Spatio-temporal variation in seawater characteristics in a semi-enclosed bay in St. John, U.S. Virgin Islands

Geoffrey Horst and Peter J. Edmunds

ABSTRACT.—An important goal of coral reef ecology is elucidating the factors driving the distribution of corals, and to this end much attention has focused on disturbances and biotic agents. In this study, small-scale variations in the abiotic characteristics of seawater along the south coast of St. John, U.S. Virgin Islands, were quantified with the objective of assessing its potential to contribute to variation in coral community structure. This goal was achieved by combining several studies that were completed between 1994 and 2005, and were designed separately to measure flow, in situ light intensities, and dissolved inorganic carbon (DIC) chemistry. Together, the results reveal a slow westward surface flow at mean speed of 3.4 cm s⁻¹, and high residency times within semi-enclosed bays. Upstream versus downstream locations periodically differed in light levels, and short-term measurements of DIC chemistry identified diel variation in aragonite saturation state that appeared to intensify in downstream locations. The association between flow and the abiotic properties of seawater suggests that small-scale patterns in water circulation are related to physical gradients that have the potential to mediate the distribution of corals.

KEYWORDS.—DIC, pH, temperature, coral, reef, Caribbean, chemistry

INTRODUCTION

Large differences in coral reef community structure are common on reefs separated in space by kilometers (Edmunds and Bruno, 1996), and in time by years or decades (Aronson et al., 2002). Such variability typically is attributed to the history of biotic phenomena (Aronson and Precht, 2001) and acute abiotic disturbances (Woodley et al., 1981). Although abiotic factors, such as gradients in flow speeds and seawater temperatures, also can contribute to variation in coral reef community structure, to date these effects have received little attention (Glynn, 1973; Monismith, 2007).

The flow of seawater affects coral community structure through multiple pathways, for example, by modulating community metabolism through the changes in temperature and seawater chemistry that occur over shallow habitats (Monismith, 2007). It also mediates the transport of pelagic larvae (Morgan, 2001), with the possibilities that larvae are dispersed, retained within a fixed area, or entrained into nearby waters dependent on the biotic characteristics of the larvae themselves, flow regimes, and bathymetry (Morgan, 2001). One aspect of the flow regime — the near-bottom, instantaneous flow — interacts with benthic roughness elements to control the transport of metabolites through the benthic boundary layer (Monismith, 2007), thereby affecting community metabolism (Carpenter and Williams 2007). The characteristics of the benthic boundary layer also can affect seawater chemistry, sometimes to a large extent in areas with low flow speeds, shallow water, and high residency times (Suzuki and Kawahata, 2003, Watanabe et al. 2006). See Monismith (2007) for a recent review of hydrodynamic processes on reefs at multiple spatial scales.

On shallow coral reefs, the CO₂ concentration of seawater can be modified within
hours-to-days as it flows over the benthic community. This effect is mediated primarily through CO_2 fluxes driven by benthic photosynthesis, respiration, and (to a lesser extent) calcification (Gattuso et al., 1996; Kleypas and Langdon 2006). The change in concentration of CO_2 alters seawater pH and the relative abundance of the different forms of dissolved inorganic carbon (DIC), which affects the aragonite saturation state (Ω) (Kleypas and Langdon 2006). Ω is the ratio of the ion concentration product ([Ca^{2+}] x [CO_3^{2-}]) to the solubility product of aragonite (K_{sp}), the mineral form of CaCO_3 that is deposited by scleractinian corals, and it plays a critical role through direct proportionality in regulating rates of coral calcification (Kleypas and Langdon, 2006).

The goal of this study was to describe the abiotic environment over a fringing reef with the objective of completing measurements on a spatial scale commensurate with the scale of biological phenomena that are of interest to reef ecologists. Specifically, we sought to define physical properties on a spatial scale that might be insightful to understanding the distribution of benthic taxa, rather than on the larger scale that typically is the domain of physical oceanographers. To achieve our goal, we focused on the fringing reefs along the south coast of St. John, U.S. Virgin Islands, and pooled the results of several studies that were completed between 1994 and 2005 and were designed for purposes differing from the one developed here. We reasoned that together these studies would attain emergent properties that would provide more information concerning the characteristics of seawater in the study location than the sum of the parts. This approach assumes that the characteristics of seawater transport (e.g., flow speed and direction) remained similar over the study period, which is reasonable for the resolution with which it was recorded. Our analyses combine kilometer-scale measurements of three abiotic factors – water motion, in situ light intensities, and the DIC chemistry of seawater – in order to explore their potential to affect coral community structure.

Materials and Methods

Study Site

All measurements were conducted between Cabritte Horn and White Point (Fig. 1), which enclose three bays characterized by calm conditions, weak flows, and shallow seawater. The reefs in the study area consist of a narrow fringing component in shallow water (<15-m depth) with low coral cover (<10%), and patches of Montastraea annularis in deeper water (Edmunds and Elahi, 2007). Overall, macroalgae dominate the substratum on virtually all these hard-bottom communities (Edmunds, 2002).

Measurement of flow

Surface flow was measured using drogues similar to those of Austin and Atkinson (2004) that were fabricated from PVC pipe with vanes (0.5 x 0.5 m) suspended at 5-m depth from a float. When the drogue study was designed, the objective was to track the movement of neutrally buoyant particles at the depth of survey areas used for the census of coral recruits (Edmunds, 2000), and therefore they were constructed with the vanes at 5-m depth. The drogues were deployed in near shore locations (<100 m from land) for short periods (<10 h) in August 1994, May/June 1995, and May/June 1996 (Fig. 1), and their positions determined by triangulation using a compass. The positions were plotted on a chart, the net direction determined, and the speed estimated by dividing the straight line between the initial and final positions by the drift duration. The results were pooled among all deployments and summarized by the direction moved (with 45° resolution) and the net speed using a two variable (direction and speed), circular histogram; Oriana 2.02e software was used for this purpose (Rockware USA, Golden, CO).

In situ light intensity

In situ light intensity on either side of the study area was recorded at 9-m depth using paired loggers (Hobo Micro Station Logger H21-002) attached to cosine corrected sensors (Onset S-LIA-M003) that recorded photosynthetically active radiation every 10 minutes.
The instruments were placed in waterproof housings (Ikelite) with the sensor beneath the flat acrylic lid. On 6 August 2005, the instruments were placed at Yawzi Point and adjacent to Tektite, with the sensor oriented in a horizontal plane using a level. The instruments were positioned to avoid early morning and late afternoon shading, and were recovered after 3 days. Inter-calibration of the sensors within the housings was accomplished by placing them adjacent to one another in the same irradiance regime.

**Dissolved Inorganic Carbon Chemistry**

DIC chemistry was quantified at six sites between Cabritte Horn and White Point (Fig. 1) during August 2003. The objective...
was to determine whether DIC chemistry varied among the sampled sites during the study period. Diel patterns in DIC chemistry were characterized by sampling every 3 h on 17/18 August and 22/23 August, as well as during the day at 07:00, 13:00 and 19:00 h on 25, 26 and 27 August. For each sampling, seawater was collected from 3-m depth, transferred to a 250 ml air-free BOD bottle, and transported to the lab for immediate processing; samples were collected from all six sites within 20 minutes. Seawater pH was measured (± 0.001 units) using a pH meter (Orion, model 920A) and combination electrode (Orion model 9157 ATC) that was calibrated before each sampling using certified buffers (Fisher). The alkalinity was measured within 2 h of collection using potentiometric titration with 0.082 M HCl (Fisher, reagent grade), and used together with the pH to calculate \( \Omega_a \) using CO2SYS software (Lewis and Wallace, 1998). \( \Omega_a \) was calculated for a standard temperature of 28.0 °C, which was the average temperature of the seawater during the sampling period. Although slight variations in seawater temperature occurred within the study areas, for example diurnally (typically < 0.4 °C) a temperature fluctuation of this magnitude would affect \( \Omega_a \) by only about 0.02 units (G. Horst, unpublished data).

Statistical analyses

A Wilcoxon's signed-ranks test was used to compare the light data between sites with the observations blocked by the sampling interval (10 minutes). The sampling for DIC chemistry at 3-h intervals was used to describe the diel fluctuations without statistical analysis because only two replicate measurements were available for the nighttime samplings. However, the daytime sampling at 6-h intervals was completed for 5 days, and therefore was statistically analyzed for site and time effects. This analysis was completed using a mixed-model, three way factorial ANOVA in which time (07:00, 13:00 and 19:00h) was a fixed factor, site a random factor, and sampling day a blocking factor; pH, alkalinity and \( \Omega_a \) were used as dependent variables in separate ANOVAs. The blocking factor was used to account for day-to-day variance attributed to weather. In the case of \( \Omega_a \), the variation among sites at each sampling interval was further resolved using additional one way ANOVAs followed by Tukey multiple comparisons. Although the results of these additional tests must be interpreted cautiously because data were selected to test for site effects independent of time effects, nevertheless they are helpful in identifying the likely processes driving the patterns of variation in \( \Omega_a \).

All statistical analyses were completed with Systat 9.2 software, and the statistical assumptions of ANOVA were tested through graphical analyses of residuals.

Results

Measurement of flow

The drogues were deployed 47 times in near shore locations between Cabritte Horn and White Point (Fig. 1), and they were released at haphazard times with regards to tidal state. The drogues were allowed to drift for 40 to 576 minutes (mean duration = 167 ± 17 minutes [± SE]), and in one case, a drogue released in Great Lameshur Bay remained in virtually the same spot for \( \approx 12 \) h. However, most drogues (60%) moved in northwesterly or southwesterly directions with speeds of 0.2-19.2 cm s\(^{-1}\) (Fig. 1). Overall, the drogues moved with a mean speed of 3.4 ± 0.5 cm s\(^{-1}\) and moved in a mean heading of 273° (Fig. 1).

In situ light intensity

In situ light intensities at both sites reached a maximum of \( \approx 700 \) μmol photons m\(^{-2}\) s\(^{-1}\) at about midday, and a between-site discrepancy in light levels developed on all four days that light was recorded (Fig. 2). Although the magnitude of the discrepancy varied, the 4-point moving average of this discrepancy reached up to 253 μmol photons m\(^{-2}\) s\(^{-1}\) by late morning, with less light penetrating to 9-m depth at Yawzi Point compared to Tektite. This quantitative analysis agreed well with observations one of us (PJE) has made during countless dives at Yawzi Point, during which a cloud of
turbid water often has been seen inundating the area from the north by mid-morning. Overall, light intensities differed significantly between sites (Wilcoxon’s Signed Ranks, $T = 50$, $n = 238$, $P < 0.001$).

**DIC chemistry**

Seawater pH varied in a diel pattern with an amplitude of $\approx 0.04$ pH units (Fig. 3), and the variation was similar among all six sites (data not shown). Overall, pH was lowest at 10:00 h and highest at 23:00 h, with gradual changes in between. The changes in pH were more systematic (i.e., they were depressed at midday) than the changes in alkalinity, which varied inconsistently throughout the day with a minimum at 19:00 h and a maximum at 22:00 h (Fig. 3). Statistical analysis of the results from 07:00, 13:00 and 19:00 h revealed a significant time x site interaction for pH and, for alkalinity, a significant effect of time (Table 1). Neither site, nor the time x site interaction, was significant for alkalinity, and for both pH and alkalinity the results were significantly affected by sampling day (Table 1). The strong effect of the time of day on pH and alkalinity also resulted in a distinctive diel pattern for $\Omega_a$ with an amplitude of $\approx 0.4$ units. The diel pattern for $\Omega_a$ was similar to the pattern for pH, with $\Omega_a$ decreasing during the night and early morning, and increasing from mid-day until early evening (Fig. 3).

Based on the seawater samples collected at 07:00, 13:00 and 19:00 h, $\Omega_a$ was significantly
affected by a time x site interaction, and also varied significantly among times and sites (Table 1, Fig. 4). Independent ANOVA’s of \( \Omega \) among sites at 07:00, 13:00 and 19:00 h only revealed a significant difference at 07:00 h (F = 6.35, df = 5,19, P = 0.002), with the values at Cabritte Horn and Tektite differing significantly from those at the NPS Dock and Donkey Bite (P < 0.05, Tukey HSD). Therefore, the time x site interaction for \( \Omega \) (Table 1) probably was a result of the higher values in the morning at the eastern sites compared to other sites, and the waning of this pattern as the day progressed. One consequence of this pattern is that the average \( \Omega \) values from 07:00, 13:00 and 19:00 h combined, differed significantly among sites (F = 2.76, df = 5,76, P = 0.024), with the values recorded deep within GLB (Donkey Bite) differing significantly from eastern headland sites (Cabritte Horn, P = 0.039; and Tektite, P = 0.05; Tukey HSD) (Fig. 4).

### Table 1. Results of a mixed-model ANOVA comparing (A) pH, (B) alkalinity and (C) aragonite saturation state (\( \Omega \)) among three sampling times (07:00, 13:00, 19:00 h: fixed factor), and six sites (random factor). Date was used as a blocking factor to account for day-to-day variation. The effect of Time was tested over the interaction of Time x Site, and all other effects were tested over the MS_error.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. pH</td>
<td>Time</td>
<td>0.0109</td>
<td>2</td>
<td>0.0055</td>
<td>11.713</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>0.0024</td>
<td>5</td>
<td>0.0005</td>
<td>4.321</td>
</tr>
<tr>
<td></td>
<td>Date</td>
<td>0.0074</td>
<td>4</td>
<td>0.0019</td>
<td>16.517</td>
</tr>
<tr>
<td></td>
<td>Time x Site</td>
<td>0.0046</td>
<td>10</td>
<td>0.0005</td>
<td>4.169</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>0.0073</td>
<td>65</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>B. Alkalinity</td>
<td>Time</td>
<td>0.0238</td>
<td>2</td>
<td>0.0119</td>
<td>30.780</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>0.0058</td>
<td>5</td>
<td>0.0012</td>
<td>1.229</td>
</tr>
<tr>
<td></td>
<td>Date</td>
<td>0.1837</td>
<td>4</td>
<td>0.0459</td>
<td>48.895</td>
</tr>
<tr>
<td></td>
<td>Time x Site</td>
<td>0.0039</td>
<td>10</td>
<td>0.0004</td>
<td>0.412</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>0.0601</td>
<td>64</td>
<td>0.0009</td>
<td></td>
</tr>
<tr>
<td>C. ( \Omega )</td>
<td>Time</td>
<td>0.2998</td>
<td>2</td>
<td>0.1499</td>
<td>6.758</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>0.1833</td>
<td>5</td>
<td>0.0367</td>
<td>4.070</td>
</tr>
<tr>
<td></td>
<td>Date</td>
<td>1.7947</td>
<td>4</td>
<td>0.4487</td>
<td>49.807</td>
</tr>
<tr>
<td></td>
<td>Time x Site</td>
<td>0.2218</td>
<td>10</td>
<td>0.0222</td>
<td>2.462</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>0.5765</td>
<td>64</td>
<td>0.0090</td>
<td></td>
</tr>
</tbody>
</table>

**Discussion**

One goal of our ongoing research in St. John is to explore the potential for small-scale variation in abiotic factors to mediate the distribution of corals, and here we take a first step in this process by focusing on the characteristics of seawater flowing over the shallow reefs. Specifically, we measured the abiotic characteristics of seawater close (<100 m) to the shore on a spatial scale (kilometer-wide or less) equivalent to that over which patterns occur in ecological events affecting the benthic community (Edmunds, 2002). Our results are important, in part because these kinds of data still are scarce for most coral reefs (but see Glynn, 1973; Genovese and Witman, 2004), but mostly because they show that the slow flow of seawater over a shallow reef can establish gradients in seawater DIC chemistry and light penetration that have the potential to influence the success of corals.

For the reefs of St. John, the mean surface flow speeds we recorded are low (i.e., 3.4 cm s\(^{-1}\)), and even the greatest speed was only 19.3 cm s\(^{-1}\). Similar, or even slower water motion (i.e., mean flow speeds of 1-8 cm s\(^{-1}\)) characterizes the near-bottom (i.e., 50 cm above the benthos) water flow at 2.9 m depth in Great Lameshur Bay and its environs (PJ Edmunds, unpublished data from the deployment of S4 current meters). The slow westward flow of water along the south shore of St. John is likely driven by prevailing winds, as occurs on other fringing reefs in the Caribbean (Glynn, 1973; Genovese and Witman, 2004) and the Pacific (Yamano et al., 1998), and is the case for
much of the westward surface flow through the Caribbean basin (Johns et al., 2002). Just south of St. John, the larger pattern of flow of surface waters in the Caribbean Sea is characterized by a strong band of westward flow moving at 25-30 cm s$^{-1}$ (Richardson, 2005), and it is possible the near shore flow along the south coast of St. John is part of this larger circulation. In addition to the overall westerly flow, the slow seawater motion along the south coast of St. John also includes ingressions into semi-enclosed bays where the seawater can remain for many hours, and it may also be augmented by eddies in the lee of the rocky headlands such as Cabritte Horn. Large (i.e., on the scale of 100’s of kilometers) cyclonic and anticyclonic eddies are common in the surface waters of the Caribbean (Richardson, 2005), but in the present study, we suspect they may operate over a kilometer-scale and were revealed occasionally by the movement of the drogues in directions contrary to the overall westerly flow.

Fig. 4. Aragonite saturation state ($\Omega_a$) at six sites between Cabritte Horn and White Point (Fig.1), expressed as means (± SE) using samples collected at 07:00, 13:00 and 19:00 h. (A) Results separated by time ($n = 5$ per site/time combination unless indicated) in order to illustrate the significant time x site interaction (Table 2). Exploratory post hoc ANOVAs comparing $\Omega_a$ among sites revealed significant differences among sites at all times ($P < 0.05$), but at 07:00 h, $\Omega_a$ was significantly higher at eastern sites (Cabritte Horn and Tektite) than at the bay sites (Donkey Bite, NPS Dock and Europa Bay). (B) Results separated by site but pooled among times ($n = 15$ per site unless indicated otherwise).
The pattern of seawater flow is associated with changes in light penetration and DIC chemistry that appear to be related functionally to the water flow. In brief, we posit that the slow westerly flow creates the opportunity for changes in DIC chemistry, most likely as result of benthic metabolism, with the consequences of these changes most strongly expressed at western sites as the water exits the study area. Against this backdrop, the in situ light intensities (Fig. 2) are helpful in elucidating the characteristics of the seawater flowing westerly, because the reduced light intensities at a western site are consistent with the hypothesized westerly flow and the likelihood that the seawater becomes more turbid as it passes through the bay. Although we did not analyze the potential sources of this turbidity, its effects are readily visible while scuba diving, and we speculate that it might be caused by mucus (from benthic taxa) and its exploitation by microbial communities (e.g., Wild et al., 2004).

The diel variations in DIC chemistry are similar to those recorded over other coral reefs (Smith, 1973; Ohde and vanWoesik, 1999), and probably are a result of processes occurring both upstream and within the study area. Such diel patterns typically are attributed to the removal of CO$_2$ by photosynthesis during the day, which drives pH and $\Omega_a$ up, and nighttime release of CO$_2$ by respiration, which causes pH and $\Omega_a$ to decline (Kayanne et al., 1995; Ohde and van Woesik, 1999). In the present case, the early morning depression of $\Omega_a$ is intensified at sites within the bays compared to those to the east and near the headlands (Fig. 4). Several factors likely intensify the impacts of nighttime respiration on the seawater pH and $\Omega_a$ that would result in lower early morning $\Omega_a$ at the head of the bays. First, water flowing into the bay has already been impacted by the metabolic activities of upstream communities. Second, the extended residence times of water in the bays would allow respired CO$_2$ from benthic communities to accumulate in the dark over a longer period of time compared to sites that are exposed to mixing with offshore water. And third, the relatively high benthic surface area relative to the volume of seawater at the heads of these shallow bays would increase the impact of benthic metabolism on the overlying water compared to communities in deeper water. The contemporaneous variation in alkalinity (Fig. 4) most likely reflects the effects of light-enhanced coral calcification during the day, when CO$_2^-$ and HCO$_3^-$ (two of the primary constituents of alkalinity) are removed (Suzuki and Kawahata, 2003). The diel changes in pH and $\Omega_a$ in St. John ($\approx 0.04$ pH and $\approx 0.4$ $\Omega_a$ units) are similar to those recorded in some Pacific lagoons, for example at Fanning Island Atoll (Smith and Pesret, 1974), but are an order of magnitude lower than the upper range of values possible, for example as recorded in Okinawa (where the diel pH variation was 0.78 [Ohde and vanWoesik, 1999]). Presumably, these differences are a result of varying CO$_2$ fluxes attributable to dissimilarities in both benthic community structure and water column properties that serve to dilute CO$_2$ fluxes. In St. John, the modest diel changes in pH and $\Omega_a$ may reflect the greater depth and low coral cover in this location (Edmunds 2002) compared to reef communities where pH, alkalinity and $\Omega_a$ often have been measured in the Pacific (e.g., Gattuso et al., 1996; Suzuki and Kawahata, 2003).

Clearly there still is considerable scope to expand the temporal scale of the present study, ideally with multiple instruments deployed simultaneously in different locations. However, our results suggest that manipulative experiments now are warranted to test the hypothesis that the flow regime and the abiotic gradients that it creates have cause-and-effect relationships with coral performance. There are several reasons to believe that such experiments will identify biologically significant relationships. For example, the unusually low flow speeds in St. John (cf. Sebens and Done, 1992) probably have implications for the flow-dependent processes affecting reef corals (Monismith, 2007). Similarly, the between-site differences in light transmission to 9-m depth could have important consequences, for instance through the effects on autotrophic nutrition (Edmunds and Davies, 1986), and conceivably the variations we recorded in $\Omega_a$ between
times and sites could affect instantaneous rates of coral calcification (Marubini et al., 2003).

Acknowledgements.—The analysis of seawater chemistry benefited from discussions with R. Buddemeier, and this portion of the research was submitted in partial fulfillment of the MS degree for G.H. Funding was provided by the VI National Park, the Sea Grant Program of the University of Puerto Rico (R-101-2-02), the Office of Naval Research (N00014-93-1-0440), the National Science Foundation (DEB 0343570), and California State University Northridge (CSUN). We thank R. Boulon and C. Rogers for the long-term support of our work, D. Swanson, C. Zilberberg, S. Vollmer, L. Allen-Requa and E. Keach for assistance in the field, V. Powell for on-site logistics, and the staff at the Virgin Islands Environmental Resource Station for making our stays productive and enjoyable. Comments from R. Carpenter, J. Leichter, R. Elahi, and L. Allen-Requa improved earlier drafts of this paper. This is contribution number xxx of the CSUN marine biology program.

Literature cited


