Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs

Christine A. Ward-Paige*, Michael J. Risk, and Owen A. Sherwood [b]

* cwardpai@dal.ca; Fax: 902-494-6889

[a]School of Geography and Geology, McMaster University, Hamilton, ON, Canada, L8S 4M1

[b]Department of Earth Sciences, Dalhousie University, Halifax, NS, Canada, B3H 4J1

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ABSTRACT: Bioerosion by *Cliona delitrix* and *Cliona lampa* was assessed at 43 sites along the Florida Reef Tract, USA, in the summer of 2001. Sponge abundances were estimated using rapid visual assessment. Tissue samples of sponges were taken for analysis of $\delta^{15}N$. Comparison samples were taken from Belize. Annual trends in sponge abundance were estimated from archived videos covering the period from 1996-2001. Sites with the greatest boring sponge size and cover were in the Backcountry and Lower Keys, where total nitrogen, ammonium, and $\delta^{15}N$ levels were highest. The sites with the largest relative increase of *C. delitrix* and *C. lampa* over the 5 year period were in the Upper Keys, where the greatest relative decline in stony coral cover has occurred. Florida sponge $\delta^{15}N$ values were 5.2 (±0.1) ‰, suggesting the influence of human waste; in comparison, offshore Belize samples were 2.1 (±0.1) ‰. These results suggest sewage contamination of the Florida Reef Tract, shifting the carbonate balance from construction to destruction.

Keywords: Eutrophication, boring sponges, $\delta^{15}N$, corals, Florida Keys

1. Introduction

The Florida reef tract is the third largest barrier reef in the world and the most extensive coral reef system in the continental United States. The reef extends 354 km from the southern tip of the Florida mainland, southwest to Key West and to the Dry Tortugas (25˚17, 80˚13 to 24˚40, 82˚48). The Florida Keys is home to more than 78 000 permanent, year round residents, plus 25 000 winter residents. More than 3 million people travel to the Keys each year, generating more than $1.3 billion annually, mostly from marine activities. Another $68 million is generated annually from the sale of commercial marine organisms (Kruczynski, 1999). Despite the value of coral reefs to the local economy, the reefs are under pressure from land-based pollution (e.g.: Lapointe and Matzie, 1996; Lipp et al., 2002; Lapointe et al., 2004).

The negative effects of land-based sources of pollution on coral reefs worldwide have been known and well documented for more than 20 years (Hallock and Schlager, 1986; Edinger et al*.,* 1998), including the Florida Keys (Dustan, 1977; Porter et al*.,* 1999; Kruczynski 1999). Significant (up to 5000 fold) nutrient enrichment in groundwaters contiguous to onsite sewage disposal systems (OSDS), was found in the nearshore waters of the Florida Keys with ammonium being the dominant nitrogenous species (Lapointe et al., 1990).There are approximately 25 000 septic tank systems, and about 4000 “unknown systems” (probably cesspits; Kruczynski, 2002, pers. comm.) in the Florida Keys, and (until recently) a shallow submerged ocean outfall for the City of Key West, 1000 m offshore. There are more than 350 shallow sewage injection wells. Recently, deep (>900

m) injection wells have been installed; it is hoped that these will reduce the amount of contamination reaching inshore waters (above discussion taken from Kruczynski, 1999; and Kruczynski, 2002, pers. comm.).

Bioerosion is a key process in the carbonate budget of any coral reef (Scoffin et al., 1980; Risk et al., 1995). On relatively healthy reefs, bioerosion and reef accretion rates are approximately equal (Hein and Risk, 1975; Scoffin et al., 1980). Increased eutrophication results in increased bioerosion levels (Rose and Risk, 1985; Sammarco, 1996; Holmes et al., 2000). Therefore, environmental changes leading to increased bioerosion can lead to a net loss of carbonate and subsequent decline of the reef itself (Edinger et al., 1998).

Clionid sponges are the most important framework bioeroders (Hein and Risk, 1975; MacGeachy, 1977; Stearn and Scoffin, 1977; Hudson 1977). Boring sponges destroy reef framework directly by excavating and encrusting coral tissue (MacGeachy and Stearn, 1976), and indirectly by compromising the structural integrity of the coral skeleton (Bromley, 1978). Their activities increase local supply of fine-grained carbonate detritus (Neumann, 1966), and produce mucus in a 1-2 cm ‘dead zone’ at the coral-sponge interface (Sullivan et al., 1983). Boring sponges account for greater than 90% of total boring in most live and dead coral heads (MacGeachy and Stearn, 1976).

Following a review of reef monitoring systems being used in the Florida Keys, we were asked by Florida Marine Research Institute (FMRI) to devise a rapid bioerosion assessment protocol that could easily be integrated into their ongoing field activities. The bioerosion assessment we devised takes approximately 60 minutes per site, depending on sponge population density. Operators can be trained in the protocol in one dive. Preliminary field observations revealed that the closely related boring sponges *Cliona delitrix* and *Cliona lampa* were abundant and widespread in the area, and these became the focus of the study.

C. delitrix and *C. lampa* are destructive bright orange-vermillion sponges that overgrow and kill coral. Both these sponges are boring sponges that overgrow the substrate in the latter stages of colony growth. Neumann (1966) and Rose and Risk (1985) showed the relation between colony size, number, and bioerosion amount. *C. lampa* usually mimics the skeletal structure of the underlying coral, and feels hard to the touch underwater compared to *C. delitrix*, which has large compound ostial papillae that mask the underlying coral skeleton. Clionid sponges penetrate coral by cellular etching, and remove up to 50% of the skeletal carbonate (Rose and Risk, 1985), which is expelled by oscula into surrounding water (Rutzler, 1975). The process is about 3 % chemical, using carbonic anhydrase, and 97 % mechanical (Rutzler, 1975).

In a study on the reefs of Grand Cayman, Rose and Risk (1985) found that density of *C. delitrix* was positively related to the numbers of water-column fecal bacteria. Other studies (Sammarco, 1996; Holmes et al., 2000) have found bioeroders to be positively correlated with nutrient levels. In this study, we combine field assessments with archived

video and stable isotope geochemistry. The results suggest land-based stresses lead to increased coral death and reef decline.

2. Methods

Study Sites

Bioerosion surveys were carried out at 43 sites along the Florida Reef Tract during the summer months of 2001. Study sites were located within 5 of the 9 Environmental Protection Agencies (EPA) water quality segments within the Florida Keys National Marine Sanctuary (FKNMS). Water quality segments are outlined in Figure 1. Further information about the ecosystem and the Environmental Protection Agency (EPA) programs may be found in Porter and Porter, 2002. The Coral Reef Monitoring Project (CRMP) installed permanent station markers in 1995; sites consisted of a maximum of 4 and a minimum of 2 stations, each with 3 transects 22 m in length (Porter et al., 2002). Table 1 categorizes each site that was used for this study (sites with *Cliona spp.* present) in its respective water quality segment.

Reefs from the Dry Tortugas, Marquesas, Backcountry, Upper, Middle, and Lower Keys were represented in this study. Site depths ranged from less than 1 m to greater than 25 m, and included hardbottom, patch, offshore deep, and offshore shallow reef types.

In addition, sponges were sampled for isotope analysis (see below) from Long Caye and Half Moon Caye at Lighthouse Reef, located approximately 75 km offshore from the mainland of Belize. There are few permanent residents in the area, and other than tourists that visit the reef, there are no other significant sources of anthropogenic nutrients.

Bioerosion

The bioerosion field assessment protocol was designed to complement the ongoing study of Florida's coral reefs by the CRMP. A 1 m wide belt transect was examined along each of the 22 m long transects. Individual colonies of *Cliona delitrix* and *Cliona lampa* were counted and their area estimated using a 5 x 5 cm transparent grid. Small (<5 g) samples of *Cliona* tissue were taken from each site (where present) for isotope analysis. Time at each site was approximately one hour. The protocol was taught to untrained collaborators within one dive. To test the methods, the same transect was repeated with multiple operators, and the agreement was greater than 95 %.

Video analyses

Each transect in the Florida sites has been filmed by the CRMP since 1996, with the exception of the Tortugas sites, which were filmed since 1999. Video was taken at a rate of 4 m minute^{-1}, at 40 cm above the bottom using a convergent laser light system (Jaap et al., 2001). Four reefs were selected for the historical study, each representing a different water quality segment: Black Coral Rock (Dry Tortugas); Cliff Green (Lower Keys); Content Key (Backcountry); Carysfort Deep (Upper Keys). Video from 1996 through 2001 was examined.

In the FMRI protocol (Wheaton et al., 1998), a length of chain, each link 5 cm in length, is laid down in each transect. We used the images of this chain to calibrate actual sponge size shown in the video. The area covered on the screen was then converted using chain-link measures. The number of colonies of *C. delitrix* and *C. lampa* were recorded, and area of each sponge colony estimated.

$\delta^{15}N$ determinations

Methods were as described in Risk et al., (2001). Sponge samples were kept on ice out of the sun until they could be put in a freezer at the lab. Samples were kept frozen until ready to be processed at McMaster University. Sponges were decalcified in 5 % HCl over the course of a few days. Once decalcified, samples were washed and centrifuged three times in deionized water. Prepared samples were freeze-dried until analyzed. Six-mm pyrex tubes were heated to 550 °C for cleaning. Tubes were loaded with 14-15 mg of sample and sandwiched between excess amounts of CuO wire that was heat treated to 900 °C. Tubes were put on a vacuum line, and sealed using a flame. Sealed tubes were combusted for 2.5 hours at 550 °C, then run within 24 hours on a dual inlet Optima mass spectrometer at McMaster University. Analytical reproducibility, as measured by the average difference of sample replicates, was ± 0.1 ‰.

Data Analysis

Sponge characteristics were measured on each transect as follows: (1) horizontal area of each sponge, and (2) total number of sponges. Averages of the (1) sponge abundance (number of sponges per transect), (2) sponge size, and (3) sponge cover (area per transect) were calculated for each site and water quality segment.

Belize $\delta^{15}N$ values were compared to Florida values. Water quality data for Florida and Belize came from Southeast Environmental Research Center (SERC; Boyer, 2003) and Lapointe (2004), respectively. This study shows regional (e.g.: Lower Keys, Backcountry, etc.) and temporal (e.g.: 1996-1998, etc.) comparisons of sponge abundance, size, cover, $\delta^{15}N$ of sponge tissue, and water quality.

3. Results

Sponge population characteristics and tissue δ^{15}N data are summarized in Table 2. Sponge samples for δ^{15}N analysis were collected at 20 of the 43 CRMP sites. Overall, *C. delitrix* was the most common species throughout the sanctuary, so it was preferentially collected. Where *C. delitrix* was absent *C. lampa* was collected instead. Compared to *C. delitrix,* δ^{15}N values from *C. lampa* were systematically higher by ca. 0.6 ‰. We report here only those δ^{15}N data for *C. delitrix*, as this was the most common species.

Regional trends in sponge coverage and δ^{15}N

The four different sponge characteristics (abundance, size, cover, and δ^{15}N) showed different regional trends (Figure 2). The sponge abundance was highest in the Upper Keys, Tortugas, and Marquesas, and lowest in the Backcountry, Lower, and Middle Keys (Figure 2a). Average sponge size and cover have a more clearly defined regional pattern (Figure 2b,c), which is approximately the inverse of the sponge abundance. The greatest sponge size was in the Backcountry and Lower Keys. Average sponge cover was also the greatest in Backcountry and Lower Keys. The Marquesas had intermediate sponge cover, while the Tortugas, Middle, and Upper Keys had relatively lower sponge cover. δ^{15}N showed similar trends with sponge size and sponge cover. The Backcountry had the highest δ^{15}N of 6.8 ‰. The Lower, Middle, and Upper Keys had similar δ^{15}N (5.3, 4.8, and 5.1 ‰ respectively). Belize had the lowest δ^{15}N at 2.2 ‰ (Figure 2d). Sponges were not collected for δ^{15}N analysis in the Tortugas, and Marquesas because we did not have permits.

Validation of video transect data

A comparison of observational field data with archived video data showed the reliability of the video methods used in this study. Note that the width of the transect in the field was 1 m, while the video was about 0.5 m. The sponge abundance recorded in the archived video was about half that of the observed data (Figure 3a). Average sponge size (Figure 3b) and average sponge cover (Figure 3c) measured by the video technique were about double that of the observed data; however, the relationship is significantly and positively correlated. These relationships suggest that small sponge colonies are better seen by underwater observers than recorded on archived video, and that physical measurements underwater are more challenging than measurements from video. Nonetheless, the overall trends from the archived video are consistent with and correlated with field data. This allows us to evaluate temporal trends in sponge parameters with confidence.

Temporal trends from 1996-2001 in sponge abundance, size, and cover from archived video showed an increase in bioerosion by *Cliona delitrix* and *Cliona lampa* in all regions of the FKNMS (Figure 4a-c). Although the Upper Keys experienced the largest relative increase in sponge abundance from 1996-2001, the average sponge cover and sponge size was only about one-fifteenth that of the Lower Keys (Figure 4b,c). Average sponge abundance nearly doubled between 1998 and 1999, sanctuary-wide. Over the same period, there was a sanctuary-wide decline in coral cover (Figure 5; Porter et al., 2002).

Sponge $\delta^{15}N$

Sponge tissue δ^{15}N data are summarized in Table 2. δ^{15}N values were highest in the Backcountry, followed by the Lower Keys, Upper Keys, and then the Middle Keys (Fig 2d). δ^{15}N of sponge tissue was positively and significantly correlated to total nitrogen (TN, Figure 6) and ammonium (NH_4^+) levels in seawater (Figure 7) for all regions of the Florida Keys. Average δ^{15}N sponge tissue values in Belize were 2.2 ‰, lower than average δ^{15}N values in Florida (average 5.2 ‰) (Figure 7).

4. Discussion

One of the most important questions facing the coral reef research community is the relative importance of sources of stress on coral reefs. We examined the scientific literature in an attempt to find studies that would allow some assessment of the factors contributing to the decline of coral reefs. The criteria were: (1) reefs had to have been sampled or assessed at the same location, (2) using similar or identical methods, (3) over a significant time interval, and (4) there had to have been some estimate of the cause of reef decline. Despite the voluminous literature available on some topics, such as coral bleaching, we were able to find only ten papers reporting on studies that met those criteria (Table 3).

Of these studies, five dealt with the effects of elevated seawater temperature and/or bleaching. Each of these noted 95-100 % recovery of corals within one year of bleaching. Despite eventual recovery, many corals did not grow during bleaching (Goreau and Macfarlane, 1990; Fitt et al., 1993) and/or were not able to complete gametogenesis in the following reproductive season (Szmant and Gassman, 1990).

The remaining papers examined the long-term effects of land-based pollution (sedimentation and sewage loading) on coral reefs. All studies found near or total coral mortality, with no recovery (Anthony et al., 1997; Hallock and Schlager 1986; Dustan and Halas 1987; Edinger et al., 1998) for as long as the stress was applied. In an urban embayment in Hawaii, redirection of sewage outflow pipes to a deep offshore location resulted in partial recovery (Grigg 1995).

In one of the first papers to note the decline, Ogden et al. (1994) used long-term photographic monitoring of the Florida Reef Tract. They reported a 40 % loss of coral cover over 5 years in the Upper Keys area, which they attributed to a decline in water quality. The authors do not attribute the loss to elevated loads of land-derived nutrients, but did find moderately elevated nutrient levels in developed nearshore areas. This study is not included in Table 3 because it does not specifically attribute the loss to nutrient loading or seawater temperature.

The number of long-term studies on reefs is not large, despite more than a century of research. To draw any firm conclusions from such a limited survey as in Table 3 would be difficult - nonetheless, it would appear that, at the present time, reef damage from land-based sources of pollution has far outstripped that from any other source, including bleaching. In addition to the above, Patterson et al. (2002) discovered that white pox disease, which kills *Acropora palmata* at a rate of 2.5 cm^2 day^{-1}, is caused by a common fecal enterobacterium.

Archived video in this study showed an increase in the boring sponge abundance, size, and cover of *C. delitrix* and *C. lampa* in all regions of the FKNMS, while the CRMP has shown an overall decline in coral species and stony coral cover from the same video footage (Jaap et al., 2001; Figure 5). The CRMP found the greatest decline of coral cover in the Upper Keys, followed by the Lower Keys, from 1996-2000 (Porter et al., 2002). During this time, there were no significant bleaching events or community changes that could be ascribed to “global change.” Average *C. delitrix* and *C. lampa* abundance, size, and cover had the greatest relative increase in the Upper Keys (2, 3, and 7 fold, respectively), while the Lower Keys had the largest sponge size and average cover - more than 50 times that of the Upper Keys.

C. delitrix and *C. lampa* are more commonly found in massive corals such as *Montastrea* and *Siderastrea*, and rarely in foliose or branching corals such as *Mycetophillia* and *Acropora*. In the Caribbean, *A. palmata* is frequently attacked by a more cryptic boring sponge, *C. vestifica*, and never by *C. delitrix* or *C. lampa*. Reasons for these differences are unclear, but the presence or absence of *C. delitrix* or *C. lampa* could be determined by the reef type.

DeNiro and Epstein (1981) determined that the nitrogen isotopic composition of animals could be used to identify food sources. $\delta^{15}N$ values are enriched with each step of the food chain because dietary ^{15}N is preferentially incorporated over ^{14}N (DeNiro and Epstein, 1981). A series of papers have documented the occurrence of elevated ^{15}N on reefs polluted with human sewage (Yamamuro and Minagawa, 1995; Heikoop, 1997; Heikoop et al., 2000), suggesting that nitrogen isotope tissue determinations are an effective objective means of evaluating sewage stress on reefs. $\delta^{15}N$ is an indicator of trophic status ($\delta^{15}N$ values are enriched up the food chain), not of nutrient levels per se. Human waste carries an isotopic signature of diet; previous studies have shown that $\delta^{15}N$ in coral tissue is an effective monitor of sewage stress on reefs (Risk et al., 1989, 1994b; Mendes et al., 1996; Heikoop, 1997). Sponge tissue $\delta^{15}N$ values in this study strongly correlate with water TN and NH_4^+; it is likely that both trends are driven by sewage loadings. TN and NH_4^+ levels are an indication of the amount of nutrient present, whereas the $\delta^{15}N$ values indicate the source. The Lower Keys and Backcountry had the greatest *C. delitrix* and *C. lampa* size and cover, as well as elevated sponge tissue $\delta^{15}N$, TN, and NH_4^+ levels.

The Backcountry segment, with less than 13 % of the human population of the Keys, had the highest $\delta^{15}N$, TN, and NH_4^+, and relatively large sponge cover and sponge size. This is likely a result of (1) local sources of NH_4^+ (large number of cesspools and septic systems; Lapointe and Clark, 1992) and/or (2) hydraulic isolation from shelf and Atlantic waters, with relatively long water residence times (Boyer and Jones, 2002). These sites are bathed in Florida Bay water, which receives discharge from the Everglades as well as a variety of non-point agricultural and recreational sources.

The Lower Keys had the largest total sponge cover, sponge size, and had elevated levels of $\delta^{15}N$, TN, and NH_4^+. Lapointe et al. (2004) also found the same trends in $\delta^{15}N$ of seagrass. The Lower Keys also has the highest effective human population density of the Keys.

The Middle and Upper Keys have significantly lower coastal population densities relative to the Lower Keys, and have a much greater mixing with relatively clean Atlantic Ocean waters (Boyer and Jones, 2002). These regions had a relatively small *C. delitrix* and *C. lampa* abundance, size, and cover, as well as low tissue $\delta^{15}N$ values.

Belize $\delta^{15}N$ values were below all measured water quality segments in the Florida Keys (note: no $\delta^{15}N$ values were taken in the Marquesas or Tortugas). Offshore Belize reefs approach pristine water levels because of minimal sources of anthropogenic nutrients coupled with mixing with open ocean waters.

The coincidence of widespread coral decline with rapid expansion in a fecal bioindicator that kills coral may not be accidental, and the relationship bears further investigation. It is greatly to be regretted that, almost 20 years after the link between *C. delitrix* and fecal loadings was established (Rose and Risk, 1985), this is the first and only follow-up study on an organism that accounts for a major proportion of the carbonate budget on Florida reefs.

Levels of bioerosion are an important part of the carbonate budget in coral reef environments (Neumann, 1966; Rutzler, 1975; MacGeachy and Stearn, 1976; Risk et al., 1995; Edinger and Risk, 1996; Holmes et al., 2000; Schonberg and Wilkinson, 2001). Examination of bioeroders is a relatively easy task that can be done by anyone with minimal experience and training. Bioerosion assessments (either some modification of the methods described herein, or the Holmes et al., 2000, rubble technique) should be an integral part of every coral reef monitoring program.

5. Conclusion

1. Sanctuary wide, coral cover declined while Clionid sponge abundance increased from 1996-2001.
2. Coral decline and relative sponge abundance increase from 1996-2001 was greatest in the Upper Keys.
3. Nitrogen isotope ratios, sponge size and sponge cover were greatest in the Lower Keys and Backcountry, where the highest values of TN and NH_4^+ occurred.
4. $\delta^{15}N$ in offshore Belize reefs are much lower than average Florida values, suggesting large differences in the source of nutrients.
5. Coral loss in the Florida Reef Tract is a result of land-based stress, rather than ‘global change’.

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References

Anthony, S.L., Lang, J.C. & Maguire, B.Jr. 1997. Causes of stony coral mortality on a central Bahamian reef: 1991-1995. In: Lessios, H.A. and Macintyre, I.G. (eds.) Proceedings of the 8th International Coral Reef Symposium, Panama 2*,* 1789-1794.

Boyer, J.N. 2003. Southeast Environmental Research Center. Florida International Research Center, Miami, Florida, USA. http://serc.fiu.edu/wqmnetwork/

Boyer, J.N. & Jones, R.D. 2002. A view from the bridge: external and internal forces affecting the ambient water quality of the Florida Keys National Marine Sanctuary (FKNMS). In: Porter, J.W. and Porter, K.G. (eds.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press, Florida, pp. 609-628.

Bromley, R.G. 1978. Bioerosion of Bermuda reefs. Palaeogeography, Palaeoclimatology, Palaeoecology 23, 169-197.

DeNiro, M.J. & Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45, 341-351.

Drollet, J.H., Faucon, M. & Martin, P.M.V. 1995. Elevated sea-water temperature and solar UV-B flux associated with two successive coral mass bleaching events in Tahiti. Marine Freshwater Research 46(8), 1153-1157.

Dustan, P. 1977. Vitality of reef coral populations off Key Largo, Florida: recruitment and mortality. Environmental Geology *2*, 51-58.

Dustan, P. & Halas, J.C. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. Coral Reefs 16, 91-106.

Edinger, E.N. & Risk, M.J. 1996. Sponge borehole size as a relative measure of bioerosion and paleoproductivity. Lethaia 29*,* 275-286.

Edinger, E.N., Jompa, J., Limmon, G.V., Widjatmoko, W. & Risk, M.J. 1998. Reef degradation and coral biodiversity in Indonesia: Effects of land-based pollution, destructive fishing practices and changes over time. Marine Pollution Bulletin 36(8), 617-630.

Fitt, W.K., Porter, J.W., Spero, H.J., Halas, J. & White, M.W. 1993. Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 Caribbean "bleaching event". Coral Reefs 12(2), 57-64.

Goreau, T.J. & Macfarlane, A.H. 1990. Reduced growth rate of *Montastrea annularis* following the 1987-1988 coral-bleaching event. Coral Reefs 8, 211-215.

Grigg, R.W. 1995. Coral reefs in an urban embayment in Hawaii: a complex case history controlled by natural and anthropogenic stress. Coral Reefs 14(4), 253-266.

Hallock, P. & Schlager, W. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. Palaios 1(4), 389-398.

Heikoop, J.M. 1997. Environmental signals in coral tissue and skeleton: examples from the Caribbean and Indo-Pacific. Ph.D. Thesis, McMaster University, Hamilton, Ontario.

Heikoop, J.M., Risk, M.J., Lazier, A.V., Edinger, E.N., Jompa, J., Limmon, G.V., Dunn, J.J., Browne, D.R. & Schwarcz, H.P. 2000. Nitrogen-15 signals of anthropogenic nutrient loading in reef corals. Marine Pollution Bulletin 40(7), 628-636.

Hein, F.J. & Risk, M.J. 1975. Bioerosion of coral heads: inner patch reefs, Florida reef tract. Bulletin of Marine Science 25, 133-138.

Holmes, K.E., Edinger, E.N., Hariyadi, Limmon, G.V. & Risk, M.J. 2000. Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. Marine Pollution Bulletin 40(7), 606-617.

Hudson, J.H. 1977. Long term bioerosion rates on a Florida reef: a new method. Proceedings of the 3rd International Coral Reef Symposium 2, 491-498.

Jaap, W.C., Porter, J.W., Wheaton, J., Hackett, K., Lybolt, M., Callahan, M., Tsokos, C. & Yanev, G. 2001. EPA/FKNMS Coral Reef Monitoring Project updated executive summary 1996-2000. Steering Committee Meeting August 1, 2001.

Kruczynski, W.L. 1999. Water quality concerns in the Florida Keys: sources, effects, and solutions. EPA Water Quality Protection Program- Florida Keys National Marine Sanctuary. EPA 904-R-99-005.

Lapointe, B.E., Barile, P.J., & Matzie, W.R. 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. Journal of Experimental Marine Biology and Ecology 308, 23-58.

Lapointe, B.E., O'Connell, J.D. & Garrett, G.S. 1990. Nutrient couplings between on-site sewage disposal systems, groundwaters, and nearshore surface waters of the Florida Keys. Biogeochemistry 10, 289-307.

Lapointe, B.E. & Clark, M.W. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. Estuaries 15(4), 465-476.

Lapointe, B.E. & Matzie, W.R. 1996. Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. Estuaries 19(2B), 422-435.

Lapointe, B.E. 2004. Phosphorous-rich waters at Glovers Reef, Belize. Marine Pollution Bulletin 48, 193-195.

Lapointe, B.E., Barile, P.J., and Matzie, W.R. 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. Journal of Experimental Marine Biology and Ecology 308, 23-58.

Lipp, E.K., Jarrell, J.L., Griffin, D.W., Lukasik, J., Jacukiewicz, J. & Rose, J.B. 2002. Preliminary evidence for human fecal contamination in corals of the Florida Keys, USA. Marine Pollution Bulletin 44, 666-670.

MacGeachy, J.T. 1977. Factors controlling species boring in Barbados reef corals. Proceedings of the 3rd International Coral Reef Symposium 2, 478-483.

MacGeachy, J.K. & Stearn, C.W. 1976. Boring by macro-organisms in the coral *Montastrea annularis* on Barbados reefs. Internationale Revue der Gesamte Hydrobiologie 61(6), 715-745.

Mendes, J., Risk, M.J., Schwarcz, H.P. & Woodley, J. 1996. Stable isotopes of nitrogen as measures of marine pollution: a preliminary assay of coral tissue from Jamaica. Proceedings of the 8th International Coral Reef Symposium 2, 1869-1972.

Neuman, A.C. 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge *Cliona lampa.* Limnology and Oceanography 11, 92-108.

Ogden, J.C., Porter, J.W., Smith, N.P., Szmant, A.M., Jaap, W.C. & Forcucci, D. 1994. A long-term interdisciplinary study of the Florida Keys seascape. Bulletin of Marine Science 54(3), 1059-1071.

Patterson, K.L., Porter, J.W., Ritchie, K.B., Polson, S.W., Mueller, E., Peters, E.C., Santavy, D.L. & Smith, G.W. 2002. The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, Acropora palmata. *Ecology: early edition*, accession no. AF389108.

Porter, J.W., Lewis, S.K. & Porter, K.G. 1999. The effects of multiple stressors on the Florida Keys coral reef ecosystem: a landscape hypothesis and a physiological test. Limnology and Oceanography 44(3), 941-949.

Porter, J.W. & Porter, K.G. (eds.) 2002. The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press, Florida.

Porter, J.W., Kosmynin, V., Patterson, K.L., Porter, K.G., Jaap, W.C., Wheaton, J.L., Hackett, K., Lybolt, M., Tsokos, C.P., Yanev, G., Marcinek, D.M., Dotten, J., Eaken, D., Patterson, M., Meier, O.W., Brill, M. & Dustan, P. 2002. Detection of coral reef change by the Florida Keys Coral Reef Monitoring Project. In: Porter, J.W., and Porter, K.G. (eds.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press, Florida, pp. 749-769.

Quinn, N.J. & Kojis, B.L. 1999. Subsurface seawater temperature variation and the recovery of corals from the 1993 coral bleaching event in waters off St. Thomas, U.S. Virgin Islands. Bulletin of Marine Science 65(1), 201-214.

Risk, M.J., Sammarco, P.W., Naim, O. & Schwarcz, H.P. 1989. Stable isotopes of carbon and environmental studies on reefs: some preliminary results from Australia and Reunion. International Society of Reef Studies, Annual Meeting (Marseilles) (abstract).

Risk, M.J., Sammarco, P.W. & Schwarcz, H.P. 1994b. Cross-continental shelf trends in $\delta^{13}C$ in coral on the Great Barrier Reef. Marine Ecology Progress Series 106, 121-130.

Risk, M.J., Sammarco, P.W. & Edinger, E.N. 1995. Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef. Coral Reefs 14(2), 79-86.

Risk, M.J., Heikoop, J.M., Edinger, E.N. & Erdmann, M.V. 2001. The assessment “toolbox”: community-based reef evaluation methods coupled with geochemical techniques to identify sources of stress. Bulletin of Marine Science 69(2), 443-458.

Rose, C.S. & Risk, M.J. 1985. Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. Marine Ecology 6(4), 345-363.

Rutzler, K. 1975. The role of burrowing sponges in bioerosion. Oecologia 19, 203-216.

Sammarco, P.W. 1996. Comments on coral reef regeneration, bioerosion, biogeography, and chemical ecology: future directions. Journal of Experimental Marine Biology and Ecology 200(1-2), 135-168.

Schonberg, C.H.L. & Wilkinson, C.R. 2001. Induced colonization of corals by a clionid bioeroding sponge. Coral Reefs 20, 69-76.

Scoffin, T.P., Stearn, C.W., Boucher, D., Frydl, P., Hawkins, C.M., Hunter, I.G. & MacGeachy, J.K. 1980. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Bulletin of Marine Science 30(2), 475-508.

Stearn, C.W. & Scoffin, T.P. 1977. Carbonate budget of a fringing reef, Barbados. Proceedings of the 3rd International Coral Reef Symposium 2, 471-476.

Sullivan, B., Faulkner, D.J. & Webb, L. 1983. Siphondictidine, a metabolite of the burrowing sponge. Siphonodictyon species that inhibits coral growth. Science 221, 1175-1176.

Szmant, A.M. & Gassman, N.J. 1990. The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs 8, 217-224.

Wheaton, J.L., Jaap, W.C., Dustan, P., Porter, J. & Meier, O. 1998. EPA Water Quality Protection Program: coral reef/hardbottom monitoring project, 1997 annual report.

Yamamuro, M. & Minagawa, M. 1995. Carbon and nitrogen stable isotopes of primary producers in coral reef ecosystems. Limnology and Oceanography 40(3), 617-621.

Figure Captions

Figure 1. Map of the FKNMS showing study sites, water quality segments, and regional pattern in benthic NH_4^+ (data from SERC, see text for details).

Figure 2. Regional differences in average (a) sponge abundance, (b) sponge size, (c) sponge cover, and (d) sponge $\delta^{15}N$. Error bars are 1 standard error, where $n > 1$.

Figure 3. Comparison of data measured by video and in the field. Both data sets are from 2001. (a) Average sponge abundance, (b) average sponge size, and (c) average sponge cover.

Figure 4. Timeseries trends in average (a) sponge abundance, (b) sponge size, and (c) sponge cover measured from video archive. Legend in (a) applies to all graphs. Note log y-axis in (b) and (c). Dotted lines bridge missing data.

Figure 5. Sanctuary-wide temporal trend in average sponge abundance, 1996 to 2001 (closed diamonds). Percent coral cover (open squares), 1996 to 2000, is plotted on the secondary y-axis (data from Porter et al., 2002).

Figure 6. Plot of $\delta^{15}N$ of sponge tissue vs. benthic TN (data from Boyer, 2003).

Figure 7. Plot of δ^{15}N of sponge tissue vs. benthic NH_4^+ (data from Boyer, 2003). Offshore Belize NH_4^+ datum from Lapointe (2004).

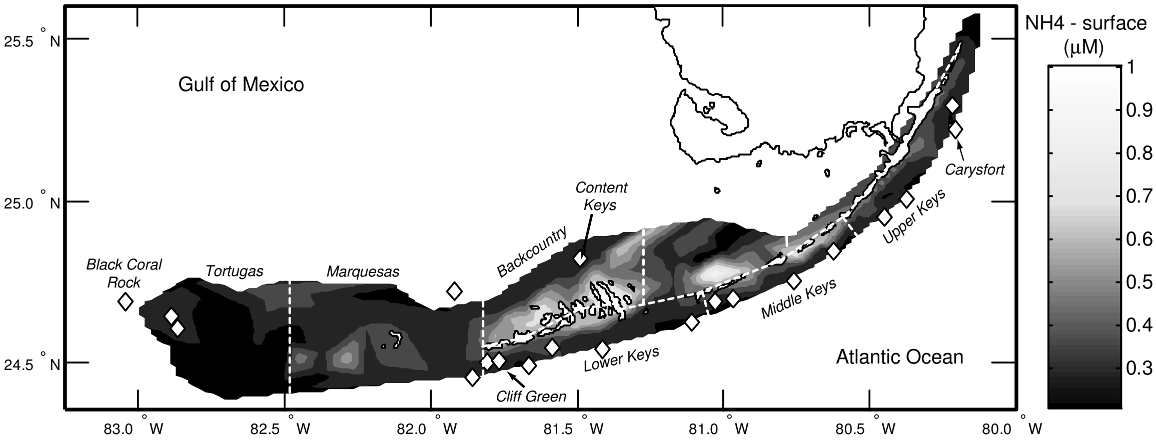

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Fig. 1

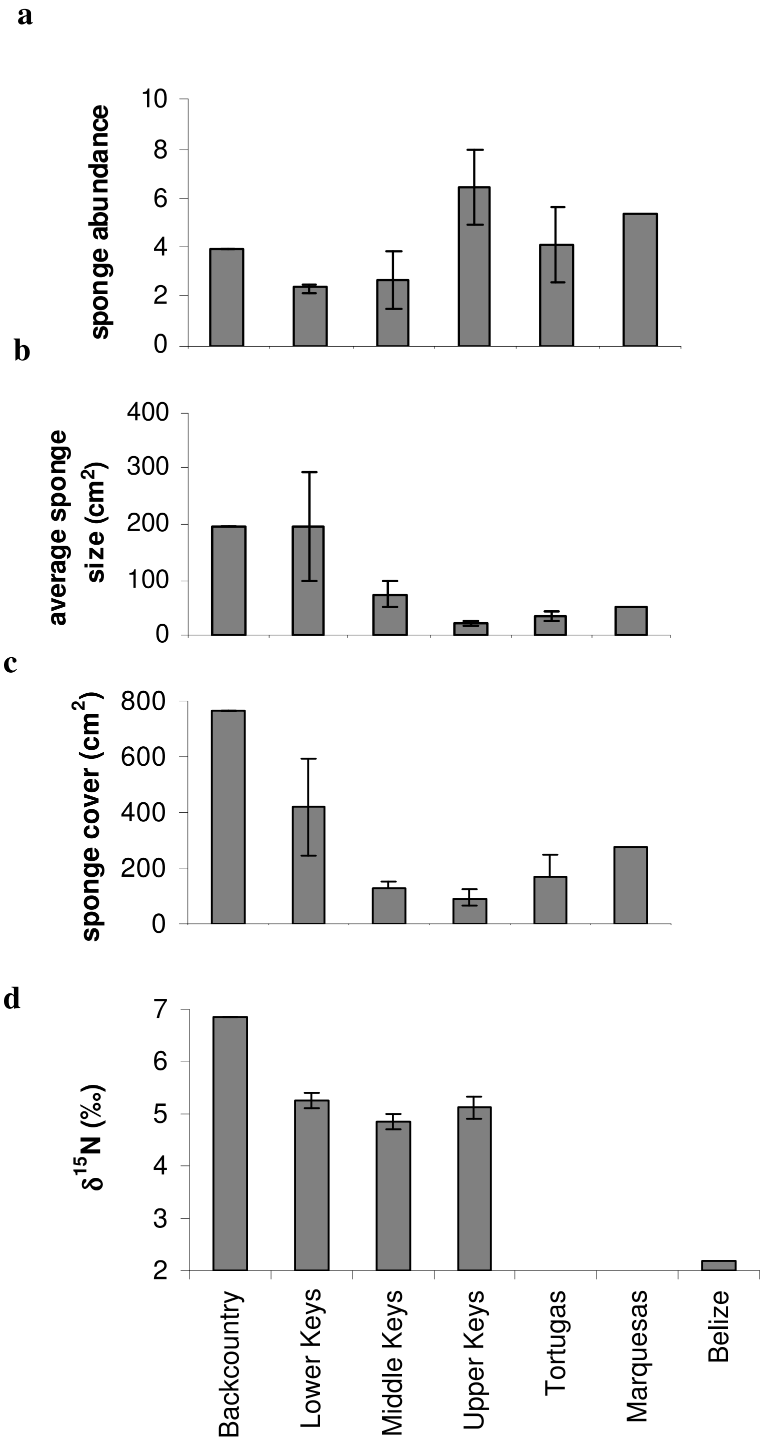
a
sponge abundance
10
8
6
4
2
0
b
average sponge size (cm^2)
400
300
200
100
0
c
sponge cover (cm^2)
800
600
400
200
0
d
$\delta^{15}N$ (‰)
7
6
5
4
3
2
Backcountry
Lower Keys
Middle Keys
Upper Keys
Tortugas
Marquesas
Belize

Figure 2

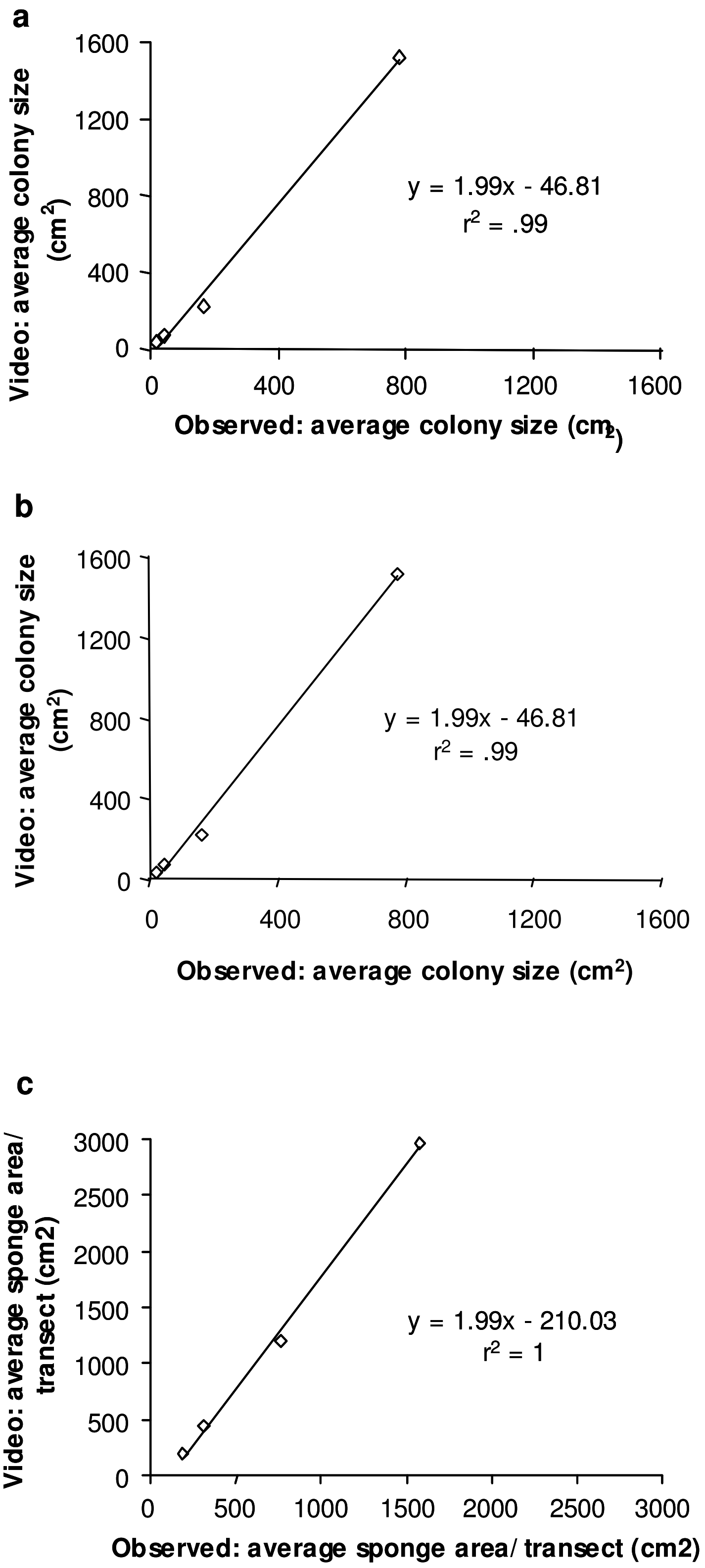
a
Video: average colony size (cm^2)
1600
1200
800
400
0
0
400
800
1200
1600
Observed: average colony size (cm^2)
y = 1.99x - 46.81
r^2 = .99
b
Video: average colony size (cm^2)
1600
1200
800
400
0
0
400
800
1200
1600
Observed: average colony size (cm^2)
y = 1.99x - 46.81
r^2 = .99
c
Video: average sponge area/ transect (cm2)
3000
2500
2000
1500
1000
500
0
0
500
1000
1500
2000
2500
3000
Observed: average sponge area/ transect (cm2)
y = 1.99x - 210.03
r^2 = 1

Figure 3

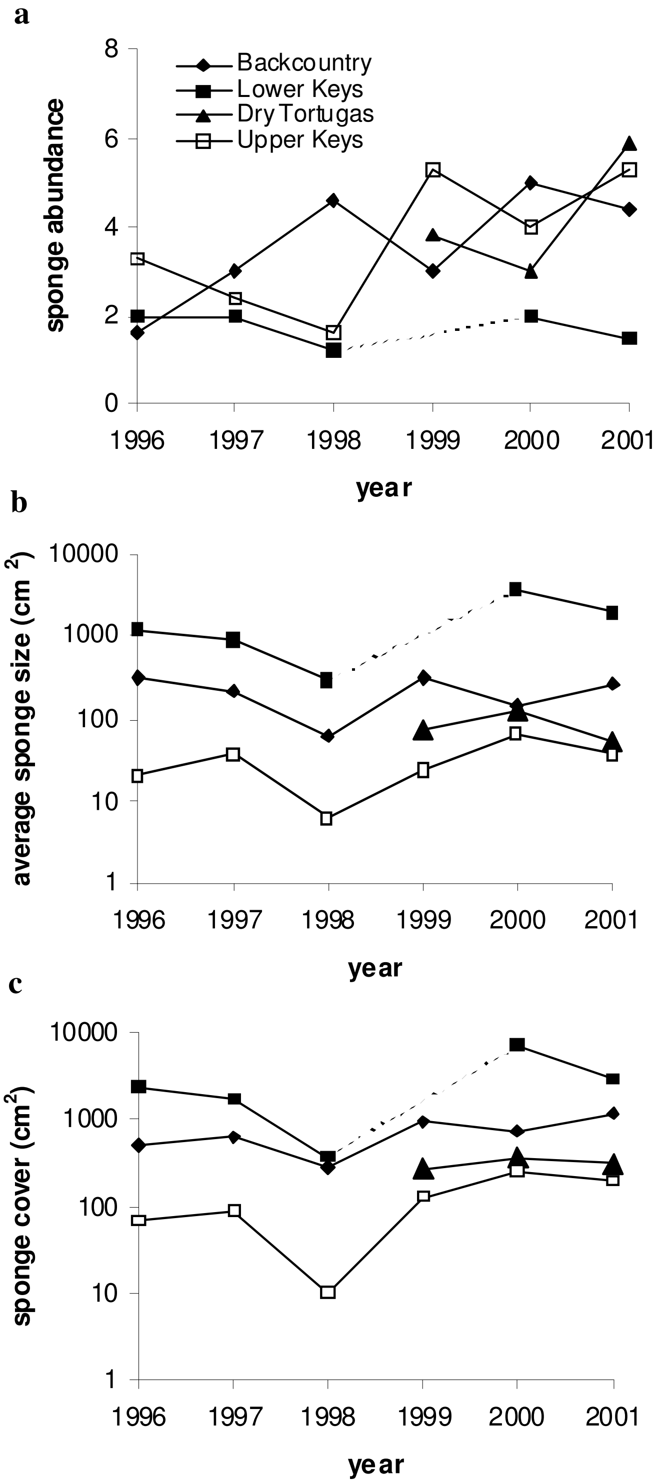
a
sponge abundance
0
2
4
6
8
Backcountry
Lower Keys
Dry Tortugas
Upper Keys
1996
1997
1998
1999
2000
2001
year
b
average sponge size (cm 2)
1
10
100
1000
10000
1996
1997
1998
1999
2000
2001
year
c
sponge cover (cm2)
1
10
100
1000
10000
1996
1997
1998
1999
2000
2001
year

Figure 4

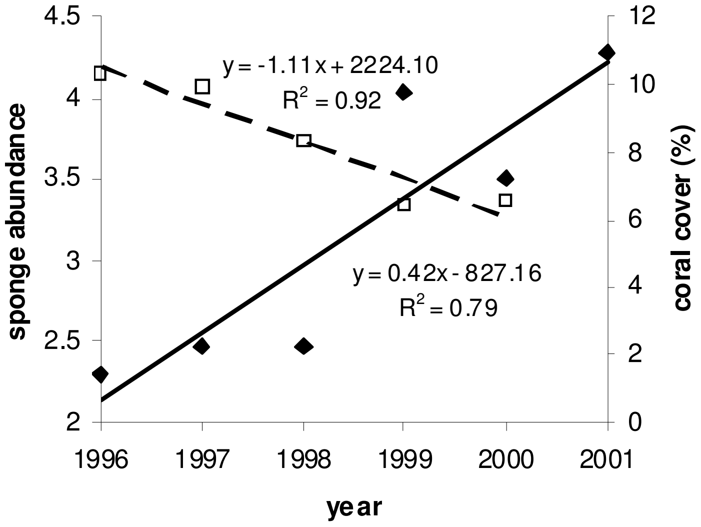
4.5
4
3.5
3
2.5
2
sponge abundance
12
10
8
6
4
2
0
coral cover (%)
1996
1997
1998
1999
2000
2001
year
y = -1.11x + 2224.10
R^2 = 0.92
y = 0.42x - 827.16
R^2 = 0.79

Figure 5

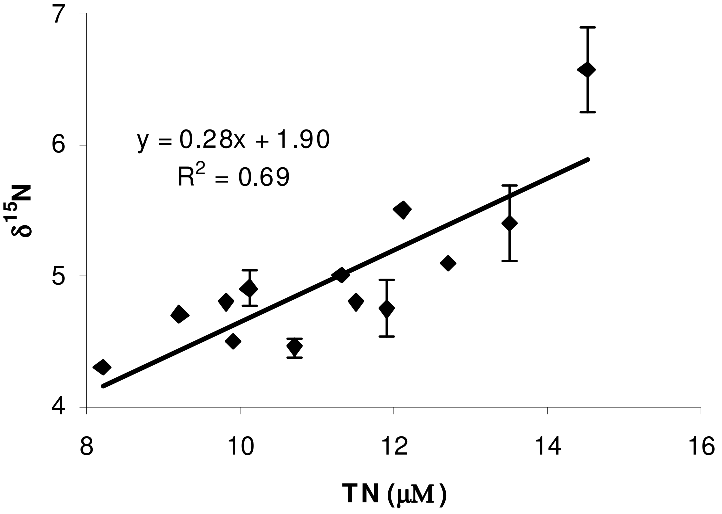

Figure 6

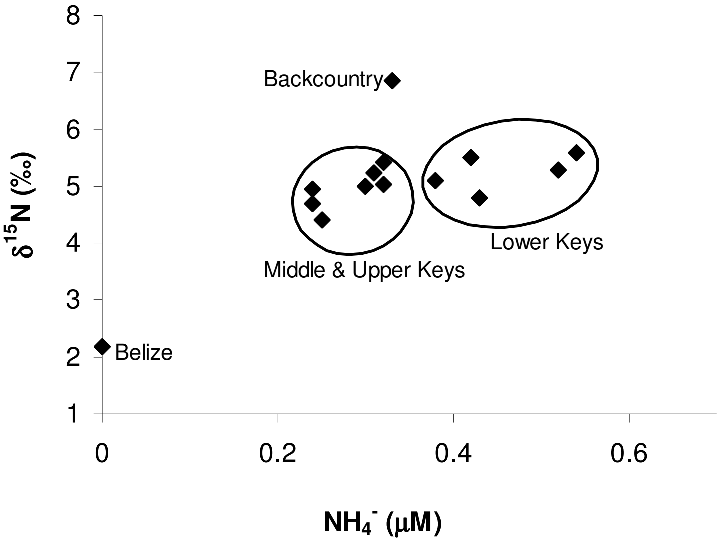
8
7
6
5
4
3
2
1
0
0.2
0.4
0.6
δ15N (‰)
NH4- (μM)
Backcountry
Middle & Upper Keys
Lower Keys
Belize

Figure 7

TABLE 1

Study regions, site names, use of observational (O), video (V) and/or isotope data (I), and list of possible sources and sinks of nitrogen.

Water quality segment	Site Name [a]	Use O/V/I	Speculated nitrogen sources/sinks
Backcountry	Content Keys (H)	O, V, I	Florida Bay, local ODS[b],fluvial and groundwater, nitrogen fixation/denitrification
Tortugas	Black Coral Rock (D)	O, V	Gulf of Mexico, Atlantic Ocean upwelling, Loop Current, nitrogen fixation/denitrification
	Bird Key (D)	O	
	White Shoal (S)	O	
Marquesas	Smith Shoal (P)	O	Gulf of Mexico, Atlantic Ocean, upwelling, nitrogen fixation/denitrification
Lower Keys	Cliff Green (P)	O, V,I	Atlantic Ocean upwelling, Key West - Big Pine Key ODS, ocean outfallsite, groundwater, nitrogen fixation/ denitrification
	Eastern Sambo Deep (D)	O, I	
	Rock Key Deep (D)	O, I	
	Western Head (P)	O, I	
	West Washerwoman (P)	O, I	
	Looe Deep (D)	O	
Middle Keys	Sombrero Deep (D)	O, I	Florida Bay, ODS, Atlantic Ocean upwelling, groundwater, nitrogen fixation/ denitrification
	Alligator Deep (D)	O, I	
	Tennessee Deep (D)	O, I	
	West Turtle Shoal (P)	O, I	
	Dustan Rocks (P)	O	
Upper Keys	Carysfort Deep (D)	O, V,I	Key Largo ODS, Atlantic Ocean upwelling, Florida Current, groundwater, nitrogen fixation/denitrification
	Conch Deep (D)	O, I	
	Molasses Deep (D)	O,	
	Turtle Patch (P)	O	

[a] Site code letters indicate site type identified by CRMP, where H= hardbottom, P= patch reef, D= offshore deep, and S= offshore shallow.

[b] ODS- Onsite Disposal System, includes cesspits, septic systems, and ‘package plants’.

TABLE 2

Summary of sponge parameters and isotope values measured in the field.

Zone	Sponge abundance	Average sponge size (cm^2)	Average cover (cm^2)	δ^{15}N (‰)*
Backcountry	Ave: 3.9 n: 1	Ave: 197 n:1	Ave: 767 n:1	Ave: 6.8 n: 1
Lower Keys	Ave: 2.3 s.d: 0.5 n: 6	Ave: 197 s.d: 235 n: 6	Ave: 420 s.d: 428 n: 6	Ave: 5.3 s.d: 0.3 n: 5
Middle Keys	Ave: 2.7 s.d: 2.5 n: 5	Ave: 77 s.d: 48 n: 5	Ave: 129 s.d: 48 n: 5	Ave: 4.8 s.d: 0.3 n: 4
Upper Keys	Ave: 6.4 s.d: 3 n: 4	Ave: 22 s.d: 6 n: 4	Ave: 89 s.d: 69 n: 4	Ave: 5.1 s.d: .4 n: 3
Tortugas	Ave: 4.1 s.d: 2.6 n: 3	Ave: 35 s.d: 16 n: 3	Ave: 169 s.d: 138 n: 3	N/A
Marquesas	Ave: 5.3 n: 1	Ave: 52 n: 1	Ave: 275 n: 1	N/A
Belize	N/A	N/A	N/A	Ave: 2.2 n:1

* n is the number of sites where sponges were sampled.

TABLE 3

Summary of the studies that fulfilled the requirements of a long-term study, in terms of location, result, and environmental factor.

Author	Location	Occurrence	Outcome
Quinn and Kojis, 1999	US Virgin Islands	1992- no bleached corals; 1993- minor bleaching of *M. annularis*	11 mo. after bleaching began, all colonies had normal pigmentation and no entire colonies dies.
Fitt et al., 1993	Florida Keys	1986-1988; 1987 mass bleaching event	No mortality of *M.annularis* in 1988 compared with 1986; possibly reduced skeletal growth, gonad development/ spawning.
Goreau and Macfarlane, 1990	Jamaica	1987-1988; 1987 mass bleaching event (nearly all corals contained some zooxanthellae)	Almost complete recovery (~95%) only 7 mo. after peak bleaching- 5% showed trace of bleaching; skeletal growth ceased during bleaching
Szmant and Gassman, 1990	Caribbean	1987 bleaching event.	Most corals survived bleaching, but did not complete gametogenesis. Bleached corals had less C and N, and abnormal distribution of zooxanthellae.
Drollet et al., 1995	Tahiti	1993-1994; bleaching episode, elevated seawater temperature and solar UV-B flux	Most corals recovered within six months of initial bleaching; no mortality.
Anthony et al., 1997	Bahamas	1991-1995; various stresses: mass bleaching, sedimentation, encrusting/ boring sponges, and macroalgae overgrowth	Partial/whole coral mortality due to sponges and macroalgae >> sedimentation >> mass bleaching
Hallock and Schlager, 1986	Geologic record	Holocene and older: Excess nutrients	Shifts in reef community from net accretion to net erosion Drowned reefs and platforms are common; Increased bioerosion
Edinger et al., 1998	Indonesia	1980-1995; Land-based pollution, including sewage, sedimentation, nearshore eutrophication, and industrial pollution.	30-60% decrease in coral species diversity. No recovery until stress is removed.
Dustan and Halas, 1987	Florida Keys	1974 -1982; physical disturbance, sedimentation, and disease.	Decreased coral abundance and size from sedimentation and disease as a result of environmental degradation
Grigg, 1995	Hawaii	1955-1977, 1982,1994; local sewage discharge (360x10^6 L/day)	Absent or severely depressed coral and a 6km area was dominated by species that favour raw sewage; recovery occurs only after redirecting pollution