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**COMMUNITY STRUCTURE, WATER COLUMN NUTRIENTS, AND WATER
FLOW IN TWO PELICAN CAYS PONDS, BELIZE**

BY

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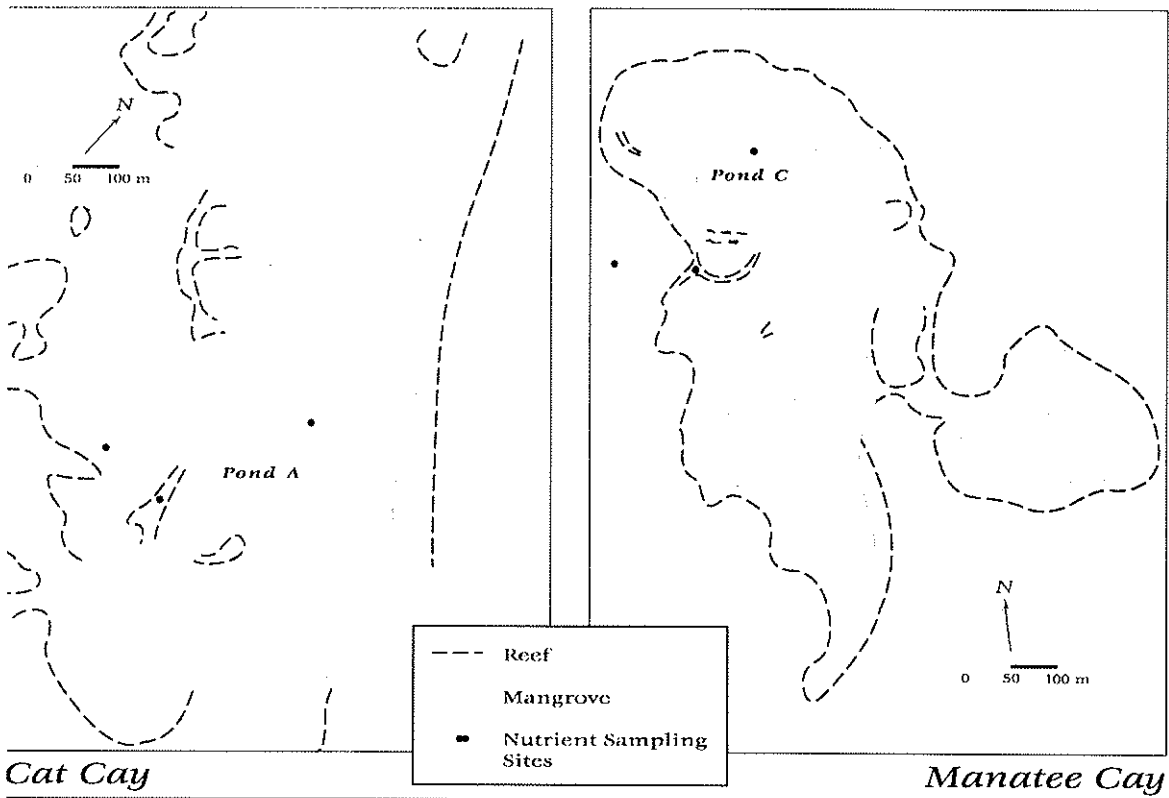
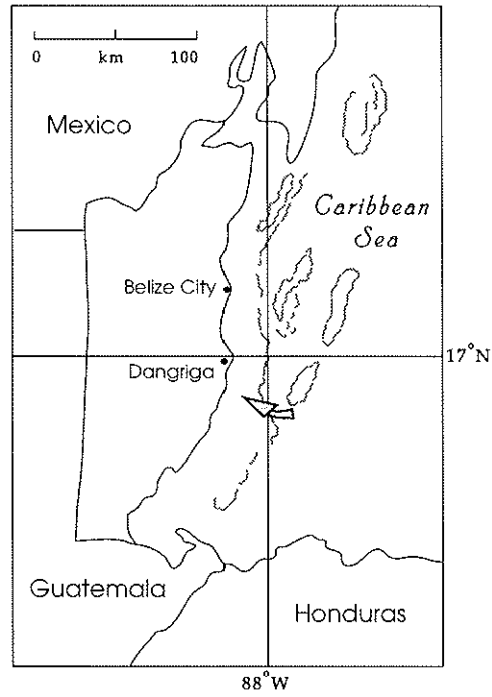


Figure 1. Map showing location of nutrient sampling sites and Ponds A and C in Cat and Manatee Cay, respectively

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ABSTRACT

Nutrient concentrations, water flow, temperature, chlorophyll *a*, and benthic community structure were measured at locations in two mangrove-ringed ponds in the Pelican Cays, Belize. Benthic community structure changed from coral dominance outside the ponds to macroalgae and seagrass dominance inside the ponds. While corals were generally absent inside Pond C, Manatee Cay, they persisted well into Pond A, Cat Cay. Dissolved inorganic nitrogen concentrations (ammonium + nitrate + nitrite) were naturally elevated along the coral ridges at the openings of the ponds and, sometimes, at the bottom of the ponds. Mean nitrate + nitrite concentrations, which ranged from 0.51 to 0.71 μM along the ridges at the entrances of both ponds between 1995 and 1997, were consistently significantly elevated compared with concentrations at nearby coral reefs and, at times, were significantly elevated above levels outside and in the center of the ponds. Soluble reactive phosphorus concentrations were generally low throughout the ponds but were occasionally elevated inside and at the bottom of the ponds. Mean chlorophyll *a* concentrations inside both ponds in 1997 were significantly elevated, indicating nutrient enrichment. Flow speeds were low at all locations in and around both mangrove ponds. Pond A (Cat Cay) has two openings, which promote flushing and exchange. Pond C (Manatee Cay) has only one opening, and therefore has greater water and nutrient retention. This retention was reflected in the significantly higher chlorophyll *a* concentrations inside Pond C. The two ponds are low-flow environments with natural elevation of dissolved inorganic nitrogen and sometimes dissolved phosphorus. These nutrients generate higher production inside the ponds (which support unique prop root suspension feeding communities) and influence benthic communities of these ponds and of the coral ridges at the entrances of the ponds.

INTRODUCTION

The Pelican Cays (16°39'N, 88°10'W) are a string of mangrove islands south of Carrie Bow Cay (CBC). Pond A (Cat Cay) and Pond C (Manatee Cay) (Fig. 1), are semi-enclosed mangrove ponds and were the focus of our descriptive study. The ponds are deep (> 10 m) circular depressions. Macintyre et al. (this volume) describe these steep-sided ponds as having

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grown as "honeycomb shoals" on top of a drowned karst pattern that has this basic shape. The coral communities in these ponds are depauperate, but soft-bodied anthozoans such as anemones and zoanthids can be abundant. The ponds support a rich community of suspension feeders such as ascidians and sponges that often

dominate the surfaces of mangrove roots along the pond edges (Goodbody, this volume; Rützler et al., this volume). At the pond openings where water flows in and out of the ponds, shallow coral ridges (< 1 m water depth) show a gradual transition from coral dominance outside to a mixed assemblage of corals, algae, seagrasses, and soft-bodied anthozoans inside (Macintyre et al., this volume). *Agaricia tenuifolia* is frequently the dominant coral along this transition and can occupy large areas inside ponds as well as outside. Aronson et al. (1998) report that *A. tenuifolia* became the dominant coral on these reefs only in the past decade. Other corals common to the ridges are *Acropora cervicornis* and *Porites divaricata*, and the hydrocoral *Millepora complanata*.

Mangrove communities adjacent to nearshore or island coral communities (Vijay Anand, 1995), can significantly alter local hydrodynamics of the region and are areas of high primary productivity that have the potential to locally elevate nutrient concentrations in the water column. Both dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) concentrations around a mangrove community can be significantly elevated compared with water from nearby coral reefs in the same region (Lapointe et al., 1992). Nutrients from natural or anthropogenic sources have the potential to shift benthic community structure from coral-dominated to a macroalgae and passive suspension feeding-dominated benthos. Lapointe et al. (1992) and Bell (1992) have suggested that when DIN concentrations are greater than $\sim 1.0 \mu\text{M}$ and SRP concentrations are greater than $\sim 0.1 \mu\text{M}$, benthic community structure will be dominated by macroalgae instead of corals and seagrasses. According to Bell (1992), chlorophyll *a* is the best indication of eutrophication and a threshold of $\sim 0.5 \mu\text{g/l}$ would be indicative for coral reef environments. With sustained nutrient elevation, macroalgae have the potential to overgrow and eliminate reef-building corals from the benthos adjacent to mangrove communities. Where corals are not overgrown by macroalgae, Atkinson et al. (1995) hypothesize, elevated nutrients could enhance coral growth. However, experiments by Marubini and Spencer-Davis (1996) have demonstrated that increased nitrate concentrations can suppress coral growth.

The coral reefs at Carrie Bow Cay and in the Pelican Cays have experienced a relatively low level of anthropogenic disturbance, and the mixed reef community of coral, algae, and seagrasses at Carrie Bow Cay has been well documented (Rützler and Macintyre, 1982). The purpose of our study was to characterize water flow, nutrient concentrations, temperature, and benthic community structure in and around two semi-enclosed mangrove ponds with such a mixed community.

METHODS

Study Site

The study was carried out in the Pelican Cays ($16^{\circ} 39' \text{N}$, $88^{\circ} 10' \text{W}$) and at Carrie Bow Cay ($16^{\circ} 48' \text{N}$, $88^{\circ} 05' \text{W}$), Belize. Samples were collected from Pond A at Cat Cay and Pond C at Manatee Cay (Fig. 1).

Water Movement

Flow speeds at locations inside and outside the ponds at Cat and Manatee Cays were measured with continuously recording Interocean S4 electromagnetic current meters. Instantaneous records are means of all 0.5-second data points, irrespective of direction. Vector-averaged records are vector-averaged means of 600 data points over a 5-min period, removing high-frequency (wave) effects on flow. Current meters were bolted to an upright PVC pipe embedded in a square cement base that could be placed in depressions among coral colonies such that the meter itself was 50 cm above the substratum. In some cases, an aluminum base was used with the same vertical PVC pipe. Water depth above the meter was 1.5 to 2.0 m. For purposes of comparison, brief deployments for several hours were carried out among habitats inside, outside, and along the tops of entrance ridges at the same time at each Cay. Long deployments lasting two days or more were also carried out on several trips during 1994–1997.

Water Quality and Temperature

Temperature measurements were made using Tidbit TM submersible temperature recorders (Onset Computer Inc.) programmed to record every five minutes for up to two days. Tidbits were placed at depths of 1.5 to 2.0 m depths inside and outside ponds, and at 6 m inside ponds for short periods (15–30 min), then left at inner and outer depths of 1.5–2.0 m for 48 hours.

On five visits to Belize (March 1995, 1996, 1997, and July 1995, 1996) water samples were collected inside and outside both Ponds A and C for inorganic nutrient analysis. On the July 1996 and March 1996 and 1997 trips, samples were also collected at a fore-reef site near CBC for comparison with the pond sites. During each visit, we made two to four trips to Ponds A and C to collect water samples at stations throughout the ponds. The following stations were sampled on each trip to Cat and Manatee ponds: a depth of 0.5 m above the bottom in the center of the pond, 0.5 m in the center of the pond, 0.5 m above the coral ridge opening, and 0.5 m at a point 100 m outside the pond (Fig. 1). Water samples were collected in acid-washed HDPE bottles and placed on ice in the dark. Upon returning to the CBC station, we fixed a subsample for ammonium (NH_4) determination with phenol solution and analyzed it within 48 hours according to methods of Parsons et al. (1984); another subsample was analyzed immediately for soluble reactive phosphorus (SRP) according to methods of Parsons et al. (1984). The remainder of the sample was filtered with a sterile GF/F filter and frozen for later analysis. The frozen subsamples were analyzed for nitrate plus nitrite ($\text{NO}_3 + \text{NO}_2$) by the Nutrient Analytical Services Laboratory at the Chesapeake Biological Laboratory in Solomons, Maryland, using standardized AutoAnalyzer methodology (D'Elia et al., 1997). Mean inorganic nutrient concentrations were calculated for each pond depth and location for each visit to Belize. Significant differences in nutrient concentrations between various locations were tested with a one-way ANOVA. Means from significant analyses were compared with an SNK test. Statistical comparisons of SRP were not performed because measures of variance could not be calculated since many measurements were below the detection limit.

Chlorophyll *a* concentrations were measured at locations inside and outside both Ponds A and C during March 1997. Replicate samples of 4 l of seawater were collected at locations inside and outside the ponds on two occasions during March 1997. The seawater samples were filtered

through GF/F filters that were then placed in 30 ml of 90% acetone on ice in the dark. The filters were returned to the CBC station and extracted overnight in a refrigerator. Chlorophyll *a* concentrations were determined according to the method of Parsons et al. (1994). Significant differences of chlorophyll *a* concentrations between locations were tested with a Student's *t*-test.

Benthic Community Structure

Benthic community structure was characterized by videotaping 30-m transects at two locations inside and two locations outside the ponds. All transects had the coral ridge as an endpoint. A 30-m transect tape was placed along a 1- to 1.5-m depth contour at locations inside and outside the ponds. These transects were videotaped using a Yashica high 8-mm camcorder that had a scale mounted on a rod approximately 30 cm in front of the camera. A swath of substrate 30 to 50 cm wide was slowly videotaped along the 30-m transects. The videos were analyzed on a high-resolution monitor using a stop-frame, random-dot analysis (Sebens and Johnson, 1991; Aronson et al., 1994). A clear plastic sheet with 10 random dots was placed over the screen, and sessile organisms that occurred under the dots were identified and recorded; the video was then advanced to a new, nonoverlapping section for analysis. Approximately 350 dots were counted for each transect.

RESULTS

There was a clear temperature variation on a diel cycle for all sites except Manatee Cay, outer ridge (Fig. 2). Water exchange between the ponds and adjacent channels is slow enough that substantial solar heating occurs within the ponds, raising their temperature up to 1° C compared with greater depths in the pond (6m, Table 1) and compared with sites outside the pond (outside, Table 1). The least temperature variation was observed at the outside site at Manatee Cay, which is adjacent to a channel between cays and is thus subject to more water movement and flushing. The outside site at Cat Cay is semi-enclosed by coral ridges, although there is a very broad opening that connects this outside site with another channel between cays.

Much of the water movement experienced by benthic organisms along the coral ridges and within the ponds was due to wind waves superimposed on slow unidirectional currents. Water flow was extremely low at most sites along coral ridges bordering the ponds at these cays and within the ponds themselves (Table 2). Flows on outer edges of the coral ridges at the entrances typically ranged from less than 1 cm s⁻¹ to just over 3 cm s⁻¹ on a given day (Table 2). Most sites, including the relatively unobstructed locations on the outer side of Manatee Cay, had flow speeds less than 5 cm s⁻¹, but there were periods when currents could be detected, producing flows well above 5 cm s⁻¹ (Fig. 3). The greatest flow speeds occur where restricted channels connect the ponds with the outer regions. Tidal or prevailing currents forcing water through those restricted channels create sustained unidirectional flows up to 12 cm s⁻¹ (Fig. 4).

Water flow at pond entrances can be tidally influenced, as at Pond E in Fisherman's Cay (Fig. 5), where the greatest flow speeds we observed coincided with the midtidal amplitudes and the direction of flow reversed on a tidal cycle. There was no such regular directional change at Pond C, where water flowed in and out slowly over a broad ridge, but also where wind blowing across the pond surface can have a large effect on transport. At Pond A, water flowed in through the southwestern channel during all segments of the tidal cycle, then flowed out through a large

Table 1. Midday temperature records at three locations each, for Manatee and Cat Cays during four days in June 1997. Outside and inside sites are as described for figure 1, inside 6 m sites are near the bottom of the ponds just below inside 1 m sites. Note that outside sites and inside 6 m sites were consistently slightly cooler than inside 1 m sites, but that all sites had a temperature range of one degree Celcius or less.

Site	Time	Date	Temperature (°C)		
			Outside 1 m	Pond 1 m	Pond 6 m
Pond A (Cat Cay)	11:00-14:00	6/22/97	30.1-30.4	30.7-30.9	29.9-30.1
Pond C (Manatee Cay)	14:00-15:00	6/22/97	30.1-30.3	30.7-30.1	30.1-30.3
Pond A (Cat Cay)	10:00-11:00	6/24/97	29.7-29.9	30.1-30.3	29.7-29.9
Pond C (Manatee Cay)	12:00-13:00	6/24/97	29.7-29.9	30.3-30.3	30.1-30.1
Pond A (Cat Cay)	10:00-11:00	6/27/97	29.3-29.5	29.3-29.5	29.3-29.5
Pond C (Manatee Cay)	11:00-13:00	6/27/97	29.0-29.2	29.2-29.5	29.4-29.6
Pond A (Cat Cay)	11:00-12:00	6/29/97	29.0-29.2	29.0-29.2	29.0-29.0
Pond C (Manatee Cay)	10:00-11:00	6/29/97	29.0-29.2	29.2-29.4	29.0-29.2

southern opening. Just after high tide, the flow speed through the southwestern opening increased, and it was at its lowest during low tide. This appeared to be a tidal flow superimposed on a unidirectional current flowing from north to south past the cays. On the inner slopes of the ponds, water flow speeds are even lower, rarely exceeding 2 cm s^{-1} (Fig. 3).

Inorganic nutrient concentrations in and around Ponds A and C were variable, but dissolved inorganic nitrogen (DIN) concentrations at certain locations in the ponds were significantly elevated compared with waters from the Carrie Bow Cay fore reef, where DIN was consistently low. $\text{NO}_3 + \text{NO}_2$ concentrations were elevated along the coral ridge at the opening of the ponds compared with surface waters inside and outside the ponds and the Carrie Bow Cay fore-reef site (Table 3). The mean $\text{NO}_3 + \text{NO}_2$ concentrations along the ridges of Ponds A and C were significantly higher ($p < 0.05$) than those from the Carrie Bow Cay fore reef during March and July 1996 and March 1997. Mean $\text{NO}_3 + \text{NO}_2$ along the ridges at the opening of Ponds A and C ranged from 0.51 to $0.71 \mu\text{M}$ while mean concentrations at Carrie Bow Cay ranged from 0.26 to $0.36 \mu\text{M}$ (Table 1).

NH_4 concentrations were also variable in and around Ponds A and C. However, there was a pattern of NH_4 elevation along the ridges and at pond bottoms, whereas concentrations measured at the Carrie Bow Cay fore-reef site were consistently low. The highest concentrations of NH_4 were measured in the bottom of the ponds in July 1996 (Table 4). NH_4 concentrations were significantly higher along the pond ridge than at Carrie Bow Cay fore reef during three sampling periods of March and July 1996 and March 1997 (Table 4). Mean NH_4 concentrations

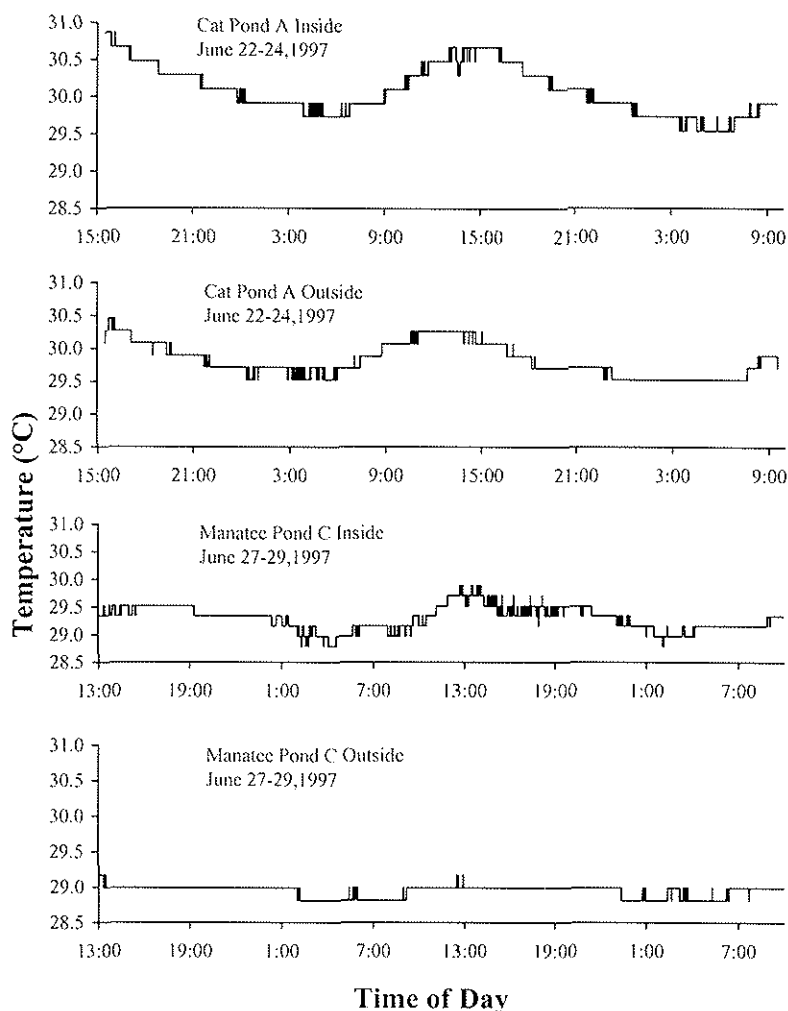


Figure 2. Temperature fluctuation at four sites in the Pelican Cays during June 1997. Inner sites are at a depth of 1-2 m along the inner pond edge, and outer sites are at a similar depth outside the pond. The Cat Cay outer site is partially enclosed, whereas the Manatee Cay outer site is adjacent to an open channel between Cays, which may explain the lower diel temperature variation.

along Pond A and Pond C ridges ranged from 0.20 to 0.30 μM , while the mean concentrations at Carrie Bow Cay ranged from < 0.10 to 0.15 μM . NH_4 in surface waters both inside and outside the ponds were generally lower than ridge and bottom concentrations. In Pond C, surface mean concentrations were significantly lower than ridge mean concentrations during the March 1996 and 1997 visits.

The DIN pattern showed elevated concentrations along the entrance ridge and at times elevated concentrations at the bottom of pond. The DIN concentrations of surface water inside and outside Pond A and C were typically low and at times below detection limits. The Carrie Bow Cay fore reef had consistently low DIN concentrations (Tables 3 and 4).

The SRP concentrations were generally low and did not exhibit a clear pattern at either of the ponds. During March 1996, SRP concentrations were elevated but variable in the ponds

Table 2. Water flow (cm sec^{-1}) maxima and minima for inner and outer sites at Manatee and Cat Cays during 1995-1997. Note that flow speeds were consistently low at all sites, but that inner sites were lower than outer.

Date	Site	Location	Max Flow (cm sec^{-1})	SD	Min Flow (cm sec^{-1})	SD	Type	Hours Deployed
3/19/95	Manatee Cay	Ridge	1.7	1.2,2.3	0.6	0.3,1.0	Vect	13
3/20/95	Manatee Cay	Ridge	1.5	1.3,1.7	0.4	0.0,1.0	Vect	24
3/21/95	Manatee Cay	Ridge	1.0	0.8,1.2	0.9	0.7,1.2	Vect	2
6/20/97	Cat Cay	Inner	1.6	0.0,2.4	0.9	0.4,1.6	Inst	12
6/21/97	Cat Cay	Inner	2.1	0.9,3.6	0.6	0.2,1.1	Inst	24
6/22/97	Cat Cay	Inner	1.2	0.6,1.9	1.0	0.4,1.7	Inst	3
6/20/97	Cat Cay	Outer	2.2	0.9,3.9	0.7	0.2,1.2	Inst	12
6/21/97	Cat Cay	Outer	3.6	1.8,5.9	0.6	0.2,1.2	Inst	24
6/22/97	Cat Cay	Outer	2.4	0.9,4.5	0.8	0.3,0.5	Inst	3
6/27/97	Manatee Cay	Inner	2.0	1.2,2.9	0.8	0.3,1.4	Inst	11
6/28/97	Manatee Cay	Inner	2.3	1.2,3.7	0.7	0.3,1.3	Inst	24
6/29/97	Manatee Cay	Inner	2.5	1.7,3.5	0.9	0.3,0.6	Inst	4
6/27/97	Manatee Cay	Outer	2.9	1.7,4.4	0.8	0.3,1.4	Inst	11
6/28/97	Manatee Cay	Outer	5.3	3.4,7.6	0.7	0.3,1.3	Inst	24
6/29/97	Manatee Cay	Outer	2.7	1.4,4.3	1.2	0.5,2.0	Inst	4

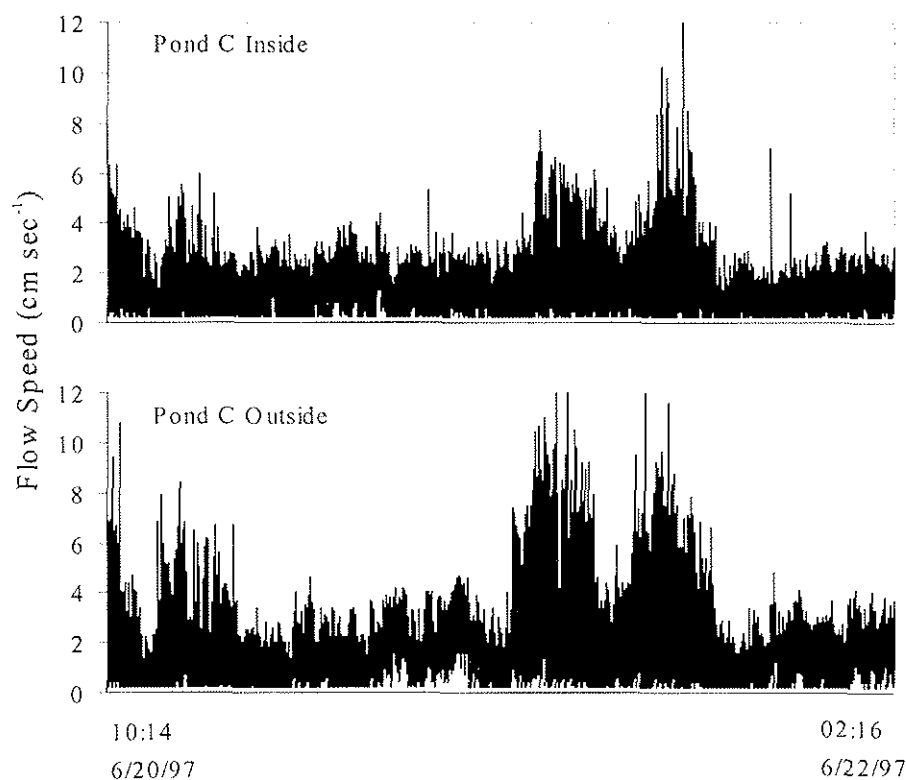


Figure 3. Instantaneous flow speeds at inner and outer locations at Pond A (Cat Cay). Note that the outer sites had consistently higher flow maxima.

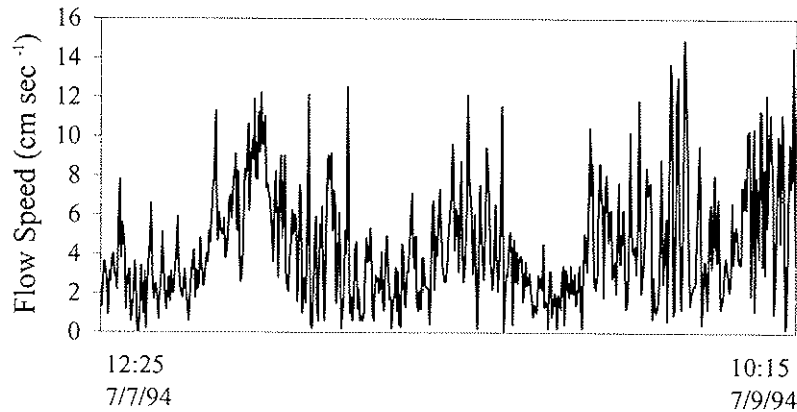


Figure 4. Vector averaged flow speeds at Cat Cay coral ridge, at a point where currents are strongest going into the pond. Note that maximum flows were generally 10-12 cm s^{-1} , 3-5 times higher than most other locations inside and outside the pond (Table 2). The most rapid flows at this site occurred close to the highest tide level, and were directed into the pond.

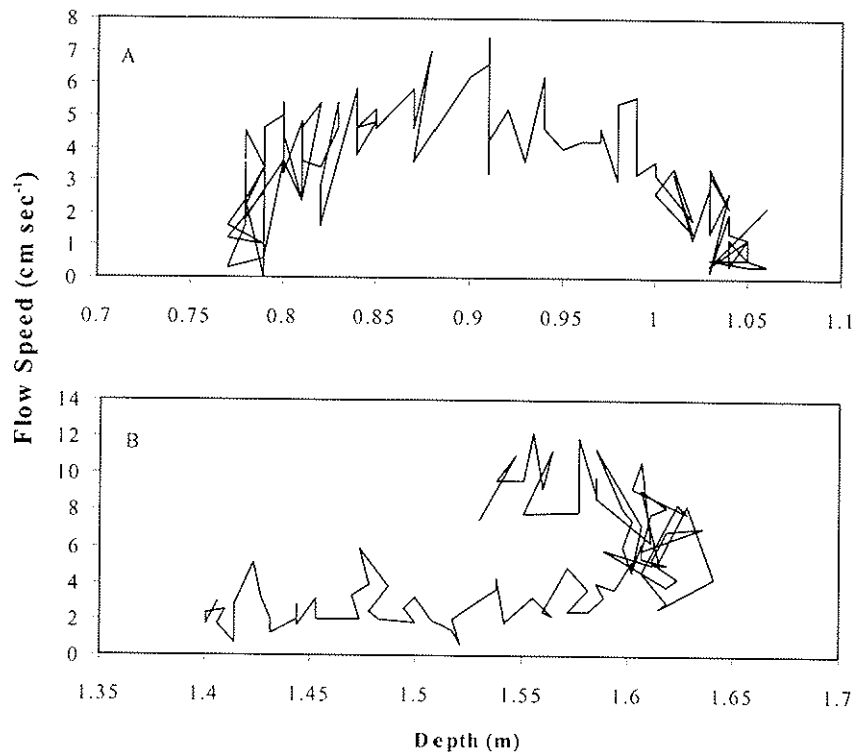


Figure 5. Vector averaged flow speeds. **A.** Fisherman's Cay, adjacent a point where currents flow in and out of the pond. The highest flows, 5-7 cm s^{-1} , occurred at mid tide at this site. **B.** Cat Cay western channel. The highest flows, 10-12 cm s^{-1} occurred close to the high tide.

Table 3. Water column $\text{NO}_3 + \text{NO}_2$ concentrations at Cat, Manatee and Carrie Bow Cays, Belize for five visits 3/95-3/97.

Location	3/95		7/95		3/96		7/96		3/97	
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Pond A (Cat)										
Bottom	0.36 (0.12)	6	0.52 (0.25)	4	0.52 (0.10)	3	0.51 (0.07)	4	0.44 (0.03)	3
Surface	0.38 (0.13)	6	0.51 (0.08)	4	0.59 (0.15)	3	0.44 (0.06)	4	0.35 (0.10)	3
Ridge	0.56 (0.19)	8	0.71 (0.23)	4	0.70 (0.03)	6	0.62 (0.09)	4	0.52 (0.11)	3
Outside	0.28 (0.09)	4	0.68 (0.81)	4	0.58 (0.02)	4	0.44 (0.08)	4	0.53 (0.04)	3
Pond C (Manatee)										
Bottom	0.37 (0.15)	4	0.36 (0.30)	3	0.37 (0.14)	3	0.49 (0.13)	4	0.23 (0.04)	3
Surface	0.13 (0.04)	4	0.33 (0.08)	3	0.25 (0.10)	3	0.37 (0.05)	4	0.22 (0.03)	3
Ridge	0.53 (0.19)	6	0.71 (0.16)	5	0.51 (0.21)	6	0.53 (0.18)	4	0.54 (0.02)	3
Outside	0.26 (0.05)	4	0.70 (0.25)	6	0.43 (0.06)	3	0.34 (0.10)	4	0.39 (0.12)	3
Carrie Bow Barrier Reef										
	NA		NA		0.36 (0.11)	7	0.26 (.07)	5	0.29 (0.06)	6

Table 4. Water column NH_4 concentrations at Cat, Manatee and Carrie Bow Cays, Belize for three visits 3/96-3/97.

Location	3/96		7/96		3/97	
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Pond A (Cat)						
Bottom	0.24 (0.12)	2	0.36 (0.09)	4	0.33 (0.04)	2
Surface	0.18 (0.13)	2	0.27 (0.04)	4	0.16 (0.05)	2
Ridge	0.20 (0.07)	4	0.27 (0.08)	4	0.24 (0.04)	2
Outside	0.17 (0.01)	4	0.21 (0.07)	4	0.15 (0.02)	2
Pond C (Manatee)						
Bottom	0.22 (0.03)	2	0.32 (0.08)	4	0.16 (0.03)	2
Surface	0.12 (0.10)	2	0.20 (0.06)	4	<0.10	2
Ridge	0.20 (0.21)	4	0.31 (0.07)	4	0.29 (0.02)	2
Outside	0.15 (0.06)	2	0.17 (0.02)	4	0.13 (0.03)	2
Carrie Bow Cay Barrier Reef						
	0.11 (0.01)	5	0.13 (0.04)	5	0.13 (0.03)	3

(Table 5). High winds that occurred during this period may have resuspended nutrients from sediments in the bottom of the lagoons. At the ponds, higher concentrations of SRP were typically found inside the ponds or along the ridges (Table 5). The SRP levels from CBC were generally lower than those at all sites within the ponds for the same sampling periods. During July 1996, most mean SRP concentrations were below the detection limit (Table 5). However, individual measurements from inside the ponds were detectable. During March 1997, only the bottom water of Pond A and the bottom and surface water of Pond C had detectable concentrations of SRP.

Chlorophyll *a* concentrations were measured inside and outside Ponds A and C. The mean

Table 5. Water column SRP concentrations at Cat, Manatee and Carrie Bow Cays, Belize for five visits 3/95-3/97.

Location	3/95		7/95		3/96		7/96		3/97	
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Pond A (Cat)										
Bottom	0.04 (0.01)	6	<0.03	4	0.07 (0.03)	2	<0.03	4	0.03 (0.01)	2
Surface	0.04 (0.02)	6	<0.03	4	0.39 (0.20)	2	<0.03	4	<0.03	2
Ridge	0.04 (0.01)	8	<0.03	4	0.25 (0.21)	4	<0.03	4	<0.03	2
Outside	0.03 (0.02)	4	<0.03	4	0.28 (0.26)	2	<0.03	4	<0.03	2
Pond C (Manatee)										
Bottom	0.14 (0.08)	5	0.04 (0.01)	3	0.11 (0.11)	2	<0.03	4	0.05 (0.01)	2
Surface	0.05 (0.01)	4	<0.03	4	0.24 (0.23)	2	<0.03	4	0.04 (0.01)	2
Ridge	0.04 (0.02)	6	<0.03	5	0.44 (0.48)	6	<0.03	4	<0.03	2
Outside	0.03 (0.01)	3	<0.03	6	<0.03	3	<0.03	4	<0.03	2
Carrie Bow										
Barrier Reef	NA		NA		0.03 (0.01)	4	<0.03	4	<0.03	2

chlorophyll *a* concentrations were significantly higher ($p < 0.05$) inside both ponds than outside the ponds (Fig. 6) and significantly higher inside Pond C than inside Pond A. The mean ($\pm 1SD$) chlorophyll *a* concentrations ($\mu g/l$) at Pond A were 0.25 (± 0.06) outside and 0.46 (± 0.06) inside and in Pond C were 0.25 (± 0.04) outside and 0.85 (± 0.23) inside.

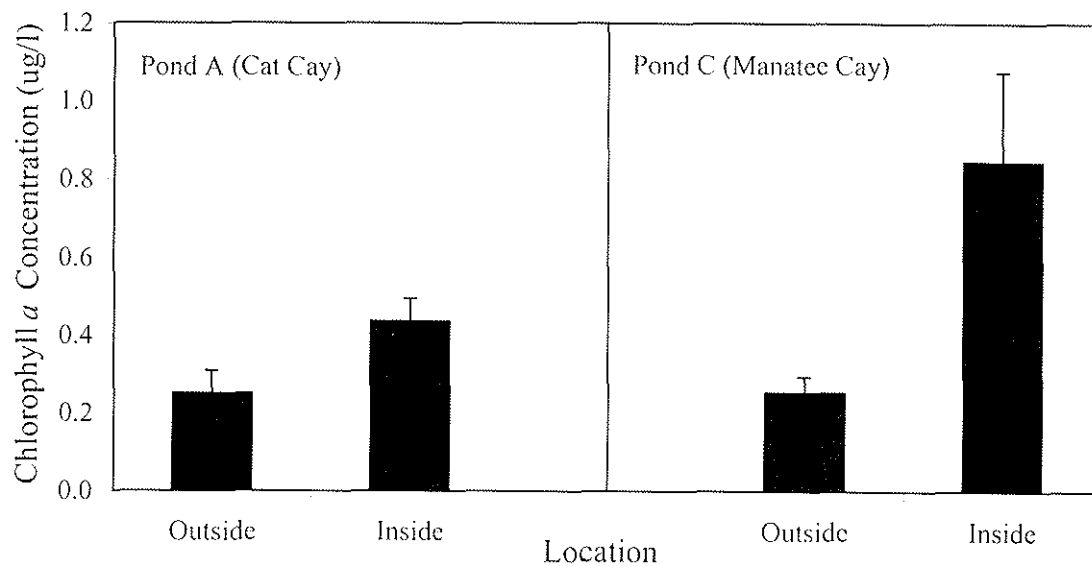


Figure 6. Mean ($\pm 1SD$) concentration of chlorophyll *a* inside and outside Ponds A and C during July 1997 ($n = 4$). Inside concentrations were significantly ($p < 0.05$) higher than outside concentrations at both locations.

At both Manatee and Cat Cays coral tends to be predominant on the outside of the opening to the ridge whereas macroalgae and seagrasses dominate the soft substrate inside the pond (Fig. 7). On the outside of these ponds, and along the ridge, live coral cover accounts for as much as 50% of the total area. At Manatee Cay there is a very sharp transition from coral dominance outside to macroalgae and seagrass dominance after crossing the coral ridge (Fig. 7). At Cat Cay, corals continue to persist inside Pond A but are gradually replaced by macroalgae and seagrasses (Fig. 6). *A. tenuifolia* is the dominant coral along all transects at Cat and Manatee Cays.

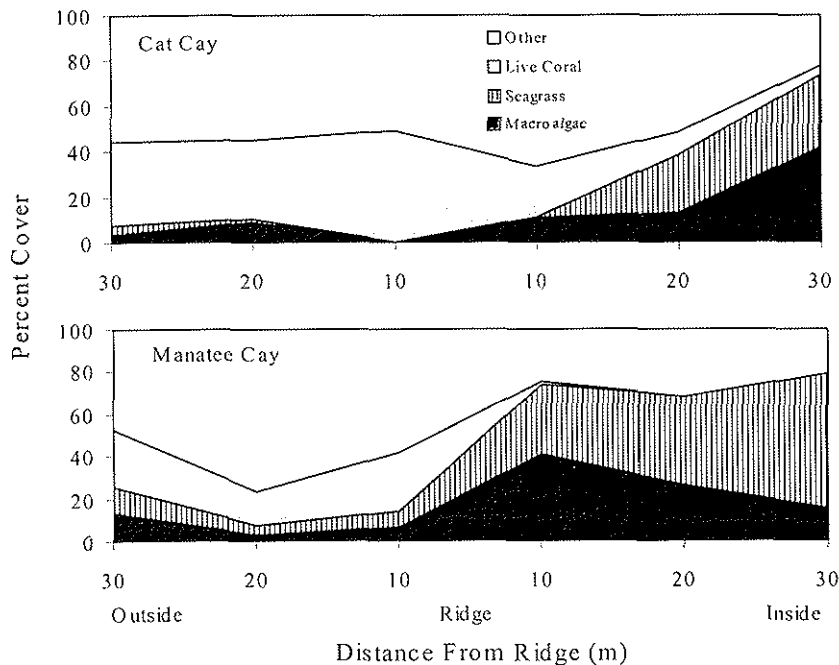


Figure 7. Percent benthic cover from combined 30 m transects along a 1-1.5 m depth contour moving from outside, onto the ridge and inside Ponds A and C at Cat and Manatee Cays, Belize, respectively (March 1995). Live corals are primarily *Agaricia tenuifolia*.

DISCUSSION

Our surveys demonstrate that Pond A in Cat Cay and Pond C in Manatee Cay are low-flow environments with some diurnal temperature fluctuations and with naturally elevated DIN concentrations in comparison with nearby reefs. Elevated DIN concentrations were measured primarily along coral ridges at the pond openings and at the bottom of the ponds. Recent investigations (Diaz and Ward, 1997; Miller-Way, personal communication) have demonstrated that common sponges and their associated cyanobacteria found on prop roots and in the benthos are capable of extremely high rates of NO_3 production. Other potential sources of DIN are

oxidation of organic materials within the reef matrix (Tribble et al., 1994), efflux from sediments (Capone et al., 1992; Williams et al., 1985), and nitrogen fixation (Wiebe et al., 1975; Capone and Carpenter, 1982), which may also contribute to the elevated DIN concentrations observed at the ponds. Concentrations of DIN and SRP were low in the central surface waters of the ponds where high chlorophyll *a* concentrations were measured. This indicates that phytoplankton are rapidly using DIN released into the ponds. DIN and SRP concentrations from the CBC fore reef were typically lower than levels measured in the pond. Other water quality studies in the area have also shown that DIN and SRP are barely detectable with conventional methods on fore-reef sites (Lapointe et al., 1992). Natural nutrient enrichment within the ponds is likely to influence the benthic community structure in and around the cays. The small difference in temperature between outside and inside sites at both Manatee and Cat Cays is unlikely to be an important factor explaining growth and survivorship differences of corals and other benthic organisms, except during periods of extreme high temperatures. During such periods, a difference of 1° could affect whether or not corals bleach (lose zooxanthellae and/or pigment), which could in turn affect their growth and survival.

The flows inside and outside the ponds are low mainly because of the protection afforded by the mangrove islands. These relatively low flows can be extremely limiting to coral energetics (Sebens, 1997) and nutrient uptake (Thomas and Atkinson, 1997; Shyka and Lipschultz, in prep.) and may be one of the factors limiting coral distribution within the ponds.

The patterns of benthic community structure, moving from outside to inside both ponds, are similar. Coral cover dominates outside the pond and onto the ridge; inside the pond, macroalgae and sea grasses are the main living components of the benthos. Lapointe et al. (1992) described a mangrove cay (Man-of-War Cay) in this region where natural nutrient elevation from a bird rookery is implicated in shifting the benthic community from a coral-dominated to macroalgae-dominated structure. The elevated concentrations of DIN, chlorophyll *a*, and low flow at the ponds probably play an important role in the transition in benthic community structure observed at Cat and Manatee Cay. At Cat Cay, corals were found further inside Pond A. The nutrient concentrations along the coral ridges at the two sites are not significantly different. Communities inside the ponds may differ in part because the structure of the ponds causes circulation differences. Pond C in Manatee Cay has only one opening, whereas Pond A in Cat Cay has two major openings and thus experiences increased circulation and flushing. Chlorophyll *a* concentrations inside Pond C are significantly higher perhaps because nutrients are retained owing to low circulation and lack of flushing. The mean chlorophyll *a* concentration in Pond C (0.84 $\mu\text{g/l}$) is well above Bell's (1992) proposed threshold of eutrophication on coral reefs (~ 0.50 $\mu\text{g/l}$). In contrast, corals persist inside Pond A, and the mean chlorophyll *a* concentration was 0.45 $\mu\text{g/l}$. Our results suggest that the ponds are semi-closed systems with respect to nutrients. Other studies have demonstrated that various components of the benthic communities can release significant amounts of DIN (Diaz and Ward, 1997; Miller-Way, personal communication). The mangroves surrounding the ponds reduce flushing and exchange; hence water column production inside the ponds is higher. The high production helps support the rich community of macroalgae and suspension feeders that release DIN. Overall, nutrients and hydrodynamics play important roles in structuring the unique community found at the ponds.

Elevated nutrient levels inside the ponds may not only cause a shift from coral to algal dominance and support the rich suspension-feeding communities inside the ponds, but may also have the potential to increase the growth rate of nearby corals (e.g., Atkinson et al., 1995). A low-

diversity but high-cover coral community was thriving along the openings of these ponds where DIN was found to be consistently elevated. However, a bleaching event in the summer of 1998 killed nearly 100% of the coral along the ridges (Precht and Aronson, personal communication). Prior to this bleaching event, *A. tenuifolia* dominated the substrate outside the ridges, which is also a relatively low flow environment. Reduced flow has been shown to decrease nutrient uptake (Thomas and Atkinson, 1998; Shyka and Lipschultz, in prep.) and photosynthesis and respiration of corals (Patterson et al., 1991; Lesser et al., 1994). In a separate study (Shyka et al., in prep.), we measured growth of corals in this environment. Coral growth rates in this low-flow, but nutrient-enriched, environment were very high. The mean increase in skeletal weight of *Acropora cervicornis* was 120% over a three-month period, March–July 1996. The mean increase in skeletal growth of *A. tenuifolia* was 70% over the same period. The growth rate of *A. tenuifolia* was significantly higher at Manatee Cay than on the fore reef at CBC at a similar depth. Manatee and Cat Cays represent unique environments in which the effects of naturally elevated nutrient concentrations may cause coral growth outside the ponds to increase, but combined with low flow and reduced circulation, may allow macroalgae and seagrass to become dominant inside the ponds. Our results suggest that the interaction of flow and nutrient concentrations plays an important role in structuring these benthic communities.

CONCLUSIONS

The ponds at Cat and Manatee Cays, Belize, are low-flow environments with naturally elevated water column DIN. The structure of the mangrove ponds reduces flow and promotes nutrient retention, which in turn elevates production inside the ponds. The elevated production most likely supports the unique suspension-feeding communities found in and around the ponds and promotes a macroalgae and seagrass-dominated benthic community. The elevated nutrients may also enhance growth rates of corals at the openings and outside the ponds. Overall, the natural eutrophication and restricted water movement have a strong influence on benthic community structure in and around the ponds.

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