# DISTRIBUTION AND PHOTOBIOLOGY OF SIDERASTREA RADIANS AND THALASSIA TESTUDINUM IN FLORIDA BAY, FLORIDA, USA

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## ABSTRACT

The distribution of *Siderastrea radians* (Pallas) Blainville and photophysiology of its symbiont in Florida Bay, USA, were examined during annual macrophyte surveys in spring 2006 and 2007. *Siderastrea radians* was present in five of the 11 sampled basins in areas with little sediment and low abundance of the seagrass *Thalassia testudinum* Banks ex König. The five basins are located along a northeast-to-southwest transect that also represents a salinity gradient from inshore, predominantly estuarine conditions adjacent to the Everglades, to offshore near-marine salinities adjacent to the Gulf of Mexico. Colony abundance was highest in the basins at the extremes of this physical range, presumably due to higher potential for larval recruitment from external reef source populations. Effective quantum yields, measured in situ by PAM fluorometry, were significantly correlated between *S. radians* and the dominant seagrass *T. testudinum* among all five basins where the two species co-occurred, albeit with a 40% reduction in mean yields of *S. radians*. These findings indicate *S. radians* may function as an alternative eco-indicator species for regions in Florida Bay where *T. testudinum* is absent.

Florida Bay is a shallow lagoonal system located at the land-sea interface between the southern tip of mainland Florida and the Florida Keys. The bay is part of the larger south Florida hydroscape that extends from north of Lake Okeechobee in central Florida to the ridges of the Florida reef tract. Historically, Florida Bay acted as the receiving body for freshwater from Lake Okeechobee that moved southward through the Everglades and mixed with the marine waters flowing in through Florida Keys channels and the open western boundary of the Gulf of Mexico, creating a rich, productive transition zone (Schomer and Drew, 1982). Soft carbonate sediments in the bay support large seagrass beds dominated by Thalassia testudinum Banks ex König (Zieman et al., 1989; Durako et al., 2002). Its dense canopy comprises approximately 92% of the habitat structure in Florida Bay, sustaining a fish and invertebrate community critical to ecosystem function as well as the local economy (Chester and Thayer, 1990; Herrnkind et al., 1994; Butler et al., 1995; Matheson et al., 1999). The annual economic return of the *T. testudinum* habitat in Florida Bay to both fisheries and tourism has been estimated in the millions of dollars for the south Florida region (Robblee and DiDomenico, 1991; Nance, 1994; English et al., 1996).

Over the last century, human development and water management projects have perturbed the natural watershed for Florida Bay via construction of canals, levees, and intensified land use. Diversion of fresh waters towards the Atlantic and Gulf of Mexico, intensified farming and development, and exponential population growth in the latter half of the 20<sup>th</sup> century exacerbated problems by all but eliminating freshwater inputs to the bay and leaving only 50% of the original Everglades system intact (Light and Dineen, 1994). Residual drainage from developed lands continue to enter the bay at low levels in pulses from the canal and levee system, frequently with concentrated nutrient and contaminant loads (Lapointe and Clark, 1992; Brand, 2002). Irregular and patchily distributed rainfall events now contribute up to 90% of the freshwater supply to Florida Bay (Nuttle et al., 2000). Higher average salinities and poor water quality were correlated with a large die-off of *T. testudinum* in western basins beginning in the late 1980s (Robblee et al., 1991). Re-suspension of sediments that increased turbidity and released trapped nutrients were linked to these losses, as were recurrent algal blooms and anoxic conditions that persisted in the bay during the early 1990s (Fourqurean and Robblee, 1999). Concern over the long-term health of Florida Bay and the adjacent Everglades led to the Comprehensive Everglades Restoration Plan (CERP). The primary goal of CERP is to restore south Florida's watershed and ecosystems via habitat and water quality modifications aimed at the re-establishment of natural drainage (www.evergladesplan.org). This requires assessment of the distribution, abundance, and condition of important ecosystem components. We present herein some preliminary baseline information to assist in satisfying these requirements.

As part of CERP monitoring efforts, the Fish Habitat Assessment Program (FHAP), instituted in 1995 following the original seagrass die-off, was expanded from 10 to 22 basins in 2005 (now termed FHAP-SF). FHAP-SF performs annual surveys to monitor trends in macrophyte abundance, distribution, and photobiology along south Florida's (SF) coastal waters, including Florida Bay, as historical drainage pathways are restored (Durako et al., 2002). The dominant macrophyte in this region, *T. testudinum*, is perceived as the best indicator of the health of the bay and its distribution, morphology and photobiology has been extensively studied since FHAP monitoring began in 1995 (Durako et al., 2002; Durako and Kunzelman, 2002; Hackney and Durako, 2004; Landry, 2005; Belshe et al., 2007, 2008).

Although most of Florida Bay has soft carbonate sediments, exposed Pleistocene calcium carbonate deposits constitute large areas of hardbottom in the central portions of many basins (Merriam et al., 1989). In these areas the lack of sediment limits rhizome development in T. testudinum. Thus, T. testudinum surveys provide limited information on community dynamics in these areas and other species that rely on such hardbottom regions may be valuable for understanding wider system function. One taxonomic group largely overlooked in the bay is hard corals. Anecdotal observations during annual FHAP surveys indicated the occurrence of Siderastrea radians (Pallas) Blainville within five of 10 surveyed basins (Durako, pers. obs.). However, no records or publications exist, to the best of our knowledge, describing the abundance or spatial distribution of this coral population in Florida Bay. A small number of peer-reviewed papers report on corals, including S. radians, in this area; however, these studies focused on paleoclimatic records and photophysiological experiments of temperature-induced stress near the Florida Keys channel systems (Swart et al., 1996; Warner et al., 1996; Thornhill et al., 2006). The significance of the S. radians population in Florida Bay is twofold: (1) Their presence in hardbottom areas of basins may allow S. radians to act as a valuable alternate eco-indicator in Florida Bay in areas where *T. testudinum* is typically absent or sparse; and (2) the photophysiology of T. testudinum can be compared to that of the coral endosymbiont, Symbiodinium spp., within *S. radians* as an additional physiological indicator of ecosystem health.

Since 2000, pulse amplitude modulated (PAM) fluorometry has been used to assess the photobiology of *T. testudinum* in a non-invasive manner during annual FHAP surveys (Durako and Kunzelman, 2002; Belshe et al., 2007, 2008). PAM fluorometry is a measure of chlorophyll fluorescence at PSII to indirectly assess the efficiency with which light energy is converted into chemical energy (Schreiber et al., 1986). PSII is considered to be the most sensitive part of the photosynthetic pathway to stress (Becker et al., 1990). This tool may provide early indications that changing environmental conditions—as may occur with restoration efforts in Florida Bay—are beneficial or detrimental to coral ecosystem health (Warner et al., 1996; Hoegh-Guldberg and Jones, 1999; Jones et al., 2000; Jones and Hoegh-Guldberg, 2001; Warner et al., 2002; Hill et al., 2004, 2005; Ralph et al., 2007).

To be used as an eco-indicator, baseline information is needed on population structure including spatial and seasonal dynamics as well as physiological response to shifts in environmental conditions (Carignan and Villard, 2002; Biber et al., 2004). This study describes the distribution, abundance, and chlorophyll fluorescence characteristics of *S. radians* and *T. testudinum* in Florida Bay during 2006 and 2007 FHAP surveys. The specific objectives of this study are: (1) to provide baseline distributional data on *S. radians* populations in Florida Bay and (2) to determine whether the photobiology of this coral population might provide relevant information on ecosystem health in Florida Bay to supplement *T. testudinum* data.

#### Methods

STUDY SITE.—Florida Bay (ca. 25°05′N, 81°45′W) is located at the southern tip of mainland Florida, bordered by the Florida Keys to the south and east, and by the Gulf of Mexico to the west (Fig. 1). The bay is divided into a suite of shallow (ca. < 2 m) basins (see Fig. 1 for basin name abbreviations used throughout this text) by a reticulated network of carbonate mud banks and mangrove islands (Schomer and Drew, 1982; Smith, 2002). Water quality follows an environmental gradient as runoff and flow constraints in the northeast create highly fluctuating and extreme salinity conditions (mean salinity from 1987 to 2007 for Duck Key Basin [DUC] = 30.8 ± 8.9, Southeast Environmental Research Center (SERC), 2002), progressing to more stable marine conditions in the south-central portions of the bay (mean salinity from 1987 to 2007 for Twin Key Basin [TWN] =  $36.2 \pm 4.3$ , SERC, 2002) as mixing with Gulf and Atlantic waters increases. Water quality among adjacent basins can also be strikingly different due to the isolation of waters by mudbanks and mangroves; low tidal flux; and the large role wind can play in directional water movement (Boyer et al., 1997). Sediments are carbonate-based and in the west are deep and nutrient-rich while eastern regions tend to have shallower sediments and more hardbottom (Zieman et al., 1989; Prager and Halley, 1997).

FHAP-SF monitors 11 of approximately 50 basins in Florida Bay which represent the full range in physical-environmental conditions in the bay. *Siderastrea radians* has been observed within five of the basins (Fig. 1) and consequently are the only basins discussed in the context of this study. These basins are located along a northeast-southwest transect that follows the environmental gradients described above (Fig. 1). Each sampled basin was subdivided into 28–30 tessellated hexagonal grids and one station randomly assigned within each polygon, to produce 28–30 stations sampled per basin. This design resulted in systematic random sampling which scales the sampling effort to basin size (Durako et al., 2002). Because sampled basins range in size from 5.8 to 62.4 km<sup>2</sup> (Durako et al., 2002), stations within each basin were sampled systematically over the course of a day (~0800–1700 h) to minimize station-to-station travel time. Stations were located using GPS.

During May 2006 and 2007, eight replicate 0.25-m<sup>2</sup> quadrats were haphazardly placed to score the presence and abundance of *T. testudinum* and *S. radians* at each station. A modified Braun-Blanquet abundance/density scale was used to assess frequency and density within quadrats: 0.1–solitary, with small cover; 0.5–few, with small cover; 1–numerous, but < 5% cover; 2–any number, with 5%–25% cover; 3–any number, with 25%–50% cover; 4–any number, with 50%–75% cover; 5–any number with > 75% cover (Braun-Blanquet,



Figure 1. Florida Bay, FL USA and basins surveyed in the current study. BLK = Blackwater Sound, DUC = Duck Key Basin, EAG = Eagle Key Basin, CAL = Calusa Key Basin, TWN = Twin Key Basin.

1972; Durako et al., 2002). Frequency and density of each species were calculated using the following formulas:

Frequency = # stations where observed/total # of stations;

Density = sum of Braun Blanquet scores/# of quads.

Transect surveys of *S. radians* were conducted in October 2006 at sites where colonies were recorded the previous May. Briefly, line transects were used in place of the Braun-Blanquet method to quantify local densities. This approach is similar to the quadrat method that was found to be the most accurate method available when determining species cover in coral mapping surveys (Jokiel et al., 2005; Leujak and Ormond, 2007). A 50 m transect was established in an east-to-west orientation. Colonies were counted when present within 0.5 m of each transect, equating to 25 m<sup>2</sup> of area covered per station. Data were compared with Braun-Blanquet scores collected in spring surveys.

SPATIAL ASSESSMENT.—Distribution and density maps of both *T. testudinum* and *S. radians* were created in ArcGIS ArcMap v.9.2 according to Landry (2005). Individual sampling events for both species were transformed into shapefiles. For *T. testudinum*, grid surfaces were interpolated from Braun-Blanquet point values using the Inverse Distance Weighted function in the Spatial Analyst extension. This technique is better suited than krigging for dealing with patchy environments. It also is not smooth, meaning it does not ignore true values and does not interpolate beyond maximum or minimum values observed. The Spatial Analyst extension applied a power of two to determine how much weight to assign distant data points. It automatically uses a 12-point variable search radius to interpolate areas without data and was assigned an output cell size of 25 to increase boundary smoothness between areas. Basin outlines were applied as an analysis mask to keep interpolated surfaces within basin boundaries, and surfaces were classified according to Braun-Blanquet values and shade coded to represent the potential range from zero to 100% cover. The distribution of *S. radians* 

was overlayed on *T. testudinum* interpolated surfaces and classified by Braun-Blanquet values using graduated size-coded symbols.

Photobiology.—Chlorophyll fluorescence was recorded in situ using a diving-PAM fluorometer (Walz, Germany). Prior to the application of saturating pulse, minimum fluorescence for the ambient light state (*F*) was measured. This steady-state fluorescence, F, represents the number of reaction centers open in the sample. The sample was then subjected to a pulse of saturating light during which a second fluorescence reading was taken ( $F_m$ ').  $F_m$ ' is the state in which all reaction centers present are considered reduced or closed. Effective quantum yield of PSII ( $\Delta F/F_m$ '), a measure of photosynthetic capacity of light-acclimated tissues, was then calculated ( $\Delta F/F_m$ ').

Apparently healthy *S. radians* colonies and *T. testudinum* short-shoots separated by > 2 m were haphazardly chosen by the diver at each station where they occurred. The instrument's fiber optic end was set at a standard geometry (30° from perpendicular) and distance (5–10 mm) to the dorsal surface of sampled corals and to the middle of the second youngest blade of seagrass short-shoots (n = 5 and n = 6 per station, respectively) using a clear acrylic distance clip. Gain and measuring intensity were minimally adjusted to maintain an *F* of approximately 150–200 throughout the day. Bottom photosynthetic active radiation (PAR) was recorded using a  $4\pi$  quantum sensor held just above the substrate.

#### Results

DISTRIBUTION.—Thalassia testudinum was observed at 97% of stations sampled while S. radians was observed at 10 and 15% of the stations in the 2006 and 2007 surveys, respectively. Thalassia testudinum did not appear to have any major shifts in cover between the two years except for small decreases in mean cover in BLK and TWN (Fig. 2, Table 1). Coral colonies were present only where *T. testudinum* was < 25% of benthic cover and mostly when *T. testudinum* cover was < 5% (Fig. 2). When present, S. radians never covered > 5% of the substratum; densities and cover were greatest in the northeast basins of BLK and DUC and southwest in TWN; lowest frequency of occurrence and % cover occurred in EAG and CAL basins (Table 1). There was no major apparent change in cover between years, however, cover as determined by the Braun-Blanquet method, was low overall in part due to the small size of individual spherical-to-hemispherical colonies, which ranged in maximum diameter from 2.0 cm to 10.0 cm with an average of 4.5 cm. Thus, even though colony frequency may be high in a given sampling area, observed percent benthic cover within a quadrat was usually quite low due to small colony size. Line transects used to reassess station densities of S. radians in October 2006 indicated cover in each basin to be comparable to values measured via the Braun-Blanquet method (Table 1).

Frequency of *S. radians* was also greater in BLK, DUC, and TWN compared to CAL and EAG. DUC had the highest frequency of occurrence at stations surveyed in both years at 27% and 20%, respectively, followed by TWN at 13% and 16% (Table 1). Colonies were rarely observed or absent among stations in both EAG and CAL at 3% and 0% for the consecutive years. It is important to note that poor visibility during 2007 surveys due to rough windy conditions caused sediment re-suspension in addition to persistent algal blooms in some areas. This may have hampered visual assessments and thus lowered overall population estimates for this year. Cover and frequency of *S. radians* among basins tended to be higher where sediment depths were shallow, while *T. testudinum* cover tended to be greater in deeper sediments (Table 1). There was no apparent trend in maximum colony diameter of *S. radians* colonies among basins (Table 1).



Figure 2. Distribution and cover of *Thalassia testudinum* and *Siderastrea radians* in Florida Bay among basins where they mutually occurred during (A) 2006 and (B) 2007 surveys. See Figure 1 for basin names.

Table 1. Benthic surveys of <i>Thalassia testudinum</i> (TT) and <i>Siderastrea radians</i> (SIDR) in 2006 and 2007
using Braun-Blanquet (BB) method. October 2006 transect surveys examined percent cover, and the mean
of maximum diameter (Max Diam) for colonies of S. radians within one station from each basin. SED
represents mean sediment depth for stations where S. radians was present. Because colonies were not
detected in CAL and EAG during 2007, sediment data were not available (indicated by -). Values are
presented as mean (± SD). FHAP: Fish Habitat Assessment Program.

	Spring FHAP								
	TT–BB		SIDR-BB		SIDR	% FREQ		Octobe	er transects
									SIDR Max
BASIN	06	07	06	07	06	07	SED (cm)	% cover	Diam (cm)
BLK	1.34 (1.25)	1.13 (1.23)	0.02 (0.07)	$0.02\ (0.06)$	14	14	1.75 (2.06)	0.64	4.78
DUC	1.37 (0.71)	1.49 (0.64)	0.09 (0.23)	0.01 (0.03)	27	20	3.00 (1.89)	0.30	3.50
EAG	1.46 (0.86)	1.55 (0.68)	0.02 (0.09)	0.0	3	0	_	0.02	4.35
CAL	1.43 (0.79)	1.55 (0.88)	0.02 (0.09)	0.0	3	0	_	0.18	7.75
TWN	2.16 (1.6)	1.84 (1.10)	0.02 (0.05)	0.02 (0.04)	13	16	8.75 (4.34)	0.31	4.42

PHOTOBIOLOGY.—Effective quantum yields ( $\Delta F/F_m'$ ) for both *S. radians* and *T. testudinum* exhibited significant among-basin variability. In 2006, these results were largely driven by the variability in ambient light among basins over the sampling period.  $\Delta F/F_m'$  in both species decreased with increasing bottom PAR (Fig. 3). These trends are not surprising as dynamic photoinhibition (or downregulation) is a typical photosynthetic response to high light, whereas increasing fluorescence yields indicate higher photochemical efficiencies at PSII under reduced light (Hoegh-Guldberg and Jones, 1999; Belshe et al., 2007, 2008).  $\Delta F/F_m'$  values for *S. radians* were typical for corals (Jones et al., 2000; Warner et al., 2002), being approximately 40% of those for *T. testudinum* (Fig. 3), but regression analyses indicated they were linearly related (P < 0.05, r<sup>2</sup> = 0.72) at stations where both species co-occurred (Fig. 4).

In 2007, *S. radians* was not observed in CAL and EAG during photophysiological assessments of *T. testudinum*. Comparisons of mean  $\Delta F/F_m$  were thus limited to



Figure 3. Mean effective quantum yields  $(\Delta F/F_m')$  for *Siderastrea radians* and *Thalassia testudinum* vs mean daily bottom PAR measured among the five basins where *S. radians* and *T. testudinum* co-occurred in 2006. Error bars represent  $\pm$  SD



Figure 4. Regression of *Thalassia testudinum* and *Siderastrea radians* mean effective quantum yields ( $\Delta F/F_m$ ) measured during May 2006 surveys. Error bars represent ± SD

only BLK, DUC, and TWN. *Siderastrea radians* in BLK and TWN exhibited similar patterns to those in 2006 in which mean  $\Delta F/F_m'$  values were 40%–50% of those measured in *T. testudinum* (Fig. 5). However, in DUC, the two species exhibited similar mean  $\Delta F/F_m'$  values. *Thalassia testudinum* in DUC maintained  $\Delta F/F_m'$  values reflecting the same trends in effective quantum yield under varying PAR as seen in 2006. Thus, the change in pattern in 2007 was a result of higher mean  $\Delta F/F_m'$  vs bottom PAR measured in *S. radians* than in the previous year.

#### Discussion

Distribution and abundance of macrophytes in Florida Bay have been extensively characterized since the large die-off of *T. testudinum* began in 1987 (Robblee et al., 1991; Hall et al., 1999; Durako et al., 2002; Fourqurean et al., 2002; Landry, 2005). These large datasets have provided management with a valuable means to assess recent macrophyte dynamics and predict how future water-management alterations under CERP may affect the macrophyte community system-wide. However, other benthic taxa have not been well documented within the bay. This work provides the first distributional assessment and physiological characterization of the dominant scleractinian coral occurring in Florida Bay, *S. radians*.

The presence of *S. radians* was minor compared to *T. testudinum* cover and frequency in the five basins where they co-occurred. However, there was an increase in coral frequency in basins at the most northeastern (BLK and DUC) and southwestern (TWN) extremes of the spatial-physical gradient. Connections between these basins and the Florida Keys reef tract may create a higher potential for larval recruitment from external reef source populations. Once established, local populations may proliferate creating higher densities in these regions compared to the more isolated and interior basins of CAL and EAG. *Siderastrea radians* is a brooding species and releases planulae on a lunar cycle rather than only once per year



Figure 5. Mean effective quantum yields  $(\Delta F/F_m)$  for *Siderastrea radians* and *Thalassia testudinum* vs mean daily bottom PAR measured among the five basins where species co-occurred in 2007. Error bars represent  $\pm$  SD

like most broadcast spawning corals (Szmant-Froelich, 1984; Richmond and Hunter, 1990). This strategy increases potential settlement and recruitment of this species as a trade off for smaller colony size (Szmant, 1986). In addition, brooded planulae settle out relatively quickly (Babcock, 1991), resulting in aggregates of colonies within a limited spatial range. Brooding corals are known to successfully recruit in habitats that are frequently disturbed due to their well-developed planulae, regular larval release throughout the year, and relatively rapid settlement (Bak and Luckhurst, 1980; Babcock, 1991). Local densities thus increase with lower likelihood of widespread distribution. This reproductive strategy is likely advantageous for corals in Florida Bay where high environmental variability and limited hardbottom may greatly impact population distributions.

Long-term survivorship of *S. radians* in the bay may also be affected by changes in sediment depth and re-suspension that may co-occur with altered flow regimes. Lirman et al. (2003) observed that experimental sediment burial of *S. radians* in Biscayne Bay severely impacted growth and mortality. Sedimentation and turbidity both play roles in restricting coral distribution through their effects on the photosynthetic activity of zooxanthellae. Short-term sedimentation significantly reduces effective quantum yields, whereas longer-term or high levels of sedimentation may kill exposed colonies (Philipp and Fabricius, 2003). Turbidity increases effective quantum yields through reductions in irradiance, but results in reduced relative electron transport rates, which may cause stress or mortality in affected corals (Piniak and Storlazzi, 2008). Thus, it may be necessary in the future to assess changes in sediment depths in regions where coral colonies exist as flow regimes are altered. A lack of differing size-frequency distributions among basins suggests colony age was not affecting among-basin responses to previous salinity fluxes and that local basin salinity conditions have not influenced age survivorship. Future monitoring surveys of *S. radians* and more comprehensive assessments of hardbottom regions, outside of those surveyed during FHAP, will better establish the distribution and abundance of this species within Florida Bay.

Thalassia testudinum and the symbiont of S. radians exhibited significantly correlated  $\Delta F/F_m$  in 2006, but to a lesser extent in 2007. Coral colonies in DUC in 2007 exhibited higher than expected  $\Delta F/F_m$  based on previous trends which may have been due to previous days' inclement weather. Prolonged windy conditions may have led to turbid waters along with drifting algal blooms from adjacent basins leading to a decrease in the ambient light field. Under such prolonged conditions, resident symbiotic algae may exhibit a more shade-adapted response. Both species responded similarly with a decrease in quantum efficiencies under increasing ambient light, a ubiquitous response in photosynthetic organisms as they downregulate as a means to avoid high excitation pressure and consequential damage to the photosynthetic apparatus (Hoegh-Guldberg and Jones, 1999; Major and Dunton, 2002). The significantly lower  $\Delta F/F_m$  values in *S. radians* compared to *T. testudinum* indicate different overall photochemical efficiencies between these species in the field. However, photochemical efficiency of PSII does not describe the full capacity of the photosynthetic pathway nor the up-regulation of photoprotective mechanisms (Logan et al., 2007). The disparity in mean quantum yields between the two species may also be affected by gross morphological differences in tissue structure, chloroplast packaging, and effects of multiple scattering (Enríquez, 2005; Enríquez et al., 2005). Under ambient light conditions, the approach by which one species enhances efficiency (i.e., changing the number of light harvesting complexes or overall tissue morphology) may dramatically differ from the other, thus exhibiting overall differences in quantum yields. However, the parallel responses to changes in light availability indicate it would be valuable to continue measuring S. radians as a complement to T. testudinum surveys, especially at sites with marginal water quality or suspected stressors.

Siderastrea radians represents a sessile invertebrate population that has not been previously sampled in FHAP monitoring due to the focus on macrophytic habitat structure (Durako et al., 2002). However, our preliminary fluorescence data suggest that this species can act as an alternative indicator of possible light stress using the same photophysiological assessment tools that have been applied to seagrasses and would account for a very different community of taxa, benthic invertebrates. Holobiont physiology is rather distinct from a seagrass outside of the similarities of their photosynthetic capabilities. As such, coral responses and related thresholds may be very different from *T. testudinum* for many variables including salinity, nutrient loading, and light. As the watershed of Florida Bay changes, *S. radians* may reveal impacts on the bay's organisms that would not be readily apparent by sampling only seagrasses and macroalgae. Furthermore, higher coral abundance in hardbottom regions provides managers with a potential alternative physiological ecoindicator measure when *T. testudinum* is absent (Zieman et al., 1989).

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