, 10 m, 20 m 4/99-9/00; 4 m 4/99-1/04. Cayo Agua 4 m 12/00-4/04. The 2 m site at Isla Colon is in the grassbed, the others at the coral reef.

 Depth	Isla Colón		Cay	o Roldán	Cayo Agua	
	Mean	Maximum	Mean	Maximum	Mean	Maximum
1m	1.15	3.07	0.80	2.81	_	_
2m	1.06	2.55	_	_	_	_
4m	0.38	1.29	0.65	2.36	.55	1.87
10m	0.34	1.29	0.47	1.54	_	_
20m	0.20	1.40	0.31	.92	_	_

present, but at other times, one level or the other would fluctuate several times a day in a pattern not related to the sun, or to the level immediately above or below it. The mean fluctuation decreased to 0.20°C at 20 m, but the maximum daily fluctuation observed was higher than the two levels above it. At 20 m, the daily signal was very weak (Fig. 4), but for brief periods each year, the temperature would fluctuate by up to a degree four or more times in the course of a day, evidently as a result of vertical mixing, and this is when the maximum daily fluctuation of 1.4°C was recorded.

The occasional periods of rapid fluctuations at 4 m and 10 m, with a random period not related to the sun, suggested vertical mixing. Often, fluctuations at one level were not observed at a shallower level, so the mechanism causing the fluctuations is probably not from wave turbulence, but may be from vertical density driven currents. Tidal currents cannot be discounted

although the mean tide range at Bocas del Toro is only 24 cm (Tides&Currents for Windows). Fluctuations at shallow depths appeared more often than those at 20 m and are not confined to the period of rapid cooling at the end of the year (Fig. 4A). At Cayo Roldán, the daily fluctuations were less than those at an equivalent depth at Isla Colón. Temperatures at Cayo Agua show fluctuations similar to Isla Colón, both at 4 m.

Over periods longer than a day, the relative fluctuations of solar radiation presumably result in increases or decreases in mean daily water temperature, but other parameters also have an effect. Wind and humidity would affect evaporative cooling of the water, air temperature, generally lower than water temperature, should cool the water, and rain mixing with the water either directly or through runoff, should also change the temperature. There would also be complex interactions among these

factors. Wind, for example, could cause vertical mixing, and the resultant change in surface temperature would affect the rate of radiative cooling. Here, however, we are not interested in a complete model of the effects of all of these factors. Solar radiation is the major source of energy into the bay, and we wanted to demonstrate the relation between it, rainfall, and changes in water temperature.

To evaluate the main effects of various meteorological parameters on the 2 m Colón grassbed water temperature, we used a multiple linear regression to compare the 72 hour change in water temperature to various 72 hour summaries of solar radiation, wind speed, rainfall, air temperature and humidity. The grassbed site was used because it is expected to show a stronger and more immediate response to meteorological parameters. A small stream entering on the northwest side of the bay may have provided more of a runoff effect than at other, more open sites. Water temperatures were smoothed over a 24 hour period centered on each hour to remove diurnal effects and then the 72 hour change in temperature was calculated for each hour. For rainfall and solar radiation, each smoothed point was the sum over the previous 72 hours. Rainfall and solar radiation totals were square root transformed to make the relation with change in water temperature linear. The solar radiation sum was divided by 3 so it would be expressed as an average daily total. For wind speed and air temperature, we calculated the mean over the previous 72 hours. Humidity was arcsine transformed before calculating the 72 hour mean. After transformations, the response and predictor variables were generally linear with respect to each other except for arcsine transformed relative humidity. At humidity values less than the mean, water temperature change was lower than expected based on the trend for values greater than the mean. Solar radiation and air temperature were similarly lower than expected but rainfall and air temperature were higher than the trend expected from higher humidity values. Most, but not all of these low humidity points were in the drier parts of the year, January to March and September to October.

We then picked the hour from 1200 to 1300 on two days each week, 3 to 4 days apart (Sundays and Wednesdays) and calculated two separate multiple linear regressions for water temperature change against the meteorological parameters, one for below average humidity, and the other for above average humidity. Both regressions were significant, the first explained 23.5% of the variance, the second 44.5%. The effect of solar radiation was significant in both (P = 0.002 and P < 0.0005 with Bonferroni adjustments, N = 69 and 61). None of the remaining effects, including humidity, were significant. The humidity and air temperature variables exhibited collinearity.

Initially, we used data from mid 2002 to the end of 2003, the period for which we had data on all 5 meteorological parameters. Since temperature and humidity did not have significant effects and we lacked data for an additional year from these two, we removed them from the analysis. We had data for the remaining parameters up to November, 2004. The second regression analysis, using solar radiation, wind speed, and rainfall, explained 40.7% of the variance and was highly significant (N = 207, P < 0.0005). Solar radiation showed the strongest effect on change in water temperature with a standardized coefficient of 0.500 and the transformed wind speed was next with a standardized coefficient of −0.184. Both effects were significant (P < 0.0005 and P = 0.008, respectively) The difference in signs indicates that solar radiation increases water temperature and wind decreases it, and the greater magnitude of the standardized coefficient for solar radiation indicates a greater effect from variations in solar radiation than from wind. The effect of wind is probably a combination of evaporative cooling mediated by air temperature and humidity and vertical mixing. It is likely to have a stronger effect less sheltered sites. The effect of rainfall was not significant (P = 0.642). When the regression used hour 8 instead of 12, a time when the effect of the most recent solar radiation is less compared to wind speed, the results are similar but the standardized coefficients for solar radiation and wind speed are 0.331 and -0.227 and the regression accounts for only 28.4% of the variation.

A similar regression against the 72 hour change in water temperature was done for solar radiation alone at depths of 2 m, 4 m, 10 m, and 20 m at the Isla Colón grassbed and coral reef sites (Fig. 8). (r²: 0.308, 0.347, 0.341, and 0.084. Regression slopes: 0.209, 0.162, 0.155, and 0.037, units are $^{\circ}$ C /kW/m²/ day, N = 196, 197, 173, and 197, P < 0.001 in all cases). For the top three levels, there was a strong effect on water temperature from solar radiation, decreasing slightly with depth. At 20 m, the effect of solar radiation was very weak, but the regression was still significant. At all four depths, the point at which the regression line crossed from a positive to negative effect was a daily average of about 4 kW/m²/day. This is approximately the median value for annual solar radiation (Fig. 5C). At 2 m, three days of solar radiation averaging 6 kW/m²/day, or 3 kW/m²/day above the median, increased the daily mean water temperature by an average of 0.62° C (= 0.209×3).

There are much longer records available for rainfall than for water temperatures, and any correlation found would be useful in estimating historical water temperature ranges. Although rainfall did not appear to affect water temperature over 72 hours, we looked for an effect of monthly total rainfall on monthly water temperature change. Because rain is accompanied by clouds and hence reduced solar radiation, and also by

stronger winds, the cumulative effect of a month of rain would be expected to reduce water temperature. Elevated humidity accompanying rainfall might be expected reduce evaporation and partially offset the cooling effects of wind. In fact, lower water temperatures in rainier years had already been observed (Fig. 4). To measure the effect of rainfall, which implicitly includes effects from wind, runoff, and humidity, we compared the monthly change in water temperature with monthly totals from the Airport data up to the end of 2001 and after that with the Daily ESP data corrected with Airport/Daily ESP regression parameters. Changes in mean daily water temperature at 4 m from the beginning to end of each month at Isla Colón were used as the dependent variable in a regression against the monthly Airport/Daily ESP data. The regression was significant (N = 48, P = 0.032), but the regression only explained 9.6% of the variance. To explain some of the reasons for the low correlation between rainfall and temperature change, two more regressions were done, one to check the effect of rain on solar radiation and another to check the effect of solar radiation on water temperature. Using monthly rain as the independent variable and mean daily total solar radiation as the dependent variable, the regression was significant (N = 22, P =0.002) and the regression explained 38.7% of the variance. Using the mean daily total solar radiation as the independent variable and the water temperature as the depen-

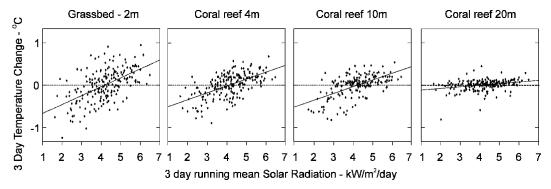


FIG. 8. Relation between solar radiation and change in water temperature. Regression between 72 hr temperature change and 72 hr total solar radiation (divided by 3 to adjust to a daily value). Temperature was first smoothed with a 24 hr running mean. Values at noon on Sundays and Wednesdays were used to avoid overlap. Data was from the Isla Colón 2 m grassbed, and the 4, 10 and 20 m coral reef sites.

dent variable, again the regression was significant (N = 22, P = 0.006), and the regression explained 31.9% of the variance, similar to the results obtained with the 72 hour regression above. The difference in N between the three regressions is because we have 48 months of combined water temperature and rainfall data starting in 1999 but we have only 22 months of combined solar radiation, rainfall and water temperature data, starting in 2002.

One year of meteorological and marine changes

To demonstrate the effect of meteorological conditions on the water temperature, a graph was prepared of the parameters over an entire year, 2003 (Fig. 9). The bottom four graphs in the figure show three day

running means and totals. The horizontal line through the wind speed graph is at 6.5 km/hr, the median annual value wind speed (Fig. 5D). Note that peaks in wind speed are often associated with peaks in rainfall but that the relative height of the rainfall peaks are not necessarily correlated with the height of the wind peaks. Since the anemometer is in a protected area, it does not accurately record wind from the NW to NE. Strong NW winds are found in other parts of Panama from late December to mid-April (Cubit 1989; Robertson et al. 1999; Windsor 1990) which would often be associated with clear skies and lack of rain. These winds are present in Bocas del Toro in more exposed areas and probably affect water conditions in these areas more than they do in our coral reef and grassbed sites on Isla Colón. However, the anemometer

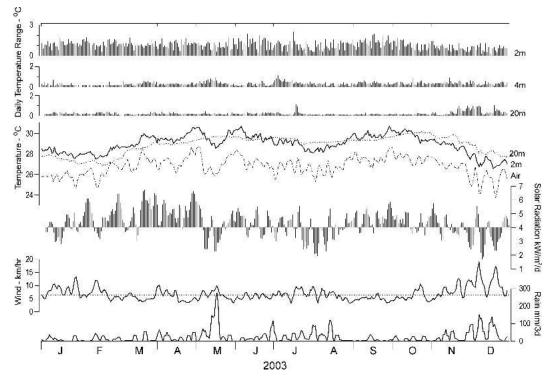


FIG. 9. Effect of rain, wind, solar radiation, and air temperature on water temperature. Data for the year 2003 are shown. Data for each day at noon are plotted. The following are running totals and means are for the 72 hours preceding the plotted point. Water temperatures are means for the 24 hours centered on noon. From the bottom up: Rain-total in mm. Wind–mean scalar wind speed in km/hr. Solar radiation: mean total daily solar radiation (divided by 3) in kW/m2/day. The values are plotted as values above and below 4 kW/m2/d. Air temperature: mean in °C. Water temperature: 24 hour running means centered on noon in °C. 2 m grassbed, 4 m coral reef, as labeled. Maximum daily temperature range at 20 m, 4 m, and 2 m: taken from the coral reef and grassbed sites.

probably provides a good indication of local wind conditions at the STRI lab and in other places along the south sides of islands in the archipelago, and so one could conclude that moderate winds are most often associated with rain there. The daily total solar radiation was plotted as anomalies from the annual median daily solar radiation, about 4 kW/m2/day (Fig. 5C).

Daily mean air temperatures and water temperatures at 2 m rise and fall together and the highs and lows are correlated with those in rain, wind, and solar radiation. Water temperature at 20 m behaved quite differently. It was much more stable, without the 1 to 2 degree changes over the course of a month, except in late November and December. At times, it didn't change at all (within the 0.18°C sensitivity of the thermometers) for over a day at a time. There were three periods during the year (mid-May, July to August, and mid-October to December) when the 20 m temperature was as much as a degree warmer than the 2 m temperature.

The top three graphs in Fig. 9 show temperature ranges, each vertical bar showing the range for one day. Temperature changes are relatively high and uniform throughout the year. At 4 m, the changes are less. Note the period of high fluctuations at the end of the year at 20 m. This was a period of heavy rainfall, high winds, low solar radiation, when the 2 m temperatures were lower than the 20 m temperatures. The pattern of relatively large (>1°C) daily fluctuation at 20 m over a short period of descending temperatures in November or December is also present in each of the four years (1999, 2001-2003) for which we have November and December data. At 4 m there are several periods of higher daily fluctuations, particularly in May and July. At these times, the fluctuations happen irregularly and are not related to changes in solar radiation.

DISCUSSION

Bocas del Toro rainfall

Rainfall in Central America is related to the ENSO (El Niño/Southern Oscillation), but not in a simple way. The sea surface temperature anomalies in the Tropical North Atlantic and in the eastern tropical Pacific play more important roles, and sometimes they are correlated with one another and with El Niño (sea surface temperature anomalies in the eastern Pacific), and sometimes not (Enfield and Alfaro 1999; Alfaro 2003).

There are two patterns of annual rainfall in Central America (Magaña et al. 1999; Alfaro 2002). The most widespread consists of a dry season from the middle of November to the middle of May with a rainy season for the remaining months, mid-spring to late fall. There is a mid-summer reduction in rain in July and August, called variously the veranillo, canicula or Mid Summer Drought. In Panama it is called the Veranillo de San Juan (Espinosa 1998). The summer rains in this cycle are a result of convective activity from the northern migration of the ITCZ as well as easterly waves, atmospheric disturbances moving westwards from April to November in the tropical North Atlantic (Magaña 2003; Enfield and Alfaro 1999). In the winter, when the ITCZ moves south with the sun, the rains stop, strong northeast winds develop, and there are high levels of solar radiation, even though the sun at noon is below the equator. Rainfall patterns in Central America are however rather variable and they are not entirely governed by maritime air masses. The mountains and the dynamics of the Central American atmosphere can cause local and seasonal variations, so much so that the second pattern is quite different from the first (Alfaro 2002).

Alfaro (2002) described the second pattern as having a nearly homogenous period from January to the middle of October, followed by a period of heavier rain at the end of the year, although he notes that this homogenous period has a minimum in March and a relative maximum in July. This pattern matched his stations along the Caribbean coast of Honduras, Costa Rica and Panama.

Bocas del Toro has this Caribbean pattern, but with some substantial differences (Fig. 5A). While there is no dry season, there is relatively dry period in February and March and another, slightly drier, in September and October. The heaviest rain comes in December, but is rivaled by a July high. This September low is found both in the 72 year record from Changuinola and the 15 year Airport record. In other words, the slight pattern in Alfaro's "nearly homogenous" period is accentuated in Bocas del Toro. Some of these differences may be attributed to Bocas del Toro's location in the far south of the range of Alfaro's sites. Sites to the south had earlier starting points for the wet season of the more common pattern, related to the earlier arrival of the ITCZ and perhaps this is related to Bocas del Toro's more extreme form of the Caribbean pattern. The heavy winter rain can be attributed to frontal systems from the north moving into the tropics (Magaña et al. 2003; Empresa de Transmision Electrica

The rainfall pattern at the STRI lab at Galeta, near Colón on the Caribbean side, follows the more common rainfall pattern with a distinct dry season during the boreal winter, but the timing of the onset of the dry season is different with heavy rain usually lasting into the middle of December (Cubit 1989). On Barro Colorado Island, Panama, the dry season is generally from January to March, and the daily pattern is the opposite of that in Bocas del Toro, with maximum rainfall occurring in the early afternoon (Windsor 1990).

The diurnal cycle of low precipitation in the late afternoon and a high early in the morning (Fig. 7A) is typical of northern hemisphere and tropical oceans adjacent to large land masses and is the opposite of the pattern normally found on land. According to one theory, on land late afternoon thundershowers develop because of solar heating of the land and produces convective currents of rising moist air. At sea, this effect is not as strong and air tends to flow towards continents to replace the rising air. At night winds flow in the opposite direction as the land cools faster than the sea, and the warm air flowing out to sea produces nighttime precipitation (Dai 2001).

A competing theory (Mapes et. al. 2003b) explains such a diurnal cycle along the coast of Columbia as the result of gravity

waves developing from land heating and propagating toward the sea. The waves operate at a higher altitude than sea breeze/land breeze theory above and do not involve horizontal translation of moisture but rather a compression and decompression of the air. During the day these waves result in a warm anomaly over the ocean which effectively cap any convective activity and reduce the amount of rain. At night, they result in a cool anomaly and enhance convective activity. The nightly seaward breeze of the first theory, according Mapes et al. (2003b) is not strong enough to produce the observed offshore convection.

An interesting element of the model used by Mapes et al. (2003a, 2003b) and observed in data from that area, is a very sharp gradient in rainfall along the coast, with more rain at sea and less over the land. They attribute this to a thin layer of cool near-surface air, below the air producing the gravity waves, which develops over the land at night and inhibits convective processes on the landward side of the coast. This would explain the lower annual mean rainfall at Changuinola, 8 km inland from the coast, 2615 mm, compared to the airport data at Bocas del Toro, 3277 mm.

Factors affecting water temperature

The relationship observed between rainfall, solar radiation, and water temperature can explain many elements of the annual cycle of temperature extremes and nutrient mixing in Bahía Almirante, as exemplified by Fig. 9. At the Colón site in Bahía Almirante and over periods of three days, solar radiation is the most important determinant of water temperature changes, followed by wind speed (Fig. 8). Rainfall does not show a strong correlation. Over periods of a month, there is a correlation between rainfall and water temperature, but as mentioned, the percent of the variation in water temperature explained by rainfall is only 9.6% while rainfall explains 38.7% of the variation in solar radiation, and solar radiation explains 31.9% of the variation in water temperature. If the factors affecting the correlation between rainfall and solar radiation are different from those affecting

the correlation between solar radiation and water temperature, then the product of the two $(0.387 \times 0.319 = 0.123)$ should approximate the relatively low proportion of the water temperature change explained by rainfall, which it does. Since it rains for only a small proportion of the time (Fig. 7A) and mostly at night, and when it does rain, most of the rain falls in an even smaller proportion of the hours (Table 2), it is not unreasonable to expect that the factors affecting the production of rain from convection clouds in the atmosphere would not be closely related to factors affecting vertical mixing in the water column. Wind, which accompanies rain and increases cooling by evaporation, is a possible exception, but it is not always closely correlated with rainfall.

Increased rainfall then can be expected to be related to lower water temperatures and vice versa, but the effect will not be a strong one and would probably only be obvious over periods longer than a month. In fact, years with heavy rainfall had generally lower water temperatures over a year than those years with less rainfall (Fig. 4), but this did not result in persistent temperature differences from the offshore temperatures into subsequent years. Note that 2002 had more rain than any year in the 78 year Changuinola record. Temperatures at 20 m for that year were generally lower than for all of the other years except for those at the end of 1999 and the beginning of 2000.

On the other hand, the 4 m temperatures in June and October of 2002 are among the highest observed, reaching a 30.7°C in early October. Even in an otherwise rainy year then, a month of clear skies can result in elevated temperatures. Of the five years for which we have nearly complete water temperature data, four had above average rainfall, and the fifth, 2003, was not appreciably below average. It is possible that a dry year, with even longer periods of above average solar radiation than observed, could have higher temperatures. But, because of the loose coupling of rainfall and water temperature, rainfall records may not necessarily indicate periods of elevated or reduced temperatures.

Another factor affecting water tempera-

ture and for which we have no direct measure is the influence of runoff from rivers. However, changes in water temperature happen uniformly over the entire bay, and this uniformity even extends to Cayo Agua at the edge of the Chiriquí Lagoon which has several large rivers draining into it (Fig. 3) and would be expected to show a different response to runoff than Bahía Almirante. This large scale uniformity in temperature response suggests that local effects, such as freshwater runoff, are not a major factor in determining water temperature. The influence of marine currents on water temperature changes has not been directly addressed in this study. We suggested above that even though the tidal range is small, subsurface currents may have been responsible for some of the rapid fluctuations found at some depths while leaving water just above and below unchanged. The strong northeast winds that are known to occur from late December to March may bring in some offshore water, particularly to Cayo Agua, but most of the cooling observed is during the period of heavy rain just before these winds develop. Most of the time, inshore water is either warmer or colder than offshore water and our argument is that local solar radiation, and other associated parameters, creates substantial differences from offshore waters, regardless of the amount of mixing.

The reason that Bahía Almirante and the outer part of Chiriqui Lagoon at Cayo Aqua has 4m temperatures higher than the surface temperatures offshore may be because the inshore waters receive relatively more solar radiation than offshore. An explanation for this could be a thin layer of cold air developing over land at night, mentioned above, which inhibits convection landward of the coastline (Mapes et al. 2003b). If the effect of this layer extended seaward, perhaps aided with a cold thermally driven slope breeze from the 3000 m mountains immediately southwest of Bahía Almirante, convection might be partially inhibited during the morning hours and the increased solar radiation would heat the water relative to the offshore water. The effect would be stronger at Cayo Roldán which is more landlocked and closer to the mountains than the other two sites.

Temperature inversions and vertical mixing

Mixing of the water column, and in particular the mixing of nutrients brought in by runoff (D'Croz 2005) depends largely on the density of the surface water relative to deeper water, and there are two opposing processes affecting this. Normally one would expect the top layers of water to be warmer than the lower layers since warm water is less dense. Less saline water is also less dense, but when it is added to the bay during rainy periods, the rain is accompanied by clouds and wind, which cool the water. If it cools too much, it will sink, but if not, it could float on top and still be colder than the underlying water. The periods when lower salinity, and presumably nutrient rich, surface water floats on top of warmer bottom water are not evenly distributed throughout the year, but are most often found during the rainier months of May to August and October to December (Fig. 4C, D). Periods without temperature inversions, February to May, and September, are associated with months having less rain, when surface warming from increased solar radiation maintains a more normal thermocline.

Presumably, the rapid daily temperature fluctuations observed annually at 20 m at the end of the year indicate vertical mixing. That the fluctuations occur without simultaneous fluctuations at more shallow depths suggest that these were the result of local subsidence events because of the drop in water temperature rather than turbulent mixing from wind. Normally the rain, and associated runoff, would be expected to decrease the density of the surface water and inhibit mixing, but the decreased temperature reduces the density enough for it to sink. The increased wind may contribute to mixing, but subsidence from increased density seems more likely since the fluctuations of the 4 m and 10 m water were often not present when the 20 m water was undergoing fluctuations. This suggests that turbulent mixing was not happening since it would have affected all depths at once.

Throughout the year, there were several times when the 2 m water, as well as the 4 m (Fig. 9) and even the 10 m water (not shown), were colder than the 20 m water for two or more weeks at a time. If they didn't mix with the underlying water even when colder, it suggests that there was very little vertical mixing with the 20 m water occurring throughout most of the year, along the lee side of Isla Colón. The diurnal stability of the 20 m water for most of 2003, except November and December and a few days in July confirms this. We don't have sufficient data to determine if this stability at 20 m extends to other parts of Bahía Almirante.

Temperature stress differences among sites and depths

Temperature increases of 1 degree above the summer mean maxima are known to damage or kill corals, (Glynn and D'Croz 1990; Jokiel and Brown 2004), so the small differences in temperature noted at different depths and at the three different sites can have a substantial impact on the corals and other organisms in the Bocas del Toro area. Of equal importance is the length of time that water temperatures stay elevated as well as the presence of other factors such as lowered salinity, turbidity, and amount of mixing of the water column.

Cayo Roldán often has 4 m temperatures more than a degree higher than Isla Colón, and these usually occur during the middle of the year when temperatures are already high. Its lowest temperatures are sometimes as low as Isla Colón (Table 1) and as the offshore surface temperatures (Fig. 3A, C), so overall, Cayo Roldán has a higher annual temperature range and higher overall temperatures. Cayo Agua often has temperatures about 0.5 degrees warmer than at Isla Colón, but these often occur during the beginning and end of the year when the water is colder (Fig. 3A, B). During the warm part of the year, temperature differences are less. In other words, the temperature at Cayo Agua does not exhibit excursions from the offshore water as extreme as at Cayo Roldán and has slightly lower excursions than at Isla Colón. This is probably because it is more exposed to the open ocean and not surrounded by as much land.

Although the annual range of temperatures is similar at all depths, there is a substantial difference in the rate and frequency of temperature changes at each depth. Observed as a seven day running mean (Fig. 4), 4 m temperatures at Cayo Roldán changed more rapidly and frequently than at 20 m (Fig. 4). Mean daily temperature fluctuations were as much as five times greater at 2 m than 20 m at Isla Colón (1.06°C vs. 0.20°C). Although the difference in maximum fluctuation values were not as extreme, large temperature fluctuations in shallow water were a daily event at 2 m, but only occurred a few times a year at 4 m and once a year at 20 m (Fig. 9). At Isla Colón, the maximum fluctuations in 1 m to 2 m of water ranged from 2.6°C to 3.1°C and were about half this at 4 m to 20 m. At Cavo Roldán, the mean daily fluctuations at 4 m and deeper were larger than those at Isla Colón, while the 1 m fluctuation was less.

The Cayo Roldán site then, is potentially the most stressful for corals and other organisms, based on its higher mean temperature (about 0.9°C) and its even higher (up to 1.3°C) differences from Isla Colón temperatures at 4 m. Cayo Agua is the least stressful based on its mean temperature being slightly lower than Isla Colón and its tending to be slightly warmer than Isla Colón during the colder parts of the year, thus reducing its overall temperature range. At all sites, temperature fluctuations are greater and more frequent at shallower depths, but even at 20 m, it is possible for animals to be subjected to short term fluctuations of over 1°C. Over several years, temperature ranges at 20 m are approximately the same as the range in daily mean temperatures at 1 m to 2 m. Besides temperature stress, shallow sites may be subjected to salinities of up to 20 ppt, and higher turbidity, particularly in small shallow bays like that at Isla Colón. All three sites were more stressful for temperature sensitive organisms than the offshore waters, which had a range of just 1.1°C between the means for the coldest and warmest months of the year.

Water temperatures can rise substantially in with just a few weeks of high solar radiation, even at 20 m. At 4 m, mean daily water temperature was observed to rise 2.8°C in just 30 days at Isla Colón. The data for this study only encompassed five years of water temperature data and one would expect that a longer record might have included periods with unusually long stretches of clear weather and subsequent higher temperatures. This could happen even if offshore temperatures were normal, just because of the vagaries of the local weather. If there were such a period of elevated temperatures, the temperature stress would probably be most extreme at the more inshore sites. Similar inshore excursions from offshore temperatures have been documented in Hawaii (Jokiel and Brown 2004).

CONCLUSIONS

Organisms inhabiting inshore waters experience a substantially different environment than those exposed to offshore waters, and these differences are often closely related to local weather phenomena. Temperatures of offshore surface water are affected by complex global weather patterns which generally also affect inshore water. But land, and in particular mountains and the shape and location of shorelines can alter these patterns. The wide variation in rainfall over short distances in Central America testifies to this.

Bahía Almirante is a small bay almost entirely surrounded by land, with a very limited watershed and relatively little circulation from the Caribbean Sea adjacent to it. The annual rainfall pattern is similar to other Caribbean coastal sites in that it does not have the pronounced dry season during the winter that most of the Pacific side and interior parts of Central America have. However, unlike other more northern Caribbean coastal sites, it has two distinct periods with lesser amounts of rain instead of just one. The water in the bay has near marine salinities and supports a wide variety of corals and other reef building organisms.

Elevated temperatures in the bay are cor-

related with periods of high solar radiation, and the converse is also true, so the primary determinate of water temperature, or more precisely its excursions from offshore water temperatures, is the amount of convective activity over the bay. When atmospheric conditions enhance convection, clouds form, sometimes accompanied by rain and wind, solar radiation during the day decreases, and the water cools. Extended periods with few clouds can result in temperatures of over 30°C. Water closer to the mainland usually has temperatures even greater than water closer to the ocean.

Elevated water temperatures, particularly those that persist for extended periods of weeks to months, cause stress to many organisms, particularly corals. Because the temperature stresses at Bocas del Toro occur as a result of differences in insolation, they are more intense at shallower depths than at 20 m, although extended elevated temperatures at 20 m also occur. Stresses from reduced salinity and turbidity accompanying rain are also present in Bahía Almirante, even though it has a relatively small watershed.

Extended cloudy periods cause temperatures at 10 m and above to drop below 20 m temperatures for a month or more. This temperature inversion is maintained by the slightly lowered salinity from rain accompanying the clouds and indicates that little vertical mixing is occurring. At the end of the year, decreased solar radiation, often accompanied by heavy rain, lowers temperatures to their annual lows and the 20 m water is then mixed with the upper layers. There is evidence that there is more frequent turbulent mixing within the upper 10 m of water.

Since water temperature in Bocas del Toro is strongly influenced by insolation and hence the amount of clouds, one might expect historical rainfall records to be a good predictor of past temperatures stresses. Unfortunately, monthly rainfall totals only explain 9.6% of the variation in monthly water temperature changes. Even during a particularly rainy year there can be several months of relatively clear skies that result in elevated temperatures. The year 2002 was the rainiest since 1926 and

yet water temperatures for June and September were among the highest recorded.

The annual range in water temperature in Bahía Almirante is more than twice that in the offshore waters, and the frequency of rapid temperature changes over periods of several weeks is also higher. Local meteorological conditions then have intensified the seasonal offshore temperature ranges and have even created a stress gradient from the outer to the inner part of the bay. Cold thermally driven breezes flowing over the bay from the mountains to the southwest may be causing this by inhibiting convection during the morning hours. The effect is mostly to increase temperature, but evaporative cooling during storms can also reduce temperatures below those offshore. Periods of clear skies for a month can result in elevated water temperatures at 4 m of almost 3°C. Other tropical embayments with restricted circulation might be subject to similar temperature increases above adjacent open ocean water.

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