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

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ABSTRACT

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

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

1. Introduction

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

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

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

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

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

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

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

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

2. Methods

2.1. Bottom water temperature and depth

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

2.2. Photoquadrat methods

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

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

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

2.3. Multivariate Analysis

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

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

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

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

3. Results

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

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

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

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

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

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

4. Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

5. Conclusions

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

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

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Figure Legends

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

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

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

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

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

Table 1

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

Table 2

Similarity percentage (SIMPER) results for taxa/morphotypes up to 90% cumulative percentage contribution of epibenthic communities $\leq 31\text{m}$ and $\geq 32.5\text{m}$.

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>Rhodomenia</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>Dictyopteris</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>Rhodomenia</i> spp. / <i>Gracilaria</i> spp. ^A	0.77	0.89	3.67

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

^A=macroalgae; ^I=sessile invertebrate

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> ¹	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 ¹	0.95	1.28	4.56
Unknown Invertebrate ¹	0.82	1.22	4.34
<i>Sargassum filipendula</i> ^A	0.98	1.21	4.31
<i>Rhodomenia</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			

Crustose Coralline / <i>Peyssonnelia</i> -like ^A	2.61	7.15	22.61
<i>Rhodomenia</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

Hydroids ^I	2.89	8.56	29.51
Unknown Invertebrate ^I	1.63	3.40	11.73
<i>Rhodomenia</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

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

^A=macroalgae; ^l=sessile invertebrate