

1 **Taxonomic distinctness in the diet of two sympatric marine**
2 **turtle species**

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21 **Key words:** marine turtle (*Chelonia mydas*, *Eretmochelys imbricata*), stomach
22 content analysis, diet, niche, taxonomic distinctness, diversity indices, keystone
23 species, ontogenetic shifts

24

25 **Abstract** Marine turtles are considered keystone consumers in tropical coastal
26 ecosystems and their decline through overexploitation has been implicated in the
27 deterioration of reefs and seagrass pastures in the Caribbean. In the present study,
28 we analysed stomach contents of green (*Chelonia mydas*) and hawksbill turtles
29 (*Eretmochelys imbricata*) harvested in the legal turtle fishery of the Turks and Caicos
30 Islands (Caribbean) during 2008-2010. Small juveniles to adult sized turtles were
31 sampled. Together with data from habitat surveys, we assessed diet composition and
32 the taxonomic distinctness (and other species diversity measures) in the diets of
33 these sympatric marine turtle species. The diet of green turtles ($n=92$) consisted of a
34 total of 47 taxa: including three species of seagrass (present in 99% of individuals),
35 29 species of algae and eight sponge species. Hawksbill turtles ($n=45$) consumed 73
36 taxa and were largely spongivorous (16 species; sponges present in 100% of
37 individuals) but also foraged on 50 species of algae (present in 73% of individuals)
38 and three species of seagrass. Plastics were found in trace amounts in 4% of green
39 turtle and 9% of hawksbill turtle stomach samples. We expected to find changes in
40 diet that might reflect ontogenetic shifts from small (oceanic-pelagic) turtles to larger
41 (coastal-benthic) turtles. Dietary composition (abundance and biomass), however,
42 did not change significantly with turtle size, although average taxonomic distinctness
43 was lower in larger green turtles. There was little overlap in prey between the two
44 turtle species, suggesting niche separation. Taxonomic distinctness routines
45 indicated that green turtles had the most selective diet, whereas hawksbill turtles
46 were less selective than expected when compared with the relative frequency and
47 biomass of diet items. We discuss these findings in relation to the likely important
48 trophic roles that these sympatric turtle species play in reef and seagrass habitats.
49

50 Introduction

51

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

57 As the most abundant marine megaherbivore in the Caribbean, green turtles
58 (*Chelonia mydas*) graze principally (but not exclusively) on the seagrass *Thalassia*
59 *testudinum*, and profoundly affect the structure, productivity and nutrient composition
60 of seagrass pastures ([Christianen et al. 2012](#); [Moran & Bjorndal 2005](#); [Moran &](#)
61 [Bjorndal 2007](#); [Thayer et al. 1982](#); [Thayer et al. 1984](#)). It has been suggested that
62 seagrass ecosystems in the Caribbean likely had very different structures and
63 dynamics in times of pre-exploitation of marine turtles, when they existed in huge
64 numbers ([Bjorndal & Jackson 2003](#); [McClenachan et al. 2006](#)). Green turtles are
65 thought to maintain grazing plots; the consistent removal of seagrass biomass is
66 thought to improve the nutritional quality of seagrass for the turtle ([Thayer et al.](#)
67 [1984](#)) and increase the speed of nutrient recycling ([Thayer et al. 1982](#)). Green turtles
68 are unusual among turtle species in that after their epipelagic-oceanic stage they are
69 generally herbivorous ([Bjorndal 1997](#)). However, they have also been known to
70 consume cnidarians, sponges and other invertebrates ([Arthur et al. 2009](#); [Bjorndal](#)
71 [1985](#); [Bjorndal 1997](#); [Cardona et al. 2009](#); [López-Mendilaharsu et al. 2008](#); [Mortimer](#)
72 [1981](#); [Seminoff et al. 2006](#); [Seminoff et al. 2002](#); [Vélez-Rubio et al. 2014](#)). Research
73 on Pacific ([Arthur & Balazs 2008](#); [López-Mendilaharsu et al. 2008](#)) and southwestern
74 Atlantic turtle populations ([Vélez-Rubio et al. 2014](#)) suggests immature green turtles
75 are omnivorous, and that conspecific adult female green turtles forage in either neritic
76 or pelagic habitats where they likely feed on macro-algae or zooplankton,
77 respectively ([Hatase et al. 2006](#)). Recent research confirmed the likely ontogenetic
78 shift of green turtles from omnivory in an epipelagic-oceanic habitat ([Witherington et](#)
79 [al. 2012](#)) during the first three to five years of their lives, to a largely herbivorous diet
80 in coastal-benthic habitats in older turtles ([Arthur et al. 2008](#); [Reich et al. 2007](#)). Prey
81 consumed therefore varies within individuals, among populations and through
82 different life stages ([Bjorndal 1997](#)). An understanding of diet shifts through the size

83 classes may contribute to our understanding of foraging ecology and the ecosystem
84 roles of green marine turtles.

85 Hawksbill turtles (*Eretmochelys imbricata*) were originally thought to be
86 indiscriminate omnivores ([Carr & Stancyk 1975](#)) but subsequent studies have
87 demonstrated that, although they also consume diverse species of algae ([Bjorndal](#)
88 [1997](#); [Mortimer 1981](#); [Van Dam & Diez 1997](#)), sponges are probably the primary prey
89 for post-pelagic life stages (but see [Bell 2013](#) for predominant algivory in Great
90 Barrier Reef hawksbills; [Meylan 1988](#)). Post-hatchling hawksbill turtles are thought to
91 have an epipelagic-oceanic stage, similar to green turtles, during which they feed
92 omnivorously on prey in *Sargassum* rafts (see [Witherington et al. 2012](#) for review)
93 before recruiting to coastal areas where they feed on benthic sponges ([Bjorndal](#)
94 [1997](#)). In juvenile coastal benthic stages and adults, hawksbill turtle diet is thought to
95 be driven by selectivity for certain sponges as well as local abundance of species
96 ([León & Bjorndal 2002](#); [Rincon-Diaz et al. 2011](#)).

97 Sessile sponges rely on toxins, spicules (spike-like skeletal structures) and
98 growth form (e.g. massive form with tough exterior) to deter predators and
99 competitors, and as such there are relatively few sponge predators ([Chanas & Pawlik](#)
100 [1995](#); [Pawlik et al. 1995](#)). Hawksbill turtles are the dominant spongivores in reef
101 ecosystems and by removing sponge biomass from reefs are thought to influence
102 total reef productivity, biomass, succession and diversity ([Bjorndal 1997](#); [Meylan](#)
103 [1988](#); [Van Dam & Diez 1997](#)); other spongivorous animals, such as nudibranchs,
104 parrotfish and wrasse ([Dunlap & Pawlik 1996](#); [Dunlap & Pawlik 1998](#); [Hill 1998](#);
105 [Pawlik et al. 1988](#); [Pawlik et al. 2013](#); [Wulff 1997](#)), do not forage to such an extent
106 ([Bjorndal & Jackson 2003](#); [Jackson 1997](#)). Hawksbill turtles reduce sponge
107 overgrowth not only by directly feeding on sponges, but also by exposing the softer
108 inner tissues of sponges, facilitating predation by other species that otherwise would
109 not be able to penetrate the tough exteriors of sponges ([Meylan 1988](#)). The decline
110 of hawksbill turtle populations in the Caribbean, principally from exploitation for their
111 shells ([McClenachan et al. 2006](#); [Meylan & Donnelly 1999](#)), has therefore
112 undoubtedly had a profound effect on reef dynamics ([Bjorndal & Jackson 2003](#)).
113 Furthermore, predicted effects of climate change on reef and seagrass habitats as a
114 result of rising sea levels and temperatures may make these habitats and associated
115 species vulnerable ([Harley et al. 2006](#); [Hawkes et al. 2009](#); [Hoegh-Guldberg et al.](#)

116 2007; Orth *et al.* 2006).

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

127 In the present study we had the opportunity to collect and analyse stomach
128 contents of green and hawksbill turtles harvested in a legal turtle fishery in the
129 Caribbean (Stringell *et al.* 2013). Using stomach contents, we set out to assess the
130 trophic role of these sympatric species in the Turks and Caicos Islands. Our aim was
131 to assess dietary preferences of the two marine turtle species, and although we
132 expected clear niche separation, we were interested in determining the extent of prey
133 overlap. We examine whether diets change with turtle body size (i.e. ontogenetic
134 shift) and expect specialisation towards herbivory in green turtles and spongivory in
135 hawksbill turtles as they reach maturity.

136

137 **Materials and methods**

138

139 Study Site.

140

141 The Turks and Caicos Islands (TCI) is a UK Overseas Territory in the Caribbean
142 located at the south-eastern end of the Bahamas (21° 45N, 71° 35W) (Fig. 1). The
143 low lying limestone islands surrounded by shallow soft sediment areas with
144 mangrove swamps and tidal creeks on the leeward side contrast with the fringing
145 reefs and steep drop-offs on the windward side ([Doran 1958](#)). The archipelago
146 supports regionally significant foraging stocks of hawksbill and green turtles
147 (Richardson *et al.* 2009; Stringell *et al.* 2015a; Stringell *et al.* 2013) that are subject to
148 one of the largest legal turtle fisheries in the Caribbean ([Humber *et al.* 2014](#); Stringell

149 *et al.* 2013). The stomach contents of juvenile and adult turtles landed by fishers at
150 Grand Turk, Providenciales and South Caicos were sampled between 2008 and
151 2010, permitting large sample sizes of both species.

152

153 Habitat surveys

154

155 To characterise the epibenthic macrofaunal communities, shallow (<10m depth)
156 snorkelling surveys were made throughout October 2010. Sixteen survey sites were
157 selected to represent turtle fishing sites, based on the information acquired during
158 fisher interviews, and turtle capture-mark-recapture (CMR) sampling sites (Authors'
159 unpublished data and Stringell *et al.* 2015b) (Fig. 1). Four reef-based habitats (reef,
160 patch reef, hard bottom and gorgonian plains) and four seagrass-based habitats
161 (seagrass, seagrass-algae, algae and coralline algae) were surveyed at these
162 locations, some of which had two or more representative habitats (supplementary
163 Table S1). Approximate survey areas ranged between 0.08 and 1.2 km² (see
164 supplementary Table S1). These surveys enabled us to quantitatively describe
165 presence, diversity and abundance of possible prey species at several locations and
166 habitats in order to compare relative proportions of species groups to those found in
167 stomach contents.

168 The communities at each habitat were described from a total of 1061
169 photoquadrat images taken at random locations using a housed Canon Powershot
170 G10 digital camera, attached to a 0.25m² quadrat framer (the quadrat was divided
171 into 25 cells). Between 14 and 48 photoquadrats were analysed from 15-105 images
172 per habitat (except at Long Cay reef where, due to water depth, only six quadrats
173 were photographed and analysed; supplementary Table S1). At each habitat in each
174 location, a sample of two to four quadrats were surveyed *in situ* to validate
175 photoquadrat data. Species abundance was enumerated by cell frequency counts
176 (see supplementary methods for further details).

177

178 Sampling turtles

179

180 For two years (from November 2008), we monitored the legal turtle fishery at key
181 landing sites throughout TCI (see Stringell *et al.* 2013 for details). Turtle capture

182 location was estimated following fisher interviews (Authors' unpublished data and
183 Stringell *et al.* 2015b). Size in juvenile to adult sized turtles ($n=91$ green turtles, $n=45$
184 hawksbill turtles) was measured along the midpoint of the carapace (Curved
185 Carapace Length (notch to tip, cm, CCL): Bolten 1999). The sex of turtles was
186 determined by gross morphology and histology of the gonads of butchered animals
187 or external morphology in adults (Stringell *et al.* 2013).

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

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

197

198 Data analysis

199

200 All multivariate statistical routines were carried out in PRIMER v6 software (Clarke &
201 Gorley 2006) with the PERMANOVA+ add on (Anderson *et al.* 2008). Univariate tests
202 were implemented in R v 2.12 (R-Development-Core-Team 2012).

203

204 *Habitat analysis*

205

206 Differences in abundance data (Bray-Curtis similarities of photoquadrat data) among
207 the eight habitats were tested with a one-way permutational multivariate analysis of
208 variance (PERMANOVA) and for differences in multivariate dispersion by
209 permutation (PERMDISP) (Anderson *et al.* 2008). Taxonomic distinctness routines
210 were used to compare species found in the photoquadrats with those expected to be
211 found in the environment (see *Relating stomach contents to habitat*
212 section for description of taxonomic distinctness, and supplementary material for
213 detailed methods).

214 Habitats were further grouped into two broad habitat types (reef-based and

215 seagrass-based habitats) and compared to hawksbill and green turtle stomach
216 content data, respectively, using a one-way analysis of similarities (ANOSIM, Clarke
217 1993).

218

219 *Stomach content analysis*

220

221 Dietary species biomass was standardised (by total) to account for differences in
222 stomach fullness, and square root transformed. Bray-Curtis similarities were used for
223 subsequent resemblance based tests and visualised in a non-metric multi-
224 dimensional scaling ordination (MDS) with a vector plot overlay of diet species most
225 correlated with the pattern (Clarke 1993). A similarity of percentages (SIMPER)
226 routine (Clarke 1993) was used to examine differences in diet species composition
227 between turtle species. Differences between turtle species and *a priori* grouping
228 factors (habitat, sex), with turtle size as a covariate, were tested using 3-way crossed
229 multivariate permutational analysis of covariance (PERMANCOVA) (Anderson *et al.*
230 2008). The PERMANCOVA used permutations under a reduced model, Type 1
231 (sequential) sums of squares, and non-significant interaction terms were sequentially
232 removed during model simplification. Differences in multivariate dispersion among
233 groups were tested using PERMDISP.

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

240 Diet species were also grouped into nine taxonomic categories (as above) and
241 visualised for differences in diet groups with size (CCL) between the two turtle
242 species, and tested with a one-way ANOSIM.

243

244 *Relating stomach contents to habitat*

245

246 Species in habitat and stomach content samples were grouped into nine
247 taxonomic categories (seagrasses, sponges, bluegreen algae, green algae, red

248 algae, brown algae, cnidarians, invertebrates and unknown). We compared the
249 relative abundance of these nine diet groups in hawksbills and green turtles against
250 the relative abundances of the same groups identified in reef and seagrass habitats,
251 and tested this using a Pearson's Chi-square analysis with Monte Carlo simulated P-
252 values from 10,000 replicates.

253 To determine how representative stomach content samples were in relation to
254 species available in the habitat, AvTD and VarTD were assessed for stomach
255 content samples by turtle species. These diversity measures are based on the
256 relatedness of species drawn at random from a sample, are independent of the
257 number of species (a better statistical sampling property than richness related
258 estimators), and can be used to compare data from differing sampling effort, spatial
259 and temporal scales (such as stomach samples and habitat species lists) (Clarke &
260 Warwick 1998; Clarke & Warwick 2001b). Here, taxonomic distinctness is defined
261 from a Linnaean tree (taxonomic aggregation file) of macrobenthic species likely in
262 TCI. A regional master list of 565 likely species was created from species identified in
263 the habitat surveys, stomach content analysis and from searches of the World
264 Register of Marine Species (WoRMS) database (Appeltans *et al.* 2012) for sponge,
265 gorgonian, coral, seagrass and algae species previously recorded in TCI and
266 neighbouring Bahamas.

267 The two taxonomic distinctness measures were used in a taxonomic
268 distinctness test (TAXDTEST, Clarke & Gorley 2006), where stomach content
269 sample data were superimposed on a funnel plot of expected AvTD and VarTD 95%
270 probability limits that were created from randomised draws of sublists of 2 to 20
271 species from the regional master list. The weighting of Linnaean tree step lengths
272 was guided by taxon richness of the master file (Clarke & Warwick 1999) and the
273 simulation of random draws was weighted by the frequencies of species found in the
274 habitat surveys (Clarke & Gorley 2006). A Mann-Whitney U test was used to formally
275 compare the differences in AvTD and VarTD between turtle species.

276

277

278 Results

279

280 Habitat surveys

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282 Species abundance differed significantly among the eight surveyed habitats and
283 these differences were driven largely by seagrass and algae species (Spearman
284 correlation >0.5) (PERMANOVA, Pseudo- $F_{(7)}=78.6$, $P_{\text{perm}}=0.001$: supplementary
285 Fig. S1). Dispersion among habitats was also significantly different (PERMDISP,
286 $F_{(7,810)}=81.9$, $P_{\text{perm}}=0.001$) with patch reefs having the highest mean dispersion
287 ($58.9 \pm \text{SE } 0.4$) and coralline algae habitats having the least (26.0 ± 1.8)
288 (supplementary Fig. S1). As expected, the relative proportions of the nine species
289 categories in photoquadrats indicated clear differences between reef and seagrass
290 habitats, such that algae and cnidarians were more common in reef habitats where
291 seagrass were absent (ANOSIM, $R=0.753$, $P=0.001$: Fig. 2).

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

306

307 Turtle stomach contents

308

309 We identified a total of 93 prey species in 137 turtle stomach samples (47 species in
310 92 green turtle stomach samples, and 73 species in 45 hawksbill samples;

311 supplementary Table S2). In green turtles, the diet was mainly herbivorous
312 (approximately 92% seagrass and algae by biomass) but with varying amounts of
313 sponge (average 7% biomass; Table 1, supplementary Table S2). The seagrass
314 *Thalassia testudinum* contributed the greatest to biomass (73%) in green turtle diet.
315 This was followed, in decreasing order, by the seagrass *Syringodium filiforme* (16%),
316 the sponge *Chondrilla caribensis* (formerly *C. nucula*) (4%), and the seagrass
317 *Halodule beaudettei* (2%). Remaining species contributed <1% each. When
318 considering, frequency of occurrence in green turtles, *T. testudinum* was found in
319 95% of all stomach samples, *S. filiforme* and *H. beaudettei* in 58%, the green algae
320 *Batophora oerstedii* in 18% and *C. caribensis* in 16%. Plastics were found in 4%
321 ($n=4$) of samples in trace amounts.

322 In hawksbill turtles, diet was more varied and omnivorous, with individuals
323 mostly consuming sponges and algae (approximately 99% by biomass) (Table 1,
324 supplementary Table S2). 27% of the hawksbill turtle diet biomass comprised of the
325 sponge *C. caribensis*, followed by the sponges *Sidonops neptuni* (17%), *Halichondria*
326 *melanadocia* (16%), *Scopalina ruetzleri* (8%), *Cinachyrella alloclada* (5%), *Erylus*
327 *formosus* (4%), the red algae *Gelidiella acerosa* (3%), and an unidentified red algae
328 (2%). Remaining species contributed <2% each. When considering frequency of
329 occurrence in hawksbill turtles, the commonest species in stomach samples were the
330 sponges *C. caribensis*, *H. Melanadocia*, *S. neptuni* (47%, 29%, 24%, respectively)
331 followed by the brown algae *Padina* spp. (22%), the red algae, *Gelidiella acerosa*
332 (18%) and the seagrasses *S. filiforme* and *T. Testudinum* in 18% and 16% of
333 samples, respectively. Plastics were found in 9% ($n=4$) of samples in trace amounts.

334 For both turtle species, no significant differences were found in diet
335 composition (Bray-Curtis similarities of standardised biomass) between sexes and
336 among habitat type in which the turtle was found. However, as expected, there was a
337 clear difference in diet composition between turtle species (Bray-Curtis similarities of
338 standardised biomass: PERMANCOVA (turtle species factor), Pseudo- $F_{(1)}=58.9$,
339 $P_{\text{perm}} < 0.001$; diet categories: ANOSIM, $R = 0.957$, $P = 0.001$; Fig. 2). A SIMPER
340 analysis confirms that *T. testudinum* and *S. filiforme* seagrasses, and *C. caribensis*,
341 *S. neptuni* and *H. melanadocia* sponges together contributed 70% to the dissimilarity
342 (or 30% similarity) between the turtle species. *T. Testudinum* made the largest
343 contribution to the difference and explained 32% of the dissimilarity, and *C.*
344 *caribensis* explained 13%, with their average abundances being highest in green

345 turtles and hawksbill turtles, respectively (Fig. 3).

346 Green turtles measured between 28.8cm and 88.0 cm CCL (mean=52.8 ± SD
347 12.6, $n=91$) and hawksbill turtles measured between 39.3cm and 91.2 cm (60.4 ±
348 14.0, $n=45$) (supplementary Fig. S3). There were no discernible diet differences with
349 size (supplementary Fig. S4), either as a continuous predictor or grouped into 10cm
350 size classes. Turtle size did not significantly explain the diversity of species in turtle
351 diet when expressed as Species richness (S), Species evenness (Simpson's), or
352 VarTD, but there was a weak suggestion of size partitioning in green turtles with the
353 taxonomic breadth of diet (AvTD) reducing with larger sizes (GAM, $P=0.04$) (Figs. 4
354 and 5).

355

356 Relating stomach contents to habitat

357

358 Diet variability (multivariate dispersion of Bray-Curtis similarities) differed significantly
359 between turtle species found at reef and seagrass habitats (PERMDISP, $F_{(3, 123)} =$
360 18.486, $P_{\text{perm}} = 0.001$). For example, diet from hawksbill turtles captured on reef
361 habitats had the highest mean dispersion of 62.6 ± 1.3 (SE) and 53.5 ± 6.3 from
362 seagrass habitats. Green turtles had significantly lower dispersion than hawksbill
363 turtles: 35.8 ± 4.0 and 25.7 ± 1.7 from reef and seagrass habitats, respectively.
364 These results suggest green turtles had the narrowest range of diet of the two
365 species, especially those from seagrass habitats.

366 The analysis of AvTD (on presence-absence stomach content data) showed
367 that all hawksbill turtle stomach samples remained within the 'funnel of 95%
368 confidence' (Fig. 6a). This indicates that hawksbill turtles fed randomly on what was
369 available in the habitat, that is, their varied diet consisted of species that were as
370 taxonomically related as those chosen at random from a species list of >500 species.
371 For green turtles, 43% ($n=40$ of 92) of the stomach content samples had significantly
372 lower ($P<0.05$) AvTD than expected (Fig. 6a). This indicates that these green turtles
373 exhibited strong dietary selectivity by having a relatively taxonomically narrow diet in
374 comparison to the habitat. However, 57% of individuals had diets that fell within the
375 habitat probability limits and were relatively taxonomically wide (Fig. 6a). There was
376 much less departure from probability limits in the case of VarTD for both species
377 (5%, $n=5$ of 92 green turtles; no hawksbill turtles), indicating similar variation in
378 taxonomic distinctness of species in turtle stomachs to those chosen at random from

379 the habitat (Fig. 6b). These results are confirmed by formal tests of these metrics
380 with significantly greater average taxonomic breadth (AvTD) found in hawksbill turtle
381 stomach samples than in green turtles (Wilcoxon, $W = 1555$, $P = 0.018$), but not for
382 VarTD ($W = 2193$, $P = 0.568$).

383 The relative percentage biomass of the nine diet groups in average hawksbill
384 turtle stomach content samples differed significantly from the relative abundances of
385 these same groups in average reef-based habitat photoquadrats ($\chi^2 = 164.89$,
386 $P_{\text{perm}} < 0.001$) and seagrass-based habitats ($\chi^2 = 171.94$, $P_{\text{perm}} < 0.001$). This indicates
387 that although many of the same species were present in stomach content samples
388 and the habitat, they were not consumed at the same relative proportions. For
389 example and as expected, in hawksbill turtle stomach content samples, sponges
390 were found in much higher proportions and brown algae at lower proportions than in
391 reef habitats (Fig. 2a). Relative proportions of diet groups in green turtle stomach
392 content samples differed significantly to the proportions of these same diet groups in
393 seagrass habitats ($\chi^2 = 25.67$, $P_{\text{perm}} < 0.001$) and reef habitats ($\chi^2 = 187.92$,
394 $P_{\text{perm}} < 0.001$) (Fig. 2b); although there was some similarity in seagrass proportions
395 between seagrass habitats and green turtle diet. These data, which are based on the
396 amounts of each diet item, have differing inferences to the results of the taxonomic
397 distinctness routines that, as diversity measures, are based on presence-absence
398 data and Linnaean relatedness.

399

400 **Discussion**

401 Knowledge of supporting habitats is essential to inform our understanding of the
402 foraging ecology and role of marine turtles in coastal ecosystems. Our results
403 demonstrate clear niche separation between the two turtle species, using relative
404 percentages and taxonomic distinctness of diet. To our knowledge, this study is the
405 first to examine taxonomic distinctness in the diet of marine turtles.

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

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

438 Apart from seagrasses, the relative proportions of prey species in green turtle
439 stomachs did not statistically match those in seagrass habitats, especially for red
440 algae, green algae and sponge proportions. This suggests a selective feeding
441 strategy and a functional linkage between consumer and habitat that supports the
442 findings of others (Table 1, [Bjorndal 1980](#); [Bjorndal 1997](#); [León & Bjorndal 2002](#);
443 [Mortimer 1981](#); [Rincon-Diaz *et al.* 2011](#); [Santos *et al.* 2011](#); [Seminoff *et al.* 2002](#); [Van
444 Dam & Diez 1997](#)). In green turtles, the AvTD routine indicates that for nearly half of

445 the stomach content samples, the relatedness of species in the diet was less
446 taxonomically distinct than that of the species available in the surrounding habitat,
447 also suggesting a degree of selective feeding. The relatively low taxonomic
448 distinctness of green turtle diet is likely a result of the narrow taxonomic distinctness
449 of seagrasses (three species from two families) that make up the majority of the
450 green turtle diet (in terms of biomass). However, the several algae species (>5%
451 frequency, mainly Chlorophytes: Table 1) found in green turtle stomachs may have
452 elevated the taxonomic distinctness of the stomach samples. Although green turtles
453 can be found in both reef and seagrass habitats, the low taxonomic distinctness of
454 green turtle diets is likely a result of seagrass-based habitats having lower species
455 diversity than reef-based habitats.

456 Hawksbill turtles are most commonly associated with reef-based habitats (but
457 see Bjorndal & Bolten 2010 for the importance of seagrass beds to hawksbill turtles).
458 Therefore, if hawksbill turtles graze randomly, we might expect them to have a diet
459 more diverse than that of green turtles and one that perhaps reflects the diversity of
460 species found in reef systems. However, in terms of relative abundance of diet type,
461 hawksbill turtle diet was not representative of reef habitat, a finding that supports
462 selective feeding mostly on sponges and algae (Bjorndal 1997; León & Bjorndal
463 2002; Rincon-Diaz *et al.* 2011; Van Dam & Diez 1997). In terms of taxonomic breadth
464 (AvTD), however, every sample fell within the funnel of taxonomic expectation,
465 suggesting they might be generalists or indiscriminate feeders that graze randomly
466 (*sensu* Carr & Stancyk 1975) and have a diet representative of available species.

467 These seemingly conflicting results may be due to several reasons: 1)
468 sponges house many symbiotic, parasitic and commensal animal and plant species
469 (which may have more nutritional value than the sponges themselves), increasing the
470 apparent taxonomic breadth of diet; 2) sponges may not be easily digestible or
471 nutritious (Bjorndal 1985) and may remain in the stomach longer than other readily
472 digestible taxa; 3) presence-absence data in taxonomic distinctness routines gives
473 equal weighting to rare species; 4) sponges are from a phylum of especially wide
474 taxonomic breadth - two species of sponge may be as distinct from each other as two
475 unrelated species drawn at random (this also applies to algae, which encompass
476 several kingdoms and phyla); and 5) Caribbean reefs are generally sponge and
477 algae dominated (McMurray *et al.* 2010; Mumby 2009), and the taxonomic routines
478 may be telling us that hawksbill turtles eat a broad range of sponges and algae which

479 dominate the reef systems in TCI (see supplementary information on habitat
480 descriptions – reef sites are dominated by various species of algae).

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

492 Many of the diet species identified in turtle stomachs are found across the
493 different habitat types and at most locations. For example, the sponge *C. caribensis*
494 occurred in both reef and seagrass habitats. The form of this sponge (*C. caribensis f.*
495 *caribensis*) commonly found in hawksbill and green turtle stomachs from our study is
496 more usually associated with seagrass habitats. Additionally, 22% of hawksbill turtle
497 stomachs contained seagrass, suggesting the importance of seagrass habitats to
498 foraging hawksbill turtles ([Bjorndal & Bolten 2010](#)). In the present study, several
499 sponge species were also found in green turtle diet. While consumption of sponges
500 by green turtles has been previously reported ([Bjorndal 1990](#)), the extent of the
501 finding is surprising. Sixteen percent of green turtle stomach samples contained *C.*
502 *caribensis*, indicating this sponge is likely to be purposefully consumed. Further, Fig.
503 3 illustrates that one green turtle had a diet dominated by sponges, perhaps
504 representing active consumption of these taxa.

505 In our study, habitat surveys were restricted to shallow depths (<10m), while
506 foraging turtles clearly dive much deeper ([Blumenthal et al. 2010](#); [Blumenthal et al.](#)
507 [2009](#)). Diving ability in marine turtles scales with body size ([Schreer & Kovacs 1997](#))
508 and size partitioning by depth is well known ([Musick & Limpus 1997](#)). Once turtles
509 recruit from the oceanic-pelagic zone and settle in coastal waters to feed benthically,
510 they are probably limited to shallow habitats that contain seagrass and patch reefs,
511 while larger turtles are able to forage at greater depths where other food types are
512 found. Consequently, we may have better surveyed the core habitat of smaller turtles

513 rather than that of larger ones. Therefore, the relative abundance of species in our
514 habitat surveys is unlikely to fully represent what is available to turtles and
515 consequently what is found in turtle stomachs. All published studies that link habitat
516 type to stomach contents, however, are also restricted to shallow survey depths and
517 typically survey only those species that were identified in stomach samples (León &
518 Bjorndal 2002; [Rincon-Diaz *et al.* 2011](#); Van Dam & Diez 1997), thereby biasing the
519 availability of species in random surveys. Thus, habitat surveys rarely (if ever) fully
520 represent the foraging breadth of aquatic consumers.

521 Taxonomic distinctness routines go some way to removing this bias by using
522 comprehensive species lists ([Clarke & Warwick 1998](#); [Clarke & Warwick 1999](#);
523 [Clarke & Warwick 2001a](#); [Clarke & Warwick 2001b](#)). In our case, a list of species
524 recorded primarily from the Bahamas region (from the WoRMS database), from our
525 habitat surveys and stomach content samples were used to compile the master
526 species list. From this list, random draws were taken to generate a habitat 'baseline'
527 (directed by the relative frequencies of species found in our habitat surveys to 'fine-
528 tune' the baseline) against which the composition of turtle stomach samples were
529 compared. This provides a more robust assessment of habitat linkage than typical
530 habitat surveys of only those species selected from stomach samples. Additionally,
531 the use of a temporally independent species list as the baseline avoids issues with
532 the differences in the timing of stomach content sample collection (Nov 2008 to Nov
533 2010) and habitat surveys (Oct 2010). In our relative abundance comparisons, the
534 timing of our habitat surveys may have had some influence on the results. However,
535 due to logistical constraints we were unable to conduct any more habitat surveys.
536 Temporally spread habitat surveys would be advised for future studies to examine
537 whether comparisons of diet and habitat composition are sensitive to temporal
538 differences.

539 Stomach contents represent only a snapshot of feeding by marine turtles and
540 may not adequately relate to what is assimilated into bodily tissue over time. This is a
541 key disadvantage with stomach content analysis ([Barrett *et al.* 2007](#); [Duffy & Jackson
542 1986](#)). Diet varies considerably among individuals and locations ([Bjorndal 1997](#)) but
543 can also vary in individuals through time, as demonstrated by the different diet
544 components found along the alimentary canal of green turtles ([Arthur *et al.* 2009](#);
545 [Vélez-Rubio *et al.* 2014](#)). Additionally, some prey species may have been completely

546 digested in stomach samples, precluding their identification. Videos from animal-
547 borne cameras on green turtles from California ([Seminoff *et al.* 2006](#)) suggest the
548 importance of cnidarians and algae to green turtle diet. It is possible, therefore, that
549 soft bodied invertebrates and readily digestible algae are underrepresented in our
550 study, although we note that most stomach samples in our study were surprisingly
551 well preserved, an observation also shared by Mortimer (1981).

552 Given the sponge and algae dominated, yet taxonomically broad, diet of
553 hawksbill turtles, and the selective grazing of green turtles, these sympatric species
554 are likely to play key grazing roles in Caribbean seagrass and reef systems. Both
555 green and hawksbill turtles are among the largest grazers in the tropics and are
556 thought to have critical roles in regulating the structure and function of reef and
557 seagrass habitats (Bjorndal & Jackson 2003). Some sponge species, notably *C.*
558 *caribensis*, are superior competitors with corals in reef habitats (Hill 1998; Wulff
559 2012). Hawksbill turtles, as spongivores, thus undoubtedly play a key role in the
560 ecological interactions between this species and many other sponges, corals and
561 algae. We are gradually building a more complete picture of the ecological dynamics
562 that relate habitat to consumers and predators. For example, Heithaus *et al.* (2007)
563 suggested that declines in seagrass beds in Bermuda may be linked to increases in
564 green turtle populations (Murdoch *et al.* 2007), which coincide with declines in tiger
565 sharks in the northwest Atlantic (Baum *et al.* 2003). This suggests top-down effects
566 of marine predators may be profound (Heithaus *et al.* 2008) not only on regulating
567 the abundance and distribution of grazers (turtles) but on the structure and function
568 of habitats ([Thayer *et al.* 1984](#)).

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585

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830

831 **Table 1** Frequency of occurrence (proportion of turtles in which present) and average (\pm SD and range) proportion of biomass of
 832 taxonomic diet groups found in stomach content samples of green turtles ($n=92$) and hawksbill turtles ($n=45$). See Supplementary
 833 Table S2 for further details
 834

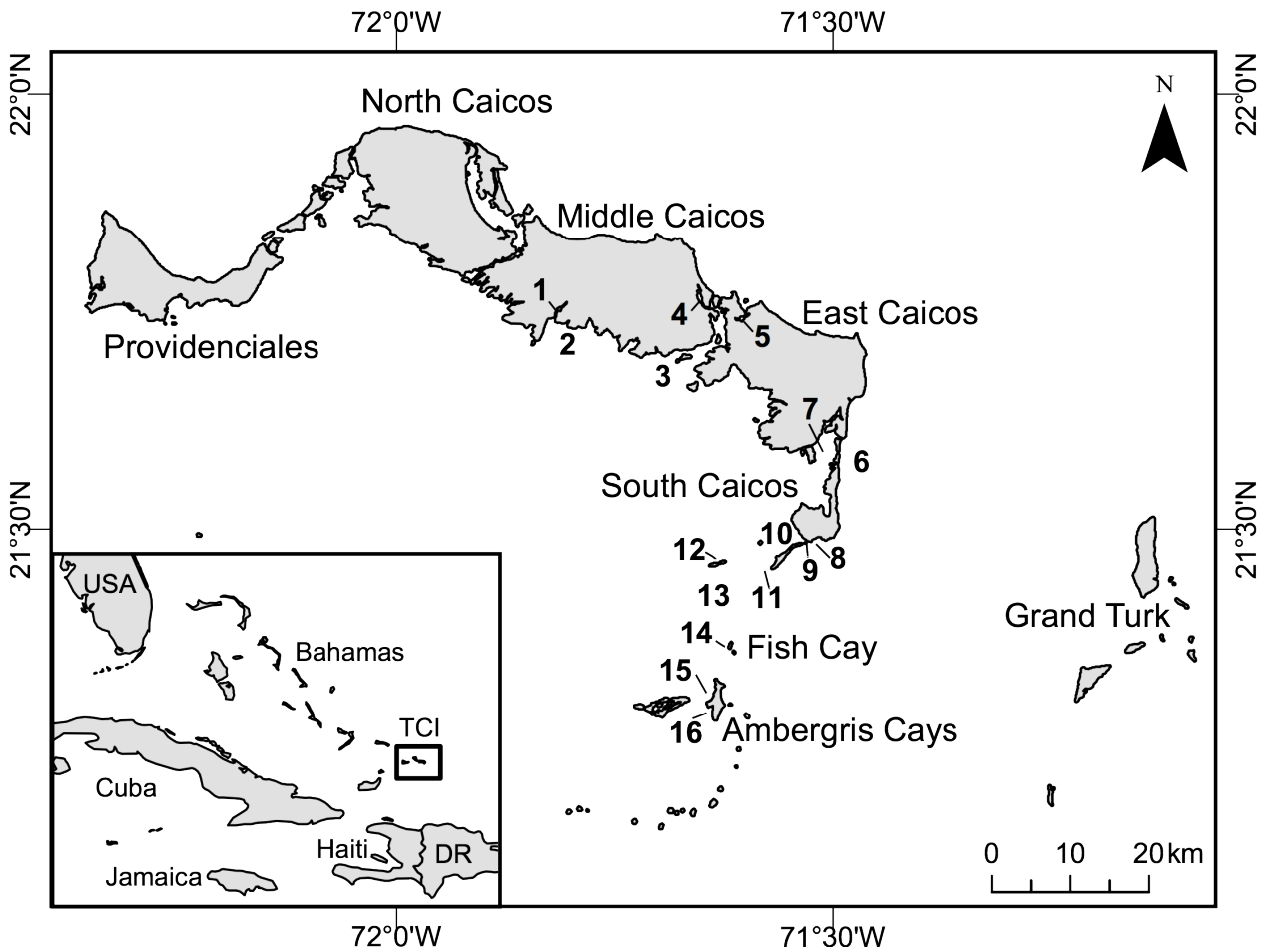
Diet group	Green turtle				Hawksbill turtle			
	Proportion of turtles	Biomass			Proportion of turtles	Biomass		
		Mean	\pm SD	Range		Mean	\pm SD	Range
Seagrasses	0.99	0.91	0.17	(0.00 - 1.00)	0.22	*	0.01	(0.00 - 0.04)
Red algae	0.26	0.01	0.10	(0.00 - 0.97)	0.49	0.10	0.20	(0.00 - 0.70)
Brown algae	0.08	*	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 [†]	0.03	*	*	(0.00 - *)	0.09	*	*	(0.00 - *)
Plastic	0.04	*	*	(0.00 - *)	0.09	*	*	(0.00 - *)

835 * = <0.01 (trace) [†] Platyhelminthes, Mollusca, Arthropoda

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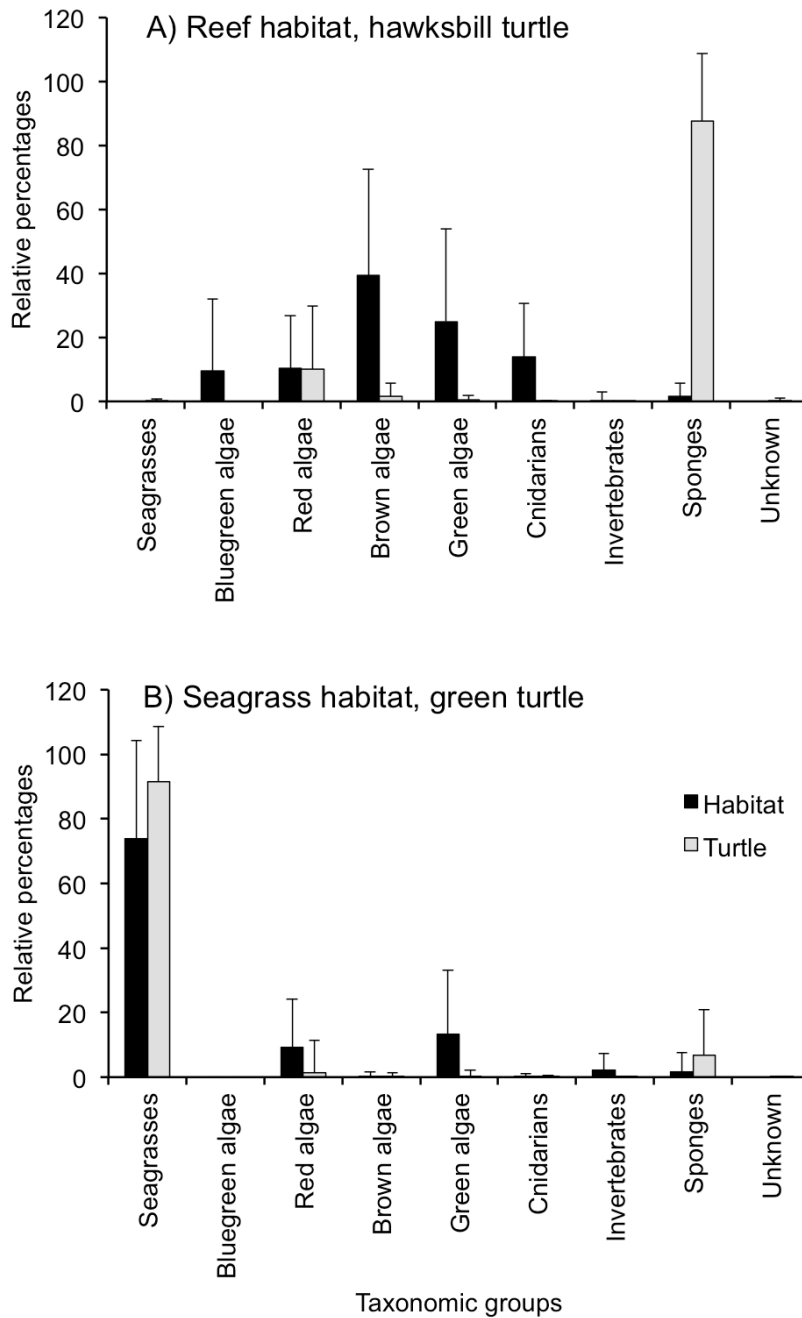


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840

841 **Fig. 1** Map of Turks and Caicos Islands (TCI) and location in Wider Caribbean
842 Region (inset, DR=Dominican Republic). Numbers indicate the following survey
843 sites: 1=Man-o-War, 2=Ocean Hole, 3=Southern Bush, 4=Lorimers Creek,
844 5=Jacksonville, 6=Eastside, 7=Nuisance Point, 8=Tuckers Reef, 9=Shark Alley,
845 10=Harbour, 11=Long Cay, 12=Six Hills, 13=Middle Reefs, 14=Fish Cay,
846 15=Ambergris, and 16=Ambergris Airport. See supplementary Table S1 for further
847 information on sites, habitats and sampling effort

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850 **Fig. 2** Average relative percentages (± 1 SD, error bars) of taxonomic diet groups.

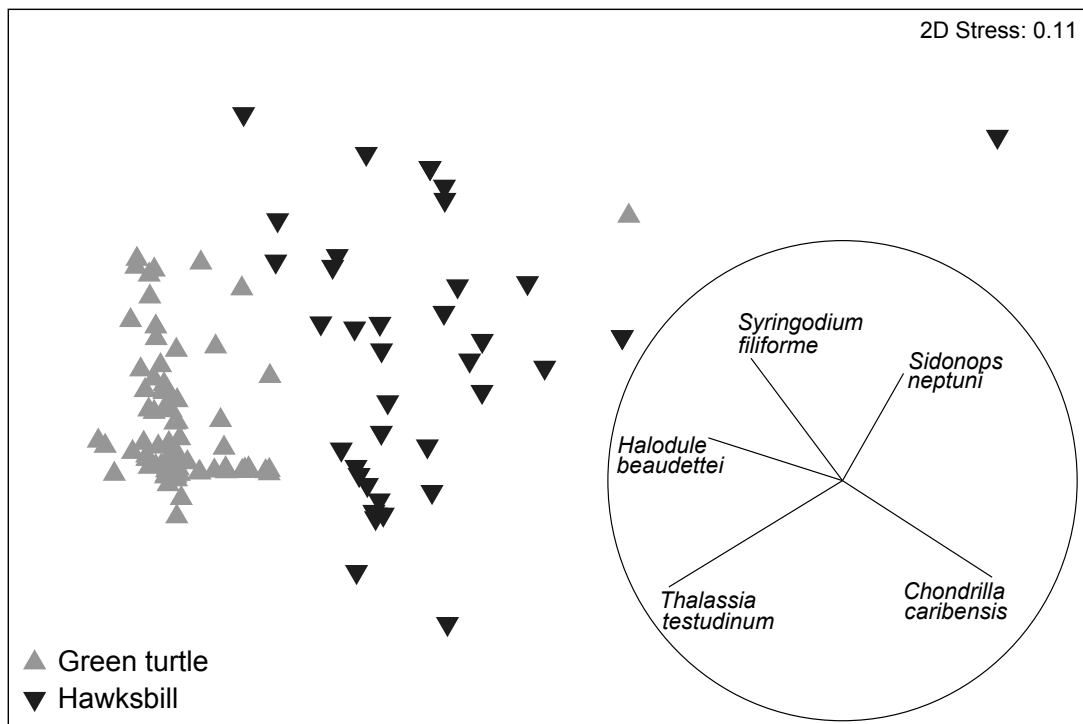
851 Reef habitat photoquadrats (abundance: $n = 406$) and hawksbill turtle stomach

852 samples (biomass: $n = 45$) are presented in panel (A). Seagrass habitat

853 photoquadrats (abundance: $n = 331$) and green turtle stomach samples (biomass: n

854 = 92) are presented in panel (B). Habitats are represented by black bars and turtle

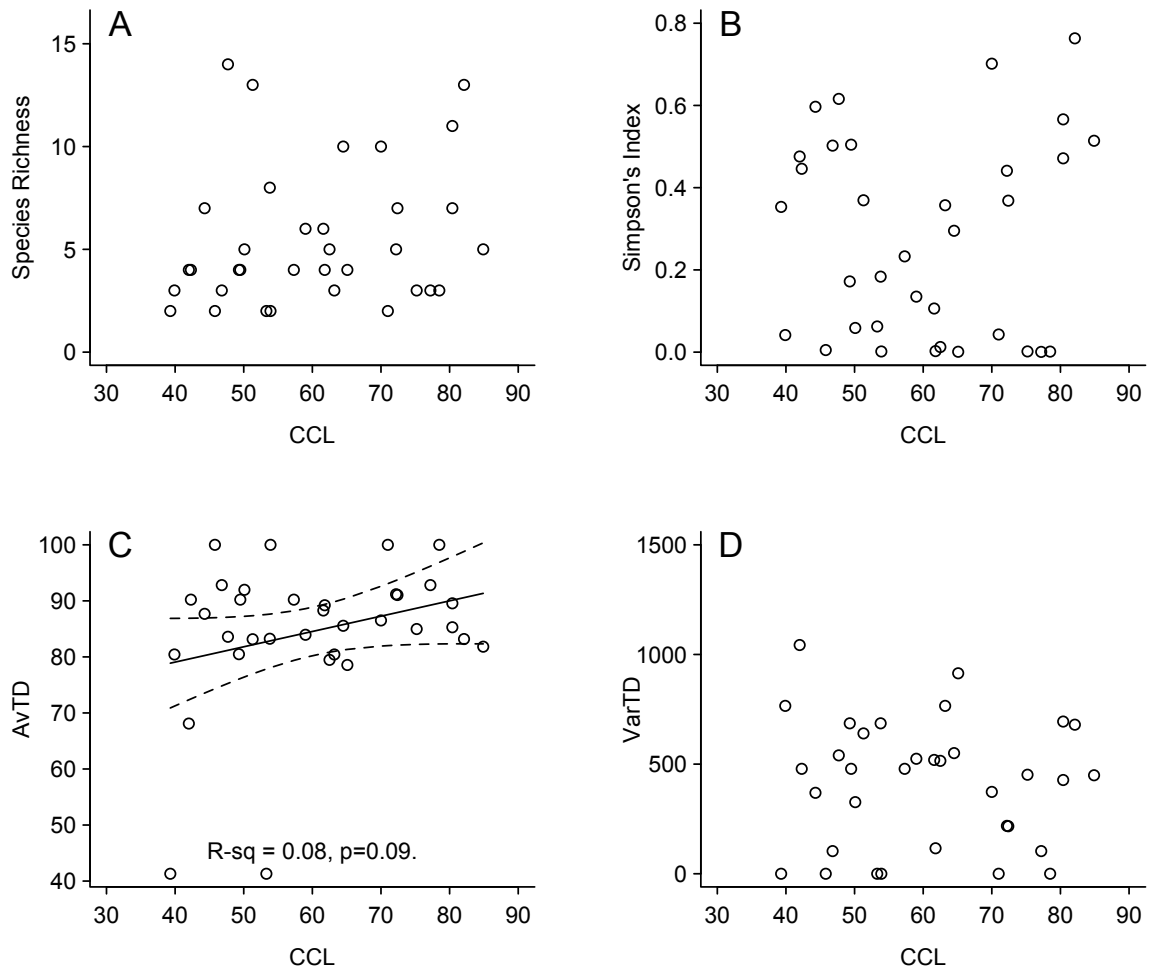
855 species by pale grey



857

858 **Fig. 3** Non-metric multidimensional scaling ordination of stomach content with vector
 859 overlay of most contributing species ($R > 0.5$ Spearman's correlation; derived from
 860 SIMPER analysis). Stomach content biomass data are standardised, square root
 861 transformed Bray-Curtis similarities. Three hawksbill turtle outliers (not shown) lie
 862 outside of plot boundary (to the northeast) and were dominated by *Sidonops neptuni*
 863 in their diet

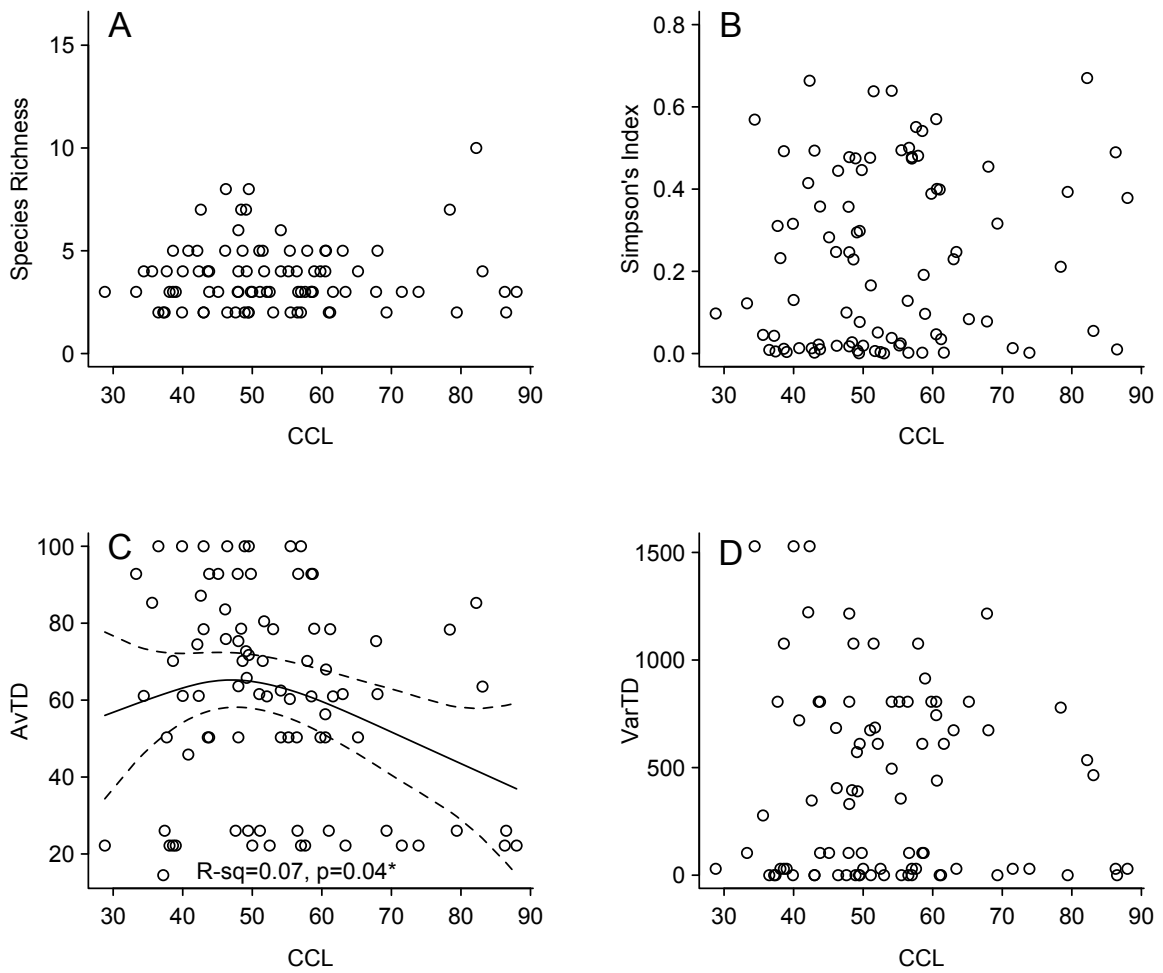
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865

866 **Fig. 4** Species diversity measures of stomach content samples against hawkbill
 867 turtle size (CCL, cm). (A) species richness, (B) Simpson's index (calculated on
 868 biomass), (C) average taxonomic distinctness, (D) variation in taxonomic
 869 distinctness

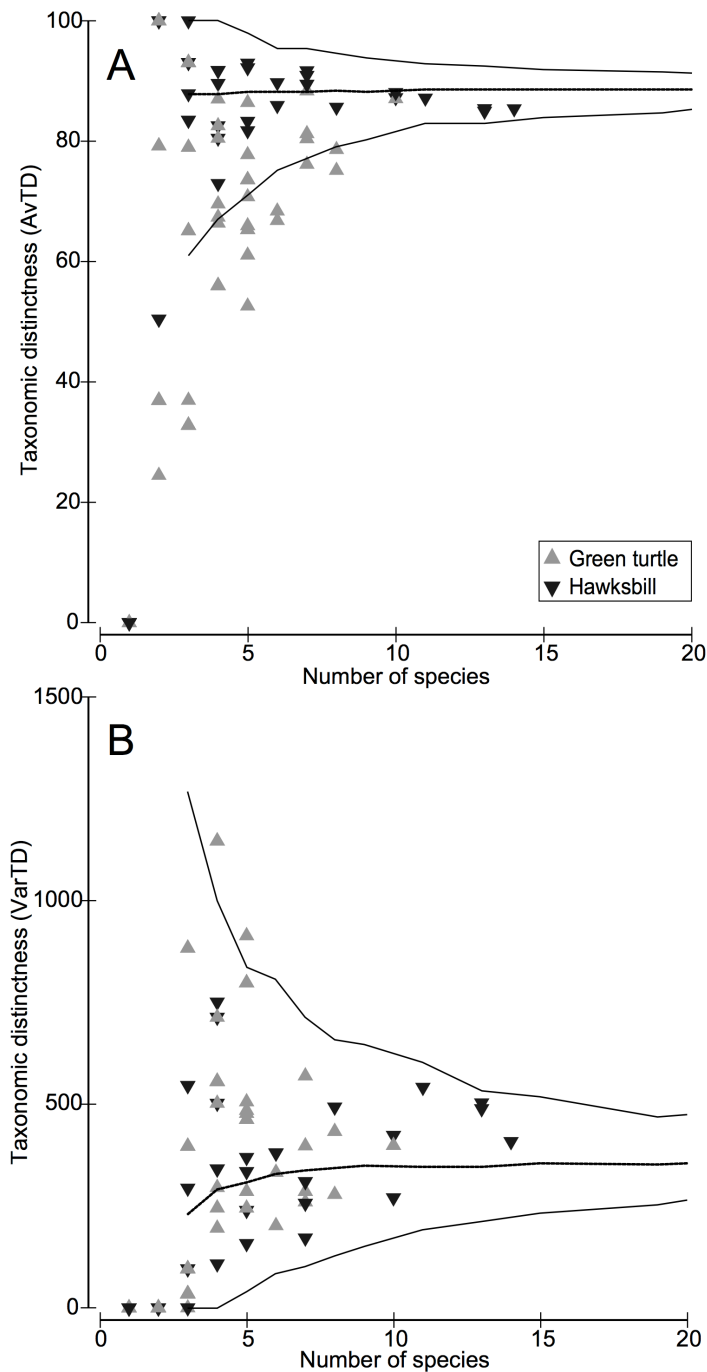
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872 **Fig. 5** Species diversity measures of stomach content samples against green turtle
 873 size (CCL, cm). (A) species richness, (B) Simpson's index (calculated on biomass),
 874 (C) average taxonomic distinctness, (D) variation in taxonomic distinctness

875



876
 877 **Fig. 6** Average (A) and variation (B) in taxonomic distinctness of stomach contents
 878 from two turtle species ($n = 45$ hawksbill turtles, $n = 92$ green turtles). Lines indicate
 879 the median and upper and lower 95% probability intervals of taxonomic distinctness
 880 created from randomised draws of sublists of 2 to 20 species from a regional master
 881 list of 565 species. Weighting of Linnaean tree step lengths was guided by taxon
 882 richness of the master list and frequencies of species found in the habitat surveys
 883 were used to weight the selection of the random species
 884