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ORIGINAL ARTICLE

Taxonomic distinctness in the diet of two sympatric marine turtle species

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Abstract

Marine turtles are considered keystone consumers in tropical coastal ecosystems and their decline through overexploitation has been implicated in the deterioration of reefs and seagrass pastures in the Caribbean. In the present study, we analysed stomach contents of green (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) harvested in the legal turtle fishery of the Turks and Caicos Islands (Caribbean) during 2008–2010. Small juveniles to adult-sized turtles were sampled. Together with data from habitat surveys, we assessed diet composition and the taxonomic distinctness (and other species diversity measures) in the diets of these sympatric marine turtle species. The diet of green turtles (n = 92) consisted of a total of 47 taxa: including three species of seagrass (present in 99% of individuals), 29 species of algae and eight sponge species. Hawksbill turtles (n = 45) consumed 73 taxa and were largely spongivorous (16 species; sponges present in 100% of individuals) but also foraged on 50 species of algae (present in 73% of individuals) and three species of seagrass. Plastics were found in trace amounts in 4% of green turtle and 9% of hawksbill turtle stomach samples. We expected to find changes in diet that might reflect ontogenetic shifts from small (oceanic-pelagic) turtles to larger (coastal-benthic) turtles. Dietary composition (abundance and biomass), however, did not change significantly with turtle size, although average taxonomic distinctness was lower in larger green turtles. There was little overlap in prey between the two turtle species, suggesting niche separation. Taxonomic distinctness routines indicated that green turtles had the most selective diet, whereas hawksbill turtles were less selective than expected when compared with the relative frequency and biomass of diet items. We discuss these findings in relation to the likely important trophic roles that these sympatric turtle species play in reef and seagrass habitats.

Introduction

Marine turtles are large and important consumers in coastal ecosystems and are generally considered keystone species. Their decline through overexploitation in recent centuries is thought to have contributed to the deterioration of reefs and seagrass pastures in the Caribbean (Jackson 1997; Jackson *et al.* 2001; Green & Short 2003; Pandolfi *et al.* 2003; Orth *et al.* 2006; Waycott *et al.* 2009).

As the most abundant marine megaherbivore in the Caribbean, green turtles (*Chelonia mydas*) graze princi-

pally (but not exclusively) on the seagrass *Thalassia testudinum*, and profoundly affect the structure, productivity and nutrient composition of seagrass pastures (Thayer *et al.* 1982, 1984; Moran & Bjorndal 2005, 2007; Christianen *et al.* 2012). It has been suggested that seagrass ecosystems in the Caribbean probably had very different structures and dynamics in times prior to major exploitation of marine turtles, when they existed in huge numbers (Bjorndal & Jackson 2003; Mcclenachan *et al.* 2006). Green turtles are thought to maintain grazing plots; the consistent removal of seagrass biomass is thought to improve the nutritional quality of seagrass for the turtle (Thayer *et al.* 1984) and increase the speed of nutrient recycling (Thayer *et al.* 1982). Green turtles are unusual amongst turtle species in that after their epipelagic-oceanic stage they are generally herbivorous (Bjorndal 1997). However, they have also been known to consume cnidarians, sponges and other invertebrates (Mortimer 1981; Bjorndal 1985, 1997; Seminoff *et al.* 2002, 2006; López-Mendilaharsu *et al.* 2008; Arthur *et al.* 2009; Cardona *et al.* 2009; Vélez-Rubio *et al.* 2014). Research on Pacific (Arthur & Balazs 2008; López-Mendilaharsu *et al.* 2008) and Southwestern Atlantic turtle populations (Vélez-Rubio *et al.* 2014) suggests that immature green turtles are omnivorous, and that conspecific adult female green turtles forage in either neritic or pelagic habitats where they probably feed on macro-algae or zooplankton, respectively (Hatase *et al.* 2006). Recent research suggested the likely ontogenetic shift of green turtles from omnivory in an epipelagic-oceanic habitat during the first 3 to 5 years of their lives, to a largely herbivorous diet in coastal-benthic habitats in older turtles (Reich *et al.* 2007; Arthur *et al.* 2008; Witherington *et al.* 2012). Prey consumed therefore varies within individuals, amongst populations and through different life stages (Bjorndal 1997). An understanding of diet shifts through the size classes may contribute to our understanding of foraging ecology and the ecosystem roles of green marine turtles.

Hawksbill turtles (*Eretmochelys imbricata*) were originally thought to be indiscriminate omnivores (Carr & Stancyk 1975) but subsequent studies have demonstrated that, although they also consume diverse species of algae (Mortimer 1981; Bjorndal 1997; Van Dam & Diez 1997), sponges are probably the primary prey for post-pelagic life stages (Meylan 1988 but see Bell 2013 for predominant algivory in Great Barrier Reef hawksbills). Post-hatchling hawksbill turtles are thought to have an epipelagic-oceanic stage, similar to green turtles, during which they feed omnivorously on prey in *Sargassum* rafts (see Witherington *et al.* 2012 for review) before recruiting to coastal areas where they feed on benthic sponges (Bjorndal 1997). In juvenile coastal benthic stages and adults, hawksbill turtle diet is thought to be driven by selectivity for certain sponges as well as local abundance of species (León & Bjorndal 2002; Rincon-Diaz *et al.* 2011).

Sessile sponges rely on toxins, spicules (spike-like skeletal structures) and growth form (*e.g.* massive form with tough exterior) to deter predators and competitors, and as such there are relatively few sponge predators (Chanas & Pawlik 1995; Pawlik *et al.* 1995). Hawksbill turtles are the dominant spongivores in reef ecosystems and by removing sponge biomass from reefs are thought to influence total reef productivity, biomass, succession and diversity (Meylan 1988; Bjorndal 1997; Van Dam & Diez 1997); other spongivorous animals, such as nudibranchs, parrotfish and wrasse (Pawlik *et al.* 1988, 2013; Dunlap & Pawlik 1996, 1998; Wulff 1997; Hill 1998), do not forage to such an extent (Jackson 1997; Bjorndal & Jackson 2003). Hawksbill turtles reduce sponge overgrowth not only by directly feeding on sponges, but also by exposing the softer inner tissues of sponges, facilitating predation by other species that otherwise would not be able to penetrate the tough exteriors of some sponges (Meylan 1988). The decline of hawksbill turtle populations in the Caribbean, principally from exploitation for their shells (Meylan & Donnelly 1999; Mcclenachan *et al.* 2006), has therefore undoubtedly had a profound effect on reef dynamics (Bjorndal & Jackson 2003). Furthermore, predicted effects of climate change on reef and seagrass habitats as a result of rising sea levels and temperatures may make these habitats and associated species vulnerable (Harley *et al.* 2006; Orth *et al.* 2006; Hoegh-Guldberg *et al.* 2007; Hawkes *et al.* 2009).

Trophic studies generally require gastric sampling to directly observe what the study species has been eating over a certain time period and at a specific location. Several studies of marine turtles have utilized stomach sampling (see Mortimer 1981 and Bjorndal 1997 for reviews; and more recent studies e.g. Brand-Gardner *et al.* 1999; León & Bjorndal 2002; Seminoff *et al.* 2002; Arthur & Balazs 2008; López-Mendilaharsu *et al.* 2008; Arthur *et al.* 2009; Rincon-Diaz *et al.* 2011; Santos *et al.* 2011; Witherington *et al.* 2012; Vélez-Rubio *et al.* 2014) Obtaining samples usually involves oesophageal/gastric lavages (see Forbes & Limpus 1993 for technique) or sampling stomachs directly from dead animals from strandings, fishery bycatch or directed take.

In the present study we had the opportunity to collect and analyse stomach contents of green and hawksbill turtles harvested in a legal turtle fishery in the Caribbean (Stringell *et al.* 2013). Using stomach contents, we set out to assess the trophic role of these sympatric species in the Turks and Caicos Islands. Our aim was to assess dietary preferences of the two marine turtle species, and although we expected clear niche separation, we were interested in

determining the extent of prey overlap. We examined whether diets change with turtle body size (*i.e.* ontogenetic shift) and expected specialization towards herbivory in green turtles and spongivory in hawksbill turtles as they increase in size.

Material and Methods

Study site

The Turks and Caicos Islands (TCI) is a UK Overseas Territory in the Caribbean located at the southeastern end of the Bahamas (21°45′ N, 71°35′ W; Fig. 1). The low-lying limestone islands are surrounded by shallow soft sediment areas with mangrove and tidal creeks on the leeward side and fringing reefs and steep coral drop-offs on the windward side (Doran 1958). The archipelago supports regionally significant foraging stocks of hawksbill and green turtles (Richardson *et al.* 2009; Stringell *et al.* 2013, 2015a) that are subject to one of the largest legal turtle fisheries in the Caribbean (Stringell *et al.* 2013; Humber *et al.* 2014). The stomach contents of juvenile and adult turtles landed by fishers at Grand Turk, Providenciales and South Caicos were sampled between 2008 and 2010, permitting large sample sizes of both species.

Habitat surveys

To characterize the epibenthic macrofaunal communities, shallow (<10 m depth) snorkelling surveys were carried out throughout October 2010. Sixteen survey sites were selected to represent turtle fishing sites, based on the information acquired during fisher interviews, and turtle capture-mark-recapture sampling sites (authors' unpublished data and Stringell *et al.* 2015b; Fig. 1). Four reef-based habitats (reef, patch reef, hard bottom and gorgonian plains) and four seagrass-based habitats (seagrass, seagrass-algae, algae and coralline algae) were surveyed at these locations, some of which had two or more representative habitats (Supporting Information Table S1). Approximate survey areas ranged between 0.08 and 1.2 km^2 (see Table S1). These surveys enabled us to quantitatively describe presence, diversity and abundance of possible prey species at several locations and habitats in order to compare relative proportions of species groups with those found in stomach contents.

The communities at each habitat were described from a total of 1061 photoquadrat images taken at random locations using a housed Canon Powershot G10 digital camera, attached to a 0.25-m^2 quadrat framer (the quadrat was divided into 25 cells). Between 14 and 48 photoquadrats were analysed from 15–105 images per habitat (except at Long Cay reef where, owing to water depth, only six quadrats were photographed and analysed; Table S1). At each habitat in each location, a sample of two to four quadrats was surveyed *in situ* to validate photoquadrat data. Species abundance was enumerated by cell frequency counts (see Materials and methods in Supporting Information for further details).

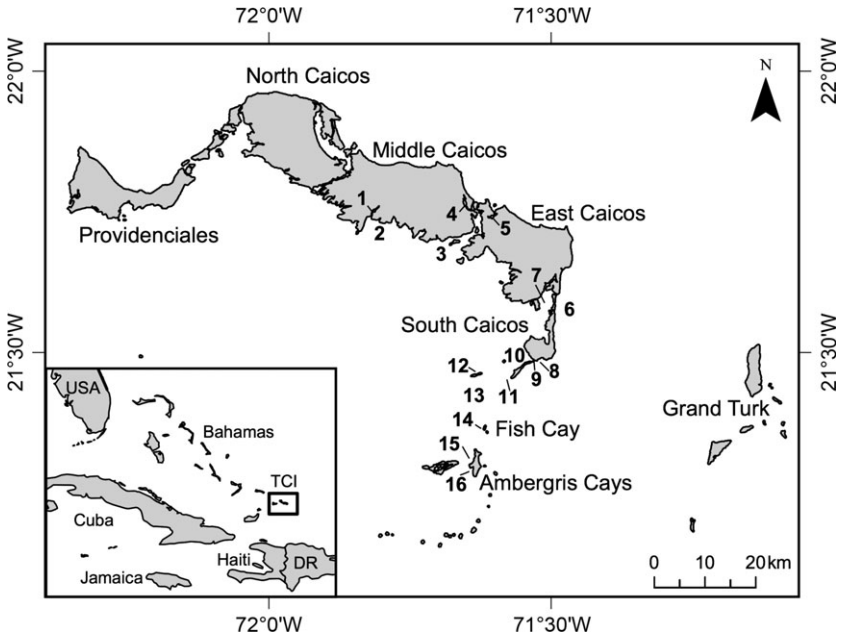

Fig. 1. Map of Turks and Caicos Islands (TCI) and location in Wider Caribbean Region (inset, DR = Dominican Republic). Numbers indicate the following survey sites: 1 = Man-o-War, 2 = Ocean Hole, 3 = Southern Bush, 4 = Lorimers Creek, 5 = Jacksonville, 6 = Eastside, 7 = Nuisance Point, 8 = Tuckers Reef, 9 = Shark Alley, 10 = Harbour, 11 = Long Cay, 12 = Six Hills, 13 = Middle Reefs, 14 = Fish Cay, 15 = Ambergris, and 16 = Ambergris Airport. See Supporting Information Table S1 for further information on sites, habitats and sampling effort.

Sampling turtles

For 2 years (from November 2008), we monitored the legal turtle fishery at key landing sites throughout TCI (see Stringell *et al.* 2013 for details). Turtle capture location was estimated following fisher interviews (authors' unpublished data and Stringell *et al.* 2015b). The size of juvenile to adult-sized turtles (n = 91 green turtles, n = 45 hawksbill turtles) was measured along the midpoint of the carapace [curved carapace length from notch to tip (CCL) in cm: Bolten 1999]. The sex of turtles was determined by gross morphology and histology of the gonads of butchered animals or external morphology in adults (Stringell *et al.* 2013).

Stomach content samples from 45 hawksbills and 92 green turtles of various sizes were collected directly from butchered animals. Owing to the large volume of digestive material in the gut we chose to collect the contents of the stomach and upper digestive tract (oesophagus and stomach); the intestine was not sampled because this was taken for food by fishers. Samples were frozen until examination.

Individual stomach contents were sorted and wet mass of each taxon weighed to the nearest 0.01 g after blotting dry (Hyslop 1980). If a species' weight was <0.01 g it was recorded as trace. Dietary items were identified to the lowest taxonomic level (see Material and methods in Supporting Information for further details).

Data analysis

All multivariate statistical routines were carried out in PRIMER v. 6 software (Clarke & Gorley 2006) with the PERMANOVA+ add on (Anderson *et al.* 2008). Univariate tests were implemented in R v. 2.12 (R Development Core Team 2012).

Habitat analysis

Differences in abundance data (Bray–Curtis similarities of photoquadrat data) among the eight habitats were tested with a one-way permutational multivariate analysis of variance (PERMANOVA) and for differences in multivariate dispersion by permutation (PERMDISP) (Anderson *et al.* 2008). Taxonomic distinctness routines were used to compare species found in the photoquadrats with those expected to be found in the environment (see 'Relating stomach contents to habitat section' later in Methods for description of taxonomic distinctness, and Material and methods in Supporting Information for detailed methods).

Habitats were further grouped into two broad habitat types (reef-based and seagrass-based habitats) and compared with hawksbill and green turtle stomach content data, respectively, using a one-way analysis of similarities (ANOSIM, Clarke 1993).

Stomach content analysis

Dietary species biomass was standardized (by total) to account for differences in stomach fullness, and square root transformed. Bray–Curtis similarities were used for subsequent resemblance-based tests and visualized in a non-metric multidimensional scaling ordination with a vector plot overlay of diet species most correlated with the pattern (Clarke 1993). A similarity of percentages (SIMPER) routine (Clarke 1993) was used to examine differences in diet species composition between turtle species. Differences between turtle species and *a priori* grouping factors (habitat, sex), with turtle size as a covariate, were tested using three-way crossed multivariate permutational analysis of covariance (PERMANCOVA) (Anderson *et al.* 2008). The PERMANCOVA used permutations under a reduced model, Type 1 (sequential) sums of squares, and non-significant interaction terms were sequentially removed during model simplification. Differences in multivariate dispersion among groups were tested using PERMDISP.

The following diversity measures of species found in stomach content samples were plotted against CCL and tested with generalized linear models (GLMs) or generalized additive models (GAMs) after initial exploration of linearity: species richness (S), Simpsons evenness (1-Lambda, calculated on Pi - proportion data: Clarke & Warwick 2001a), average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD) (Clarke & Warwick 1998, 2001b; see below).

Diet species were also grouped into nine taxonomic categories (see next section for list) and visualized for differences in diet groups with size (CCL) between the two turtle species, and tested with a one-way ANOSIM.

Relating stomach contents to habitat

Species in habitat and stomach content samples were grouped into nine taxonomic categories (seagrasses, sponges, bluegreen algae, green algae, red algae, brown algae, cnidarians, invertebrates and unknown). We compared the relative abundance of these nine diet groups in hawksbill and green turtles against the relative abundances of the same groups identified in reef and seagrass habitats, and tested this using a Pearson's Chi-square analysis with Monte Carlo simulated P-values from 10,000 replicates.

To determine how representative stomach content samples were in relation to species available in the habitat, AvTD and VarTD were assessed for stomach content samples by turtle species. These diversity measures are based on the relatedness of species drawn at random from a sample, are independent of the number of species (a better statistical sampling property than richness related estimators), and can be used to compare data obtained with differing sampling efforts and at different

spatial and temporal scales (such as stomach samples and habitat species lists; Clarke & Warwick 1998, 2001b). Here, taxonomic distinctness is defined from a Linnaean tree (taxonomic aggregation file) of macrobenthic species likely to be present in TCI. A regional master list of 565 likely species was created from species identified in the habitat surveys, stomach content analysis and from searches of the World Register of Marine Species (WoRMS) database (Appeltans *et al.* 2012) for sponge, gorgonian, coral, seagrass and algae species previously recorded in TCI and neighbouring Bahamas.

The two taxonomic distinctness measures were used in a taxonomic distinctness test (Clarke & Gorley 2006), in which stomach content sample data were superimposed on a funnel plot of expected AvTD and VarTD 95% probability limits that were created from randomized draws of sublists of two to 20 species from the regional master list. The weighting of Linnaean tree step lengths was guided by taxon richness of the master list (Clarke & Warwick 1999) and the simulation of random draws was weighted by the frequencies of species found in the habitat surveys (Clarke & Gorley 2006). A Mann–Whitney *U*-test was used to formally compare the differences in AvTD and VarTD between turtle species.

Results

Habitat surveys

Species abundance differed significantly among the eight surveyed habitats and these differences were driven largely by seagrass and algae species (Spearman correlation >0.5; PERMANOVA, Pseudo-$F_{(7)} = 78.6$, $P_{perm} = 0.001$: Supporting Information Fig. S1). Dispersion among habitats was also significantly different (PERMDISP, $F_{(7,810)} = 81.9$, $P_{perm} = 0.001$), with patch reefs having the highest mean dispersion (58.9 ± SE 0.4) and coralline algae habitats having the least (26.0 ± 1.8) (Fig. S1). As expected, the relative proportions of the nine species categories from photoquadrat data indicated clear differences between reef and seagrass habitats, such that algae and cnidarians were more common in reef habitats where seagrass were absent (ANOSIM, R = 0.753, P = 0.001: Fig. 2).

We identified 108 species of plants and animals from the photoquadrat images. Green algae (Chlorophyta) were the most diverse taxonomic group with 22 species; *Halimeda* was the most common genus in this group. Reef habitats were most diverse (had the greatest species richness), but the gorgonian habitat at site 10 (see Fig. 1 for location) was the single most diverse site, with 41 species identified (Supporting Information Table S1). Seagrass density ranged from 15.6–148.5 shoots·m^{-2} (Table S1). Reef-based habitats (reef, patch reef, hard bottom and gorgonian plains) were more taxonomically distinct than seagrass-based habitats (seagrass, seagrass-algae, algae, coralline algae). Reef photoquadrats mostly fell within the 95% AvTD funnel of the regional expectation, but were generally more variable than expected (VarTD) (Supporting Information Fig. S2). The opposite pattern was found for seagrass-based habitats, reflecting the lower diversity of these habitats. These findings indicate that our habitat surveys were likely to be representative of the species found in the region.

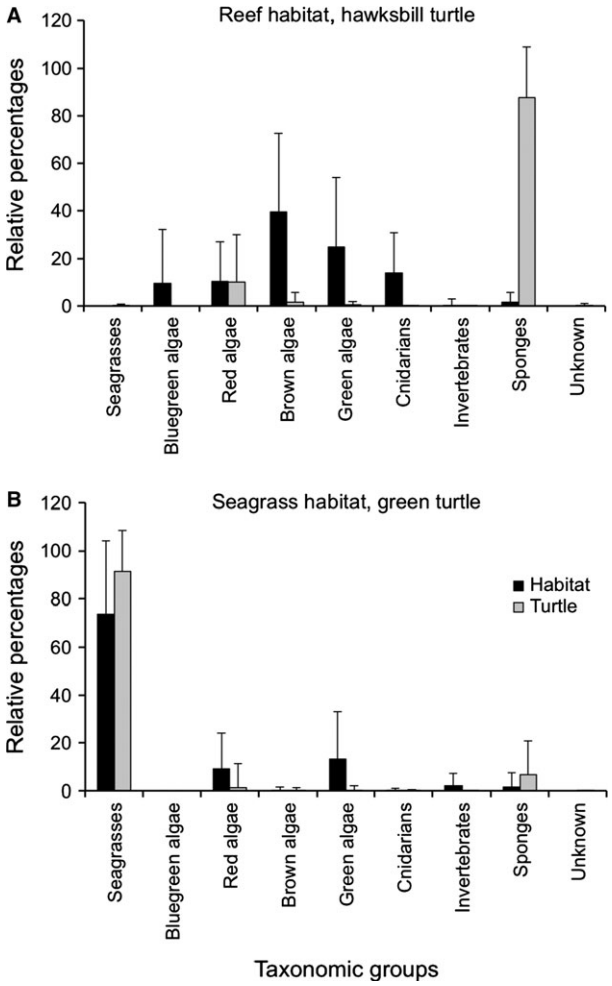

Fig. 2. Average relative percentages (±1 SD, error bars) of taxonomic diet groups. (A) Reef habitat photoquadrats (abundance: n = 406) and hawksbill turtle stomach samples (biomass: n = 45). (B) Seagrass habitat photoquadrats (abundance: n = 331) and green turtle stomach samples (biomass: n = 92).

Turtle stomach contents

We identified a total of 93 prey species in 137 turtle stomach samples (47 species in 92 green turtle stomach samples, and 73 species in 45 hawksbill samples; Supporting Information Table S2). In green turtles, the diet was

Table 1. Frequency of occurrence (proportion of turtles in which present) and average (±SD and range) proportion of biomass of taxonomic diet groups found in stomach content samples of green turtles (n = 92) and hawksbill turtles (n = 45). See Supporting Information Table S2 for further details.

	green turtle				hawksbill turtle			
		biomass				biomass		
diet group	proportion of turtles	mean	±SD	range	proportion of turtles	mean	±SD	range
seagrasses	0.99	0.91	0.17	(0.00–1.00)	0.22	*	0.01	(0.00–0.04)
red algae	0.26	0.01	0.10	(0.00–0.97)	0.49	0.10	0.20	(0.00–0.70)
brown algae	0.08	*	0.01	(0.00–0.10)	0.49	0.02	0.04	(0.00–0.18)
green algae	0.32	*	0.02	(0.00–0.18)	0.49	*	0.01	(0.00–0.07)
unknown algae	0.03	*	*	(0.00–0.01)	0.04	*	0.01	(0.00–0.07)
sponges	0.28	0.07	0.14	(0.00–0.55)	1.00	0.88	0.21	(0.30–1.00)
cnidarians	0.03	*	*	(0.00–0.04)	0.02	*	*	(0.00–0.01)
other invertebrates[a]	0.03	*	*	(0.00–*)	0.09	*	*	(0.00–*)
plastic	0.04	*	*	(0.00–*)	0.09	*	*	(0.00–*)

*<0.01 (trace).

[a]Platyhelminthes, Mollusca, Arthropoda.

mainly herbivorous (approximately 92% seagrass and algae by biomass) but with varying amounts of sponge (average 7% biomass; Tables 1 and S2). The seagrass *Thalassia testudinum* contributed the most to biomass (73%) in green turtle diet. This was followed, in decreasing order, by the seagrass *Syringodium filiforme* (16%), the sponge *Chondrilla caribensis* (formerly *Chondrilla nucula*) (4%) and the seagrass *Halodule beaudettei* (2%). The remaining species contributed <1% each. In terms of the frequency of occurrence in green turtles, *T. testudinum* was found in 95% of all stomach samples, *S. filiforme* and *H. beaudettei* in 58%, the green algae *Batophora oerstedii* in 18% and *C. caribensis* in 16%. Trace amounts of plastics were found in 4% (n = 4) of samples.

In hawksbill turtles, diet was more varied and omnivorous, with individuals mostly consuming sponges and algae (approximately 99% by biomass; Tables 1 and S2). Twenty-seven per cent of the hawksbill turtle diet biomass comprised of the sponge *Chondrilla caribensis*, followed by the sponges *Sidonops neptuni* (17%), *Halichondria melanadocia* (16%), *Scopalina ruetzleri* (8%), *Cinachyrella alloclada* (5%) and *Erylus formosus* (4%), the red algae *Gelidiella acerosa* (3%) and an unidentified red algae (2%). The remaining species contributed <2% each. When considering the frequency of occurrence in hawksbill turtles, the commonest species in stomach samples were the sponges *C. caribensis*, *H. melanadocia* and *S. neptuni* (47%, 29%, 24%, respectively), followed by the brown algae *Padina* spp. (22%), the red algae *G. acerosa* (18%) and the seagrasses *Syringodium filiforme* and *Thalassia testudinum* in 18% and 16% of samples, respectively. Trace amounts of plastics were found in 9% (n = 4) of samples.

For both turtle species, no significant differences were found in diet composition (Bray–Curtis similarities of standardized biomass) either between sexes or among the habitat types in which the turtle was found. However, as expected, there was a clear difference in diet composition between turtle species [Bray–Curtis similarities of standardized biomass: PERMANCOVA (turtle species factor), Pseudo-$F_{(1)} = 58.9$, $P_{perm} < 0.001$; diet categories: ANOSIM, $R = 0.957$, $P = 0.001$; Fig. 2]. A SIMPER analysis confirmed that *Thalassia testudinum* and *Syringodium filiforme* seagrasses, and *Chondrilla caribensis*, *Sidonops neptuni* and *Halichondria melanadocia* sponges together contributed 70% to the dissimilarity (or 30% similarity) between the turtle species. *Thalassia testudinum* made the largest contribution to the difference and explained 32% of the dissimilarity, and *C. caribensis* explained 13%, with their average abundances being highest in green turtles and hawksbill turtles, respectively (Fig. 3).

Green turtles measured between 28.8 and 88.0 cm CCL (mean = 52.8 ± SD 12.6, n = 91) and hawksbill turtles measured between 39.3 and 91.2 cm (60.4 ± 14.0, n = 45) (Supporting Information Fig. S3). There were no discernible diet differences with size (Supporting Information Fig. S4), either as a continuous predictor or grouped into 10-cm size classes. Turtle size did not significantly explain the diversity of species in turtle diet when expressed as S, species evenness (Simpson's) or VarTD, but there was a weak suggestion of size partitioning in green turtles with the taxonomic breadth of diet (AvTD) reducing with larger sizes (GAM, P = 0.04) (Figs 4 and 5).

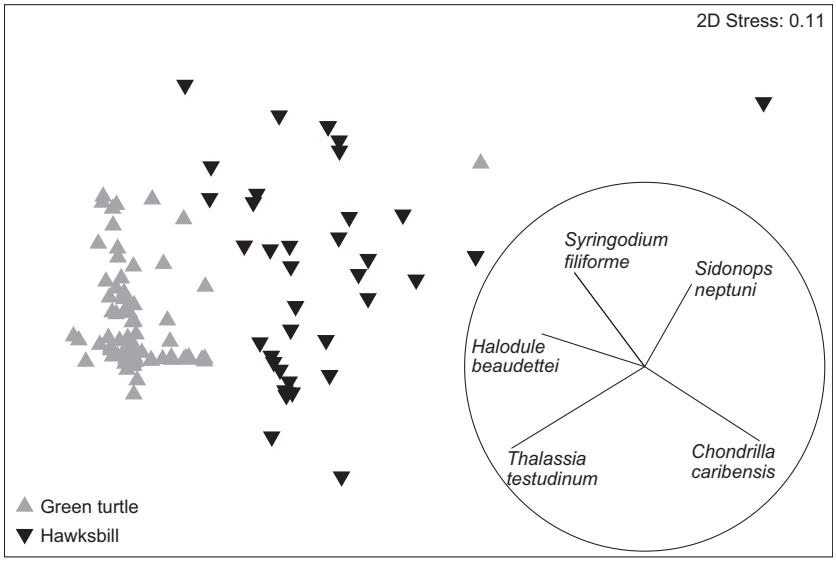

Fig. 3. Non-metric multidimensional scaling ordination of stomach content sample data. Vector overlay indicates species most correlated with the pattern ($R > 0.5$ Spearman's correlation; derived from similarity of percentages analysis). Stomach content biomass data are standardized, square root-transformed Bray–Curtis similarities. Three hawksbill turtle outliers (not shown) lie outside of plot boundary (top right) and were dominated by *Sidonops neptuni* in their diet.

Relating stomach contents to habitat

Diet variability (multivariate dispersion of Bray–Curtis similarities) differed significantly between turtle species found in reef and seagrass habitats (PERMDISP, $F_{(3,\ 123)} = 18.486$, $P_{perm} = 0.001$). For example, the diet of hawksbill turtles captured in reef habitats had higher mean dispersion [62.6 ± 1.3 (SE)] than the diet of individuals captured in seagrass habitats (53.5 ± 6.3). Green turtles had significantly lower dispersion than hawksbill turtles: 35.8 ± 4.0 and 25.7 ± 1.7 from reef and seagrass habitats, respectively. These results suggest that green turtles had the narrower range of diet of the two species, especially those from seagrass habitats.

The analysis of AvTD (on presence-absence stomach content data) showed that all hawksbill turtle stomach samples remained within the 'funnel of 95% confidence' (Fig. 6A). This indicates that hawksbill turtles fed randomly on what was available in the habitat, that is, their varied diet consisted of species that were as taxonomically related as those chosen at random from a species list of >500 species. For green turtles, 43% (n = 40 of 92) of the stomach content samples had significantly lower AvTD ($P < 0.05$) than expected (Fig. 6A). This indicates that these green turtles exhibited strong dietary selectivity by having a relatively taxonomically narrow diet in comparison to the habitat. However, 57% of individuals had diets that fell within the habitat probability limits and were relatively taxonomically wide (Fig. 6A). There was much less departure from probability limits in the case of VarTD for both species (5%, n = 5 of 92 green turtles; no hawksbill turtles), indicating similar variation in taxonomic distinctness of species in turtle stomachs to those chosen at random from the habitat (Fig. 6B). These results are confirmed by formal tests of these metrics with significantly greater average taxonomic breadth (AvTD) found in hawksbill turtle stomach samples than in green turtles (Wilcoxon, $W = 1555$, $P = 0.018$), but not for VarTD ($W = 2193$, $P = 0.568$).

The relative proportions of biomass of the nine diet groups in average hawksbill turtle stomach content samples differed significantly from the relative abundances of these same groups in average reef-based habitat photoquadrats ($X^2 = 164.89$, $P_{perm} < 0.001$) and seagrass-based habitats ($X^2 = 171.94$, $P_{perm} < 0.001$). This indicates that although many of the same species were present in stomach content samples and the habitat, they were not consumed at the same relative proportions. For example and as expected, in hawksbill turtle stomach content samples, sponges were found in much higher proportions and brown algae at lower proportions than in reef habitats (Fig. 2A). Relative proportions of diet groups in green turtle stomach content samples differed significantly from the proportions of these same diet groups in seagrass habitats ($X^2 = 25.67$, $P_{perm} < 0.001$) and reef habitats ($X^2 = 187.92$, $P_{perm} < 0.001$) (Fig. 2B); although there was some similarity in seagrass proportions between seagrass habitats and green turtle diet. These data, which are based on the amounts of each diet item, have differing inferences to the results of the taxonomic distinctness routines that, as diversity measures, are based on presence-absence data and Linnaean relatedness.

Discussion

Knowledge of supporting habitats is essential to inform our understanding of the foraging ecology and role of marine turtles in coastal ecosystems. Our results demon-

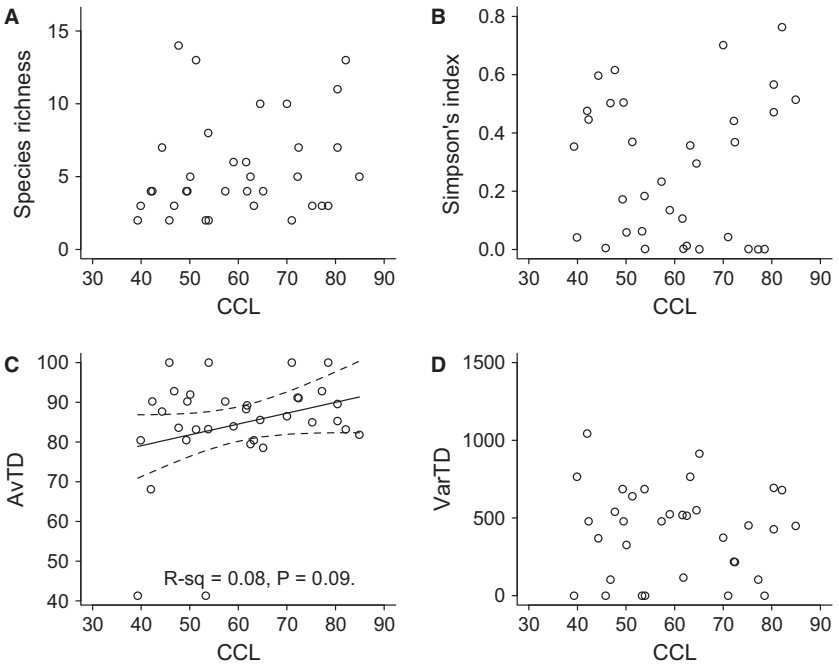

Fig. 4. Species diversity measures of stomach content samples against hawksbill turtle size [curved carapace length from notch to tip (CCL), cm]. (A) species richness; (B) Simpson's index (calculated on biomass); (C) average taxonomic distinctness (AvTD); (D): variation in taxonomic distinctness (VarTD).

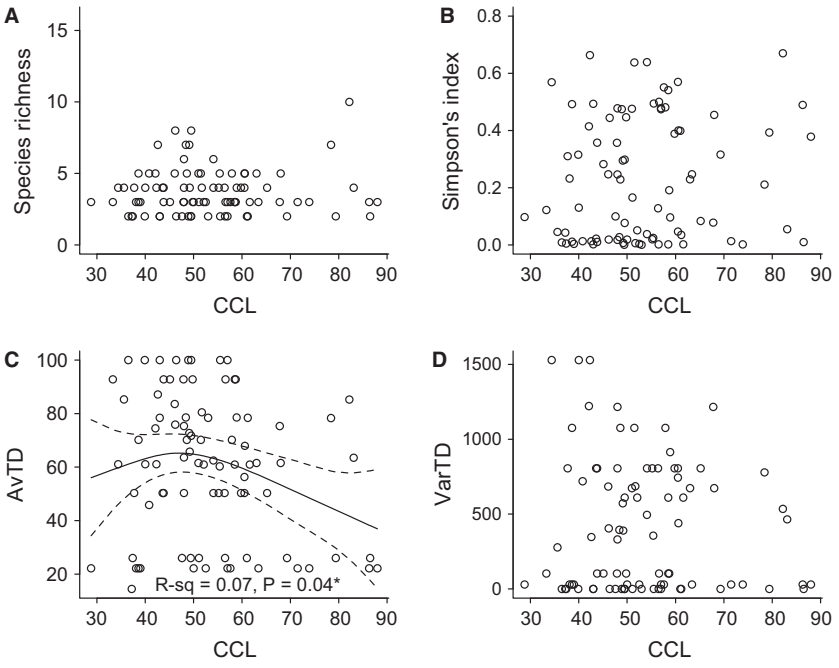

Fig. 5. Species diversity measures of stomach content samples against green turtle size [curved carapace length from notch to tip (CCL), cm]. (A) species richness; (B) Simpson's index (calculated on biomass); (C) average taxonomic distinctness (AvTD); (D): variation in taxonomic distinctness (VarTD).

strate clear niche separation between the two turtle species, using relative proportions and taxonomic distinctness of diet. To our knowledge, this study is the first to examine taxonomic distinctness in the diet of marine turtles.

Green turtles undergo ontogenetic shifts whereby small oceanic-pelagic juveniles recruit to coastal-benthic habitats and switch from omnivorous/carnivorous to herbivorous feeding. This has been effectively demonstrated using stable isotope analysis (Reich *et al.* 2007; Arthur *et al.* 2008; Stringell 2013; although see Cardona *et al.* 2009 for alternative patterns of omnivory in green turtles). Stringell (2013) suggested that a similar ontogenetic shift also occurs in hawksbill turtles. Part of the present

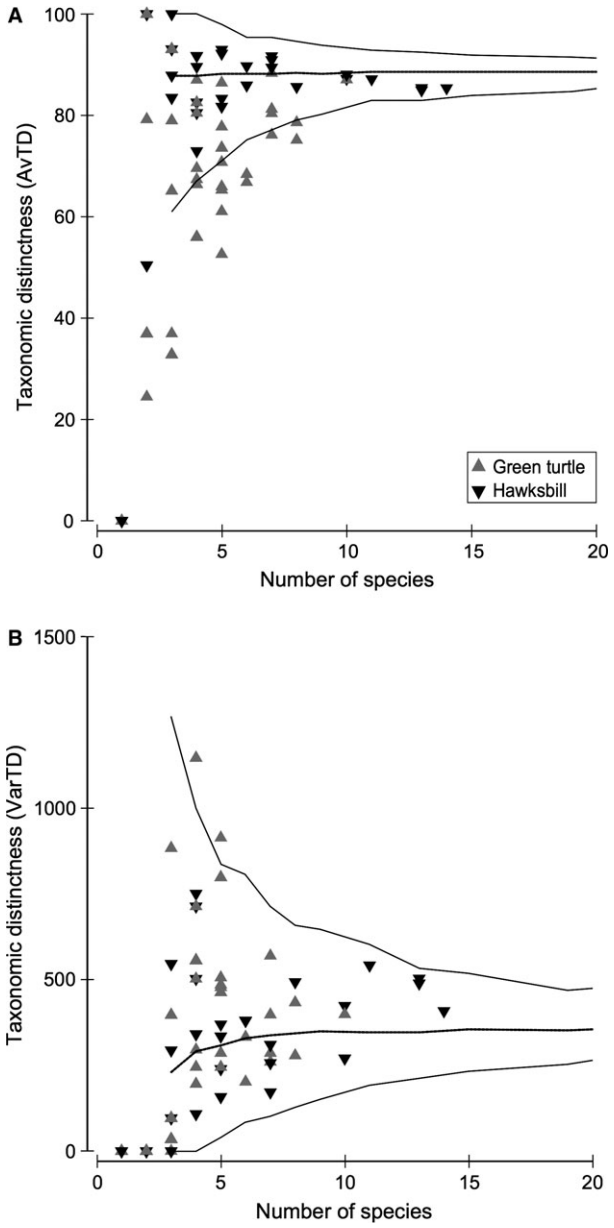

Fig. 6. Average (A, AvTD) and variation (B, VarTD) in taxonomic distinctness of stomach contents of two turtle species (n = 45 hawksbill turtles, n = 92 green turtles). Lines indicate the median and upper and lower 95% probability intervals of taxonomic distinctness created from randomized draws of sublists of two to 20 species from a regional master list of 565 species.

study was to investigate if a similar shift in diet across turtle sizes could be observed in stomach contents. We might expect to see a shift from omnivory/carnivory to herbivory in green turtles, and to omnivory at a lower trophic level (owing to intake of sponges rather than animal taxa of higher trophic level) in hawksbill turtles. The results of our stomach contents analyses, however, did not readily show this shift. Dietary composition (abundance and biomass) did not change significantly with turtle size (see Supporting Information Fig. S4). Examination of stomach samples from the smallest green turtles (minimum 28.8 cm CCL) did not show discernible diet differences (in terms of abundance and biomass) with larger turtles. However, average taxonomic distinctness in green turtles indicated a significant non-linear change with size (AvTD was lower in larger green turtles), which suggests a possible diet shift. One possible explanation for this lack of clear evidence of ontogenetic shifts is that small, newly recruited animals were unlikely to have been well represented in our sample of the fishery; small turtles are less desirable to eat because of the low meat yield and are below legal catch size, a regulation that fishers generally respect (Stringell *et al.* 2013). Larger size green turtles (large juveniles to adults) were also not well represented in the fishery, most likely because of the effort required to catch them and their relative abundance at these sizes (Stringell *et al.* 2013). Additionally, the size at which hawksbill turtles recruit to coastal habitats is thought to be smaller than that of green turtles (Meylan *et al.* 2011). Therefore, the smallest hawksbill turtle in our study (39.9 cm CCL) may well have been resident for some time and it is possible that our entire sample of hawksbills represents turtles that had already completed ontogenetic shifts in their feeding. Consequently, although the present study had a large sample size, some size classes were not well represented and further sampling of small and large animals would help address this bias.

Apart from seagrasses, the relative proportions of prey species in green turtle stomachs did not statistically match those in seagrass habitats, especially for red algae, green algae and sponge proportions. This suggests a selective feeding strategy and a functional linkage between consumer and habitat that supports the findings of others (Table 1; Bjorndal 1980, 1997; Mortimer 1981; Van Dam & Diez 1997; Seminoff *et al.* 2002; León & Bjorndal 2002; Rincon-Diaz *et al.* 2011; Santos *et al.* 2011). In green turtles, the AvTD routine indicates that for nearly half of the stomach content samples, the relatedness of species in the diet was less taxonomically distinct than that of the species available in the surrounding habitat, also suggesting a degree of selective feeding. The relatively low taxonomic distinctness of green turtle diet is probably a result of the narrow taxonomic distinctness of seagrasses (three species from two families) that make up the majority of the green turtle diet (in terms of biomass). However, the several algae species (>5% frequency, mainly Chlorophytes: Table 1) found in green turtle stomachs may have elevated the taxonomic distinctness of the stomach samples. Although green turtles can be found in both reef

and seagrass habitats, the low taxonomic distinctness of green turtle diets is probably a result of seagrass-based habitats having lower species diversity than reef-based habitats.

Hawksbill turtles are most commonly associated with reef-based habitats (but see Bjorndal & Bolten 2010 for the importance of seagrass beds to hawskbill turtles). Therefore, if hawksbill turtles graze randomly, we might expect them to have a diet more diverse than that of green turtles and one that perhaps reflects the diversity of species found in reef systems. However, in terms of relative abundance of diet type, hawksbill turtle diet was not representative of reef habitat, a finding that supports selective feeding mostly on sponges and algae (Bjorndal 1997; Van Dam & Diez 1997; León & Bjorndal 2002; Rincon-Diaz *et al.* 2011). In terms of taxonomic breadth (AvTD), however, every sample fell within the funnel of taxonomic expectation, suggesting they might be generalists or indiscriminate feeders that graze randomly (*sensu* Carr & Stancyk 1975) and have a diet representative of available species.

These seemingly conflicting results may be due to several reasons: (i) sponges house many symbiotic, parasitic and commensal animal and plant species (which may have more nutritional value than the sponges themselves), increasing the apparent taxonomic breadth of diet; (ii) sponges may not be easily digestible or nutritious (Bjorndal 1985) and may remain in the stomach longer than other readily digestible taxa; (iii) presence-absence data in taxonomic distinctness routines give equal weighting to rare species; (iv) sponges are from a phylum of especially wide taxonomic breadth – two species of sponge may be as distinct from each other as two unrelated species drawn at random (this also applies to algae, which encompass several kingdoms and phyla); and (v) Caribbean reefs are generally sponge and algae dominated (Mumby 2009; Mcmurray *et al.* 2010), and the taxonomic routines may be telling us that hawksbill turtles eat a broad range of sponges and algae, which dominate the reef systems in TCI (see Supporting Information on habitat descriptions [Tables S1, S3, S4; Fig. S1] – reef sites are dominated by various species of algae).

Caution must therefore be taken when making comparisons with other studies that used abundance or biomass measures, because taxonomic distinctness assesses diversity (taxonomic relatedness) rather than abundance. Taxonomic distinctness complements rather than replaces analyses of relative abundance and these should be viewed together to provide a diversity perspective on diet selectivity. Furthermore, the findings of the present work using these measures are reflected in a stable isotope analysis of the same population of hawksbill turtles that showed mixed diet sources (not only sponges), suggesting more of a generalist diet (Stringell 2013). Recent work by Bell (2013) found that hawksbill turtles in the Great Barrier Reef predominantly fed on algae. Thus, our work using taxonomic distinctness supports a departure from obligate spongivory in hawksbill turtles (Meylan 1988).

Many of the diet species identified in turtle stomachs are found across the different habitat types and at most locations. For example, the sponge *Chondrilla caribensis* occurs in both reef and seagrass habitats. The form of this sponge (*C. caribensis* f. *caribensis*) commonly found in hawksbill and green turtle stomachs from our study is more usually associated with seagrass habitats. Additionally, 22% of hawksbill turtle stomachs contained seagrass, suggesting the importance of seagrass habitats to foraging hawksbill turtles (Bjorndal & Bolten 2010). In the present study, several sponge species were also found in green turtle diet. Although consumption of sponges by green turtles has been previously reported (Bjorndal 1990), the extent of the finding is surprising. Sixteen per cent of green turtle stomach samples contained *C. caribensis*, indicating that this sponge is likely to be purposefully consumed. Further, Fig. 3 illustrates that one green turtle had a diet dominated by sponges, perhaps representing active consumption of these taxa.

In our study, habitat surveys were restricted to shallow depths (<10 m), whereas foraging turtles clearly dive much deeper (Blumenthal *et al.* 2009, 2010). Diving ability in marine turtles scales with body size (Schreer & Kovacs 1997) and size partitioning by depth is well known (Musick & Limpus 1997). Once turtles recruit from the oceanic-pelagic zone and settle in coastal waters to feed benthically, they are probably limited to shallow habitats that contain seagrass and patch reefs, whereas larger turtles are able to forage at greater depths where other food types are found. Consequently, we may have better surveyed the core habitat of smaller turtles rather than that of larger ones. Therefore, the relative abundance of species in our habitat surveys is unlikely to fully represent what is available to turtles and consequently what is found in turtle stomachs. All published studies that link habitat type to stomach contents, however, are also restricted to shallow survey depths and typically survey only those species that were identified in stomach samples (Van Dam & Diez 1997; León & Bjorndal 2002; Rincon-Diaz *et al.* 2011), thereby biasing the availability of species in random surveys. Thus, habitat surveys rarely (if ever) fully represent the foraging breadth of aquatic consumers.

Taxonomic distinctness routines go some way to removing this bias by using comprehensive species lists (Clarke & Warwick 1998, 1999, 2001a,b). In our case, a list of species recorded primarily from the Bahamas region (from the WoRMS database), from our habitat

surveys and from stomach content samples was used to compile the master species list. From this list, random draws were taken to generate a habitat 'baseline' (directed by the relative frequencies of species found in our habitat surveys to 'fine-tune' the randomization) against which the compositions of turtle stomach samples were compared. This provides a more robust assessment of habitat linkage than typical habitat surveys of only those species selected from stomach samples. Additionally, the use of a temporally independent species list as the baseline avoids issues with the differences in the timing of stomach content sample collection (November 2008 to November 2010) and habitat surveys (October 2010). In our relative abundance comparisons, the timing of our habitat surveys may have had some influence on the results. However, owing to logistical constraints we were unable to conduct any more habitat surveys. Temporally spread habitat surveys would be advised for future studies to examine whether comparisons of diet and habitat composition are sensitive to temporal differences.

Stomach contents represent only a snapshot of feeding by marine turtles and may not adequately relate to what is assimilated into body tissue over time. This is a key disadvantage with stomach content analysis (Duffy & Jackson 1986; Barrett *et al.* 2007). Diet varies considerably amongst individuals and locations (Bjorndal 1997) but can also vary in individuals through time, as demonstrated by the different diet components found along the alimentary canal of green turtles (Arthur *et al.* 2009; Vélez-Rubio *et al.* 2014). Additionally, some prey species may have been completely digested in stomach samples, precluding their identification. Videos from animal-borne cameras on green turtles from California (Seminoff *et al.* 2006) suggest the importance of cnidarians and algae to green turtle diet. It is possible, therefore, that soft-bodied invertebrates and readily digestible algae are under-represented in our study, although we note that most stomach samples in our study were surprisingly well preserved, an observation also shared by Mortimer (1981).

Given the sponge- and algae-dominated, yet taxonomically broad, diet of hawksbill turtles, and the selective grazing of green turtles, these sympatric species are likely to play key grazing roles in Caribbean seagrass and reef systems. Both green and hawksbill turtles are among the largest grazers in the tropics and are thought to have critical roles in regulating the structure and function of reef and seagrass habitats (Bjorndal & Jackson 2003). Some sponge species, notably *Chondrilla caribensis,* are superior competitors to corals in reef habitats (Hill 1998; Wulff 2012). Hawksbill turtles, as spongivores, thus undoubtedly play a key role in the ecological interactions between this species and many other sponges, corals and algae. We are gradually building a more complete picture of the ecological dynamics that relate habitat to consumers and predators. For example, Heithaus *et al.* (2007) suggested that declines in seagrass beds in Bermuda may be linked to increases in green turtle populations (Murdoch *et al.* 2007), which coincide with declines in tiger sharks in the Northwest Atlantic (Baum *et al.* 2003). This suggests that top-down effects of marine predators may be profound (Heithaus *et al.* 2008), not only on regulating the abundance and distribution of grazers (turtles) but on the structure and function of habitats (Thayer *et al.* 1984).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of TCI sampling sites, their habitats and descriptions with tidal state and height (m) (tidal phase indicated by S = Springs, N = Neaps) and sampling water depth at time of sampling.

Table S2. Species in diets of green turtles (n = 92) and hawksbill turtles (n = 45).

Table S3. Rapid assessment of habitats: biological characteristics measured using the SACFOR abundance scale (see http://jncc.defra.gov.uk/page-2684), substrate type (%), physical characteristics ranked 1–5 (5 = high relief, many patches, high density, unstable sediment, many crevices, deep sediment).

Table S4. Classification of habitats surveyed. Dense = >1 individuals m^{-2} for solitary species, or >50% cover for algae/seagrass.

Figure S1. Non-metric multi dimensional scaling ordination of habitat photoquadrats and vector overlay of species most correlated with the pattern ($R > 0.5$ Spearman's correlation; derived from SIMPER analysis).

Figure S2. Average (A) and variation (B) in taxonomic distinctness of habitat quadrats.

Figure S3. Size class histogram of curved carapace length (CCL, cm) in sampled green turtles (left panel; n = 91) and hawksbill turtles (right panel; n = 45).

Figure S4. Trellice plot of relative percentage biomass of five main diet groups (brown, green and red algae, seagrasses and sponges) found in gut content indicates no apparent relationship exists with turtle carapace size class.