Ecological Responses of Seascape Heterogeneity

Dinorah H. Chacin

University of South Florida

Follow this and additional works at: https://digitalcommons.usf.edu/etd

Part of the Ecology and Evolutionary Biology Commons

Scholar Commons Citation

This Dissertation is brought to you for free and open access by the USF Graduate Theses and Dissertations at Digital Commons @ University of South Florida. It has been accepted for inclusion in USF Tampa Graduate Theses and Dissertations by an authorized administrator of Digital Commons @ University of South Florida. For more information, please contact digitalcommons@usf.edu.
Ecological Responses of Seascape Heterogeneity

by

Dinorah H. Chacin

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Marine Science with a concentration in Marine Resource Assessment
College of Marine Science
University of South Florida

Co-Major Professor: Christopher D. Stallings, Ph.D.
Co-Major Professor: Susan Bell, Ph.D.
    Ernst Peebles, Ph.D.
    Joshua Kilborn, Ph.D.
    David Kimbro, PhD

Date of Approval
November 12th, 2019

Keywords: positive interactions, oyster reefs, intertidal zones, herbivory, macroalgal beds, mangroves

Copyright © 2019, Dinorah H. Chacin
DEDICATION

I dedicate this dissertation to my parents who have always believed in me and encouraged me to pursue my dreams.
ACKNOWLEDGMENTS

First, I am deeply thankful to all the funding sources that made my PhD possible. These include the National Science Foundation Graduate Research Fellowship Program, Graduate Research Opportunities Worldwide, the Explorers Club – Florida Chapter, the Swedish Research Council, the Alfred P. Sloan Foundation Minority Ph.D. Program, the McKnight Doctoral Fellowship, the ARCS Foundation Scholar Award, and the University of South Florida Bridge to the Doctorate Endowed Graduate Fellowship. I am extremely lucky to have been awarded all these fellowships.

I thank my advisors Christopher Stallings and Susan Bell for their advice, guidance, and support throughout my PhD path and for their numerous thorough edits of my work. I also want to thank my committee members Ernst Peebles, Joshua Kilborn, and David Kimbro for their extensive knowledge, advice, time, and contribution to the work presented in this dissertation. I am also immensely grateful to David Jones for his assistance and support in statistical analysis since I started in the College of Marine Science many years ago. He will always be dearly missed and I will take all the lessons learned in his classes and from working with him anywhere I go. I also want to especially thank my collaborator from Sweden Charlotte Berkström, whom I met and instantly established a great relationship that grew into an international collaboration. In this collaboration I had the privilege of being part of a team of young and inspiring scientists including Maria Eggertsen, Carolina Åkerlund, and Yessenia Rojas-Sepulveda whom I lived and
worked with in Tanzania for three months. Several publications and collaboration are presently on-going with this talented group.

I lovingly thank my family. My parents Rosa Elena Amorena Rojas and Eduardo Enrique Chacin Landaeta, my siblings Deborah Chacin Amorena, Dennis Chacin Amorena, and my grandparents Esther Chacin Landaeta and Eduardo Chacin Briñez for their constant love and support and for always being there for me. Their encouragement has been key in all my accomplishments. I lovingly thank my husband Francis Joseph Stankiewicz for experiencing this adventure with me and for being exceptionally supportive every single day. I adore his kind heart. I want to thank our dog Lilo for her unconditional love every day and for giving the very best hugs especially during difficult times.

Last but not least I want to thank my friends and especially my peer support group in St. Pete: Abdiel E. Laureano Rosario, Ileana Freytes-Ortiz, Loraine Martell Bonet, Natalia López Figueroa, María Vega Rodriguez, and Natasha M. Méndez Ferrer. More than my friends they have become my family and I am extremely grateful for their support through out my PhD path, which has kept me sane.
# TABLE OF CONTENTS

List of Tables ......................................................................................................................... iii

List of Figures ........................................................................................................................ iv

Abstract ................................................................................................................................ vi

Chapter 1: Introduction – Oyster reefs from a multi-scale perspective ..................................... 1
  1.1. Oyster reef growth and comparison to other landscape-forming habitats ..................... 4
  1.2. Factors that mold oyster seascapes: salinity and hydrodynamics influence location and development of oyster reefs ................................................................. 8
  1.3. Oyster reefs; intertidal systems in a seascape .............................................................. 13
  1.4. Dissertation outline .................................................................................................... 24
  1.5. References .................................................................................................................. 26

Chapter 2: Eastern Oyster demographic rates and habitat adjacency in an estuarine transition zone .................................................................................................................. 40
  2.1. Abstract ....................................................................................................................... 40
  2.2. Introduction ................................................................................................................ 41
  2.3. Method ......................................................................................................................... 44
    2.3.1. Study location ....................................................................................................... 44
    2.3.2. Study species ........................................................................................................ 45
    2.3.3. Experimental deployment .................................................................................... 47
    2.3.4. Oyster density and factors that may influence demographic rates of oysters .......... 49
    2.3.5. Statistical analyses ............................................................................................... 50
  2.4. Results ........................................................................................................................ 51
    2.4.1. Environmental variables ....................................................................................... 57
  2.5. Discussion .................................................................................................................... 57
    2.5.1. Conclusion ............................................................................................................ 64
  2.6. Acknowledgments ....................................................................................................... 65
  2.7. References .................................................................................................................. 65

Chapter 3: Red Mangroves positively influence the Eastern Oyster along an intertidal gradient ......................................................................................................................... 73
  3.1. Abstract ....................................................................................................................... 73
  3.2. Introduction ................................................................................................................ 74
  3.3. Methods ....................................................................................................................... 78
    3.3.1. Study location ....................................................................................................... 78
    3.3.2. Study species ........................................................................................................ 79
    3.3.3. Oyster demography and predators ...................................................................... 81
LIST OF TABLES

Table 3. 1 Non-parametric one-way analysis of variance test for main effects of mangrove prop root intertidal zone on density of juvenile oysters ........................................... 88

Table 3. 2 Non-parametric one-way analysis of variance test for main effects of mangrove intertidal zone on density of adult oysters ................................................................. 88

Table 3. 3 Non-parametric one-way analysis of variance test for main effects of reef intertidal zone on density of juvenile oysters .................................................................................. 90

Table 3. 4. Non-parametric one-way analysis of variance test for main effects of reef intertidal zone on density of adult oysters .................................................................................. 90

Table 3. 5. Non-parametric one-way analysis of variance tests for main effects of mangrove prop roots intertidal zone on percent of gaping oysters ................................................. 92

Table 3. 6. Average temperature recorded weekly during the HOBO deployment period and average and maximum temperature recorded during the hours of air exposure ......................................................................................................................................... 97

Table B. 1. Average salinity and water temperature recorded on study locations in Tampa Bay ........................................................................................................................................... 120
LIST OF FIGURES

Figure 1. 1. A visual representation of the hierarchical array formed by oysters. ...................5

Figure 1. 2. Oyster reefs adjacent to (a) Smooth Cordgrass and (b) Red Mangroves.................6

Figure 1. 3. Conceptual framework depicting processes and factors that might generate spatial zonation within intertidal oyster reefs (a), and how the factors might change if the reef is subtidal (b) .............................................................................................. 15

Figure 2. 1. Study sites selected in the Guana Tolomato Matanzas National Estuarine Research Reserve for the experimental deployment of juvenile oysters..............45

Figure 2. 2. Juvenile oysters (spat) attached to ceramic tile (a) were assigned to one of three predator exposure levels: (b) predator absent consisted of a tile inside a cage completely closed off to predators, (c) cage-control to account for potential caging artifacts, and (d) predator accessible consisted of a tile completely exposed and therefore open to predators. ............................................................48

Figure 2. 3. Survival rates of juvenile oysters in all predator levels and habitat types .............52

Figure 2. 4. Mean survival rates (a), predator effects (b), and growth rates (c) of juvenile oysters on reefs adjacent to saltmarsh grass, Black Mangroves, and oyster bars isolated from habitats .................................................................54

Figure 2. 5. Mean oyster density (a), barnacle density (b), Crown Conch density (c), and density of associated organisms (d), per 0.25 x 0.25 m quadrat on reefs adjacent to saltmarsh grass, Black Mangroves, and oyster bars isolated from habitats........................................................................................................55

Figure 2. 6. Mean density of Xanthid crabs in oyster reefs (in general) north and south of the Reserve .................................................................................................................56

Figure 2. 7. Monthly mean environmental variables ± standard error of the mean from January 2014 until December 2016 for Matanzas River (left column) and Pellicer Creek (right column) .................................................................59

Figure 3. 1. Conceptual model of potential interactions between Red Mangroves and the Eastern Oysters ........................................................................................................78
Figure 3. 2. Map of Tampa Bay, Florida, USA, showing the study locations indicated with black circles

Figure 3. 3. Average density ± standard error of adults, juveniles, and total oysters in mangrove prop roots and oyster reefs

Figure 3. 4. Average density ± standard error adults, juveniles, and total (adults + juveniles) oysters per mangrove sample at different locations (bottom of root, middle of root, top of root)

Figure 3. 5. Average density ± standard error of adults, juveniles, and total (adults + juveniles) oysters per quadrat at different intertidal locations (bottom, middle/slope, top/crest) on oyster reefs

Figure 3. 6. Percent of gaping oysters (± standard error) per sample at different intertidal zones (bottom, middle, and top) on mangrove prop roots (a) and on oyster reefs (b)

Figure 3. 7. Survival of oyster recruits ± standard error at different locations (bottom, middle, and top) on oyster reefs and mangrove prop roots

Figure 3. 8. The percent of tiles deployed covered by barnacles in mangroves and in reefs in general (a), top intertidal location on both habitats (b), middle intertidal location on both habitats (c), and bottom intertidal zone on both habitats (d)

Figure 3. 9. Weekly average water depth in meters collected by HOBO Onset U20L-02 water level logger at top and bottom intertidal zones of oyster reefs and Red Mangrove prop roots
ABSTRACT

A core aim of landscape ecologists as well as conservation and management practices has been to understand how processes that structure communities vary as a function of landscape context. Landscape heterogeneity (i.e. landscape composition, configuration) and fine-scale habitat characteristics can influence ecological interactions across habitat patches at a range of scales. Therefore, the main objective of this work is to apply a landscape ecology perspective to understand how seascape heterogeneity can influence demographic rates, community patterns, and ecological processes. To accomplish this overall goal, I conducted a literature review on oyster reefs from a seascape ecology perspective (Chapter 1) and I carried out three independent research studies (Chapters 2-4) using observational and experimental approaches.

In Chapter 2, I assessed demographic rates of oysters in reefs adjacent to various habitat types in a transition zone. In northeast Florida, the dominant coastal habitat transitions from Smooth Cordgrass (*Sporobolus alterniflorus*; temperate species) to Black Mangroves (*Avicennia germinans*; tropical species). These two foundation species may affect the demographic rates of the Eastern Oyster (*Crassostrea virginica*), another foundation species commonly located adjacent to them. Therefore, I deployed juvenile oysters in cage experiments comprising three levels of predator exposure on (a) oyster reefs bordering Smooth Cordgrass, (b) reefs bordering Black Mangroves, and (c) isolated oyster bars, to quantify survival and growth rates north and south in the Guana Tolomato Matanzas National Estuarine Research Reserve. Additionally, I analyzed three datasets with information on the abundances of oysters, associated organisms,
potential predators, and other biotic (e.g., chlorophyll \( a \)) and abiotic factors (e.g., salinity, dissolved oxygen) across the seascape. The results of this chapter indicated that neighboring habitats and regional variation in the seascape may influence demographic rates of oysters.

Although oyster demographic rates across intertidal zones have been examined in oyster reefs at higher latitudes, far less is known about them at subtropical locations where desiccation stress is expected to be greater due to higher temperature. Furthermore, little is known about oyster demographic rates when in association with a macrophyte intertidal habitat, which may reduce desiccation stress and positively influence oysters at higher intertidal zones. In Chapter 3, I measured demographic rates of oysters along intertidal zones on oyster reefs and on oyster clusters associated to Red Mangrove prop roots in Tampa Bay, Florida. This study addressed: (a) how do demographic rates of the Eastern Oyster vary along intertidal zones (bottom, middle, and top) on oyster reefs and on prop roots and (b) whether the association of oysters with mangroves may reduce desiccation stress, thus positively influencing oysters at higher intertidal zones. I found oysters on prop roots to be at higher densities and had higher survival. Consistent with density and survival, water loss (a proxy for desiccation stress) was lower on the prop roots, suggesting that the mangrove canopy may have provided a positive effect on oysters. This chapter contributes to our understanding of fine-scale zonation patterns on two biogenic habitats that exist in close association.

In tropical seascapes, beds of benthic macroalgae occur naturally interspersed within or nearby other habitats, but it is unclear what roles they play to support marine fauna. Even less is known about how the introduction of non-native macroalgal habitats (e.g., macroalgal farms) into tropical seascapes may affect ecological processes that influence ecosystem function and its comparison to seascapes with natural macroalgal beds. To address this knowledge gap, in
Chapter 4, I surveyed fish assemblages and deployed macroalgal assays to quantify herbivory within naturally-occurring macroalgal habitats, macroalgal farms, as well as at varying distances in the seascape near Mafia Island, Tanzania. The results showed that macroalgal beds had a higher species richness of fish and lower herbivory, while higher herbivory occurred in farmed seascapes likely to the farms attracting herbivores. This chapter advances our understanding of the effects that alteration of tropical seascapes (due to the introduction of farms) may have on patterns of community assembly and ecological processes.

Overall, the findings of this dissertation suggested that neighboring habitat patches can influence demographic characteristics of organisms, but the responses may be contextual upon location in the seascape due to variation in regional factors. Moreover, fine-scale variation in biotic and abiotic factors in intertidal habitats can affect demographic rates of organisms and the presence of other foundation species may influence these patterns. Lastly, seascape alterations can influence patterns of community assembly and ecological processes thus affecting ecosystem structure and function. As seascapes continue to be altered due to climate change (e.g., poleward movement of foundation species) and anthropogenic activities (e.g., farming practices), studies that assess the ecological responses of such changes will improve our understanding on the cascading effects within ecosystems and the services they provide.
CHAPTER 1: INTRODUCTION – OYSTER REEFS FROM A MULTI-SCALE PERSPECTIVE

Landscape ecology is a multidisciplinary field that uses concepts derived from geography and ecology to understand the causes, changes, and ecological consequences of spatial patterns and processes occurring across heterogeneous mosaics at a range of scales (Turner et al. 2001, Turner 2005). The field of landscape ecology, which started as early as 1940s in Europe and 1980s in North America, has developed analytical tools and concepts that have resulted in valuable contributions to the understanding and management of terrestrial environments. Given this discipline was developed for terrestrial managers, landscape-ecology studies have focused on vegetation as the type of land cover that creates spatial structure and composes the landscape (e.g., forests, grasslands, agricultural fields). In the early 1990s, landscape-ecology concepts were introduced in the study of marine landscapes and thus a sub-discipline formally termed “Seascape Ecology” emerged.

Many similarities exist between terrestrial landscapes and seascapes. For example, the spatial arrangement that marine biogenic-habitats exhibit produce “patches” which are embedded within a background matrix (e.g., sand, mud; Dunning et al. 1992). Seascapes (like landscapes) can also be composed of mosaics of habitat patches that result in highly heterogeneous areas. Well-known coastal spatial patterns include the dendritic structure that tidal channels form in wetlands, the spatial zonation occurring in rocky shores as well as in saltmarsh grass habitats, and the mosaics of patches formed by seagrass beds, coral reefs, and mangrove forests (Pittman et al. 2007).
Additionally, numerous coastal organisms are often associated with benthic habitat structure, similar to that reported for terrestrial environments. Due to the recognition of the spatially structured nature of marine habitats and the similarities to terrestrial systems, it is logical that many of the concepts and techniques developed by terrestrial ecologists are applicable to aquatic benthic environments.

Even though water and air are two physically and chemically different media that possibly influence ecological processes and spatial structure, the application of landscape principles to the study of marine environments has gained popularity and the number of studies using such approaches has increased over time (Bell and Furman 2017). Consequently, seascape ecology has been applied to the study of a variety of shallow and coastal subtidal and intertidal biogenic habitats across a range of scales (see Boström et al. 2011 for a review of the literature). Seagrasses have been the species/habitat primarily studied from a landscape perspective (Boström et al. 2011) due to their resemblance to terrestrial environments (e.g., grasses) and their spatial and temporal structure (Robbins and Bell 1994). Seagrasses have been studied generally using the patch-matrix model (focal seagrass patches surrounded by unvegetated sand matrix) to examine spatial processes and the ecological consequences of fragmentation in terms of patch-size change, number of patches, and isolation (Bell et al. 2001, Hovel and Regan 2008). Also, several studies have revealed that species associated with seagrasses respond to the spatial arrangement of the patches. For example, juxtaposition, contiguity, fine-scale complexity (e.g., blade density), and inter-patch distances can affect predator-prey relationships by influencing refuge, predation risk, and mobility among habitats (Irlandi and Crawford 1997, Micheli and Peterson 1999, Grober-Dunsmore et al. 2007, Chacin and Stallings 2016).
Seascape studies on intertidal plants such as saltmarsh grasses and mangroves are also available (Costanza et al. 1990). Similarly to studies in seagrass beds, responses especially of macroinvertebrates to saltmarsh spatial structure (e.g., patch size, patch density, edge effects) have been reported (Baltz et al. 1993, Minello et al. 1994, Peterson and Turner 1994, Cicchetti and Diaz 2000, West and Zedler 2000, Minello and Rozas 2002, Haas et al. 2004, Guest and Connolly 2006, Long and Burke 2007, Roth et al. 2008). Fewer studies have been conducted on mangroves and these have revealed that percent cover of mangroves can influence fish diversity in coastal seascapes (Pittman et al. 2004). Other landscape-forming habitats generated by animals (e.g., coral reefs and oyster reefs) can also create large spatial structures, and these have begun to be studied from a landscape perspective more recently (Boström et al. 2011).

Oysters are bivalve mollusks that can live in marine or brackish environments, subtidally and intertidally, and have been a recent target of landscape investigations (Grabowski et al. 2005, Hanke et al. 2017, Ziegler et al. 2018). Oysters aggregate to form clusters, which in turn form reefs. Sets of reefs can form small to large spatial structures (1-10s m) embedded within a background matrix, typically mud and reefs are the usual elements considered in seascape studies. It is this hierarchical spatial nature of oyster reefs that renders them ideal habitats to study from a multi-scale perspective. However, in comparison to other coastal habitats, oyster reefs have been understudied from a multi-scale perspective (but see Grabowski et al. 2005, Hanke et al. 2017), even though the approach has been advocated to provide an advantageous conceptual framework for furthering our understanding of oyster reef ecology and restoration ecology (Eggleston et al. 1998, 1999, Boström et al. 2011).

This review builds on the theme of coastal landscapes and discusses (1) variation in spatial structure of oyster reefs as landscape-forming habitats, (2) the influence of salinity and
hydrodynamics on the development of oyster reefs within coastal settings, and (3) patterns of intertidal zonation within oyster reefs that set the stage for ecological investigations and their comparison to other well-studied intertidal marine ecosystems.

1.1. Oyster reef growth and comparison to other landscape-forming habitats

Oyster reefs share a variety of similarities with other landscape-forming habitats. Oyster landscapes can be formed in a hierarchical array (Figure 1.1). At very fine (e.g., millimeter) scales, individual oysters may grow away from sediment with the developing edges oriented upwards (Figure 1.1a; Bahr and Lanier 1981). Upon this oyster shell many other oysters can settle, physically attach, and grow, forming an oyster cluster (Figure 1.1b; Winslow 1882). Therefore, the presence of other conspecifics and hard substrate is necessary for starting the process of reef formation. The oyster cluster forms a three-dimensional structure composed of live oysters and shells from dead oysters creating a hard bottom that can expand laterally and upward, the latter which may potentially allow reefs to keep pace with sea-level rise (Figure 1.1c; DeAlteris 1988, McCormick-Ray 1998, Ridge et al. 2017). This three-dimensional reef structure increases habitat complexity and seascape heterogeneity in soft-sediment systems, augmenting species abundance and diversity (Meyer and Townsend 2000, Gutiérrez et al. 2003, Peterson et al. 2003, Walles 2015). The oyster clusters over time may accumulate more individual oysters and form a patch/oyster reef, and at this point, these patches can be visible at scales of centimeters to meters (Figure 1.1c). Dynamics of growth contribute to fine-scale habitat complexity of the reef patches. Oyster reefs that have a high proportion of live oysters growing closely wedged together display high structural complexity, while those in which dead shells form a higher proportion of the reef, are less complex.
Spatial configuration of oyster reefs (Eggleston et al. 1998) range from sparse and fragmented reefs, to aggregated clusters that form large continuous reefs (extending over 1 km; Figure 1.1d; Eggleston et al. 1999) across the seascape. Oysters are found in nearshore coastal areas and the reefs they create are distinct from the surrounding sediment matrix, making their boundaries/edges visually identifiable. Oysters also form reefs adjacently to other habitats creating a patchwork of mosaics within the coastal matrix. For example, in the northern Gulf of Mexico and the east coast of the United States of America (USA), oyster reefs formed by *Crassostrea virginica* can be found juxtaposed to saltmarsh grass (Figure 1.2a) and seagrass beds
(McCormick-Ray 2005, van de Koppel et al. 2015). In Florida, oysters can grow attached to prop roots of Red Mangroves (*Rhizophora mangle*) and reefs can be found adjacent to mangroves (Figure 1.2b).

Figure 1.2. Oyster reefs adjacent to (a) Smooth Cordgrass and (b) Red Mangroves.
Oyster reefs differ from other landscape-forming habitats in terms of the growth pattern of patch expansion. In terrestrial settings, canopy elements of vegetation are a main characteristic often measured. Change in the vertical range and structure of the canopy is typically of interest, as this metric is reported to influence foliage diversity, structural complexity, and epiphytic cover (Spies 1998, Robbins and Bell 1994, Zellweger et al. 2013). Seascapes shaped by coral reefs are formed by the settlement of free-swimming coral larvae onto submerged hard structures. Once settled, the coral polyps build skeletons beneath the tissue creating and offering more substrate for other coral larvae to settle as well as increasing the surface area upon which other organisms (e.g., calcifying macroalgae and benthic invertebrates) may attach. On the other hand, oyster reefs expand by the settlement of new oyster recruits into the reefs and through the accumulation of biodeposits. Suspended small inorganic particles are repackaged by oysters and other bivalves into feces and pseudofeces and oysters biodeposit them into the sediments (Widdows et al. 1998). The deposition of biodeposits is an important process, which contributes to reef stability and modulates reef sediment supply on and around reefs (Widdows et al. 1998). Biodeposition and shell material contribute to reef accretion by filling the interstitial space, which helps elevate the reef structure. Oyster reefs also offer substrate for many organisms, such as mussels, sponges, anemones, and barnacles, to settle (Wells 1959) and this further contributes to the cementing process of the reef structure. Therefore, the combination of oyster recruitment, biodeposition, and the settlement of other benthic organisms over time allow the oyster reefs to expand three-dimensionally.
1.2. Factors that mold oyster seascapes: salinity and hydrodynamics influence location and development of oyster reefs

It has been well established that salinity and hydrodynamic processes can play an important role in the distribution, growth, and recruitment processes of most estuarine organisms (Zeineldin 1963, Barletta et al. 2005). Cyrus and Blaber (1992) identified salinity as one of the major factors driving fish distributional patterns in the Embley estuary, Australia. Furthermore, hydrodynamic processes such as freshwater inflow have the potential to transport larvae towards or away from settlement habitats influencing recruitment and survival of organisms (Tolley et al. 2012). Oysters are known for thriving in the transition zone between freshwater and saltwater environments (Galtsoff 1964, Wilber 1992). At broad scales, variation in salinity and hydrodynamic processes are well established. Therefore, it is expected that oyster reef development, distribution, persistence, and location would be related to the salinity regimes and the hydrodynamics of estuarine systems.

At the population level, oysters can survive highly variable salinity regimes, including low and high salinity events (Butler 1952, Pollack et al. 2011). However, the frequency, timing, and duration of salinity extremes can affect oyster physiology, alter the distribution of oyster predators, and influence the prevalence of disease-carrying pathogens. The effects of salinity regimes on such factors can affect oyster survival and population success, thereby impacting the development and location of oyster reefs within the seascape.

Salinity is one of the main factors affecting oyster physiology. The timing and duration of low extreme salinities may result in dramatic changes in oyster population dynamics by affecting recruitment, growth, and mortality of different life stages. For example, in the Northern Gulf of Mexico, La Peyre et al. (2013) observed that extended low salinities (< 5 ppt) in combination to
high temperatures (>25 °C) during the summer season negatively impacted oyster recruitment, survival, and growth. Examination of the oyster plasma showed evidence that these oysters were not able to osmoconform and lower their plasma osmolality, resulting in excessive valve closure to minimize energetic demands. The extended period of valve closure caused hypoxia, acidosis of the hemolymph or starvation, leading to oyster death (de Zwaan and Wijsman 1976, Lombardi et al. 2013). Lack of feeding in oysters has also been reported in salinity levels under 3 ppt and reduced growth at salinities under 7.5 ppt (Loosanoff 1953, 1965). Low salinities, in general, make oysters depress or arrest gametogenesis (Loosanoff 1953), delay spawning (Allen and Turner 1989), and reabsorb gonadal material (Livingston 1997). Oysters may experience 100% mortality within one week of exposure to 1 ppt (Rybovich et al. 2016) and result in low spat production and extremely high valve closure at salinities levels below 14 ppt (Shumway 1996, Volety et al. 2008). All of these effects ultimately can lead to recruitment failure or post settlement mortality, deterring oyster reef growth and, consequently, reef persistence.

In addition to strongly affecting oyster physiology, salinity may also influence oyster reef structure and location of oyster reef formation. Disarticulation rate of oysters has been shown to be higher in increased salinity areas than in those within low salinity locations (Christmas et al. 1997). Possible explanations included the more diverse proteolytic bacteria (found in high salinity settings), which can mediate degradation of the hinge ligament and influence reef complexity and structure. Salinity has also been identified as a major driver of intertidal oyster reefs distribution in North Carolina (Theuerkauf 2017) given that intertidal reefs have not been found below a salinity threshold of ~27 ppt in Pamlico and Core Sound. Conversely, Eleuterius (1977) found that oyster reefs were distributed in salinity-suitable locations in the Mississippi Sound within salinity range of 2 to 22 ppt that average between 10 and 16 ppt. They concluded
that salinity levels under such threshold could affect reef persistence due to unsuccessful reproduction, whereas higher values could expose the oysters to the predator, *Thais haemastoma*.

Diseases caused by parasites have the potential to cause extensive mortalities of oysters (Haskin and Andrews 1988, Andrews 1996) and have been associated with increased salinities levels. Volety (2008) found high prevalence and infection intensity of *C. virginica* oyster by the highly pathogenic parasite *Perkinsus marinus* in locations downstream of the Caloosahatchee Estuary where salinity was higher compared to upstream locations. Possible explanations included physiological limitations of the pathogens in lower salinity environments. The transmission and progression of infections by *P. marinus* have also been related to variability in rainfall, which alters salinity patterns and temperature (Ford and Tripp 1996, Powell et al. 1996, Kim and Powell 1998, Malek 2010, Soniat et al. 2006). In the Gulf of Mexico, reduced rainfall and warmer waters during La Niña events have also lead to epizootic events of *P. marinus* (Powell et al. 1996, Kim and Powell 1998). Furthermore, oyster infections and mortality caused by *P. marinus* in Chesapeake Bay tend to increase in the summer season, which corresponds to higher temperatures and elevated salinities. Infections by *P. marinus* can result in alterations to individual oyster morphology such as smaller shells and decreased tissue growth (Menzel and Hopkins 1955, Paynter and Burreson 1991). Infections can also affect the biochemical composition of the oyster mantle tissue (Soniat and Koenig 1982), reduce the oyster gametogenic development, and result in mortality of the host. Therefore, by affecting oyster morphology diseases can influence the structural complexity of reefs, and by inducing high mortality rates diseases also affect reef persistence.

High salinity levels can also impact oyster population success through the effects of predation. Predators whose distribution is dictated by salinity have the potential to decimate
oyster reefs. When salinities exceed 15 ppt predation can overwhelm recruitment in subtidal oyster reefs. For instance, the Southern Oyster Drill (*Stramonita haemastoma*) is an oyster predator known for occurring when salinities rise over 15 ppt (Garton and Stickle 1980). Other predators such as the Stone Crab (*Menippe adina* and *Menippe mercenaria*) and the Blue Crab (*Callinectes sapidus*) prey on small oysters and are also found in marine (higher salinity) environments (Menzel et al. 1966, Eggleston 1990, Brown and Haight 1992). Studies have also shown that predators can influence reef persistence. Miller et al. (2017) developed an oyster suitability model by studying oyster growth, mortality, and recruitment across a salinity gradient in the Louisiana coast, Gulf of Mexico. The authors found that over a two-year period the highest salinity study sites demonstrated a low likelihood for sustainable reef development over time due to the high oyster mortality resulting from predation. A decline of oyster reefs in the Matanzas River estuary in northeast Florida occurred in 2008 (Garland and Kimbro 2015). The primary cause for the loss of reefs was an increase in water salinity due to a regional drought, which positively influenced the reproductive success of the oyster predator, the Crown Conch, (*Melongena corona*). Similarly, Kimbro et al. (2017) showed through *in situ* experiments that regional drought in combination with water withdrawals led to elevated salinity levels in Apalachicola Bay. Under these conditions, abundance of predatory snails increased and high mortality of oysters due to intense predation followed, thus contributing to the collapse of the oyster fishery. Consequently, it may be advantageous for oyster reef restoration efforts to target locations with moderate salinities in order to reduce oyster mortality associated with the high and low salinity conditions thus preventing oyster reef decimation and ensuring reef persistence.

Oyster bed morphology can be highly variable at the individual bed scale reflecting variation within and among beds and the complex relationships with hydrodynamic processes.
(McCormick-Ray 1988). However, oyster bed morphology and orientation has been related to hydrodynamic processes. For example, long linear reefs have been shown to form oriented perpendicularly to tidal currents (Grinnell 1974, Grave 1905). The suggested mechanism is that small oyster clusters along the shoreline undergo high flow rates at the leading edge and consequently experience ideal conditions for settlement and growth. The shortest axis on this type of reefs is in the direction of tidal flow and turbulent eddies that slow flow are minor. Water velocity over the reefs increases due to restriction of space in the water column as the water travels over the reef crest (Colden 2014). The higher water flow may lead to increased food delivery and may result in higher survival and growth, enhancing vertical reef accretion (Kennedy and Sanford 1999, Lenihan 1999). These conditions result in elongation of the oyster reef away from the shoreline (Colden 2014, Grave 1905). Lastly, oyster clusters falling from the crest into adjacent locations, due to fast water flow, can initiate the formation of another reef in a similar process.

Oyster reef orientation and axial position can also be influenced by channel conditions (Colden 2014). Fringing oyster reefs can border tidal channels. Oyster clusters in these locations might experience fast flow produced by the water that travels in the channels. The fast-flowing water through the channel might be rich in food source for oysters, presenting ideal conditions for fast growth (Powell et al. 1995, Kennedy and Sanford 1999, Smith et al. 2003). Moreover, as oyster larvae are transported through the channel, the closely located oysters might be the first available substrate the larvae encounter resulting in the elongation and development of the fringing reefs (Colden 2014).

Oyster patch reefs are another type of oyster reef morphology. They are characterized by not having a clearly defined shape, which causes them to propagate out from the center of
development (Haven and Whitcomb 1983, Kennedy and Sanford 1999, Smith et al. 2003). Oyster patch reefs have been described historically to form in locations where there is no strong bidirectional flow, such as in the mouth of rivers (Haven and Whitcomb 1983, Kennedy and Sanford 1999). Overall, estuarine hydrodynamics are able to influence oyster reef patch shape while salinity influences patch structural complexity and oyster reef distribution.

1.3. Oyster reefs; intertidal systems in a seascape

Models of community organization have shown that biotic and abiotic factors can affect the spatio-temporal patterns of abundance and distribution of organisms (Menge and Sutherland 1987, Menge and Olson 1990). Biotic factors such as the presence of consumers might affect an organism’s distribution by their direct consumption and by influencing their selection of habitats (Turner and Mittelbach 1990, Pawlik 1998, Johnson and Smee 2014). Abiotic factors such as temperature and oxygen levels can also pose physiological stress on organisms, which can increase susceptibility to infections and lead to mortality (Menge 1976, Menge and Olson 1990, Lenihan et al. 1999, La Peyre et al. 2009). The interplay of biotic and abiotic factors and their influence on zonation of benthic marine organisms has been widely investigated in intertidal systems such as rocky shores and saltmarsh grass habitats.

Experimental work on the rocky intertidal shores has shown the upper limits in vertical zonation can be determined by direct effects of the physical environments such as high wave energy, high temperature due to increased solar radiation, and freezing conditions (Connell 1972). For example, the upper level distribution of barnacles in a variety of studies has been related to desiccation stress (Hatton 1938, Foster 1969, Wethey 1983). Menge (1976) observed that the barnacle *Balanus balanoides* abundance in the high intertidal zone during long-term experiments decreased significantly during the summer season due to desiccation stress produced...
by a series of neap tides occurring on calm warm days. Meanwhile, biological interactions such as competition (Connell 1961), predation (Paine 1966), or disturbance (Dayton 1971) may be more important in setting the lower limits of species distributions in vertical zonation in rocky intertidal shores. For instance, while *Chthamalus stellatus* can survive at different shore levels, its restriction to high shore levels in Scotland is caused by competition with another barnacle *B. balanoides* for space in the lower intertidal zone. Furthermore, in the intertidal rocky shores of Washington, Paine (1974) showed that *Mytilus californianus* and *Balanus glandula* were able to survive at lower shore levels if predators such as *Pisaster ochraceus* were removed.

Alternatively, in saltmarsh grass habitats the upper limits are set by competition between plant species (e.g., *Spartina alterniflora* and *Spartina patens*) while the lower limits are set by their tolerance to inundation (Bertness 1991, Pennings and Bertness 2001). Overall biotic and abiotic factors have been shown to vary across intertidal habitats and structure community patterns in a variety of coastal systems (see appendix A, Box 1).

Similar factors to those mentioned above, which have been shown to influence community distribution in intertidal systems such as rocky shores, may possibly operate in other systems such as those formed by oyster reefs. Oysters are sessile and thrive within the intertidal zone and subtidal habitats worldwide. Intertidal oyster reef patches can protrude above the water during ebb tides becoming aerially exposed and become completely submerged during high tide. This vertical tidal gradient can influence biotic and abiotic factors that shape oyster reef ecology and may produce patterns of intertidal zonation (Figure 1.3). In contrast to rocky intertidal systems, only one species (the oyster) is the main occupant of reefs across all tidal elevations. In this sense, interspecific competition for space may not be as strong as in rocky intertidal systems in driving spatial patterns of distribution along tidal elevations.
Conceptual framework depicting processes and factors that might generate spatial zonation within intertidal oyster reefs (a), and how the factors might change if the reef is subtidal (b). The relative influence of these factors may vary spatially and temporally. These factors might influence oysters differently depending on the intertidal elevation. Oysters located on an intertidal oyster reef above mean water level can experience higher desiccation stress. Boat wakes may affect oysters that settle on the reef crest but have a lesser impact on the oysters that are located below water level. Settlement of oyster larvae might depict a vertical gradient in which more larvae can settle in lower sections of oyster reefs. Similarly, oysters that settle in the lower section of the reef might experience higher food delivery in comparison to oysters in the reef crest. Oysters at lower intertidal elevations that are subtidal may be exposed longer to diseases transmitted through the water column. Oysters living in the lower intertidal zone may also experience smothering by sedimentation. At lower intertidal zones oysters might experience increased competition for space with other intertidal organisms and higher predation.
Intraspecific differences in oyster survivorship across tidal elevations may exist however. Oysters located within the high intertidal portions of reefs are exposed to more stressful physical conditions such as higher temperatures and higher wave energy, while subtidal oysters and those oysters in lower intertidal elevations experience longer submersion period, which could lead to increased intra and interspecific competition and consumer pressure (Ortega 1981, Fodrie et al. 2014).

Tidal emersion may influence a variety of factors and processes that affect fine-scale structure in oyster reefs (Figure 1.3). Larval delivery is one of these processes. Settlement and early recruitment of *C. virginica* oyster larvae in North Carolina (Fodrie et al. 2014), Connecticut, New York (Prytherch 1929), and Virginia (Loosanoff 1932, Mackin 1946, Roegner and Mann 1990, Bartol and Mann 1997) while found at all depths studied, were higher subtidally and near mean low water in intertidal oyster reefs. Furthermore, studies of vertical distribution of settlement of *Ostrea denselamellosa*, *O. edulis*, and *C. gigas* have shown similar patterns of higher oyster larval recruitment towards subtidal locations (Suki and Tanaka 1931, Korringa 1940, Cahn 1950). Numerous possible explanations have been related to the observed patterns of higher settlement in the lower tidal zone and one of them is longer submergence time. Prolonged submergence allows oyster larvae in the water column become exposed to subtidal substrate substantially longer than intertidal substrate and consequently the larvae can experience a wider period in which to settle. Another possible explanation is the vertical segregation of different stages of oyster larvae within the water column. The pediveliger larvae are more abundant near the benthos compared to surface waters (Carriker 1951, Kunkle 1957, Baker 1994, Bartol and Mann 1997), which might contribute to the higher settlement patterns observed in subtidal oyster substrate. In addition, since later stages of oyster larvae have higher sinking rates (Dekshenieks
et al. 1996), prefer low energy areas (Ortega 1981, Abbe 1986), and lower flow (Bushek 1988) the larvae might actively seek oyster substrate located closer to the benthos when settling. The input of oyster settlers into the reefs allows for substrate to be created and for reef structure to be persistent in the seascape over time. While several invertebrates settle on the reef and may influence the reef complexity, the settling and cementing process carried out by oysters allow the reef structure to be generally created by oysters. This contrasts with rocky reef intertidal systems in which zones of multiple organismal distribution can be observed as distinct horizontal bands influenced by predation and competition.

Tidal emersion may also influence competition and predation in oyster reefs. Despite increased settlement of oyster larvae towards the bottom substrates of reefs, oyster reefs developed in intertidal zones have been shown to support greater densities of adult oysters compared to those in subtidal locations. This is possibly related to higher oyster survival in intertidal reefs as a result of shorter exposure to marine predators and biofouling organisms compared to oyster substrate located below mean water level in intertidal oyster reefs or in subtidal reefs (Nichy and Menzel 1967). For example, Fodrie et al. (2014) used predator surveys and faunal sampling to quantify Stone Crab burrows and predatory gastropods and recorded higher abundances in deep versus mid intertidal zones. Correspondingly, oyster abundance was higher in mid intertidal zones thereby suggesting that higher predation occurs at lower intertidal zones. Johnson and Smee (2014) also found that oyster mortality rate was higher in subtidal habitats compared to intertidal reefs. Additionally, oyster spat was able to survive and grow in subtidal areas but only when protected from consumers, suggesting that predation was higher in subtidal habitats (Johnson and Smee 2014). It is also possible, that oysters located below mean water level are closer to the boundaries of reefs thus experiencing edge effects (Ries et al. 2004,
Gorman et al. 2009) as shell cover and habitat complexity can be lower along reef edges, leading to increased predation pressure (Hanke et al. 2017). Therefore, it appears to be well established that oysters living below mean water level will most likely experience higher mortality rates due to predation pressure than that recorded in mid or intertidal locations.

Overgrowth by marine organisms might also be more predominant for oysters located in the lower portions of oyster reefs or deeper reefs due to prolonged submergence periods (Bahr and Lanier 1981, Johnson and Smee 2014). MacDougall (1943) found that no oyster spat survived below low water level due to smothering caused by hydroids, tunicates, sponges, and encrusting organisms. Similarly, Chestnut and Fahy (1953) after a month of exposing oysters at low water level and below mean water level, found that the shells were heavily encrusted with bryozoans, hydroids, barnacles, and tunicates with the highest mortality of oysters produced by Oyster Drills (Urosalpinx cinerea) near the bottom. Furthermore, interference competition of oyster spat with canopy-forming fouling organisms has been shown to increase with decreasing aerial exposure (Brodeur 2016). Hence, biological interactions such as consumer pressure and competition can influence structural complexity of oyster reefs at lower intertidal zones.

Oysters located in subtidal oyster reefs and below mean water level might be exposed to higher food delivery due to prolonged submergence compared to oysters located higher on intertidal oyster reefs (e.g., reef crest). The difference in submergence may result in differential growth patterns observed at relatively fine scales in the reefs. For example, Roegner and Mann (1955) found that oysters area growth was slower in reefs that became 25% percent aerially exposed, compared to those located in the lower intertidal and subtidal reefs that were submerged longer. Likewise, Kingsley-Smith and Luckenbach (2008) observed that growth rates of C. virginica and C. ariakensis across tidal treatments were the greatest in the subtidal
treatments compared to higher tidal levels. On the other hand, longer submergence may also lead to intense development of fouling suspension feeding organisms, which may locally compete for food resources, add energetic costs, and reduce growth of hosts resulting in reverse or paradoxical patterns of expected growth and distribution across the tidal gradient (Peterson and Black 1987, Bishop and Peterson 2006, Brodeur 2016). Ultimately, different levels of aerial exposure can result in variation in food availability and competitive interactions at lower intertidal locations.

The deposition of sediments and erosion have been identified as some of the leading causes of oyster reef failure, reef burial, and lack of persistence (Bahr and Lanier 1981, Taylor and Bushek 2008, Powers et al. 2009). Sediments both suspended and deposited can harm gill tissue, induce metabolic stress, and cause oyster mortality (Suedel et al. 2014). Despite the critical role sediments may play in reef persistence, few studies have conducted experimental manipulations to investigate the effects of sedimentation on oyster survival (but see Colden and Lipcius 2015), and no studies to my knowledge have experimentally examined the effects of sedimentation on oyster reef demography across tidal gradients. Oysters positioned closer to reef edges could experience higher sedimentation rates where flow is the slowest causing mortality and leading to a localized decrease in oyster shell cover and complexity (Hanke 2017, Lenihan 1999). Intertidal reefs can experience higher shifting of sediments, due to storms (Taylor and Bushek 2008), which could affect reef accretion and elevation. Further experimental work is needed however to tease apart the possible relationship of sedimentation with tidal elevation and its effects on fine and broader landscape structure of oyster reefs.

Desiccation stress may also play a role in oyster survival and contribute to zonation patterns within oyster reefs. During emersion, intertidal oysters especially those located in the upper
locations of reefs, (e.g., reef crests) experience increased solar radiation exposure, which can lead to high percentage of tissue water loss and result in mortality (Kingsley-Smith and Luckenbach 2008). The intertidal Sydney Rock Oyster (*Saccostrea commercialis*) suffers from heat kills when unusually low tides coincide with abnormally high temperatures (Porter and Hill 1982). With experimental deployments Nichy and Menzel (1967) found that mortality of *C. virginica* was the highest at the upper tidal level of the reefs during hot weather and low tide. Similarly, Roegner and Mann (1995) exposed newly settled *C. virginica* oysters to subtidal and intertidal levels and found that all recruits in the mid intertidal and above died during high temperature periods in contrast to low intertidal and subtidal oysters which survived. This is likely the reason why the structure of intertidal oyster reefs has a vertical limit and above this threshold it is impossible for oysters to survive. Therefore, it is established that similar to rocky shore intertidal systems, patterns of zonation at fine scales in oyster reefs can occur with mortality at high intertidal zones driven by desiccation stress.

In rocky intertidal settings the presence of macroalgae can facilitate intertidal organisms by ameliorating stressful conditions (Hay 1981, Bertness and Grosholz 1985). It is unclear however, whether the presence of macrophytes nearby oysters or adjacent to oyster reefs might influence desiccation stress and overall biotic and abiotic factors across the intertidal gradient. For instance, oysters located on reefs bordering macrophytes, such as mangroves, may experience lower desiccation stress due to amelioration of conditions by the canopy cover (see appendix A Box 2). Similarly, mangroves can provide substrate for oyster settlement across the intertidal zone and potentially influence biotic and abiotic factors across the intertidal zone. Formal tests of these hypotheses remain to be conducted.
Diseases affect the survival of oysters potentially influencing oyster reef structure. A variety of diseases and parasites infect oysters (see Lauckner 1983, Andrews 1984, Brower et al. 1994 for detailed reviews), but *Perkinsus marinus*, *Haplosporidium nelsoni* (MSX) and *H. costale* (SSO) are among the most common disease-producing protozoans. Despite the prevalence of diseases on oysters at broad geographic scales, infections by parasites such as *P. marinus* have been suggested to not vary with intertidal elevation on reefs (Burrell et al. 1984, O'Beirn et al. 1994, Ybanez 2007, Malek and Breitburg 2016). Tidal elevation (specifically duration of emersion of oysters) however might influence parasite infection (Malek 2010). The duration of emersion dictates how long the oysters can be exposed to parasites in the water column. Oysters that are exposed less to parasites (e.g., those located of reef crests or above mean water level) could potentially have lower infection rates. Increased internal temperatures, large temperature fluctuations, and increased CO$_2$ levels experienced by intertidal oysters (especially on reef crests), may reduce the ability of parasites (e.g., *P. marinus*) to proliferate at fast rates (Milardo 2001). On the other hand, bivalves when exposed to air can stop oxygen exchange with the atmosphere and might experience physiologically challenging conditions, becoming stressed (Burnett 1997) and more susceptible to infection (Allen and Burnett 2008). Malek and Byers (2017) through experimental manipulations of *C. virginica* in the southeastern USA, investigated the effect of tidal elevation on the heterogeneity of *P. marinus* prevalence, the intensity in prevalence of *H. nelsoni*, and the co-occurrence of both parasites. The results indicated that tidal elevation affected the intensity of *P. marinus* and the prevalence of *H. nelsoni*, which were significantly higher intertidally than subtidally. The authors attributed the patterns to the extreme variability that host oysters in the intertidal zone can experience in abiotic conditions (e.g., temperature, oxygen) at fine spatial scales, which can negatively affect the host physiology and
consequently host-parasite interactions. Conversely, a study conducted in Delaware Bay by Littlewood et al. (1992), investigated the effect of 5 different intertidal elevations on *H. nelsoni* and found no effect on parasite infection intensity or prevalence. However, abiotic conditions such as temperature in intertidal reefs can vary significantly between northeastern USA and southeastern locations such as South Florida and the Gulf of Mexico. Therefore, the effect of tidal elevation on host-parasite interactions might vary geographically. Since studies have found contrasting results, further research is needed in order to understand patterns of parasite infections across scales and tidal elevations. Furthermore, oysters of the same age heavily infected with *P. marinus* have shown to cease growth and oysters lightly infected grow slower than uninfected oysters (Menzel and Hopkins 1955). Differential oyster growth produced by parasites in combination with parasite variation at fine scales within reefs need to be investigated as it may result in structural complexity alterations of oyster reefs, an important feature that mediates predator-prey interactions and food web ecology in oyster reefs (Grabowski 2004, Grabowski and Kimbro 2005, Grabowski et al. 2008, Hesterberg et al. 2017).

Wave action and boating activity may also result in fine-scale spatial patterns in vertical zonation on intertidal oyster reefs and may also alter overall reef distribution and reefs patterns throughout the seascape. Vertical reef growth and morphology may be strongly related to wave action (Bahr and Lanier 1981). Waves and currents can transport sediment to and from the oyster reefs. High wave energy might also clear substrates, create substrate instability, inhibit the settlement of oyster larvae, and consequently prevent reef development. For instance, at exposed mid and high intertidal seawall locations in Beaufort, North Carolina where wave action is high, *C. virginica* only covered 10% of the structure while other species more resistant to wave action such as the mussels, barnacles, and algae occupied most of the available space (Ortega 1981).
Furthermore, consistent boating activity and accompanying wake effects might also alter oyster reef patterns in the seascape at broader scales. Grizzle et al. (2002) using historical aerial photography showed that oyster reefs in the vicinity of major navigation channels in the Mosquito Lagoon displayed evidence of dead margins. At fine scales, the dead margins of reefs consisted of empty and disarticulated shells that mounded up to a meter above the high water level. At broader scales, reefs initially located next to the channels migrated over time away from the channels, while those located far from the channel remained in the same location. Wall et al. (2005) collected in situ data on oyster recruitment, survival, sediment load data, slit/clay fraction, and water motion on reefs that displayed dead margins (impacted reefs) and compared them with pristine reefs. Recruitment did not vary among reefs, while survival was low and sediment load, percent silt/clay, and water motion were significantly higher in impacted reefs. This suggested that impacted reefs experienced lower survival of recruits due to high water motion and sediment load that resulted from persistent boating activities. Tank experiments have also found that wave energy could move clusters of intertidal oysters and reorient them into positions that result in lower survival (Campbell 2015). Therefore, reef structural complexity, shape, persistence, and location can be shaped by exposure to wave action and boating activities.

Based on all the literature surveyed, it is evident that the combination of biotic and abiotic factors is able to influence oyster reef seascapes at fine and broad scales. These factors can also influence oysters differently depending on the tidal elevation at which oysters are located. This renders oyster reefs as ideal study systems in which to evaluate questions regarding patterns of zonation across tidal gradients. Furthermore, the fact some species of oysters such as *C. virginica* are present across latitudes it allows the evaluation of the complex interplay between broad- and local- scale processes and the consistency of factors in regulating community structure. For
example, at lower latitudes desiccation stress may play a larger role in structuring oyster demographic rates on higher intertidal zones. However, it is unclear whether or not this effect stays consistent as latitude increases and high temperature becomes less extreme. Additional multi-scale investigations in oyster reef systems are needed to advance our understanding of oyster reef seascapes, their development, and their persistence. Moreover, these studies will contribute relevant and critical information (e.g., variation of oyster reef habitat structure and landscape context) for consideration in future designs of oyster reef restoration to maximize oyster biological output as well as the provision of habitat for other organisms.

1.4. Dissertation outline

The overall goal of this dissertation is to apply a seascape ecology perspective to understand how seascape heterogeneity can influence demographic rates, community patterns, and ecological processes. In general, oyster reefs have been understudied (compared to other coastal habitats) from a multi-scale perspective (Pittman et al. 2011) even though 85% of oyster reefs have been either lost or degraded (Barbier et al. 2010, Beck et al. 2011) and a spatially explicit approach could provide valuable insights for restoration practices (Boström et al. 2011). In addition, oyster reefs formed by the Eastern Oyster have proven to be an excellent model system to test questions related to zonation patterns along tidal gradients due to some oyster reefs spatial structures being located within intertidal locations. Nevertheless, how biotic and abiotic factors across the intertidal zone compare between oysters living on oyster reefs and those on mangrove prop root systems is not fully understood. Moreover, the patchwork of mosaics that oyster reefs form with other coastal habitats also render them ideal to test questions related to habitat adjacency and its potential influence on ecological processes. Indeed while information exists on oyster reefs
spatial patterns within the seascape, assessments of Eastern Oyster demographic rates in different habitat settings including seascapes where mangroves and oysters coexist, remain scarce.

In addition to oyster reefs, tropical macroalgal beds are in general understudied coastal habitats (compared to temperate macroalgal beds) and have not been investigated from a seascape perspective. Even less is known about how the alteration of tropical seascapes, through the introduction of non-native macroalgal habitats, may affect ecological processes that influence ecosystem function and how it compares to seascapes with natural macroalgal beds. Therefore, to address these knowledge gaps, I have divided my dissertation into three main study chapters.

In northeastern Florida, the dominant coastal habitat transitions from Smooth Cordgrass (*Sporobolus alterniflorus*; temperate species) to Black Mangroves (*Avicennia germinans*; tropical species). These two foundation species may affect the demographic rates of the Eastern Oyster (*Crassostrea virginica*), another foundation species commonly located adjacent to them. Therefore, I deployed juvenile oysters in cage experiments comprising three levels of predator exposure on (a) oyster reefs bordering Smooth Cordgrass, (b) reefs bordering Black Mangroves, and (c) isolated oyster bars, to quantify survival and growth rates north and south in the Guana Tolomato Matanzas National Estuarine Research Reserve. The results obtained in this study provided insights into the effects the encroachment of Black Mangroves into temperate saltmarsh-dominated habitats may have on demographic characteristics of the Eastern Oyster and associated fauna.

Although oyster demographic rates across intertidal zones have been examined in oyster reefs at higher latitudes, far less is known about them at subtropical locations where desiccation stress is expected to be greater due to higher temperature. Furthermore, little is known about oyster demographic rates when in association with a macrophyte intertidal habitat, which may
reduce desiccation stress and positively influence oysters at higher intertidal zones. In Chapter 3, I measured demographic characteristics of oysters along intertidal zones on oyster reefs and on oyster clusters associated to Red Mangrove prop roots in Tampa Bay, Florida. This study addressed: (a) how do demographic rates of the Eastern Oyster vary along intertidal zones (bottom, middle, and top) on oyster reefs and on prop roots and (b) whether the association of oysters with mangroves may reduce desiccation stress, thus positively influencing oysters at higher intertidal zones. This chapter contributed to our understanding of oysters and Red Mangrove relationships.

In tropical seascapes, beds of benthic macroalgae occur naturally interspersed within or nearby other habitats, but it is unclear what roles they play to support marine fauna. Even less is known about how the introduction of non-native macroalgal habitats (e.g., macroalgal farms) into tropical seascapes may affect ecological processes that influence ecosystem function and its comparison to seascapes with natural macroalgal beds. To address this knowledge gap, in Chapter 4, I surveyed fish assemblages and deployed macroalgal assays to quantify herbivory within naturally-occurring macroalgal habitats, macroalgal farms, as well as at varying distances in the seascape near Mafia Island, Tanzania. This study helped us understand the ecological roles that native macroalgal beds and introduced macroalgal farms play as habitats and food resource for fish assemblages in the East African region.

1.5. References


Grant, J., and McDonald J. 1979. Desiccation tolerance of Eurypanopeus depressus (Smith) (Decapoda: Xanthidae) and the exploitation of microhabitat. – Estuaries 2: 182–177.


CHAPTER 2: EASTERN OYSTER DEMOGRAPHIC RATES AND HABITAT ADJACENCY IN AN ESTUARINE TRANSITION ZONE

2.1. Abstract

The dominant habitat types found in a seascape can influence demographic rates and trophic interactions for many coastal organisms located in adjacent habitat patches. Thus, transition zones where habitat dominance changes can be informative for separating seascape-level effects from broader regional ones. For example, the dominant coastal habitat in the southeastern United States transitions from Smooth Cordgrass (Sporobolus alterniflorus; temperate species) to Black Mangroves (Avicennia germinans; tropical species) in northeastern Florida. These two foundation species may affect the demographic rates of the Eastern Oyster (Crassostrea virginica), another foundation species commonly located adjacent to them. In this study I used experimental and observational approaches to measure demographic rates of the Eastern Oyster on reefs adjacent to Smooth Cordgrass and Black Mangroves located within the transition zone (i.e., the seascape-scale effects), as well as on isolated reefs that were not adjacent to these coastal habitats to account for broader, regional-scale effects. Survival rates of oysters were lower on isolated oyster bars in the northern region of the transition zone, consistent with the higher abundance of predatory xanthid crabs found in this region. Likewise, growth was lower in the northern region, likely due to higher chlorophyll a concentrations in the south. Compared to their regional controls, both survival and growth was higher next to saltmarsh and lower next to mangrove habitats. The mechanisms for the influences of these adjacent habitats were not clear,
but appear to have been related to both consumptive and non-consumptive effects of predators. This study indicated that neighboring habitats and regional variation in the seascape may influence demographic rates of oysters. As coastal habitats continue to undergo change, such as tropical foundation species moving to higher latitudes, the influence of habitat adjacency on other organisms is not well understood, but could have important effects on ecosystems and the services they provide.

2.2. Introduction

A core aim of landscape ecologists, as well as conservation and management practices, is to understand how processes that structure communities vary as a function of landscape context (Fahrig 2007, Cushman et al. 2011, Schmucki et al. 2012). Landscape composition (i.e., types of habitat present) and habitat configuration (e.g., habitat adjacency) can influence interactions across habitat patches and thus affect demographic rates of organisms (Rilov and Schiel 2006a, 2006b, 2011, Donadi et al. 2013). In terrestrial landscapes for example, the proximity to different neighboring habitat patches can alter emigration success and predation of birds and mammals highlighting the importance of habitat adjacency (Andrén 1994, Gustafson and Gardner 1996). Habitat patches can be interlinked within the landscape, hence the quality of a patch can be a function of neighboring habitat types, which affect demographic rates (e.g., mortality) and persistence of organisms (Hobbs 1992, Tischendorf and Fahrig 2000, Thomas et al. 2001, Fischer and Lindenmayer 2007).

Regional factors can also influence ecological patterns and processes in the landscape matrix within which habitat patches are embedded, thus creating spatial discrepancies in organismal responses. For instance, variation in regional-scale factors, such as host-bird abundance and predator composition, influence ecological responses such as survival rates of birds in forest...
habitats (Donovan et al. 1997). In marine landscapes (termed ‘seascapes’) regional factors can be prominent since seawater is the connecting medium of habitat patches and it can vary (chemically and physically) depending on location. More specifically, hydrological (e.g., water velocity) and water quality parameters (e.g., dissolved oxygen, salinity) may vary regionally and consequently influence organismal dispersal, resource distribution, and physiological regulation of marine organisms. For example, differences in freshwater input into two closely located northeastern estuaries in the Gulf of Mexico resulted in contrasting salinity patterns, which affected the abundance of oyster predators and contributed to differences in oyster mortality between the two estuaries (Kimbro et al. 2017). Furthermore, Baillie and Grabowski et al. (2019) concluded that regional factors and processes can influence the persistence of oyster reefs and the success of their restoration after noticing that the relationship between vertical relief and oyster demographic characteristics yielded similar results in Chesapeake Bay (Schulte et al. 2009) and North Carolina (Lenihan 1999), but did not follow the same pattern in the Northeastern US. This suggests that oyster demographic characteristics can be context-dependent due to variations in biotic and abiotic factors. Understanding and accounting for such factors in restoration practices will ensure optimal allocation of resources in large-scale restoration efforts and spatially-explicit conservation practices (Fodrie et al. 2014).

Oysters are sessile organisms that live within estuarine seascapes that can vary in biotic and abiotic factors across multiple spatial and temporal scales. Oysters are foundation species that create complex habitats for associated faunal communities, many which are of commercial and recreational importance (Wells 1961, Bahr and Lanier 1981, Lenihan et al. 1998, Stunz et al. 2010). Oysters also provide a variety of valuable ecosystem services (Dayton 1972, Grabowski et al. 2012). Oyster reefs have become one of the most degraded habitats worldwide as a result of
anthropogenic activities influencing estuarine ecosystems (Peterson et al. 2003, Lotze et al. 2006, Worm et al. 2006, Beck et al. 2011). In addition to overharvesting and destructive harvesting practices, diseases, predator outbreaks, and the introduction of invasive species further threaten oyster populations (Lenihan and Peterson 1998, Kirby 2004, Kimbro et al. 2009, zu Ermgassen et al. 2012). In Northeast Florida, an ecoregion where oysters are commercially harvested, the abundance of the Eastern Oyster (Crassostrea virginica) has declined, which has led to concern from the scientific community, stakeholders, and regional management as the causes of decline are poorly known and age specific sources of mortality largely undetermined (Marcum et al. 2018). Possible causes suggested to underlie the decline include a combination of increased abundance of the oyster predator, the Crown Conch (Melongena corona) with ensuing higher predation rates, and a prolonged regional drought, which alters salinity and temperature increasing disease and desiccation stress (Garland and Kimbro 2015).

In Northeast Florida, intertidal Eastern Oyster reefs can be found within the estuarine seascape displaying distinct habitat features such as isolated oyster bars (with no immediate habitat adjacent to the reef) or oyster reefs bordered by other vegetated habitats, such as Smooth Cordgrass (Sporobolus alterniflorus previously Spartina alterniflora; Hosier 2018). The oyster reefs in Northeast Florida have also become recently rimmed by mangroves (most commonly Black Mangroves, Avicennia germinans, followed by Red Mangroves, Rhizophora mangle), which have been expanding their geographic range poleward beyond a previous northern historical limit at ~30°N along the east Florida coast (Kangas and Lugo 1990, Cavanaugh et al. 2014, McMillan and Sherrod 1986, Cook-Patton et al. 2015) thereby forming a coastal transition zone. North of the transition zone, oyster reefs can be found with saltmarsh grass as the dominant vegetation cover in coastal temperate climates, while just south of this region an ecotone persists
where oyster reefs, saltmarsh, and mangroves coexist at the apex of subtropical conditions (Cavanaugh et al. 2014).

The current study took place in the transition zone between subtropical and temperate climates in Northeast Florida and investigated how demographic rates of the Eastern Oyster were influenced by (a) habitat types (adjacency to saltmarshes and Black Mangroves) and (b) regional factors (north or south) within the seascape. To address these questions, a combination of field surveys and experimental deployments were conducted to quantify the seascape-level effects on survival and growth of juvenile oysters, and on the abundance of oysters (both juvenile and adults) and associated organisms. The results obtained in this study provide insights into the effects the encroachment of Black Mangroves into temperate saltmarsh-dominated habitats may have on demographic characteristics of the Eastern Oyster and associated fauna.

2.3. Method

2.3.1. Study location

The study was conducted in the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR) in Northeast Florida (Figure 2.1). The GTMNERR is located south of Jacksonville in St. Johns and Flagler counties and is divided by the city of St. Augustine (Frazel 2009). The Reserve is linked to the Atlantic Ocean through the St. Augustine and the Matanzas inlets. The Reserve has approximately 64,487 acres of submerged lands and uplands, which includes saltmarshes, mangrove tidal wetlands, oyster bars, estuarine lagoons, upland habitat, and coastal beaches (Frazel 2009). In the Reserve, some of the potential oyster predators include the Mud Crab (*Panopeus herbstii*; Kimbro et al. 2014), Oyster Toadfish (*Opsanus tau*; Grabowski 2004, Grabowski and Kimbro 2005, Kimbro et al. 2014), Stone Crab (*Menippe mercenaria*; Kimbro et al. 2017), Blue Crab (*Callinectes sapidus*), Crown Conch, and Sheepshead fish (*Archosargus*...
probatocephalus). The Reserve is also known for containing the northernmost extent of mangrove habitat on the east coast of the United States (Zomlefer et al. 2006). The study sites were located in a subsection of the Reserve, which is associated with the Matanzas River estuary, extending from Moultrie Creek to south of Pellicer Creek (Figure 2.1).

![Figure 2.1](image)

Figure 2.1. Study sites selected in the Guana Tolomato Matanzas National Estuarine Research Reserve for the experimental deployment of juvenile oysters.

### 2.3.2. Study species

The Eastern Oyster is found in estuarine and coastal habitats along the east coast of North America from the Gulf of St. Lawrence to South Florida, throughout the Caribbean, and along the coasts of Brazil and Argentina (Parker et al. 2013). In the United States, the Eastern Oyster is commercially important due to its fishery value (Kirby 2004). In addition, the Eastern Oyster is important ecologically as oyster reefs provide a variety of ecosystem services such as filtration of coastal waters (zu Ermgassen et al. 2012), removal of excess nutrients from estuarine ecosystems

Mangroves and saltmarshes are the dominant flora in coastal estuarine ecosystems of Florida (Ball 1988, Day et al. 1989, Alongi 1998, Bianchi 2007). Both plants are tolerant to salt and co-occur at lower latitudes globally (Comeaux et al. 2012). Mangrove propagules can get trapped within saltmarsh grass (Lewis and Dunston 1975) and compete for space with saltmarsh plant species (Pickens and Hester 2010). Saltmarshes can provide foraging grounds and protection from predation for many estuarine organisms (Weisberg et al. 1981, Weisberg and Lotrich 1982, Minello and Zimmerman 1983, Boesch and Turner 1984, Fitz and Weigert 1991, Beck et al. 2001). Saltmarshes are a main source of carbon detritus and, for this reason, play a major role in the secondary production of invertebrate prey that may be transferred in the food web to nearby tidal creeks and bays (Hettler 1989, Galvan 2008, Haynert et al. 2017). In Northeast Florida saltmarsh grass is dominated by the Smooth Cordgrass. Mangrove forests are among the most productive habitats, which are important ecologically and economically through the diverse ecosystem services provided. These services include food, nursery grounds for commercially and recreationally important fish and invertebrates, nesting sites, recreation, and shoreline protection (Ewel et al. 1998, Aburto-Oropeza et al. 2008). Although the Red Mangrove is present in the Reserve, the Black Mangrove is the dominant species there.
2.3.3. Experimental deployment

Survival and growth of juvenile oysters was experimentally assessed in oyster reefs with no immediate adjacent vegetation, oyster reefs adjacent to saltmarsh grass, and on reefs adjacent to Black Mangroves. Four sites were selected, two each north (N1 and N2) and south (S1 and S2) in the Reserve (Figure 2.1). Sites north were characterized by oyster reefs, which exist as oyster bars (isolated reefs at least by 10 m from vegetative habitats) and as reefs adjacent to saltmarsh. Sites in the south were characterized by oyster bars and by reefs adjacent to saltmarsh and reefs adjacent to mangroves. Therefore, 10 representative reefs adjacent to Smooth Cordgrass saltmarsh (n = 5 per site) and 6 oyster bars (n = 3 per site) were selected north in the Reserve, while 10 reefs adjacent to Black Mangroves (n = 5 per site) and 6 oyster bars (n = 3 per site) were selected south in the Reserve (N = 32 total oyster reefs). During June 2015 juvenile oysters (spat) were deployed in experimental cages comprising three levels of predator exposure (Figure 2.2a) at each of the 32 reefs. The predator absent level (P-), consisted of a tile placed inside a cage completely closed off to predators (Figure 2.2b), the cage control level had two sides removed (Figure 2.2c) to allow access by predators and mimic the potential artifacts of the cages on oyster (survival), and the predator accessible level (P+), consisted of a tile completely exposed (no sides present) and therefore open to predators (Figure 2.2d). The experiments were attached to a PVC pipe and deployed on the boundary of oyster reefs with adjacent habitats (when present) and similar tidal height in the absence of habitats. In all three levels of predator exposure, six oyster spat were attached with marine epoxy (i.e., z-spar) to a tile, which was then cable-tied to a mesh Vexar base. Shell heights (mm) of all spat were measured at the time of deployment and after one month spat were checked and status (dead or alive) recorded. Survival was calculated as the proportion of oysters alive out of the total at the time of retrieval. Survival
rates in predator-accessible tiles did not differ from survival rates in cage controls (all p > 0.05), except for reefs adjacent to saltmarsh grass ($t = 2.23, p = 0.034$).

Figure 2. 2. Juvenile oysters (spat) attached to ceramic tile (a) were assigned to one of three predator exposure levels: (b) predator absent consisted of a tile inside a cage completely closed off to predators, (c) cage-control to account for potential caging artifacts, and (d) predator accessible consisted of a tile completely exposed and therefore open to predators.

Juvenile oysters within the predator absent level were deployed for two additional months (June-September) to quantify growth. I re-measured their size after three months of deployment to calculate juvenile oyster growth rates (final size minus initial size of each individual live
oyster and dividing the difference by 90 days). Growth rates were averaged within each cage and by habitat type.

2.3.4. Oyster density and factors that may influence demographic rates of oysters

In addition to the experimental deployments, I acquired three data sets to investigate oyster density and other biotic and abiotic factors that could have influenced patterns of oyster demographic rates observed in caging experiments. The GTMNERR conducted sampling of oyster reefs in the Reserve from 2014 until 2016 along the Matanzas River and Pellicer Flats locations that overlapped the locations where the juvenile oyster experiments were conducted. For this study only non-harvested oyster reefs were included in the analysis. GTMNERR selected oyster reefs using a stratified random sampling design (Marcum et al. 2018). They collected oysters and associated organisms from quadrats (0.25 m x 0.25 m) excavated to a depth of 15 cm (Rodriguez et al. 2014) from which barnacles, mussels, clams, and porcelain crabs were counted and individual oyster shell height was measured for each sample.

The reefs sampled by GTMNERR were classified for this study by region in the seascape (north or south in the Reserve) and by habitat type. Habitat types were defined as: (a) isolated oyster bars, which consisted of reefs > 10 m distance from adjacent habitats, (b) oyster reefs adjacent to saltmarsh grass (≤ 10 m distance from habitat), or (c) reefs adjacent to mangroves (≤ 10 m distance from habitat). This classification was accomplished by locating each georeference-sampled reef and measuring the distance to the closest habitat using ArcGIS v 10.5. Mean oyster density, percent cover of live oysters, barnacle density, density of Crown Conchs, and density of associated organisms (barnacles, mussels, clams, and porcelain crabs), were calculated for each reef. In total, 50 oyster reefs were sampled by the Reserve in the selected regions for this study. Of these reefs, 16 reefs were adjacent to saltmarsh grass, three were adjacent to Black
Mangroves, and the remaining 31 reefs were oyster bars. More oyster reefs were sampled north in the Reserve (36) compared to the south (14).

Xanthid crab abundance surveys were conducted in July 2015 (D. Kimbro unpublished data) since they are predators of juvenile oysters (Kimbro et al. 2014, Micheli and Peterson 1999). Xanthid crabs were quantified on 12 oyster reefs north and 12 oyster reefs south in the Reserve using two quadrats (0.25 m x 0.25 m) on each reef. The density of xanthid crabs greater than 8mm in carapace width was then averaged by reef, and compared north and south in the Reserve.

Water quality (i.e., salinity, temperature, and dissolved oxygen) and chlorophyll a data were acquired from two stations (one north of the Reserve and one south) monitored by GTMNERR from January 2014-December 2016. Daily measurements were pooled into monthly averages during the three years of monitoring for seascape location comparisons.

2.3.5. Statistical analyses

Due to presence of regional differences between north and south in the Reserve and experimental design, oyster demographic rates were compared (1) on oyster reefs in the absence of vegetation (oyster bars) north and south, (2) on northern oyster bars and reefs adjacent to saltmarsh grass, and (3) on southern oyster bars and reefs adjacent to Black Mangroves. Survival rates of juvenile oysters in the absence of predators (in cages) were first assessed and compared (as explained above) to examine any potential mortality not linked to predation that could have been related to regional or adjacent habitat effects. Then, survival rates in the presence of predators (exposed tiles) were compared (as explained above) to examine any potential mortality linked to predation. To fully isolate the predator effects, survival rates in the absence of predators were subtracted from survival rates in the presence of predators at each reef and averaged by habitat type. Predator effects were then compared (as explained above) to examine any regional or adjacent...
habitat effects. Similarly, growth rates of juvenile oysters in cages were compared for regional and adjacent habitat effects. All comparisons were conducted using non-parametric, permutation-based (np) t-tests.

The density of oysters, barnacles, Crown Conchs, and all associated organisms, were compared similarly as above (1) on oyster reefs in the absence of vegetation (oyster bars) north and south, (2) on northern oyster bars and reefs adjacent to saltmarsh grass, and (3) on southern oyster bars, reefs adjacent to Black Mangroves, and reefs adjacent to saltmarshes since the GTMNERR sampled these reefs also south of the Reserve. Np t-tests and np analysis of variance (ANOVA; Anderson 2001) were used to examine the effects of region (north and south) and adjacent habitats on the density of organisms. Xanthid crab density and other abiotic and biotic variables (percent of oyster cover, salinity, temperature, dissolved oxygen, and chlorophyll a) were compared between north and south in the Reserve with np t-tests.

Homogeneity of dispersion for all data was verified with the function np-disp, (non-parametric dispersion) which is equivalent to Levene’s test (Anderson 2006, Anderson et al. 2006), and when needed data were square-root transformed to meet assumptions. All statistical analyses were conducted using Matlab and the Fathom toolbox (Jones 2017) and 1,000 permutations.

2.4. Results

Overall, juvenile oysters in the absence of predators (in cages) had a survival rate of 0.89 ± 0.03. In the absence of predators and adjacent habitats, survival rates of juvenile oysters in isolated oyster bars did not differ significantly between north and south in the Reserve (t = 2.24, p = 0.191; Figure 2.3). However, in the absence of predators survival rates were 0.08 higher in the north compared to the south. In the absence of predators, survival rates of juvenile oysters in
isolated oyster bars did not differ significantly from reefs adjacent to saltmarshes ($t = 1.15, p = 0.49$; Figure 2.3). However, in the absence of predators when adjacent to saltmarshes survival rates were 0.03 lower compared to survival in isolated oyster bars. In the absence of predators, survival rates of juvenile oysters in oyster bars did not differ significantly from reefs adjacent to Black Mangroves ($t = 1.37, p = 0.183$; Figure 2.3). However, in the absence of predators survival rates were 0.17 lower when adjacent to Black Mangroves compared to in isolated oyster bars.

![Survival rates of juvenile oysters in all predator levels and habitat types.](image)

**Figure 2.3.** Survival rates of juvenile oysters in all predator levels and habitat types. *Predator −* refers to oysters placed inside a mesh-built cage and therefore protected from predators. *Cage control*, refers to juvenile oysters in cages with two sides removed thus accessible by predators (used for controlling the presence of mesh material). *Predator +* refers to tiles completely exposed and therefore accessible to predators.

In isolated oyster bars survival rates of juvenile oysters within predator-accessible tiles were two times higher south ($0.5 \pm 0.17$) than north in the Reserve ($0.25 \pm 0.19$, $t = 2.66, p = 0.03$; Figure 2.4a), suggesting regional effects. Survival rates of juvenile oysters in the absence of
adjacent habitats in isolated oyster bars did not differ significantly from reefs adjacent to
saltmarshes ($t = 0.37, p = 0.717$; Figure 2.4a). However, survival rates was 0.20 higher adjacent
to saltmarsh than isolated oyster bars. Although not significant at the alpha 0.05 level, there was
5.2% support for survival rates of juvenile oysters being higher in isolated oyster bars ($0.37 \pm
0.13$) compared to oyster reefs adjacent to Black Mangroves ($t = 2.20, p = 0.052$; Figure 2.4a). In
close contrast to the patterns in reefs adjacent to saltmarshes, survival rates were 0.38 lower when
adjacent to Black Mangroves compared to isolated oyster reefs.

In isolated oyster bars there was a 5.5% support for predator effects on juvenile oysters being
higher north ($0.75 \pm 0.14$) than south in the Reserve ($0.42 \pm 0.09, t = 1.97, p = 0.055$; Figure
2.4b), suggesting regional effects. Predator effects on juvenile oysters in isolated oyster bars did
not differ significantly from reefs adjacent to saltmarshes ($t = 1.25, p = 0.221$; Figure 2.4b).
However, predator effects were 0.23 lower adjacent to saltmarshes compared to northern isolated
oyster bars. Predator effects on juvenile oysters in oyster bars did not differ significantly from
reefs adjacent to Black Mangroves ($t = 1.51, p = 0.153$; Figure 2.4b). However, predator effects
were 0.25 higher adjacent to Black Mangroves compared to southern oyster bars.

Growth rates (mm/day ± standard error) in isolated oyster bars were higher south ($0.15 \pm
0.001$) than north in the Reserve ($0.07 \pm 0.01, t = 4.41, p = 0.004$; Figure 2.4c). Growth rates in
oyster bars did not differ significantly from reefs adjacent to saltmarshes ($t = 1.31, p = 0.199$;
Figure 2.4c). However, growth rates were 0.034 higher when adjacent to saltmarshes compared
to oyster bars. Growth rates in oyster bars did not differ significantly from reefs adjacent to
Black Mangroves ($t = 1.28, p = 0.207$; Figure 2.4c). However, growth rates were 0.051 lower
adjacent to Black Mangroves compared to oyster bars.
Figure 2.4. Mean survival rates (a), predator effects (b), and growth rates (c) of juvenile oysters on reefs adjacent to saltmarsh grass, Black Mangroves, and oyster bars isolated from habitats. Data used for these graphs include experimental deployments conducted north and south sites of the Reserve. For survival, exposed tiles to the presence of predators were used. To calculate predator effects, survival rates in predator absence (P –, completely closed off cages) were subtracted from tiles exposed to the presence of predators (P +). For growth calculations only oysters in completely closed off cages were used.

Overall, across the Reserve the mean (± standard error) density of oysters was 133.6 ± 13.2 per 0.0625 m². In the south there was a mean density of oysters (± standard error) of 193.4 ±
36.8 while 110.3 ± 9.3 oysters per 0.0625 m$^2$ were quantified north. In isolated oyster bars, density of oysters was higher south compared to north in the Reserve ($t = 2.99$, $p = 0.004$; Figure 2.5a). Density of oysters in oyster bars did not differ significantly from reefs adjacent to saltmarshes ($t = 0.72$, $p = 0.504$; Figure 2.5a). Oyster density did not differ among oyster bars, reefs adjacent to Black Mangroves, and reefs adjacent to saltmarsh south in the Reserve ($F_{2,11} = 0.45$, $p = 0.661$).

![Graphs showing mean oyster density, barnacle density, Crown Conch density, and density of associated organisms per 0.25 x 0.25 m quadrat on reefs adjacent to saltmarsh grass, Black Mangroves, and oyster bars isolated from habitats. Data used for these graphs include sampling conducted by GTMNERR north and south sites in the Reserve.]

Figure 2.5. Mean oyster density (a), barnacle density (b), Crown Conch density (c), and density of associated organisms (d), per 0.25 x 0.25 m quadrat on reefs adjacent to saltmarsh grass, Black Mangroves, and oyster bars isolated from habitats. Data used for these graphs include sampling conducted by GTMNERR north and south sites in the Reserve.

Density of barnacles in isolated oyster bars was higher south compared to north in the Reserve ($t = 2.79$, $p = 0.011$; Figure 2.5b). Density of barnacles in isolated oyster bars did not differ significantly from reefs adjacent to saltmarshes ($t = 0.10$, $p = 0.919$; Figure 2.5b). Density
of barnacles did not differ among oyster bars, reefs adjacent to Black Mangroves, and reefs adjacent to saltmarsh south in the Reserve \( (F_{2,11} = 0.34, p = 0.719; \text{Figure 2.5b}) \).

Density of organisms in oyster bars was higher south compared to north in the Reserve \( (t = 4.56, p = 0.001; \text{Figure 2.5d}) \). Density of organisms in oyster bars did not differ significantly from reefs adjacent to saltmarshes \( (t = 0.47, p = 0.663; \text{Figure 2.5d}) \). Density of organisms did not differ among oyster bars, reefs adjacent to Black Mangroves, and reefs adjacent to saltmarsh south in the Reserve \( (F_{2,11} = 0.29, p = 0.754; \text{Figure 2.5d}) \).

The percent cover of live oysters was significantly higher in oyster bars north (27.8%) compared to south (19.2%) in the Reserve \( (t = 2.42, p = 0.029) \). No Crown Conchs were found in surveys conducted north in the Reserve, and their density did not differ among habitat types in the south \( (F_{2,11} = 0.89, p = 0.474; \text{Figure 2.5c}) \). Mean density of xanthid crabs (± standard error) was significantly higher north \( (3.1 ± 0.04) \) compared to south \( (1.6 ± 0.5) \) in the Reserve \( (t = 2.28, p = 0.031; \text{Figure 2.6}) \).

![Figure 2.6](image-url)  

**Figure 2.6.** Mean density of Xanthid crabs in oyster reefs (in general) north and south of the Matanzas Inlet. Data used for these graphs include sampling conducted by Kimbro et al (unpublished data) north and south sites of the Reserve.
2.4.1. Environmental variables

Mean temperature (C° ± standard error) did not differ between north (23.02 ± 0.31) and south in the Reserve (23.75 ± 0.51, \( t = 0.56, p = 0.595 \); Figure 2.7a,b). Mean salinity (psu ± standard error) was higher north (33.5 ± 0.45) compared to south in the Reserve (15.46 ± 2.74, \( t = 17.39, p = 0.001 \); Figure 2.7c,d). Mean dissolved oxygen (mg/l ± standard error) was higher (6.54 ± 0.07) north of compared to south in the Reserve (5.61 ± 0.11, \( t = 3.33, p = 0.001 \); Figure 2.7e,f). Mean chlorophyll \( a \) (µg/l ± standard error) was lower (3.91 ± 0.44) north compared to the south (7.95 ± 1.11, \( t = 3.26, p = 0.002 \); Figure 2.7g,h).

2.5. Discussion

Understanding how seascape context can influence demographic rates and trophic interactions for many coastal organisms is important for the management and conservation of ecosystems. Yet understanding how context dependency may operate in transition zones where the dominant vegetation is changing within estuarine seascapes presents a major challenge. In this study, experimental and observational approaches were used to quantify demographic rates of Eastern Oysters in various habitat types within an estuarine transition zone where Black Mangroves have started to become established as a result of their range expansion towards higher latitudes. Specifically, this study showed that neighboring habitat patches can influence demographic characteristics of oysters such as survival and growth. In addition, regional variation in biotic and abiotic factors may also occur in estuarine seascapes and strongly affect oyster demographic rates.

Survival rates of juvenile oysters differed among the cage types, as expected, due to varying levels of predator access. Survival rates in the absence of predators were generally high (~89%). However, in the absence of predators, survival rates in isolated oyster reefs decreased (~8%)
south in the Reserve suggesting regional non-consumptive mortality. In the present study, water salinity was higher north of the Reserve. While parasitic diseases (e.g., *Perkinsus marinus*, *Haplosporidium nelsoni*) are usually associated with higher salinities (Ford and Tripp 1996, Powell et al. 1996, Kim and Powell 1998, Soniat et al. 2006, Volety et al. 2008, Malek 2010) long exposure to low salinity levels may be detrimental for oysters. For example, in the northern Gulf of Mexico, La Peyre et al. (2013) observed that extended low salinities (< 5 ppt) in combination to high temperatures (>25 °C) during the summer season negatively impacted oyster recruitment, survival, and growth. Examination of the oyster plasma showed evidence that these oysters were not able to osmoconform and lower their plasma osmolality, resulting in excessive valve closure to minimize energetic demands. The extended period of valve closure caused hypoxia, acidosis of the hemolymph or starvation, leading to oyster death (de Zwaan and Wijsman 1976, Lombardi et al. 2013). Therefore, lower salinity levels south of the Reserve might have influenced oyster survival but further research is needed to clarify this pattern. In addition, the lower salinities observed south of the Reserve contrasts with Garland and Kimbro (2015) findings. Possible reasons for the patterns observed include the ending of the drought period, resulting in lower salinity values due to increased freshwater discharge from Pellicer Creek into the southern sites. Another possibility for the discrepancy in findings is that the water quality station south in the Reserve is located close to the mouth of the creek, which could have influenced the low salinity values recorded relative to those measured by handheld YSI occurring closer to the oyster reefs by Garland and Kimbro (2015).
Figure 2. 7. Monthly mean environmental variables ± standard error of the mean from January 2014 until December 2016 for Matanzas River (left column) and Pellicer Creek (right column). Variables include temperature (a and b), salinity (c and d), dissolved oxygen (e and f), and chlorophyll a (g and h).
Survival rates in the absence of predators were lower (~17%) when adjacent to Black Mangrove habitats in comparison to southern isolated oyster bars, suggesting regional and non-consumptive mortality adjacent to Black Mangrove habitats. These findings were surprising since in chapter 3 of this dissertation I found that mangrove canopy (through reduction of desiccation stress) might positively influence oysters living on Red Mangrove prop roots within the Tampa Bay estuary. Similarly, Aquino-Thomas and Proffitt (2014) found that mangrove height (used as a proxy for shading by the canopy) also positively influenced oysters. However, both of the mentioned studies occurred in southern Florida estuaries where oysters were associated to Red Mangroves while the at present study location Black Mangroves dominated. Therefore the lower (non-consumptive) mortality found in this study may be due to specific biotic or abiotic characteristics associated with Black Mangroves. Differences in fine-scale habitat structure as well as broad scale stand-level attributes exist among the different mangrove species and saltmarsh grass (Johnstone and Guner 2018). At fine-scales, habitat structure of estuarine vegetation varies in terms of pneumatophores, prop roots, and grass shoots. At broader scales, mangrove-dominated seascapes differ in stand-level attributes such as more woody substrates, larger canopies, mangrove-derived productivity, and associated chemical cues (Odum 2002, Johnstone and Guner 2018). In saltmarsh-dominated seascapes grass-based substrate, marsh-derived productivity, and associated cues are the common stand-level attributes. These differences among vegetative patches can influence sorting of associated fauna at different scales (Johnstone and Guner 2018) and possibly may also alter biotic and abiotic conditions that influence demographic rates of organisms such as survival and growth rates in oysters, though this requires further investigation.
Survival rates of juvenile oysters in predator accessible tiles in isolated oyster bars were lower north of the Reserve and corresponding predator effects were higher compared to the south. This is consistent with predatory xanthid crab densities. For example, xanthid crabs (>8 mm) were more abundant in oyster reefs north compared to the south and therefore could have been a factor contributing to lower survival rates as adult xanthid crabs feed on juvenile oysters (Kimbro et al. 2014). There has also been an increase in density of the Crown Conch, one of the major oyster predators in the Reserve, presumably due to reduced regulation from its predators the Stone Crab and the Horse Conch (*Triplofusgus giganteus*; Garland and Kimbro 2015). Interestingly, Crown Conchs were absent north and present only in oyster reefs in the south. This finding is consistent with Garland and Kimbro (2015) who also found that no Crown Conchs were present in northern oyster reefs in the same Reserve. Crown Conchs have been demonstrated to mainly target adult oysters and not juveniles (Garland and Kimbro 2015). This might the reason why despite Crown Conch density being higher south of the Reserve, juvenile oysters survival rates in oyster bars were not lower south compared to oyster bars located north in the Reserve.

The survival rates of juvenile oysters in the predator accessible tiles differed among habitat types. Specifically, survival rates of juvenile oysters were lower on oyster reefs that were adjacent to Black Mangroves (~10%) with higher predator effects compared to southern oyster bars (~50%), which had lower predatory effects. This suggests that juveniles in oyster reefs adjacent to Black Mangroves face a higher mortality risk related to predation compared to other oyster-reef habitat types. Micheli and Peterson (1999), found that survival of hard clams (*Mercenaria mercenaria*) was higher on oyster reefs that were separated from saltmarshes and seagrass beds because the predatory Blue Crab used vegetated habitats as corridors, which
facilitated the access of Blue Crabs to oyster reefs and enhanced predation intensity on the clams. It is possible that in the present study a predator associated with Black Mangrove habitats may have easier access to adjacent oyster reefs. Indeed, Aquino-Thomas and Proffit (2014) found that increasing numbers of mangroves in the shoreline could have negative effects on oysters living on the benthic substrate nearby and attributed it to the ability of mangroves to provide habitats for a variety of predators and competitors of oysters (Ashton et al. 2003, Manson et al. 2005). Potential predators associated with mangroves include wetland-associated birds and other marine predators, such as xanthid crabs. Wading birds and sea birds frequently nest, roost, and raise their young in the mangrove canopies due to the relative isolation from terrestrial predators and close proximity to food resources. Adult xanthid crabs, which include Stone Crabs and Mud Crabs, are known for preying on juvenile oysters (Micheli 1997, Kimbro et al. 2014) and can be abundant in mangrove wetlands. However, xanthid crab abundance was higher in the north where oyster reefs were not adjacent to Black Mangroves. In chapter 3 of this dissertation I found no differences in xanthid crab abundance between clumps of oysters on Red Mangrove prop roots and oyster bars. This suggests that xanthid crabs might be similarly abundant in oyster bars and reefs adjacent to mangroves making it challenging to explain the difference in predation observed in the present study. The observations in chapter 3 however, were made on Red Mangroves in a different Florida estuary (Tampa Bay), while in northeast Florida Black Mangroves dominate the mangrove vegetation and taxon-specific differences may occur. Johnston and Gruner (2018) compared associated marine fauna among Smooth Cordgrass, Black Mangroves, and Red Mangroves and observed that penaeid shrimp was associated to pneumatophore structure of Black Mangroves. Hence it is possible that penaeid shrimp could predate on juvenile oysters in adjacent oysters reefs. However, more research is needed to
examine whether this is the case or if another predator might be responsible for observed patterns of decreased oyster survival adjacent to Black Mangroves.

Juvenile oyster survival rates in the predator accessible tiles did not differ significantly between reefs adjacent to saltmarshes and oyster bars. This pattern is consistent with the findings of Micheli and Peterson (1999) where no differences in juvenile oyster survival were observed among reefs that were isolated from vegetation and oyster reefs adjacent to saltmarshes. One possible reason attributed to these patterns (in the mentioned study) was that xanthid crabs did not differ in abundance between saltmarshes and isolated oyster reef (Micheli and Peterson 1999). The database analyzed in the present study did not have the spatial resolution for investigating the effects of habitat type on xanthid crab abundance, thus I could not assess whether the same pattern occurs in northeast Florida. Nevertheless, survival was 20% higher when oyster reefs were adjacent to saltmarshes compared to northern oyster reefs, which had higher predatory effects. These results suggest that more favorable conditions with fewer predators may occur in reefs adjacent to saltmarsh vegetation north in the Reserve.

Growth rates of juvenile oysters were higher in isolated oyster bars south compared to north in the Reserve. This is potentially related to the higher concentration of chlorophyll $a$ found in this location of the Reserve, which could have served as food source for oysters. High chlorophyll $a$ may result in higher levels of secondary production, which was likely the case in this study since high abundance of associated fauna (barnacles, mussels, clams, and porcelain crabs) was also observed. It is important to note however, that while juvenile oyster growth rates were higher on oyster bars south of the Reserve, oyster reefs in this location were mainly composed of juvenile oysters (Marcum et al. 2018). Thus, while juveniles grew faster in southern
reefs by Pellicer Creek, once they reach a size threshold they may most likely be targeted by the abundant Crown Conch, which was absent in the northern sites.

Local differences in the seascape with respect to Crown Conch abundance and oyster recruitment pulses may have also influenced oyster reef patterns. Oyster density was higher and more variable south of the Reserve relative to the north, while there was a higher percent cover of live oysters in oyster bars located in the north. These findings seem contradictory, however there was a higher proportion of smaller oysters in the south (Marcum et al. 2018) resulting in higher overall density of oysters but not necessarily higher cover.

2.5.1. Conclusion

This study found that the type of habitat patches adjacent to oyster reefs may influence the Eastern Oyster demographic rates in the Northeast Florida ecoregion as suggested by the differences in growth rates and survival rates observed in the different oyster reef habitats. However variation in regional biotic and abiotic factors likely strongly influenced the Eastern Oyster demographic characteristics highlighting the importance of studies assessing regional-scale variation in populations. Future studies could be enhanced by increasing the sample size of surveys of oyster demographic characteristics and associated predator communities in the different oyster habitat settings to allow for a more balanced design. Indeed constraints of this study include low sample size and limited spatial resolution in the acquired datasets. Furthermore, this study was conducted in a transition zone where Black Mangroves are starting to encroach saltmarsh-dominated estuaries. Therefore, it is possible that drastic effects associated with mangrove encroachment are not yet strongly noticeable. However, with the continued mangrove expansion poleward, changes in vegetation abundance and composition are expected, which presents an exciting new frontier for ecological studies concerning estuarine habitats with
implications for coastal wetland communities. This study presents a first step towards understanding how oysters residing in oyster reefs occurring in subtropical-temperate settings may respond to changes in neighboring habitat types.

2.6. Acknowledgments

I thank all the field assistance provided by Tim Pusack, Mattew Farnum, and Owen Stokes-Cawley. I also thank all the researchers and agencies that collected and shared datasets analyzed in this chapter; these include David Kimbro from Northeastern University, Nikki Dix and her research team from the Guana Tolomato Matanzas National Estuarine Research Reserve, and the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanic and Atmospheric Administration.

2.7. References


Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. – In: Parker, B. (ed) Proceedings of
the Colloquium on Conservation Problems in Antarctica. Allen Press. Lawrence, Kansas, pp. 81–95.


CHAPTER 3: RED MANGROVES POSITIVELY INFLUENCE THE EASTERN OYSTER ALONG AN INTERTIDAL GRADIENT

3.1. Abstract
In intertidal habitats, desiccation and heat stress increase from low to high intertidal zones. However the presence of macrophytes may ameliorate stressful conditions at high intertidal zones, thus positively influencing associated organisms. Although oyster demographic rates across intertidal zones have been examined in oyster reefs at higher latitudes, far less is known about them at subtropical locations where desiccation stress is expected to be greater due to higher temperature. Furthermore, little is known about oyster demographic rates when in association with a macrophyte intertidal habitat, which may lower desiccation and positively influence oysters at higher intertidal zones. The Eastern Oyster (*Crassostrea virginica*) is a sessile invertebrate, which can form two types of intertidal habitats – oyster reefs and oyster clusters on Red Mangrove prop roots. Higher intertidal zones of these habitats can protrude above the water throughout ebb tides during which they are exposed aerially, but become completely submerged during high tide. This vertical tidal gradient influences biotic and abiotic factors, which may affect oyster demographic rates. Therefore this study addresses (a) how do demographic rates of the Eastern Oyster vary along intertidal zones (bottom, middle, and top) on prop roots and oyster reefs and (b) whether the association of oysters with mangroves may reduce desiccation stress, thus positively influencing oysters at higher intertidal zones. To address these questions, I used experimental and observational approaches to measure
demographic rates and conducted an evaporative water loss experiment on mangrove prop roots and oyster reefs. Compared to reefs, I found oysters on prop roots to be at higher densities and had higher survival. Consistent with density and survival, water loss (a proxy for desiccation stress) was lower on the prop roots, suggesting that the mangrove canopy may have provided a positive effect on oysters. Lower density of oysters was observed at lower intertidal zones on both habitats and may have been related to longer exposure to marine predators. The results suggest that in stressful intertidal habitats positive interactions can occur when oysters are associated to Red Mangroves due to canopy shade, which reduces desiccation stress for oysters. As temperature increases with climate change, mangroves may provide a desiccation refuge for associated oysters.

3.2. Introduction

Traditional conceptual models of community organization mainly focused on physical stresses and biological processes such as competition, predation, and recruitment (Menge and Sutherland 1987, Tilman 1994, Bertness and Callaway 1994, Altieri et al. 2007, Bruno et al. 2003, Hacker 2009, Nummi et al. 2019). Experimental work on rocky intertidal shores has demonstrated that upper limits in vertical zonation can be determined by direct effects of the physical environments such as high wave energy and temperature (Hatton 1938, Foster 1969, Connell 1972, Menge 1976, Wethey 1983). Meanwhile, biological interactions such as competition (Connell 1961) and predation (Paine 1966), or disturbance (Dayton 1971) operate frequently on lower intertidal zones and therefore set the lower limits for species in intertidal habitats. In other systems such as saltmarsh habitats, the pattern is reversed with the upper limits set by competition between plant species (e.g., Sporobolus alterniflorus, previously Spartina alterniflora (Hosier 2018), and Spartina patens), while the lower limits are set by plant tolerance to saltwater inundation
(Bertness 1991, Pennings and Bertness 2001). Therefore, across elevation distinct processes are responsible for molding zonation patterns. These models of community organization have been instrumental for the development of community ecology, however the presence of positive interactions had been underreported and thus comparatively understudied.

In the last three decades, ecologists have advanced our understanding of how positive interactions can be important drivers of community organization and biological diversity (Hacker and Bertness 1996, Bruno and Bertness 2001, Callaway et al. 2002, Bruno et al. 2003, Brooker et al. 2008, Hacker 2009, He et al. 2013, Cavieres et al. 2014, Vega-Alvarez et al. 2018). Positive interactions can result in better survival, growth, or reproduction thus increasing the fitness of species and enhancing the chances of co-occurrence (Hacker 2009, Cavieres et al. 2014). For instance, some plants can ameliorate micro-climates (Valiente-Banuet and Ezcurra 1991), accumulate nutrients, and offer protection to other plants from herbivory (McAuliffe 1988), consequently enhancing the performance of neighboring species (Callaway 2002) and maintaining diversity (Cavieres and Badano 2009) in plant communities. In communities organized by positive interactions, foundation species can facilitate the occupation of the habitat by additional organisms through the amelioration of environmental stressful conditions (Angelini et al. 2011). For example, the presence of macroalgae can enhance water retention beneath its canopy in rocky intertidal habitats and reduce the stressful effects of high temperature caused by solar radiation at low tide, further facilitating the establishment, survival, and/or performance of snails, mussels, crabs and other macroalgae (Brawley and Johnson 1991, Bertness et al. 1999, Molina-Montenegro 2005). In environmentally harsh habitats, positive interactions (i.e., facilitation) are expected to be pervasive forces in communities (Bertness and Callaway 1994). For instance, in sub-alpine and alpine forests, competition generally dominates interactions at
lower elevations where conditions are less stressful, while at high elevations where abiotic stress is high, the interactions among plants are primarily positive (Callaway et al. 2002). Positive interactions have been frequently reported in harsh environments such as deserts (Valiente-Banuet et al. 1991, Tirado and Pugnaire 2003), sub-alpine forests (Rebertus et al. 1991, Callaway 1995, Callaway et al. 2002, Cavieres et al. 2002), rocky intertidal zones (Molina-Montenegro 2005), and saltmarshes (Hacker and Bertness 1996, Bertness and Leonard 1997, Callaway and Pennings 2000).

Factors demonstrated to influence community assembly across stress gradients may also operate in other systems such as those formed by intertidal oyster reefs. Oysters are a sessile foundation species inhabiting the intertidal and subtidal zones from tropical to temperate latitudes (Galtsoff 1964, Shumway 1996). The Eastern Oyster (*Crassostrea virginica*) in intertidal zones can form reef patches that protrude above the water surface being aerially exposed throughout ebb tides, but are completely submerged during high tide (Loosanoff 1932, Mackin 1959, Roegner and Mann 1990, Bartol and Mann 1997). This vertical tidal gradient of influences biotic and abiotic factors that may affect oyster demographic characteristics (Nichy and Menzel 1967, Potter and Hill 1982, Michener and Kenny 1991). For example, oysters located within the high intertidal zone might be strongly affected by physical factors such as high temperature, while those located along the lower intertidal zone may more likely be influenced by predation and competition, resulting from longer submersion periods (Johnson and Smee 2014). Thus demography of oysters can vary across tidal gradients due to the relative strengths of biotic and abiotic factors (Fodrie et al. 2014), which may result in vertical zonation patterns analogous to well-studied saltmarsh systems (e.g., Bertness 1991) and rocky intertidal shores (e.g., Paine 1980, Menge 1995).
In addition to forming oyster reefs, the Eastern Oyster can also settle, aggregate, and grow on Red Mangrove (*Rhizophora mangle*) prop roots forming oyster clusters that grow outward from the root both vertically and horizontally. Therefore, the Eastern Oyster can co-occur with the Red Mangrove, another foundation species in intertidal zones, across tropical and subtropical latitudes (Aquino-Thomas and Proffitt 2014). In these lower latitude settings, high temperatures (up to 40 °C during the summer season) can produce harsh conditions that increase desiccation stress for oysters in higher intertidal zones (Roegner and Mann 1995, Michener and Kenny 1991). High temperature can affect oyster’s oxygen consumption rate, metabolic activities, feeding rates, and ultimately cause mortality (Shumway and Koehn 1982, Loosanoff 1958). Since high intertidal zones are exposed to high temperature for longer periods compared to lower tidal levels, reduction in desiccation stress from shading by the Red Mangrove canopy may occur. Therefore, oysters growing on mangrove prop roots in the high intertidal zone in particular should benefit from the association with the Red Mangrove (Figure 3.1). While some information about sources of mortality and desiccation stress has been gleaned from studies in temperate oyster reefs (Kingsley-Smith and Luckenbach 2008, Fodrie et al. 2014), we know comparatively less about these across the intertidal gradient in lower latitudes where abiotic factors can be more extreme (e.g., temperature). This study addresses (a) how do demographic rates of the Eastern Oyster vary along intertidal zones (bottom, middle, and top) on oyster reefs and on prop roots and (b) whether the association of oysters with mangroves may reduce desiccation stress, thus positively influencing oysters at higher intertidal zones.
3.3. Methods

3.3.1. Study location

This study was conducted in Tampa Bay, Florida, USA (Figure 3.2) during a nine-month period from June 2018 to February 2019. Tampa Bay is the largest shallow-water estuary in Florida with a mean depth of < 5m and a surface area of ~1000km² (Chen et al. 2007). Three locations (Upper Tampa Bay Park, Clam Bayou, and Ft. De Soto State Park) were selected in Tampa Bay. These study locations were selected due to the presence of oyster reefs as well as considerable oyster growth on mangrove prop roots along the shoreline. This presented the ideal seascape composition for examining oyster demographic rates on both habitat types. These locations are
found within a salinity gradient occurring from low salinity in the upper Bay to higher salinity in the lower Bay closer to the Gulf of Mexico (See appendix B).

Figure 3. 2. Map of Tampa Bay, Florida, USA, showing the study locations indicated with black circles. UP stands for Upper Tampa Bay Park, CB for Clam Bayou, and FS for Fort De Soto Park.

3.3.2. Study species

The Eastern Oyster (*Crassostrea virginica*) inhabits estuarine and coastal habitats along the east coast of North America from the Gulf of St. Lawrence to southern Florida, throughout the Caribbean to the Yucatan Peninsula of Mexico, and along the coasts of Venezuela, Brazil, and
Argentina (Parker et al. 2013). A variety of ecological services and economic benefits are provided by the Eastern Oyster including food and essential habitats for many estuarine organisms, nutrient transfer between the benthos and the water column, erosion reduction, shoreline stabilization, and water quality improvement (Bahr and Lanier 1981, Lenihan and Peterson 1998, Beck et al. 2011). The harvesting of Eastern Oysters for consumption has occurred since before Europeans colonized North America (MacKenzie et al. 1997) and continues to support commercial and recreational fisheries along the Gulf and Atlantic coasts of the United States (Drexler et al. 2014).

The Eastern Oyster can tolerate a broad range of abiotic factors that can influence survival and growth (Shumway 1996), including temperature and salinity fluctuations, and sedimentation (Galtsoff 1964, Shumway 1996, Aquino-Thomas and Proffitt 2014). Biotic factors such as diseases, predation, and competition with biofouling organisms can also influence oyster populations (Hanley et al. 2019, Pusack et al. 2019, Booth et al. 2018, Pusack et al. 2018, Kimbro et al. 2017). These biotic and abiotic factors can vary along intertidal gradients producing microclimates for the organisms living in a particular location along the gradient. For example, in high intertidal zones temperatures can reach high levels due to air exposure and increased solar radiation compared to lower intertidal zones (which can be submerged longer). The periods of air exposure and more intense solar radiation can lead to high desiccation stress especially for sessile marine organisms (e.g., oysters, Foster 1969, Hatton 1938, Menge 1976). During emersion oysters can also be exposed to land predators such as seabirds or terrestrial predators. In lower intertidal zones, desiccation stress is lower, but there is longer exposure to marine predators, disease transmission, and competition with biofouling organisms (Connell 1961, Paine 1966, Malek et al. 2016).
The Red Mangrove occurs in estuarine systems throughout the tropics and can form very productive forests supporting diverse assemblages of organisms (Krauss et al. 2008, Ewel et al. 1998). The prop roots of Red Mangroves can modify sediment deposition through leaf breakdown, stabilize shorelines, and offer storm protection by attenuating wave action (Proffitt and Devlin 2005, Carlton 1974, Brooks and Bell 2002). Red Mangroves grow in the intertidal zone and aerial prop roots originate from the trunk or branches and extend towards the soil. Where the prop root meets the sediment, an underground root system can develop (Carlton 1974). Prop roots do not necessarily always meet the sediments and can also ramify resulting in an arching system of roots, which are complex in structure (Gill and Tomlinson 1971, Brooks and Bell 2002). This root structure provides extra support for the mangrove, additional access to oxygen in anoxic sediments, and can offer substrate for many sessile organisms to live on such as sponges, mussels, algae, tunicates, anemones, barnacles, and the Eastern Oyster (Odum et al. 1982, Krauss et al. 2008, Aquino-Thomas and Proffit 2014). The prop roots can also provide shelter for mobile species such as crabs, isopods, shrimps, lobsters, sea urchins, and fishes (Macnae 1968, Lugo and Snedaker 1974, Tomlinson 1986). The Red Mangrove can reach a height of up to 35m and the canopy, formed by leaves that grow in clusters at the end of branches, can be dense, complex, and continuous, hence providing shade for organisms that settle directly below (Proffit and Travis 2010, Aquino-Thomas and Proffit 2014).

3.3.3. Oyster demography and predators

The densities of oysters were determined by destructively sampling ~0.25m² areas in both mangrove prop roots and oyster reefs from June through November 2018. Since one of the study questions was to examine patterns of zonation in mangrove prop roots and oyster reefs, three zones within each habitat were selected. Mangrove prop roots were sampled by randomly
selecting a mangrove that did not have an oyster reef directly adjacent to it. Once the initial root was selected, five additional adjacent roots with ~4cm diameter were selected. For each root, the bottom, middle, and top intertidal zones were delineated based on 10.5cm height increments. Therefore, the density of oysters were measured on ~31.5cm of each prop root. This zone delineation method was chosen by randomly selecting 21 prop roots and measuring the length of the root covered by oysters from the lowest point, yielding an average (± standard error) of 29.6 ± 1.4 cm. Therefore, 31.5cm (i.e., the mean ± 1se) was sampled and divided into the three intertidal zones. Furthermore, six roots composing a total length of 1.89m (31.5cm x 6) were analyzed per sample. Using the prop root radius of 2 cm, the surface area sampled was approximated by using the formula for a cylinder:

\[
\text{Surface area} = 2\pi \times h
\]

where r is the radius and h is the height (the length) of prop root sampled. This resulted in a total surface area of mangrove of ~0.24 m² for all six roots per sample. In oyster reefs, oysters were sampled by randomly placing a 0.25m² quadrat at three tidal elevations: at the top location on the crest of the reef above mean water level, at the middle location found in the slope of the reef (half-way distance between top and bottom) approximately around mean water level, and at the bottom edge of the reef, which was the area right where the reef began to become sparse and below mean water level. In each quadrat, excavation was performed to a depth at which no live oysters were found. In each sample (prop roots or quadrat), adults (≥25mm in shell height), juveniles (<25mm in shell height), and total oysters (juveniles + adults) were quantified. Oyster mortality was quantified by measuring the number of gaping oyster shells (two shell valves still attached to each other by the hinge and gaping open with no tissue left) within a sample (Ford et al. 2006, Jordan 1995). All Mud Crabs (*Panopeus herbstii*) and Crown Conchs (*Melongena*...
corona) encountered within a quadrat were also quantified as potential oyster predators. Despite the efforts to standardize the surface area sampled in both habitats (~ 0.25 m²), the depth excavated on the reefs may have differed from the distance that oysters can grow from the prop root surface outwards resulting in different volumes sampled. Therefore, caution must be used in the interpretation of results.

3.3.4. Oyster recruitment and survival

Ceramic tiles were deployed in the three study locations to quantify recruitment and survival of recruits across the intertidal zones of both mangrove roots and oyster reefs (May-July 2018). Recruitment of juvenile oysters was quantified by the deployment of seventy-two ceramic tiles (116.6 cm²) across both habitat types and intertidal zone (bottom, middle, top). Three separate mangroves and three oyster reefs were chosen per each study location and tiles were deployed at each intertidal zone (3 individuals x 2 habitat types x 3 study locations x 3 intertidal zones n = 54 tiles). Due to logistical constraints (e.g., tidal time limitation), the three additional separate prop roots and three reefs at each study location only had tiles placed in the middle intertidal zone (3 individuals x 2 habitat types x 3 study locations x 1 intertidal zones n = 18). This resulted in slightly higher number of replicates for middle intertidal zones for both habitats (mangroves and reefs). All oyster recruits that settled on the ceramic tiles were counted one-month post-deployment.

To quantify recruit survival, seventy-two additional tiles were deployed using the same design as explained for recruitment. After a month of deployment, the tiles were checked, dried carefully with a hand towel, and settled oysters (five maximum) were marked with a black sharpie circle on the tile and subsequently deployed for another month. After the second month,
marked individuals were checked for survival. Survival was calculated as the proportion of recruits alive out of the initially marked.

3.3.5. Condition index

Approximately 15 oysters were randomly selected for analysis of condition from the mangroves and reefs at each intertidal zone (bottom, middle, top) and study site \( (N = 279) \). Each oyster was cleaned to remove any attached organisms (e.g., barnacles, mussels) and total wet weight was recorded. Next, the internal tissue from each oyster was placed in a tared aluminum container. The tissues and oyster shells were then dried at 80 °C for 48 hours to obtain the dry tissue weight (DTW) and dry shell weight (DSW), respectively. Condition index of oysters was then calculated using the equation:

\[
\text{Condition index} = \left( \frac{\text{DTW}}{\text{DSW}} \right) \times 100 \quad \text{(Lucas and Beninger 1985)}
\]

3.3.6. Barnacle cover

During the deployment of the tiles for the recruitment and survival experiments, barnacle presence was noted and categorized (0 barnacles = no barnacles, < ~33% = low barnacle cover, \( \geq ~33\% \) and \( \leq < ~66\% \) = medium barnacle cover, or \( > ~66\% \) = high barnacle cover) to gain insights about potential competitors.

3.3.7. Evaporative water loss experiment and microclimatic measurements

To test whether evaporative water loss was reduced under the canopy of Red Mangroves compared to oyster reefs during the low tide, \( 10 \times 15 \) cm semitransparent white mesh bags were filled with 10g of vermiculite and placed on the top intertidal zone in both habitat types during February 2019. Fifteen bags were placed on the top intertidal zone on mangrove prop roots and 15 on the top of oyster reefs (3 bags \( \times \) 5 reefs) for 2.5 hours during low tide, where bags were
completely out of the water and not at risk of being splashed by waves. Prior to the initiation of the experiment, all the bags were submerged in seawater until reaching a constant weight (g), and each bag was weighed immediately before being placed into prop root or reef. After the experimental period, each bag was transferred to a sealed plastic bag, stored in a dark cooler, and weighed again upon return to land. The differences in weights were used to calculate percent water loss. During the experimental period, air temperature and water temperature were measured in both habitat types five times (every 0.5 hours) and the differences between habitats compared.

3.3.8. Physical variables

Water level loggers (Onset HOBO U20L-02) were deployed to gather data on the tidal variation occurring at the top and bottom intertidal zones in both prop roots and reefs. The loggers recorded pressure at 15-min intervals for ~ 25 weeks starting in September 2018. The same loggers also measured temperature. Measurements were binned into weekly-intervals, and the binned data were averaged. Salinity was measured manually with a YSI meter in the field monthly at each study site from June through September 2018.

3.3.9. Statistical analyses

Differences in density of oysters (juveniles, adults, total), gaping oysters, predators, number of recruits, and survival were compared separately across (1) habitat types (two levels) using permutation-based, non-parametric $t$-tests and (2) intertidal zones (three levels) using permutation-based, non-parametric analysis of variances (np-ANOVAs; Anderson 2001). One thousand permutations were used for all analyses. Pairwise comparisons were included for the tests involving intertidal zones. Homogeneity of dispersion was verified with the function npdisp, which is equivalent to Levene’s test (Anderson 2006, Anderson et al. 2006), and when
needed data were square-root transformed. All statistical analyses were conducted using Matlab and the Fathom toolbox (Jones 2017). The level of significance for all tests was based on an alpha value of 0.05 and 1,000 permutations were used.

3.4. Results

3.4.1. Oyster demography and predators

The density of total oysters was higher on mangrove prop roots than oyster reefs ($t = 3.90, p = 0.001$; Figure 3.3). This pattern was consistent for both juvenile ($t = 4.69, p = 0.001$) and adult oysters ($t = 2.33, p = 0.012$). On prop roots, the density of juvenile oysters was higher than adults ($t = 5.02, p = 0.001$). On reefs, the densities of juveniles and adults did not differ ($t = 0.46, p = 0.879$).

![Figure 3.3](image-url) (Reefs and Mangroves)

Figure 3. 3. Average density ± standard error of adults, juveniles, and total oysters in mangrove prop roots and oyster reefs. Area sampled in both habitats ~ 0.25m$^2$. 
On the mangrove prop roots, the density of juvenile oysters differed among the intertidal zones \( F_{2, 30} = 3.76, p = 0.008 \); Table 3.1; Figure 3.4). Specifically, they were higher in the middle compared to the bottom \( t = 2.56, p = 0.003 \) and top of mangrove prop roots \( t = 2.60, p = 0.002 \), and similar between bottom and top of mangrove prop roots \( t = 0.65, p = 0.859 \). The adult oyster density also differed among intertidal zones \( F_{2, 30} = 4.46, p = 0.004 \); Table 3.2; Figure 3.4). The adult oyster density was higher in the middle compared to the bottom \( t = 1.88, p = 0.048 \) and top of mangrove prop roots \( t = 2.90, p = 0.002 \), and was similar between bottom and top of mangrove prop roots \( t = 1.28, p = 0.147 \).

![Figure 3.4](image)

Figure 3.4. Average density ± standard error of adults, juveniles, and total (adults + juveniles) oysters per mangrove sample at different locations (bottom of root, middle of root, top of root).
Table 3. 1 Non-parametric one-way analysis of variance test for main effects of mangrove prop root intertidal zone on density of juvenile oysters. Values in bold indicate significant differences.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertidal zone</td>
<td>2</td>
<td>0.654</td>
<td>0.327</td>
<td>3.757</td>
<td><strong>0.008</strong></td>
</tr>
<tr>
<td>Residual</td>
<td>30</td>
<td>2.609</td>
<td>0.087</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>32</td>
<td>3.263</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Comparison among habitats*</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom versus middle</td>
<td>2.559</td>
<td><strong>0.003</strong></td>
</tr>
<tr>
<td>Bottom versus top</td>
<td>0.646</td>
<td>0.859</td>
</tr>
<tr>
<td>Middle versus top</td>
<td>2.596</td>
<td><strong>0.002</strong></td>
</tr>
</tbody>
</table>

* Pair-wise *a posteriori* tests of juvenile oyster density among intertidal zones on mangrove prop roots.

Table 3. 2 Non-parametric one-way analysis of variance test for main effects of mangrove intertidal zone on density of adult oysters. Values in bold indicate significant differences.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertidal zone</td>
<td>2</td>
<td>0.704</td>
<td>0.352</td>
<td>4.464</td>
<td><strong>0.004</strong></td>
</tr>
<tr>
<td>Residual</td>
<td>30</td>
<td>2.364</td>
<td>0.078</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>32</td>
<td>3.068</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Comparison among habitats*</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom versus middle</td>
<td>1.879</td>
<td><strong>0.048</strong></td>
</tr>
<tr>
<td>Bottom versus top</td>
<td>1.284</td>
<td>0.147</td>
</tr>
<tr>
<td>Middle versus top</td>
<td>2.899</td>
<td><strong>0.002</strong></td>
</tr>
</tbody>
</table>

* Pair-wise *a posteriori* tests of adult oyster density among intertidal zones on reefs.
The density of juvenile oysters differed among intertidal zones of reefs \((F_{2,24} = 6.21, p = 0.001;\) Table 3.3; Figure 3.5), but the patterns were different than those on mangrove prop roots. Juvenile oyster density was lower in the bottom of reefs compared to the middle \((t = 3.83, p = 0.001)\) and top of oyster reefs \((t = 2.03, p = 0.018)\), but was similar between the middle and top zones \((t = 1.34, p = 0.215)\). The density of adult oysters followed the same pattern as juveniles, differing among intertidal zones of reefs \((F_{2,24} = 3.75, p = 0.007;\) Table 3.4; Figure 3.5). Density of adults was lower on the bottom zone of reefs compared to the middle \((t = 2.23, p = 0.004)\) and top \((t = 2.21, p = 0.005)\), but was similar between the middle and top zones \((t = 0.39, p = 0.826)\).

Figure 3. 5. Average density ± standard error of adults, juveniles, and total (adults + juveniles) oysters per quadrat at different intertidal locations (bottom, middle/slope, top/crest) on oyster reefs.
Table 3. 3 Non-parametric one-way analysis of variance test for main effects of reef intertidal zone on density of juvenile oysters. Values in bold indicate significant differences.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertidal zone</td>
<td>2</td>
<td>1.243</td>
<td>0.621</td>
<td>6.213</td>
<td>0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>2.401</td>
<td>0.100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>26</td>
<td>3.644</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Comparison among habitats*

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom versus middle</td>
<td>3.829</td>
<td>0.001</td>
</tr>
<tr>
<td>Bottom versus top</td>
<td>2.029</td>
<td>0.018</td>
</tr>
<tr>
<td>Middle versus top</td>
<td>1.337</td>
<td>0.215</td>
</tr>
</tbody>
</table>

* Pair-wise *a posteriori* tests of juvenile oyster density among intertidal zones on reefs.

Table 3. 4. Non-parametric one-way analysis of variance test for main effects of reef intertidal zone on density of adult oysters. Values in bold indicate significant differences.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertidal zone</td>
<td>2</td>
<td>0.758</td>
<td>0.379</td>
<td>3.753</td>
<td>0.007</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>2.423</td>
<td>0.101</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>26</td>
<td>3.181</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Comparison among habitats*

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom versus middle</td>
<td>2.229</td>
<td>0.004</td>
</tr>
<tr>
<td>Bottom versus top</td>
<td>2.212</td>
<td>0.005</td>
</tr>
<tr>
<td>Middle versus top</td>
<td>0.389</td>
<td>0.826</td>
</tr>
</tbody>
</table>

* Pair-wise *a posteriori* tests of adult oyster density among intertidal zones on reefs.
The percent of gaping oysters (± SE), indicative of mortality, was over two times lower on mangrove prop roots (6.6 ± 0.9) compared to oyster reefs (15.6 ± 3.0; \(t = 3.06, p = 0.02\)). Although not significant at the alpha 0.05 level, there 5.6 % support for gaping oysters differing among the intertidal zones on mangrove prop roots \(F_{2, 30} = 2.15, p = 0.056;\) Table 3.5). The percent of gaping oysters was higher in the middle (− 8%) compared to the top of mangrove prop roots (− 4 %, \(t = 1.68, p = 0.042\)), but similar between bottom and the top of prop roots \(t = 1.58, p = 0.070\), and between the bottom and middle zones of mangrove prop roots \(t = 0.27, p = 0.917;\) Figure 6a). The percentage of gaping oysters was similar among the intertidal locations on the reefs \(F_{2, 24} = 2.20, p = 0.091\), although the largest and most variable percent of gapers was found at the lowest tidal elevation of reefs (Figure 6b).

Figure 3.6. Percent of gaping oysters (± standard error) per sample at different intertidal zones (bottom, middle, and top) on mangrove prop roots (a) and on oyster reefs (b)
Table 3. Non-parametric one-way analysis of variance tests for main effects of mangrove prop roots intertidal zone on percent of gaping oysters. Values in bold indicate significant differences.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertidal zone</td>
<td>2</td>
<td>0.416</td>
<td>0.208</td>
<td>2.146</td>
<td>0.056</td>
</tr>
<tr>
<td>Residual</td>
<td>30</td>
<td>2.909</td>
<td>0.097</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>32</td>
<td>3.326</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Comparison among habitats*

<table>
<thead>
<tr>
<th></th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom versus middle</td>
<td>0.268</td>
<td>0.917</td>
</tr>
<tr>
<td>Bottom versus top</td>
<td>1.577</td>
<td>0.070</td>
</tr>
<tr>
<td>Middle versus top</td>
<td>1.682</td>
<td>0.042</td>
</tr>
</tbody>
</table>

* Pair-wise *a posteriori* tests of gaping oysters among intertidal zones on reefs.

The density of Mud Crabs (± SE) did not differ significantly between habitats (mangroves = 31 ± 6 Mud Crabs/0.25 m², reefs = 34 ± 5 Mud Crabs/0.25 m²; *t* = 2.95, *p* = 0.217). The density of Mud Crabs did not differ among the different intertidal zones on the reefs (bottom = 35 ± 6, middle = 57 ± 9, top = 35 ± 8; *F*<sub>2, 24</sub> = 2.18, *p* = 0.076). Crown Conchs were not present on the mangrove prop roots sampled. The density of Crown Conchs was higher in the bottom (0.89 ± 0.45/0.25 m<sup>2</sup>) and middle zones (0.89 ± 0.42/0.25 m<sup>2</sup>) of oyster reefs compared to the top of reefs (0.22 ± 0.42/0.25 m<sup>2</sup>).

### 3.4.2. Oyster recruitment and survival

The total number of recruits on tiles overall was strikingly similar between mangrove prop roots and oyster reefs (17.8 ± 4.6; *t* = 1.29, *p* = 0.195). The number of oyster recruits differed among intertidal zones on mangrove prop roots (*F*<sub>2, 33</sub> = 1.48, *p* = 0.028) but not on oyster reefs (*F*<sub>2, 33</sub> = 1.59, *p* = 0.203). The number of recruits did not differ between the bottom and middle zones (*t* =
1.32, \( p = 0.176 \)). The number of recruits was lower on the top of the prop root compared to the middle (\( t = 1.76, p = 0.04 \)) and bottom intertidal zones (\( t = 2.28, p = 0.009 \)).

The survival of recruits was similar between mangrove prop roots and oyster reefs (\( t = 1.77, p = 0.083 \)) and did not differ among intertidal locations on either mangrove prop roots (\( F_{2, 18} = 0.39, p = 0.672 \); Figure 3.7) or oyster reefs (\( F_{2, 21} = 1.11, p = 0.366 \)). However, recruit survival in the top zone of mangrove prop roots was higher than on reefs (\( t = 2.95, p = 0.022 \); Figure 3.7), but did not differ in the other zones (all \( p > 0.05 \)).

### 3.4.3. Condition index

Condition index of oysters did not differ between habitats or intertidal zones within them (all \( p > 0.05 \)) and was on average (± SE) 2.29 ± 0.04.
3.4.4. Barnacle cover

Eighty-four percent of deployed tiles on mangrove prop roots had barnacles compared to 98% percent of the tiles on oyster reefs (Figure 3.8a). Over twice as many tiles on oyster reefs (33%) had high cover of barnacles compared to tiles on mangrove prop roots (15%). A high percentage of the tiles deployed had low cover of barnacles on both mangrove prop roots (~61%) and oyster reefs (~66%) and on the top intertidal zone (Figure 3.8b). Additionally, within the top intertidal zone, ~5% of the tiles deployed on mangrove prop roots had a high cover of barnacles compared to ~11% of tiles deployed on oyster reefs. In the middle intertidal zone, the percent of tiles deployed on mangrove prop roots and oyster reefs were similarly covered with high barnacles (30% and 31%, respectively; Figure 3.8c). Within the lower tidal zone, the ~11% of the tiles deployed on mangrove prop roots had high cover of barnacles compared to ~61% percent of the tiles deployed on oyster reefs (Figure 3.8d).

3.4.5. Evaporative water loss experiment and microclimatic measurements

The percentage of water loss from experimental bags was significantly lower underneath the canopy of Red Mangroves (13.02 ± 0.67 %) compared to the bags on the top of reefs (22.26 ± 0.94 %; \( t = 7.87, p = 0.001 \)). The mean microsite temperatures in oyster reefs were 0.62 °C higher in the air and 0.93 °C higher in the water than by the mangrove prop roots under the canopy during the water loss experiment.
Figure 3. The percent of tiles deployed covered by barnacles in mangroves and in reefs in general (a), top intertidal location on both habitats (b), middle intertidal location on both habitats (c), and bottom intertidal zone on both habitats (d). Overall, a greater percentage of high cover of barnacles (potential competitors for space) was found in oyster reefs compared to mangrove prop roots across tidal zones.

3.4.6. Physical variables

Mean salinity during low tide in Tampa Bay was 25.51 ± 0.80 ppt. In general, salinity in mangroves had an average of 24.67 ± 3.95 ppt, with 24.44 ± 4.09 ppt at the bottom, 25.08 ± 4.05 ppt at the middle, and 24.20 ± 3.95 ppt at the top. Salinity in general in reefs had an average of
26.29 ± 3.56 ppt, with 26.03 ± 3.65 ppt at the bottom, 26.56 ± 3.44 ppt at the middle, and 26.03 ± 3.73 ppt at the top. Water temperature was on average 23.80 ± 0.04 °C during the entire deployment of the HOBOs. The average temperature over the entire deployment period was 22.54 ± 0.05 °C at the top of mangrove prop roots, and 24.95 ± 0.04 °C at the bottom of mangrove prop roots, 23.32 ± 0.02 °C at the top of the reefs, with 22.79 ± 0.00 °C at the reef bottom. The average temperature at the top of mangrove prop roots during the hours of air exposure was 20.30 ± 0.12 °C with a maximum of 33.41 ± 0.72 °C. At the bottom zone on the mangrove prop roots when exposed to the air the average temperature was 17.77 ± 0.18 °C with a maximum of 32.19 ± 0.59 °C. During the hours of air exposure, the average temperature at the reef top was 20.99 ± 0.14 °C and the maximum 41.49 ± 0.57 °C. No air exposure temperature was recorded for the reef bottom location since the HOBO was consistently submerged during the deployment period (Figure 3.7; Table 3.6). The mangrove top was exposed an average of 2.92 ± 0.94 hours a day and mangrove bottom prop root 1.34 ± 0.17 hours, while the reef top was exposed to the air an average of 4.39 ± 0.29 hours daily. The average reef height sampled was taken as 0 cm in the bottom of the reef, 29.29 ± 2.63 cm in the middle intertidal zone, and 47.74 ± 4.40 cm in the high intertidal zone.

3.5. Discussion

Using a combination of field surveys and experiments, I found that Eastern Oyster demographic rates differed between mangrove prop roots and intertidal oyster reef habitats. Compared to reefs, I found oysters on prop roots to be at higher densities and had higher survival. Consistent with density and survival, water loss (proxy for desiccation) was lower on the prop roots, suggesting that the mangrove canopy may have provided a positive effect on oysters. I also found that demographic rates of oysters were not consistent when examined across tidal
elevations on both habitats. For example, lower density of oysters was observed at lower tidal elevations on both habitats (likely due to longer exposure to marine predators), but higher survival of oyster recruits occurred at the upper intertidal zone on prop roots. Overall, these results indicated that positive interactions between mangroves and oysters may help shape the community assemblage that develops on the prop roots.

Table 3. 6. Average temperature recorded weekly during the HOBO deployment period and average and maximum temperature recorded during the hours of air exposure. NA stands for not applicable.

<table>
<thead>
<tr>
<th></th>
<th>Average temperature (C°) during entire HOBO deployment period</th>
<th>Average temperature (C°) during exposed hours</th>
<th>Maximum temperature (C°) during exposed hours</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Reefs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top</td>
<td>23.32 ± 0.02</td>
<td>21.0 ± 0.1</td>
<td>41.49 ± 0.57</td>
</tr>
<tr>
<td>Bottom</td>
<td>22.79 ± 0.00</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><strong>Mangroves</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top</td>
<td>22.54 ± 0.05</td>
<td>20.30 ± 0.12</td>
<td>33.4 ± 0.72</td>
</tr>
<tr>
<td>Bottom</td>
<td>24.95 ± 0.04</td>
<td>17.77 ± 0.18</td>
<td>32.19 ± 0.59</td>
</tr>
</tbody>
</table>

Red Mangrove prop roots provide hard substrate on which oyster larvae may settle and complete their life cycle and the high complexity created by the presence of multiple roots (e.g., see Brooks and Bell 2002) may provide a refuge for oysters from predation by decreasing the foraging efficiency of some predators (e.g., demersal fishes). This might be the reason why the densities of juvenile and adult oysters observed in the surveys were higher in mangrove habitats compared to oyster reefs despite that the surface area sampled was slightly smaller in mangrove prop roots (~ 0.24 m²) than in oyster reefs (0.25 m²). These findings are comparable to those encountered by Drexler et al. (2014) in other Tampa Bay locations in that higher density of oyster was found on mangroves than on reefs. Habitat complexity can provide refuge from
predation in many soft and hard benthic environments (Sih et al. 1985, Stoner 2009, Chacin and Stallings 2016) and it may have also played a role in this system, although the exact mechanisms need to be further investigated. Moreover, the percentage of gaping oysters overall was lower on prop roots compared to oyster reefs, which suggests that higher mortality occurred on oyster reefs. While the density of Mud Crabs (a known oyster predator) did not differ between the two habitats, it was surprising that no Crown Conchs were observed in the mangrove prop roots sampled. This suggests there might be a physical impediment for these invertebrates to successfully access and feed upon oysters on prop roots. Other sources of mortality may have contributed to the patterns observed. A lower percentage of tiles placed on mangrove prop roots were highly covered in barnacles compared to those placed oyster reefs and although the reasons behind these patterns are unclear, interspecific competition for settlement space might be more intense in oyster reefs than in oyster clusters on mangrove prop roots.

The densities of juvenile and adult oysters varied across the intertidal zones on mangrove prop roots and oyster reefs. It is important to acknowledge that since the sampling of oysters at lower intertidal zones on oyster reefs was done on areas where oysters started to become sparse denoting the edge of the reef, the sampling could have been biased toward having relatively fewer oysters. Densities of juvenile and adult oysters were higher at the middle of mangrove prop roots and oyster reefs compared to the bottom of both habitats and could have been related to submergence time. Indeed the tidal loggers showed that the bottom zone on both habitats were submerged the longest compared to the other intertidal zones, which could have resulted in longer exposure of oysters to marine predators, overgrowth by biofouling organisms, and disease carrying vectors. Through predator surveys and faunal sampling, Fodrie et al. (2014) found that Stone Crab burrows and predatory gastropods were predominant in deeper oyster reefs, while
oyster abundance was the highest in middle intertidal zones, suggesting that higher predation occurs on lower intertidal zones. In the present study, the density of Mud Crabs (one of the most abundant predators of oysters in the Tampa Bay estuary) did not vary among intertidal zones on oyster reefs. However, Mud Crabs may possibly feed at higher rates in less stressful environments such as those lower in the intertidal zone, while they might seek refuge from desiccation in the oyster shell structure at higher intertidal zones (Van Horn and Tolley 2009). In contrast, the density of Crown Conchs was higher in the bottom and middle zones of oyster reefs compared to the top of reefs, which may have contributed higher predation rates and lower density of oysters at the bottom of reefs. Through field manipulations, Johnson and Smee (2014) found that oyster mortality rate was higher in subtidal habitats compared to intertidal reefs. Similarly, in this study, the percentage of gaping oysters was higher and more variable in the bottom zones of prop roots and oyster reefs, suggesting higher mortality of oysters occur in these zones. Furthermore, Chestnut and Fahy (1953) found that the oyster shells were heavily encrusted with bryozoans, hydroids, barnacles, and tunicates after a month of exposure at low-water level and below mean water level. During settlement, I observed that the bottom intertidal zone of reefs had a higher percentage of tiles that were highly covered (~ 60%) with barnacles compared to the other intertidal zones (~ 30% on the middle and ~ 10% on the top). Overall, these observations suggest that in addition to longer exposure to predators, oysters on the lower intertidal zone also faced increased competition for substrate with barnacles, which could have led to lower density of oysters and more variable percentage of gaping oysters on the lower intertidal zone.
The number of oyster recruits that settled on the deployed tiles was similar between mangrove prop roots and oyster reefs, which suggest that the supply of larvae was similar for both habitat types during the time of sampling. The survival rates of oyster recruits were much higher on top intertidal zones on mangrove prop roots (85%) compared to oyster reefs (35%). This increased survival in mangrove prop roots may be related to the reduction of desiccation stress via canopy shading. In the top zone, mangroves had shorter aerial exposure periods (2.9 hrs in mangroves vs. 4.3 hrs in reefs) and ~40% reduction of water loss compared to that of oyster
reefs. The water loss experiment was conducted during February in Florida when the temperature is among the lowest, while solar radiation is more intense and consequently higher percentage of water loss is expected to occur during the summer. This suggests that the mangrove canopy can reduce desiccation stress on oysters in high intertidal zones, and possibly increase survival rates. A previous study using tree height, as a proxy for canopy shading also reported a positive effect on oysters (Aquino-Thomas and Proffitt 2014). Positive interactions among foundation species have been also observed in other intertidal habitats. For example, positive association patterns occurred in two macroalgae species in rocky intertidal habitats (Molina-Montenegro 2005).

Beneath the canopy of the kelp *Macrocystis pyrifera* at high intertidal zones, the macroalgae *Ulva lactuca* experienced lower evaporation, temperature, and photosynthetic active radiation, which enhanced physiological performance. Similarly, Red Mangroves may positively influence oysters beneath the canopy on prop roots by lowering desiccation stress and reducing predation risk.

The condition index of oysters did not vary between habitat types or intertidal zones within the habitats, which is consistent with Drexler et al. (2014). Therefore, oyster condition index may be influenced by other factors that are not habitat-specific. In general, the condition index of the oysters calculated in this study were lower than those found by Drexler et al. (2014) during the same seasonal period in Tampa Bay. While it is expected that oyster condition index decreases in the fall months because oyster tissue mass is reduced when spawning stops and the gamete production ceases, the values were comparably low. The range of condition index values measured here was more comparable to those previously observed in the St. Lucy estuary (Arnold et al. 2008).
In environmentally stressful habitats, such as those occurring along abiotic gradients, positive interactions can affect the structure of community organization (Bertness and Leonard 1997, Hacker and Bertness 1996, Bruno et al. 2003, Molina-Montenegro et al. 2005). The results of this study suggest that positive interactions may also occur in intertidal gradients where Eastern Oysters co-occur with Red Mangroves. Mangrove canopy can alter desiccation stress by reducing evaporative water loss and shortening aerial exposure periods, which may result in higher survival rates of oyster juveniles. This study has noteworthy implications for the management and conservation of Eastern Oysters as habitats and food resource. Eastern Oyster populations have faced severe declines throughout the mid-Atlantic, southeastern US, and northeastern Gulf of Mexico due to a combination of overharvesting, habitat destruction, diseases, predation intensity, and changes in upstream freshwater removal (Grabowski and Peterson 2007, Kimbro et al. 2017). Additionally, increased solar radiation and temperature associated with global climate change may significantly affect marine organisms (Brierley and Kingsford 2009) and is likely a threat to Eastern Oysters in intertidal habitats by increasing desiccation stress. Red Mangroves (through canopy shading) have recently been identified as potential refuge from increased temperatures related to climate change to diverse coral communities (Yates et al. 2014). The present study provides evidence for Red Mangroves as a potential refuge for oysters from increased solar radiation through the shading provided by the canopy. Furthermore, as oyster reef restoration has proven unsuccessful in many locations and continues to be a challenge (Mann and Powell 2007), special attention can be given to alternative forms of substrate for oyster recruits such as those provided by the mangrove prop roots in tropical and subtropical locations. As mangrove habitat range continues to expand poleward
(Cavanaugh et al. 2014, Comeaux et al. 2012) further research is necessary to advance our understanding of the interactions between these two foundational species.

3.5.1. Implications and future directions

The results of this study suggest that as Red Mangroves shift their distributions toward higher latitudes, oysters that settle on prop roots may experience a refuge from predation or desiccation stress. The results of this study also set a baseline for further scientific inquiry. For instance, subsequent studies could examine to what extent (e.g., threshold) prop root structure impedes foraging efficiency of predators (mobiles and more sluggish ones, e.g., Crown Conchs), potentially providing predation refugia for oysters. It would also be of interest to examine whether similar processes (to those occurring on oysters clusters associated with mangroves) occur on oyster reefs directly adjacent to Red Mangroves. Finally, the findings of this study could have a practical use in building living shorelines. For example, projects that intend to increase oyster survival on shorelines for water quality improvement could consider adding artificial prop roots, which may enhance complexity and lower predation risk. Projects could also consider planting Red Mangroves on shorelines to provide the combined effect of substrate, shelter, and lower desiccation stress for settling oysters.

3.6. Acknowledgments

I am thankful for all the field assistance provided by Cynthia Lupton, Nathan Reineld, Garrett Monfre, Francis Stankiewicz, Rosa Amorena, Xavier Chacin, Ileana Freytes-Ortiz, Michael Schram, Meaghan Faletti, Garrett Miller, Natasha Mendez-Ferrer, and Abdiel Laureano-Rosario. This study was supported by the National Science Foundation Graduate Research Fellowship (grant no. 1144244), The Explorers Club – Florida Chapter, and the University of South Florida, College of Marine Science.
3.7. References


Hatton, H. 1938. Essais de bionomle explicative sur quelques especes intercotidales d'algues et d'animaux. Annls Inst, oceanogr. – Monaco I: 241-238


CHAPTER 4: ALTERED TROPICAL SEASCAPES INFLUENCE PATTERNS OF FISH ASSEMBLAGE AND ECOLOGICAL FUNCTIONS IN EAST AFRICA

Note to reader

This chapter was submitted for publication in the peer-reviewed journal *Oecologia* and is included in the Appendix C. The full citation is Chacin, D.H., Stallings, C.D., Eggertsen, M., Åkerlund, C., Halling, C., Berkström, C. 2019. Altered tropical seascapes influence patterns of fish assemblage and ecological functions in East Africa. Oecologia (submitted).
CHAPTER 5: CONCLUSION

Similar to terrestrial landscapes coastal biogenic habitats exist as heterogeneous interlinked mosaics in the seascape. Such heterogeneity can determine distribution and interactions of organisms as well as ecological processes within an ecosystem (Boström et al. 2011). For example, seagrass patches adjacent to saltmarsh are used as corridors by predators, which influences predator behavior and predation risk of shellfish (Micheli and Peterson 1999). Hence, the investigation of seascape heterogeneity can be useful for improving our understanding of ecosystem structure and function. The research presented in this dissertation is consistent with this statement.

In chapter 2, I found that in a northeast Florida estuarine seascape, adjacent habitats to intertidal oyster reefs can influence oyster demographic rates. For example, survival rates of juvenile oysters were lower and more variable in reefs adjacent to Black Mangroves than on reefs adjacent to Smooth Cordgrass and isolated oyster bars. I also found that survival was lower on oyster bars north in the reserve likely due to predation by xanthid crabs, which were at a higher density compared to the south. Likewise, growth was lower in the northern region, likely due to higher chlorophyll $a$ concentrations in the south. Compared to their regional controls, both survival and growth was higher next to saltmarsh and lower next to mangrove habitats. The mechanisms for the influences of these adjacent habitats were not clear, but appear to have been related to both consumptive and non-consumptive effects of predators. This study indicated that
neighboring habitats and regional variation in the seascape may influence demographic rates of oysters.

In chapter 3, in the Tampa Bay estuary I found that oysters on Red Mangrove prop roots had a higher density (both adults and juveniles) and had a lower proportion of dead oysters compared to oyster reefs. In addition, percent of water loss was lower and survival of oyster recruits was higher at upper intertidal zones on mangrove prop roots compared to reefs. The results of this study suggest that in stressful intertidal habitats (such as those occurring at lower latitudes where temperature can be high) oysters associated to Red Mangroves may be positively affected due to the canopy reducing desiccation stress for oysters.

In chapter 4, in tropical East Africa I found that fish and habitat composition and herbivory differed between seascapes with macroalgal beds and those with introduced macroalgal farms. The results showed that macroalgal beds had a higher species richness of fish and lower herbivory, while overall higher herbivory occurred in farmed seascapes likely to the farms attracting herbivores. However, macrophyte characteristics and fish abundance was similar in macroalgal beds compared to macroalgal farms. Additionally, fish assemblage patterns and herbivory varied with distance from the focal macroalgal habitat patches. The results of this chapter indicated that introduced monospecific macroalgal farms do not host the same fish assemblages as natural macroalgal beds. This suggests alterations of tropical seascapes by farming practices can have consequences on fish community composition and the ecological functions performed, thus positioning of farms should be carefully considered in management and conservation plans.

Specific follow-up recommendations emerged from each chapter. In chapter 2, characterization of habitat-specific predators will help disentangle different sources of juvenile
oyster mortality. Allocating more sampling effort to increase sample size of surveys on oyster reefs adjacent to Black Mangroves will also improve robustness of results. In Chapter 3, a noteworthy finding was that no Crown Conchs were present on Red Mangrove prop root samples. Consequently, Crown Conch behavioral experiments in mangrove roots would help elucidate any potential accessibility issue as well as identify possible predation refuges for oysters in these habitats. Another recommendation is to examine whether prop root structure impedes foraging efficiency of predators in general, potentially increasing survival rates of associated oysters. The characterization of communities supported by the association of oysters and mangroves and examination of potential facilitation cascades could be another follow-up study. In chapter 4, comparison of growth rates between farmed macroalgae and native macrophytes as well as investigating allelopathic interactions could improve our understanding of mechanisms by which farmed macroalgae could directly affect other habitat-forming organisms.

In this dissertation I have demonstrated the usefulness of assessing ecological responses of seascape heterogeneity to improve our understanding of ecosystem structure and function. Chapter 2 suggested that regional variation in biotic and abiotic factors and habitat adjacency can affect demographic rates of organisms in estuarine transition zones where vegetation dominance is changing. This chapter provides us with insights into how organisms living in temperate saltmarsh-dominated coastal zones may respond to undergo encroachment of Black Mangroves. Chapter 3 indicated that habitat associations between two foundation species of ecological and economic importance can positively interact across intertidal gradients resulting in zonation patterns of organisms. About 85% of oyster reefs have been either lost or degraded (Barbier et al. 2010, Beck et al. 2011) and evaluation of landscape context such as the one
presented in this dissertation could provide valuable insights for restoration practices. Chapter 4 suggested that the introduction of macroalgal farms can alter the composition of fish assemblages and processes like herbivory in tropical seascapes. Accordingly, this chapter provides insights for management in terms of the introduction and placement of farms in the seascape and possible outcomes. Overall, seascape heterogeneity influences patterns and processes in ecosystems and as such, the employment of a spatially-explicit approach is recommended for improving our understanding of ecosystems and their effective management.

5.1. References


Box 1. Applying community organization models of rocky shores to saltmarsh, soft sediments, and oyster reefs – A brief comparison among intertidal systems.

**Competition:** competition for space (leading to competitive exclusion) is intense in rocky shores and results in sharp boundaries among competing sessile organisms and distinct bands in monocultures (Connell 1961). In soft sediments in contrast, residents do not compete for space, but compete (less intensely) for food resources that are brought up by the tide, thus distributional patterns of residents occur in more gradual changes (Peterson 1991). In contrast, competition for space in saltmarsh is intense and conspicuous and operates across sharp gradients of stress resulting in zonation patterns of plant species (Bertness and Shumway 1991). In comparison, competition may be an important process in oyster reefs as oyster larvae settles in hard substrate, thus potentially exhibiting intraspecific competition as well as competing for space with other settling organisms such as barnacles and hydroids (MacDougall 1943). Since oysters are sessile invertebrates they can be subjected to overgrowth, dislodgement, and crushing by other oysters and organisms possibly more intensely in lower intertidal zones.

**Predation/consumers:** in rocky shores, predation by sluggish marine invertebrates is more intense in lower intertidal zones (Paine 1966). In contrast in soft sediments, mobile predators such as birds, fish, swimming crabs, and sluggish predators (e.g., snails) exert predation across the intertidal zone (Quammen 1984). However, predation rates for both predator types could be more intense in lower intertidal soft sediments contributing to zonation patterns (Peterson 1991). Herbivory occurs in saltmarsh and it is estimated that only 5-10% of the carbon is consumed by herbivores. Nevertheless, a variety of herbivores and parasitic plants can influence the distribution and abundance of marsh plants (Lynch et al. 1947, Shanholtzer 1974, Turner 1987, Ford and Grace 1998, Bertness et al. 1987, Ellison 1991, Bertness and Shumway 1992). In comparison, predation in oyster reefs by marine predators (including sluggish and mobile) is likely higher during high tide (Fodrie et al. 2014) and by terrestrial predators during low tide.

**Physiological stress:** in rocky shores, the steep vertical environment creates a gradient in physiological stress, where at higher elevation only those species that are tolerant to longer air exposure are found. Therefore, physiological stress produces boundaries of organismal distribution at high intertidal elevations in rocky shores (Menge 1976, Wethey 1983). In soft sediments, the direct effects of air exposure and solar radiation are buffered by the overlying sediment layer, which acts as a blanket retaining moisture and lowering water evaporation. Therefore, physiological stress does not seem to be a strong structuring factor in soft sediment communities (Peterson 1991). In saltmarsh communities, stressful gradients of salinity across the intertidal can occur due to tidal variation and flushing at lower elevations and by freshwater input from terrestrial sources and rain at the terrestrial side (Pennings and Bertness 2001). This
gradient can vary geographically. In soils with increased salinities, more salt-tolerant plants will occur, while in more flushable sediments competition increases among different plants. In intertidal oyster reefs in comparison, a stress gradient of aerial exposure occurs. Oysters are stress tolerant sessile invertebrates and therefore occur across a range of intertidal zones. However, physiological stress can limit oyster distribution as well as other settling invertebrates at the high intertidal zone. This gradient similarly to saltmarsh communities might also vary geographically. For instance, oyster reefs can be found in tropical, subtropical, and temperate climates and therefore variation in solar radiation is expected to influence desiccation stress more strongly in warmer climates affecting survival and condition. However, this hypothesis remains untested.

**Habitat modification and positive interactions:** in rocky shores, mussel beds can provide three-dimensional structures enhancing assemblages of smaller invertebrates, which would be absent otherwise. In soft sediments, bioturbators can create burrows and thus positively influence species that depend on the provision of three-dimensional subterranean structure for their habitat (Reise 1985). In saltmarsh, habitat modification is very common and prominent and is a process that mediates the structure and organization of communities. For example, halophytic plants are critical players because they invade high salinity/low oxygen sediments, accumulate and stabilize sediments, ameliorate wave stress, and consequently facilitate the settlement of other plants (Pennings and Bertness 2001). In comparison, oyster reefs can create complex three-dimensional structures that support assemblages of invertebrates. Oysters can also form reefs that are adjacent to Red Mangroves or oysters can grow on mangrove prop roots. The close association between these two foundation species (in tropical and subtropical latitudes) may provide benefits for both. Oysters can use the mangrove structure for settling and protection, and benefit from the canopy shade, which might reduce desiccation stress. Likewise, oysters might help stabilize substrate and fertilize the soil benefitting mangroves. Formal tests of these hypotheses are in need (but see chapter 3 of this dissertation).

**Disturbance:** In soft sediments, wave action is a source of disturbance and can help set patterns of zonation since it reaches a maximum at higher elevations. This can result in the movement and sorting of sediments according to size across the intertidal zone, creating a zonation of invertebrates based on feeding types as they process sediments for organic food (Peterson 1991). In saltmarsh, disturbance can occur in different forms (e.g., ice, floating debris, herbivores, fire, and sediment) and play a role in plant community dynamics with variations across latitudes (Pennings and Bertness 2001). For example, ice damage at high latitudes (e.g., Alaska, Canada) can limit the development of marsh on the lower intertidal, which is continuously scoured (Desplanque 1983, Adam 1990). At moderate latitudes on the other hand, ice disturbance is less severe and not an important factor as uninterrupted sediment deposition allows for the development of plants at lower elevations (Wiegert and Freeman 1990). In oyster reefs, disturbance can occur in the form of wave action. Wave action might influence patterns of zonation with pronounced effects at higher elevations as sediments shift and oyster clusters move. Disturbance for oysters might also vary geographically with frost or hurricane disturbances occurring in higher frequency at specific locations. These hypotheses however, remain untested.
Box 2. Can positive interactions occur between mangroves and oysters?

Since desiccation stress plays a critical role influencing intertidal communities, positive interactions resulting from neighbors buffering one another from stressful conditions are predicted to be an important force structuring communities (Bertness and Callaway 1994, Bertness and Leonard 1997). The majority of the work studying zonation patterns in intertidal ecology has been conducted in cooler temperate habitats in which positive interactions (including amelioration of desiccation stress) might not be as critical and may be more pertinent in warmer climates. In southern Florida and the Caribbean, oysters can grow attached to mangrove prop roots and form reefs bordering mangroves. Temperature in these locations can also reach high ranges (31-33 °C), and pose greater desiccation stress on oysters compared to temperate locations. It may be possible that oysters growing on mangrove prop roots and those growing on reefs adjacent to mangroves experience less desiccation stress due to shading produced by the mangrove canopy, which allows oysters trap moisture for longer. Furthermore, prop roots may be an initial point for oyster settlement due to provision of hard structure (Aquino-Thomas and Proffitt 2014). Once enough oysters adhere and form a large oyster clusters, these clusters may eventually develop into oyster reefs. In exchange, oyster reefs may stabilize the sediment, preventing erosion of mangrove shorelines (Meyer et al. 1997) and benefitting mangroves (Figure below; see Thomsen et al. 2010 for a review on facilitation cascades). An analogous situation occurs in an intertidal cordgrass bed community on New England cobblestone beaches. The cordgrass *Spartina alterniflora* by baffling waves and providing shade facilitates an assemblage of organisms including mussels, snails, and seaweeds, which in turn stabilize the substrate (Altieri et al. 2007). Furthermore, in the east coast of Australia, a fucalean macroalgae *Hormosira banksii* patches within mangrove pneumatophores facilitate molluscan assemblages by increasing mollusk abundance and species richness (Bishop et al. 2009). Therefore, it is possible that in lower latitudes, where mangroves coexist with oysters, a facilitative process exists, however formal tests of this hypothesis remain to be investigated.
Table B. 1. Average salinity and water temperature recorded on study locations in Tampa Bay

<table>
<thead>
<tr>
<th>Bay locations</th>
<th>Red Mangrove (ppt) ±</th>
<th>Oyster reef (ppt) ±</th>
<th>Grand total (ppt) ±</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Tampa Bay</td>
<td>11.37 ± 1.51</td>
<td>14.16 ± 1.46</td>
<td>12.78 ± 1.05</td>
</tr>
<tr>
<td>Clam Bayou</td>
<td>30.68 ± 0.93</td>
<td>30.89 ± 0.52</td>
<td>30.79 ± 0.51</td>
</tr>
<tr>
<td>Ft. de Soto</td>
<td>33.35 ± 0.63</td>
<td>34.47 ± 0.36</td>
<td>33.92 ± 0.36</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Bay locations</th>
<th>Red Mangrove (°C) ±</th>
<th>Oyster reef (°C) ±</th>
<th>Grand total (°C) ±</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Tampa Bay</td>
<td>29.82 ± 0.51</td>
<td>29.38 ± 0.55</td>
<td>29.60 ± 0.37</td>
</tr>
<tr>
<td>Clam Bayou</td>
<td>26.72 ± 0.69</td>
<td>27.15 ± 0.81</td>
<td>29.74 ± 0.53</td>
</tr>
<tr>
<td>Ft. de Soto</td>
<td>28.88 ± 0.43</td>
<td>30.58 ± 0.41</td>
<td>29.60 ± 0.31</td>
</tr>
</tbody>
</table>
APPENDIX C: ALTERED TROPICAL SEASCAPES INFLUENCE PATTERNS OF FISH ASSEMBLAGE AND ECOLOGICAL FUNCTIONS IN EAST AFRICA

# Oecologia

**Altered tropical seascapes influence patterns of fish assemblage and ecological functions in East Africa**

--Manuscript Draft--

<table>
<thead>
<tr>
<th>Manuscript Number:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Full Title:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altered tropical seascapes influence patterns of fish assemblage and ecological functions in East Africa</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Article Type:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecosystem ecology – original research</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Corresponding Author:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dinorah Chacin</td>
</tr>
<tr>
<td>University of South Florida</td>
</tr>
<tr>
<td>UNITED STATES</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Order of Authors:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dinorah Chacin</td>
</tr>
<tr>
<td>Christopher Stallings</td>
</tr>
<tr>
<td>Maria Eggertsen</td>
</tr>
<tr>
<td>Carolina Åkerlund</td>
</tr>
<tr>
<td>Christina Halling</td>
</tr>
<tr>
<td>Charlotte Berström</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Suggested Reviewers:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kenneth Heck</td>
</tr>
<tr>
<td>University of South Alabama</td>
</tr>
<tr>
<td><a href="mailto:kheck@disl.org">kheck@disl.org</a></td>
</tr>
<tr>
<td>Mark Hay</td>
</tr>
<tr>
<td>Georgia Institute of Technology</td>
</tr>
<tr>
<td><a href="mailto:mark.hay@biology.gatech.edu">mark.hay@biology.gatech.edu</a></td>
</tr>
<tr>
<td>Kevin Hovel</td>
</tr>
<tr>
<td>University of California San Diego</td>
</tr>
<tr>
<td><a href="mailto:khovel@sdsu.edu">khovel@sdsu.edu</a></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Opposed Reviewers:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Funding Information:</th>
</tr>
</thead>
<tbody>
<tr>
<td>National Science Foundation (1144244)</td>
</tr>
<tr>
<td>Swedish Research Council (2015-05848, 2015-01257, E0344801)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mrs. Dinorah Chacin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dr. Charlotte Berström</td>
</tr>
</tbody>
</table>
**Abstract:**

The arrangement and composition of habitats within landscapes and fine-scale habitat characteristics influence patterns of community structure and ecological processes. Anthropogenic activities can alter fine-scale habitat characteristics and the composition of habitats in landscapes, thus affecting associated communities. Farming of macroalgae is a common practice in tropical settings. The introduction of farms can alter the natural structure and composition of seascapes by introducing patches of monocultures. The farmed macroalgae may also grow faster or be less palatable compared to native macroalgae, influencing herbivory. The present study aims to understand how the alteration of tropical seascapes through the introduction of macroalgal farms might influence fish assemblages, herbivory, and how these farms may differ from naturally-occurring macroalgal beds. We surveyed fish assemblages and deployed macroalgal assays within macroalgal habitats and macroalgal farms, as well as at varying distances from the habitats near Mafia Island, Tanzania. Fish and habitat compositions and herbivory differed between macroalgal beds and farms. Additionally, fish assemblage patterns and herbivory were not consistent across the seascapes and varied with distance from the focal habitats. However, macrophyte characteristics and fish abundance was similar in macroalgal beds compared to macroalgal farms. The results of the present study indicate that introduced macroalgal farms do not host the same fish assemblages as natural macroalgal beds. This suggests alterations of seascapes by farming practices can have consequences on fish assemblage and the ecological functions performed, thus positioning of farms should be carefully considered in management and conservation plans.
Dinorah H. Chacin, MSc
PhD Candidate
University of South Florida, College of Marine Science
830 1st St S. St. Petersburg, FL 33701

October 2nd, 2019

Dear Oecologia Editorial Office,

I am pleased to submit an original manuscript titled "Altered tropical seascapes influence patterns of fish assemblage and ecological functions in East Africa" to be considered for publication in Oecologia as a research article. This manuscript evaluates how the alteration of tropical seascapes through the introduction of macroalgal farms might influence patterns of fish community assembly, ecological processes such as, herbivory and how these may differ from naturally occurring macroalgal beds. By surveying fish assemblages and deploying experimental macroalgal assays within the focal macroalgal habitats and at varying distances from the habitats we observed that patterns of fish assemblage, habitat heterogeneity, and percent of macroalgal loss differed between macroalgal beds and macroalgal farms and were not consistent throughout the seascapes. These results add to our understanding of seascapes subjected to human practices and suggest that alterations of tropical seascapes by farming practices can have consequences on fish community composition and the ecological functions performed.

This study addresses several themes that will be of keen interest to readers of Oecologia including herbivory, the role of multiple habitat patches in the landscape, species introductions, and the use of controlled experiments.

This manuscript has not been published and is not under consideration for publication elsewhere. We have no conflicts of interest to disclose.

We suggest the following reviewers:

1) Kenneth Heck – University of South Alabama – kheck@disl.org
2) Mark Hay – Georgia Tech – mark.hay@biology.gatech.edu
3) Kevin Hovel – San Diego State University – khovel@sdsu.edu
4) Ivan Nagelkerken – The University of Adelaide – ivan.nagelkerken@adelaide.edu.au

Thank you for considering this submission.

Sincerely,
Dinorah Chacin
Altered tropical seascapes influence patterns of fish assemblage and ecological functions in East Africa

Chacin, D.H.*1; Stallings, C.D.1; Eggertsen, M.2; Åkerlund, C.2; Halling, C.2; Berkström, C.2,3

1College of Marine Science, University of South Florida, 140 7th Avenue South, St. Petersburg, FL 33701, USA

2Department of Ecology, Environment, and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden

3Department of Aquatic Resources, Institute of Coastal Research, Swedish University of Agricultural Sciences, Skolgatan 6, SE-742 42 Oregrund, Sweden

*Corresponding author: dchacin@mail.usf.edu

Author Contributions: DHC conceptualization, funding acquisition, data collection, formal analysis, manuscript writing – original draft, writing – review and editing. CDS conceptualization, writing – review and editing. ME data collection, writing – review and editing. CA data collection, writing – review and editing. CH funding acquisition, writing – review and editing. CB conceptualization, funding acquisition, writing – review and editing.
Abstract

The arrangement and composition of habitats within landscapes and fine-scale habitat characteristics influence patterns of community structure and ecological processes. Anthropogenic activities can alter fine-scale habitat characteristics and the composition of habitats in landscapes, thus affecting associated communities. Farming of macroalgae is a common practice in tropical settings. The introduction of farms can alter the natural structure and composition of seascapes by introducing patches of monocultures. The farmed macroalgae may also grow faster or be less palatable compared to native macroalgae, influencing herbivory. The present study aims to understand how the alteration of tropical seascapes through the introduction of macroalgal farms might influence fish assemblages, herbivory, and how these farms may differ from naturally-occurring macroalgal beds. We surveyed fish assemblages and deployed macroalgal assays within macroalgal habitats and macroalgal farms, as well as at varying distances from the habitats near Mafia Island, Tanzania. Fish and habitat compositions and herbivory differed between macroalgal beds and farms. Additionally, fish assemblage patterns and herbivory were not consistent across the seascapes and varied with distance from the focal habitats. However, macrophyte characteristics and fish abundance was similar in macroalgal beds compared to macroalgal farms. The results of the present study indicate that introduced macroalgal farms do not host the same fish assemblages as natural macroalgal beds. This suggests alterations of seascapes by farming practices can have consequences on fish assemblage and the ecological functions performed, thus positioning of farms should be carefully considered in management and conservation plans.

Keywords: seaweed, exotic species, consumer, rabbitfish, agro-ecosystems
Introduction

The spatial arrangement and composition of habitats within landscapes along with fine-scale habitat characteristics influence patterns of community structure and ecological processes (Turner 1989, Weins 1989, Levin 1992, Dunning et al. 1992, Boström et al. 2011). For example, the abundance and diversity of native pollinators (and the process of pollination) in agricultural settings is strongly influenced by spatial characteristics of the landscape, such as the relative proportion of natural habitats neighboring farmed patches (Kremen et al. 2002). Similarly, in forest settings, organismal fire refuge depends on the composition, fine-scale structure, and spatial arrangement of the vegetation within the landscape (Robinson et al. 2013). Anthropogenic activities such as land use can influence fine-scale habitat characteristics and the composition of habitats in the landscape, thus affecting associated communities across the globe (Chapin et al. 2000, Michel et al. 2006, Kirk et al. 2011). Landscape alterations can influence habitat heterogeneity, and ultimately food resource quality and availability, resulting in modification of trophic structure, biodiversity, and ecosystem function (Connell and Glasby 1999, Tilman et al. 2001, Tylianakis et al. 2008). For instance, agricultural intensification of landscapes has been shown to lower heterogeneity resulting in reduced refuge, feeding areas, and dispersal corridors for birds consequently influencing their diversity, density, and breeding success (O’Connor and Shrub 1986, Galbraith 1988, Benton et al. 2003). Land-use patterns can therefore affect the persistence of regional metapopulations and the structure of biological communities (Lubchenco et al. 1991, Andrén 1994). This may also be the case in marine systems where alterations of seascape composition and heterogeneity within habitats will likely affect ecosystem functioning.

Farming and harvesting of macroalgae is a common practice in tropical settings (McHugh 1991, Jensen 1993). Macroalgal farming has been increasingly advocated as a sustainable alternative form of aquaculture due to lack of fertilizers or medicines applied (e.g., compared to shrimp farms) for many local communities in developing countries and is expanding rapidly worldwide (Ask et al. 2001, Rönnbäck et al. 2002, FAO 2014, Abhilash et al. 2019). Despite the practice being promoted as a means to improve
coral-reef health through poverty reduction and reduced fisheries exploitation (Petterson-Löfqquist and 
Lindberg 2001, Rönnbäck et al. 2002), the ecological effects and benefits of macroalgal farming remain 
unclear, partly because studies have shown contrasting results (Hehre and Meeuwig 2016).

In tropical seascapes, the introduction of macroalgal farms can alter the natural structure and 
composition in several ways. Typically farms consist of numerous ropes arranged in a dense and parallel 
fashion over large areas on the coast (Hehre and Meeuwig 2016). Macroalgae thalli are tied to the ropes, 
introducing habitat patches of monocultures in areas otherwise naturally covered by sand, seagrasses, 
native macroalgae, and coral patches (Bergman et al. 2001, de la Torre-Castro and Rönnbäck 2004). The 
macroalgae taxa used in the farming practices may not be native to the farming location, resulting in the 
introduction of a potentially invasive species, which may spread from the farms into neighboring 
components of the seascape (Halling et al. 2013; Tano et al. 2015). The farmed macroalgae may also 
grow faster or be less palatable compared to native macroalgae, resulting in changes in the consumption 
rate of macroalgae through herbivory (Conklin and Smith 2005). The readily available aggregations of 
farmed fleshy macroalgae may also attract herbivores within the seascape. All these factors have the 
potential to influence fish assemblages and the ecological functions the fishes perform, which may 
depend on the fine-scale heterogeneity within habitats as well as on the arrangement and composition of 
tropical habitat patches. Therefore, the alteration of tropical seascapes through the introduction of 
macroalgal farms has the potential to affect the entire ecosystem structure and function.

In contrast to macroalgal farms, beds of native canopy-forming macroalgae occur naturally 
interspersed within or adjacent to other habitats (e.g., seagrass beds, coral reefs) comprising a mosaic of 
interlinked patches. Despite the fact that canopy-forming macroalgae in temperate systems has long been 
recognized as important habitats for fishes (Carr 1994, Bertocci et al. 2015), tropical macroalgal beds 
have only recently been recognized as important fish habitat offering structural complexity and a variety 
tropical systems can cover extensive areas (Garrigue 1995, Kobryn et al. 2013) and enhance productivity 
by providing habitat and food resources to numerous organisms including fishes and invertebrates
While our knowledge on the ecological role of macroalgal beds in tropical seascapes is advancing, information on the process of herbivory (e.g., rates of macroalgae consumption, identification of consumers) within these habitats or on patterns of herbivory and fish assemblages in the surrounding seascapes is scarce (but see Eggertsen et al. 2019). Even less is known about how the alteration of seascapes, through the introduction of non-native macroalgal habitats, may affect ecological processes that influence ecosystem function and how it compares to seascapes with natural macroalgal beds.

Indeed, macroalgal farming has been demonstrated to influence organismal communities of bacteria (Johnstone and Ólafsson 1995), meiofauna (Ólafsson et al. 1995), benthic macrofauna (Eklöf et al. 2005), fish (Bergman et al. 2001), and corals (Russell 1983). Macroalgal farms have also influenced fishery catch composition and ecosystem structure and function within seagrass beds (Eklöf et al. 2006a, Eklöf et al. 2006b). However, there are no previous studies in the tropics that compare macroalgal farms to natural macroalgal beds and the surrounding seascapes in terms of fish community structure and ecological processes. The goal of this study was to understand how the alteration of tropical seascapes through the introduction of macroalgal farms might influence patterns of fish community assembly, ecological processes such as, herbivory, and whether these differed from naturally-occurring macroalgal beds. We hypothesized that habitat heterogeneity would be higher in naturally-occurring macroalgal beds compared to macroalgal farms (due to methods of algae cultivation) and subsequently fish abundance and richness would be higher in macroalgal beds. We also hypothesized that macroalgal farms attract herbivorous fishes, such as browsers that feed on macroalgae, thus their abundance as well as the associated macroalgae loss (through herbivory) would be higher in the interior and edge of macroalgal farms compared to natural macroalgal beds and the surrounding seascapes. Therefore, we expect macroalgae loss to be context dependent and affected by habitat arrangement and fish assemblages present in the seascapes.

Materials and Methods
Study location

This study was conducted during September-November 2016 in the southern region of Mafia Island off the east coast of Tanzania (Fig. 1). Mafia Island is located 60 km south of Dar es Salaam and 21 km east of the Rufiji delta (Garpe and Ohman 2003). The backreef areas around Chole Bay, where the study was conducted, have a maximum depth of 15 m, except in the deep channels that connect the Bay with the open ocean (McClanahan 1988). Mafia Island is influenced by the East African Coastal Current (EACC) and has semi diurnal tides with 3.3 m in average amplitude (Garpe and Ohman 2003).

In East Africa, macroalgal farming began on the Zanzibar archipelago, Tanzania in the late 1980s, with the introduction of Philippine strains of *Eucheuma denticulatum* and *Kappaphycus alvarezii* (Msuya et al. 2014) and is currently practiced along the East African coast, with Zanzibar being the largest producer (Msuya et al. 2014). These two red macroalgae are farmed in shallow coastal areas for their polysaccharide carrageenan content, which is widely used by the pharmaceutical, food, cosmetics, and textile industries for gelling constituents, medicines, and toothpaste among other products (Msuya 2006). In addition to tourism, macroalgal farming has become one of the most important industries bringing foreign revenue into the local economy through exports and raising living standards of rural communities (Rönnbäck et al. 2002, Msuya 2013, FAO 2014). For this study, we selected *E. denticulatum* as our farmed study species over *K. alvarezii* since it’s farming is more prevalent in the study area (Tano et al. 2015, Eggertsen et al. 2019).

The focal habitats compared in this study included natural macroalgal beds (Fig. 2a), and macroalgal farms (Fig. 2b). The macroalgal beds were dominated by *Sargassum aquifolium* and *Turbinaria conoides* with the occasional presence of other species including *Padina spp.*, *Portiera harveyi*, *Ulva* spp., and *E. denticulatum*. The macroalgal beds were also heterogeneous with irregular patches of sand, coral, sponges, and rubble mixed in with the macroalgae. Macroalgal farms of *E. denticulatum* are placed in shallow, accessible, and well-flushed coastal areas. The farms require no addition of fertilizers or pesticides, only sufficient water motion and natural light (Eklöf et al. 2012, Valderrama et al. 2015). The macroalgae is farmed by using the “peg-and-line” or “off-bottom” method, in which macroalgal fronds
are tied using ribbons, known as “tie-ties,” to ropes that are extended and tied to wooden pegs on the
marine sediment (Valderrama et al. 2015). The size and spacing of macroalgal fronds was variable, with
the size of fronds ranging from ~10-30 cm in diameter and tending to be evenly spaced with ~40-60 cm of
rope in between. Other macrophytes such as seagrasses (Syringodium and Thalassia spp.) were
occasionally found on the substrate beneath the macroalgae fronds, otherwise sand was the most common
substrate. Both the macroalgal bed and macroalgal farm sites selected were similar in area (~600 m²) and
seawater temperature (26-28 °C).

The study sites were located within and in the vicinity of Chole Bay, which is an area comprising
shallow mosaics of macroalgal beds, seagrass meadows, mangrove shorelines, and coral reefs (Berkström
et al. 2013, Horrill et al. 1996). Three macroalgal beds and three macroalgal farms with their surrounding
seascape (up to 100 m distance from focal habitat patches) were selected for this study (Fig. 1). We
surveyed fish assemblages and conducted field experiments within the focal macroalgal habitats and at
varying distances from the habitats in the seascape to characterize fish assemblages and gain insight into
herbivory of the different macroalgae.

Fish assemblage surveys
To determine whether fish assemblages differed among macroalgal beds, macroalgal farms, and the
neighboring seascape, fish surveys (25 m x 2 m strip transects) were conducted in focal macroalgal
habitats and at different distances (edge/boundary of focal patches, 10 m, 50 m, and 100 m) from the
habitats. Fishes were identified to the lowest taxonomic level possible (usually species) and their total
lengths were estimated to the closest centimeter. The highly mobile species were counted first, followed
by the more cryptic and demersal species. Sea urchins encountered in our surveys were also included
since they are known for their importance as herbivores in benthic marine habitats (Ogden and Lobel
1978, Lawrence and Agatsuma 2013, Wall and Stallings 2018). Surveys were conducted between 0900
and 1630 hours to reduce variability in fish density associated with periods of high activity due to diurnal
influences during crepuscular periods. At the end of every survey, benthic substrate composition was
categorized (e.g., sand, macroalgae, seagrass, sponges) and quantified within 0.25 m² quadrats every 5 meters on the transect line.

We compared fish community structure from field surveys among focal habitats within the seascape. Permutation-based, non-parametric analysis of variance (np-ANOVA) was used to compare fish densities and species richness between the two focal macroalgal habitats and among the different locations in the seascape. Fish assemblages were compared between macroalgal beds and macroalgal farms by conducting a permutation-based, non-parametric multivariate analysis of variance (np-MANOVA; Anderson 2001; McArdie and Anderson 2001) on square-root transformed data. This test is a multivariate equivalent of Fisher’s F-statistic and it was employed to test the null hypothesis of no difference among groups (Anderson 2001). To identify which species were significantly indicative of each group (i.e., macroalgal bed vs. macroalgal farm) the indicator value method (IndVal; Dufrène and Legendre 1997) was used. The test was followed by a canonical analysis of principal coordinates (CAP; Anderson and Willis 2003, Legendre and Legendre 2012) to create a bi-plot and a correlation vector plot to visualize the main species driving the observed differences. Homogeneity of dispersion was verified with the function np-disp, which is equivalent to Levene’s test (Anderson 2006, Anderson et al. 2006), and when needed data were square-root transformed. All statistical analyses were conducted using MATLAB and the Fathom toolbox (Jones 2017).

**Maceralgal assays field experiments**

To test potential differences in herbivory among macroalgal beds, macroalgal farms, and the surrounding seascapes, a fully-orthogonal field experiment was conducted. Macroalgal species were collected from the field by hand, placed in buckets filled with seawater, and brought back to the laboratory. At the laboratory the macroalgae samples were rinsed and epiphytes removed. The macroalgae were divided into smaller single-thallus pieces and were spun in a salad spinner for ten seconds to remove any excess water. Single-thallus pieces of *Sargassum aquifolium* and farmed *Eucheuma denticulatum* were tethered within each focal habitat (i.e., macroalgal beds of *Sargassum* spp., macroalgal farms of *E. denticulatum*) for 24 hrs and at different distances (edge of focal patches, 10 m, 50 m, and 100 m) from each focal habitat to
quantify percent of macroalgal loss throughout the surrounding seascape. We hypothesized that the percent loss of the native macroalgae *S. Aquifolium* would be higher compared to the farmed *E. denticulatum* due to its higher nutritional content (Rojas-Sepulveda 2017), however this pattern would be context-dependent upon location of deployment.

The macroalgal assays were created from a 40 cm long PVC pipe where two thalli of each macroalgal species were fixed in place with a transparent plastic line and separated by approximately 8 cm (Fig. 3). For a subset of the macroalgal assays, a video camera (GoPro Hero Session, Black) was placed facing directly toward the assay, and allowed to record for 20 minutes. At five and ten minutes into the recordings, any fishes that came into the field of view of the camera were noted and identified to the lowest taxonomic level possible. The macroalgae were weighted before and after the deployment and percent of macroalgal loss per unit time calculated. The rate of macroalgal loss was then compared between focal macroalgal habitats using permutation-based, non-parametric analysis of variances (np-ANOVA). To control for the effects of handling or algal growth, a caged control with two thalli pieces of each species was deployed during each sampling event and changes in macroalgal biomass were used in the calculations to adjust experimental macroalgal biomass accordingly.

**Results**

Habitat heterogeneity was markedly different between macroalgal beds and farms while no differences in macrophyte characteristics (i.e. cover, height) were detected between the focal habitats. More specifically, the mean percent cover (= standard error of the mean) of hard substrate (e.g., rubble, rocks, reef) was over four times higher in macroalgal beds (39.63 ± 4.89) compared to macroalgal farms (9.42 ± 5.84; $F_{(1, 30)} = 13.34, p = 0.002$). The mean macrophyte cover (including seagrass and farmed/non-farmed macroalgae; $F_{(1, 30)} = 3.18, p = 0.08$) and height ($F_{(1, 30)} = 3.18, p = 0.38$) were similar between the focal macroalgal beds and macroalgal farms. Although not significant at the alpha 0.05 level, there was a marginal support for higher species richness of macrophytes in natural macroalgal beds (6.4 ± 0.5 species) than in macroalgal farms (4.8 ± 0.4 species; $F_{(1, 30)} = 4.17, p = 0.057$).
In total, 4,464 fish were quantified from 97 visual surveys (Table S1). Fish abundance (mean number of fish per transect = standard error of the mean) was similar between the interior of focal habitats, with 51.0 ± 6.9 fish observed in macroalgal beds and 39.0 ± 12.2 fish in macroalgal farms ($F_{1, 30} = 2.15, p = 0.09$). Fish abundance did not differ between the interior and edge of macroalgal beds ($t = 0.50, p = 0.72$) but decreased significantly with distance away from the macroalgal beds ($F_{4, 43} = 4.42, p = < 0.01$; Fig. 4a). In contrast, fish abundance tended to increase with distance away from farms in the seascape (Fig. 4a). However, this pattern was not statistically significant ($F_{4, 43} = 1.78, p = 0.06$).

Fish species richness (= standard error of the mean) was higher in the macroalgal beds (16.5 ± 1.8 fish species) than in the macroalgal farms (6.7 ± 1.3 fish species; $F_{1, 30} = 10.7, p = < 0.01$). Species richness decreased drastically within 10 meters from the edge of macroalgal beds and stayed rather constant with distance away from the edge of macroalgal beds ($F_{4, 43} = 5.52, p = < 0.01$; Fig. 4b). Species richness in macroalgal farms, on the other hand, was constant throughout the seascape ($F_{4, 43} = 1.78, p = 0.07$; Fig. 4b).

On average, a greater percentage of turf, sponges, and macroalgae were observed in the interior and edge of macroalgal beds while the percentage of seagrass (dominated by *Thalassodendron ciliatum*) increased with distance away from the focal habitat (Fig. 4c). In seascapes with macroalgal farms, macroalgae and seagrass beds were the most common benthic substrate while turf and sponges constituted comparatively lower percentages (Fig. 4d). While seagrass beds were a common component of the substrate composition in the seascape, *Cymodocea* spp. and *Thalassia hemprichii* were the dominant species in the interior and edge of macroalgal farms. In the seascape surrounding macroalgal farms, *Enhalus acoroides* dominated the seagrass composition.

Fish assemblage composition differed significantly between macroalgal beds and farms ($F_{1, 30} = 5.33, p = 0.001$). The ten species with highest indicator power values were identified and visualized with a CAP plot (Table 1). The CAP demonstrated through the correlation vectors with the longest components on canonical axis I, that wrasses such as *Thalassoma hebraicum*, *Labroides dimidiatus*, the goatfish *Parupeneus macronema*, and damselfishes *Plectroglyphidodon lacrymatus*, *Dascyllus aruanus*, and
Chrysiptera unimaculata were the taxa most indicative of the macroalgal beds driving the assemblage patterns. Parrotfishes such as Leptoscarus vaigiensis and juvenile scarids, the wrasse Cheilinus inermis, and the emperor Lethrinus harak were the taxa most indicative of macroalgal farms (Fig. 5).

In general, macroalgal loss during the macroalgae assay field experiments was higher and more variable in macroalgal farm seascapes compared to macroalgal bed seascapes ($F_{(1, 336)} = 14.60, p = 0.001$; Fig. 6). Furthermore, percent loss of S. aquilotum did not differ from E. denticulatum in the seascapes for either natural macroalgal beds ($F_{(1, 212)} = 1.79, p = 0.21$; Fig. 6) or farms ($F_{(1, 172)} = 0.002, p = 0.953$). There was no difference in mean loss of S. aquilotum among the different distances away from macroalgal beds ($F_{(4, 10)} = 0.84, p = 0.53$; Fig. 7a) or among distances away from the macroalgal farms ($F_{(4, 10)} = 0.42, p = 0.82$; Fig. 7a). The percent loss of E. denticulatum did not differ among the different distances in the macroalgal beds ($F_{(4, 10)} = 1.75, p = 0.131$; Fig. 7b). In addition to higher percentage of E. denticulatum loss in the macroalgal farms compared to natural macroalgal beds, the percentage of macroalgae loss was both higher and more variable at 10 and 50 meters from the farms compared to the other locations within the seascapes ($F_{(4, 10)} = 3.01, p = 0.02$; Fig. 7b).

In terms of trophic composition, the surveys demonstrated that territorial grazers, other grazers, and scrapers were common in the interior and edge of macroalgal beds, and the percentage of territorial grazers decreased in the surrounding seascapes (Fig. 7c). In the interior and edge of macroalgal farms, a greater percentage of browsers was present compared to the surrounding seascapes wherein the percentages of browsers decreased with increasing distance from farms. Instead, the percentage of scrapers and excavators increased in the surrounding seascapes compared to the interior and edge of the macroalgal farms (Fig. 7d). Furthermore, the abundance of browsers was also higher in the interior and edge of macroalgal farms, and both lower and more consistent in macroalgal beds and neighboring seascapes (Fig. 8a). Sea urchins were nearly absent from macroalgal bed seascapes and not abundant in the interior and edge of the farms (Fig. 8b). Sea urchin abundance was higher and more variable in the neighboring seascapes of the macroalgal farms (Fig. 8b). Invertivores in contrast, were more common in
macroalgal beds and the surrounding seascape compared to the macroalgal farms and the surrounding seascape.

Discussion

As hypothesized, patterns of fish assemblage, habitat heterogeneity, and percent of macroalgae loss differed between macroalgal beds and macroalgal farms in tropical East African seascapes. Additionally, fish assemblages and rates of herbivory were not consistent across the seascapes and varied with distance from the focal habitat patches likely due to the presence of other benthic habitats in the seascape.

However, contrary to predictions, macrophyte characteristics (cover and height) were not different and fish abundance was not higher in natural macroalgal beds compared to macroalgal farms. The results of the present study indicate that introduced macroalgal farms such as those of monospecific *Eucheuma denticulatum* do not host the same fish assemblage as natural macroalgal beds. Similar to Bergman et al. (2001) and Anyango et al. (2017), macroalgal farms also differed in fish trophic composition from surrounding uncultivated habitats (e.g., seagrass beds, macroalgal patches) in the seascape. This suggests alterations of tropical seascapes by farming practices can have consequences on fish community composition and the ecological functions performed.

Fish abundance was similar among macroalgal beds and macroalgal farms and may be explained by similar habitat characteristics and food resource availability among habitats. Habitat characteristics such as macrophyte cover and height, which provide structural complexity in ecosystems, were similar between the two focal habitat types examined. The dense structure of macrophytes can impede effective foraging by predators, consequently reducing predation rates (Savino and Stein 1982) and macroalgal density, height, and percent cover have been identified as important drivers of fish abundance and distribution in temperate reefs (Anderson 1994, Levin and Hay 1996). Similarly, canopy height, density of holdfasts, and coverage of macroalgal habitat patches are important predictors of fish assemblages in other tropical locations (Wilson et al. 2014, Lim et al. 2016, Wenger et al. 2018). Additionally, high seagrass blade density (which is usually correlated with macrophyte cover) and the presence of
macroalgae can reduce mortality rates of fishes (Horinouchi 2007, Chacin and Stallings 2016) and many invertebrates (Orth et al. 1984, Heck and Crowder 1991, Johnson 2006, Gregor and Anderson 2016), suggesting that the structural complexity provided by the two macroalgal habitats in Mafia Island likely offered similar refuge to fishes.

Fish species richness was higher in macroalgal beds compared to farms and both habitats hosted different fish assemblages, which may have been related to the higher macrophyte species richness and greater percentage cover of hard substrate found in natural macroalgal beds. Hard substrate and different macrophyte species provided higher fine-scale heterogeneity, thus increasing structural complexity and potentially greater food and habitat resources for fishes (Rossier and Kulbicki 2000). Similarly, monocultures in agricultural fields on land can have lower within-habitat heterogeneity and decrease species richness of associated organisms compared to natural uncultivated vegetative habitats (Arnold et al. 1987; Bretagnolle et al. 2018). Furthermore, the interior of macroalgal beds in the present study also had higher percentages of sponges, corals, and filamentous algal turf (compared to the interior of the macroalgal farms), and these may have offered crevices and holes for a variety of species to use as refuge (Eggertsen 2019). For instance, van Lier et al. (2018) observed that hard complexity coupled with soft canopy structure of tropical macroalgal beds in Western Australia provided a large number of microhabitat types, and thus supported a high number of species likely due to niche partitioning (Harding 1960; Hortal et al. 2009). This has also been found in tropical macroalgal beds in Brazil (Eggertsen et al. 2017). It is likely the reason why the territorial pomacentrid P. lacreanus, which feeds on the epilithic algal matrix (Wilson and Bellwood 1997) that it farms on hard substrates (Horn 1989), and the inverteores T. hebraticum and P. macronema were found to highly influence assemblage patterns in macroalgal beds. Overall, higher fine-scale heterogeneity most likely provided more refuge and food resources and hence contributed to higher fish species richness in natural macroalgal beds compared to macroalgal farms. Similar patterns have been observed in Cichlid fish communities in lakes in central Africa and in bat populations at the Iberian Peninsula where habitat heterogeneity allows partitioning of resources and supports diverse assemblages (Genner et al. 1999, Arrizabalaga-Escudero et al. 2018).
In contrast, the macroalgal farms had lower percentage of hard substrate and filamentous algal turf, and were mainly composed of macroalgae and seagrass. This is likely the reason why macroalgal farms comprised a different fish assemblage with higher percentage of herbivorous fishes and a lower percentage of carnivores, omnivores, and corallivores compared to natural macroalgal beds. Similar results have been observed in terrestrial agronomic practices where for instance, ground beetle assemblages in uncultivated fields differed from those in harvested fields (Carcamo et al. 1995). In the present study the parrotfish *L. vaigiensis*, and juvenile scarid labrids were the most abundant herbivores and some of the most indicative taxa in macroalgal farms. The high presence of parrotfish *L. vaigiensis* in farms may be explained by its feeding ecology. It feeds on both algae and seagrass blades and may do so both within the farms and in the nearby surrounding seagrass patches (Locham et al. 2015). Other studies have observed high abundances of siganids (rabbitfishes—common browsers in Indo-Pacific tropical seascapes) within macroalgal farms in Zanzibar, Tanzania (Bergman et al. 2001; Eklöf et al. 2006b; Anyango et al. 2017). Surprisingly, siganids were recorded at low numbers in the visual surveys. However, in 43% of the deployed videos the rabbitfish *Siganus sutor* was frequently observed swimming in the macroalgal farms suggesting this species evades human presence (likely due to siganids being a common catch by artisanal fishers) and was probably the reason we did not observe them frequently in our visual surveys. In Southeast Asia (Indonesia, Malaysia, and the Philippines), siganid catches have increased disproportionally with macroalgal farming (Hehre and Meeuwig 2016). While it is unclear whether a similar increase in siganid abundance is occurring in East Africa, where farming is performed at a substantially smaller-scale, it is not surprising to observe the siganids swimming in and out the macroalgal farms. Overall, these patterns suggest that while both macroalgal habitats (beds and farms) may provide similar structural complexity for fishes (to some extent), the identity of the macroalgae and the available amount of hard structural complexity can influence the composition of the assemblage, determining the ecological functions performed by the fishes.

Fish abundance and species richness in the surrounding seascapes differed between the two types of macroalgal habitats. In seascapes where macroalgal beds were located, fish abundance and species
richness were similar between the interior and edge of the focal habitat, and generally decreased with
distance from the habitat. These patterns were likely influenced by the change of benthic composition
from structurally diverse habitats including turf and sponges to a benthic cover of the monospecific
*Thalassodendron ciliatum* seagrass, resulting in reduced habitat heterogeneity as distance increased away
from natural macroalgal beds. As previously discussed, high fine-scale habitat heterogeneity offers a
range of resources, both in terms of refuge and feeding grounds, hence attracting a more diverse fish
assemblage (Öhman and Rajasuriya 1998; Gratwicke and Speight 2005). In addition, lower epiphytic
cover in seagrass beds compared to those of other benthic habitats in tropical settings may also provide
less food resources and thus lower abundance and richness of associated fish. In contrast, both epiphytic
growth on seagrass and fish abundance is high in subtropical and temperate seagrass beds (Humphries et
al. 1992, Nelson 2017). The abundance and species richness of fishes was similar across the seascapes
where macroalgal farms were located, even as distance increased from the focal habitat. Other types of
benthic habitats present in the vicinity of the farms likely influenced these patterns. Patches of seagrasses
mainly dominated by the long-bladed *Enhalus acoroides* may have provided refuge for many fishes
similar to the mix of seagrass and algae in the macroalgal farms, thus explaining the consistent pattern of
fish species richness across the seascapes surrounding the farms (Gullström et al. 2011). High fish density
and diversity has been previously associated with patches of *E. acoroides* as several taxa are able to rely
on *E. acoroides* as a food source (Vonk et al. 2008, Gullström et al. 2011).

Macroalgae loss due to herbivores was generally higher in seascapes where macroalgal farms were
located compared to seascapes where macroalgal beds were present. These patterns were likely related to
the greater amount of browsers in seascapes with farms. Indeed, abundance of browsers was higher inside
the macroalgal farms suggesting the readily available farmed *E. denticulatum* served as a viable food
source. Additionally, *E. denticulatum* was intensively grazed while under cultivation in the present study
and has been found in the stomachs of browsers (e.g., *Siganus* spp.) in the East African region (Bergman
et al. 2001, Anyango et al. 2017). It was also the most frequently found macroalgae in the stomachs of the
rabbitfish *Siganus sutor*, caught in the same macroalgal farms as the present study (Rojas-Sepulveda
Comparably, in terrestrial farmlands granivorous bird species (i.e., those with a substantial seed component in the diet) can feed off cereal grain and the seeds of many plants cultivated in the farmlands and thus benefit from these harvestable habitats (Wilson et al. 1999).

Biomass loss of *E. denticulatum* and *S. aquifolium* was low in the natural macroalgal beds and did not differ significantly in the surrounding seascapes. These patterns were likely related to the low percentage of browsers and low abundance of grazing urchins in the surrounding seascapes. Instead, invertivores and omnivores constituted a high percentage of the fishes observed in the surrounding seascapes of macroalgal beds. Tanzanian macroalgal beds comprise a high abundance and diversity of epifaunal invertebrates (Tano et al. 2016), thus these habitats can serve as feeding grounds, not only for herbivorous fishes, but also for a number of invertivores and omnivores.

In contrast to the surrounding seascapes of natural macroalgal beds, the percent loss of *E. denticulatum* was not consistent across the seascapes with macroalgal farms. It was lower in the interior and edge of the farms compared to the rest of the seascapes despite the high abundance of browsers observed. This may be explained by the high availability of *E. denticulatum* fronds in the farms, resulting in lower browsing intensity on the tethered *E. denticulatum*. The biomass loss of *E. denticulatum* was higher and more variable with distance from the farms despite the decrease in abundance of browsers and might have been related to less available farmed macroalgae as a food source in the surrounding seascapes. It may have also been influenced by the sporadically high abundance of grazing urchins found in the vicinity of the farms.

Interestingly, patchy aggregations of sea urchins, including *Diadema savigni*, *D. setosum*, *Echinometra mathaei*, and *Echinotrix diadema* were encountered in the vicinity of the farms but not within them.

Occasionally, during low tide, the macroalgal farms were exposed to the air and thus unavailable as feeding grounds for marine herbivores. Air exposure can be detrimental to marine invertebrates due to desiccation stress (Menge 1976). This is possibly the reason why the sea urchins were found nearby the farms and not in their interior and why the percent loss of macroalgae in general tended to be more variable in the vicinity of the farms.
In this study we demonstrated that alteration of seascapes through the introduction of macroalgal farms may modify habitat heterogeneity with secondary effects on fish community assembly and ecological processes. We also observed that macroalgal farms differed from naturally-occurring macroalgal beds, both in terms of habitat heterogeneity and fish species richness. If the intensity of the macroalgal farming were to increase (such as in Southeast Asia), it could cause strong homogenization and degradation of coastal habitats across the seascapes leading to losses in the diversity of macrophytes and fishes with repercussions on ecosystem function. In agricultural terrestrial systems increased land use intensity can cause loss of habitat heterogeneity resulting in declines of species richness of birds and arthropods (Siriwardena et al. 1998; Krebs et al. 1999; Benton et al. 2003; Heikkinen et al. 2004; Dauber et al. 2005; Hendrix et al. 2007). As such, the placement of farms and farming intensity might have significant implications for associated fauna and ecological processes. Alternatively, macroalgae farming if practiced properly could have positive effects, such as carbon sequestration to mitigate carbon emissions (Froehlich et al. 2019). Therefore, further studies are recommended to understand generalities.

This study allowed us to gain a greater understanding of how seascapes alterations through “land-use” practices can influence patterns of community assembly and ecological processes and was an attempt to attain a more holistic view of tropical African seascapes subjected to human practices.

Acknowledgments – We are grateful for all the assistance provided by Dr. Amelia Buriyo at University of Dar es Salaam with respect to logistics, Karlina See Kee for her help with the fieldwork, and Yessenia Rojas with preparation of macroalgal assays. We also thank the staff at the Mafia Island Marine Park (MIMP), Big Blu Mafia Island Dive Centre, and Mafia Island Diving for their support. We are incredibly thankful for our Tanzanian boat captain, Mr. Nahoda Salamala for his invaluable contribution and local knowledge of the marine habitats in Mafia Island. We are grateful for the reviews provided by Dr. Susan Bell from University of South Florida. This study was supported by the National Science Foundation Graduate Research Fellowship and the Graduate Research Opportunities Worldwide (grant no. 1144244 to D.H.C), the Swedish Research Council (grant nos. 2015-05848, 2015-01257, E0344801), and the University of South Florida, College of Marine Science.
References


483  landscapes. Oikos 65:169–175
484  Eggertsen L, Ferraira CE, Fontoura L, Kautsky N, Gullström M, Barkström C (2017) Seaweed beds support more
485  juvenile reef fish than seagrass beds: Carrying capacity in a south-western Atlantic tropical seascape. Estuar. Coast.
488  https://doi.org/10.1007/s00227-019-3498-0
489  Eklöf JS, de la Torre-Castro M, Adelsköld L, Jiddawi NS, Kautsky N (2005) Differences in macrofaunal and
491  Eklöf JS, Heurriksson R, Kautsky N (2006a) Effects of tropical open-water seaweed farming on seagrass ecosystem
495  Eklöf JS, Musya FE, Lyimo TJ, Buriyo AS (2012) Seaweed Farming in Chwaka Bay: A Sustainable Alternative in
496  Aquaculture? – In: de la Torre-Castro, M. and T. J. Lyimo (eds), People, Nature and Research in Chwaka Bay,
498  Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery
504  25:487–503
505  Garrigue C (1995) Macrophyte associations on the soft bottoms of the south-west lagoon of New Caledonia:


Ambio 24:455–469


Lim IE, Wilson SK, Holmes TH, Noble MM, Fulton, C (2016) Specialization within a shifting habitat mosaic
underpins the seasonal abundance of a tropical fish. Ecosphere 7(2):e01212. 10.1002/ecs2.1212
Lubchenko J, Olson AM, Brubaker LB, Carpenter SR, Holland MM, Hubbell SP, Levin SA, MacMahon JA, Matson
PA, Malillo JM, Mooney HA, Peterson CH, Pulliam HR, Raal LA, Ragel PJ, Risser PG (1991) The sustainable
McArdis BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based
redundancy analysis. Ecology 82:290–297
Hydrobiologia 221:19–29
Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition, and
Michel N, Bural F, Butet A (2006) How does landscape use influence small mammal diversity, abundance and
Msuya FE (2006) The impact of seaweed farming on the social and economic structure of seaweed farming
Authoritative Reference System. Amsterdam: ETI BioInformatics
Msuya FE (2013) Social and economic dimensions of carrageenan seaweed farming in the United Republic of
Carrageenan Seaweed Farming Fisheries and Aquaculture Technical Paper No. 580. FAO, Rome, Italy, pp 115–146
Msuya FE, Buriyo A, Omar I, Pascal B, Narrain K, Ravina JIM, Mrsbu E, Wakibia JG (2014) Cultivation and
utilisation of red seaweeds in the Western Indian Ocean (WIO) Region. J. Appl. Phycol. 26:699–705
Nelson WG (2017) Development of an epiphyte indicator of nutrient enrichment: a critical evaluation of
observational and experimental studies. Ecol. Indic. 79:207–227
Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. Environ Biol Fish
3:49. https://doi.org/10.1007/BF00006308


https://doi.org/10.1371/journal.pbio.0060122.


Environ. 75:13–30
Table 1. Results of IndVal analysis comparing macroalgal beds versus macroalgal farms. The 10 species with highest indicator power values (ranges from 0-100%) were selected and used for visualization in the CAP plot.

<table>
<thead>
<tr>
<th>Group</th>
<th>Family</th>
<th>Taxa</th>
<th>$I$</th>
<th>$p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macroalgal bed</td>
<td>Labridae (wrasses and parrotfishes)</td>
<td>Thalassoma hebraicum</td>
<td>76.19</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Labridae (wrasses parrotfishes)</td>
<td>Labroides dimidiatus</td>
<td>57.14</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>Pomacentridae (damselfishes)</td>
<td>Plectroglyphodon lacrymanus</td>
<td>52.38</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>Pomacentridae (damselfishes)</td>
<td>Chrysiptera unimaculata</td>
<td>46.44</td>
<td>0.057</td>
</tr>
<tr>
<td></td>
<td>Pomacentridae (damselfishes)</td>
<td>Dascyllus auratus</td>
<td>42.86</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td>Mullidae (goatfishes)</td>
<td>Parupeneus macronema</td>
<td>38.85</td>
<td>0.034</td>
</tr>
<tr>
<td>Macroalgal farm</td>
<td>Labridae (wrasses and parrotfishes)</td>
<td>Leptoscarus vaigiensis</td>
<td>70.10</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Labridae (wrasses and parrotfishes)</td>
<td>Juvenile scardis</td>
<td>49.67</td>
<td>0.066</td>
</tr>
<tr>
<td></td>
<td>Labridae (wrasses parrotfishes)</td>
<td>Chelidae inermis</td>
<td>43.74</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td>Lethrinidae (emperors)</td>
<td>Lethrinus harak</td>
<td>27.27</td>
<td>0.025</td>
</tr>
</tbody>
</table>
Figure 1. Study sites in Mafia Island, Tanzania. Black circles indicate locations of macroalgal farms and white triangles indicate locations of macroalgal beds.

Figure 2. Image of a macroalgal bed (a) and a macroalgal farm (b).

Figure 3. Tethering unit with macroalgae *Eucheuma denticulatum* and *Sargassum Aquifolium*. The tethering units were deployed within focal macroalgal patches (macroalgal farms and natural macroalgal beds), at the edges and at 10 m, 50 m, and 100 m from the habitats.

Figure 4. Average (± standard error) fish density (a) and species richness (b) in macroalgal beds, macroalgal farms, and neighboring locations in the seascape. Benthic composition in macroalgal beds (c) and and macroalgal farms (d) and neighboring locations within each habitat’s seascape. The term *interior* refers to the interior of the focal habitat, *edge* refers to the boundary of the focal habitat, *10 m* refers to 10 meters from the edge of the focal habitat, *50 m* refers to 50 meters from the edge of the focal habitat, and *100 m* refers to 100 meters from the edge of the focal habitat.

Figure 5. Canonical Analysis of Principal Coordinates of Mafia Island, Tanzania fish assemblage structure (a). Circles represent data points in macroalgal beds and crosses represent data points in macroalgal farms. The Y-axis data are jittered to ease visual assessment of the assemblage patterns. Fish species vectors pointing to the right correspond to those species mainly found in macroalgal farms and those vectors pointing to the left correspond to those observed in the macroalgal beds (b).

Figure 6. Percent loss of macroalgae (mean ± standard error) in macroalgal bed seascape and macroalgal farm seascape ± standard error of the mean.

Figure 7. Percent loss (mean ± standard error) of *Sargassum aquifolium* (a) and *Eucheuma denticulatum* (b) in macroalgal beds, macroalgal farms, and neighboring locations in the seascape. Trophic composition in macroalgal beds (c) and macroalgal farms (d) and neighboring locations within the seascape of each habitat. The term *interior* refers to the interior of the focal habitat, *edge* refers to the boundary of the focal habitat, *10 m* refers to 10 meters from the edge of the focal habitat, *50 m* refers to 50 meters from the edge of the focal habitat, and *100 m* refers to 100 meters from the edge of the focal habitat. Negative values indicate macroalgal growth within the 24-hr deployment period.

Figure 8. Average density (± standard error) of browsers (a) and sea urchins (b) in macroalgal beds, macroalgal farms, and neighboring locations in the seascape.
Figure 1.
Figure 3.
Figure 4
Figure 5.
Figure 6.
Figure 7.
Figure 8.