

1 **Epibenthic community assessments indicate high spatial and temporal variability**
2 **among continental shelf hard bottom sites in a marine transition zone**

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20 **ABSTRACT**

21 We studied 19 hard bottom sites within Onslow Bay, North Carolina during 2007-2010
22 using photoquadrat analyses to investigate the role of temperature, depth, and fish
23 community variables in the structure of the epibenthic (macroalgae and sessile
24 invertebrates) community. Although significant variation in community structure was
25 found both by site and year, depth was the most important factor in structuring these
26 epibenthic communities with significant differences found among five depth categories:
27 18-20 m; 24-29.2 m; 31 m; 32.5-37 m; 38.5-42 m. The largest community difference was
28 found between depths ≤ 31 m and ≥ 32.5 m, resulting in a shift from macroalgae
29 dominance at the shallower sites to shared macroalgae and sessile invertebrate
30 dominance at deeper sites. Depth is a complicated variable as it relates to structuring
31 the epibenthic community in this region because it reflects varying winter bottom water
32 temperatures, light levels, and periodicity of nutrient influxes. The location of North
33 Carolina marine habitats at the transition from cold-temperate to warm-
34 temperate/tropical zones, and the spatial compression of this transition zone along
35 inshore to offshore transects make this an ideal area for tracking climate change related
36 shifts in marine communities. However, a better understanding of the relationship among
37 variables such as depth, light, temperature and nutrients and the epibenthic community,
38 as well as seasonal and short annual community variation, is needed before climate
39 related shifts can be determined.

40

41 *Keywords:* community structure; hard bottoms; marine algae; sessile invertebrates;
42 Onslow Bay, North Carolina; LINKTREE analysis

43

44 **1. Introduction**

45 The marine waters of North Carolina are biogeographically important because
46 they encompass a transition zone between cold-temperate and more southerly warm-
47 temperate/tropical regions of the North American East Coast (Searles and Schneider,
48 1980; Spalding et al., 2007). At Cape Hatteras, cooler temperate waters originating from
49 the Labrador Current converge with the warm-water Gulf Stream flowing north creating a
50 sharp north-south temperature gradient. South of Cape Hatteras there is also an
51 inshore-offshore bottom water temperature gradient in winter, characterized by cooler
52 nearshore (shallower) waters that transition to the warmer offshore (deeper) waters
53 moderated by the Gulf Stream. This results in large temperature ranges for the areas
54 near the coast where intracoastal sound and near shore water temperatures vary
55 seasonally by as much as 30°C, while offshore waters have more stable temperatures
56 (Schneider, 1976; Atkinson et al., 1983). Bottom topography, wind and current
57 influenced Gulf Stream upwelling events cause offshore bottom water temperature
58 fluctuations (Atkinson et al., 1983; Pietrafesa et al., 1985); however, usually not on the
59 order of the seasonal fluctuations found in nearshore waters (<20 m deep).

60 Onslow Bay is the area of continental shelf waters extending from Cape Lookout
61 south to Cape Fear, North Carolina (Fig. 1), and it contains the most extensive rock
62 outcrops (“hard bottom”) in the mid-Atlantic (Searles, 1984; Riggs et al., 1996). The large
63 amount of hard bottom substrate and varying bottom water temperatures create a variety
64 of environments suitable for the attachment and survival of diverse epibenthic
65 communities (e.g. Searles and Schneider, 1978). Understanding the structure of
66 epibenthic communities in this region is important because their composition and
67 biomass affect the recruitment and productivity of fish communities (Levin and Hay
68 1996; 2002; Kendall et al., 2009). It is also important because the sessile invertebrates

69 and macroalgae within this transition zone are potential indicator species for
70 understanding climate change (e.g. Precht and Aronson, 2004; Hawkins et al., 2008;
71 Wernberg et al., 2011; Tanaka et al., 2012). Accelerated sea level rise, warming waters,
72 and a slowing Gulf Stream are radically changing the United States East Coast,
73 specifically the mid-Atlantic (Kemp et al., 2009; Sallenger et al., 2012; Ezer et al., 2013).
74 The inshore-offshore winter water temperature gradient in Onslow Bay is a
75 geographically restricted area that reflects community changes within the wider East
76 Coast climatic transition zone. Whitfield et al. (2014) found separate fish communities
77 within Onslow Bay that were related to this winter bottom water temperature gradient
78 and suggested candidate species whose distributions within Onslow Bay could be used
79 as ecological indicators of climatic changes. The epibenthic hard bottom community may
80 be similarly used.

81 Comparisons with studies from the 1970s have found different abundances and
82 distributions of macroalgae in Onslow Bay, and northward range expansions of at least
83 ten species previously restricted to more tropical waters (Schneider and Searles, 1991;
84 Freshwater and Idol, 2013; Freshwater and Whitfield, unpubl. data). However, the
85 variables controlling epibenthic community structure are poorly understood, and defining
86 the influence of depth, bottom water temperature and ecological variables on macroalgal
87 and sessile invertebrate distributions in this region will be critical for developing a better,
88 more predictive, understanding of climate-associated responses in marine hard bottom
89 communities.

90 There have been relatively few studies that describe epibenthic communities off
91 North Carolina or in the Southeast United States Large Marine Ecosystem (SEUSLME).
92 Wenner et al. (1983) found a high diversity of sessile invertebrates that they related to
93 the complexity of bottom types in a central portion of the SEUSLME (southern South
94 Carolina to northern Florida), and that the sessile invertebrate community varied with

95 both depth and season. Further studies off the Georgia coast found different sponge
96 communities associated with specific ledge habitats and related these differences to a
97 combination of biotic (e.g. competition, predation) and abiotic (e.g. sedimentation,
98 currents) factors (Freeman et al., 2007; Ruzicka and Gleason, 2009). Schneider (1976)
99 and Schneider and Searles (1979) reported variable depth and latitudinal distributions of
100 marine algae species off the North Carolina coast, and Goldberg and Heine (2012)
101 found variable macroalgal species richness among sites within Georgia's Gray's Reef
102 National Marine Sanctuary, all suggesting community differences at varying spatial
103 scales. Seasonal and yearly variation in the sessile invertebrate and macroalgal
104 communities at a single Onslow Bay hard bottom site were observed by Peckol and
105 Searles (1983; 1984). This variation resulted from physical disturbance, herbivory,
106 recruitment, and species-specific timing of growth and reproduction. In a subsequent
107 study of two deeper hard bottom sites, Peckol and Ramus (1988) found differences in
108 the dominant macroalgae species at 30 m and 42 m depth that they believed resulted
109 from opposing selective pressures acting in these low light, low nutrient environments.
110 Renaud et al. (1997) observed inter-annual variation in the abundance of dominant
111 macroalgae at three Onslow Bay sites, and this variability was enhanced by periodic
112 storm events that altered substrate availability.

113 Given the general paucity of information on epibenthic (macroalgae and sessile
114 invertebrates) community structure within the SEUSLME, we examined hard bottom
115 communities within Onslow Bay, North Carolina, USA as part of a more comprehensive
116 ecological characterization of the fish communities (Whitfield et al., 2014). The
117 objectives of this study were to provide an initial assessment of the spatial and temporal
118 stability of these communities and examine the role of temperature, depth, and fish
119 community parameters in shaping epibenthic community structure. This is a critical first

120 step in determining the utility of epibenthic communities for monitoring climate change
121 effects within this important marine transition zone.

122

123 **2. Methods**

124 *2.1. Bottom water temperature and depth*

125 To investigate bottom water temperature effects on benthic community structure
126 in Onslow Bay, daily bottom water temperature data were collected from each site using
127 annually retrieved HOBO® water temp pro data loggers (Onset Computer Corp.,
128 Bourne, MA, USA). The data loggers were attached near the substrate and recorded
129 one temperature observation every 30 minutes and averaged by day. Analyses of these
130 data by Whitfield et al. (2014) found summer temperature to be nearly homogeneous
131 across Onslow Bay; accordingly only winter bottom water temperature data were
132 included in this study. Mean winter bottom water temperature each year was calculated
133 for each site, based on the daily average from the three coldest winter months: January,
134 February, and March (Figueira and Booth, 2010; Whitfield et al., 2014). Depth at each
135 site was confirmed in situ, but for analyses depths were calculated using NOAA chart
136 number 11520 by averaging the closest charted depths (<4 km).

137

138 *2.2. Photoquadrat methods*

139 Photoquadrat analyses of the epibenthic community were conducted along 50 m
140 transects as part of a comprehensive characterization of the temperate reef communities
141 that included diver-based fish community surveys along the same transects (Whitfield et
142 al., 2014). The hard bottom reefs, also known as ledges due to their linear geography,
143 ranged from depths of 18-42 m and were chosen to represent a gradient of temperature
144 and depth across the shelf in Onslow Bay (Fig. 1). Surveys were conducted between

145 April and September during 2007–2010, with the exact dates and number of sites
146 surveyed each year dependent on ship time and availability (Table S1, see Appendix A).

147 Photoquadrats were taken by SCUBA divers every 5 m along 50 m transects
148 placed parallel to the upper edge of the hard bottom ledges where the highest reef
149 structure and complexity is generally found. Eleven images were captured along most
150 transects however dive conditions limited some transects to six. Images were framed
151 using a 30 cm² quadrat and captured with Olympus 5060 (6 megapixel) and 7070 (7
152 megapixel) cameras within a Light & Motion underwater housing with a Sea & Sea
153 strobe. Photoquadrats were analyzed using a randomized point intersect method in the
154 Coral Point Count with Excel extension software (CPCe, Kohler and Gill, 2006). An array
155 of 50 random stratified points within a 25 cm² area was projected on each image and
156 macroalgae or sessile invertebrates identified under each point. The number of points
157 was determined based on assessments of species accumulation curves for multiple
158 images taken during 2007 surveys. Species were identified to the lowest taxonomic
159 level possible or classified within morphotypes when identification from images was not
160 possible and percent cover was then calculated. While taxa such as *Solieria filiformis*
161 may be identified to species within photoquadrats, the 16 reported species of crustose
162 coralline and *Peyssonnelia*-like red algae in North Carolina (Suyemoto, 1980; Schneider
163 and Reading, 1987; Schneider and Searles, 1991) could only be classified within a
164 broad group representing multiple species and genera. This was especially problematic
165 when scoring sessile invertebrates, which are poorly studied in Onslow Bay and for the
166 majority, would require destructive sampling to accurately identify. Diversity of
167 taxa/morphotypes is discussed with the understanding that they do not necessarily
168 represent equivalent levels of classification or that the same classification level
169 represents equivalent evolutionary/ecological units.

170

171 *2.3. Multivariate Analysis*

172 The percent cover of each taxa/morphotype from the CPCe photoquadrat data
173 was analyzed using Primer (v. 6, Clarke and Gorley, 2006). Only total benthic biota
174 (macroalgae + sessile invertebrates) was analyzed. The abiotic component was
175 excluded from this analysis. Total benthic biota was first square-root transformed to
176 reduce the influence of common species, and converted into Bray-Curtis similarity
177 matrices in PRIMER (Clarke and Warwick, 2001; Clarke and Gorley, 2006). The
178 categorical variables, year and study site, were examined using analysis of similarity
179 (ANOSIM) (Clarke and Gorley, 2006). The influence of 18 continuous explanatory
180 variables (Table 1) on benthic community structure was examined using the BEST
181 followed by the LINKTREE and SIMPER procedures (Clarke et al., 2008).

182 The continuous explanatory variables were derived from site-specific winter
183 bottom water temperature, depth, habitat height, and fish community surveys conducted
184 from 2007-2010 at the same locations (Table 1). The methods used to collect and
185 process these variables are described in detail in Whitfield et al. (2014) and include fish
186 community density data from two survey types; a larger transect (500 m²) focused on
187 conspicuous mobile fishes and a smaller transect (100 m²) focused on the smaller
188 bodied (<10 cm) cryptic fish community. Site-specific densities for each transect type
189 were calculated for total fish, total predators (carnivorous fish >50 cm), omnivores,
190 herbivores, carnivores, invertivores, piscivores and the invasive Indo-Pacific lionfish.

191 All continuous variables were first observed in draftsman plots, transformed (if
192 needed to correct skewness), normalized and converted to a resemblance matrix using
193 the Euclidean distance coefficient (Clarke and Warwick, 2001). Winter bottom water
194 temperature and depth were found to be collinear ($r > 0.9$) and consequently analyzed
195 separately (Clarke et al., 2008; Whitfield et al., 2014). Next, the BEST procedure was
196 used to examine the importance of the continuous variables in structuring the total

197 benthic biota and once the variable or group of variables comprising the highest
198 Spearman rank correlation were identified, they were used within the LINKTREE
199 procedure to determine actual breaks or thresholds within those data that constitute
200 statistically significant ($p < 0.05$) community differences. Then, the individual
201 taxa/morphotypes responsible for the significant LINKTREE clusters of $B\% > 60$ were
202 further examined using the similarity percentage analysis (SIMPER) procedure. $B\%$
203 represents the absolute measure of the group differences as calculated from the original
204 similarity matrix (Clark and Gorley, 2006). $B\% > 60$ represents a higher significance
205 threshold for the explanatory depth variable and although not chosen a priori, it is similar
206 to the significance threshold chosen for SIMPER analysis of the fish community in the
207 same region (Whitfield et al., 2014).

208

209 **3. Results**

210 Epibenthic communities at all studied sites were found to be significantly different
211 from each other within and across years with the exception of sites 23-1 and CDan1 in
212 2007 (one-way ANOSIM, Global $R = 0.563$, $p = 0.001$). Likewise, when sites were
213 grouped by year, all years were also significantly different (one-way ANOSIM, Global R
214 $= 0.229$, $p = 0.001$). Given that year-to-year differences may result from uneven sampling
215 across the shelf both spatially and seasonally (Table S1, see Appendix A), the data were
216 pooled by site to better examine the general trends. Due to the high correlation between
217 depth and temperature within the area surveyed in Onslow Bay (see Fig. 2 in Whitfield et
218 al. 2014), the role of each was examined separately in the BEST and LINKTREE
219 analysis to avoid statistical problems associated with covariance. Results of the BEST
220 analyses for total sessile biota (macroalgae + invertebrates) indicated that of the 18
221 factors examined, depth was the most important in explaining the structure of this
222 community ($p = 0.311$). Similar to depth, when mean winter temperature was included in

223 analyses (depth excluded due to covariance) it was also the most important in
224 determining epibenthic community structure ($\rho = 0.277$). Since depth, in this case, has a
225 higher spearman rank correlation and is a proxy for multiple factors including
226 temperature, only results of the analysis based on depth are presented.

227 Results from the LINKTREE analysis revealed clustering of the biotic community
228 ($B\% > 60$) into five depth categories: 18-20 m; 24-29.2 m; 31 m; 32.5-37 m; 38.5-42 m
229 (Fig. 2). The largest amount of separation occurred between sites at depths ≤ 31 m and
230 ≥ 32.5 m ($B\% = 77.3$). SIMPER analysis based on these two clusters indicated a distinct
231 difference in the composition of the benthic communities within these depth zones. The
232 ratio of total percent community contribution of macroalgae to sessile invertebrates in the
233 ≤ 31 m depth zone was 7.88 while only 0.65 in the ≥ 32.5 m depth zone. Twelve of the 14
234 taxa/morphotypes, accounting for 91.7% of the community for sites ≤ 31 m were
235 macroalgae. Unknown invertebrates (those lacking distinguishing characteristics in
236 images) were the highest contributing non-algae at 4.10% (Table 2). Crustose coralline
237 and *Peyssonnelia*-like red algae (CCA/P) dominated with a nearly 30% contribution to
238 the community structure, followed by the red alga *Solieria filiformis* (10.8%), the brown
239 alga *Zonaria tournefortii* (7.8%), and unknown red algae (7.4%). These were the only
240 taxa/morphotypes with individual community contributions greater than 5%. In contrast,
241 within sites ≥ 32.5 m, ten taxa/morphotypes accounted for the top 90.8% of the
242 community composition and they were evenly split between invertebrates and
243 macroalgae (Table 2). The highest contributions came from hydroids (21.04%) and
244 unknown invertebrates (20.75%), with the next two highest contributors being brown
245 algae *Dictyota* spp. (12.76%) and CCA/P red algae (11.79%). The top four
246 taxa/morphotypes combined account for over 66% of the community contribution.
247 Dissimilarity between the ≤ 31 m and ≥ 32.5 m depths were driven primarily by the top
248 three taxa/morphotypes within each of the depth zones - CCA/P red algae; hydroids;

249 *Solieria filiformis*; unknown invertebrates; *Dictyota* spp., and *Zonaria tournefortii* (Fig. 2,
250 Table S2, see Appendix A). All other taxa/morphotypes had a <5% individual
251 contribution to the dissimilarity between these depth zones.

252 The greater overall importance of macroalgae in the shallower epibenthic
253 communities was also apparent when examining the contributions of organisms within
254 the five more restricted depth zones identified in the linkage tree analysis (Table 3).
255 Macroalgae were the dominant contributors to the three depth zone communities
256 identified between 18 and 31 m with macroalgae to sessile invertebrate percent
257 contribution ratios of 4.41, 8.38, and 8.97 (Fig. 3). The top community contributors were:
258 18-20 m – *Solieria filiformis* (37.32%) and CCA/P (24.84%); 24-29.2 m - CCA/P
259 (27.43%) and *Zonaria tournefortii* (17.31%); 31 m - CCA/P (22.61%) and *Rhodymenia*
260 spp./*Gracilaria* spp. (18.80%). The only invertebrate taxa/morphotype with a contribution
261 greater than ten percent in any of these communities was the octocoral *Titanideum*
262 *frauenfeldii* at 15.30% within the 18-20 m depth zone. No invertebrate taxa/morphotype
263 contributed >7% to communities within the 24-29.2 m and 31 m depth zones (Table 3).

264 The number and percent contribution of invertebrate taxa/morphotypes was greater
265 within the 32.5-37 m and 38.5-42 m depth zones (Fig. 3). The macroalgae to sessile
266 invertebrates percent community contribution ratios were 0.97 and 0.63, respectively
267 within these zones. While the number of macroalgae taxa/morphotypes that contribute to
268 the top 90% of the 32.5-37 m community was still larger than that of invertebrates,
269 hydroids (29.51%) and unknown invertebrates (11.73%) were the top two contributors.
270 Only three macroalgae taxa/morphotypes contributed to the top 90% of the 38.5-42 m
271 community (Table 3), while unknown invertebrates (26.71%), branching Bryozoans
272 (11.72%), hydroids (11.72%), encrusting Sponges (7.32%), and Tunicates (2.62) made
273 up nearly 60% of the community.

274

275 **4. Discussion**

276 The structure of epibenthic hard bottom communities in Onslow Bay was found to
277 be dynamic and significantly different between nearly all sites and sampling dates at
278 specific sites. The 2007 and 2009 samplings occurred during the summer season and
279 the observed epibenthic communities were more alike than in other sampling years but
280 still significantly different. The 2010 sampling was done during the late summer season
281 but was within 3-8 days of a category-two hurricane passing near the study area that
282 removed large amounts of foliose macroalgae from ledge epibenthic communities
283 (authors' observations). Sampling in 2008 occurred during the spring season with a
284 reduced number of sites visited. Despite this variation, major trends in the differences
285 between epibenthic communities were related primarily to depth (although winter bottom
286 water temperature is also important), and LINKTREE analysis clustered hard bottom
287 sites within specific depth zones (Fig. 2). Macroalgae were the most dominant
288 organisms for structuring communities within the shallower depth zones (≤ 31 m), and
289 both macroalgae and invertebrates were important in the deeper depth zones (≥ 32.5 m)
290 (Fig. 3). In addition, neither the height of the hard bottom structure nor any of the fish
291 community variables were found to have a significant influence on total epibenthic
292 community structure.

293 There is a correlation between depth and both mean winter bottom water
294 temperatures (Whitfield et al., 2014, see Fig. 2) and mean annual temperature range on
295 the southeastern North Carolina continental shelf. The proximity of the warm Gulf
296 Stream current along the outer shelf results in warmer winter bottom water temperatures
297 and a more narrow annual temperature range at greater depths, while shallower depths
298 experience colder winter bottom water temperatures and a wider annual temperature
299 range (Fig. 4). Onslow Bay fish communities between 5–46 m depth were found to be
300 structured by a depth gradient that corresponded to the winter mean temperatures

301 (Whitfield et al., 2014). While winter mean temperatures were important in this study,
302 multiple other factors related to depth such as light and periodicity of nutrient influxes,
303 may influence the structure of the epibenthic hard bottom communities.

304 Differences between the epibenthic depth zone communities were driven largely
305 by compositional differences in the taxa/morphotypes that make the largest contributions
306 to community structure, but quantitative differences were also in play. For example,
307 *Solieria filiformis* and hydroids were only top contributors to the shallower and the
308 deeper communities, respectively, illustrating a shift in community structure across the
309 shelf (Fig. 5). These compositional differences gave hydroids and *Solieria filiformis* the
310 second and third highest contribution to the dissimilarity between the ≤ 31 m and ≥ 32.5
311 m major split identified by the LINKTREE analysis (Fig. 2, Table S2, see Appendix A). In
312 contrast, CCA/P species were important components of communities in all depth zones
313 (ca. >10% community contribution, Fig. 5). However, SIMPER dissimilarity analysis
314 indicated that differences in their community contribution were also a major driver of
315 differences between depth zones.

316 Although limited, previous studies have found differences in Onslow Bay
317 macroalgal community structure related to depth. Schneider (1976) related the
318 distribution of algal species on the continental shelf to available hard bottom habitat as
319 well as the depth related variables of temperature and bottom turbidity. Notably, the
320 inner shelf zone (ca. <20 m), where the least macroalgal diversity was found, included
321 depths where wave induced bottom turbidity (Day et al., 1971) impacted available light
322 for photosynthesis, and water temperatures were highly variable. Miller and Hay (1996)
323 recorded decreased abundance of macroalgae at shallow sites that they also related to
324 turbidity induced light attenuation. The shallowest sites in this study (18–20 m depth)
325 were within this turbulence zone and characterized by relatively large community
326 contributions coming from only a few taxa/morphotypes (Table 3). Interestingly the

327 taxa/morphotypes in this depth zone that had the highest average abundances and
328 made the greatest community contributions were structurally different. The two top
329 contributors were red algae, but one, *Solieria filiformis*, has a highly branched three
330 dimensional structure, while the other, CCA/P species, are crusts with a two dimensional
331 structure. Species with a three dimensional or multilayered structure may have a
332 competitive advantage in high light environments but they lose this advantage when light
333 decreases because of self-shading (Hay, 1986). Multilayered species may alleviate the
334 low light disadvantage through coordinated environmental and life history cycles. For
335 example, *Solieria*, essentially an aseasonal annual (see Sears and Wilce [1975] for
336 explanation of seasonal periodicity categories), is present on hard bottoms for much of
337 the year, but its maximum abundance occurs during seasons of greatest light (i.e. late
338 spring to early fall) (Peckol, 1982; Schneider and Searles, 1991; Idol, 2012). In contrast,
339 CCA/P species are perennials. Although there is reported variation in the photosynthetic
340 capacity of different crustose coralline and *Peyssonnelia* species, they are often low light
341 adapted (e.g. Häder et al., 1998; Chisholm, 2003; Schwarz et al., 2005; Martin et al.,
342 2013) and photoacclimation enables individual species to grow under highly variable
343 light conditions (Payri et al., 2001).

344 Whereas the 18-20 m depth zone sites were at the transition to the shallower
345 coastal turbulence zone and differences between these communities and those of
346 deeper sites ≤ 31 m were relatively subtle, a sharper contrast existed between
347 communities ≤ 31 m and ≥ 32.5 m depth. Both the 24-29.2 m and 31 m depth zone
348 communities included contributions from a relatively large number of macroalgal
349 taxa/morphotypes (Table 3) that demonstrate different structural forms and life cycle
350 periodicities. The top contributor in both depth zones was CCA/P species, perennial,
351 two-dimensional crusts. The next highest contributors, *Zonaria tournefortii* in the 24-29.2
352 m zone and *Rhodymenia* spp./*Gracilaria* spp. in the 31 m zone, were also perennials or

353 pseudoperennials (Peckol, 1982; Schneider and Searles, 1991). However, *Zonaria* has a
354 branched three-dimensional structure where the foliose lamina die back seasonally to
355 perennial stalks (pseudoperennial), while *Rhodymenia* spp./*Gracilaria* spp. have a two
356 dimensional structure of relatively thick, perennial strap-like blades. Other important
357 macroalgal contributors in the 24-29.2 m depth zone included *Lobophora variegata*, a
358 perennial species with decumbent two-dimensional structure, *Solieria filiformis*, a three-
359 dimensional aseasonal annual, and *Sargassum filipendula* a seasonally large
360 pseudoperennial with three-dimensional structure. Additional macroalgae with high
361 contributions within the 31 m depth zone were *Champia* spp./*Lometaria* spp., *Pallisada*
362 *corallopsis*, *Botryocladia occidentalis*, and *Solieria filiformis*, all seasonal or aseasonal
363 annuals with three-dimensional structure. Macroalgae that could only be classified in
364 photoquadrats as “Unknown Red Algae” were also important contributors in both depth
365 zones. Taxonomic assessments of study site collections revealed that some of the
366 species included under this classification were the perennial two-dimensional
367 *Petroglossum undulatum*, annual two-dimensional *Sarcodiotheca divaricata*, and annual
368 three-dimensional *Wrightiella tumanowiczii*.

369 There was a large decrease in the community contribution of macroalgae within
370 the 32.5-37 m and 38.5-42 m depth zones (Fig. 3). Space is an important resource on
371 subtidal hard bottoms (e.g. Osman, 1977; Whitman, 1987) and any reduction in the
372 abundance of macroalgae is generally reciprocated by an increase in the abundance of
373 sessile invertebrates. Light is an important factor in the space competition between
374 marine algae and sessile invertebrates. At shallower depths, marine algae are dominant
375 on surfaces in full light, while sessile invertebrates are more dominant under overhangs
376 and on vertical or shaded substrates (e.g. Baynes, 1999; Irving and Connell, 2002; Miller
377 and Etter, 2008). As light decreases with depth, macroalgae abundance on surfaces
378 exposed to full light decreases and sessile invertebrate abundances increase (e.g.

379 Whitman and Cooper, 1983; Whitman and Dayton, 2001). Peckol and Ramus (1988)
380 estimated bottom light at a 42 m Onslow Bay study site to be half that recorded at a 30
381 m site and this reduced light availability may be a factor in the decreased macroalgal
382 abundance at these deeper depths. For example, hydroids are outcompeted by algae for
383 substrate in well-lit environments (Gili and Hughes, 1995), and in this study they were
384 not a significant part of epibenthic communities ≤ 31 m but top contributors to those at
385 ≥ 32.5 m depth (Fig. 5, Table 3).

386 There are multiple mechanisms by which macroalgae may negatively impact
387 sessile invertebrates including shading and overgrowth (e.g. Paine, 1976; Davis et al.,
388 1997), allelopathic effects (Nys et al., 1991; Rasher and Hay, 2010; Rasher et al., 2011),
389 and decreased feeding efficiency (Coyer et al., 1993; River and Edmunds, 2001;
390 Titlyanov et al., 2007).

391 Peckol and Ramus (1988) found that many of the macroalgae tested from their 30
392 m and 42 m sites were nitrogen limited. The offshore waters of Onslow Bay are
393 generally oligotrophic, but topographically enhanced Gulf Stream upwelling events
394 intermittently bring nutrient rich slopewaters onto the shelf (Atkinson et al., 1983;
395 Pietrafesa et al., 1985). Macroalgae that can take advantage of nutrient pulses and
396 efficiently harvest light will have an advantage in this environment. The macroalgae with
397 the greatest contribution to community structure at the two deepest sites (*Dictyota* spp.,
398 CCA/P species, and *Rhodymenia* spp./*Gracilaria* spp. [Tables 2 and 3]) demonstrate
399 different strategies for seasonally varying light and nutrient pulses. Nutrient uptake rates
400 and photosynthetic capacity are positively correlated with surface area to volume ratios
401 (Littler and Arnold, 1982; Rosenberg and Ramus, 1982a; 1982b; 1984). *Dictyota* spp.
402 are two-dimensional annuals that have high surface area to volume ratios and also
403 produce secondary metabolites that deter herbivory (Pereira et al., 2000; Barbosa et al.,
404 2004). Three species, the erect growing *Dictyota ciliolata* and *D. pleiacantha*, and an

405 unidentified procumbent species, have been collected at these sites. These species are
406 a good fit for the hypothesized advantage of species with a high surface to volume ratio.
407 The CCA/P and *Rhodomenia/Gracilaria* species also have two-dimensional structure,
408 but have more robust thalli and are longer lived, which may allow them to survive
409 through periods of low nutrients and seasonally low light.

410 Although macroalgal-invertebrate interactions in cold-temperate, epibenthic
411 communities have been the focus of numerous studies (see Whitman and Dayton,
412 2001), only Peckol and Searles (1983) and Miller and Hay (1996) have addressed the
413 nature of these interactions on North Carolina hard bottoms. Additional studies are
414 needed to better understand the interactions of macroalgae and sessile invertebrates
415 within Onslow Bay and how these affect the structure of hard bottom communities in this
416 dynamic system.

417 As a first step, the seasonality of growth and annual variation in occurrence of
418 epibenthic species needs to be determined. A better understanding of the species
419 comprising the epibenthic community is also needed. While a comprehensive guide to
420 Octocorals of the SEUSLME has recently been published (DeVictor and Morton, 2010),
421 new resources for the identification of other sessile invertebrate species are lacking, and
422 the marine algal flora of the region has not been updated since the development of
423 modern molecular identification techniques. Additional physical measures are needed to
424 reveal the multiple factors tied to depth that control epibenthic community composition.
425 Whitfield et al. (2014) showed the tight linkage of temperature to depth across the
426 continental shelf, but the relationships with other factors such as light and nutrients are
427 less well understood and basic data are lacking.

428 Epibenthic communities are ideal for monitoring climate induced ecosystem
429 changes because community composition shifts through relatively slowly occurring
430 population decline and colonization events (Walther et al., 2002). The wintertime thermal

431 transition zone across the NC continental shelf provides a laboratory for modeling
432 climate change effects on epibenthic communities. There are numerous potential effects
433 with the simplest being an increase in the presence of tropical species in NC waters.
434 This has already been reported for fishes (Parker and Dixon, 1998) and some marine
435 algae (Freshwater and Idol, 2013; NCCOS, 2014). Overall warming of shelf waters may
436 result in a shift towards more tropical epibenthic communities in nearshore waters where
437 low winter temperatures now exclude many of the species found along the outer shelf.
438 Increasing ocean acidification will have a deleterious effect on the competitive abilities of
439 the coralline algae that are important components of NC epibenthic communities, as well
440 as calcified herbivores such as urchins (e.g. Hall-Spencer et al., 2008; McCoy and
441 Kamenos, 2015).

442 More complex effects may also be realized. Extended periods of warm, or cold,
443 water temperatures may alter the phenology of epibenthic species and affect their
444 reproductive cycles. The amplitude of seasonal water temperature changes across the
445 shelf may also increase, and this could potentially decrease community diversity by
446 selecting for more eurythermic species. Another possible effect of climate change is an
447 increase in tropical storm intensity (e.g. Knutson et al., 2010). Concomitant epibenthic
448 community disturbances may result in greater inter-annual community variation
449 depending upon the timing of disturbances in relation to the reproductive cycles of the
450 constituent epibenthic organisms.

451

452 **5. Conclusions**

453 The structure of North Carolina hard bottom epibenthic communities is both
454 spatially and temporally dynamic. Community composition and structure are related to
455 depth, which is a complicated variable that reflects varying winter bottom water
456 temperatures, light levels, and periodicity of nutrient influxes. Species traits provide clues

457 as to their contribution to community structure, but a detailed examination of the marine
458 algae and sessile invertebrates of these hard bottoms is needed to understand the
459 morphological, physiological and life history characteristics that control their varying
460 levels of dominance. The position of North Carolina waters at the transition from cold-
461 temperate to warm-temperate/tropical marine zones, and the spatial compression of this
462 transition along inshore to offshore transects make this an ideal area for tracking climate
463 change related shifts in marine communities. However, seasonal and short annual
464 community variation must be understood before climate related shifts can be
465 determined.

466

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485

486 **Appendix A. Supplementary data**

487 Supplementary material related to this article can be found online at

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489

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- 703

704 Figure Legends

705 Fig. 1. Position of continental shelf hard bottom study sites within Onslow Bay, North
706 Carolina. Details on the dates sites were surveyed are included in Table S1 (see
707 Appendix A).

708 Fig. 2. LINKTREE analysis showing divisive clustering of sites from Bray Curtis similarity
709 of percent cover of biotic organisms, constrained by inequalities of the abiotic variable
710 depth. Horizontal position of sites is scaled to their depths, and depth ranges (m) for
711 clusters defined by partitions are shown on dendrogram branches. Optimal ANOSIM R,
712 and B% statistics are shown for each binary partition (node) in the lower right table. B%
713 represents the absolute measure of the group differences as calculated from the original
714 similarity matrix (Clark and Gorley, 2006). The top taxa/morphotypes for the groups at
715 the threshold of B%>60 were examined using the SIMPER procedure. The dissimilarity
716 results from SIMPER procedure are shown for top taxa/morphotypes in the primary
717 partition only. Cluster name abbreviations when they include multiple sites: NWP
718 (2NWP3 & 3NWP6); SWL (SWL1&2); Witz (Witz1&2); CDan (CDan1&2); 210 (210 &
719 210N); Woo (Woo2&6).

720 Fig. 3. Percent contribution of macroalgal and sessile invertebrate taxa/morphotypes to
721 Onslow Bay hard bottom communities in five depth zones. Macroalgae:Sessile
722 Invertebrate contribution ratios are shown above bars for each depth zone.

723 Fig. 4. Mean winter bottom water temperature and mean annual bottom water
724 temperature range for five depth zones in Onslow Bay, North Carolina. The winter mean
725 temperature observations and range are averaged over 4 years from 2007-2010, the
726 time period of benthic sampling for the study.

727 Fig. 5. SIMPER percent community contribution values for *Solieria filiformis*, Crustose
728 Coralline/*Peyssonnelia*-like algae (CCA/P), and hydroids in five depth zones.

729 **Table 1**

730 Continuous explanatory variables examined in BEST and if significant also in the
 731 LINKTREE analysis. The fish community density data were from two survey types; a
 732 larger transect (500 m²) focused on conspicuous mobile fishes and a smaller transect
 733 (100 m²) focused on the smaller bodied (<10 cm) cryptic fish community. yes – indicates
 734 the variable was derived from this transect, no – indicates this variable was not derived
 735 from this transect type and was not included in the analyses, n/a – indicates it was not
 736 applicable to derive the variable from a transect, ns – indicates that where applicable the
 737 variables from both transects were not significant in the BEST analysis and therefore the
 738 LINKTREE Analysis was not conducted (nc).

Variable	Transect Type		Analyses	
	Conspicuous (500 m ²)	Prey (100m ²)	BEST	LINKTREE
total fish density	yes	yes	ns	nc
total predators	yes	no	ns	nc
omnivores	yes	yes	ns	nc
herbivores	yes	yes	ns	nc
carnivores	yes	yes	ns	nc
invertivores	yes	yes	ns	nc
piscivores	yes	yes	ns	nc
Indo-Pacific lionfish	yes	no	ns	nc
winter bottom water temperature	n/a	n/a	$\rho = 0.277$	yes
depth	n/a	n/a	$\rho = 0.311$	yes
habitat height	n/a	n/a	ns	nc

739

Table 2

Similarity percentage (SIMPER) results for taxa/morphotypes up to 90% cumulative percentage contribution of epibenthic communities ≤31m and ≥32.5m.

Taxa/Morphotypes	Average Abundance	Average Similarity	% Contribution
18 – 31 m			
Crustose Coralline / <i>Peyssonnelia</i> -like ^A	2.57	7.62	29.92
<i>Solieria filiformis</i> ^A	1.73	2.75	10.79
<i>Zonaria tournefortii</i> ^A	1.59	1.98	7.77
Unknown Red Algae ^A	1.11	1.89	7.42
<i>Rhodymenia</i> spp. / <i>Gracilaria</i> spp. ^A	0.97	1.26	4.94
Unknown Invertebrate ^I	0.76	1.04	4.10
Encrusting Sponge ^I	0.79	0.97	3.83
Filamentous Red Algae ^A	0.79	0.95	3.74
<i>Dictyota</i> spp. ^A	0.85	0.92	3.62
Filamentous Green Algae ^A	0.80	0.92	3.62
<i>Sargassum filipendula</i> ^A	0.83	0.86	3.39
<i>Dictyopteria</i> spp. ^A	0.90	0.75	2.94
<i>Amphiroa beauvoisii</i> ^A	0.77	0.72	2.83
<i>Lobophora variegata</i> ^A	0.77	0.71	2.79
32.5 – 42 m			
Hydroids ^I	2.06	5.09	21.04
Unknown Invertebrate ^I	1.93	5.02	20.75
<i>Dictyota</i> spp. ^A	1.52	3.09	12.76
Crustose Coralline / <i>Peyssonnelia</i> -like ^A	1.16	2.85	11.79
Branching Bryozoan ^I	1.23	1.79	7.38
Encrusting Sponge ^I	0.97	1.70	7.01
<i>Rhodymenia</i> spp. / <i>Gracilaria</i> spp. ^A	0.77	0.89	3.67

Filamentous Red Algae ^A	0.69	0.66	2.75
Tunicates ^l	0.48	0.49	2.02
Filamentous Green Algae ^A	0.41	0.41	1.68

740

741 ^A=macroalgae; ^l=sessile invertebrate

742

743

Table 3

Similarity percentage (SIMPER) results for taxa/morphotypes up to 90% cumulative percentage contribution of epibenthic communities for sites clustered within five depth ranges.

Taxa/Morphotypes	Average Abundance	Average Similarity	% Contribution
18 – 20 m			
<i>Solieria filiformis</i> ^A	3.82	13.14	37.32
Crustose Coralline / <i>Peyssonnelia</i> -like ^A	2.56	8.75	24.84
<i>Titanideum frauenfeldii</i> ^I	1.95	5.39	15.30
Unknown Red Algae ^A	0.96	2.08	5.91
<i>Dictyopteris</i> spp. ^A	0.99	1.16	3.29
Filamentous Green Algae ^A	0.80	0.77	2.19
<i>Sargassum filipendula</i> ^A	0.71	0.60	1.70
24 – 29.2 m			
Crustose Coralline / <i>Peyssonnelia</i> -like ^A	2.64	7.72	27.43
<i>Zonaria tournefortii</i> ^A	2.50	4.87	17.31
Unknown Red Algae ^A	1.03	1.58	5.60
<i>Lobophora variegata</i> ^A	1.10	1.47	5.21
<i>Solieria filiformis</i> ^A	1.18	1.35	4.79
Encrusting Sponge ^I	0.95	1.28	4.56
Unknown Invertebrate ^I	0.82	1.22	4.34
<i>Sargassum filipendula</i> ^A	0.98	1.21	4.31
<i>Rhodymenia</i> spp. / <i>Gracilaria</i> spp. ^A	0.94	1.10	3.89
Filamentous Red Algae ^A	0.82	1.01	3.59
<i>Dictyota</i> spp. ^A	0.89	1.00	3.57
<i>Dictyopteris</i> spp. ^A	1.07	0.96	3.41
Filamentous Green Algae ^A	0.75	0.85	3.03
31 m			

<hr/> Crustose Coralline / <i>Peyssonnelia</i> -like ^A	2.61	7.15	22.61
<i>Rhodymenia</i> spp. / <i>Gracilaria</i> spp. ^A	2.12	5.95	18.80
<i>Champia</i> spp. / <i>Lomentaria</i> spp. ^A	2.24	3.12	9.85
Unknown Red Algae ^A	1.52	2.62	8.29
<i>Pallisada corallopsis</i> ^A	1.57	2.35	7.44
<i>Botryocladia occidentalis</i> ^A	1.38	2.23	7.05
Hydroids ^I	1.46	1.99	6.28
<i>Solieria filiformis</i> ^A	1.28	1.45	4.58
Filamentous Red Algae ^A	0.90	1.30	4.10
<i>Amphiroa beauvoisii</i> ^A	0.98	0.84	2.67
 32.5 – 37 m			
<hr/> Hydroids ^I	2.89	8.56	29.51
Unknown Invertebrate ^I	1.63	3.40	11.73
<i>Rhodymenia</i> spp. / <i>Gracilaria</i> spp. ^A	1.40	2.94	10.15
Crustose Coralline / <i>Peyssonnelia</i> -like ^A	1.22	2.53	8.72
<i>Dictyota</i> spp. ^A	1.33	2.03	7.00
Filamentous Red Algae ^A	1.20	1.71	5.89
Encrusting Sponge ^I	0.95	1.54	5.32
<i>Eucheuma isiformis</i> ^A	1.13	1.48	5.10
Unknown Red Algae ^A	0.79	0.88	3.05
Filamentous Green Algae ^A	0.62	0.60	2.07
Branching Bryzoan ^I	0.60	0.46	1.59
 38.5 – 42 m			
<hr/> Unknown Invertebrate ^I	2.19	6.61	26.71
<i>Dictyota</i> spp. ^A	1.73	4.28	17.28
Crustose Coralline / <i>Peyssonnelia</i> -like ^A	1.17	3.08	12.45
Branching Bryzoan ^I	1.58	2.90	11.72
Hydroids ^I	1.30	2.57	10.36
Encrusting Sponge ^I	1.01	1.81	7.32

	Tunicates ^l	0.56	0.65	2.62
	Filamentous Green Algae ^A	0.42	0.50	2.03
744	<hr/>			
745	^A =macroalgae; ^l =sessile invertebrate			
746				

Figure 1
[Click here to download high resolution image](#)

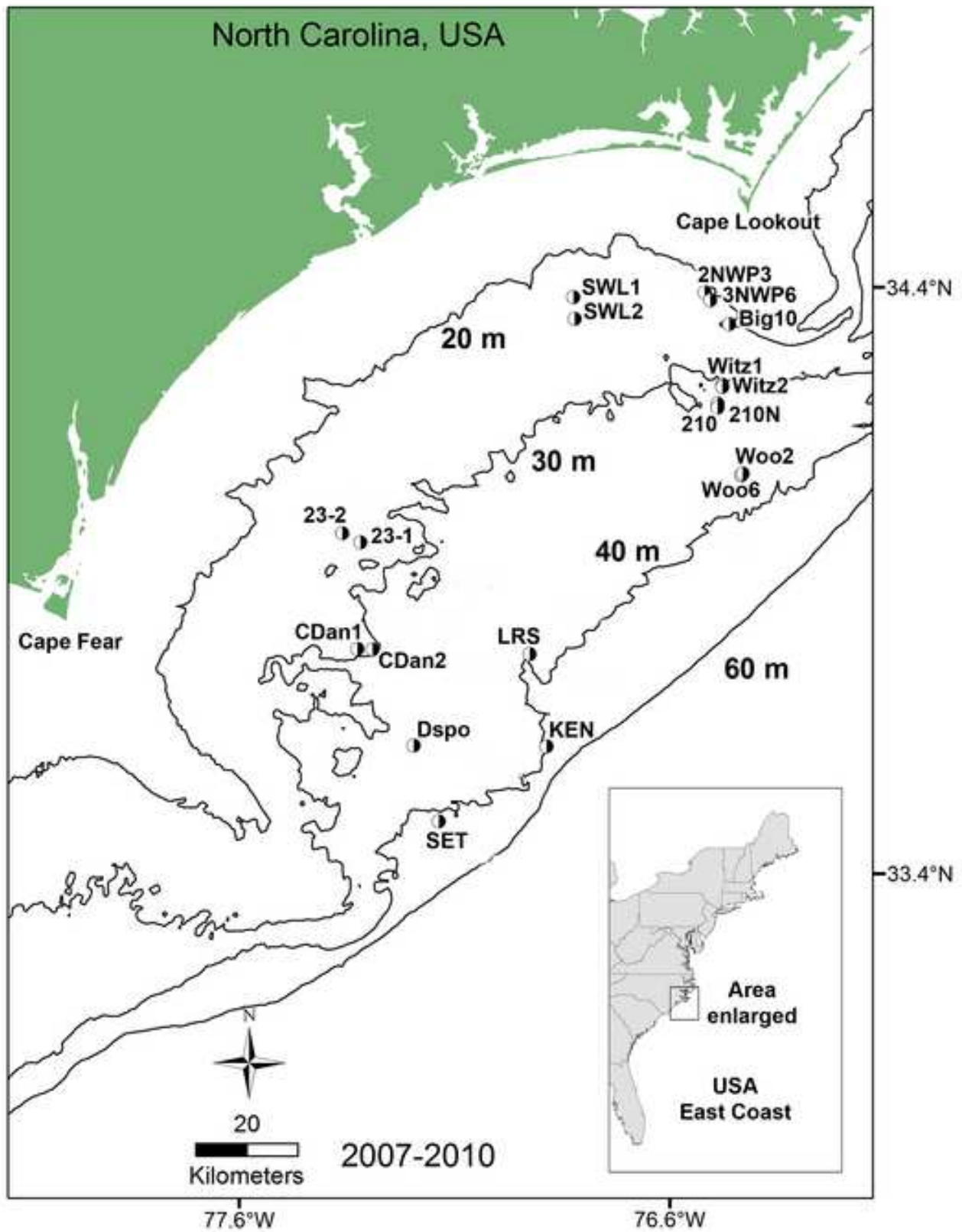


Figure 2

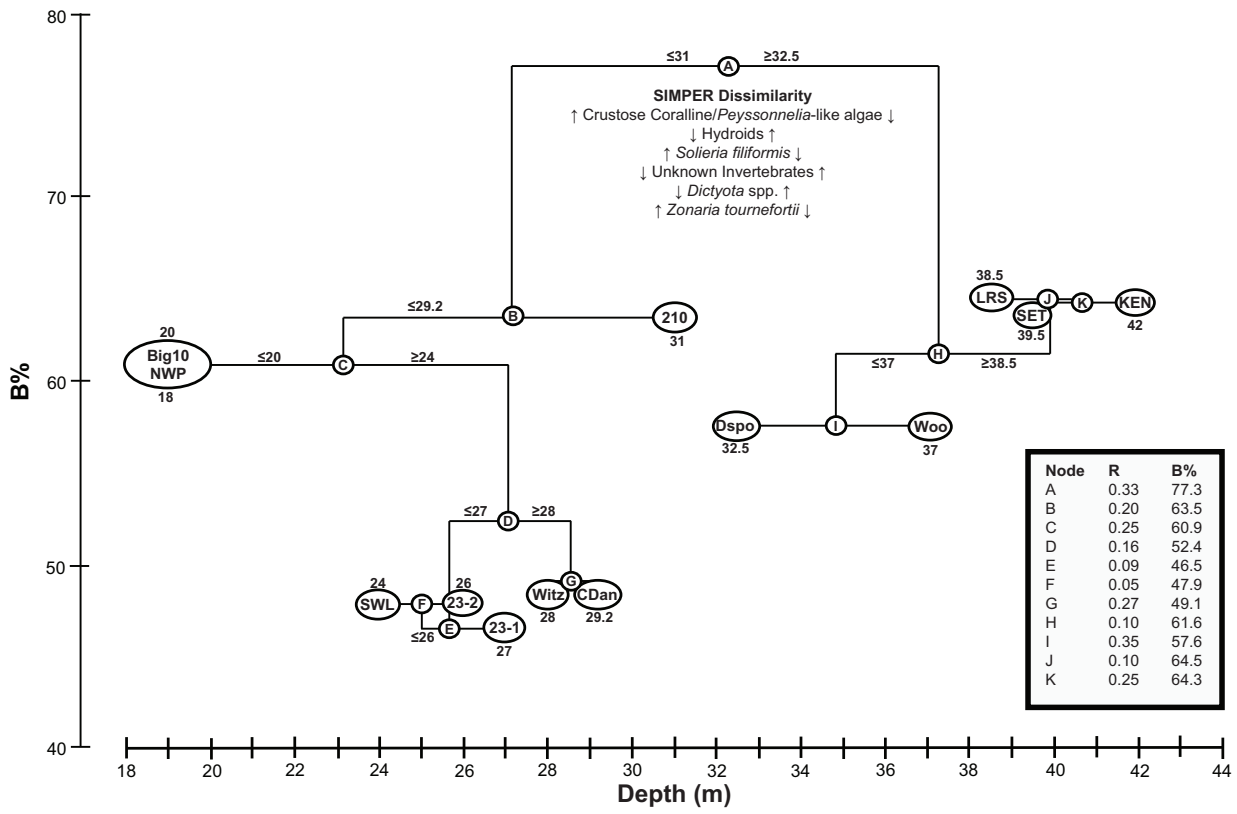


Figure 3

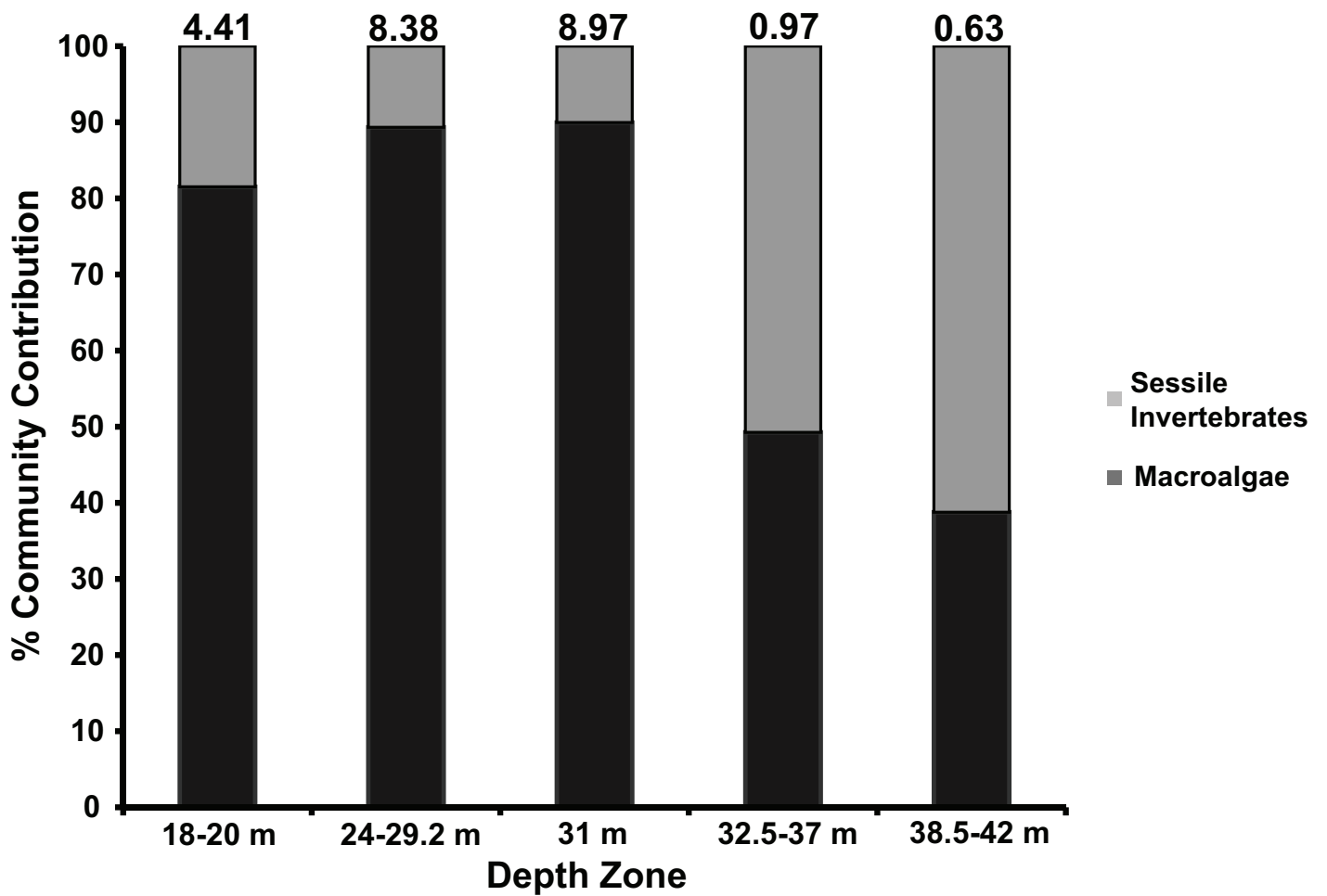


Figure 4

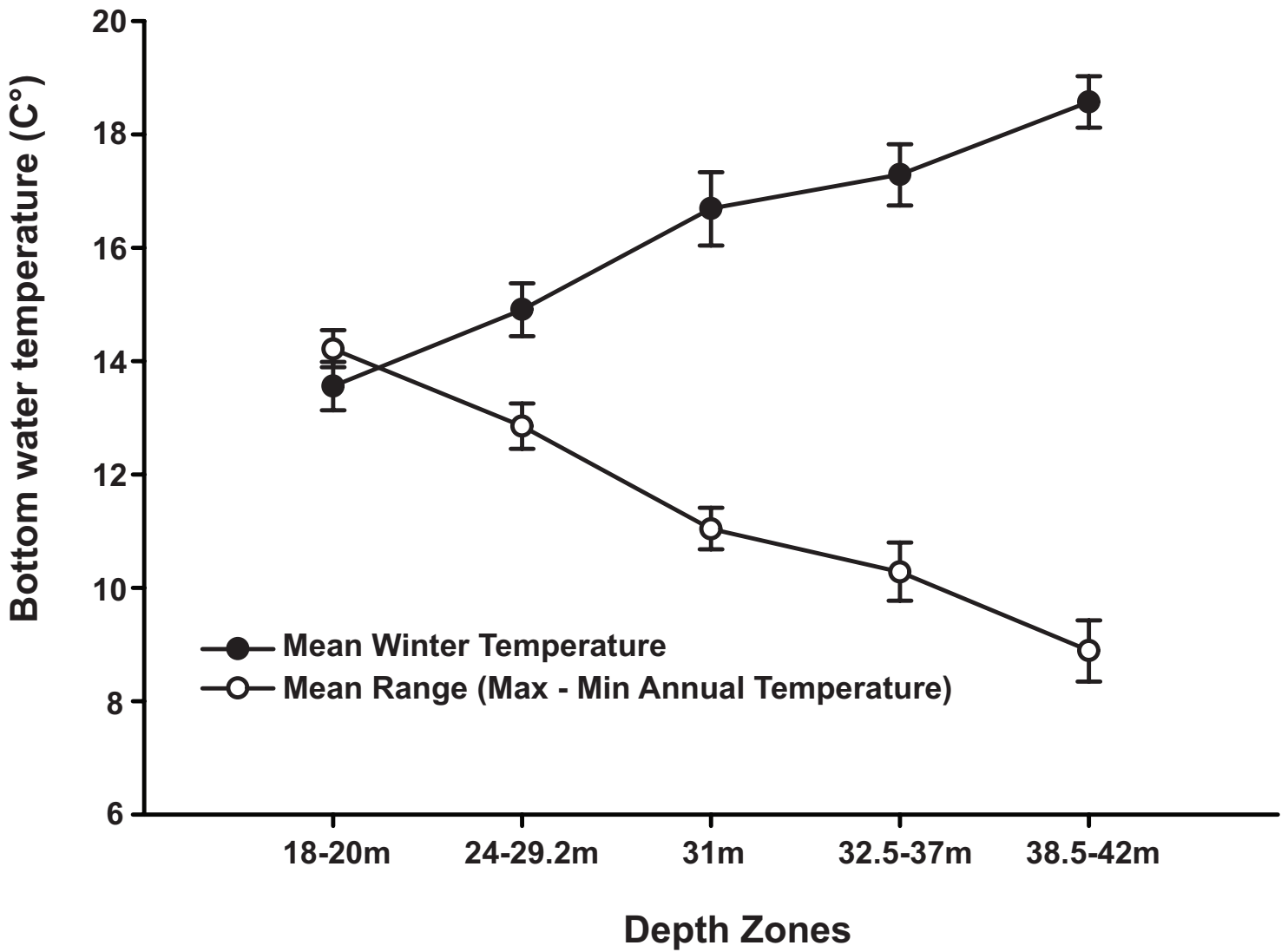
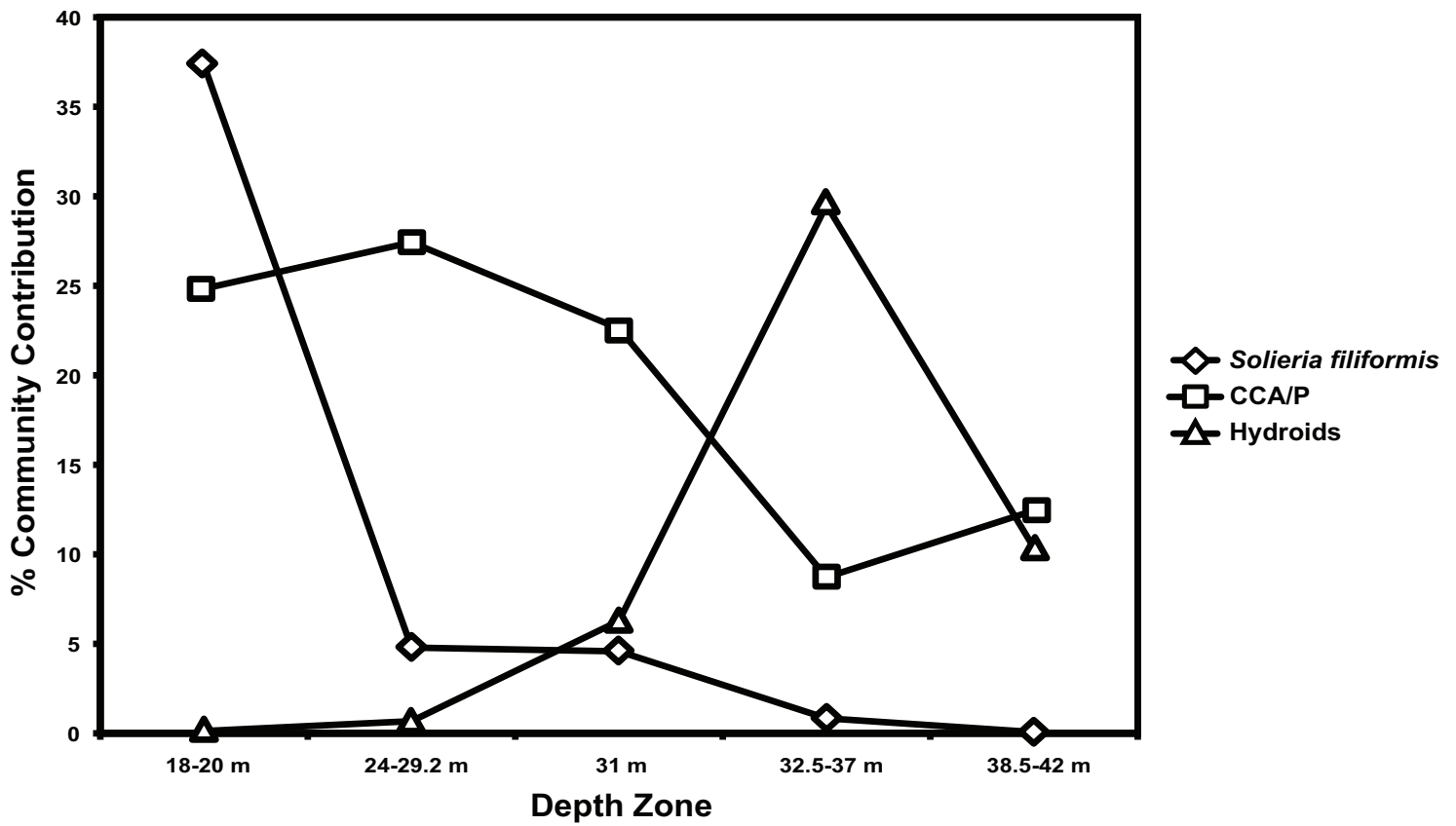


Figure 5



Highlights (for review)

Highlights

- Onslow Bay, NC epibenthic communities varied significantly both by site and year.
- Depth was the most important factor in structuring Onslow Bay epibenthic communities.
- Macroalgae dominate the community at shallower sites.
- Macroalgae and sessile invertebrates share dominance at deeper sites.
- Depth in Onslow Bay reflects varying winter bottom water temperatures and light.