ATOLL RESEARCH BULLETIN

NO. 535

WATER COLUMN STRUCTURE AND CIRCULATION IN THE MAIN CHANNEL, TWIN CAYS, BELIZE

BY

STEVEN R. KIBLER, MARIA A. FAUST, MARK W. VANDERSEA,
SABRINA M. VARNAM, R. WAYNE LITAKER, AND PATRICIA A. TESTER

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
NOVEMBER 2005

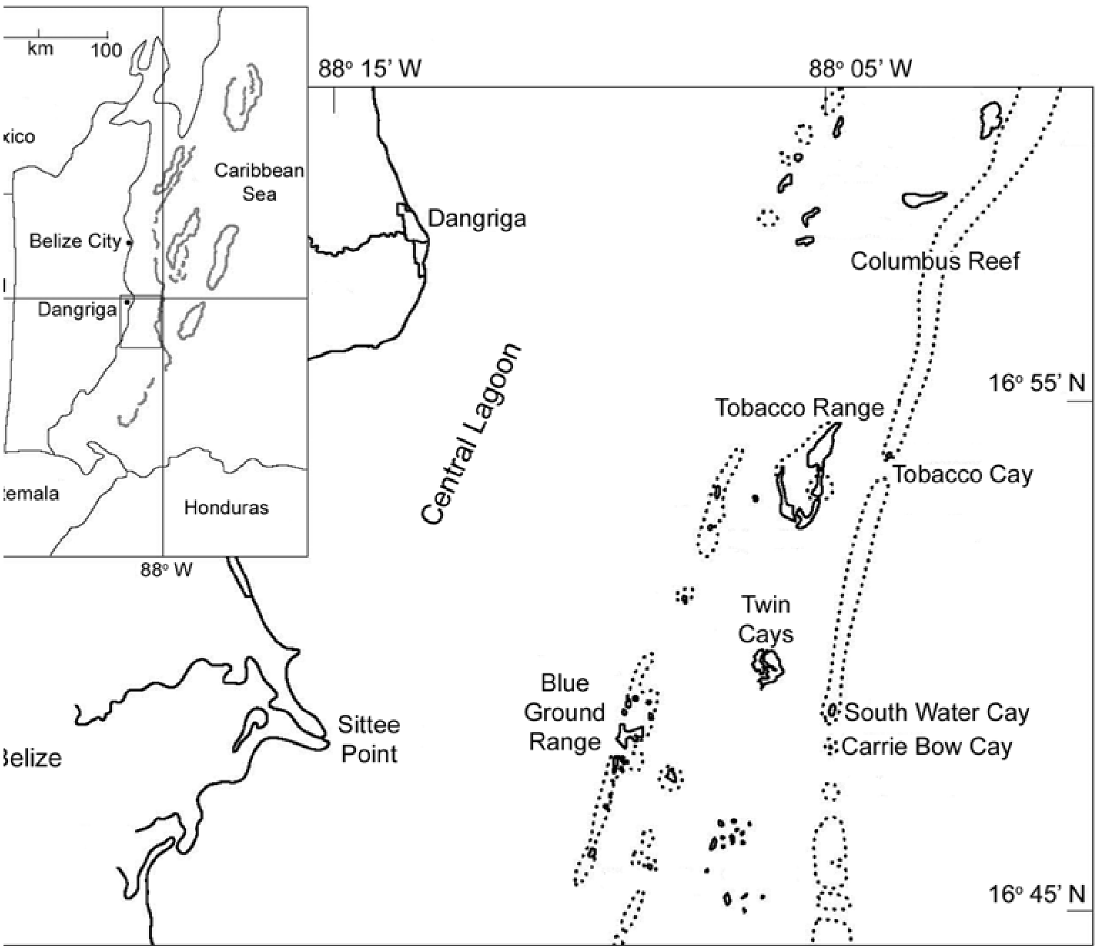

Figure 1. Regional map of the Belizean central lagoon showing Twin Cays and surrounding islands. Map drawn by M. Ryan, Department of Invertebrate Zoology, NMNH, Smithsonian Institution, Washington, D.C.

WATER COLUMN STRUCTURE AND CIRCULATION IN THE MAIN CHANNEL, TWIN CAYS, BELIZE

BY

STEVEN R. KIBLER,[1] MARIA A. FAUST,[2] MARK W. VANDERSEA,[1] SABRINA M. VARNAM,[1] R. WAYNE LITAKER,[1] AND PATRICIA A. TESTER[1]

ABSTRACT

The hydrographic structure of the Main Channel at Twin Cays, Belize was surveyed in the morning and on the afternoon of 18 May 2004. Transects conducted along the channel revealed the northern and southern portions of the system were characterized by very different hydrographic conditions. In the afternoon, the deeper southern portion of the Main Channel was characterized by two-layer circulation in which warm (~ 30 ºC) surface water flowed outward from the Main Channel and cooler (28.6-28.7 ºC) bottom water moved northward from the lagoon. The southern channel was also characterized by a plume of high temperature (~29 ºC) and high salinity (~37.4) bottom water from the neighboring Lair Channel.

Strong afternoon stratification occurred in the southern channel as evidenced by Brunt-Väisälä frequencies of 20-50 cycle h^{-1}. In contrast, the northern part of the channel was characterized by more shallow (< 2 m), poorly stratified waters (0-10 cycle h^{-1}) that were divorced from the surrounding lagoon by shoals and patch reefs. Average water temperatures were lower in the southern channel due to inflow of lagoon water and more rapid diel heating of the shallow waters to the north. The shallow bathymetry in the north also prevented cooler bottom waters from entering the northern channel. Salinity was lower (~36.6) in the northern channel due to input of rainwater from the interior of the islands. The hydrographic structure of the Main Channel also influenced the distribution of chlorophyll and dissolved oxygen. The southernmost part of the Main Channel was characterized by relatively high chlorophyll fluorescence (> 25 RFU) at the surface, which was attributed to a phytoplankton bloom fueled by outwelling of nutrients from the mangrove fringe. In contrast, relative fluorescence was highest (20-30 RFU) along the bottom of the northern channel due to an abundance of subsurface microalgae. Shallow areas in the northern channel were marked by the high rates of photosynthetic O_2 production (22 µmol O_2 L^{-1} h^{-1}) resulting in O_2 saturation in excess of 150%.

[1] Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA.

[2] Department of Botany, National Museum of Natural History, Smithsonian Institution 4210 Silver Hill Road, Suitland, Maryland 20746, USA.

Manuscript received 19 July 2005; revised 9 September 2005.

INTRODUCTION

The mangrove islands in the central lagoon of Belize are surrounded by a complex fringe environment that includes channels, ponds, coves and other small embayments. These shallow (< 4 m) habitats are characterized by a mixed assemblage of fish, corals, sponges, macroalgae and other organisms (Macintyre et al., 2000). Water flow among these habitats supplies nutrients, food particles and dissolved oxygen to fringe biota and eliminates wastes. Flow is also crucial for transport of organic matter that supports the extensive detrital food web in the mangrove fringe (Alongi et al., 1989; Ambler et al., 1994). However, circulation between fringe habitats and the surrounding central lagoon waters is often restricted because of the dense mangrove vegetation that dampens wind stress and prevents mixing. This situation is compounded by lack of tidal mixing because of the minimal tides in the region (~20 cm). As a result, the mangrove embayments and ponds in the central lagoon are often poorly flushed, exhibiting stratified and sometimes stagnant conditions (Urish, 2000; Villareal, 2000).

Twin Cays (16° 49.4′ N; 88° 6.1′ W) is a group of small peat-based islands located 12 km from the Belizean mainland (Fig. 1). This site is characterized by a series of bays and channels (Fig. 2), some of which are poorly flushed. Twin Cays are largely covered with mangroves (*Rhizophora mangle* L.; *Avicennia germinans* L.) and are bisected by the relatively deep Main Channel (Fig. 2) (McKee et al., 2002). While much is known about the ecology of the mangroves at Twin Cays, very little is known about the hydrography of the Main Channel and how water circulation relates to the distribution of aquatic biota. The few hydrographic data available represent attempts to measure flow rates within the mangrove channels or to characterize flushing of water from the interior of the islands (ex., Wright, 1991; Ferrari et al., 2003). On 18 May 2004, we undertook a hydrographic survey of the Main Channel at Twin Cays as part of a more extensive investigation into factors controlling productivity in the nearby Lair and Lair Channel (Fig. 2) (Kibler et al., in preparation). Here we report the results of our survey with respect to vertical structure and circulation within the Main Channel and how environmental conditions varied over the course of a single day during the Belizean dry season.

METHODS

Study Site

The Main Channel at Twin Cays (Fig. 2) is a system encompassing 0.1-0.2 km^2 and is navigable by small boats along most of its length. Water depth varies from 4-5m near the southern end of the Main Channel (Stas. TL-MC2) to 1-3 m in the northern channel (Fig. 2, Table 1). The northern terminus of the channel is narrow (10-15 m) and is obstructed by shoals and patch reefs that restrict exchange with the lagoon. In contrast, the southern end of the Main Channel is significantly wider (> 100 m) and opens into a wide bay covered in seagrass and small patches of coral. In this study, the southern end of the Main Channel is referred to as the mouth because of the greater depth and breadth in this part of the system.

Most of the Main Channel is protected from the prevailing NE trade winds (meteorological convention) by mangroves that overhang the channel in many locations. Because of the small tidal range (~20 cm), currents are normally less than 20 cm s^{-1}. The prevailing current is southward (~5 cm s^{-1}) in the northern part of the channel and is strongest in Cuda cut, the first of two openings along the northwestern side of the channel (Rützler et al., 2004). South of the Lair Channel (Fig. 2), currents are tidally driven northward during flood (~5 cm s^{-1}) and southward during ebb (~5 cm s^{-1}) (Ferrari et al., 2003).

Hydrographic Data

Hydrographic data were collected at Twin Cays using a model 6600 Sonde in profiling mode (YSI Inc., Yellow Springs, Ohio). The unit was equipped with sensors to measure temperature and conductivity (YSI model 6560) as well as dissolved O_2 (model 6562) and chlorophyll fluorescence (model 6025). Because in situ fluorometric measurements were not calibrated to absolute chlorophyll concentrations, data collected with the YSI fluorometer were termed chlorophyll fluorescence and represent a relative measure of phytoplankton abundance (RFU, relative fluorescence units). All other sensors were calibrated in accordance with the instructions provided by the instrument manufacturer. Irradiance was quantified with a model LI-1925A PAR sensor (Li-Cor Inc., Lincoln, Nebraska) fixed on a side arm to the instrument. Hydrographic data were collected at a series of 10 stations situated along a transect between the northern terminus of the Main Channel (Sta. 10) and the lagoon to the south (Sta. TL, Fig. 2). Vertical profiles were collected at each of these stations in the morning and afternoon of 18 May 2004.

Data Analyses

Hydrographic data from each station were compiled and MATLAB 7.04 (The Mathworks Inc., Natick, Massachusetts) was used to create vertical sections of the Main Channel. Data were cubic spline interpolated and gridded using depth measurements from each station. Distance was estimated using a spatially referenced aerial photograph of Twin Cays (Rodriguez and Feller, 2004). An electronic image of the map was spatially calibrated with Metamorph 5.0 software (Universal Imaging Inc., Downingtown, Pennsylvania). Distances between stations and surface area of the Main Channel were then calculated using the software's linear and area analysis functions.

RESULTS

Physical Conditions

The lowest average water temperatures were observed at Sta. TL in both morning (28.2 ºC) and afternoon (29.0 ºC) transects (Table 1). In the morning, temperature increased from the southern to the northern end of the channel with the highest water temperatures at Sta. 10. In contrast, afternoon temperatures were highest at the shallow sites in the northern channel between Stas. 6 and 9 (Table 1). To simplify comparisons among stations, depth, temperature and salinity values were averaged at each station with respect to both depth and time and were plotted versus station depth (Fig. 3). The results of a linear regression indicated temperature declined with station depth ($r^2 = 0.68$, $p = 0.003$) as a result of more rapid heating of shallow sites relative to deeper sites (Fig. 3A). Distribution of mean temperature data on the graph also suggested values were distributed among two groups, one comprised of shallow stations in the northern channel with high temperature (Stas. 5, 6, 7, 9, 10), and the other including deeper stations in the southern channel with cooler temperatures (Stas. TL, 1, 2, 4, MC2). A similar comparison of mean salinity among stations (Fig. 3B) revealed salinity was lower in the shallow northern part of the channel but the relationship was not significant ($p > 0.05$).

To better illustrate vertical structure of the water column along the length of the system, morning and afternoon vertical profile data were used to create vertical sections of temperature and salinity in the Main Channel (Figs. 4, 5). In the morning, the mouth of the channel was characterized by an outflow of relatively warm (> 28 ºC) surface water and a subsurface inflow of cooler (< 28.5 ºC) lagoon water (Fig. 4A). Pockets of warmer surface water also were evident near the midpoint of the Main Channel and at its northern extent. A narrow band of warm bottom water was also present at MC2, reflecting outflow of bottom water from the Lair Channel. After entering the Main Channel, this plume moved southward along the bottom before mixing with cooler water near Sta. TL (arrows, Fig. 4A). Morning salinities ranged from 36.6 to 36.7 along the surface, increasing to ~36.9 near the Lair Channel (Fig. 5A). Water with the lowest salinity was present in northern Main Channel where salinity declined to ~36.6. This low salinity lens was attributed to outflow from the interior of the islands following rainfall on the morning of 18 May. High salinity water was present in two regions of the Main Channel. The first of these was at the bottom of Sta. MC2 as a result of high salinity (~37.4) water from the Lair Channel which moved southward along the bottom (arrows, Fig. 5A). Salinity was also high at the bottom of Sta. 10 reflecting the restricted exchange at the north end of the Main Channel (Fig. 5A).

By afternoon, water temperatures increased along the length of the Main Channel. Stations 5-9 exhibited the greatest increase in temperature, which averaged 5-7% higher in the afternoon versus the morning hours (compare Figs. 4A, B). The two-layer structure in the southern channel was more pronounced in the afternoon, a strong thermocline being present southward of Sta. MC2 (Fig. 4B). Outwelling of warm surface water, which was evident along most of the southern Main Channel, was balanced by inflow along the bottom. The difference between surface and bottom temperatures increased from <0.5 ºC in the morning to >1 ºC (Stas. 1-4) by the afternoon. The warmest water (> 30 ºC) was present between Stas. 5 and 10 with a slightly cooler subsurface inflow from Cuda Cut evident at Sta. 7 (Fig. 4B).

Transect data showed that outflow from the Lair Channel continued through the afternoon (arrows, Figs. 5A, B). High salinity (> 37) bottom water along the southern Main Channel was overlain by a lens of low salinity (< 36.7) water extending from the surface to ~2 m (Fig. 5B). This low salinity lens represents surface water from the northern channel that was advected southward by the ebbing tide. Low salinity water was also observed in the Lair and Lair Channel during the same part of the day (data not shown), suggesting surface outflow from the Lair Channel may have been significant in reducing salinity in the southern Main Channel.

Comparison of morning and afternoon density structure in the channel (Fig. 6) revealed the effect of bathymetry as well as diel heating upon circulation between the Main Channel and the lagoon. Contours of σ_t illustrated a low-density region in the northern portion of the channel and a high-density region in the southern half of the channel. In the northern channel, this partitioning was partly governed by bathymetry where the shallows between Stas. 5 and 6 prevented subsurface exchange. Longitudinal density gradients prevented low salinity water at Stas. 5-6 from mixing with the higher salinity water to the north and south (Fig. 6). The bathymetry of the channel also restricted circulation further north resulting in a pool of high density water at the bottom of Sta. 10 (Fig. 6A, B). The outflow from the Lair Channel was also evident in morning and afternoon sections as high-density bottom water at Sta. MC2 (Fig. 6).

In order to better illustrate the influence of salinity and temperature upon the vertical structure of the water column at each station, a comparison of thermal and salinity gradients was made using profile data from morning and afternoon transects. The influence of temperature ($\alpha\partial T/\partial z$) and salinity ($\beta\partial S/\partial z$) upon stratification was quantified (Table 2), where α, β, $\partial T/\partial z$ and $\partial S/\partial z$ are the thermal expansion coefficient, haline contraction coefficient, vertical temperature gradient, and vertical salinity gradient (respectively). In the morning, positive vertical salinity gradients dominated the structure at Stas. 4, MC2 and 10 due to high-salinity bottom water at these sites (Table 2, Fig. 5A). Strong negative thermal gradients dominated vertical structure in the morning at Stas. 6 and 9. The remaining stations exhibited slight-to-moderate temperature and salinity gradients in the morning (Table 2). In contrast, afternoon structure was mostly dominated by temperature that greatly exceeded salinity effects in the southern half of the Main Channel (Stas. TL-4). Stations MC2 and 10 were characterized by strong negative vertical temperature gradients combined with strong positive vertical salinity gradients (Table 2). The effect of these gradients upon the vertical stratification of the water column is evident in Fig. 6.

Stratification was quantified at each station using the Brunt-Väisälä frequency (N) that describes the oscillation that results when the pycnocline is displaced (Mann and Lazier, 1996). This metric was calculated with the expression N (rad s^{-1}) = $(g/\rho\ \partial\rho/\partial z)^{1/2}$ where g is the gravitational constant (m s^{-2}) and ρ is density (Kg m^{-3}). To simplify comparisons, N was converted to units of cycles h^{-1} using $N/2\pi$. In general, the water column in the southern Main Channel was moderately stratified ($10 < N < 20$ cycles

h^{-1}) in the morning and more significantly stratified ($N \geq 20$ cycles h^{-1}) in the afternoon. In the morning, stratification was most evident at Sta. MC2 where high-salinity bottom water occurred in close proximity to low-salinity surface water (Fig. 7A). As a result of thermal stratification, Brunt-Väisälä frequencies were greatest in the afternoon at Stas. MC2, 4 and 2, and reached a maximum at a depth of ~2m (Fig. 7B). Stratification was also evident at Sta. 10 due to warm surface waters and high-salinity bottom water in Cassiopea Cove.

Irradiance

Light penetration in the water column varied greatly along the Main Channel reflecting interaction between the visibly colored mangrove fringe waters and the more transparent waters of the lagoon. Irradiance data from vertical profiles collected at each station were used to calculate K_{PAR}, the attenuation coefficient with respect to PAR (300-700nm) using the expression K_{PAR} (m^{-1}) = [-Ln (I_z / $I_{0.1}$)] / z, where z (m) is depth, $I_{0.1}$ and I_z represent irradiance (µmol photons m^{-2} s^{-1}) measured at 0.1 m and just above the bottom, respectively. Light attenuation was relatively low (< 0.4 m^{-1}) at Stas. TL, 1 and 2 where lagoon waters were more prevalent (Fig. 8). Attenuation generally increased to 0.4-0.6 m^{-1} northward from Sta. 4 although K_{PAR} was <0.4 m^{-1} at Sta. 5. The greater light attenuation in the northern Main Channel was attributable to plankton and particulates in the water column as well as to dissolved organic matter from the mangrove sediments that comprise the islands. The highest attenuation coefficient was observed in the afternoon at Sta. 4, where K_{PAR} exceeded 0.62 m^{-1} (Fig. 8). The results of a t-test indicated morning and afternoon attenuation were not significantly different ($p > 0.5$).

Dissolved Oxygen

Dissolved oxygen levels were relatively high throughout the Main Channel and were strongly impacted by solar radiation. The lowest average O_2 saturation levels were observed in the morning at Stas. 6 (89%) and 10 (90%, Table 3). The highest mean saturation occurred in the afternoon ranging from 112% at Sta. 10 to 170% at Sta. 7 (Table 3). Overall, O_2 concentrations averaged 37% higher in the afternoon relative to morning. Regression results showed a linear relationship between mean O_2 saturation and depth ($r^2 = 0.70$, $p = 0.001$), indicating deeper stations, on average, had higher levels of O_2 saturation than shallow stations (Fig. 9). This negative relationship was attributable to lower morning O_2 saturation in the northern Main Channel relative to the southern channel sites.

A vertical section of the Main Channel, created with profile data from each station, showed a significant longitudinal gradient in O_2 saturation and lesser variation with depth (Fig. 10). Low oxygen levels were evident in the morning, reaching minimum saturation along the bottom of the mid-to-northern Main Channel (Fig. 10A). Highest morning O_2 saturation (~110%) occurred along the bottom near Sta. TL reflecting mixing with lagoon waters. By afternoon all stations exhibited very high O_2 concentrations (6.4-10.5 mg L^{-1}). Afternoon oxygen concentrations were highest at Sta. 7 where saturation exceeded 160% near the surface and declined to 110-120% near the bottom (Fig. 10B).

Some of the lowest afternoon O_2 concentrations (7-7.2 mg L^{-1}) were associated with the low salinity lens near the surface of Sta. 4. Similarly, O_2 saturation was low at the bottom of Sta. MC2 owing to outflow of high temperature, high salinity bottom water from the Lair Channel.

Chlorophyll Fluorescence

Similar to temperature, salinity and dissolved oxygen, fluorescence data indicated phytoplankton were distributed differently in the southern and northern portions of the Main Channel. In the morning, fluorescence was low (<1 RFU) through most of the system but exceeded 25 RFU in the upper 0.5 m of the water column at Stas. TL and 1 (Fig. 11A). High fluorescence was also recorded along the bottom at Stas. 5, 6 and 10 (20-30 RFU). This distribution suggests phytoplankton were largely concentrated near the surface at the mouth of the channel but showed a near-bottom distribution in the northern channel (Fig. 11A). Morning fluorescence was also moderately high (4-6 RFU) at the bottom of Sta. MC2 reflecting the plume of bottom water from the Lair Channel (see Figs. 11A, 6A). Afternoon contours showed very low fluorescence (< 1 RFU) throughout the system with very narrow bands of higher fluorescence at the bottom of Stas. 2, 4, 9 and 10 (Fig. 11B). Unlike in the morning, the surface waters at the mouth of the Main Channel were characterized by low fluorescence (compare Figs. 11A, B). This low fluorescence may be attributed to the advection of phytoplankton cells out of the channel with the ebbing tide.

Diel Changes

The effect of solar radiation upon mean temperature, salinity and O_2 saturation at stations in the Main Channel was quantified using ΔT, the diel change in mean temperature, ΔS, the diel change in mean salinity, and ΔO_2, the diel change in oxygen saturation (Fig. 12). Stations in the southern channel (Stas. TL-MC2) underwent a temperature increase of 2-3% by afternoon while the shallow sites in the northern channel (Stas. 5-9) exhibited a diel increase of 6-8%. Similarly, northern channel sites increased in salinity by ~1% as opposed to those in the southern channel which increased very little or declined slightly (Fig. 12). Diel shifts in T and S at Sta. 10 were comparable to those near the mouth of the Main Channel, signifying exchange with the lagoon to the north. Oxygen saturation followed a similar pattern where saturation increased significantly at stations above MC2. The largest gain in O_2 saturation occurred at Stas. 6 and 7 where ΔO_2 exceeded 75% (Fig. 12).

DISCUSSION

The vertical and longitudinal structure of the Main Channel at Twin Cays is characterized by two distinct hydrographic zones. The first of these is the southern portion of the channel (Stas. TL-MC2) that is strongly influenced by exchange with the waters of the central lagoon. In contrast, circulation is more restricted in the shallow northern part of the channel (Stas. 5-10) where environmental conditions are more closely governed by diel heating and outwelling of water from the interior of the islands. The distribution of chlorophyll and dissolved oxygen reflected the hydrographic structure of the Main Channel.

The southern portion of the Main Channel represents a transitional environment influenced by exchange of water between the channel and the lagoon. This exchange was most evident in the distribution of temperature and salinity at Stas. TL, 1, 2, and MC2. Both morning and afternoon transects demonstrated a distinct two-layer circulation pattern whereby an outflow of warm surface water from the channel is balanced by inflow of lagoon water along the bottom. The cooler, denser water from the lagoon is little influenced by diel heating thereby buffering the lower water column from the rapid shifts in temperature and salinity that characterize the northern channel sites. The benthic biota that reside in the southern channel benefit from this stability enabling reef-type organisms such as corals, seagrasses and sponges to survive in close proximity to the mangrove fringe. The interaction between lagoon and fringe waters in such environments may account for the high diversity of corals, sponges and other benthic biota that has been documented in similar mangrove cay habitats (Richardson, 2000; Rützler et al., 2000).

The two-layer structure that occurs in the southern Main Channel is influenced by outflow from the Lair Channel. Diel heating and evaporation in the sheltered waters of the Lair result in formation of high temperature and high salinity bottom water along the length of the Lair Channel. This dense bottom water spills into the Main Channel where it moves southward (Kibler et al., in preparation). Lair Channel water was visible in vertical sections of the Main Channel as a band of warm (~29 ºC) saline water (37.1-37.2) that collected at the bottom of Sta. MC2 and moved southward at a depth of 3-4 m (Figs. 4, 5). The bottom water that emerges from the Lair Channel was also characterized by low oxygen and high chlorophyll (Figs. 10, 11), suggesting the outflow may be a significant source of benthic microalgae from the Lair (see Faust, 2004). The Lair Channel plume, which was detectable as far south as Sta. TL, may be a regular feature of circulation during the dry season.

In contrast to the mouth of the Main Channel, exchange between the northern portion of the channel and the lagoon is very limited. The region north of Sta. MC2 is more shallow than the rest of the system (Table 1). The shallow bathymetry restricts exchange by preventing intrusion of lagoon water along the bottom. More rapid heating of the shallow water column in the northern Main Channel also generates a steep longitudinal density gradient (Fig. 6) which further restricts exchange between the northern and southern channel. Although some inflow of lagoon water occurs through Cuda Cut, the flow rates are low and circulation is poor (Rützler et al., 2004).

The shallow part of the system is highly dynamic and is strongly impacted by diel heating and precipitation (Figs. 4, 5). The dynamic conditions in the northern channel were exemplified by moderate rainfall that developed over Twin Cays on the morning of 18 May. The rainfall resulted in a lens of low salinity surface water in the northern channel (Stas. 5-9, Fig. 5A). In contrast, salinity near the channel mouth was less affected by this precipitation indicating rainwater was directed into the northern channel from the surrounding mangroves. The shallow ponds in the northwest quarter of East Island (Turtle pond, Candy's pond, Fig. 2) commonly collect rainwater that is then funneled into the Main Channel through Turtle creek and other outlets (Rützler et al., 2004). Similarly, outflow from the interior of West Island may enter the system through a channel near Sta. 5 (Wright et al., 1991). Rainfall, in concert with strong solar heating, caused rapid shifts in temperature and salinity in the shallow waters of the northern Main Channel. Organisms residing in this dynamic environment are likely to experience greater physiological stress than those residing elsewhere in the system. This physiological stress has the greatest impact upon sessile invertebrates and other benthic biota that are unable to migrate to more favorable habitats during periods of stress. The degree of environmental stress, in turn, has a direct impact upon diversity and distribution of benthic and epiphytic biota in the system (Goodbody, 2004; Rützler et al., 2004).

Circulation within the Main Channel was also influenced by vertical stratification. This stratification was reflected in the Brunt-Väisälä frequency where strong stratification was indicated by frequencies in excess of 20 cycle h^{-1} (MacIntyre et al., 2002). Stratification was weak (< 1) in the shallow portions of the northern Main Channel (Stas. 5, 6) where vertical salinity and temperature gradients were slight. Stratification increased slightly in the afternoon (Fig. 7B) with moderate Brunt-Väisälä frequencies at Cuda Cut (Sta. 7) and Cassiopea Cove (Sta. 10). In contrast, the two-layered circulation within the southern Main Channel resulted in a sharp afternoon pycnocline at mid-depth (~2 m) representing the boundary between outflowing Main Channel water and inflowing lagoon water (Fig. 7). Strong afternoon stratification occurred in the southern channel (Stas. TL, 1) as evidenced by Brunt-Väisälä frequencies of 20-30 cycle h^{-1} (Fig. 8B). Further north, low salinity surface water combined with bottom water from the Lair Channel increased N to 40-50 cycle h^{-1} (Fig. 5B). The strong vertical stratification observed in the southern Main Channel is more typical of estuaries where strong vertical salinity gradients result in classic estuarine circulation (Pritchard, 1989). Considering the depth of the system (< 5 m), the degree of stratification observed in the Main Channel is therefore surprising and exemplifies the strong influence of solar heating upon vertical structure in mangrove fringe waters. Because salinity gradients across the entire system were relatively weak, thermal gradients had much more of an effect upon stratification (Table 2). A very similar pattern of thermal dominance occurs in lakes and reservoirs as well as other marine systems with near uniform salinity (Mann and Lazier, 1996; Talling, 2001).

In concert with bathymetry, water-column structure and circulation patterns in the Main Channel tend to segregate portions of the system into distinct zones. These zones encompass a spectrum of environmental conditions ranging from lagoonal reef-type habitats with clear water to those more typical of turbid mangrove ponds. The largest of these zones is the southern Main Channel which is characterized by low turbidity, low light attenuation and more constant temperature and salinity. Inflow of subsurface lagoon water buffers the southern water column from the rapid shifts in environmental conditions that occur closer to the mangrove fringe. As a result, the benthic organisms that reside in the southern Main Channel are typical of reef-and-seagrass communities elsewhere in the central lagoon. Some common examples of these organisms include numerous corals, macroalgae and sponges (Rützler et al., 2004). Conversely, the northern portion of the water column is characterized by outflow of surface water from the Main Channel. In addition to having higher temperature and often lower salinity than lagoon water, the outflowing surface water is characterized by higher concentrations of dissolved nutrients and organic matter that may fuel productivity at the mouth of the Main Channel (Kibler et al., in preparation). Mangrove fringe water typically contains relatively high concentrations of dissolved nutrients due to remineralization of leaf litter and other organic matter (Moran et al., 1991). The high surface chlorophyll levels observed at the mouth of the Main Channel may reflect enrichment of phytoplankton by these nutrients.

Inflow of water from the mangroves may also represent a source of nutrients to the seagrasses and microalgae in the northern Main Channel. Both interstitial and surface waters in the interior of the islands contain high concentrations of nutrients (Feller, 1995; McKee et al., 2002), some of which undoubtedly leach into the Main Channel. Where outflow from the inland ponds occurs, seagrass density and biomass of associated epiphytes are elevated relative to other sites at Twin Cays (Richardson, 2004). Nutrient input may also promote phytoplankton growth as evidenced by the high subsurface chlorophyll levels observed at the northern channel sites (Fig. 11).

The greater abundance of seagrass and microalgae in the northern Main Channel may have also influenced O_2 saturation. Due to lower O_2 levels in the morning, average O_2 saturation tended to be slightly higher at deeper sites than shallow stations but diel O_2 production was dramatically higher in the northern channel (Fig. 9). The shallow stations in the northern channel (Stas. 5, 6, 7, 9) exhibited an average of 12% greater daytime oxygen production than stations in the southern channel (Stas. TL, 1, 2, MC2). The highest rate of oxygen production was observed at Sta. 7, where O_2 concentrations increased by 4.3 mg L^{-1}. This production was equivalent to a rate of 22 µmol O_2 L^{-1} h^{-1}. At best, stations in the southern channel produced no more than 1.1 µmol L^{-1} h^{-1} during the same time period (Sta. MC2). The increased production in the northern channel could not be attributed to dissolution of atmospheric oxygen as water temperature and salinity, factors which would reduce gas solubility, were both higher in the afternoon. Instead, high O_2 saturation was attributable to in-situ production by seagrass and microalgae at these sites.

Unlike the remainder of the stations in the Main Channel, Sta. 10 exhibited low oxygen production relative to its depth (Figs. 10, 12). Cassiopea Cove is characterized by turbid, organic rich water similar to the Lair and other ponds at Twin Cays. Its muddy, flocculent sediment is unsuitable for seagrasses (Rützler et al., 2004) and oxygen production at this site was correspondingly low. The restricted circulation at this site promotes retention of organic matter, a factor which may increase the biochemical demand for oxygen in the water column. This demand is compounded by elevated water temperatures resulting from high levels of solar radiation.

Solar radiation is responsible for the physical structure of the water column and directly influences the distribution of dissolved oxygen and phytoplankton in the Main Channel. The effect of solar radiation is both direct, through solar heating of the water column, and indirect, by influencing the vertical distribution of phytoplankton and production of oxygen in Main Channel waters. The absorption of solar energy by fringe waters generates vertical temperature gradients and drives evaporation. The resulting thermohaline structure governs circulation and controls the distribution of nutrients, dissolved oxygen and organic matter in the channels and bays at Twin Cays. Light attenuation, and therefore heat transfer, is greatest at the shallow stations in the northern channel (Fig. 4). The result is a very rapid increase in water temperature at these sites relative to the deeper, more transparent lagoon waters at the mouth of the Main Channel.

The greater light attenuation in the northern Main Channel may also govern oxygen production and phytoplankton distribution. Oxygen production and chlorophyll fluorescence were greatest at the stations where light attenuation was greatest (Figs. 8, 11). This pattern may be attributed to a reduction in photic stress at these sites. Photic stress is common in shallow tropical systems where high light levels may depress rates of photosynthesis and cause cellular damage (Fleischman, 1989; Lesser, 1996; Chróst and Faust, 1999). Increased photoproduction may therefore account for the very high O_2 levels in the northern Main Channel (Figs.10,12, Table 3). Similarly, the near-benthic distribution of chlorophyll may be a photoprotective strategy employed by microalgae to avoid photic stress near the surface.

Although the distribution of biota at Twin Cays and similar mangrove environments may be tied to meteorological forcing, the manifestation of such forcing may be subtle requiring a better understanding of variability occurring at short time scales (days, hours) and/or spatial scales (centimeters). For example, dinoflagellates and other phytoplankton associated with the mangrove fringe can be abundant in surface waters from the same portion of the Main Channel where lagoonal organisms like corals are found (Faust, unpublished; Rützler et al., 2004). These cells are advected from mangrove fringe waters with the low-density surface water via the channel. Alternatively, phytoplankton concentrations at the mouth of the Main Channel may develop in situ as a result of nutrients in the same surface layer. It is the structure of the water column in the southern Main Channel that makes this mix of lagoon and mangrove species possible. Clearly, both vertical and horizontal circulation are important determinants affecting the distribution of benthic and planktonic biota at Twin Cays. The vertical and longitudinal zonation of the Main Channel should be considered when future surveys of benthic and other biota are conducted at Twin Cays and elsewhere in the central lagoon.

CONCLUSIONS

This study represents one of the first attempts to characterize physical structure and thermohaline circulation in the Main Channel at Twin Cays. The data presented here demonstrate the manner in which the longitudinal density structure, vertical stratification and channel bathymetry act to create distinct zones in the Main Channel, each experiencing a different suite of environmental conditions. The southern portion of the Main Channel is characterized by a two-layer pattern of circulation in which warm surface water flows outward from the Main Channel and cooler bottom water moves northward from the lagoon. The surface outflow represents a source of nutrients and organic matter that promotes phytoplankton growth in the waters to the south of the island. The northern part of the Main Channel is characterized by shallow waters divorced from the oligotrophic waters of the lagoon. These shallow sites are strongly influenced by diel heating, evaporation and rainfall and biota may undergo rapid shifts in environmental conditions. Nevertheless, this region of the channel is marked by the highest rates of photosynthetic O_2 production in the system. Restricted exchange in the northern channel may harbor microalgae, which were indicated by high chlorophyll levels along the bottom.

ACKNOWLEDGEMENTS

We are very grateful to K. Rützler and M. Carpenter for the use of the Carrie Bow Cay field station and for the support we received, to K. Parson and B. Pfieffer for their assistance with fieldwork, to J. Pinckney for HPLC analyses, and to C. Holland, A. Dubois and M. West for laboratory support while we were in Belize. This paper is contribution No. 730 from the Caribbean Coral Reef Ecosystem Program of the Smithsonian Institution.

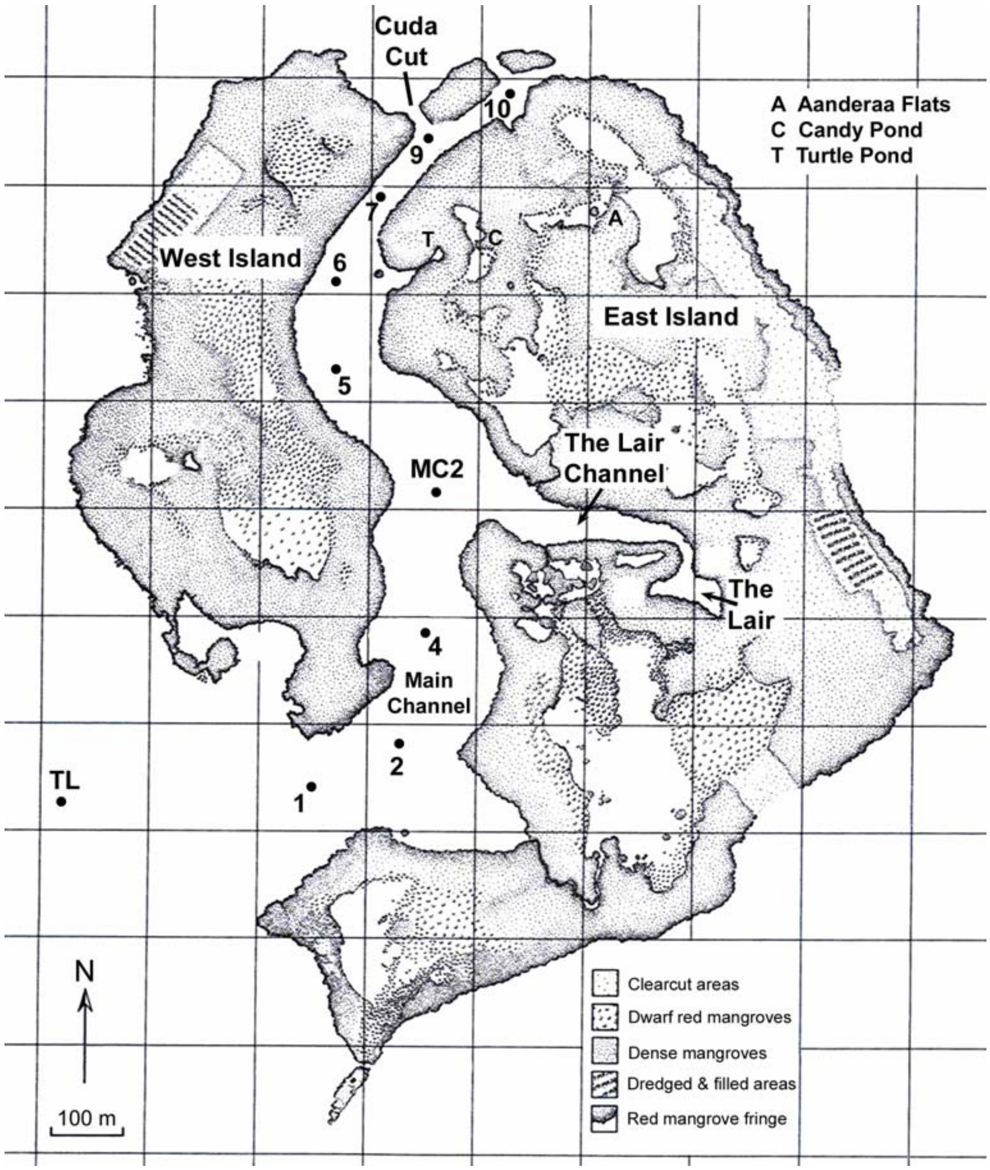

Figure 2. Map of Twin Cays showing sampling stations in the Main Channel. Map drawn by M. Ryan, Department of Invertebrate Zoology, NMNH, Smithsonian Institution, Washington D.C. Gridlines represent nominal scale.

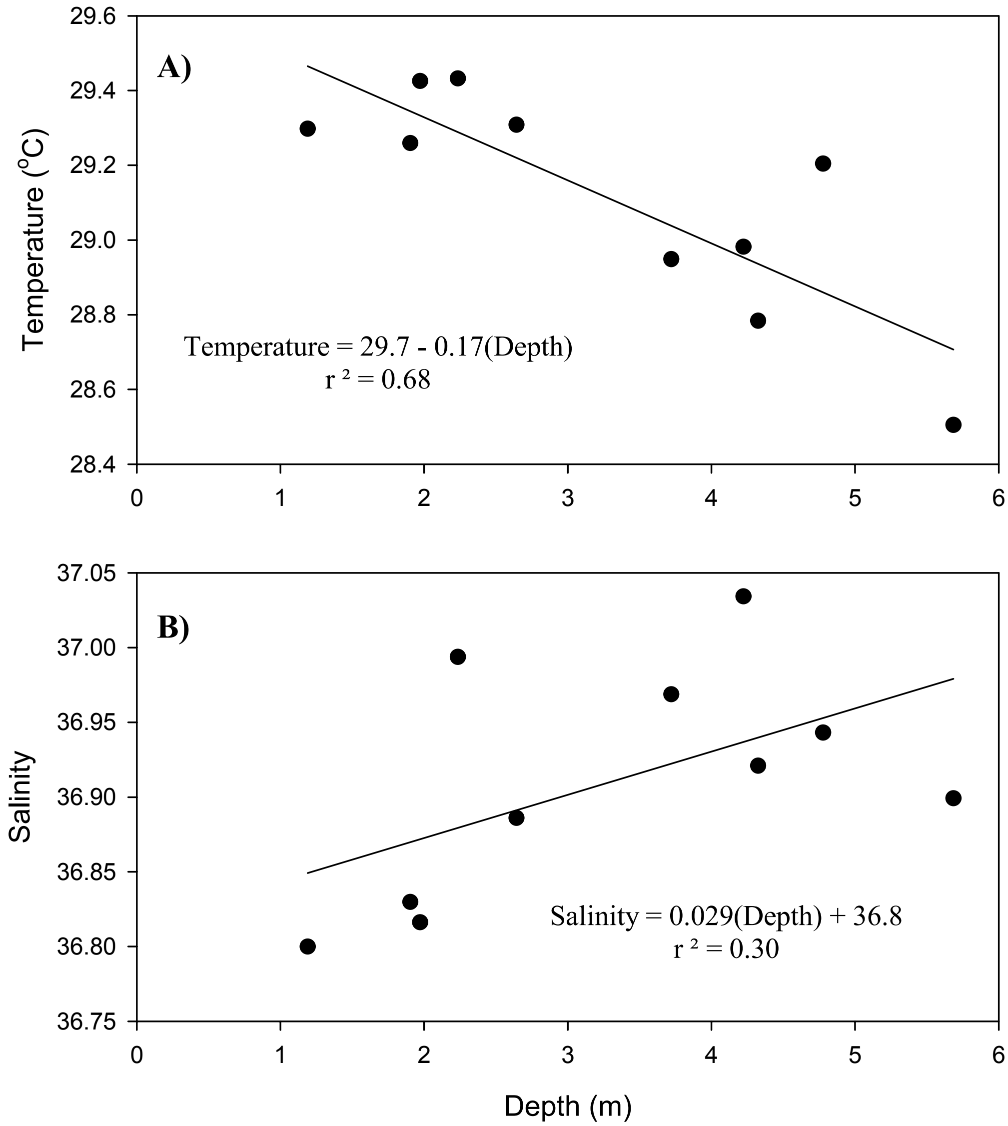

Figure 3. Linear relationship between A) temperature and depth and B) salinity and depth for stations in the Main Channel at Twin Cays, Belize. Temperature and salinity data were averaged with respect to depth and time.

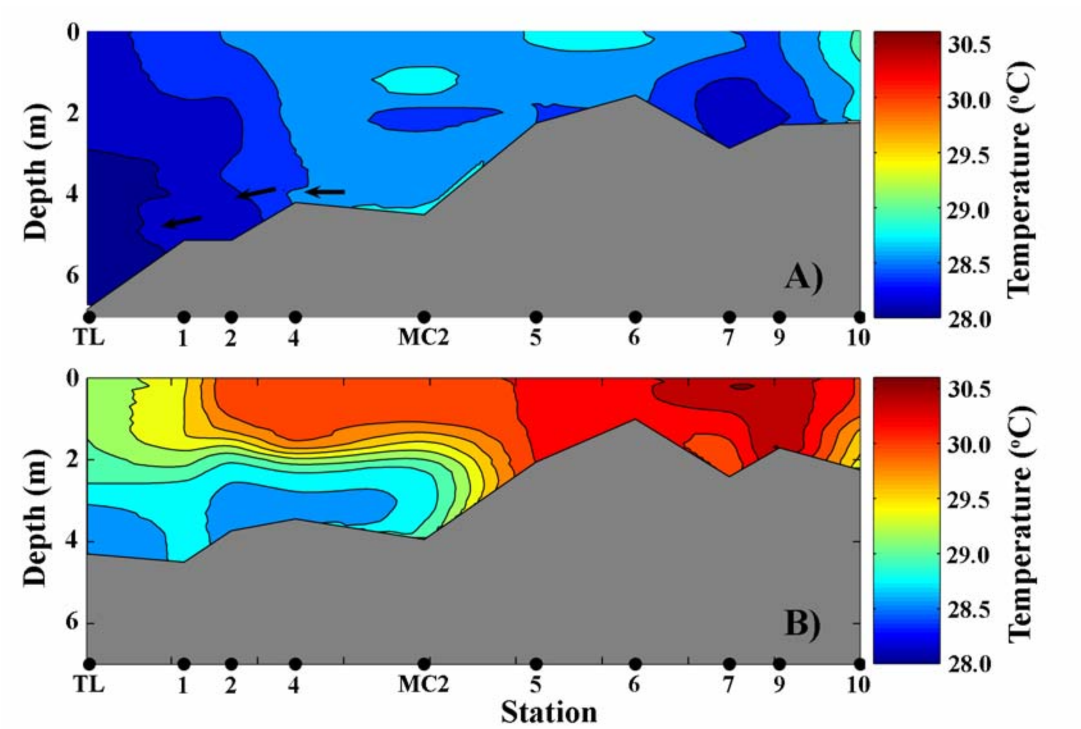

Figure 4. Morning vertical sections of (A) temperature (ºC) and (B) salinity from the Main Channel at Twin Cays, Belize. See Fig. 2 for stations. Arrows represent southward flow of bottom water from the Lair Channel (Sta. MC2).

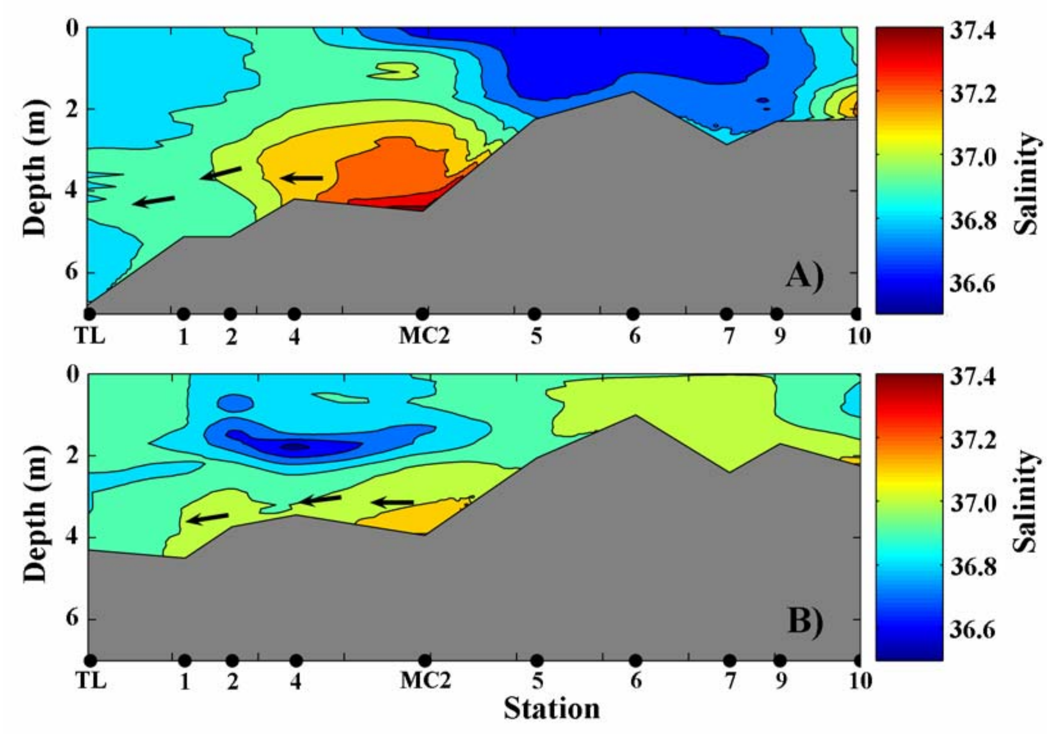

Figure 5. Afternoon vertical sections of (A) temperature (ºC) and (B) salinity from the Main Channel at Twin Cays, Belize. See Fig. 2 for stations. Arrows represent southward flow of bottom water from the Lair Channel (Sta. MC2).

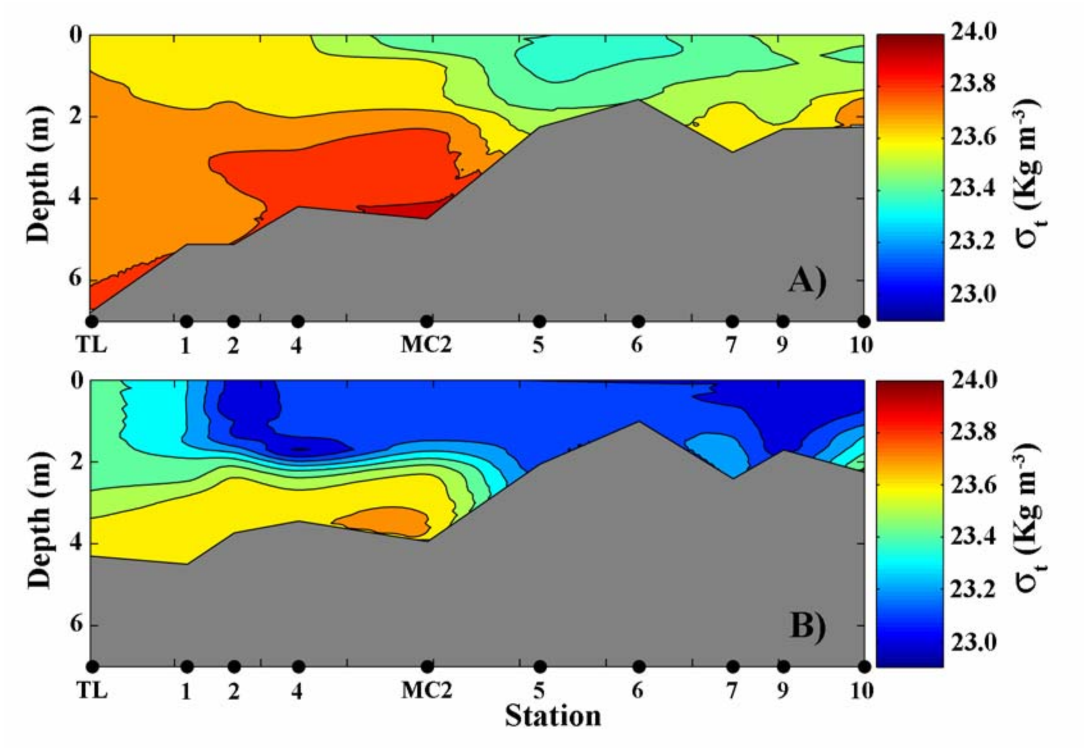

Figure 6. Density sections (σ_t) of the Main Channel created from (A) morning (am) and (B) afternoon (pm) profile data. See Fig. 2 for stations.

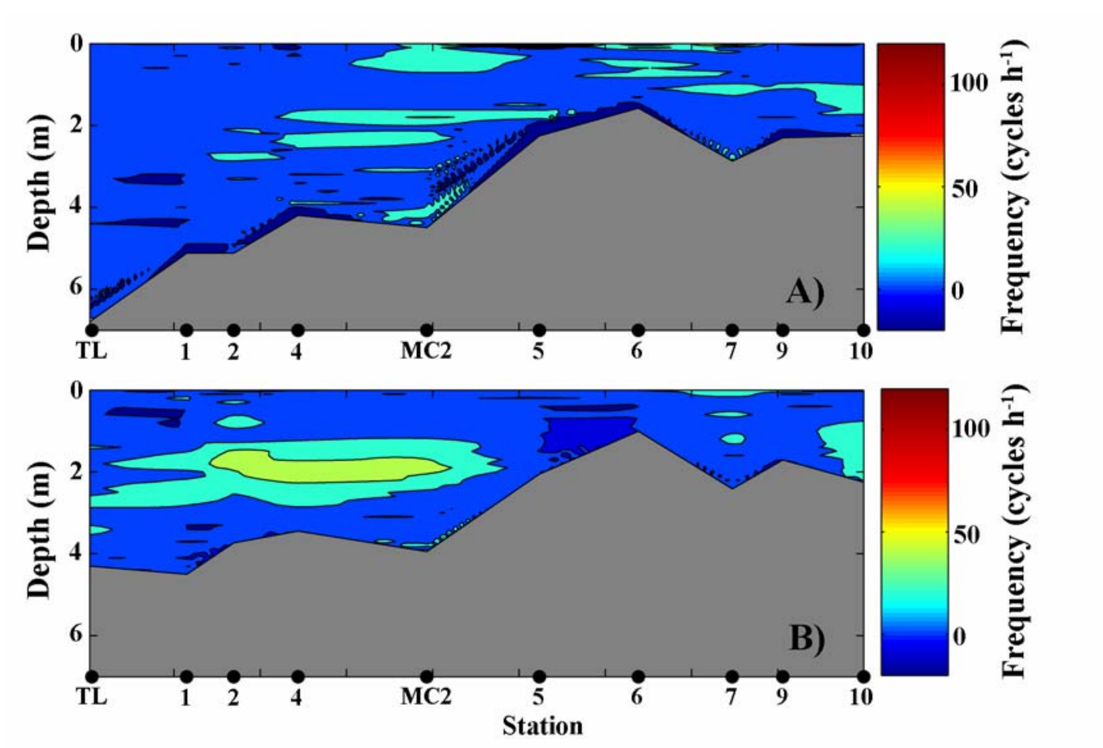

Figure 7. Vertical sections of the Brunt-Väisälä frequency (N) in the Main Channel created from (A) morning and (B) afternoon profile data. See Fig. 2 for station map.

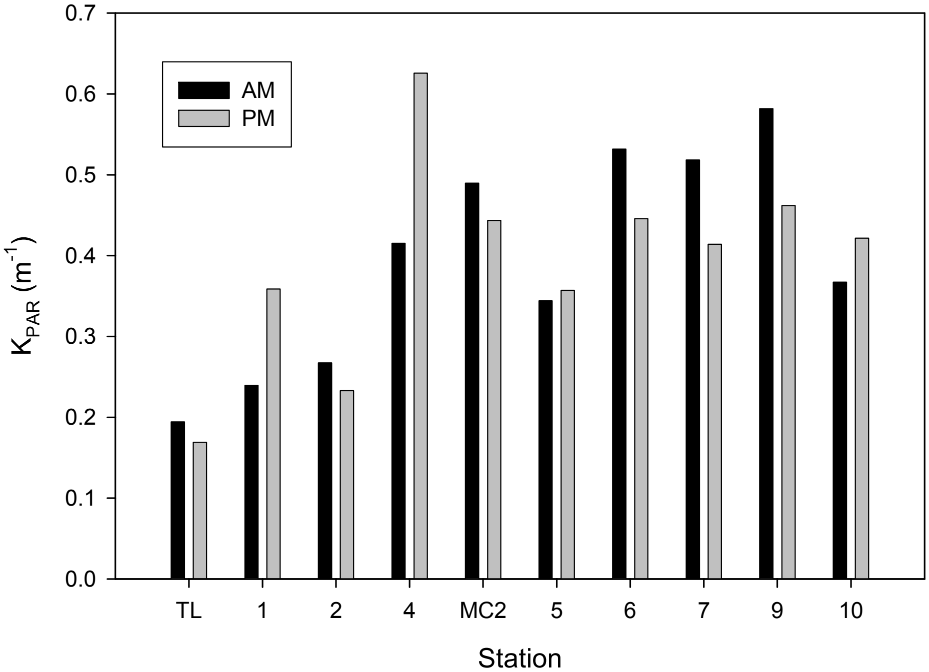

Figure 8. A comparison of light attenuation at stations in the Main Channel, Twin Cays. Attenuation was quantified as K_{PAR}, the light attenuation coefficient relative to PAR (400-700 nm) calculated from morning (AM) and afternoon (PM) profile data.

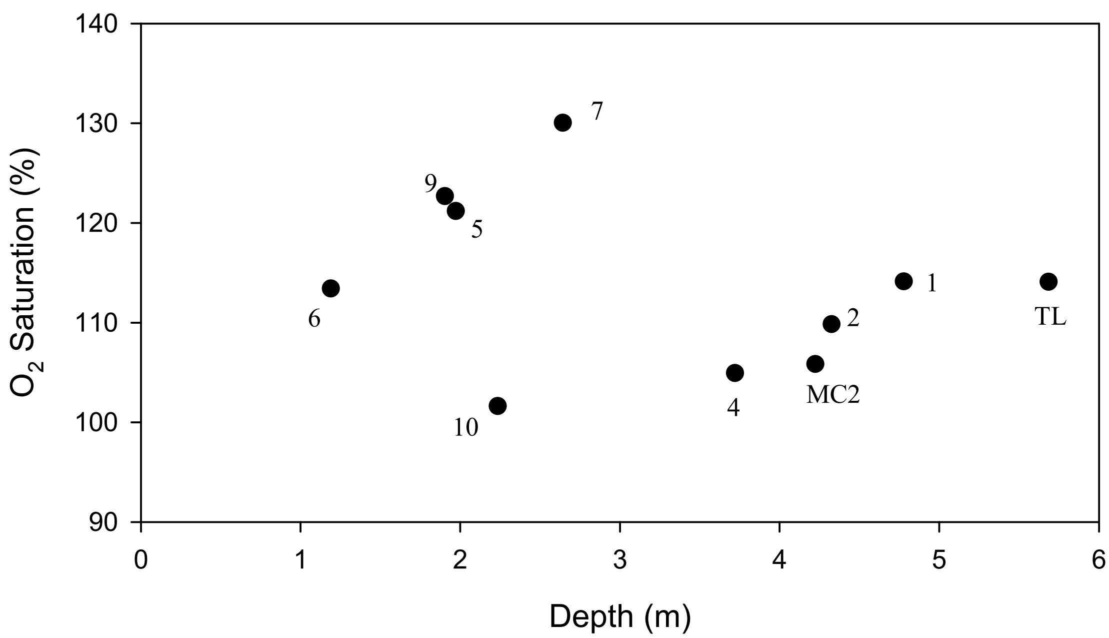

Figure 9. Relationship between mean dissolved O_2 saturation and depth at stations in the Main Channel. Data were averaged with respect to time.

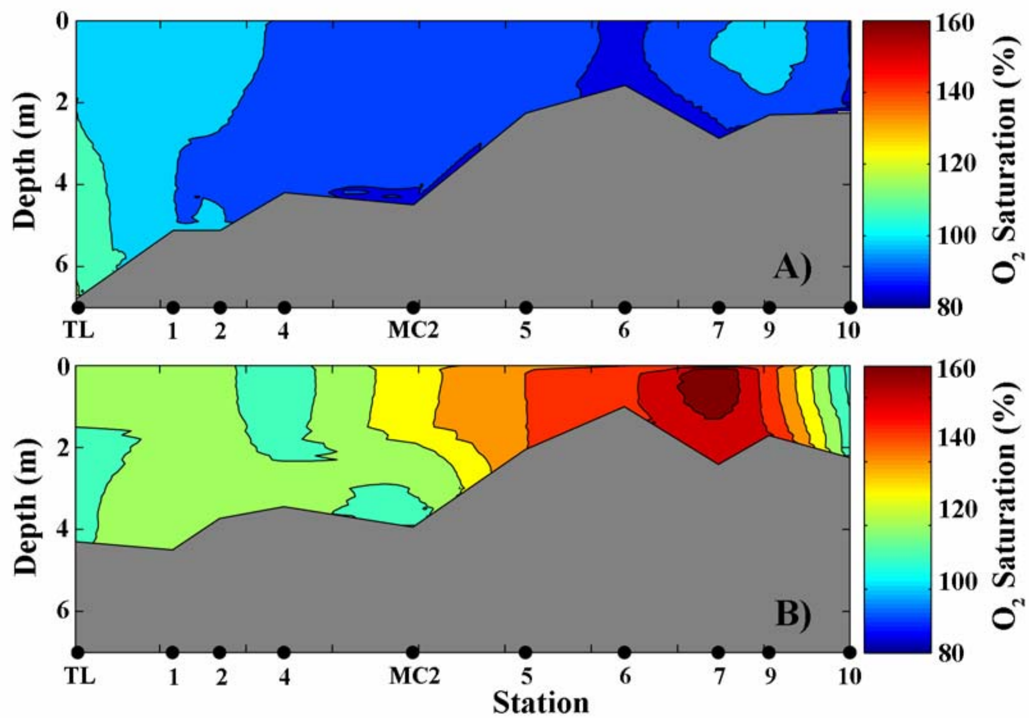

Figure 10. Dissolved O_2 saturation (%) sections of the Main Channel created from morning (am) and afternoon (pm) profile data. See Fig. 2 for station map.

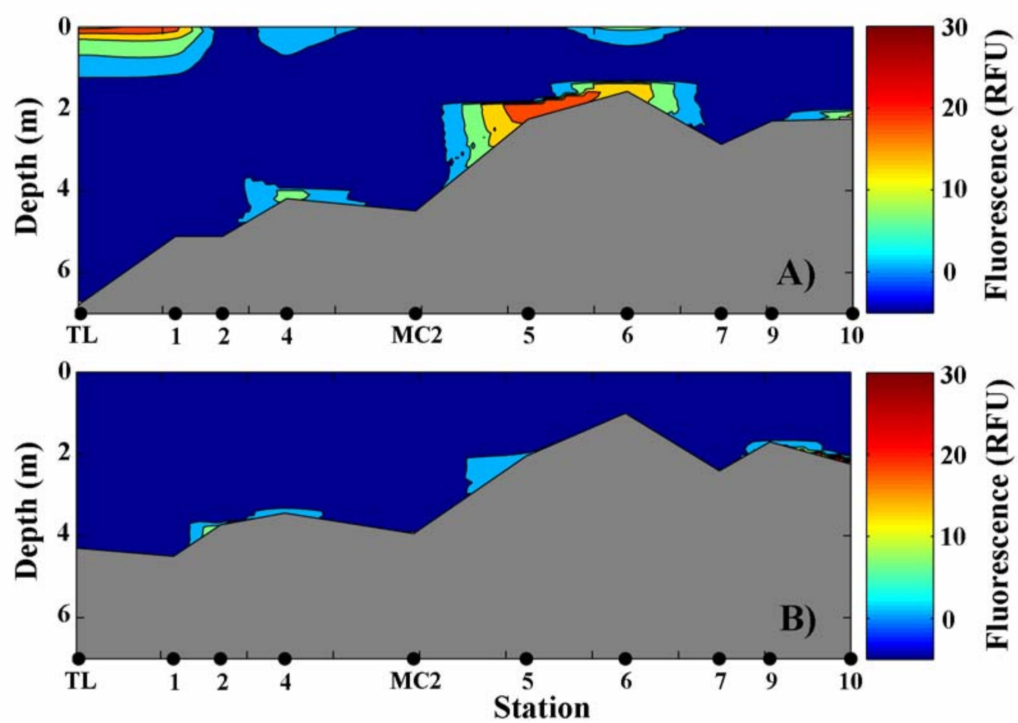

Figure 11. Vertical sections chlorophyll fluorescence (RFU) created from (A) morning and (B) afternoon profile data. See Fig. 2 for station map.

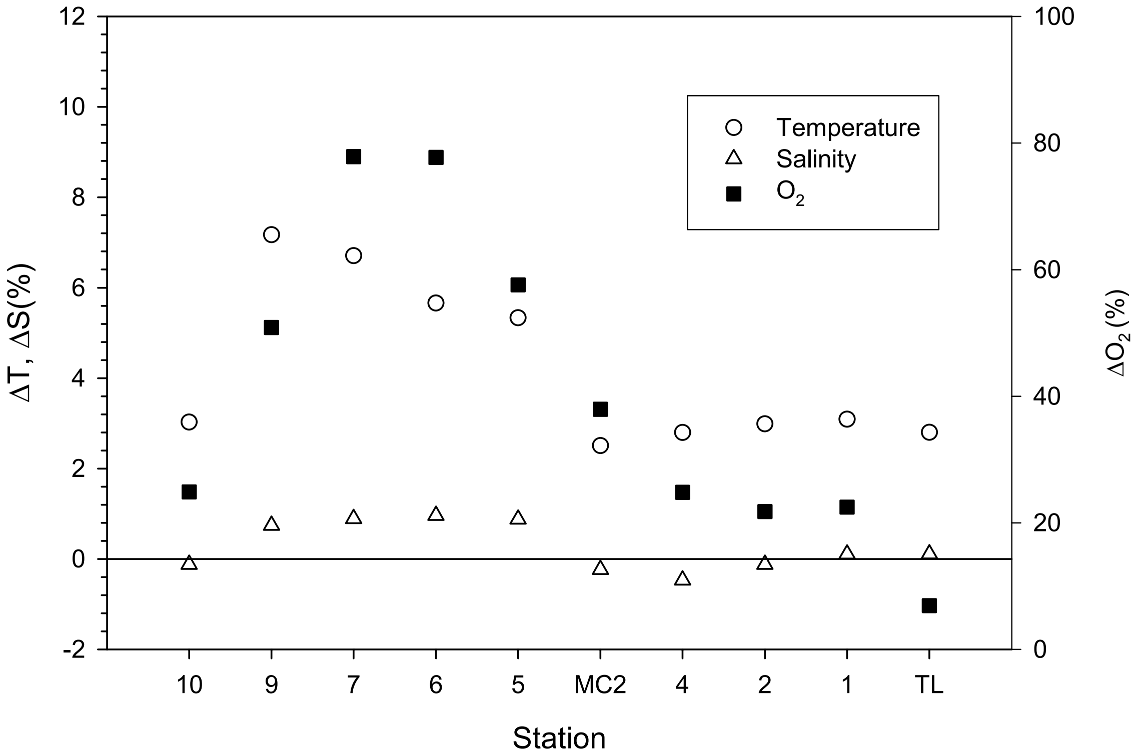

Figure 12. Diel shifts in temperature (ΔT), salinity (ΔS) and oxygen saturation (ΔO_2) at stations along the length of the Main Channel at Twin Cays, Belize. Data represent the difference between afternoon and morning values of mean (depth-averaged) temperature, salinity and O_2 saturation.

Table 1. Average depth (D), temperature (T) and salinity (S) at stations in the Main Channel, Twin Cays, Belize. Mean values represent depth-averaged data.

Station	D (m)	am T (ºC)	am S	pm T (ºC)	pm S
10	2.2	28.96	37.018	29.84	36.973
9	1.9	28.52	36.730	30.56	37.004
7	2.6	28.42	36.734	30.33	37.061
6	1.2	28.73	36.678	30.36	37.030
5	2.0	28.70	36.663	30.23	36.985
MC2	4.2	28.72	37.066	29.44	36.980
4	3.7	28.64	37.037	29.44	36.862
2	4.3	28.45	36.939	29.30	36.893
1	4.8	28.33	36.903	29.20	36.943
TL	5.7	28.21	36.884	29.00	36.925

Table 2. Vertical gradients of temperature and salinity measured in the Main Channel, Twin Cays in the morning (am) and afternoon (pm) of 18 May 2004. Negative gradients indicate bottom values were higher than surface values.

Station	**am** $\alpha\ \partial T_z/\partial z$ **(10^{-3} m^{-1})**	**am** $\beta\ \partial S_z/\partial z$ **(10^{-3} m^{-1})**	**pm** $\alpha\ \partial T_z/\partial z$ **(10^{-3} m^{-1})**	**pm** $\beta\ \partial S_z/\partial z$ **(10^{-3} m^{-1})**
10	7.87	86.6	-115	87.5
9	-44.8	5.36	8.75	32.4
7	-16.8	30.4	-46.7	-8.22
6	-132	21.4	0.00	0.00
5	-33.6	48.5	-3.04	-1.95
MC2	13.9	116	-82.4	62.1
4	-3.35	36.6	-143	34.0
2	-8.59	0.24	-105	36.3
1	-16.3	8.28	-38.0	12.8
TL	-12.3	-6.28	-53.7	1.13

Table 3. Average oxygen saturation in the Main Channel, Twin Cays in the morning (am) and afternoon (pm) of 18 May 2004. Values were averaged with respect to depth.

Station	**am** O_2 **Saturation (%)**	**pm** O_2 **Saturation (%)**
10	89.6	112
9	104	156
7	95.4	170
6	88.6	158
5	95.1	150
MC2	92.9	128
4	95.7	119
2	101	123
1	101	124
TL	111	119

REFERENCES

Alongi, D.M, K.G. Boto, and F. Tirendi
1989. Effect of exported mangrove litter on bacterial productivity and dissolved organic carbon fluxes in adjacent tropical nearshore sediments. *Marine Ecology Progress Series* 56:133-144.

Ambler J.W., J. Alcala-Herrera, and R. Burke
1994. Trophic roles of particle feeders and detritus in a mangrove island prop root ecosystem. *Hydrobiologia* 292/293:437-446.

Chróst, R.J., and M.A. Faust
1999. Consequences of solar radiation on bacterial secondary production and growth rates in subtropical coastal water (Atlantic Coral Reef off Belize, Central America). *Aquatic. Microbial Ecology* 20:39-48.

Faust, M.A.
2004. The dinoflagellates of Twin Cays, Belize: biodiversity, distribution, and vulnerability. *Atoll Research Bulletin* 514:1-20.

Feller, I.C.
1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs* 65(4):477-505.

Ferrari, F.D, J.A. Fornshell, L. Ong, and J.W. Ambler
2003. Diel distribution of copepods across a channel of an overwash mangrove island. *Hydrobiologia* 499:147-159.

Fleischman, E.M.
1989. The measurement and penetration of ultraviolet radiation into tropical marine water. *Limnology and Oceanography* 34(8):1623-1629.

Goodbody, IG.
2004. Diversity and distribution of Ascidians (Tunicata) at Twin Cays, Belize. *Atoll Research Bulletin* 524:1-23.

Kibler, S.R., M.A. Faust, S.M. Varnam, R.W. Litaker, and P.A. Tester
In prep. Phytoplankton Distribution in a Mangrove Embayment, Twin Cays, Belize.

Lesser, M.P.
1996. Elevated temperatures and ultraviolet radiation cause oxidative stress and inhibit photosynthesis in symbiotic dinoflagellates. *Limnology and Oceanography* 41(2):271-283.

Macintyre, I.G., I. Goodbody, K. Rützler, D.S. Littler, and M.M. Littler
2000. A general biological and geological survey of the rims of the ponds in the major mangrove islands of the Pelican Cays, Belize. *Atoll Research Bulletin* 467:13-44.

MacIntyre, S., J.R. Romero, and G.W. Kling
2002. Spatial-temporal variability in surface layer deepening and lateral advection in an embayment of Lake Victoria, East Africa. *Limnology and Oceanography* 47:656-671.

Mann, K.H., and J.R.N. Lazier
1996. *Dynamic of Marine Ecosystems* Blackwell Science, Cambridge.

McKee, K.L, I.C. Feller, M. Popp, and W. Wanek
2002. Mangrove isotopic ($\delta^{15}N$ and $\delta^{13}C$) fractionation across a nitrogen vs. phosphorus limitation gradient. *Ecology* 83(4):1065-1075.

Moran, M.A., J.W. Wicks, and R.E. Hodson
1991. Export of dissolved organic matter from a mangrove swamp ecosystem: evidence from natural fluorescence, dissolved lignin phenols, and bacterial secondary production. *Marine Ecology Progress Series* 76:175-184.

Pritchard, D.W.
1989. Estuarine classification – A help or a hindrance. Pages 1-38 in B.J. Neilson, A. Kuo and J. Brubaker (eds). *Estuarine Circulation*. Humana Press, Clifton, New Jersey.

Richardson, S.L.
2000. Epiphytic Foraminifera of the Pelican Cays, Belize: Diversity and distribution. *Atoll Research Bulletin* 475:207-228.

Richardson, S.L.
2004. Seasonal variation in epiphytic foraminiferal biotas from *Thalassia* seagrass habitats, Twin Cays, Belize. *Atoll Research Bulletin* 517:1-39.

Rodriguez, W., and I.C. Feller
2004. Mangrove landscape characterization and change in Twin Cays, Belize using aerial photography and IKONOS satellite data. *Atoll Research Bulletin* 513:1-22.

Rützler, K., I. Goodbody, M.C. Diaz, I.C. Feller, and I.G. Macintyre
2004. The aquatic environment of Twin Cays, Belize. *Atoll Research Bulletin* 512:1-35.

Rützler, K., M.C. Diaz, R.W.M. Van Soest, S. Zea, K.P. Smith, B. Alvarez, and J. Wulff
2000. Diversity of sponge fauna in mangrove ponds, Pelican Cays, Belize. *Atoll Research Bulletin* 476:229-248.

Talling, J.F.
2001. Environmental controls on the functioning of shallow tropical lakes. *Hydrobiologia* 458:1-8.

Urish, D.W.
2000. Preliminary hydrographic surveys of some ponds in the Pelican Cays, Belize. *Atoll Research Bulletin* 469:59-85.

Villareal, T.A., S.L. Morton, and G.B. Gardner
2000. Hydrography of a semienclosed mangrove lagoon, Manatee Cay, Belize. *Atoll Research Bulletin* 470:87-103.

Wright, R.M., D.W. Urish, and I. Runge
1991. The hydrology of a Caribbean mangrove island. Pages 170-184 in G. Cambers and O.T. Magoon (eds). *Coastlines of the Caribbean*. American Society of Civil Engineers, New York.