

Episodic nutrient transport to Florida coral reefs

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Abstract

This study documents the changes in nutrient fluxes associated with internal tidal bores arriving on Florida Keys coral reefs and points to biological use of subthermocline nitrate brought onshore by this mechanism. Internal bores on Conch Reef, Florida Keys, are associated with concentrations of 1.0–4.0 $\mu\text{mol L}^{-1}$ nitrate (NO_3^-) and 0.1–0.3 $\mu\text{mol L}^{-1}$ soluble reactive phosphate (SRP) and onshore flow velocities of 0.1–0.3 m s^{-1} . The arrival of internal bores causes 10–40 fold increases in nutrient concentrations and 1–2 orders of magnitude increases in nutrient flux relative to ambient, nonbore conditions. The magnitude and duration of cool-water nutrient transport events increases significantly with increasing depth on reef slopes. In June 2001, the gradient of increased exposure to subsurface water with depth corresponded to increased percentage of N and $\delta^{15}\text{N}$ and decreased C:N ratio in a common benthic macroalga, *Codium isthmocladum*. Internal tidal bores are widespread throughout the Florida Keys reef tract, with cool-water episodes influencing reefs up to 10%–25% of the time during summer months and with significant variability among years. Estimated inputs of nitrogen and phosphorus by internal tidal bores to Florida Keys reef slopes are as much as 40-fold larger than published estimates of inputs to near-shore waters from waste water and storm water runoff. Internal tidal upwelling represents an important, previously underestimated, episodic source of nutrients on the Florida Keys reef tract. In order to assess nutrient availability in this system accurately it is essential to understand natural sources of high-frequency variability.

Concern over the recent, rapid decline of corals and the widespread shifts from coral to macroalgal dominance on many coral reefs has produced a focus of research attention on anthropogenic factors associated both with reductions in herbivore populations and the input of dissolved nutrients to reef environments (e.g., Done 1992; Lapointe 1997, 1999; Hughes et al. 1999; McCook 1999). While patterns of herbivory appear to exert proximate control over macroalgal abundance in many instances (Hughes et al. 1999; McCook 1999; Edmunds and Carpenter 2001; Jompa and McCook 2002), the availability of dissolved nitrogen and phosphorus

can have far-reaching direct and indirect consequences for primary productivity, species composition, and the overall condition of coral reefs (Smith et al. 1981; Bell 1992; Lapointe 1997). Dissolved nutrients on coral reefs can originate from a range of sources including in situ fixation, fluxes out of reef matrices, terrestrial runoff and outflow of coastal water, onshore transport of oceanic water masses, and localized upwelling of nutrient-rich subsurface waters (reviewed in D'Elia and Wiebe 1990). While a variety of physical mechanisms may cause high-frequency variation in nutrient availability, the nature and importance of rapid fluctuations in nutrient fluxes on coral reefs are poorly understood. Most nutrient sampling regimes have, for logistic reasons, been limited to relatively coarse temporal and spatial sampling scales (e.g., weekly, monthly, quarterly sampling at widely separated sites) with implicit assumptions that background nutrient concentrations on coral reefs tend to be low and relatively static. Thus, the complexity and importance of episodic nutrient inputs to coral reef systems may have been significantly underestimated, and this compounds the difficulty of assessing possible direct and indirect effects of anthropogenic nutrient inputs.

The relatively recent study of the impact of internal tidal bores as an important source of high-frequency upwelling for the Florida Keys (Leichter et al. 1996) led directly to the present effort to quantify nutrient inputs by this mechanism. Physical variability associated with internal tidal activity has been reported from a wide variety of habitats and ocean basins (Leichter et al. 1996). On the slopes of Florida Keys

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coral reefs, internal bores appear to be generated by breaking internal waves and at the leading edge of the internal tide, and cause rapid drops in temperature and sharp increases in onshore flow near the bottom at roughly semidiurnal frequencies, especially in summer (May through September). Leichter et al. (1996) speculated that the subthermocline water forced onshore by this mechanism is likely to contain elevated concentrations of nitrate and phosphate relative to surface waters and that availability of nitrate from two large internal bores per day could equal or exceed availability for the rest of a given day. However, that study lacked high-frequency nutrient sampling on the reef slope. Additional studies have pointed to the potential for significant nutrient inputs associated with upwelling along and seaward of the Florida Keys reef tract (Lapointe and Smith 1987; Lee et al. 1994; Szmant and Forrester 1996); however those studies did not directly consider the role of high-frequency internal tidal bores as a source of subsurface water arriving on shore. In an effort to understand broad-scale patterns of nutrient availability, Boyer and Jones (2002) have monitored concentrations of a range of dissolved nutrients in shallow water throughout much of the Florida Keys at approximately quarterly intervals since 1995. Patterns include generally low nitrate ($\text{NO}_3^- < 0.2 \mu\text{mol L}^{-1}$) and soluble reactive phosphate ($\text{SRP} < 0.01 \mu\text{mol L}^{-1}$) on the Florida Keys reef tract with marked increases closer to shore. Occasional periods of high NO_3^- and SRP concentrations near the reef tract have been detected and putatively linked to upwelling; however, defining the importance of nutrient inputs related to upwelling has not been a part of the broad-scale sampling design (Boyer and Jones 2002).

The goal of this study was to measure the delivery of dissolved nutrients associated with internal tidal upwelling on the Florida Keys reef tract and to examine potential links between the availability of subsurface nutrients and the tissue chemistry of a common benthic primary producer. Data from detailed hydrographic, nutrient, and algal sampling at Conch Reef in the upper Florida Keys in the summers of 2000 and 2001 were combined with data collected in 1997–2001 as part of a larger scale, continuous study of high-frequency temperature variability at six sites spanning approximately 200 km of the Florida Keys reef tract.

Methods

Study sites—In late 1996, J. Leichter established sites for collection of high-frequency temperature data on six reefs in the Florida Keys: Carysfort Reef (CF), The Elbow Reef (EL), Conch Reef (CR), Tennessee Reef (TN), Looe Key Reef (LK), and Sand Key Reef (SK) (Fig. 1). In addition, detailed hydrographic, nutrient, and algal sampling were conducted in June of both 2000 and 2001 at the central study site, Conch Reef ($24^\circ 57.0' \text{N}$, $80^\circ 27.3' \text{W}$). The Florida Keys reef tract lies approximately 5–8 km offshore of the Florida Keys and represents primarily Holocene reef development along the Pleistocene margin of south Florida (Shinn et al. 1989). At each study site, a reef crest lies in 5–10-m water depth, adjacent to a moderately sloping fore-reef that extends to approximately 30–35-m depth, where the coral spur and

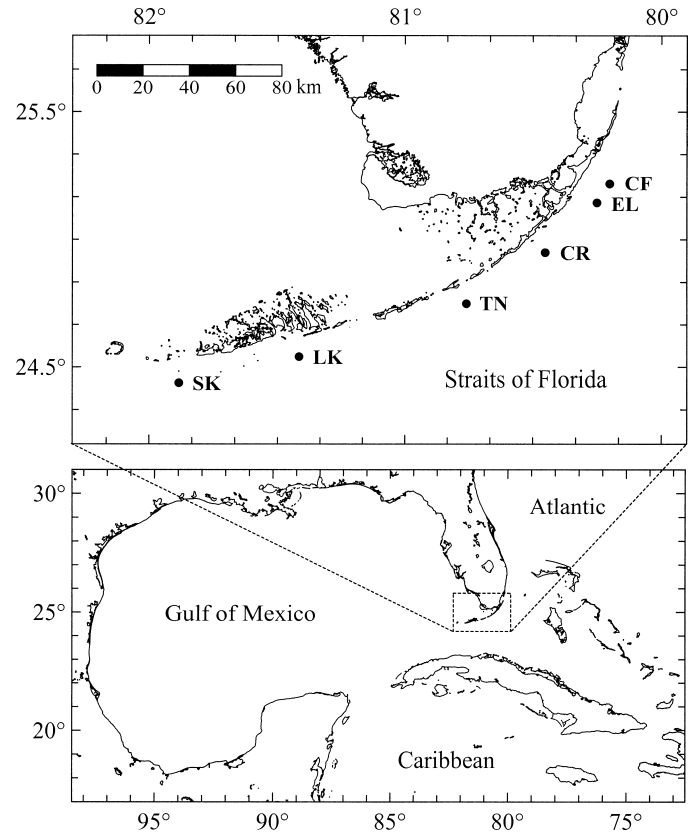


Fig. 1. Study region along the Florida Keys reef tract near the southern tip of Florida. Sites: Carysfort Reef (CF), The Elbow (EL), Conch Reef (CR), Tennessee Reef (TN), Looe Key (LK), and Sand Key (SK).

groove formations break up into semiisolated patches separated by sand. Seaward of the reefs, the bottom slopes gradually, with depth increasing approximately 10–20 m per kilometer offshore. At roughly 20–35 km offshore, the bottom slope angle increases into the deep channel of the Florida Straits where depths range from roughly 800 to 1,500 m at 60–80 km offshore. In summer (May–September) the water column seaward of the Florida Keys reef tract is typically well stratified with a warm, isothermal surface layer to approximately 50–80-m depth. The Florida current is characterized by strong surface flows as swift as $0.5\text{--}1.5 \text{ m s}^{-1}$ to the northeast (NE). The central axis of the Florida current typically runs closer to shore in the upper (NE) than in the lower (southwest) keys, ranging from roughly 10–20 km off CF to as much as 20–100 km off SK. Surface tides in the Florida Keys are mixed semidiurnal with mean amplitude of 0.25–0.5 m.

Broad-scale temperature measurements—Pairs of individual temperature recorders were deployed 1 m above the reef slope at depths of 10, 20, and 30 m on each study site from December 1996 through 2001. In 1996–2000 two Onset Computers Stowaway ITX-32 temperature loggers (0.2°C resolution, 0.5°C accuracy) were deployed at each station. These loggers were contained in individual pressure housings with external probes and had response times of

20–30 s. Data were sampled continuously at 2 Hz and recorded as 10-min averages. Where both loggers recorded successfully the paired data were averaged. In 2000 and 2001 one Seabird SBE-39 temperature logger (0.0001°C resolution 0.002°C accuracy) sampling every 60 s and one Onset Stowaway ITX-32 sampling at 2 Hz recording 10-min averages were deployed at each station. Data from the Onset loggers were used only if the higher resolution Seabird loggers failed. In summer, exposure to periods of cool subsurface water on the reef slopes was quantified by calculating the percent of total observations that corresponded to temperature <25.0°C for 1 May through 30 September (hereafter %*T* < 25). %*T* < 25 was calculated for each study depth on each reef and each summer from 1997 to 2001. The exposure to water <25°C as a function of depth on Conch Reef was also examined in detail for a 36-d period from 12 May to 17 June 2001. SBE-39 temperature loggers were deployed at depths of 7, 10, 18, 23, 26, 29, and 32 m, recording continuously at 10-s intervals. Exposure to water <25°C was expressed as total degree hours <25°C for each depth, calculated as

$$\text{deg h} = \frac{\sum (25 - \text{obs}) \times 10}{3600}$$

where obs is the value of each 10-s observation <25°C.

Hydrographic and high-frequency nutrient sampling—Hydrographic conditions were measured seaward of Conch Reef in June of 2000 and 2001 by profiling from the surface to within 5 m of the bottom with a Seabird Electronics SBE-19 conductivity-temperature-depth recorder with attached WETLabs fluorometer (CTD-F). CTD-F casts were made at 1.8-km intervals along a 9-km line running directly offshore (150°) from Conch Reef. A single cast was made at each station, with the entire transect repeated on 3 d in each sampling session (7, 15, and 20 June 2000; 9, 15, and 21 June 2001). On 15 June 2000 and 15 June 2001, 1.8-liter Niskin bottles were used to collect water samples at the maximum depth, midway through the water column and 1 m below the surface at each CTD-F station. Water samples were immediately filtered (Whatman GF/F), kept dark on ice on the boat, and frozen on shore for subsequent analysis of inorganic nitrogen and soluble reactive phosphate (SRP) concentrations using an Alpkem RFA 300 autoanalyzer. CTD-F data were postprocessed with Seabird Electronics recommended standard filters to remove the up-casts, align temperature and conductivity, calculate salinity and density, and average data to 1-m depth bin. Since chlorophyll *a* values from water samples were not available for cross-calibration, fluorescence was expressed in relative units for each sampling day. Spatial contour plots of the CTD-F and nutrient concentration data were produced by kriging with linear variogram and no nugget effect, using Surfer 8 software (Golden Software).

Water samples were collected 1 m above the slope of Conch Reef at 21–32-m depth by SCUBA divers during intensive study periods in June of 2000 (95 samples) and 2001 (51 samples). These study periods included two 8-d periods of saturation diving, staged from the National Oceanic and

Atmospheric Administration Aquarius habitat at 15-m depth. Saturation diving allowed the collection of discrete samples at intervals of 20 min to several hours over periods of 8–18 h per day. Samples were collected both at regular intervals and in response to diver-observed fluctuations in near-bottom temperature and hydrographic conditions associated with the arrival of individual internal bores. As part of this sampling, a time series of water samples at 32-m depth was collected at approximately 20-min intervals over nearly 18 h from 0815 h (local daylight time, GMT – 4 h) on 18 June 2000 until 0200 h on 19 June 2000. All diver samples were collected in clean 140-cm³ syringes and returned to the surface where they were filtered and frozen for subsequent analysis of inorganic nitrogen and soluble reactive phosphate concentrations as described above. Water temperature was measured with a hand-held Seabird SBE-39 temperature recorder as each syringe sample was collected.

Along with the reef nutrient sampling, water column currents above the reef slope at Conch Reef were measured with an upward-looking RD Instruments Workhorse 600 kHz acoustic Doppler current profiler (ADCP) positioned on the bottom at 32-m depth at the seaward edge of the reef slope. Data were sampled continuously at 1.33 Hz and stored as 1-min averages in 2-m depth bins. The ADCP north and east component vectors for each depth bin were rotated to the alongshore (60°/240°) and onshore/offshore (330°/150°) components, and temporal contour plots of the onshore/offshore and alongshore velocities were produced by kriging with linear variogram and no nugget effect, using Surfer 8 software (Golden Software).

Estimates of nutrient inputs by internal bores—The input of nitrogen and phosphorus to the Florida Keys reef tract by internal bores was estimated by multiplying the range of measured NO₃⁻ and SRP concentrations by estimates of the volume of water transported onshore per bore. A low estimate was made by taking the height of a bore as 5 m, the onshore flow speed as 0.10 m s⁻¹, the total time of upslope flow as 20 min, and the concentrations of NO₃⁻ and SRP as 1.0 and 0.1 μmol L⁻¹, respectively. A high estimate was made by taking the height of the bore as 10 m, the onshore flow speed as 0.30 m s⁻¹, the total time of upslope flow as 30 min, and the concentrations of NO₃⁻ and SRP as 4.0 and 0.3 μmol L⁻¹, respectively. The parameters used in both the low and the high estimates fall within the range of measured values. Although the alongshore extent of individual internal bores is unknown, the phenomenon of internal tidal upwelling is observed along the entire reef tract. Therefore, the estimates made on a per-linear-meter of reef tract basis were subsequently multiplied by the length of the reef tract, taken as 200 km. Estimates of the number of cool-water forcing events in both 2000 and 2001 were made by scanning the entire temperature records from 30-m depth at Conch Reef and counting all large (Δ*T* > 3°C) and small (1.5°C < Δ*T* < 3°C) internal tidal events. This likely underestimates the actual total number of onshore surges because events characterized by multiple pulses of onshore flow are treated as single events. An estimate of the overall total input of nitrogen and phosphorus due to internal tidal bores in each year was then produced by multiplying the per-bore input esti-

mates by 1.0 times the number of large plus 0.5 times the number of small events. Both the estimated per-bore and overall total nitrogen and phosphorus input associated with internal tidal upwelling were then compared with an estimate of overall daily nutrient loading from waste water and storm water (WW + SW) sources in the Florida Keys (Kruczynski and McManus 2002 based on U.S. Environmental Protection Agency 1993 estimates).

Macroalgal sampling—Possible biological utilization of episodic subsurface nitrogen pulses on Florida Keys reefs was examined by measuring both the distribution and tissue chemistry of the common macroalga *Codium isthmocladum* (Div. Chlorophyta). Densities were estimated at 10-, 15-, 20-, 25-, and 32-m depth using 10 1-m² quadrats positioned randomly along each of three 30-m transects within each depth in June 2001. The linear distance along the reef slope from the shallowest to the deepest collection site was approximately 240 m. Samples for tissue chemistry analysis were collected across depths from 9 to 34 m on Conch Reef on 19–24 June 2001. Of approximately 80 individual *C. isthmocladum* samples collected, 35 covering the entire depth range sampled were randomly selected for tissue chemistry analysis. In addition, temporal variation *C. isthmocladum* tissue chemistry was examined in samples collected at 33-m depth on Conch Reef in June 2000 ($n = 11$), November 2000 ($n = 6$), May 2001 ($n = 7$), and June 2001 ($n = 14$). After collection, all samples were briefly rinsed in deionized water to remove external salt, dried at 60°C, and stored for subsequent determination of tissue percentage C, percentage N, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ by combustion and mass spectrometry in the Center for Stable Isotope Geochemistry at the University of California at Berkeley. ^{15}N and ^{13}C are expressed as δ values (‰) relative to atmospheric N_2 and PeeDee Belemnite C standards, respectively, following the equation:

$$\delta = \left\{ \left[\frac{R(\text{sample})}{R(\text{standard})} \right] - 1 \right\} \times 1000$$

where R is the ratio $^{15}\text{N}:^{14}\text{N}$, or $^{13}\text{C}:^{12}\text{C}$.

Results

Broad-scale temperatures—Patterns of temperature variability were similar across the six reef sites, with seasonal variation consisting of predictable alternation between summer warming and winter cooling. Superposed on the low-frequency patterns were concentrated periods, particularly in summer, of high-frequency variability characterized by numerous temperature fluctuations as large as 2–8°C within 1–20 min. The complete temperature record for Conch Reef in 2000–2001 is shown in Fig. 2 (top panels) along with detailed views (lower panels) showing a 5-d period of high temperature variability in each year. The high-frequency variability is similar to patterns described in Leichter et al. (1996), occurring on a predominantly semidiurnal basis and reflecting the arrival of surges of cool water forced onshore by internal tidal bores. Periods of high temperature variability were concentrated in May–June and July–August of 2000, and in June–July and September of 2001.

At all six reef sites, the magnitude and duration of cool-water events increased significantly with depth from 10 to 30 m. 1 May–30 September % $T < 25$ as a function of depth showed strong similarity among sites as well as significant variability among years (Table 1). In summer 1998 % $T < 25$ was 19.5–25.6 at 30-m, 11.0–13.6 at 20-m, and 4.5–8.9 at 10-m depth across sites. By contrast, in 1999 these values were 2.3–5.0 at 30 m, 0–1.7 at 20 m, and 0–1.6 at 10 m. The ranking of sites with respect to % $T < 25$ was relatively consistent across years. At 30-m depth, SK experienced the greatest % $T < 25$ in all years, while TN showed the lowest values in 4 out of 5 years. At depths of 10 and 20 m, the largest % $T < 25$ were generally at LK and EL. Averaged over five summers, % $T < 25$ was 7–13 at 30 m, 3–4 at 20 m, and 2–3 at 10 m. At the fine scale of the period 12 May–17 June 2001 on Conch Reef, a similar clear increase in exposure to cool water with depth was evident, with the total degree hours $< 25^\circ\text{C}$ increasing from 0 at 7 and 10 m to 313 at 32 m (Table 2).

Hydrography and nutrients—Water column hydrographic profiles with accompanying nutrient concentrations seaward of Conch Reef on 15 June 2000 and 15 June 2001 are shown in Fig. 3. On both days the water column showed stable density stratification typical of summer conditions, with a warm, isothermal, surface layer overlying cooler subsurface water. However, the stratification was much sharper, with the thermocline much shallower and subsurface water much colder, on 15 June 2001 than on 15 June 2000. Fluorescence showed marked subsurface peaks indicating well-defined chlorophyll *a* maximum layers associated with the thermocline on both days. Concentrations of NO_3^- and SRP were low to undetectable near the surface but increased sharply below the thermocline, especially for the very sharp thermocline on 15 June 2001 when concentrations in subthermocline waters ranged from 6.7 to 20.5 $\mu\text{mol L}^{-1}$ for NO_3^- and 0.3 to 1.3 $\mu\text{mol L}^{-1}$ for SRP. The water column profiles also varied among days within each year (not shown), although these differences were more subtle than those evident between years. In June 2000 the strength of stratification decreased and the thermocline moved deeper from the 7th to 15th and through the 20th. In June 2001 the strength of stratification increased and the thermocline moved shallower from the 9th to the 15th and stratification then decreased somewhat as the thermocline moved deeper from the 15th to the 21st.

A 3-h segment of near-bottom temperature and the onshore/offshore component of flow in the water column are shown in Fig. 4, corresponding to a single, large internal bore event on 9 June 2000. Conditions were warm and flow was relatively quiescent prior to the arrival of cool water. Rapid cooling 1 m above the bottom was detected first at 30-m depth and subsequently at 20 m. Above the 30-m site, the cooling was accompanied by a sharp rise in onshore flow with maximum velocities reaching 0.25–0.28 m s^{-1} within the bottom 8 m of the water column. A simultaneous offshore flow with velocities of 0.20–0.34 m s^{-1} occurred in the top 10–15 m of the water column, indicating surface water moving offshore as deep water surged onto the reef slope. In this event, cool water did not reach the station at

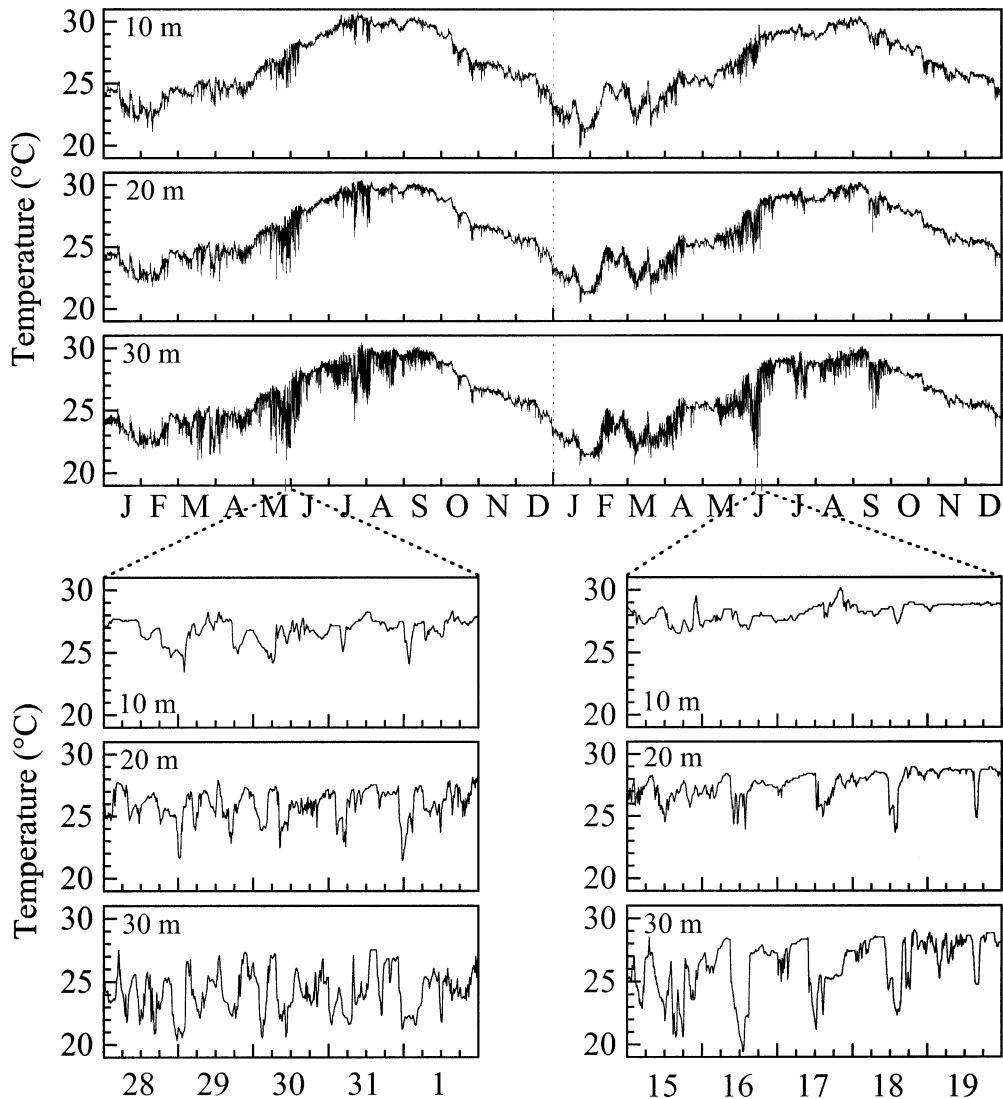


Fig. 2. Temperature 1 m above the surface of Conch Reef at 10-, 20-, and 30-m depth (top three panels) January 2000 through December 2001. Data recorded as 10-min averages, plotted as 60-min averages for clarity. Lower panels show 10-min average data during two 5-d periods of high temperature variation: 28 May–1 June 2000 and 14–19 June 2001.

10 m on the reef slope. A return to preevent warm conditions started approximately 30–50 min after the initial cooling and was accompanied by moderate offshore flow close to the bottom. Temperature at 30 m had returned to preevent levels approximately 120 min after the initial cooling. These patterns of cool water flowing onshore near the bottom accompanied by surface water flowing offshore followed by near-bottom offshore flow and gradual return to warm temperatures were typical of events observed in both 2000 and 2001 and previously described by Leichter et al. (1996). The magnitude of cooling and associated on-shore flow speeds varied considerably among events, with the largest cooling generally associated with the largest magnitudes of onshore flow. In some cases the initial cooling was produced by a series of closely spaced cool-water pulses, likely representing the arrival of a packet of internal bores, with temperature stepping down in each pulse. Flow during nonbore

periods was predominantly alongshore with tidal reversal of direction and peak velocities of $0.30\text{--}0.45\text{ m s}^{-1}$ in the upper 10–15 m of the water column.

Nutrient concentrations 1 m above the slope of Conch Reef were highly variable in both June 2000 and June 2001 (Fig. 5). When warm surface waters were present across the reef slope, for example on 18 June 2000, ambient NO_3^- and SRP were low to undetectable. The arrival of a single, isolated cool-water event on 18 June 2000 produced a sharp increase from 0 to $0.18\ \mu\text{mol L}^{-1}\ \text{NO}_3^-$ and from 0 to $0.025\ \mu\text{mol L}^{-1}\ \text{SRP}$ as temperature dropped from 28.2°C to 26.1°C (Fig. 5). A small, unexplained rise in SRP concentrations appears also to have occurred just before the arrival of the bore in this case. However, this may not represent a significant change since SRP concentrations were very low and close to detection limits throughout the entire event. On 13–17 June 2000 temperature varied from 28.2°C to 25.0°C

Table 1. Percent of time, 01 May through 30 Sep of temperature <25.0°C. Reef sites: Carysfort (CF), Elbow (EL), Conch (CR), Tennessee (TN), Looe Key (LK), Sand Key (SK). Avg = average within site and depth across years. Dash indicates sites with insufficient data.

Site	Depth (m)	1997	1998	1999	2000	2001	Avg
CF	10	0.7	4.9	0.2	1.2	3.8	2.1
EL	10	0.4	6.8	0.1	1.2	0.3	1.7
CR	10	—	4.5	0.2	0.7	2.3	1.9
TN	10	—	5.1	—	0.5	0.6	2.1
LK	10	0.0	4.6	1.6	0.1	1.9	1.6
SK	10	0.0	8.9	0.0	—	—	3.0
CF	20	1.3	11.9	0.3	2.1	4.0	3.9
EL	20	1.3	13.6	1.0	2.5	2.6	4.2
CR	20	—	11.0	0.7	1.9	2.4	4.0
TN	20	—	11.0	1.0	2.1	0.9	3.7
LK	20	—	11.4	1.7	0.2	4.2	4.4
SK	20	0.1	12.0	0.0	0.1	2.1	2.9
CF	30	4.5	21.0	2.3	7.0	10.3	9.0
EL	30	4.5	20.9	3.0	7.9	6.6	8.6
CR	30	6.7	20.7	4.3	6.5	8.5	9.3
TN	30	2.9	19.5	3.7	5.4	5.3	7.3
LK	30	5.4	21.5	3.9	6.0	10.6	9.5
SK	30	8.6	25.6	5.0	8.7	15.3	12.6

as a series of internal bores arrived on the reef slope, and NO_3^- concentrations varied from 0 to $0.6 \mu\text{mol L}^{-1}$, while SRP concentrations varied from 0.05 to $0.15 \mu\text{mol L}^{-1}$. In June 2001, temperature changes were as large as 9°C with minimum temperatures as low as 19.1°C . During this period the majority of NO_3^- values were $>1.0 \mu\text{mol L}^{-1}$, ranging as high as $4.2 \mu\text{mol L}^{-1}$. SRP concentrations were mostly $>0.1 \mu\text{mol L}^{-1}$, ranging as high as $0.2 \mu\text{mol L}^{-1}$. The overall relationships between temperature and the concentrations of NO_3^- and SRP measured at 32-m depth are shown in Fig. 6. Concentrations of both nutrients increased with decreasing temperature, especially with temperatures $<25^\circ\text{C}$, but both nutrients also show a high degree of variance at any given temperature.

Ammonium concentrations were low ($0.1\text{--}0.5 \mu\text{mol L}^{-1}$) in all of the June 2000 samples and in most of the June 2001 samples, but with occasional peaks between 1.0 and $2.2 \mu\text{mol L}^{-1}$. Ammonium showed no clear relationship with temperature; however, on several occasions in June 2001, divers noted the arrival on the reef slope of high concentrations of zooplankton and greenish/brown water, possibly representing the subsurface chlorophyll maximum layer. Ele-

vated ammonium concentrations associated with the subsurface chlorophyll maximum layer may have resulted from ammonia production by zooplankton.

Estimated N and P inputs—Table 3 presents estimates of nitrogen and phosphorus input due to internal tidal bores on the Florida Keys reef tract. The estimated nitrogen input across the reef tract ranges from 1.68×10^3 to 6.1×10^4 kg per internal bore. Estimated phosphorus input ranges from 3.7×10^2 to 10.0×10^3 kg per internal bore. Estimated nutrient loading to nearshore waters from WW + SW sources is 1.36×10^3 kg N d^{-1} and 4.42×10^2 kg P d^{-1} (Kruczynski and McManus 2002). The ratios of estimated nutrient input per internal bore to estimated WW + SW loading per day range from 1.2 to 44.7 for nitrogen and 0.8 to 22.7 for phosphorus. The number of internal bores estimated from the temperature data for Conch Reef was 85 large and 37 small events over a period of 182 d in 2000, and 52 large and 32 small events over a period of 224 d in 2001. The ratios of estimated total nutrient input from internal bores to input from WW + SW over the same time period range from 0.6 to 21.0 for nitrogen and 0.4 to 10.7 for phosphorus.

Codium density and tissue chemistry—In June 2001 maximum densities of 20–28 individuals m^{-2} for *Codium isthmocladum* on Conch Reef were observed at depths >20 m, while densities decreased markedly in shallower water. Fig. 7 shows percentage N, C:N, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ for a total of 35 *C. isthmocladum* samples collected across depths in June 2001. Tissue percent nitrogen increased significantly with depth, from 0.5%–0.7% at 9 m to 1.1%–1.4% at 34 m, while percent carbon (not shown) varied from 10% to 26% but with no clear trends with depth. C:N ratios decreased from 26–30 at 9 m to 16–23 at 34 m. *C. isthmocladum* tissue showed marked enrichment of ^{15}N with increasing depth,

Table 2. Cumulative degree hours $<25.0^\circ\text{C}$ across the reef slope of Conch Reef, 12 May–17 June 2001.

Depth (m)	Degree hours $<25^\circ\text{C}$
7	0
10	0
18	17
23	63
26	121
29	204
32	313

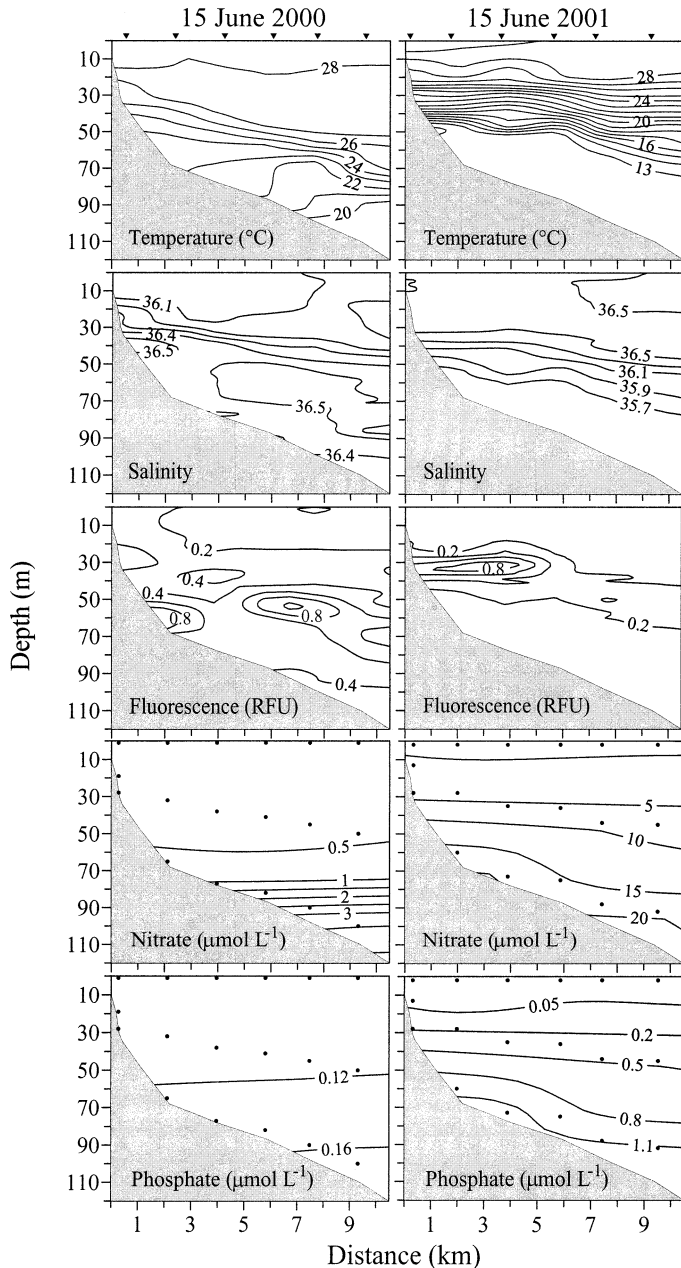


Fig. 3. Hydrographic profiles of temperature, salinity, relative fluorescence (RFU), and concentrations of nitrate and soluble reactive phosphate seaward of Conch Reef on 15 June 2000 and 15 June 2001. Position of individual CTD casts is represented by arrows along top axis. Depth of water samples taken at the surface, middle water column, and near bottom at each cast for nutrient measurements are shown by solid points in the panels for nitrate and phosphate.

with $\delta^{15}\text{N}$ ranging from 2.6‰–2.7‰ at 9 m to 4.3‰–5.0‰ at 34 m. $\delta^{13}\text{C}$ values decreased with depth ranging from –11.8‰ to –12.5‰ at 9 m to –13.7‰ to –15.4‰ at 34 m. Correlations between depth and percentage N, C:N, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ were all highly significant ($p < 0.01$), with variation in depth explaining 59%–82% of the variance in tissue chemistry and isotopic composition (Fig. 7). $\delta^{15}\text{N}$ across the

reef slope in June 2001 also showed a close relationship to total degree hours $< 25^\circ\text{C}$ as a function of depth for the 36-d period prior to sample collection (Fig. 8). Seasonal variation in mean $\delta^{15}\text{N}$ values at 33-m depth were reflected in lower values in November 2000 ($3.58\text{‰} \pm 0.26\text{‰}$, mean \pm SE, $n = 6$) and early May 2001 ($3.19\text{‰} \pm 0.09\text{‰}$, mean \pm SE, $n = 7$) than in June 2000 ($5.42\text{‰} \pm 0.42\text{‰}$, mean \pm SE, $n = 11$) or June 2001 ($4.70\text{‰} \pm 0.19\text{‰}$, mean \pm SE, $n = 14$).

Discussion

High-frequency internal tidal upwelling represents a significant, widespread, and episodic source of high nitrate and phosphate fluxes on Florida Keys reef slopes. The patterns of *Codium isthmocladum* tissue nitrogen content and stable isotope composition with depth on Conch Reef suggest use of the transiently upwelled nitrate by this benthic primary producer. While internal tidal bores primarily impact the reef slopes, they do at times reach the reef crests at 10-m depth, and it is likely that some upwelled water is advected into back reef environments. The results of this study have significance for understanding nutrient dynamics on the Florida Keys reef tract, as well as implications for studying the impact of oceanographic forcing mechanisms and their variation in space and time on coral reefs in general. In particular, this study highlights the importance of understanding, documenting, and including high-frequency variation in studies of reef nutrient dynamics.

Patterns of internal tidal upwelling—Upwelling in general has been suggested as a source of allochthonous nutrients for coral reefs, especially for the outer Great Barrier Reef (Andrews and Gentien 1982; Wolanski and Pickard 1983; D’Elia and Wiebe 1990; Wolanski 1994), and the observation of a significant pool of dissolved nutrients below the thermocline seaward of the Florida Keys reef tract is consistent with previous reports. For example, Lee et al. (1994) reported subthermocline nitrate concentrations of 3–15 $\mu\text{mol L}^{-1}$ offshore of Looe Key. Cold water intrusions were observed in low-frequency data from Looe Key (Lapointe and Smith 1987), and it has been suggested that upwelling associated with gyres in the Florida current could be followed by onshore movement of nutrient-rich waters to the Florida Keys reef tract (Lee et al. 1992, 1994; Szmant and Forrester 1996). However, the actual arrival of nutrients onshore has not been previously measured at frequencies fast enough to resolve internal tidal forcing. The present study is the first to document the role of internal tidal bores in high-frequency nutrient transport to Florida reefs and to quantify the large magnitude of associated nutrient fluxes. This study is also the first to show the broad spatial impact of high-frequency upwelling in the Florida Keys and to point to a possible biological response to this physical process.

High-frequency internal tidal forcing exists within the context of regional oceanographic variability. The continuous temperature records for Conch Reef show significant internal bore activity starting in March and becoming strongest throughout the summer (May–September) but then decreasing significantly in October–January. This likely re-

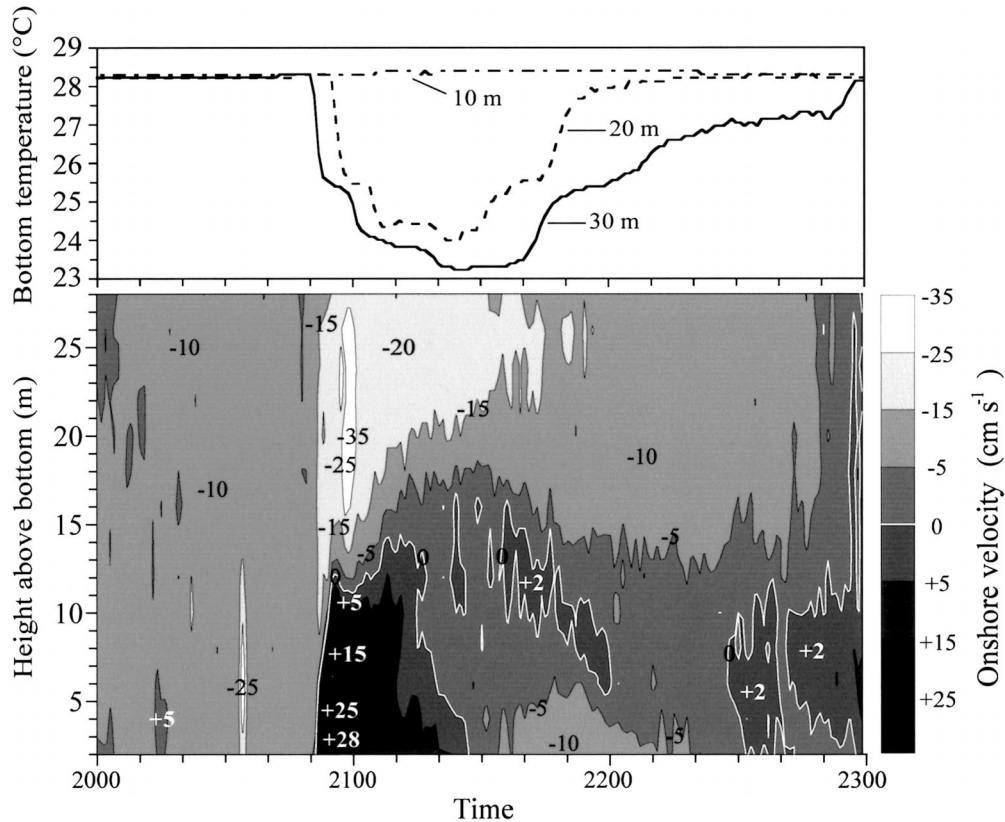


Fig. 4. Water column profile of onshore/offshore flow speed (lower panel) measured with an acoustic Doppler current profiler (ADCP) at 32-m depth at the seaward edge of Conch Reef, and temperature (top panel) 1 m above the bottom at 30-, 20-, and 10-m depth on the reef slope, during a cold water intrusion event on 9 June 2000. Positive values of onshore flow represent flow at 330° , negative values represent flow at 150° . Flow was not resolved for the top (surface) and bottom 2 m of the water column.

flects seasonal changes in the depth and strength of the offshore pycnocline. On shorter time frames, the variance in near-bottom temperature increases episodically over periods of 5–7 d at irregular intervals within the summer. This modulation of internal bore activity appears to occur nearly synchronously across multiple sites (J. Leichter unpubl. data) and likely reflects fluctuations in the mean depth of the offshore pycnocline. The CTD profiles in June 2000 and June 2001 showed variations among days and between years that corresponded to differences in magnitude of temperature fluctuations recorded on the reef slope. For example, observation of a sharp, shallow thermocline on 15 June 2001 corresponded to a period of very cool water reaching the reef slope. The deepening of the offshore thermocline from 7 through 20 June 2000 corresponded to a decrease in temperature variation on the reef slope. While the mechanisms of variation in thermocline depth and modulation of the internal tidal forcing signal are not evident from the present data, these are likely to include processes associated with Florida Current meanders and gyres and/or wind forcing (Lee and Mayer 1977; Mooers and Brooks 1977; Lee et al. 1985, 1992, 1994).

Nutrient input from internal bores—While background NO_3^- and SRP concentrations on Conch Reef are typically

on the order of 0.1–0.2 and 0.01–0.02 $\mu\text{mol L}^{-1}$, respectively, levels measured during June of 2000 and 2001 were elevated as much as 10–40 fold to 1.0–4.0 $\mu\text{mol L}^{-1}$ NO_3^- and 0.1–0.3 $\mu\text{mol L}^{-1}$ NO_3^- SRP in association with the presence of cool water on the reef slope. The most obvious patterns in the nutrient data are a trend of increased concentration with decreased temperature, especially temperature $<25^\circ\text{C}$ (Fig. 6), and increases in both the mean and the variance on days with repeated, large cooling events (Fig. 5). In several cases, concentrations of NO_3^- and SRP showed clear, step-like increases associated with the initial upslope flow of individual internal bores. For example, on 18 June 2000 the arrival of a single bore stood out clearly against a background of ambient, warm conditions and was associated with marked increases in NO_3^- and SRP (Fig. 5). In several cases, such as on 25 June 2001, cool water transported onto the reef slope remained in a visible layer, one to several meters thick, close to the bottom. Nutrient concentrations were high in these cool, near-bottom layers. However, at times, nutrient concentrations were also relatively high in water that was not associated with sharply defined thermal discontinuities. This is likely to arise from mixing associated with the onshore flow of internal bores and their interaction with the rough surface of the reef slope. The entire June 2001 sampling effort coincided with a period of intense cool-

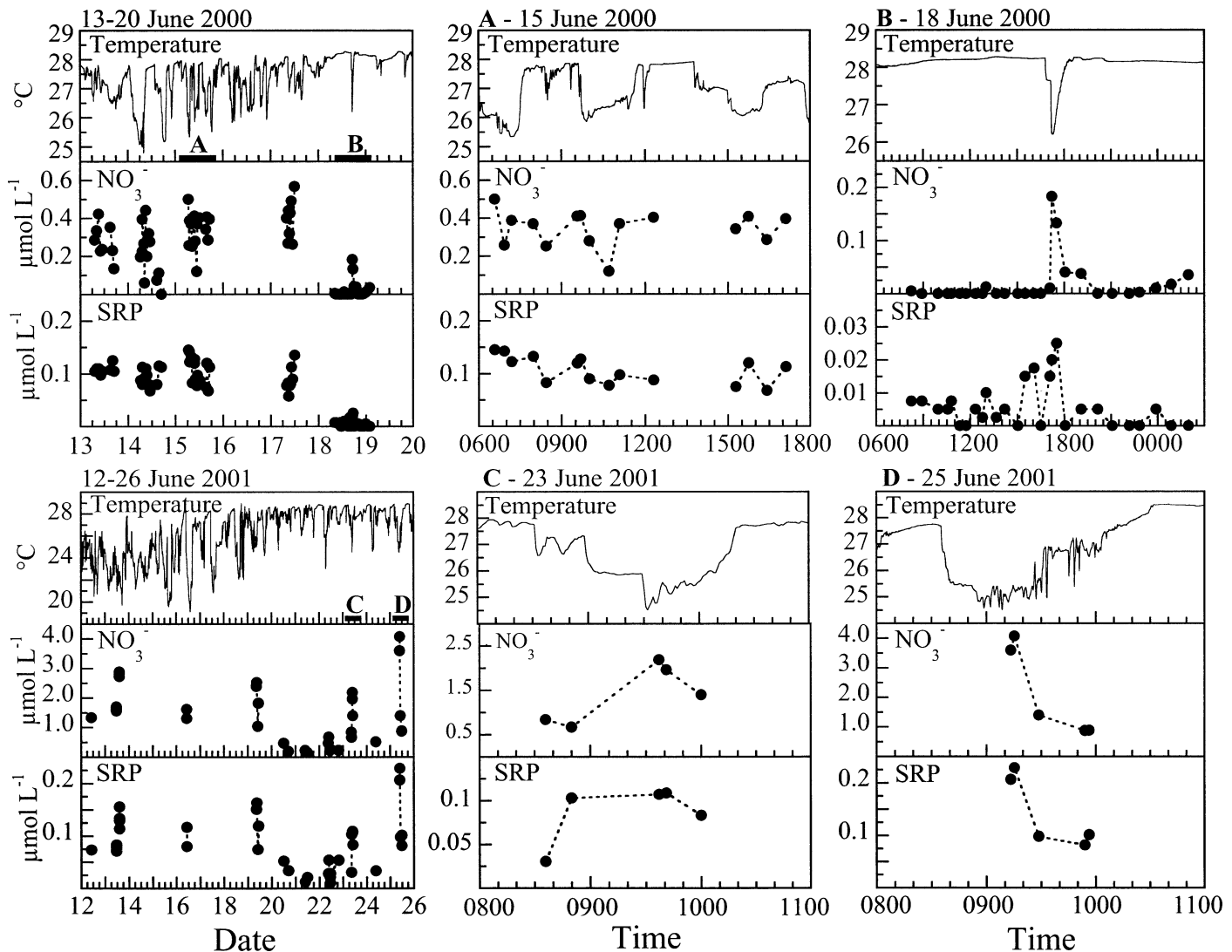


Fig. 5. Temperature time series (1-min interval), and concentrations of nitrate (NO_3^-) and soluble reactive phosphate (SRP) measured at irregular intervals, 1 m above the bottom on Conch Reef at 32-m depth during two study periods: 13–20 June 2000 (top left) and 12–26 June 2001 (bottom left). Expanded views of the sections labeled A and B in the June 2000 record are shown in the top center and top right panels. Expanded views of the sections labeled C and D in the June 2001 record are shown in the bottom center and bottom right panels. Scale of axes varies among panels.

ing, with minimum temperatures on the reef slope as low as 19.5°C . NO_3^- concentrations during this period were as much as an order of magnitude higher than in June 2000. A period of large temperature fluctuations and minimum temperatures comparable to those observed in June 2001 did occur in May–June 2000 just prior to the sampling effort that year. Although nutrients were not sampled on those days, from the magnitude of cooling and frequency of internal bores it seems likely that concentrations were similar to those measured in June 2001.

Because the transport of nutrients to benthic organisms may be limited by flux across benthic boundary layers, nutrient availability is sensitive to both concentrations and flow speeds (Atkinson and Bilger 1992; Bilger and Atkinson 1995; Larned and Atkinson 1997). The increases in nutrient concentrations associated with the arrival of internal tidal

bores tend to be accompanied by large increases in flow speeds close to the reef surface and can result in very large increases in near-bottom nutrient flux. For example, the cooling event shown in Fig. 4 was associated with flow speeds in the bottom 5–8 m of the water column increasing from approximately 0.05 to 0.25 m s^{-1} as temperature dropped 5°C . Although nutrient concentrations were not measured during this event, data for other events of this magnitude of cooling show NO_3^- concentrations as high as 2.0 – 4.0 $\mu\text{mol L}^{-1}$. Assuming pre-event NO_3^- concentrations on the order of 0.2 $\mu\text{mol L}^{-1}$, the resulting increase in instantaneous NO_3^- flux per m^2 normal to the onshore flow would have been roughly 50–100 fold, from approximately 10 $\mu\text{mol s}^{-1}$ under ambient conditions to 500 – $1,000$ $\mu\text{mol s}^{-1}$ during the up-slope flow of the internal bore.

The frequency and duration of internal bore events on

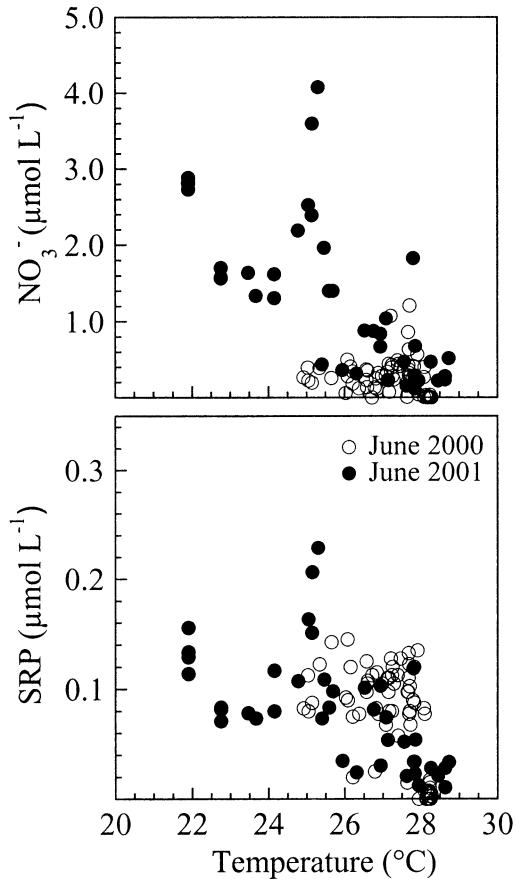


Fig. 6. Relationships between temperature and the concentrations of nitrate (NO_3^-) and soluble reactive phosphate (SRP) for the data depicted in Fig. 5, measured 1 m above Conch Reef at 32-m depth in June 2000 ($n = 74$) and June 2001 ($n = 42$).

Conch Reef suggest a very significant input of dissolved nutrients to the reef by this mechanism. However, attempting to quantify the overall input of nitrogen and phosphorus to the Florida Keys reef tract by internal tidal upwelling is complicated by several factors.

First, while the arrival of cold water on the reef is a useful indicator of times of likely high nutrient concentrations, and almost all of the water samples taken when temperature was $<25.0^\circ\text{C}$ at Conch Reef had concentrations in the range of $0.5\text{--}4.0 \mu\text{mol L}^{-1} \text{NO}_3^-$ and $0.1\text{--}0.3 \mu\text{mol L}^{-1} \text{SRP}$, reef temperature alone is not a good proxy for nutrient concentrations. Mixing associated with the run-up of internal bores on the reef slope appears to blur the tight relationships observed between temperature and nutrient concentrations in the water column offshore. In both 2000 and 2001, the variance in nutrient concentrations at a given temperature measured on the reef slope was always higher than that measured in the water column offshore. On days with significant numbers of cold pulses, high nitrate concentrations were found on the reef even in samples from relatively warm water (e.g., $0.5\text{--}2.0 \mu\text{mol L}^{-1} \text{NO}_3^-$ at $26\text{--}28^\circ\text{C}$). By contrast, $26\text{--}28^\circ\text{C}$ water sampled offshore always contained $<0.2 \mu\text{mol L}^{-1} \text{NO}_3^-$. Using temperature on the reef as a direct proxy for nutrient concentrations via the relationships between temperature and

nutrients measured offshore would be likely to underestimate overall nutrient delivery to the reef.

Second, the waters overlying the reef tract do not represent a stationary, confined pool, and the residence time of upwelled water on reef slopes is likely to be highly variable. Following the strong upslope flow at the start of a cooling event, some portion of the subthermocline water transported onshore is likely to mix with surface layers and be subject to alongshore advection, while the cool, dense water remaining on the reef will eventually tend to recede offshore in gravity currents as shown in Fig. 4. Roughness at a range of scales from individual coral heads to the morphology of the spur and groove formation on individual reefs is likely to lead to spatial patchiness in residence times and overall nutrient availability. Following internal bore events, pockets of cool water can be found in reef depressions and under large coral heads long (e.g., 60–120 min) after temperature just above the reef surface has returned to ambient, warm levels (unpubl. data and pers. obs.).

Third, assessing the relative contribution of nutrients to the reef tract by internal tidal upwelling is compounded by limited quantification of other potential sources including in situ nitrogen fixation, fluxes out of the reef matrix, and inputs, including sources reaching the reef tract from back reef and near-shore waters. In addition, internal tidal upwelling does not represent a point source of nutrients but rather occurs at a broad spatial scale across the entire reef tract. However, from the available data it is possible to make order of magnitude estimates of nutrient input to the reef tract by internal tidal bores and to compare these with recent estimates of inputs from near-shore nutrient sources.

The estimates presented in Table 3 suggest that nitrogen and phosphorus inputs to the slopes of the Florida Keys reef tract from internal bores are at least as large and possibly as much as 20–40 times greater than estimated daily inputs to near-shore waters from waste water and storm water. The estimated annual input of nitrogen and phosphorus from internal bores ranges from roughly half to 10–20 times the annual input to near-shore waters from waste water and storm water. WW + SW estimates represent nitrogen and phosphorus loading to near-shore waters in close proximity to the Florida Keys. Nutrients input to near-shore waters are likely to be rapidly taken up by benthic and water column primary producers as well as diluted by mixing before possibly reaching the reef tract 5–8 km offshore. Only a small (but unknown) fraction of this loading would be expected to reach the reef tract (Szmant and Forrester 1996; Kruczynski and McManus 2002). Thus, it seems likely that for Florida Keys reef slopes, nitrogen and phosphorus availability from internal tidal upwelling will be one to several orders of magnitude larger than availability directly from near-shore waste water and storm water sources. It is, however, important to recognize that this will not be the case near shore and in back reef habitats where internal bores do not penetrate. Szmant and Forrester (1996) attempted to estimate potential nutrient upwelling associated with transient gyres of the Florida current and suggested approximately 40-fold more nitrogen and 25-fold more phosphorus could be injected into the system by upwelling than by WW + SW sources. That study, however, did not show evidence that upwelled water

Table 3. Estimated N and P input to the Florida Keys reef tract by internal tidal bores and comparison with estimated input from waste water and storm water (WW + WS) (Kruczynski and McManus 2002) from USEPA 1993.

Parameter	Low estimate	High estimate
NO ₃ ⁻ concentration (μmol L ⁻¹)	1.00	4.00
SRP concentration (μmol L ⁻¹)	0.10	0.30
Upslope flow speed (m s ⁻¹)	0.10	0.30
Height of bore (m)	5	10
Time of upslope flow (min)	20	30
Length of reef tract (km)	200	200
Volume transported (m ³ bore ⁻¹)	1.20×10 ⁸	1.08×10 ⁹
N transported across reef tract (kg bore ⁻¹)	1.68×10 ³	6.05×10 ⁴
P transported across reef tract (kg bore ⁻¹)	3.72×10 ²	1.00×10 ⁴
Transport events, 2000: 85 large, 37 small in 182 d		
Transport events, 2001: 52 large, 32 small in 224 d		
Total estimated bore N input (kg) 2000	1.74×10 ⁵	6.26×10 ⁶
Total estimated bore N input (kg) 2001	1.14×10 ⁵	4.12×10 ⁶
Total estimate bore P input (kg) 2000	3.85×10 ⁴	1.04×10 ⁶
Total estimate bore P input (kg) 2001	2.53×10 ⁴	6.82×10 ⁵
Estimated WW+SW N input (kg d ⁻¹)	1.36×10 ³	1.36×10 ³
Estimated WW+SW P input (kg d ⁻¹)	4.42×10 ²	4.42×10 ²
N input (bore ⁻¹)/WW+SW N input (kg d ⁻¹)	1.2	44.7
P input (bore ⁻¹)/WW+SW P input (kg d ⁻¹)	0.8	22.7
Total bore N input (kg)/total WW+SW N input (kg)	0.6	21.0
Total bore P input (kg)/total WW+SW P input (kg)	0.4	10.7

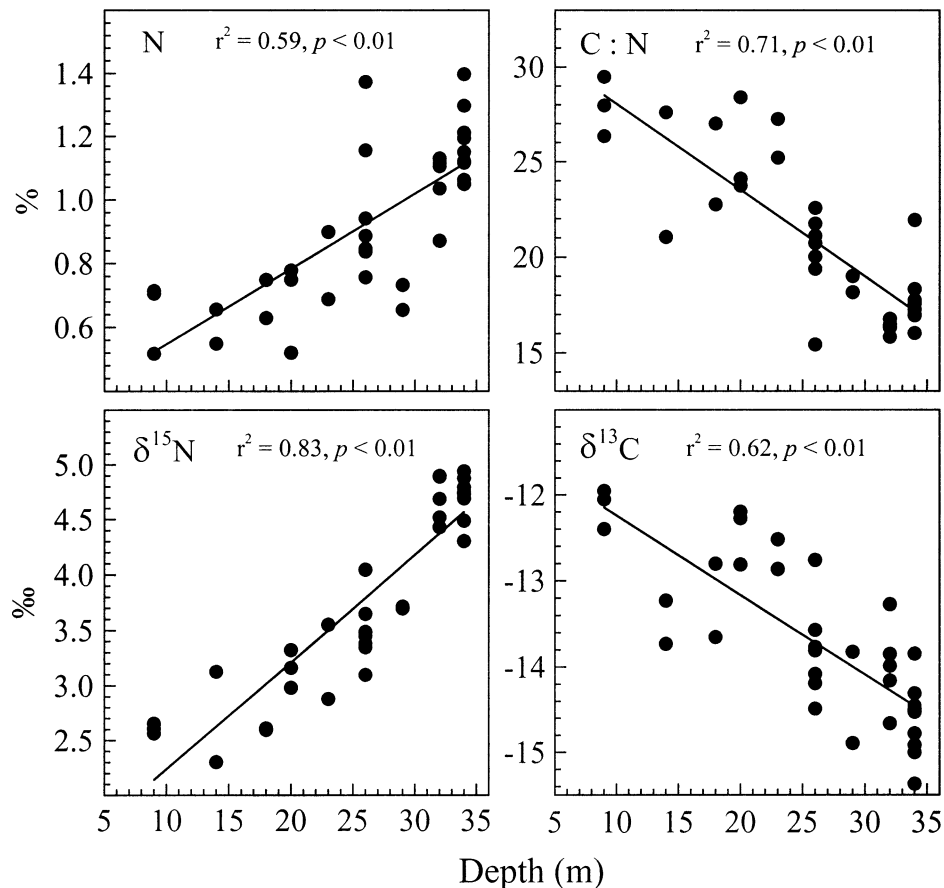


Fig. 7. *Codium isthmocladum* tissue percentage N, C:N ratio, $\delta^{15}\text{N}$ (‰), and $\delta^{13}\text{C}$ (‰) as a function of depth on the slope of Conch Reef, June 2001. $n = 35$ samples. r^2 and significance p values are indicated for linear correlation of each variable with depth.

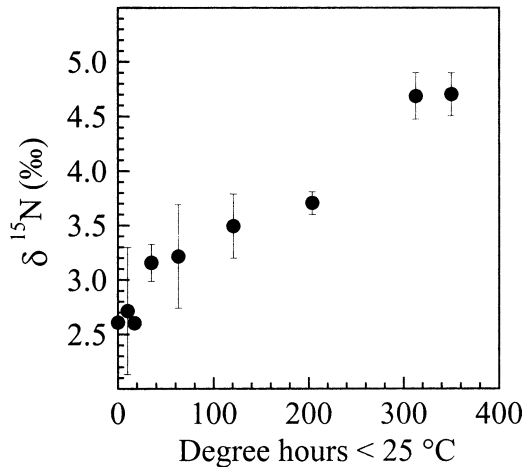


Fig. 8. Mean *Codium isthmocladum* tissue $\delta^{15}\text{N}$ for samples collected from Conch Reef 19–24 June 2001, plotted against depth-specific total degree hours $<25^\circ\text{C}$ for the prior 36-d period 12 May–17 June 2001. Error bars represent ± 1 standard error. Degree hours for at 15-, 20-, and 34-m depth are interpolated from a best-fit line to the data in Table 2.

actually reaches the reef tract and based its estimates on offshore, subthermocline concentrations of NO_3^- ($22 \mu\text{mol L}^{-1}$) and SRP ($2 \mu\text{mol L}^{-1}$) that are much higher than any concentrations observed on the slope of Conch Reef in the present study.

Algal use of subthermocline nitrate—An important consequence of the impact of internal bores on the Florida Keys reef tract is that the availability of nutrients is highly variable, with large transient peaks. In order to assess nutrient availability in this system accurately, it is essential to understand the sources of high-frequency variability and to sample at relevant temporal scales. Although intermittent sampling regimes will likely miss high-frequency pulses, macroalgae can continually “sample” available nutrients and are well equipped for rapid uptake during transient pulses and subsequent nutrient storage. Thus, they will be likely to experience overall nutrient regimes quite different from those estimated by low-frequency measurements. *Codium isthmocladum* tissue showed clear patterns of increasing percentage N, decreasing C:N, elevated $\delta^{15}\text{N}$, and decreasing $\delta^{13}\text{C}$ with depth on Conch Reef in June 2001. As discussed above, increasing depth on the reef slope is tightly associated with increasing magnitude and duration of cooling during internal tidal upwelling events. The patterns of *C. isthmocladum* percentage N and C:N suggest increasing nitrogen availability with increasing depth; however, the overall low percentage N ($<1.5\%$) and C:N significantly greater than the Redfield ratio also suggest N limitation at all depths (Hanisak 1979, 1983). Under conditions of nitrogen limitation, macroalgal growth rates can be highly sensitive to internal nitrogen content. For example, in the North Atlantic species, *Codium fragile*, Hanisak (1979) showed sharp increases in growth rates with increasing nitrogen up to approximately 2%. Assuming a similar relationship between growth rates and internal nitrogen content for *C. isthmo-*

cladum, it is likely that the increases in nitrogen content with increasing depth will result in significantly enhanced growth rates and possibly to changes in other physiological parameters as well. Preliminary data (J. Leichter, unpubl. data) for May–June 2001 showed higher *C. isthmocladum* growth rates at 33 m than at 21 m on Conch Reef. At shallower depths on Conch Reef, J. Smith (pers. comm.) has found higher growth rates of *Halimeda tuna* at 20 m than at 7 m, likely due to increased nutrient availability with depth.

Many macroalgae are capable of rapid uptake of transiently available nutrients, and in situ incubations designed to simulate short-term NO_3^- pulses ($0.5\text{--}2.0 \mu\text{mol L}^{-1} \text{NO}_3^-$ for 2–4 h) point to significant uptake of NO_3^- by *C. isthmocladum* (H. Stewart, J. Leichter unpubl. data). Under nitrogen-limited conditions, macroalgae are likely to take up and assimilate most or all available nitrogen with limited resulting isotopic fractionation. Thus, the resulting isotopic composition of tissue nitrogen can be expected to be relatively close to that of the nitrogen source pool. Subthermocline NO_3^- seaward of the Florida Keys is likely to have $\delta^{15}\text{N}$ values in the range of $+4\text{‰--}+7\text{‰}$ as reported for subsurface, oceanic NO_3^- in other regions (Michener and Schell 1994). Thus, the *C. isthmocladum* $\delta^{15}\text{N}$ values suggest use of subsurface NO_3^- , and the variation in $\delta^{15}\text{N}$ with depth can be explained by variation in exposure to transiently upwelled water. The relationship between mean $\delta^{15}\text{N}$ and total degree hours $<25^\circ\text{C}$ for the 36-d period preceding sample collection (Fig. 8) points to cumulative effects of the magnitude of cooling and duration that algae are exposed to subthermocline water. While variation in nitrogen fractionation associated with variation in light intensity could contribute to patterns of $\delta^{15}\text{N}$ with depth, this seems an unlikely explanation of the patterns observed here. Decreased light intensity with increasing depth has been suggested to explain decreasing $\delta^{15}\text{N}$ values in corals from both Jamaica and Zanzibar (Muscatine and Kaplan 1994; Heikoop et al. 1998), a pattern in the opposite direction of the one observed here for macroalgae.

Measurement of stable isotopes can be a powerful tool for examining nitrogen sources in marine environments (Michener and Schell 1994). Positive $\delta^{15}\text{N}$ values for corals growing along the outer margin of the Great Barrier Reef have been attributed to nitrogen sources associated with upwelling (Sammarco et al. 1999). Values of $\delta^{15}\text{N}$ in two benthic algal species on reefs in the Ryukyu Islands, Japan, have been used to infer patterns of terrestrial nitrogen input close to shore (Umezawa et al. 2002). In the present study, in addition to varying with depth, $\delta^{15}\text{N}$ values in *C. isthmocladum* tissue also varied seasonally at a given depth. Internal tidal upwelling is strongest from May to September, and the May 2001 samples were collected shortly before the onset of a period of strong upwelling that lasted into June 2001. Lapointe (1997) showed a temporal pattern of positive $\delta^{15}\text{N}$ values ($+2\text{‰--}11\text{‰}$) in *C. isthmocladum* collected off Jupiter Inlet near Ft. Lauderdale, Florida, and concluded these represented a signal of land-derived nitrogen reaching offshore reefs in association with strong, seasonal rainfall events. However, that study failed to consider deep-water nitrogen sources that appear to offer a simpler explanation for the positive $\delta^{15}\text{N}$ values (Hughes et al. 1999). Terrestrial nitrogen input is not a viable explanation for the increasing

positive $\delta^{15}\text{N}$ values with increasing depth that we measured within a small (200 m) cross-shore spatial scale at Conch Reef.

Values of $\delta^{13}\text{C}$ in the June 2001 *C. isthmocladum* samples decreased significantly with increasing depth. The causes of variation in isotopic composition of carbon in macroalgae are likely to be complex, and isotopic fractionation possibly in relation to light availability may be significant (Raven and Farquhar 1990; Raven et al. 1995), especially since carbon does not appear to be limiting growth in this case. It is interesting to note that decreasing $\delta^{13}\text{C}$ correlates with increasing percentage N. Increased tissue nitrogen might lead to altered physiological function and an increased ability to discriminate against ^{13}C . However, a number of factors may have contributed the observed $\delta^{13}\text{C}$ pattern with depth in the present study, and the cause of these patterns is unclear at present.

Conclusions

Recognition of the highly complex, naturally varying nutrient availability in this system, as well as the strong potential for similar effects in other locations, supports the view that it is unrealistic to expect simple concentration thresholds such as $1.0 \mu\text{mol L}^{-1} \text{NO}_3^-$ to cause phase shifts to algal dominance on coral reefs (Bell 1992; Lapointe 1997; Hughes et al. 1999; McCook 1999). Further, the possible signal of anthropogenic nutrients reaching the Florida Keys reef tract is likely to be small relative to the large fluctuations in background concentrations and thus very difficult to detect. Periods of strong internal tidal upwelling may explain rapid algal growth including reported blooms of *C. isthmocladum* (Hanisak 2001) on Florida reefs, and it appears likely that natural availability of nutrients, including high-frequency nutrient pulses, is sufficient to support significant growth of macroalgae in this system (Hanisak and Siemon 2000). Considering the natural availability of nutrients in this system, it seems much more likely that recent increases in macroalgal cover and changes in community composition on Florida reefs are related to factors such as herbivory, changes in water clarity, sedimentation, and coral diseases (all of which may have anthropogenic components) than to direct anthropogenic nutrient inputs. However, this does not rule out the possibility of important effects related to anthropogenic nutrients reaching the reef tract. Although Szmant and Forrester (1996) found no evidence in Florida Keys reef tract sediments of anthropogenic nutrient enrichment, there is widespread consensus that conditions on the Florida Keys reefs and back reef environments have changed dramatically in recent years and that anthropogenic activities are a major cause (e.g., Porter and Porter 2002 and papers therein). The data presented here clearly suggest that natural inputs of nitrogen and phosphorus during strong bouts of internal tidal upwelling would swamp out the possible signal of anthropogenic nutrients reaching the reef tract. However, there also are significant periods between pulses of upwelling and long periods particularly in October–December in each year when internal tidal upwelling is minimal. One consequence of anthropogenic nutrient inputs may have been subtle alterations

in baseline nutrient concentrations and shifts toward a situation of more continuous, chronic nutrient availability in a system naturally characterized by large but highly episodic inputs. It is also reasonable to speculate that warming of surface waters associated with climate change may have, and/or could in the future, lead to increased water column stratification. A possible effect could be an increase in the number of internal bores reaching Florida reef slopes and significant increases in reef slope nutrient availability.

The physical processes observed here are likely to occur on other reefs adjacent to strong, relatively shallow thermoclines and in proximity to mechanisms of internal wave generation such as strong alongshore currents and tidal exchange over abrupt shelf topography (Baines 1986; Wolanski 1994). Frequent bouts of strong internal tidal upwelling with associated low temperatures and significant nutrient input are probable contributors to the less-than-optimal conditions for scleractinian corals in the Florida Keys reflected in relatively low rates of reef accretion during the last 2,000–4,000 yr (Shinn et al. 1989). Periods of intensified upwelling, such as those observed in May–August 2000 and June–July and September 2001, are likely related to regional-scale oceanographic variability associated with the Florida current (Lee et al. 1985, 1994). At long temporal scales, changes in processes that control high-frequency upwelling such as water column stratification and the trajectory of coastal currents may result in significant changes in reef nutrient dynamics. At more immediate temporal scales, with the increasing need to understand rapid ecological change on coral reefs comes a critical need to evaluate and understand high-frequency oceanographic forcing mechanisms and their consequences for these and other complex marine ecosystems.

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