Ecological Correlates of Green Turtle (*Chelonia mydas*) Abundance on the Nearshore Worm Reefs of Southeastern Florida

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ABSTRACT

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Juvenile green turtles (*Chelonia mydas*) differ in abundance on nearshore reefs, but why some sites are preferred over others is unknown. Our study had two objectives: to quantify site-specific differences in turtle abundance over time (1 y) and to determine what ecological factors were correlated with those differences. We conducted quarterly surveys on reefs in Palm Beach and Broward Counties, Florida, and compared reef sites with respect to (1) water depth, (2) algal abundance, (3) algal species richness, and (4) fluctuations in reef area caused by sand burial (which kills the algae used as forage by the turtles). Turtles were most abundant on reefs located in shallow water and exposed to bright ambient light. More turtles were also seen at sites where algae were both abundant and composed of many species. Reefs with those characteristics tended to remain uncovered by sand ("stable") for longer time periods. We hypothesize that foraging by turtles on preferred reefs may prevent any one species of algae from dominating the site, making room for others to colonize. If true, then both physical stability (reef exposure time) and biological activity (turtle grazing) may make some reefs more attractive to turtles than others.

ADDITIONAL INDEX WORDS: *Habitat, ecological stability, algal diversity.*

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INTRODUCTION

Nearshore hard-bottom reef habitats (*Anastasia* formations and Sabellariid worm rock reefs) are found in shallow water along Florida's east coast between Brevard and Miami-Dade counties (Kirtley and Tanner, 1968; Lindeman *et al.,* 2009). These habitats are typically found within 200 m of the shoreline and at water depths of ≤7 m. These reefs run parallel to the shoreline and exist as either long tracts or as patches separated by areas of sand (Bush *et al.,* 2004; Kirtley and Tanner, 1968).

Nearshore hard-bottom reef habitats offer shelter for many animals and provide a substrate on which invertebrates and many types of marine algae can attach and grow (Moyer *et al.,* 2003; Zale and Merrifield, 1989). As a result, these reefs support a diverse community of marine flora, invertebrates (*e.g.*, arthropods, cnidarians, bryozoans, sponges), fish, and sea turtles (Lindeman and Snyder, 1999; Lindeman *et al.,* 2009). Nearshore reef habitats are breeding and spawning sites for many marine organisms, but the majority of fishes and sea turtles found on these reefs are juveniles (Baron, Jordan, and Spieler, 2004; Moyer *et al.,* 2003; Musick and Limpus, 1997).

Habitats occupied by green sea turtles (*Chelonia mydas*) change with turtle size and age (Bolten, 2003; Guseman and

Ehrhart, 1990; Musick and Limpus, 1997; Witherington, Hirama, and Hardy, 2012). Green turtles spend approximately 3–5 years in an oceanic stage of development (Reich, Bjorndal, and Bolten, 2007). During this time, they hide from predators in *Sargassum* mats (Carr, 1987; Smith and Salmon, 2009; Witherington, Hirama, and Hardy, 2012) and feed as omnivores, making shallow dives to capture prey near the surface (Bolton, 2003; Salmon, Jones, and Horch, 2004; Witherington, Hirama, and Hardy, 2012). Green turtles recruit to shallow developmental habitats as juveniles at a carapace length of about 25–35 cm (Bjorndal, 1997; Reich, Bjorndal, and Bolten, 2007). Return to coastal waters is accompanied by a gradual dietary shift, as the turtles begin feeding primarily on benthic macroalgae and seagrasses (Bjorndal, 1997). Green turtles are specialized to feed as herbivores, a feeding adaptation that, among marine turtles, is uncommon (Bjorndal, 1997). Juvenile turtles also use nearshore reef habitat for shelter. When resting, turtles often wedge their head and body under ledges present along the reef (Makowski, Seminoff, and Salmon, 2006; Mott and Salmon, 2011; Seminoff, Resendiz, and Nichols, 2002).

Developmental habitats are those occupied by marine turtles for portions of their ontogeny between the juvenile and adult life history stages (Bass and Witzell, 2000; Bjorndal and Bolten, 1997; Bolten, 2003; Meylan, Meylan, and Gray, 2011; Musick and Limpus, 1997). Carr (1987) first used this term with regard to sea turtles when he recognized that most sea turtles only spent a portion of their lives as oceanic creatures and returned to nearshore waters to complete growth to sexual maturity. He used the term "developmental migrations" (Carr, 1980) to

Table 1. *Location, length, and depth where surveys for juvenile green turtles were conducted in this study. Reefs are listed from north to south. The Breakers and Boca Raton reefs are located in Palm Beach County. See Figure 1 for photographs.*

Location	Latitude Range	Longitude	Length (km)	Depth Range (m)
Breakers	26°42′40.7″ N–26°41′59.4″ N	80°01′ W	1.3	2.1–3.4
Boca Raton South	26°19′34.2″ N–26°19′03.3″ N	80°04′ W	1.1	1.2–5.2
Broward North	26°18′55.2″ N–26°18′18.4″ N	80°04′ W	1.2	2.4–4.6
Broward Middle	26°18′18.4″ N–26°17′26.2″ N	80°04′ W	1.6	3.0–6.1
Broward South	26°17′26.2″ N–26°16′52.8″ N	80°04′ W	1.1	4.9–7.0

describe transitions among habitats at different life history stages.

Developmental habitats contain resources required for survival such as food (seagrasses and macroalgae for green turtles) and shelter. Residents (juvenile stage animals) may occupy developmental habitats seasonally (at northern latitudes) or for longer periods (at subtropical or tropical locations). Site fidelity is also common (Hart and Fujisaki, 2010; Makowski, Seminoff, and Salmon, 2006; McClellan and Read, 2009; Meylan, Meylan, and Gray, 2011; Seminoff, Resendiz, and Nichols, 2002). Such areas that contain resources required for daily growth and survival are called home ranges. Thus, developmental habitats are age-specific home ranges.

Previous studies suggest that among green turtles, there is a strong correlation between home range size and the spatial distribution of food (Brill *et al.,* 1995; Makowski, Seminoff, and Salmon, 2006; Mendonca, 1983; Renaud *et al.,* 1995; Seminoff, Resendiz, and Nichols, 2002). Where food resources are spatially concentrated, home ranges are small (0.77–2.88 km^2; Brill *et al.,* 1995; Makowski, Seminoff, and Salmon, 2006; Mendonca, 1983; Renaud *et al.,* 1995). However, at sites where food resources are widely scattered, home range areas are, on average, over 5 times greater (16.62 km^2; Bahia de Los Angeles in the Gulf of California; Seminoff, Resendiz, and Nichols, 2002), forcing the turtles to forage over greater distances. Smaller home ranges may be preferred by juvenile green turtles because less time and energy is required for traveling, leaving more energy for growth. While many studies suggest that food availability is related to growth rates, we know of no studies in which growth rates of marine turtles have been related to foraging (or other) costs. Also, we know of no studies done to examine how juvenile green turtles select developmental habitats or why they may prefer some sites over others.

The goals of this study were (1) to quantify juvenile green turtle abundance on local near shore reefs, (2) to determine if those differences remained seasonally consistent, and (3) to reveal the ecological correlates associated with those differences in turtle abundance. Results show that over 1 year of observations, there were consistent differences between reefs in turtle abundance, and that this variation was correlated with reef depth, algal abundance (proportion of area occupied by any algae), algal species richness (the number of species present), and the length of time that the reef remained uncovered by sand (reef "stability").

METHODS

This study was conducted over sections of shallow (≤7 m) nearshore reef habitat in Palm Beach (Breakers reef, Boca reef) and Broward (Broward North, Broward Middle, Broward South

reefs; Table 1) counties, Florida, U.S.A., during 2010–2012. The Breakers site is located 45 km north of Boca Raton and consists of a continuous reef, 1.3 km long. This site was selected because green turtles are known occupants (Makowski, Slattery, and Salmon, 2005; Makowski, Seminoff, and Salmon, 2006) and because the spatial separation from the other study sites clustered to the south provided an independent measure of seasonal effects on green turtle abundance. The remaining sites were located south of the Boca Raton Inlet (Figure 1).

Turtle Surveys

Each study site was surveyed for turtles using the in-water "Shark Fishing" method (Makowski, Slattery, and Salmon, 2005). Two observers with snorkeling gear were towed slowly (2–4 km/hr) ~5 m behind a small (6 m long) power boat traveling directly over the reef and parallel to the shore. Observers visually scanned the reef directly below them and to their right (starboard observer) or left (port observer) side. When a turtle was located, observers notified the boat operator who recorded the time, water depth (m), species (most often green turtles), and location (latitude and longitude). Sites were surveyed quarterly, weather permitting, during January–March (winter), April–May (spring), June–August (summer), and September–November (fall). We attempted to perform each survey twice, once in a north-to-south (NS) direction and once in a south-to-north (SN) direction. Each directional survey was done at an interval separated by several days or weeks.

We plotted all turtle sightings using ArcMap 10 GIS mapping software to provide a spatial platform on which to view changes in turtle distribution with respect to survey location and season. We used chi-square tests (corrected for continuity) to determine whether turtle abundance differed by study site (Siegel and Castellan, 1988; Zar, 1999). We used the maximum number of turtles observed in one survey direction at each site, then normalized these numbers for a reef length of 1 km. Partitioning was used to determine which sites were responsible for significant differences (Siegel and Castellan, 1988). The normalized numbers were compared with an expected abundance at three sites (Breakers reef, Boca reef, Broward North) where all of the surveys were completed; no analyses were performed at two sites (Broward Middle, Broward South) where due to adverse weather, surveys were incomplete. Chi-square tests (and partitioning) were also used to determine if there were seasonal differences in turtle abundance between these three sites. In all statistical tests, the null hypothesis of no difference from the expected abundance was rejected when $p \leq 0.05$.

We summarized the distribution of turtles observed at each depth, then separated our sample into two portions: those of
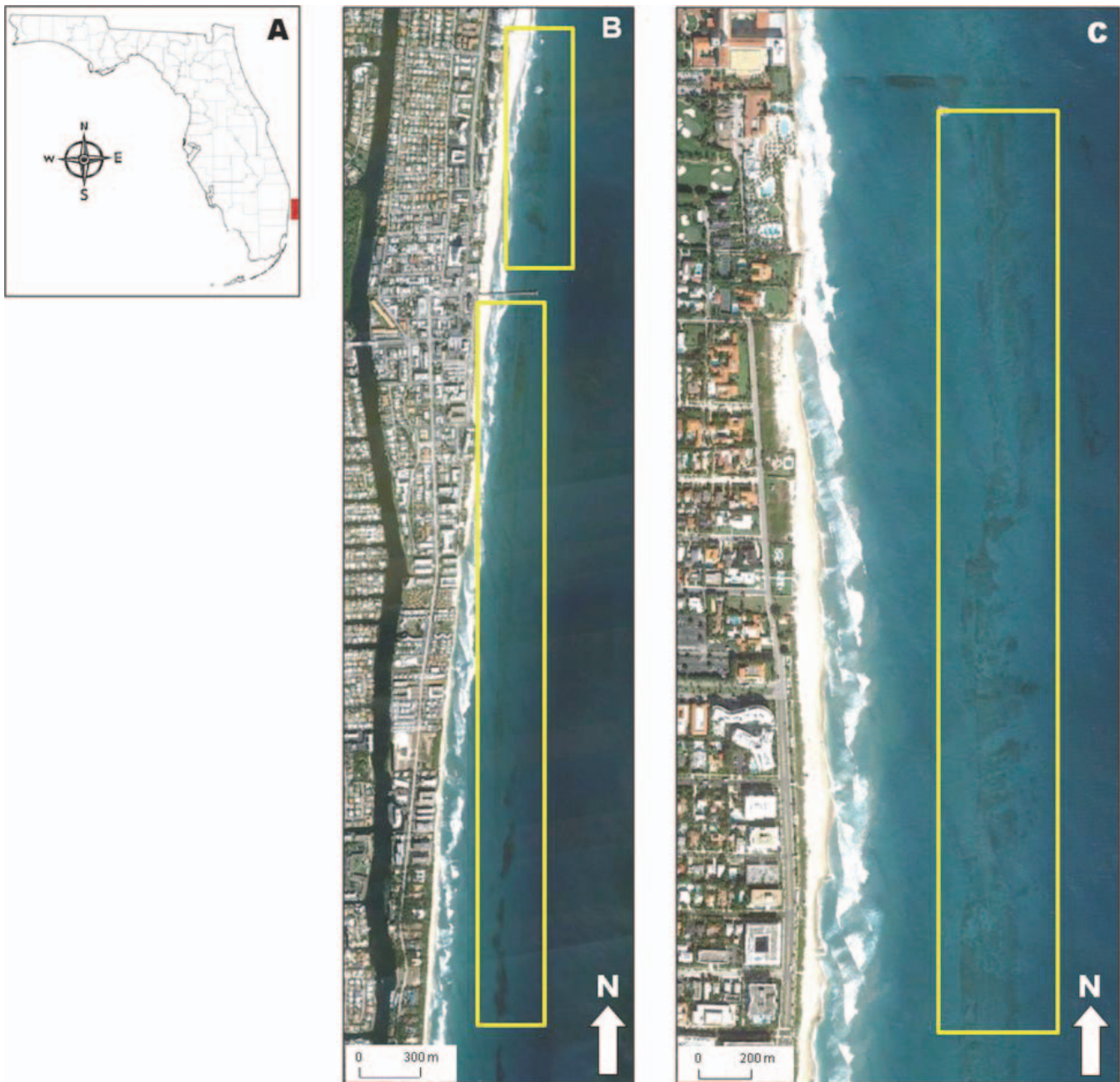
Figure 1. (A) Location of study sites (red) in Palm Beach and Broward Counties. (B) Boca reef and Broward County study sites. (C) Breakers reef site. Darker areas within yellow rectangles are the shallow-water reefs, oriented as streaks in a north–south direction. (Color for this figure is available in the online version of this paper.)

turtles observed at less than or equal to the median depth and those of turtles observed at depths greater than the median. A chi-square test was used to determine if turtle abundance differed significantly from expected equivalence (Siegel and Castellan, 1988; Zar, 1999). The null hypothesis of no difference in turtle abundance between the two depth categories was rejected when $p \leq 0.05$.

Algae Surveys

To characterize the abundance and distribution of algal species, we positioned five transects (labeled T1–T5) in an east–west direction across the north–south oriented Boca Raton reef (Figure 2). We hypothesized that turtle abundance might be correlated with differences in algal density and/or species richness (a count of species, regardless of their abundance;
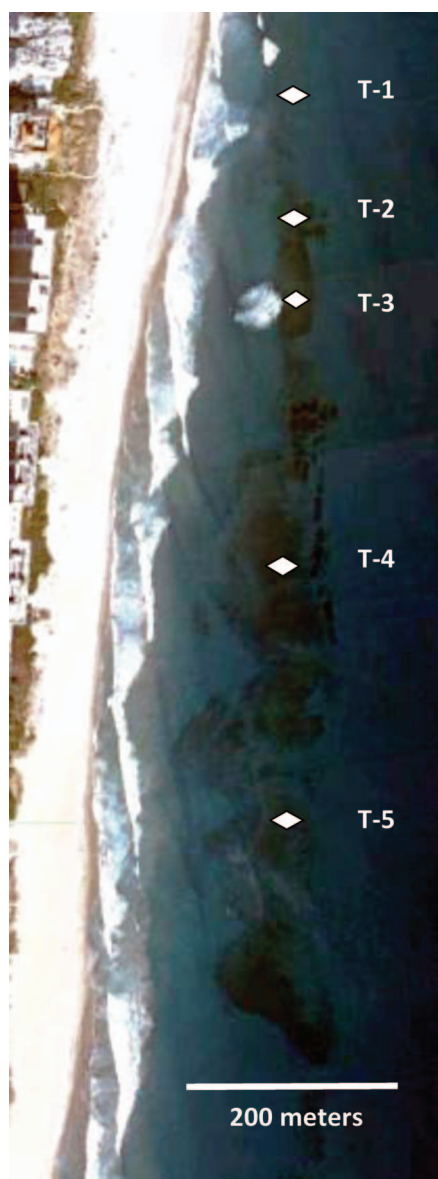
Figure 2. Filled diamonds indicate transect survey site locations (T1–T5) at the Boca Raton reef. Sites were selected based upon differences in turtle densities observed during surveys. See the text for details. (Color for this figure is available in the online version of this paper.)

Colwell and Coddington, 1994). To test that idea, our transect locations were determined by the turtle densities observed during shark fishing surveys. Two transects were done where turtle densities were high (>22 turtles), two where turtle densities were intermediate ("medium", 11–21 turtles), and one where turtle densities were low (≤10 turtles).

Transects were spaced approximately 70–300 m apart with start and end points defined by GPS coordinates. A tape measure placed on the bottom was used to record reef width. The tape measure also served as a guide for the placement of a square of polyvinyl chloride pipe measuring 50 cm long on each

side. The square was placed on the bottom at 10 locations along the guide, spaced apart by 2–3 m within each transect. Water depth was measured at each location using an Oceanic Veo 1.0 dive computer. Algae within the square were photographed at a distance of 60 cm from above using either a SeaLife Mini 2 or a Nikon E4300 digital camera contained within an underwater housing.

Algae were identified and their abundance estimated from the 10 photographs within each transect. Algae were classified as one of three types (green algae or Chlorophyta, brown algae or Phaeophyta, red algae or Rhodophyta) and one functional group (turf algae; Littler, Littler and Taylor, 1983). The latter refer to a multispecies assemblage of other types characterized by their filamentous structure and low height (≤10 mm). The abundance of all algae was estimated using the "ACFOR" scale, which stands for: 5, abundant [81–100%]; 4, common [61–80%]; 3, frequent [41–60%]; 2, occasional [21–40%], and 1, rare [1–20%]; (Crisp and Southward, 1958; Simkanin et al., 2005). We added "0" (not present) to photos where none of these specimens were seen.

We used the 10 ACFOR abundance scores for each transect to determine (1) whether each algal type was equally abundant across the five transects, and (2) whether the transects differed from one another in their overall (total algal abundance) scores. Both analyses were done using Kruskal-Wallis tests (Zar, 1999). In all cases, our null hypothesis was that there were no differences in algal abundance. That hypothesis was rejected when test probabilities (H statistic) were ≤0.05.

Where possible, we identified algae to species to obtain a measure of species richness. These data came from the quadrat photographs. We also took some algae samples during surveys to identify epiphytic algal species not visible in the photographs. Identification to species also made it possible to compare our findings with previous studies where lavage data were used to document the ingestion of specific algal food sources.

Reef Area Mapping and Stability Measurements

We measured reef area from calibrated aerial images (obtained from the Palm Beach County Department of Environmental Resource Management) made once annually between 2000 and 2011 to determine whether reef stability, defined as a change in reef area through time, varied significantly among the nearshore reefs in Palm Beach County. Our measure of change was the percentage change in reef area from one year to the next, except for one pair of comparisons (2001 to 2003) where no aerial imagery was available for 2002. We categorized reef stability as "low" if at any time across sample years that reef experienced >250% change in area (whether positive [increased area] or negative [decreased area]), "medium" if it experienced a 125–250% change, and "high" if that reef experienced <125% change.

The county conducts aerial imagery missions once annually. (Copies may be requested from the county.) Imagery is obtained from low-flying planes during the summer because weather conditions are calm and water clarity is best for reef visibility. The county contracts with the Department of Geosciences at Florida Atlantic University (FAU) to map reef area. It also specifies requirements for flights (tide level, time of day, cloud

Table 2. *Reef segments in Palm Beach County used for analysis of annual changes in area, listed from north to south.*

Reef Segment	Location
Palm Beach	11.0 km N of Palm Beach Inlet
Breakers reef	9.2 km S of Palm Beach Inlet
Boynton Beach	12.7 km N of the Boynton Inlet
Boca Raton North	4.6 km N of the Boca Raton Inlet
Boca Raton South	2.1 km S of the Boca Raton Inlet

conditions, and water clarity). These procedures are effective for recording reef dimensions at water depths up to $\sim$9 m and at a resolution of $\leq$30 cm.

A completed geodatabase was obtained from FAU for the years 2000–2001 and 2003–2009, and maps were added for 2010 and 2011 using the methods set forth by the FAU Department of Geosciences for digitizing reefs (Pitti, 2011). We determined how reef area changed annually by digitizing polygons (using ArcMap 10 GIS software) on top of each reef's image. ArcMap calculated reef area (in hectares) automatically when the last point of each polygon was digitized. That value was stored in the attribute table of the map.

Since some nearshore reef structures were not continuous, we digitized several polygons within one reef location. We obtained the calculated reef areas from ArcMap for each of the individual polygons and summed them to yield one value for the reef section of interest.

We divided the entire Palm Beach County reef tract into five segments (Table 2) and analyzed each for changes in reef area over time.

RESULTS

We saw 351 juvenile green turtles, some of which were observed repeatedly (as determined by the location of scars, barnacles, or wounds on the flippers or carapace). The majority of the turtles were seen feeding on the reef; the remainder were swimming, breathing at the surface, or resting on the bottom. Three turtles had flipper tags, but we were never close enough to read the tag numbers. Though most of sightings were green turtles, one hawksbill (*Eretmochelys imbricata*; Breakers) and one Kemp's ridley (*Lepidochelys kempii*; Broward Middle) were also observed. On surveys performed during the nesting season, three adult green turtles (Broward South) and one adult loggerhead (*Caretta caretta*; Breakers) were observed.

Turtle Abundance

Turtle abundance varied at the three sites (Breakers reef, Boca reef, and Broward North reef) where surveys were complete (Table 3). The number of turtles per kilometer observed at each site and normalized for reef length (29, 77, and 44, respectively) differed significantly from an expected abundance (of $n = 50$ turtles; $X^2 = 24.12$, 2 degrees of freedom [df], $p < 0.0001$). Partitioning revealed that turtle abundance at the Boca Raton site was significantly greater than turtle abundance at the Breakers reef and Broward North sites ($X^2 = 21.07$, $p < 0.0001$) but that differences in turtle abundance between the Breakers reef and Broward North site did not achieve significance ($X^2 = 3.08$, $p = 0.08$).

The number of turtles observed during each season (winter, 44; spring, 48; summer, 57; fall, 26; Table 3) differed from an expected average abundance ($n = 44$; $X^2 = 11.63$, 3 df, $p = 0.009$). Partitioning revealed no significant differences in turtle abundance between the winter, spring, and summer seasons. However, significant differences were found between the summer (greater than expected) and fall (less than expected) seasons ($X^2 = 11.58$, 1 df, $p < 0.001$).

Turtles were observed at depths between 1.2 and 7 m, with the median value of 4.0 m. Most were seen at depths between 1.8 and 4.6 m (Figure 3). The number of turtles observed at shallow depths (1.2–4.0 m, $n = 265$ turtles) significantly exceeded the number observed at deeper depths (4.2–7.0 m, $n = 86$; $X^2 = 47.8$, 1 df, $p < 0.0001$), when compared with equivalence.

Algae Surveys

The green, brown, and red algal types differed significantly in abundance between transects, but there were no compa-

Table 3. *Numbers of turtles observed during seasonal in-water surveys at five reef locations conducted during 2010–2012. NS and SN indicate the direction travel during each survey. Totals observed are the largest counts (bold) made during a survey at any one location during any one season. Turtles/km corrects for differences in reef length (See Table 1) for the Breakers, Boca reef, and Broward North sites where surveys in both directions were completed. A dash (—) denotes reef locations where surveys were incomplete.*

Reef Location	Winter (Jan–Mar)	Spring (Apr–May)	Summer (June–Aug)	Fall (Sept–Nov)	Totals Observed[a]	Turtles per km
Breakers						
NS	6	5	**12**	2	**37**	**29**
SN	**11**	**9**	4	**5**		
Boca South						
NS	10	16	18	11	**85**	**77**
SN	**16**	**24**	**33**	**12**		
Broward North						
NS	6	6	**12**	**9**	**53**	**44**
SN	**17**	**15**	5	5		
Broward Middle						
NS	14	10	9	10	43	
SN	12	—	—	—	12	
Broward South						
NS	7	3	4	1	15	
SN	8	—	—	—	8	

[a] Seasonal totals (using the largest count [in bold]) observed for the Breakers, Boca, and Broward North reefs) are winter, **44**; spring, **48**; summer, **57**, fall, **26**.
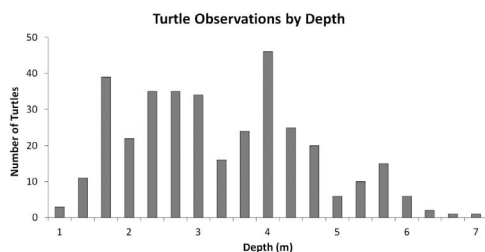
Figure 3. Number of observed turtles ($n = 351$) at all sites, as a function of water depth.

rable statistical differences in turf abundance among the transects (columns, Table 4). Total algal abundance scores for transects T1–T4 were statistically identical, but algal abundance in transect T5 was significantly lower than in all other transects (rows, Table 4). The most abundant algal types were Chlorophyta (total abundance score = 155) and turf (153), followed by Rhodophyta (102) and Phaeophyta (90; Table 4).

Rhodophyta were the most species rich group of algae present, followed by Chlorophyta and Phaeophyta (Table 5). Species richness did not differ statistically among the transects compared with an expected average ($X^2 = 5.78$, 4 df, $p = 0.22$). Nevertheless, the number of species found in Transect T5 was less than half of the number found in all of the other transects.

The dominant algae were *Halimeda* spp. (type: Chlorophyta) and *Heterosiphonia* sp. (type: Rhodophyta). Other common algae genera present in transect locations and identified from photographs included *Dasycladus vermicularis*, *Chondria* sp., *Crouania* sp., *Dasya* spp., *Galaxaura* sp., *Hydropuntia* sp., *Hypnea* sp., *Dictyota* spp., and *Padina* sp. Epiphytic algae were present on collected samples of larger algae. These were identified as *Ceramium* spp., *Jania adhaerens*, *Laurencia* spp., and *Polysiphonia* spp.

Reef Area Mapping and Stability

Reef stability was measured by the percentage change in the available area of the reef. Between date pairs, the reef tracts

Table 4. *ACFOR abundance scores at the Boca reef, analyzed separately for each algal type and the turf functional group (columns), and for all algal summed by abundance score in each transect (rows, T1–T5). See Methods for details. Abundance scores for each algal type differed significantly among transects (by a Kruskal-Wallis test, 4 df) except for turf, which showed no statistical differences in abundance (n.s.). Summed abundance for all algal types was statistically similar in Transects T1 through T4 but was significantly lower in Transect T5 than in the other transects (H = 36.65, p < 0.001, 4 df). See text for further details.*

Transect	Chlorophyta	Phaeophyta	Rhodophyta	Turf	Range (median)
T1	38	16	16	29	16–38 (27.0)
T2	23	25	32	32	23–32 (27.5)
T3	41	25	24	29	24–41 (32.5)
T4	45	16	19	35	19–45 (32.0)
T5	8	8	12	28	8–28 (18.0)
H	35.69	15.04	19.25	3.36	
P	<0.001	<0.01	<0.001	n.s.	

Table 5. *Numbers of algal species identified by type from 10 photographs taken along each of the five Boca Raton reef transects. At two transect locations (T2, T3) turtle densities were high (>22 turtles), at two (T1, T4) turtle densities were medium (11–21 turtles), and at one site (T5) turtle densities were low (≤10 turtles).*

Transect	Turtle Density	Chlorophyta	Phaeophyta	Rhodophyta	Species Total
T1	Medium	7	2	11	20
T2	High	5	3	11	19
T3	High	7	3	12	22
T4	Medium	6	2	11	19
T5	Low	2	1	6	9

north of the Boca Raton Inlet, the Boynton Beach Inlet and the Palm Beach Inlet experienced the most variation in reef area over time, exhibiting minimally one period of substantial change (≥125%) in reef area between 2001 and 2010 (Table 6). The Breakers and Boca Raton reef tracts exhibited the least change (greatest stability) in available area during observations (Table 6).

DISCUSSION

Results of this study reveal that turtle abundance on nearshore reefs varies significantly by location and season, and that this variation is correlated with habitat characteristics such as water depth, algal abundance and species richness, and reef area stability.

Turtle Abundance on Shallow Reefs

We observed more turtles at or below median water depths (4.0 m; Figure 3). This pattern could be a function of light availability, which in marine habitats is in part determined by water depth (Dennison, 1987; Dennison *et al.*, 1993; Markager and Sand-Jensen, 1992). Macroalgae, the primary food source for turtles on the reefs, are photosynthesizing organisms that rely on exposure to sunlight for growth and survival.

Predator avoidance and size class may also explain the attraction of small juvenile green turtles to reefs located in shallow water. Shallow water may offer protection from predators such as sharks (Bresette, Gorham, and Peery, 1998; Heithaus *et al.*, 2005; Musick and Limpus, 1997). Heithaus *et al.* (2005) found that juvenile green turtles in Shark Bay, Australia, were most abundant in shallow nearshore water and mangrove areas while adults were more abundant in deeper off-shore waters also inhabited by tiger sharks. Bresette *et al.* (2010) found the same water depth–size distribution pattern in green turtles residing near the Marquesas Keys, an area also inhabited by tiger sharks. Juvenile turtles are more vulnerable to attacks by large predators than adult turtles, and shallow nearshore reef habitats may afford them some protection from large predators that cannot maneuver in shallow water.

The abundance of juvenile green turtles in nearshore reefs showed a distinct seasonal pattern characterized by near-uniform turtle densities during the winter, spring, and summer and a decline in the fall (Table 3). This pattern differs from the summer peak in turtle abundance documented for shallow-water lagoon habitats in SE Florida (Bresette, Gorham, and Peery, 1998; Ehrhart, Redfoot, and Bagley, 2007). Turtles in lagoons usually depart for oceanic waters in late fall, when

Table 6. *Changes in reef area (ha) and the percentage of change (in parentheses) for the reefs located in Palm Beach County (see Tables 1 and 2 for their locations). Values show comparisons to the previous year except for 2003, which is compared with 2001, as no imagery was available for 2002. Positive values represent an increase, while negative values indicate a decrease in area. Bold values indicate a pronounced change (≥125%) compared with the previous year. A dash (—) denotes reef sections that were not mapped in 2010 and 2011.*

Year	S Boca Reef	N Boca Reef	Boynton Inlet	Breakers Reef	Palm Beach
2000	4.8	0.7	25.4	48.1	28.2
2001	4.8 (0)	1.0 (37.7)	24.6 (−3.4)	49.8 (3.5)	19.9 (−29.4)
2003	4.4 (−8.5)	0.6 (−36.5)	8.9 (−63.9)	49.3 (−0.9)	10.9 (−45.5)
2004	4.5 (2.6)	0.3 (−45.3)	**25.0 (181.7)**	49.9 (1.2)	7.8 (−27.9)
2005	3.2 (−28.9)	**0.9 (179.0)**	34.2 (36.9)	56.2 (12.7)	**50.2 (540.9)**
2006	6.4 (99.3)	**4.3 (356.9)**	37.8 (10.4)	60.3 (7.2)	44.2 (−12.0)
2007	3.6 (−44.1)	2.4 (−44.6)	30.4 (−19.5)	50.1 (−16.9)	33.0 (−25.5)
2008	5.3 (48.0)	2.5 (4.2)	21.4 (−30.0)	45.6 (−9.0)	39.6 (20.1)
2009	5.9 (10.7)	0.8 (67.0)	5.2 (−75.6)	70.8 (55.3)	23.4 (−40.91)
2010	5.6 (−5.3)	—	—	75.6 (6.9)	—
2011	5.8 (4.9)	—	—	72.7 (−4.0)	—

temperatures can decline rapidly (Milton and Lutz, 2003; Witherington and Ehrhart, 1989). By doing so, they avoid the risk of "cold stunning" (Milton and Lutz, 2003; Morreale *et al.*, 1992; Schwartz, 1978) and move into habitats where temperatures remain higher and fluctuate less (Epperly, Braun, and Veishlow, 1995). The turtles return to the lagoon and achieve peak abundance during the summer months (Inwater Research Group, Inc., 2010; Mendonca and Ehrhart, 1982).

At our study sites, the turtles were seasonally abundant except during the fall (Table 3). Why that decrease should occur is unknown. The fall season is when wind and wave action increase, reefs are more likely to experience greater scouring and/or increased probability of covering by sand, and both are associated with seasonal storms (Table 6; Lindeman *et al.*, 2009). A shortening day length during the fall may also reduce algal growth and abundance, forcing the turtles to seek alternative habitats for food. More studies on the seasonal movements of turtles toward or away from shallow oceanic reef sites are needed to fully understand the underlying cause(s) of these movements.

Algal Abundance

Algae surveys at the Boca reef revealed an abundance of macroalgae that have been previously documented as forage for juvenile green turtles (Table 7). These algae include *Hypnea* sp., *Gelidium* spp., and *Halimeda* spp. (Wershoven and Wershoven, 1992); *Acanthophora* sp., *Caulerpa* spp., *Ceramium* spp., *Gelidium* spp., *Laurencia* sp., and *Padina* sp. (Jones *et al.*, 2005); *Gelidium* spp., *Ceramium* spp., *Chondria* spp., *Dasya* spp., *Jania* sp., and *Ulva* spp. (Holloway-Adkins, 2001,

2005); *Acanthophora* sp., *Dictyota* spp., *Jania* sp., and *Dasycladus vermicularis* (Makowski, Seminoff, and Salmon, 2006). In those previous studies, Rhodophyta were the most common algal type consumed (Table 7). Turtles at the Boca reef site were often observed foraging on turf algae and Rhodophyta species, including the abundant *Heterosiphonia gibbesii*, a Rhodophyta species not previously documented as a food source for green turtles in Florida.

Multispecies assemblages of turf algae were consistently and uniformly abundant at all of our transect locations (Table 4). Turtles were often observed feeding on turf algae both in this and in other studies on juvenile green turtles (Gilbert, 2005; Holloway-Adkins, 2001; Lindeman *et al.*, 2009; Table 7). The majority of turf algae at our study site consisted of both Rhodophyta and Chlorophyta algae species. Turf algae are adapted to flourish in stressed environments such as areas close to shore exposed to wave action and storm activity (Airoldi, 1998; Cheroske, Williams, and Carpenter, 2000), as well as areas with high grazing pressures (Hay, 1981; Littler, Littler, and Taylor, 1983; Steneck and Dethier, 1988). Turf algae are also able to reestablish quickly, displaying rapid growth after periods of covering by sand or disturbance by grazers (Cheroske, Williams, and Carpenter, 2000; Littler, Littler, and Taylor, 1983). These characteristics suggest that turf algae probably represent an abundant and usually stable food source for foraging juvenile green turtles, one that can thrive under conditions that other groups of algae cannot endure. At the same time, turf algae abundance *per se* seems relatively unimportant in determining which areas of the reef are preferred by the turtles (Table 4).

Table 7. *The number of algal species identified in six studies by lavage and direct observations on foraging juvenile green turtles. All studies were done on shallow reefs present along the SE coast of Florida. Numbers from this (current) study are species that were identified from transect photographs and by samples collected during transect surveys. The abundance of algae species within each algal type reported here is consistent with the data found in the previous studies.*

Reference	Total Species	Chlorophyta	Rhodophyta	Phaeophyta
Wershoven and Wershoven (1992)	9	2	6	1
Holloway-Adkins (2001)	32	5	23	4
Jones *et al.* (2005)	14	3	10	1
Gilbert (2005)	25	5	16	4
Holloway-Adkins (2005)	16	4	11	1
Makowski, Slattery, and Salmon (2005)	12	5	5	2
Current study	28	8	17	3

The Rhodophyte, *Gracilaria mammillaris*, was absent from all sampling sites in the Boca Raton reef location. This species has been documented as a preferred food item for juvenile green turtles found on reefs in Brevard (Holloway-Adkins, 2005), Palm Beach (Makowski, Seminoff, and Salmon, 2006), and Broward (Wershoven and Wershoven, 1992) Counties, Florida. *Gracilaria mammillaris* may not be present at the Boca reef site, or it may be present during seasons other than the summer, when we did our algal survey. Previous studies acknowledge that seasonal changes in algal abundance exist (Lindeman *et al.*, 2009; Lirman and Biber, 2000; Riegl *et al.*, 2005). However, we found no studies that documented any seasonal patterns of abundance for algal species at the Boca Raton reef site.

Ecological Effects of Grazing by Marine Turtles

We found a correlation between where turtles were most abundant on the reef and where algae were both most abundant (Table 4) and species rich (Table 5). Previous studies suggest that these circumstances might involve a positive feedback loop between the foraging activity of predators (the turtles) and the settlement and growth activities of their prey (the algae). Briefly, these studies show that predator "cropping" can enhance prey abundance through a variety of effects: by reducing interactions between dominant and less competitive prey species, by opening space on the reef for new recruits, and by reducing the unanticipated effects of "overgrowth." Such broad-scale considerations require an understanding of the resource requirements of all of the interacting species, as well as each species' impact on the abundance and distribution of those resources (Leibold, 1995).

These positive effects, unfortunately, are now seen in reverse (Bjorndal and Jackson, 2003), since the decline of marine turtle populations caused by humans has had serious impacts on both the turtles and the resources that they consume. We describe these below.

As a consequence of the historic decline of Caribbean green sea turtle populations, the general health of their primary food, the seagrass *Thalassia testudinum,* has declined (Bjorndal and Jackson, 2003). Historically abundant green turtle populations maintained the health of seagrass populations, since constant grazing kept productivity and overall quality of the resource high. However, when green turtle populations plummeted, seagrass blades grew too tall and blocked sunlight, caused self-shading that in turn led to hypoxia, heightened root decomposition in the sediment, and increased susceptibility to pathogens. The result was a die-off of many seagrass beds (Jackson *et al.*, 2001; Bjorndal and Jackson, 2003). Clipping experiments over a 16 month period were done to simulate foraging by historically dense populations of green turtles. These resulted in compensatory plant growth without a decline in blade or rhizome biomass, as well as significantly higher energy and higher nitrogen and phosphorus content in the shortened, younger blades (Moran and Bjorndal, 2005, 2007).

The hawksbill example may more closely approximate conditions described in this study where turtles feed on sessile reef organisms. Hawksbill sea turtles feed primarily on sponges, organisms that contain glass-like supporting elements (spicules) that most other animals cannot ingest without injury (Meylan, 1988; Meylan, Meylan, and Gray, 2011). Sponges are prolific organisms and are often important competitors for reef space (Bjorndal and Jackson, 2003). A direct effect of hawksbill predation on sponges is control of the sponge population. An indirect effect is the maintenance of reef diversity, since when sponges are consumed, space is made available for other reef species, such as corals, to attach and grow. Hawksbill predation on aggressive sponge species also promotes competition among less competent sponge competitors, with the result that species diversity is increased (Leon and Bjorndal, 2002; van Dam and Diez, 1997). However, historic declines in hawksbill sea turtle populations throughout the Caribbean have led to less predation pressure on the most competitive sponge species. Corals must then compete against aggressive sponge species for space and resources on the reef. The end result has been coral die-offs and an overall decrease in reef species diversity (Bjorndal and Jackson, 2003).

Correlations between Reef Stability and Turtle Grazing

Our study revealed an interesting correlation between turtle abundance and reef stability. The Breakers and Boca Raton reef sites exhibited relatively little change in reef area over the observation period of 11 years (Table 6). Juvenile green turtles have been documented on these reefs in previous studies in numbers similar to what we found in this study (Jones *et al.*, 2005 for the Boca reef site; Makowski, Slattery, and Salmon, 2005 for the Breakers site). Those results suggest that turtles tend to be found in greatest abundance on reefs that are infrequently covered by sand, and therefore show little change in reef area over time. Those reefs should represent favorable sites because they retain their algal colonies.

Conversely, the reef tracts north of the Palm Beach Inlet and north of the Boca Inlet showed greater fluctuations in area over time (Table 6). The most dramatic changes occurred between 2004 and 2006, which were strong storm years for Florida. In 2004, the east coast of Florida experienced hurricanes Charley, Frances, Ivan, and Jeanne. In 2005, hurricanes Ophelia, Wilma, and Katrina, as well as tropical storm Tammy, also affected Florida's east coast. During these years, the reef tracts north of the Palm Beach Inlet and north of the Boca Inlet gained reef area, as new reef was exposed. There was a subsequent, drastic decline in reef area in both locations in the years that followed. While the Boca Raton reef showed a small increase in area during 2006, it soon returned to its original state (Table 6).

Reef stability should be an important factor when considering whether a given nearshore habitat is suitable for juvenile green turtles. Abundance and some measure of species diversity in ecological communities, both marine and terrestrial, are decidedly affected by different levels of habitat disturbances (Connell, 1978; Dayton, 1971; Death and Winterbourn, 1995; Paine and Levin, 1981; Robinson and Minshall, 1986; Sousa, 1984). Previous studies have arrived at the same basic conclusion: the number of species present declines in areas of high disturbance and low stability because species are unable to reproduce fast enough to combat disturbance-related increases in mortality (Wootton, 1998).

Habitats that exist in areas of low disturbance are also at risk of species decreases because they may be dominated by a small number of effective competitors that displace other species (Death and Winterbourn, 1995; Wootton, 1998). However, habitats exposed to "intermediate" levels of disturbance often have higher measures of species diversity and richness (Death and Winterbourn, 1995; Paine and Levin, 1981; Sousa, 1979; Wootton, 1998). Intermediate disturbance levels apparently encourage species diversity. The effects of habitat disturbance are often seasonal (Robinson and Minshall, 1986). The diversity of intertidal and nearshore benthic organisms is increased by other seasonal disturbances, such as wave action, grazing, and the movement of nearshore rocks and boulders (Dethier, 1984; Lubchenco, 1978; Paine and Levin, 1981; Robinson and Minshall, 1986; Sousa, 1979). In terrestrial habitats, the effects of occasional fire and fallen trees encourage plant species diversity (Connell, 1978; Keeley *et al.*, 1981; Sousa, 1984).

We hypothesize that at sites where green turtles were most abundant (Breakers and Boca Raton reefs), such an intermediate disturbance pattern may be important. Both sites can be characterized as experiencing relatively little physical disturbance due to wave action from storms or sand coverage during the last 11 years (Table 6). But at both sites the feeding activities of many green turtles may have prevented any one algal species from dominating available space. Preferred algal food was present at both sites (Table 7); at the Breakers site, preferred algal food was actually consumed by juvenile green turtles (Makowski, Seminoff, and Salmon, 2006).

CONCLUSIONS

This study for the first time seeks to understand why more green turtles are found over some reefs than others. Our observations in Florida waters suggest that reefs preferred as developmental habitats by juvenile green turtles may be characterized by two factors: physical stability through time, as well as an abundant supply of different species of algal prey. That abundant supply may be maintained by the grazing activity of the turtles. However, our conclusions are based upon correlation, not causation, and remain to be tested experimentally. We hope that the ideas presented here lead ecologists in the future to test the validity of these conclusions with well designed and controlled experiments.

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