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Spatial Dynamics of Vegetated Seascapes and the Influence on Fish and Crustaceans

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UNIVERSITY OF MIAMI

SPATIAL DYNAMICS OF VEGETATED SEASCAPES AND THE INFLUENCE ON
FISH AND CRUSTACEANS

By

Rolando O. Santos Corujo

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

December 2014

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SPATIAL DYNAMICS OF VEGETATED SEASCAPES AND THE INFLUENCE ON
FISH AND CRUSTACEANS

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Spatial Dynamics of Vegetated Seascapes and the
Influence on Fish and Crustaceans

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My dissertation adopted concepts and spatial tools of seascape ecology, the marine counterpart of landscape ecology, to understand the broad-scale structural attributes that make submerged aquatic vegetation (SAV) seascapes resilient to anthropogenic disturbances, drivers of fauna community structure, and productive fisheries habitats. My research was designed to address the relative and interrelated ecological effects of broad-scale changes in SAV habitat amount (habitat loss) and configuration (fragmentation). SAV seascapes in nearshore areas of Biscayne Bay have been subject to constant anthropogenic disturbances associated to freshwater pulses from canals over the last 50 years; thus, these seascapes served as a model system to link water management practices, seascape transformation (e.g., habitat loss and fragmentation), and to evaluate cascading effects on marine fauna. First, I performed a long-term analysis of SAV seascape characteristics using archived black-white aerial photographs, from 1938 to 2009, to assess the spatio-temporal trends of SAV habitat fragmentation independently of habitat loss within Biscayne Bay's nearshore habitats. Habitat loss and fragmentation were significantly higher along the shoreline compared to offshore seascapes removed from freshwater influences. All sites exhibited higher fragmentation in 2009 compared to 1938, and while areas adjacent to canals had significantly higher SAV cover, they still experienced wide fluctuations in cover and fragmentation over time. Two organism-

habitat relationship studies were designed and implemented to explore the nature of the ecological responses to SAV seascapes. First, I compared fish and crustacean community assemblages and diversity between spatially continuous and fragmented SAV seascapes. Fragmented seascapes supported significantly higher species richness of fish and crustaceans and higher biomass of carnivorous fishes than did continuous seascapes. The community patterns were also influenced by salinity, indicating that both water quality and spatial properties of SAV seascapes play an important role in structuring faunal communities. Second, I applied multivariate non-linear models to evaluate patterns of abundance of the most common fish and shrimp species to document species-specific responses to SAV seascape characteristics, and to determine whether habitat amount and configuration thresholds exist in the response of organisms to seascape structure. The amount of SAV habitat and its patch configuration (and the interactions between these two metrics), were the most influential predictors of faunal abundance, and outperformed fine-scale habitat characteristics such as seagrass cover and canopy height as predictors of faunal responses. Abundance thresholds were identified for all species in response to patch complexity and habitat composition and configuration which help to determine the minimum amount of habitat and maximum level of fragmentation that could sustain fish and crustacean populations. Finally, field experiments using baited remote underwater video surveys (BRUVs) and tethering with *Farfantepenaeus duorarum* (pink shrimp) were designed to test whether predation and predation-risk effects are key mechanisms generating patterns in fish and crustacean abundance in relation to habitat amount and configuration. Both BRUVS and tether experiments identified higher predation risk at boundaries of the seagrass meadows (at mangrove-seagrass edges, and seagrass seaward

edges). Based on allocation time and pecking rate, it was evident that habitat shifts occur in response to seascape spatial properties and risk of predation. In conclusion, the transformation of the SAV seascape in Biscayne Bay has been induced mainly by salinity patterns associated with freshwater inflow into the bay. Moreover, seascape characteristics and transformations directly linked to the abundance and distribution of SAV-associated fish and crustacean assemblages. These patterns are most likely attributed to the role that seascape play in species interactions and trophic dynamics. Thus, my work showed how seascape ecology concepts could be used to evaluate questions about ecological dynamics and patterns induced by anthropogenic disturbances and the spatial transformation of essential fish and crustacean habitats.

I dedicate this work to my Mom, Cindy Corujo, for her unconditional support, and for encouraging me to be a good conscious citizen, student and scientist, and for teaching me the invaluable lessons of commitment, sacrifice, and perseverance

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TABLE OF CONTENTS

	Page
LIST OF FIGURES	x
LIST OF TABLES	xi
Chapter	
1 INTRODUCTION AND DISSERTATION OBJECTIVES	1
Seascape Ecology	1
Biscayne Bay and the Comprehensive Everglades Restoration Plan.....	5
Dissertation Objectives.....	5
Key Findings and Implications for Management.....	8
2 LONG-TERM SPATIAL DYNAMICS IN VEGETATED SEASCAPES: FRAGMENTATION AND HABITAT LOSS IN A HUMAN-IMPACTED SUBTROPICAL LAGOON	16
Summary	16
Background	17
Materials and Methods.....	21
Study site.....	21
Study design.....	21
Benthic habitat mapping	22
Spatial-pattern analysis	24
Results	28
SAV cover and SAV seascape fragmentation	28
Temporal trends in SAV cover and fragmentation.....	29
SAV loss and fragmentation dynamics.....	29
Discussion	30
3 INFLUENCE OF FRAGMENTED VERSUS CONTINUOUSLY VEGETATED SEASCAPES ON MARINE ASSEMBLAGES IN A SUBTROPICAL BAY..	48
Summary	48
Background	49
Materials and Methods.....	52
Study site.....	52
Seascape mapping.....	52
Quantifying the spatial structure of seascapes	54
Fish and crustacean sampling design	55
Sample and data processing.....	56
Statistical analyses	57

Results	59
Do fragmented and continuous seascapes differ in faunal occurrence, abundance and biomass?.....	59
Are there more predators' abundance and biomass in fragmented versus continuous seascapes?.....	60
Is species richness higher in fragmented seascapes versus continuous seascapes?	61
Discussion	62
Assemblage composition in continuous vs fragmented seascapes	62
Patterns of functional groups and biomass	64
Faunal diversity associated with SAV seascapes.....	65
Geographical influence on seascape faunal patterns	66
Management relevance of a seascape approach.....	67
4 ECOLOGICAL RESPONSES OF THREE MARINE ORGANISMS TO THE SPATIAL STRUCTURE OF SEAGRASS HABITAT: HABITAT LOSS AND FRAGMENTATION THRESHOLDS	78
Summary	78
Background.....	79
Materials and Methods.....	83
Study site.....	83
Sampling design.....	83
Seascape mapping.....	84
Seascape spatial structure	84
Within-patch structure	86
Statistical analyses	87
Seascape simulations under different salinity environments.....	89
Results	91
Seascape spatial pattern trends.....	91
Within-patch structure	92
Model validation	93
Seascape simulation <i>F. duorarum</i> abundance	93
Discussion.....	94
Spatial scale of abundance responses	95
Importance of seascape spatial properties.....	96
Tradeoffs and interactions.....	98
Seascape scenarios and management implications.....	100
5 PREDATION RISKS IN FRAGMENTED SAV SEASCAPES.....	111
Summary	111
Background.....	112
Materials and Methods.....	115
Study site.....	115
Sampling design.....	116
Seascape metrics	120

Statistical analyses	121
Results	122
Tethering experiments	122
BRUVs	123
Discussion	124
Shrimp predation and SAV seascape fragmentation	125
Predation risks indirect effects	126
Gradient in the “Seascape of Fear”	128
6 Conclusions	143
Key Findings	143
Spatio-temporal Dynamics of SAV Seascapes	144
Limitation and future work	145
Faunal Responses to SAV Seascape Patterns	145
Limitation and future work	147
Ecological Mechanisms Behind Responses	147
Limitation and future work	149
Emerging Priorities and Research Questions	150
References	154
Appendices	175

LIST OF TABLES

Table 2.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne Bay	38
Table 2.2. Patterns of change in SAV area in western Biscayne Bay over the >70-year record evaluated here (1938– 2009)	39
Table 2.2. Principal component analysis (PCA) eigenvalues and variable loadings .	40
Table 3.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne	70
Table 3.2. Results from the similarity percentages (SIMPER) analysis for the a) occurrence, b) abundance and c) biomass data	71
Table 4.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne	102
Table 4.2. Measures of the abundance (A_{gam}) and occurrence (O_{gam}) generalized additive model performance based on the spatial pattern sub-models (i.e., abundance and occurrence response to habitat amount and configuration within each seascape sample unit).	103
Table 4.3. Results of the abundance (A_{gam}) and occurrence (O_{gam}) generalized additive models for each species	104
Table 4.4. Validation measures for the full abundance (A_{gam}) and occurrence (O_{gam}) generalized additive models for each species	105
Table 5.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne Bay.....	133
Table 5.2. Percentage of deviance explained by the generalized linear models (GLMs) and the significance of the models based on Chi-square tests	134
Table 5.3. Generalized linear models (GLMs) regression coefficients	135

LIST OF FIGURES

Figure 1.1. Illustration of a vegetated seascape, a spatially heterogeneous area composed of various discrete habitat patches	10
Figure 1.2. Illustration of metrics used to quantify habitat amount and configuration	11
Figure 1.3. Illustration of habitat loss and fragmentation	12
Figure 1.4. Illustration of a seascape analysis with patch and patch-mosaic perspectives	13
Figure 1.4. Illustration of a seascape multiscale approach.....	14
Figure 1.5. Conceptual diagram of the hierarchical structure of this dissertation.....	15
Figure 2.1. Study site: Biscayne Bay, Miami, Florida	41
Figure 2.2. Classification of fragmentation seascape state within each site	42
Figure 2.3. SAV cover and Fragmentation Index over time measured within the 500m from shore spatial extent	43
Figure 2.4. SAV cover and Fragmentation Index over time measured within the shoreline habitats and offshore habitats	44
Figure 2.5. SAV seascape patterns calculated for the period 1938 to 2009.....	45
Figure 2.6. Vector lengths calculated from the coordinates of PCA biplot quantifying the magnitude of fragmentation and defragmentation by canal treatment.....	46
Figure 2.7. Conceptual SAV seascape transformation illustrating habitat loss/gain and fragmentation.....	47
Figure 3.1. Study area, seascape map, superimposed 500 x 500 m grid and areas classified and selected as continuous (light green) and fragmented (red) SAV seascapes	72
Figure 3.2. Relative abundance of faunal species within assemblages sampled from the nearshore area of Biscayne Bay by: seascape and zone	73
Figure 3.3. Multi-dimensional scaling (MDS) plots of the occurrence, abundance and biomass community data	74

Figure 3.4. Abundance and biomass for functional groups (error bars: standard deviation): invertivores of sessile prey (IvS), invertivore of small mobile prey (IvSm), invertivore and piscivore (Iv/Pi) and piscivores (Pi)	75
Figure 3.5. W-statistic compared between continuous and fragmented SAV seascapes	76
Figure 3.6. Species diversity indices (error bars: standard deviation): species richness (s), Shannon-Weiner ($H'(\log_e)$), Simpson diversity (1-Lambda), and variation in taxonomic distinctness (Lambda+) compared between continuous and fragmented SAV seascapes	77
Figure 4.1. Illustration of the study area within Biscayne Bay, SAV seascape map with the 100 x 500 m plots randomly located along the shoreline, and the locations of the three replicate seines that were randomly placed within distance-to-shore zones	106
Figure 4.2. Bar graphs illustrating the percentage contribution of each predictor variable to the total deviance explained in the abundance (A_{gam}) and occurrence (O_{gam}) generalized additive models	107
Figure 4.3. Additive effect smooth terms (y axis) of each covariate on <i>Farfantepenaeus duorarum</i> , <i>Lagodon rhomboides</i> and <i>Lucania parva</i> abundance model..	108
Figure 4.4. Additive effect smooth terms of each variable on <i>Lagodon rhomboides</i> (pinfish) probability of occurrence	109
Figure 4.5. Predicted <i>Farfantepaneaus duorarum</i> abundance (# of individuals * hectare) within the 9 simulated seascapes	110
Figure 5.1. Illustration of the study area within Biscayne Bay, SAV seascape map with the 100 x 500 m plots randomly located along the shoreline, and the locations of the four BRUVs and tethering replicates that were randomly placed within distance-to-shore zones	136
Figure 5.2. Illustration of the a) BRUVs design and b) sample video frames from one of the BRUVs	137
Figure 5.3. Mean (black dot) and standard error (bars) of the abundance (MaxN – max # of individuals*minutes ⁻¹) per site and for each functional group: invertivore/piscivore generalists (IvPi), invertivores of small prey (IvSm), mesopredators (MesoP)	138
Figure 5.4. Probability of shrimp predation with respect to distance-to-shore, seascape fragmentation, and soaking time of the tethered lines	139

Figure 5.5. Probability of occurrence of mesopredators (Mesop), invertivores of small prey (IvSm), and invertivore/piscivore generalists.	140
Figure 5.6. Time in view (TiV) and pecking rate (PRate) for Invertivores of small prey (IvSm) in relation to fragmentation levels and distance-to-shore for habitats with different SAV cover values.	141
Figure 5.7. Time in view (TiV) and pecking rate (PRate) for Invertivore/Piscivore generalists (IvPi) in relation to fragmentation levels (F) and distance-to-shore (D) for habitats with different SAV cover values.....	142

Chapter 1: Introduction and dissertation objectives

Seascape Ecology

Submerged aquatic vegetation (SAV) habitats composed of seagrass and macroalgae species, provide key ecological and economic services such as primary production, carbon sequestration, nutrient cycling, and sediment stabilization (Orth et al. 2006). In addition, these ecological engineers provide essential habitat for commercial and recreationally important fish and invertebrate species (Heck Jr. et al. 2003, Gillanders 2007). However, significant declines have been documented for SAV habitats worldwide, caused by a combination of human and natural stressors (Duarte 2002). To date, the majority of studies of SAV function, structure, and patterns of decline have focused their attention at a considerably fine spatial scale (meters to tens of meters) that is ecologically relevant for many fishes, and operationally meaningful for management (Pittman et al. 2011). At broader spatial scales, these habitats form distinct patch-mosaics, or seascapes (i.e., a spatially heterogeneous area composed of various discrete habitat patches – **Figure 1.1**) that are known to influence species abundance, diversity and connectivity (Bell et al. 2007). Here, I apply a seascape ecology approach to evaluate the role that broad-scale (up to 100s of m) spatial patterns of SAV seascapes have on:

- 1) the resistance and resilience of these habitats over long temporal scales (> 70 years);**
- 2) the structuring of associated faunal communities, and;**
- 3) the predation risk and predation patterns of abundant fish and crustacean species.**

My dissertation adopted concepts and spatial tools of seascape ecology, the marine counterpart of landscape ecology, to scale and address ecological questions to the study of marine seascapes. The application of landscape ecology concepts to the marine realm can provide new perspectives on the study and understanding of broad-scale spatial marine habitat dynamics (Robbins & Bell 1994b, Pittman & McAlpine 2003). For example, several studies have described how fish communities associated with mangroves, coral reefs, and salt marshes can respond to patchiness, fragmentation, and spatial heterogeneity of neighboring SAV habitats (Irlandi & Crawford 1997, Pittman et al. 2004, Mumby et al. 2004, Grober-Dunsmore et al. 2007). These studies suggest that heterogeneous SAV seascapes support diversity by enhancing recruitment and providing multiple resources needed to maintain different types of species, as well as influence the outcome of biological interactions such as competition, predation, foraging behavior. Nevertheless, there are still large knowledge gaps on the response of fish and crustaceans communities to SAV seascape characteristics across spatial and temporal scales, taxonomic groups, and ecological regions (Connolly & Hindell 2006, Boström et al. 2011).

Broad-scale structural attributes of benthic habitats (i.e., seascape spatial attributes) can influence the persistence, distribution, abundance, diversity, and trophic interactions of associated fauna by exerting control over resource availability by influencing functional connectivity and foraging behaviour of associated fauna (Fahrig 1998, Grober-Dunsmore et al. 2009, Villard & Metzger 2014). The spatial attributes of the SAV seascape that were explored here included habitat amount (proportion of the seascape occupied by SAV habitat or habitat extent) and configuration (patch density,

shape, clustering) of SAV patches within seascapes. Metrics quantifying habitat amount or composition are commonly used to document habitat loss or gains, whereas metrics of configuration are used to quantify the patterns of habitat fragmentation (**Figure 1.2**).

These two types of metrics are rarely evaluated separately in seascape ecology studies, and their relative importance as drivers of ecological processes, community composition and abundance, and species persistence is a current topic of debate. Changes in habitat amount (habitat loss) and configuration (fragmentation) can occur simultaneously (Haila 2002, Fahrig 2003) and their effects are often confounded (Smith et al. 2009)(**Figure 1.3**). Moreover, many studies have failed to address the relative and interrelated ecological effects of both types of spatial habitat properties (Smith et al. 2009, Didham et al. 2012, Villard & Metzger 2014). In this dissertation, SAV amount and configuration within the seascape were explicitly quantified to provide an efficient way to assess the relative and interrelated effects of habitat loss and fragmentation on the spatial and temporal dynamics of SAV seascapes, and the abundance and distribution of associated fish and crustacean species.

Another important knowledge gap in the emerging field of seascape ecology is the understanding of the role of patch-mosaic attributes on the relationship between organisms and habitat spatial properties. The majority of seascape ecology studies have focused on the faunal response to individual patch attributes (e.g., edge, size, perimeter:area ratio), while only a few studies have assessed faunal responses from the patch-mosaic perspective used in this dissertation (Boström et al. 2011)(**Figure 1.4 – patch vs patch-mosaic perspective**). Biased conclusions have likely been made in studies that have inferred landscape patterns and ecological responses from patch-scale data

(McGarigal & Cushman 2002, Didham et al. 2012). For example, patch-scale studies have implicitly attributed all variance in faunal response to habitat fragmentation by ignoring the interdependence of habitat amount and configuration; thus, providing results that do not reflect the actual spatial structure of target populations. Habitat fragmentation is a process that occurs at the seascape level, and in the end, the effects of habitat fragmentation can be only understood at this level, and not at the patch level (McGarigal & Cushman 2002). Therefore, emphasis was given here to the patch-mosaic perspective when designing my dissertation studies to separate the effects of habitat amount and habitat configuration on SAV-associated faunal responses.

When assessing the response organisms to habitat fragmentation, the range, also known as ecological neighborhood, over which the organism moves during usual activities should be considered to determine the appropriate spatial scale or extension (e.g., 100s m² to hectares) to assess organism-habitat relationships (McGarigal & Cushman 2002, Pittman & MacAlpine 2003). In addition, different mechanisms controlling species abundance, distribution and persistence may be hierarchically structured operating over a range of spatial resolutions (e.g., seascape characteristics vs patch structural/complexity characteristics) (Pittman et al. 2004). Therefore, a broader multi-scale approach is necessary to observe any possible relationship between seascape characteristics and fish metrics (Pittman et al. 2004, Mellin et al. 2009). This dissertation integrated multi-scale approaches to address the spatial scaling of organism-seascape relationships in Biscayne Bay (**Figure 1.5**).

Biscayne Bay and the Comprehensive Everglades Restoration Plan

My dissertation work concentrated in Biscayne Bay, a shallow subtropical lagoon adjacent to the city of Miami (population 2.5 million) and downstream of the Florida Everglades. The natural hydrology of the Biscayne Bay watershed was modified with the construction of the Central and Southern Florida Project (CS&F) water-drainage system completed in the 1960s (Browder & Ogden 1999). This modification has caused changes in the salinity regimes of the bay that are, in turn, linked to significant changes in the SAV community composition and distribution (Lirman et al. 2014) and SAV seascape characteristics (Santos et al. 2011). Nearshore habitats of Biscayne Bay, including seagrass meadows and mangrove forests, will be directly affected by the activities of the Comprehensive Everglades Restoration Plan (CERP), which plans to modify the delivery of freshwater from the Everglades into the coastal bays of South Florida (Caccia & Boyer 2005). The nearshore SAV seascapes are of special concern within the restoration framework since these are the areas presently exhibiting the widest fluctuations in salinity and where the impacts of restoration projects would be concentrated. Consequently, it is essential to understand the functional linkage between habitats, as well as how seascape properties influence the abundance, distribution, and diversity of associated marine and estuarine organisms to quantify, mitigate, and manage the ecological implications associated with CERP activities.

Dissertation Objectives

A seascape approach that incorporates theories and tools of landscape ecology was designed with the purpose of: **(1) developing novel methods to assess the spatio-**

temporal trends of SAV habitat fragmentation independently of habitat loss (Chapter 2), (2) use SAV seascape dynamics in Biscayne Bay as a case study to understand how patterns of habitat loss and fragmentation relate to watershed management (Chapters 2 and 3), and (3) determine how SAV seascape patterns may have cascading effects on the abundance, distribution, and predator-prey interactions of fish and crustacean communities (Chapters 4 and 5).

The dissertation research chapters followed a hierarchical design with three levels of study (**Figure 1.6**). Chapter 2 is considered to be the "upper level" or "pattern level" since it addresses the dynamics of spatial parameters that provided context to the data and analyses presented in the subsequent chapters. Chapters 3 and 4 were the "focus level" of the dissertation, and they explored the ecological responses of fish and crustaceans to the spatial patterns described in Ch 2. Using different seascape approaches, both faunal response chapters, addressed how fish and crustacean species distribution, diversity and assemblage structure responded to habitat amount and configuration within nearshore SAV seascapes. Chapter 5 was designed as a lower explanatory level that explored the "why" of the patterns described in Ch 3 and 4. Chapter 5 employed survey sampling and experimental design to test the predation model as a main mechanism behind the responses to seascape properties.

Chapter 2 was designed to meet the first two objectives of this dissertation. A long-term analysis of SAV seascape characteristics was conducted over a 70-year period to: 1) develop novel methods to assess the spatio-temporal trends of SAV habitat fragmentation independently of habitat loss; and 2) use SAV seascape dynamics in Biscayne Bay as a case study to understand how patterns of habitat loss and

fragmentation relate to water quality and watershed management. A fragmentation index was developed to quantify temporal trends of SAV seascape fragmentation, and compare them to trends in habitat loss. This was performed using archived black and white aerial photographs that were subject to different analysis approaches such as overlapped analysis in GIS, quantification of spatial pattern metrics, and ordination and vector analyses.

The following two research chapters (Chapter 3 and 4) explored the nature of the ecological responses of SAV-associated fauna to spatial properties of SAV seascapes found in nearshore areas of Biscayne Bay. In both chapters the fish and crustacean community associated with SAV seascapes were sampled nocturnally seines deployed following a stratified random design. In Chapter 3, a binary patch-mosaic approach was employed to compare fish and crustacean community assemblages and diversity between spatially continuous and fragmented SAV seascapes. The ultimate goal of this effort was to identify and quantify potential linkages among water management practices, seascape fragmentation, and cascading effects on marine fauna. This study was used as an example of the classic factorial analysis used to assess faunal responses to habitat fragmentation (Fahrig 2003, Boström et al. 2011). In contrast, the study in Chapter 4 used the abundance of the most prevalent fish and shrimp species in the bay as test subjects to examine in detail the relative and interrelated effects of habitat amount and configuration on the abundance and distribution of species with economic and ecological importance. Detailed mapping of the SAV seascape and collections of fish and shrimp were combined to document species-specific responses to seascape characteristics and to determine whether habitat amount and configuration thresholds exist for key epibenthic species

associated with seagrass habitats. In addition, field data and statistical models were combined to develop simulation scenarios and evaluate the response of pink shrimp (*Farfantepenaeus duorarum*) to changes in habitat amount and configuration under different SAV community assemblages associated to distinct salinity environments (i.e., halohabitats). This simulation exercise was conducted to reveal the spatial SAV seascape characteristics that may sustain pink shrimp population under expected halohabitats influenced by water management actions in South Florida as part of the Comprehensive Everglades Restoration Plan (CERP).

The final data chapter of this dissertation (Chapter 5) examined possible mechanisms behind the faunal response patterns observed in Chapter 3 and 4. Predation and predation-risk effects were hypothesized as key mechanisms generating patterns in fish and crustaceans abundance in relation to habitat amount and configuration. This chapter combined two field experiments to assess the occurrence of predators across the seascapes, the relative predation rate on a small prey, and to determine how predation risks influence food harvesting and safety behavior of foragers and how these interact with seascape features.

Key Findings and Implications for Management

This dissertation focused on the faunal responses and interactions with seascape composition and configuration in Biscayne Bay, Miami, Florida, U.S.A., where nearshore habitats are subjected to environmental changes associated with the Everglades Restoration activities, thereby providing a direct test of the impacts of biological and human interactions at the seascape level. The results of this dissertation will provide an

understanding of the temporal resolution at which large-scale seascape characteristics respond to environmental factors influenced by coastal management decisions. In addition, these findings could determine priorities for conservation planning in response to seagrass habitat loss and fragmentation. More importantly, the outcome of this research will help explain how future impacts of restoration and management activities may affect optimal seascape types and determine whether critical ecological thresholds could be exceeded in nearshore habitats of Biscayne Bay; and how possible disruption to ecological thresholds could influence (positively or negatively) the functional connectivity within the mangrove-seagrass ecotone.

Figure 1.1. Illustration of a vegetated seascape, a spatially heterogeneous area composed of various discrete habitat patches. The map in the right shows different types of delineated habitat patches (dense SAV cover - green, intermediate SAV cover - yellow and sparse SAV cover - red) that constitute this vegetated seascape

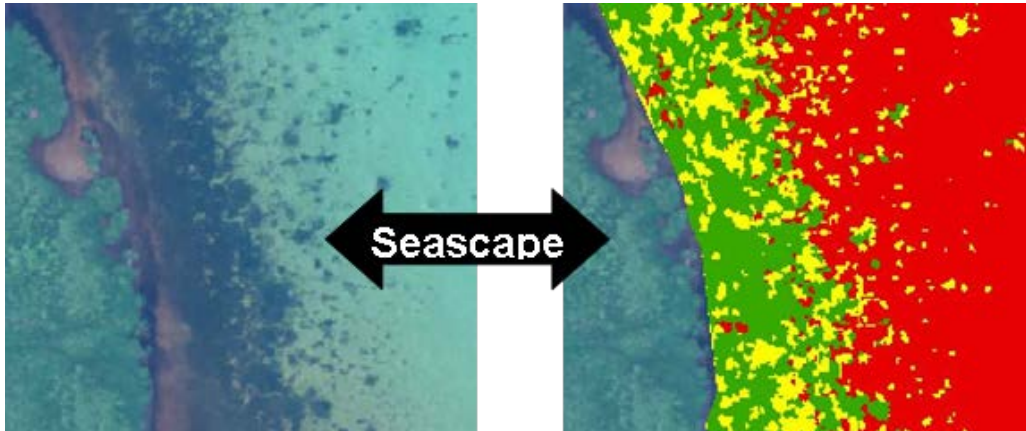


Figure 1.2. Illustration of metrics used to quantify habitat amount (a) and configuration (c). Changes in habitat amount and configuration depict habitat loss (b) and fragmentation (d), respectively. For example, in (b) habitat loss resulted from the reduction in area of the figures in (a) (dotted line equal to the original print of the figures to the left). In contrast, habitat fragmentation in (d) resulted from the splitting and perforation of the figures in (c)

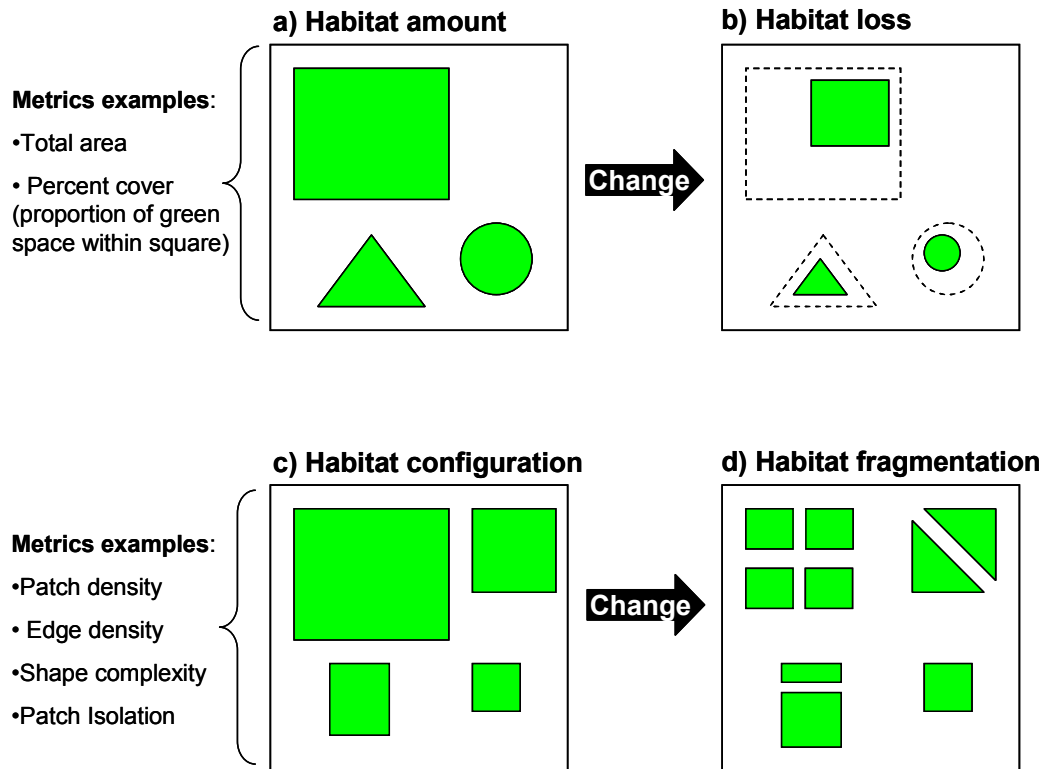


Figure 1.3. Illustration of habitat loss (y axis, dashed line) and fragmentation (x axis, solid line). Habitat patches appear in black. Habitat loss and fragmentation most often occur simultaneously (diagonal dotted line).

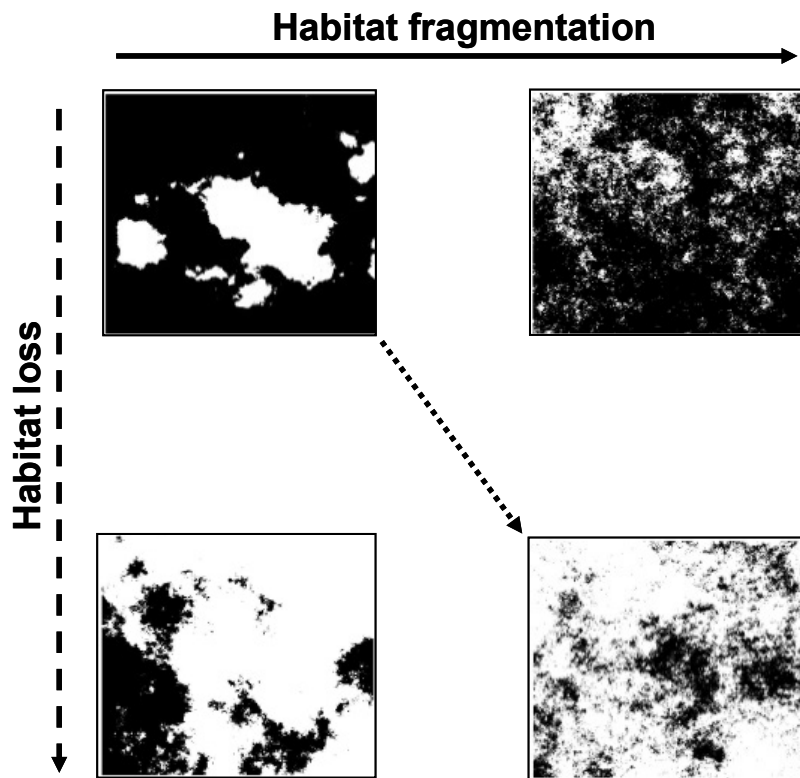


Figure 1.4. Illustration of a seascape analysis with patch (a) and patch-mosaic (b) perspectives. Red dots and black x illustrate sampling points. In a patch perspective, faunal responses (Y_i) are compared between patches (p_i) with different characteristics (e.g., area, shape, perimeter-area ratio) or between habitat core (dot) and edge (x) (right panel). In contrast, in a patch-mosaic perspective, faunal responses (Y_i) are explored between different seascapes (S_i) with distinct amounts and arrangement of patches or within the organisms' home range (dashed circles).

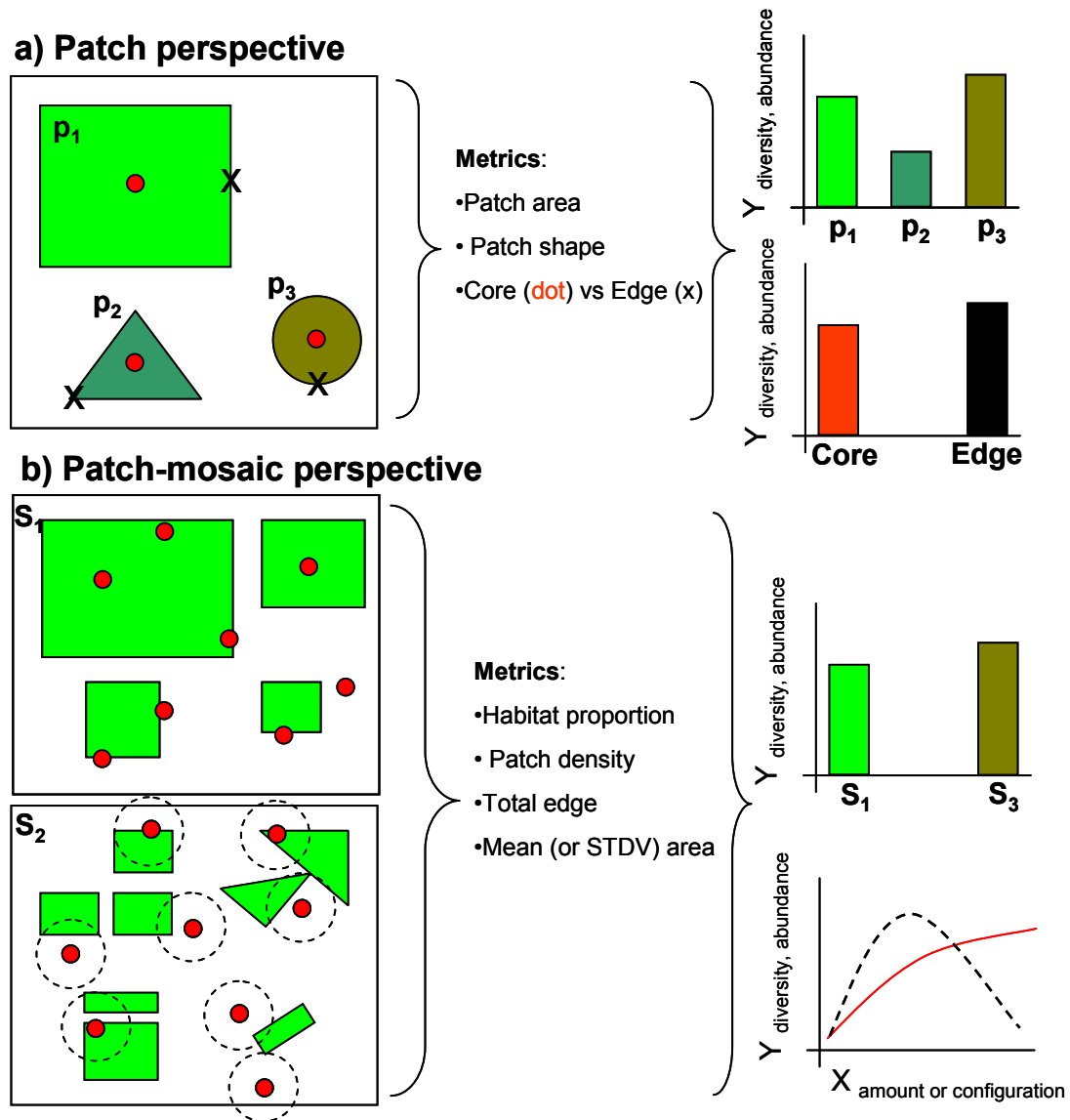


Figure 1.5. Illustration of a seascape multiscale approach. Faunal responses could be a function of seascape characteristics within different spatial extents (seascapes within different radii –50, 100 or 150m) and/or within patch structural properties (within-patch level –percent cover of seagrass and macroalgae, canopy height).

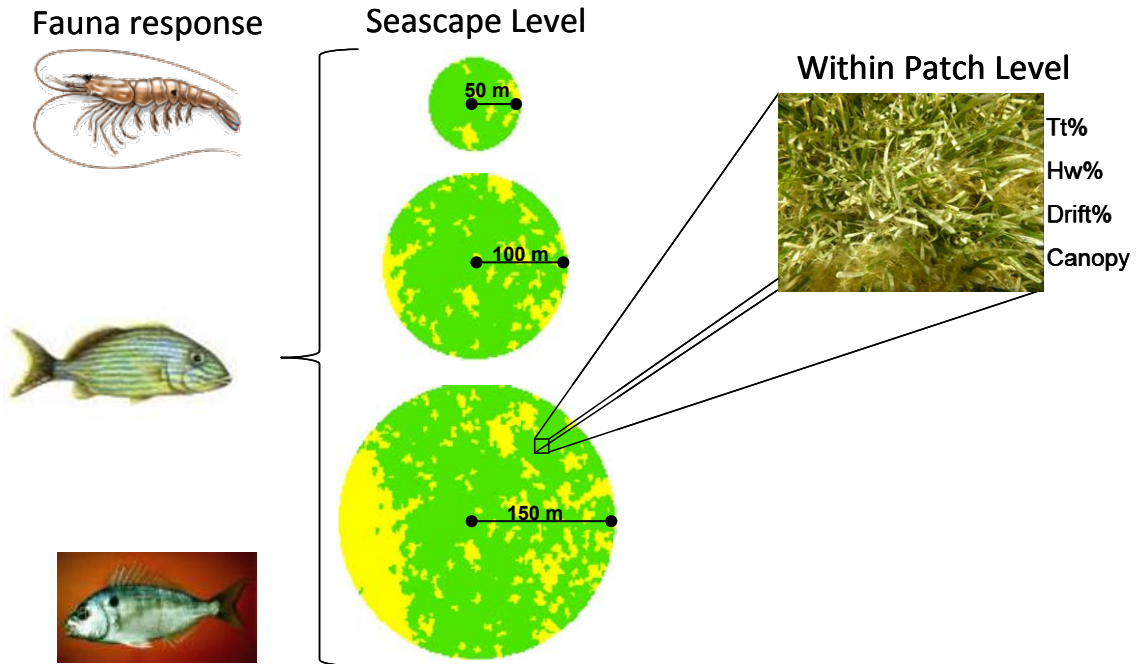
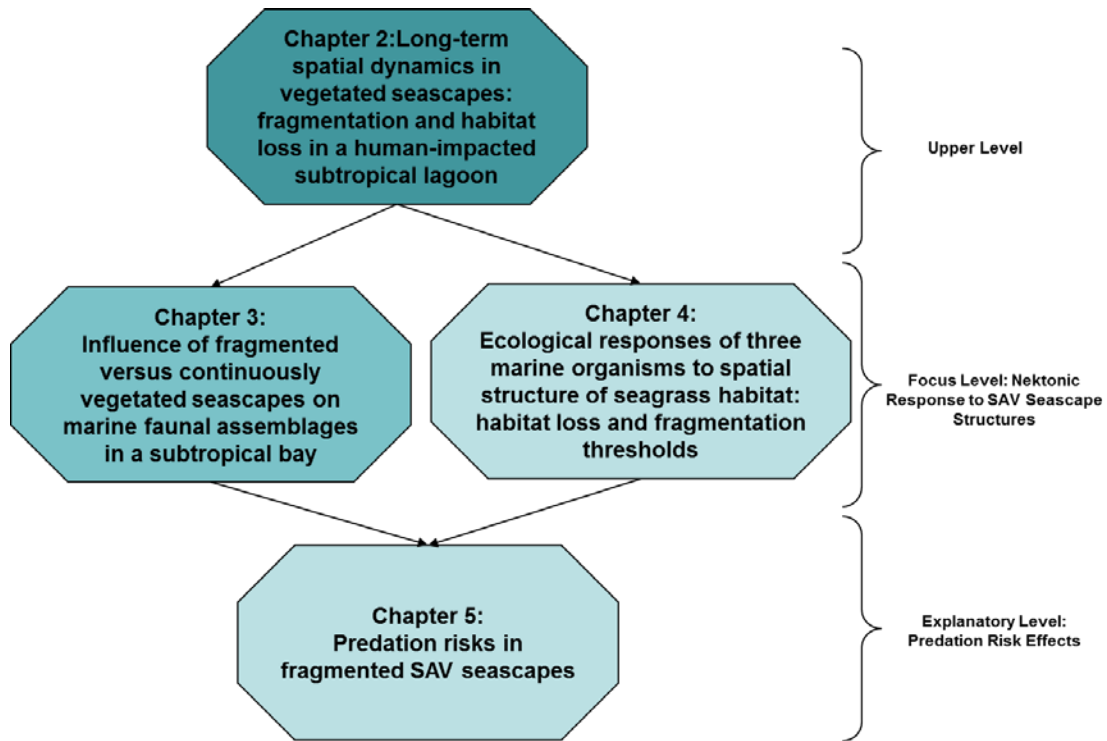


Figure 1.6. Conceptual diagram of the hierarchical structure of this dissertation. The first data chapter (Ch. 2) explores the spatio-temporal variability of vegetated seascape properties. The chapters at the focus level (Ch. 3 and 4) were designed to study the faunal responses to the seascape patterns observed in Chapter 2. The last data chapter (Ch. 5) was designed to investigate whether predation risk effects are the main mechanism behind the patterns observed at the focus level.



*Adapted from: Turner et al., 2001

Chapter 2: Long-term spatial dynamics in vegetated seascapes: fragmentation and habitat loss in a human-impacted subtropical lagoon

Summary

Vegetated coastal seascapes exhibit dynamic spatial patterning, some of which is directly linked to human coastal activities. Human activities (e.g., coastal development) have modified freshwater flow to marine environments, resulting in significant changes to submerged aquatic vegetation (SAV) communities. Yet, very little is known about the spatially complex process of SAV habitat loss and fragmentation that affects ecosystem function. Using habitat mapping from aerial photography spanning 71 years (1938-2009) for Biscayne Bay (Florida, USA), I quantify both SAV habitat loss and fragmentation using a novel fragmentation index. To understand the influence of water management practices on SAV seascapes, habitat loss and fragmentation were compared between nearshore and offshore locations, as well as locations adjacent and distant from canals that transport freshwater into the marine environment. Habitat loss and fragmentation were significantly higher along the shoreline compared to offshore seascapes. Nearshore habitats experienced a net loss of 3.31% of the total SAV mapped (2.57 km²) over the time series. While areas adjacent to canals had significantly higher SAV cover, they still experienced wide fluctuations in cover and fragmentation over time. All sites exhibited higher fragmentation in 2009 compared to 1938, with four sites exhibiting high fragmentation levels between 1990s and 2000s. I demonstrate that freshwater inputs into coastal bays modify the amount of SAV and the fragmentation dynamics of SAV habitats. Spatial changes are greater close to shore and canals indicating that these coastal developments have transformative impacts on vegetated habitats, with undetermined consequences for the provisioning of ecosystem goods and services.

Background

Submerged aquatic vegetation (SAV) assemblages composed of seagrasses and macroalgae are keystone components of coastal benthic ecosystems where they provide important ecological, societal, and economic services (Orth et al. 2006, Barbier et al. 2011). SAV assemblages are known to significantly contribute to carbon sequestration (Duarte et al. 2005), provide food and shelter to economically and ecologically important species (Gillanders 2007), and are essential habitat for endangered marine species such as the green turtle (*Chelonia mydas*), West Indian manatee (*Trichechus manatus*) and dugongs (*Dugon dugon*) (Hemminga & Duarte 2000). SAV habitats also influence water quality by the uptake of nutrients and the deposition and binding of sediments (Koch et al. 2007a), and facilitate organic, inorganic, and trophic transfers to adjacent habitats such as salt marshes, mangroves, and coral reefs (Davis et al. 2014, Hyndes et al. 2014). Thus, SAV habitats are essential for the resilience of marine and estuarine ecosystems, and the growth, development, and survival of juveniles and adult populations of key marine taxa (e.g., herbivorous fishes, apex predators) (Gillanders et al. 2003, Mumby et al. 2004, Olds et al. 2012). In this study, I use a unique data-set of aerial images from 1938-2009 to evaluate historical patterns of change in SAV communities of Biscayne Bay, Florida, USA, and determine whether water management actions have influenced the extent (cover) and spatial pattern (fragmentation) of SAV seascapes.

Like other coastal ecosystems (i.e., coral reefs, mangroves), SAV communities have experienced significant global declines in the recent past as a consequence of anthropogenic disturbances (Waycott et al. 2009). Seagrass habitats have disappeared worldwide at a rate of $110 \text{ km}^2\text{yr}^{-1}$ between 1980 and 2006 (Waycott et al. 2009), with an

estimated 14% of seagrass species experiencing an elevated risk of extinction (Short et al. 2011). Declines in SAV abundance worldwide are mostly caused by water quality degradation, especially due to nutrient loading and sediment runoff (Fourqurean & Robblee 1999a, Duarte 2002, Santos et al. 2011). Other disturbances such as thermal pollution, dredging, vessel grounding, and boat propeller scaring have also been associated with significant SAV losses (Orth et al. 2006).

Concepts and analytical techniques developed in terrestrial landscape ecology provide a framework that can be readily applied to assess broad-scale SAV patterns and disturbance impacts (Wedding et al. 2011). A benthic seascape, analogous to a terrestrial landscape, is applied here to describe a spatially heterogeneous area of the seafloor composed of various discrete habitat patches (Grober-Dunsmore et al. 2009, Pittman et al. 2011). The degradation and transformation of SAV seascapes may be characterized by two main aspects: habitat loss and fragmentation. The former is the reduction in the amount or the proportion of habitat occupied by SAV within the seascape, while the latter refers to the breaking apart of large, continuous patches into smaller units. Both habitat loss and fragmentation change the spatial arrangement of the seascape. A growing body of evidence, mostly from terrestrial landscape ecology, has demonstrated distinct ecological impacts of habitat loss and fragmentation (Fahrig 2003, McGarigal et al. 2005, Liao et al. 2013). The terrestrial ecology literature suggests that the effects of habitat fragmentation are generally much weaker than the effects of habitat loss (Fahrig 2003); however, critical thresholds for organisms and ecosystem function will vary depending on the system (Andren 1994, Pardini et al. 2010). For example, negative effects of habitat loss and fragmentation on forest patches are dependent on the dispersal strategies,

intraspecific competition, and growth rates of organisms (With & Crist 1995, Bonte et al. 2010, Liao et al. 2013), which in turn have the potential to change the species composition, successional stages, and local extinction rates of plant species (Laurance et al. 2006, Pütz et al. 2011). While planning for conservation, these two processes of habitat degradation should be quantified separately since they can be managed independently with different restoration approaches (e.g., conserving large areas versus many small areas), and their effects on populations and biodiversity may differ in magnitude and direction (Ewers & Didham 2006a, Smith et al. 2009).

Habitat loss and fragmentation studies in marine ecosystems are relatively rare (Boström et al. 2011). Both of these types of degradation can have either independent or interactive effects on the resilience and persistence of SAV and influence faunal connectivity among habitats, species diversity, and ecological interactions (e.g., competition, predation, foraging behavior)(Irlandi & Crawford 1997, Hovel & Lipcius 2001, Fahrig 2003). Until recently, historical mapping and monitoring studies have concentrated on changes in the areal extent of SAV (i.e., habitat loss or recovery), largely ignoring spatial configuration and fragmentation and how these may influence seagrass ecology (Cunha & Santos 2009, Santos et al. 2011, Cuttriss et al. 2013). Here, using a historical record of >70 years (1938 to 2009), I quantified, independently, habitat loss and fragmentation to provide a better understanding of how SAV seascapes respond to anthropogenic disturbances such as the modification of freshwater deliveries.

In Biscayne Bay, Florida, SAV seascapes are influenced by water-management practices that regulate freshwater discharges into littoral areas. Over the last 50 years, the hydrology of the South Florida watershed has been modified by the construction of a

massive water management system that has altered the quantity, quality, and delivery method of fresh water into the coastal bays (Browder & Ogden 1999). The modifications to the watershed hydrology have resulted in significantly lower total freshwater delivery, a reduction in the proportion of fresh water delivered through overland sheet flow and groundwater sources, and a switch from historical diffuse deliveries to pulsed, point-sources of discharge through man-made canals (Wang et al. 2003, Lirman et al. 2008b, Stalker et al. 2009). These hydrological modifications have affected the abundance and composition of Biscayne Bay's nearshore SAV communities. For example, previous research has shown that abundance and plant species composition of SAV are directly related to salinity patterns, with areas of low and highly variable salinity (i.e., adjacent to canals that discharge fresh water) exhibiting lower SAV abundance and high variability in percent cover (Lirman et al. 2008b). Applying a landscape ecology approach, Santos et al. (2011), observed distinct SAV seascape structures related to salinity regimes using data from only one year and one season. As a significant expansion of this previous research, a temporal change-analysis of SAV seascape characteristics was conducted over a 70-year period to: 1) develop novel methods to assess the spatio-temporal trends of SAV habitat fragmentation independently of habitat loss; and 2) use SAV seascape dynamics in Biscayne Bay as a case study to understand how patterns of habitat loss and fragmentation relate to watershed management. I hypothesize: (H¹) a significant regional decrease in SAV habitat cover and increase in SAV seascape fragmentation over the 71 year study period; (H²) Seascapes in close proximity to shore and canals experience greater loss of SAV and fragmentation than more distant seascapes; and (H³) Seascapes

in close proximity to canals experience more dynamic patterns of SAV habitat cover and fragmentation than more distant seascapes.

Materials and Methods

Study site

The study area was the western shoreline of Biscayne Bay, Florida (**Figure 2.1**), a shallow subtropical lagoon adjacent to the city of Miami (population 2.5 million) and downstream of the Florida Everglades. The natural hydrology of the Biscayne Bay watershed was modified with the construction of the Central and Southern Florida Project (CS&F) water-drainage system completed in the 1960s (Browder & Ogden 1999). The Comprehensive Everglades Restoration Plan (CERP) has been designed, in part, to recover the natural and historical hydrology of the Everglades and coastal lagoons of South Florida. CERP has specific goals to restore the amount of fresh water reaching Florida and Biscayne Bay, as well as to modify the way the fresh water is delivered (Light & Dineen 1994, McIvor et al. 1994, Browder & Ogden 1999). The nearshore SAV seascapes are of special concern within the restoration framework since these are the areas presently exhibiting the widest fluctuations in salinity and where the impacts of restoration projects would be concentrated.

Study design

Six sites were selected along the western shore of central Biscayne Bay (**Figure 2.1**). The study sites were divided into two types: 1) "Distant" from freshwater canals (N = 3, mean distance to canal = 2.77 km \pm 0.94), and 2) "Adjacent" to freshwater canals (N = 3 sites, mean distance to canal = 0.54 km \pm 0.10). The canals adjacent to survey sites

were: Snapper Creek, Black Point, and Mowry Canal. These canals have high discharge rates (average flow of 4 m³/sec; SFWMD-DBHYDRO, Browder et al. 2010), and were constructed >50 years ago, resulting in long-term patterns of discharge. There are other sources of fresh water (e.g., natural creeks, groundwater seepages) for Biscayne Bay; however, the freshwater contribution of these sources have been significantly reduced over the years (Caccia & Boyer 2005, Stalker et al. 2009). Freshwater pulses from man-made structure haven been linked to changes in the salinity and nutrients regimes of the bay (Caccia & Boyer 2005).

Following Santos et al. (2011), sites adjacent to canals were located in close proximity to canals with the largest average discharge rates. The sites distant from canals were randomly selected along the shoreline, but were all located >1 km² from a canal. Within sites, the habitats were further divided into shoreline (< 200 m from shore) and offshore (> 200 m) based on previous work that identified the shoreline habitats as areas with significantly lower and more variable salinity (Santos et al. 2011, Lirman et al. 2014). For the historical analyses, 9 representative periods, 5-10 years apart, were selected from aerial photographs collected from 1938-2009 (**Appendix A1**). The selection of specific years for analysis was based on the availability and quality of the aerial imagery.

Benthic habitat mapping

Image processing

The SAV seascape maps for each year were created using high-resolution, digital black and white aerial photographs obtained from digital archives held by federal and

state agencies digital archives (**Appendix A1**). All imagery was first processed to standardize the resolution, optical properties, and area of sampling, and then geo-rectified using the USGS topographic map as a spatial reference. The resolution of all aerial photographs was re-sampled to 1-meter pixel size, and histogram equalization and convolution filtering technique was applied to control for the contrast and textural optical variability between years and sites. The majority of the aerial photographs had 1 m pixel size, but the most recent years (1991-2009) had 0.35 m pixel size (Appendix A1); therefore, the most recent years were re-sampled to 1 m to standardize the mapping procedure. The 1-m resolution still provided adequate pixel size to delineate even the smaller patches observed. Like the filtering technique, the resampling of the aeriels helped in the smoothing of the image and therefore in the reduction of noise and salt-pepper effects. Finally, a 500-m radial buffer was used to extract and standardize the area mapped for each site. A radius of 500 m was used since this distance includes the extent of the nearshore habitats where the influence of the CERP canals and projects will be concentrated (Lirman et al. 2008a, Lirman et al. 2008b).

Mapping procedure

SAV seascape maps were created by hand-digitizing and delineating individual SAV patches. The digitization procedure was standardized by setting all photographs to a 50% contrast level and a 1:2,500 scale, with a minimum mapping unit of 20 m² (the size of the digitization cursor). Seagrass patches were manually digitized because the optical properties (i.e., brightness, tone, texture) varied significantly within and between photographs. The contrast level used to analyze the photographs clearly highlighted patches with dense SAV cover (> 50% cover), which facilitated the digitization process

and reduced misclassification. All photo interpreters (N = 3) were trained to follow a set of digitization rules to limit variability among observers/interpreters. In addition, all preliminary maps were subjected to quality assessment by the lead interpreter using the digitization rules and by comparing preliminary maps to a computer automated classification. The availability of ground-truth points was scarce since the majority of the images were taken before 2005 when the nearshore seagrass monitoring program was initiated in Biscayne Bay (Lirman et al. 2008a, Lirman et al. 2008b). Prior spatial accuracy using ground validation surveys showed that this mapping procedure produced classified benthic maps with a spatial accuracy of 60-80% (Santos et al. 2011). Similar studies have used archived aerial photographs to monitor seascape changes in nearshore areas with high thematic accuracy (Sheppard et al. 1995; Zharikov et al. 2005). The total area of seagrasses mapped within 6 sites was 2.57 km², with a mean area per site of 0.43 km² (± 0.16 SD).

Spatial-pattern analysis

Spatial-pattern metrics

Spatial-pattern metrics provide quantitative information that measure and describe the spatial patterning of seascapes and can be grouped broadly into two categories: those that quantify the composition of the patch mosaic, and those that quantify the configuration or spatial arrangement of seascape elements (McGarigal & Cushman 2002, Wedding et al. 2011). Metrics quantifying seascape composition are used to document habitat losses and gains, whereas metrics of configuration are used to assess habitat fragmentation. Spatial-pattern metrics were applied to benthic habitat maps with the software FRAGSTATS v4

(McGarigal et al. 2012) to quantify the spatial composition (percentage cover) and configuration (fragmentation) of SAV seascapes (**Table 2.1**). As recommended by Sleeman et al. (2005) and McGarigal et al. (2005), patch density (PD), landscape division (LD), area-weighted mean perimeter to area ratio (AWMPAR), and mean radius of gyration (GYRATE_MN) were selected here to quantify the spatial configuration of SAV patches and measure the rate of SAV seascape fragmentation over time. These metrics quantify four distinct characteristics of spatial pattern: habitat size, compactness, habitat subdivision, and habitat geometry (McGarigal et al. 2005)(**Table 2.1**) and are robust across spatial scales (i.e., grain and/or extent size)(Wu et al. 2002, Wu 2004), total areal coverage and aggregation of the target habitat (Neel et al. 2004, Sleeman et al. 2005, Cushman et al. 2008), and have been utilized previously to assess the effects of SAV seascape fragmentation on tropical and temperate fish and invertebrate species (Hovel & Lipcius 2001, Salita et al. 2003, Boström et al. 2011).

Habitat loss and fragmentation patterns

Spatio-temporal patterns in metric values were explored and analyzed using principal component and vector analyses followed by linear regression models.

An index of area change (G) (RW.ERROR - Unable to find reference:281) was applied to quantify the proportion of the total area of SAV either lost or gained between two consecutive sampling periods. G was calculated as follows:

$$G = (\text{area lost} + \text{area gained}) / (\text{area lost} + \text{area gained} + \text{area unchanged})$$

The index, which ranges from 0 (no change) to 1 (a complete change in SAV area with either 100% lost or gained), is used to quantify changes in seascape composition independent of measurements of spatial configuration.

The configuration metrics used to quantify fragmentation were analyzed using two approaches: 1) a multivariate principal component analysis (PCA) followed by a vector analysis (VA) to examine the contribution of each metric to fragmentation patterns, as well as the magnitude of fragmentation between consecutive sampling periods; and 2) a simple metric of fragmentation, the "fragmentation index" as described below:

Multivariate Analyses: The multivariate data (i.e., values for the 4 seascape metrics) calculated for each site and time interval were used in a PCA ordination. The coordinates of each site within the PC1 and PC2 plane were used to measure the direction and length of the vector connecting sites between consecutive sampling periods. The resulting vectors were used to measure the magnitude (i.e., length of vector) and direction (i.e., movement towards fragmentation or expansion/clustering, referred hereafter as defragmentation) of change in SAV seascape state between intervals (**Appendix A2**). The vector length was standardized by the number of years elapsed between images. Lastly, a hierarchical cluster analysis (CA) was used to discern robust groupings of sites/years that shared similar values of the metrics used to evaluate spatial and temporal patterns of SAV fragmentation. The CA was performed using the Euclidean dissimilarity matrix of the PCA scores of each site/year. The PCA and CA were performed in PRIMER v6.

Fragmentation Index: Since the four spatial-pattern metrics used quantify different aspects of spatial properties (habitat size, compactness, habitat subdivision, and habitat geometry), these metrics were integrated into a single fragmentation index for simplicity. By developing a single fragmentation index, a simpler temporal analysis can be used to assess the trajectory of SAV seascapes. Similar approaches have been used previously to assess the effects of fragmentation on species diversity, probability of occurrence, and abundance of terrestrial and marine species independent of habitat loss (McGarigal & McComb 1995, Trzcinski et al. 1999, Kaufman 2011). The metrics used here were collapsed into the following fragmentation index (FragIndex):

$$\text{FragIndex} = \sqrt[4]{(\text{PD} * \text{LD} * \text{AWMPAR} * 1 / \text{Gyrate_MN})}$$

All metrics were standardized to produce a FragIndex ranging from 0 (low fragmentation) to 1 (high fragmentation).

Statistical analyses were performed using JMP v10. A Shapiro-Wilk test on the dependent variables was used to test for normality and check for other assumptions of parametric analyses. Variables were Box-Cox transformed when the normality test failed. One-way analyses of variance (ANOVA) were used to test for differences in the index of relative change, fragmentation index, and changes in SAV composition between areas distant and adjacent to freshwater canals (testing for H^1 and H^3). Analyses of covariance (ANCOVA) were used to evaluate differences in loss of SAV and SAV seascape fragmentation between areas distant and adjacent to freshwater canals (testing for H^2).

Results

SAV cover and SAV seascape fragmentation

A regional decrease in SAV cover and transition to a more fragmented SAV seascape was detected (PCA results below). A net amount of 0.085 km² of SAV was lost across all sites over the whole study period (1938 – 2009), representing a loss of 3.31% of the total SAV mapped (2.57 km²) (**Table 2.2**). Areas adjacent to freshwater canals showed higher average net loss than areas distant from canals. Two of the three sites adjacent to canals, BP and SC, had a net loss of 11.4% and 11.5% respectively. Unexpectedly, the highest net loss (17.8%) was recorded for BL, one of the sites distant from canals. Two of the three distant sites, CK and TP, presented net gains of 1.2% and 9.9% (**Table 2. 2**). No statistics were performed to test for the significant of this pattern due to the limited number of sites examined.

The PCA based on the spatial-pattern metrics selected to describe the fragmentation of SAV habitats (e.g., PD, LD, AWMPAR, and GYRATE_MN) showed that 91% of the variation in SAV spatial configuration was explained by the first two principal components (**Table 2.3, Appendix A3** in supplementary material). The first PC explains 71% of the variation, and separate sites based on the level of fragmentation, with higher values representing higher fragmentation (**Table 2.3**). This first axis was positively correlated with PD, LD, and AWMPAR, which indicate, respectively, an increase in the number of patches, the probability that two randomly selected locations within the seascape are not situated in the same contiguous habitat patch, and the shape complexity of the patches. GYRATE_MN was negatively associated with PC1 since an

increase in this metric represents an increase in continuity or structural connectedness of the patches. Using a cluster analysis and the scores on the first PC, the PCA biplot was divided into three regions representing low, medium, and high fragmentation (**Figure 2.2 and Appendix A3**). All sites exhibited higher fragmentation in 2009 compared to 1938, with four sites exhibiting highest fragmentation levels between 1990s-2000s (**Figure 2.2**).

Temporal trends in SAV cover and fragmentation

SAV cover decreased significantly over time, while fragmentation increased significantly over time (**Figure 2.3**). Contrary to what I hypothesized, the rates of change (i.e., slopes of the fitted lines) of fragmentation and SAV cover were not statistically different between the canal adjacent and distant treatments (ANCOVA, $p > 0.05$) (**Figure 2.3**). However, when the metrics were separated into shoreline (0-200 m) and offshore buffers (200-500 m), there was a significantly higher rate of habitat loss and fragmentation in shoreline habitats compared to offshore habitats (**Figure 2.4**). Within the shoreline buffer, sites adjacent to canals had higher rates of habitat loss and fragmentation; however, the difference between the canal adjacent and distant treatments was not statistically significant.

SAV loss and fragmentation dynamics

Looking only at the initial and final values spanning a >70-year interval masks the highly dynamic changes that have taken place between decades that show that the SAV seascape along Biscayne Bay's western shoreline is indeed influenced by the presence of freshwater canals and the historical transformation of the bay's salinity regimes. While

areas adjacent to canals had, on average, significantly higher SAV cover (one-way ANOVA, $p < 0.05$), the temporal changes in the amount of SAV were significantly more dynamic in these areas, as illustrated by the higher relative change index in sites adjacent to canals (one-way ANOVA, $p < 0.05$) (**Figure 2.5a**). This is further illustrated by the significantly higher proportion of SAV habitat that was lost and gained in areas adjacent to canals (one-way ANOVA, $p < 0.05$) (**Figure 2.5b**).

The vector analysis measured the magnitude of fragmentation (black vectors pointing right within the PCA biplot) and defragmentation (grey vectors pointing left) between sampling intervals adjusted by the number of years between images (**Figure 2.3**). The magnitude of fragmentation and defragmentation (black and gray vectors) was not significantly different (**Figure 2.6**), thus explaining the limited net change in SAV cover recorded over the > 70 year record (**Table 2.2**). However, the magnitude of both vectors was significantly higher (two-way ANOVA, $p < 0.05$) in areas adjacent to canals (**Figure 2.6**), indicating more spatially dynamic conditions within these areas.

Discussion

Our analysis of the structure of nearshore SAV habitats of Biscayne Bay, Florida, USA over a 71-year time period has shown declines in SAV cover and increases in seascape fragmentation for this highly modified coastal lagoon located adjacent to the city of Miami. However, the net loss in SAV cover was relatively low (approx. 3%) across the study period (1938-2009). This is in clear contrast to recent reports of significant declines in worldwide seagrass abundance (Duarte 2002, Waycott et al. 2009), but in agreement with examples of seagrass populations that have been stable or

increasing over time (Frederiksen et al. 2004b, Hernandez-Cruz et al. 2006, Lyons et al. 2010, Lyons et al. 2013). In contrast, the spatial configuration of the SAV seascapes shifted significantly from continuous (i.e., seascape dominated by few large patches) to fragmented seascapes (i.e., many small patches, perforated SAV meadows) over the same time period. These conflicting patterns (i.e., small change in SAV cover but significant fragmentation) highlight the importance of incorporating both composition and configuration metrics in comprehensive assessments of SAV habitats. The low taxonomic resolution of the mapping approach used in this historical analysis may mask changes in species and community composition such as replacements of euhaline (e.g., *T. testudinum*, *Halimeda* spp.) for more ephemeral mesohaline taxa (*H. wrighttii*, *Laurencia* sp.) (Collado-Vides et al. 2011). Such species replacements (i.e., from slower-growing to fast-growing SAV species) may add to the highly dynamic nature of a stressed SAV community and may be partly responsible for the patterns documented here.

Historically, few large-scale mapping and monitoring studies have considered the significance of SAV seascape fragmentation dynamics and how this spatial transformation may influence the resilience of SAV populations (Cunha & Santos 2009, Montefalcone et al. 2010, Cuttriss et al. 2013). Fragmentation of SAV seascapes is likely to have a greater effect on bed persistence than changes in cover (Sleeman et al. 2005). Within-bed SAV cover can be highly dynamic as significant changes in plant biomass are often recorded between seasons (Lirman et al. 2014). In contrast, bed expansion through the colonization of new propagules or the extension of existing clones through rhizome elongation can be a slow process. Evidence of this is the common lack of recovery of propeller scars within *Thalassia testudinum* beds in Florida where rhizomes are not able

to bridge the denuded gap and persist for years or decades. Seagrasses, the main ecosystem engineers within SAV patches in Biscayne Bay, rely heavily on rhizome extension for recovery after disturbance and bed expansion (Duarte & Sand-Jensen 1990, Kendrick et al. 2005, Sintes et al. 2005). Therefore, the fragmentation of SAV habitats that creates gaps among patches and increases the amount of edges, influences seagrass ecosystem function directly (Duarte & Sand-Jensen 1990, Kendrick et al. 2005) and can make plant populations more vulnerable to local extinction (Liao et al. 2013). The high mortality associated with small SAV patches could be linked to lower anchoring capabilities and higher erosion influenced by the higher edge/area ratio of fragmented habitats, leading also to higher susceptibility to physical disturbances (Vidondo et al. 1997, Kendrick et al. 2005, Duarte et al. 2007). In contrast, continuous SAV seascapes composed of larger patches can be more stable and resilient by stabilizing sediments, reducing erosion and re-suspension, and enhancing resource accumulation and allocation (Fonseca & Bell 1998, Sintes et al. 2005).

In this study, for the first time, the long-term spatial dynamics of SAV habitat loss and fragmentation were quantified in relation to the disturbance associated with freshwater discharges into a coastal bay. Net habitat loss from 1938-2009 was more common within the sites adjacent to freshwater canals (2 out of 3 sites). In contrast, 2 out of 3 sites classified as distant from canals showed net gains. The rate of habitat loss and fragmentation was higher within shoreline habitats that are close to the point of freshwater discharge. By exploring the trajectories of individual sites over > 70 years, we can begin to understand how composition and configuration may be responding differently to the environment and providing seemingly contradictory results (e.g., loss of

SAV cover with a concurrent decrease in fragmentation) (**Figure 2.7**). There are different alternative scenarios of SAV habitat loss and SAV seascape fragmentation associated with different seascape transformation types (e.g., perforation, dissection, subdivision, shrinkage and attrition) and tradeoffs between disturbance and succession processes (Forman 1995, McGarigal et al. 2005). Sites can exhibit an increase in cover without a reduction in fragmentation if the SAV patches increase the above-ground biomass and a steadily expansion of large patches over time concentrated on one edge of the seascape, but fail to expand into denuded areas (illustrated by a downward progression along the SAV cover vertical axis in **Figure 2.7**). Conversely, sites can exhibit reduced cover without a change in fragmentation if remaining patches only "thin out" in unfavorable environmental conditions. Within sites, resources need to be allocated to the maintenance of above-ground biomass (which influences SAV cover) and below-ground biomass that results in rhizome extension and thus bed expansion. Under favorable conditions, SAV patches can increase in biomass/cover as well as expand into suitable habitat and fill out gaps among patches. When conditions are not consistently favorable, trade-offs may lead to conflicting and dynamic patterns such as documented here. Under extreme or persistent unfavorable conditions, this may lead to both habitat loss and fragmentation (illustrated by the black dashed line in **Figure 2.7**). Under this scenario, the SAV seascape is subject to habitat perforation, subdivision, and shrinkage and attrition processes that lead to a gradual breakdown and formation of discrete fragments (Forman 1995). The site south of Black Point Canal (BP) was the only location that showed both significant habitat loss and fragmentation. The pulsed discharge of freshwater from this canal creates a highly variable salinity environment that can experience low-salinity

conditions within a few hours and remains < 5 psu for several days (Wang et al. 2003, Lirman et al. 2008b). These pulsed freshwater disturbances have been associated with the reduction in SAV cover and dominance, and abundance of species with high turn-over rates (Lirman et al. 2008a, Collado-Vides et al. 2011), therefore contributing to both the loss and fragmentation of SAV habitats. Depression of productivity and short-shoot mortality of *T. testudinum*, the dominant seagrass species of Biscayne Bay, have been previously associated with low-salinity events, and high and frequent salinity fluctuations (Lirman & Cropper Jr. 2003, Herbert & Fourqurean 2009).

Sites that showed only habitat loss were subject to localized removal of biomass and/or shrinkage and attrition of existing patches (illustrated by dotted and dash-dot arrows in **Figure 2.7**). Sites that showed only fragmentation were subject to a balance between habitat subdivision, shrinkage, and the formation of small patches. The Convoy Point site located close to Mowry Canal showed the highest rate of fragmentation, but not declines in cover. Similar patterns were observed at Turkey Point, a site classified as distant from canals. Although fragmentation patterns at Turkey Point could not be associated with freshwater pulses, there are other localized disturbances in this area that could have influenced such spatial processes. For example, the Turkey Point Nuclear Generating Station has been operating in this area since 1967 (Dolan 2012) and studies have observed significant decline in the abundance and density of seagrass up to a 1 km from the heated effluent of this power plant (Zieman & Wood 1975, Dolan 2012). In addition to thermal stress, hypersalinity conditions which are known to be detrimental to seagrass (Koch et al. 2007b, Herbert & Fourqurean 2009) could be associated with the fragmentation observed at this site (FPL 2009; Hughes et al. 2009; Dolan 2012).

Other studies that used spatial pattern metrics in addition to areal extent identified an increase in the fragmentation state of SAV seascapes and an increase or neutral trend in SAV cover (Cunha et al. 2005; Cuttriss et al. 2013). Hernandez-Cruz et al. (2006) observed an expansion of seagrass cover within an embayment, but the nearshore portion of the study area influenced by effluent discharges revealed increases in patchiness and fragmentation. Montefalcone et al. (2010) noticed that the abundance patterns of seagrasses in the Mediterranean Sea were not correlated with coastal development, but that fragmentation measures were indeed influenced by human-induced disturbances on seagrass meadows.

A confounding environmental factor that may have played a role in the observed SAV historical patterns is the increase in nutrient availability associated with freshwater discharges. Habitats of Biscayne Bay in proximity to canals have been shown to have high N availability (Caccia & Boyer 2005). This was confirmed by studies that showed high N-content within the tissue of macroalgae and seagrasses within western Biscayne Bay (Collado-Vides et al. 2011; Lirman et al. 2014). While not tested, it is possible that increased nutrients result in faster growth and higher SAV cover in closer proximity to canals (Herbert & Fourqurean 2008), supporting our observation of higher SAV cover near canals. The increased above-ground productivity, however, may not necessarily translate into high resilience to the negative salinity impacts and may not prevent seascape fragmentation. In addition, increased sediment organic content linked with elevated productivity and turnover rates has the potential to create sulfate-reducing conditions that have been implicated in seagrass die-offs in neighboring Florida Bay (Fourqurean & Robblee 1999; Koch et al. 2007b). Thus, the temporally and spatially

dynamic influence of salinity and nutrients on SAV may have been responsible for the patterns of composition and configuration reported here and may explain why both cover and fragmentation were higher in some of the areas adjacent to canals. Clearly, controlled experiments that isolate the effects of low salinity and high nutrient concentrations on above and below-ground seagrass biomass and algal productivity are needed to provide further insights into the influence of water management practices on SAV seascapes.

In conclusion, the SAV seascape in Biscayne Bay has been highly dynamic in time and space during the span of 71 years included in this study, with changes in SAV composition and configuration being greatest in the habitats closest to shore and freshwater canals. More importantly, our results highlight the importance of quantifying habitat loss and habitat fragmentation independently to tease apart patterns related to the amount and removal of SAV habitat versus those related to the spatial arrangement and configuration of SAV patches. These results illustrate the importance of incorporating measurements of SAV seascape spatial characteristics to existing monitoring and restoration programs to have a complete indication and accurate projection of coastal habitat resilience and recovery from anthropogenic disturbances. In addition, seascape spatial characteristics are especially relevant when evaluating the cascading effects that changes in SAV seascapes can have on associated macrofauna. Studies in terrestrial ecology have indicated that thresholds exist beyond which abrupt decline in habitat suitability occurs and where fragmentation effects become significant (Fahrig 2003); however, there is still a limited understanding about how marine nektonic populations response to fragmentation independently and interactively with the amount of habitat within the seascape. Therefore, a seascape approach is essential to comprehend how

marine habitats spatial properties influence the growth, survivorship, and ecological interactions of marine species, and hence the quality of nursery functions and fisheries productivity of nearshore environments. By combining remote sensing techniques with landscape ecology and conventional marine ecology, our study provides a quantitative framework from which change in seascape spatial patterning can be monitored and measured to support the implementation of adaptive management strategies.

Table 2.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne Bay. ZLAND was used to assess habitat loss, and the remaining four metrics were used to create the fragmentation index (FragIndex = $\sqrt[4]{(PD*LD*AWMPAR*1/Gyrate_MN)}$)

Metric	Acronym	Category	Aspect	Description	Formula
Percentage of Landscape	PLAND	Composition	Area/Density	Percentage of the total landscape made up of the corresponding class	$PLAND = \frac{\sum_{j=1}^n a_{ij}}{A} (100)$
Patch Density	PD	Configuration	Area/Density	Number of patches of a certain class divided by the total landscape area	$PD = \frac{n_i}{A}$
				N patches/ha	
Mean Radius of Gyration	GYRATE_MN	Configuration	Area/Density	Measure of patch extensiveness Larger patches will have higher GYRATE values	$GYRATE_MN = \frac{\sum_{j=1}^n [\sum_{r=1}^z (\frac{h_{ijr}}{2})]}{n_i}$
Landscape Division	LD	Configuration	Interspersion/Contagion	Probability that two randomly chosen pixels in the landscape are not situated in the same patch	$LD = \left[1 - \sum_{i=0}^n \left(\frac{a_i}{A} \right)^2 \right]$
Area-Weighted Mean Perimeter-Area Ratio	AWMPAR	Configuration	Shape	Measure of patch-shape complexity	$AWMPAR = \frac{\sum_{i=1}^{i=NP} \frac{p_i}{a_i} \cdot a_i}{\sum_{i=1}^{i=NP} a_i}$

Table 2.2. Patterns of change in SAV area in western Biscayne Bay over the >70-year record evaluated here (1938– 2009). Percent net change calculated as the proportion of net area change across all years with the areal extent sampled at each site (Site Area). Percent net positive and negative change highlighted in bold grey and black, respectively

Site	Name	Canal Treatment	Site Area (km ²)	Net Area Changes (km ²)	%Net Change
BL	Black Point Lagoon	Distant	0.41	-0.073	-17.78
CK	Chicken Key	Distant	0.34	0.004	1.17
TP	Turkey Point	Distant	0.71	0.07	9.93
BP	Black Point Canal	Adjacent	0.39	-0.044	-11.42
CP	Convoy Point	Adjacent	0.33	0.003	0.94
SC	Snapper Creek	Adjacent	0.39	-0.045	-11.55
		Total	2.57	-0.085	-3.31

Table 2.3. Principal components analysis (PCA) eigenvalues and variable loadings. Four variables that measure different spatial components of habitat fragmentation were considered in the PCA. Variable loadings in axis 1 were used to quantify spatial configuration and fragmentation temporal dynamics

Eigenvalues and variable loadings		Axis 1	Axis 2
Eigenvalues		2.87	0.79
Percentage		71.70	19.60
Cumulative percentage		71.70	91.30
PCA variable loadings:			
	Patch Density (PD)	0.57	-0.152
	Mean radius of gyration (GYRATE_MN)	-0.46	0.64
	Area-weighted mean perimeter to area ratio (AWMPAR)	0.54	0.138
	Landscape division (LD)	0.42	0.74

Figure 2.1. Study site: Biscayne Bay, Miami, Florida. Six sites were selected: 3 adjacent to freshwater canals (in black) and 3 distant from canals (in grey)

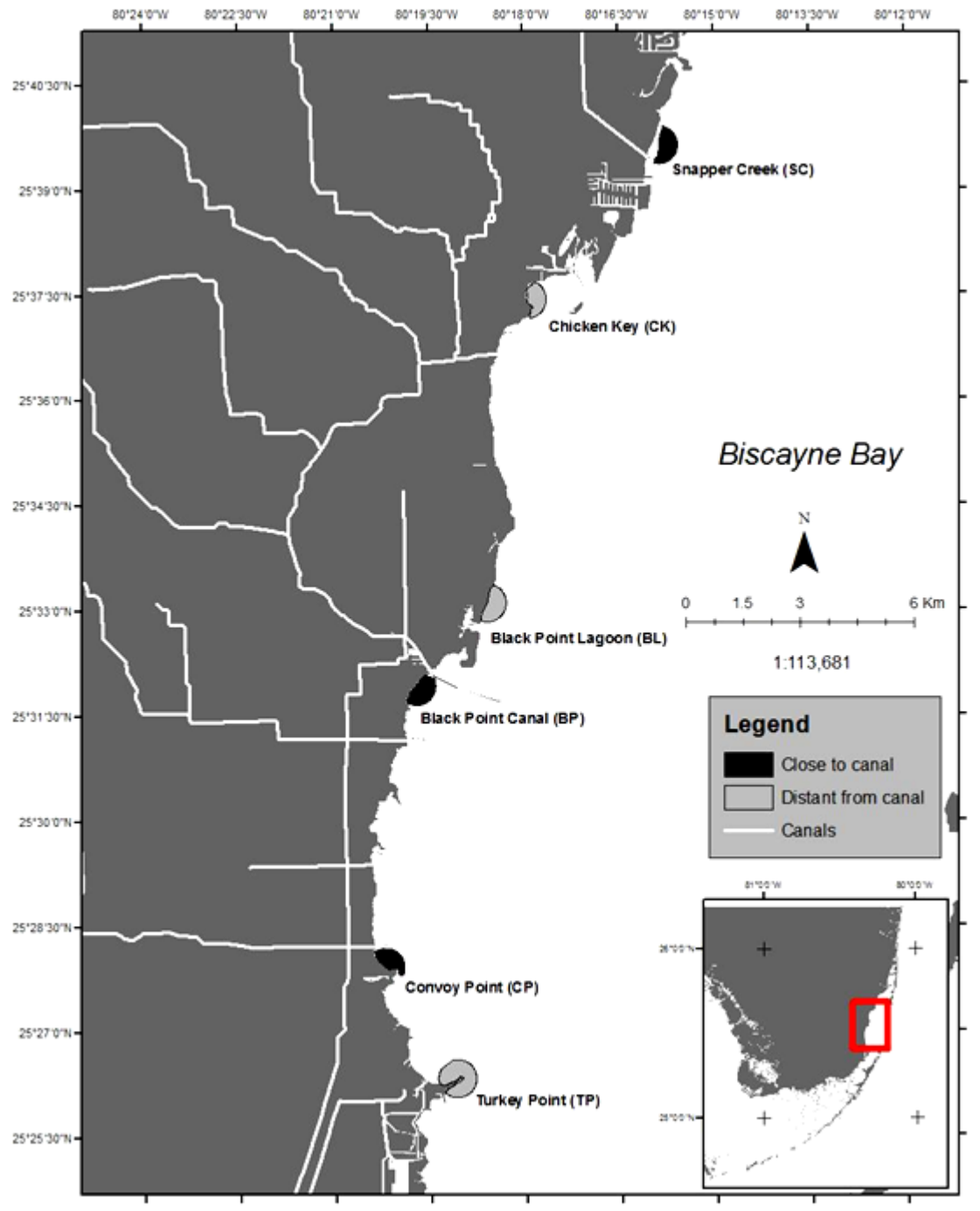


Figure 2.3. SAV cover and Fragmentation Index over time measured within the 500m from shore spatial extent. Solid and dashed lines (standard error = shaded area) represent temporal trend in habitat loss and fragmentation within areas adjacent and distant from a freshwater canal. Based on the ANCOVA results, the rate of habitat loss and fragmentation appears to be equal in both canal treatments; however, lines within SAV habitat cover were not coincident (i.e., parallel with different intercept – different initial and final values)

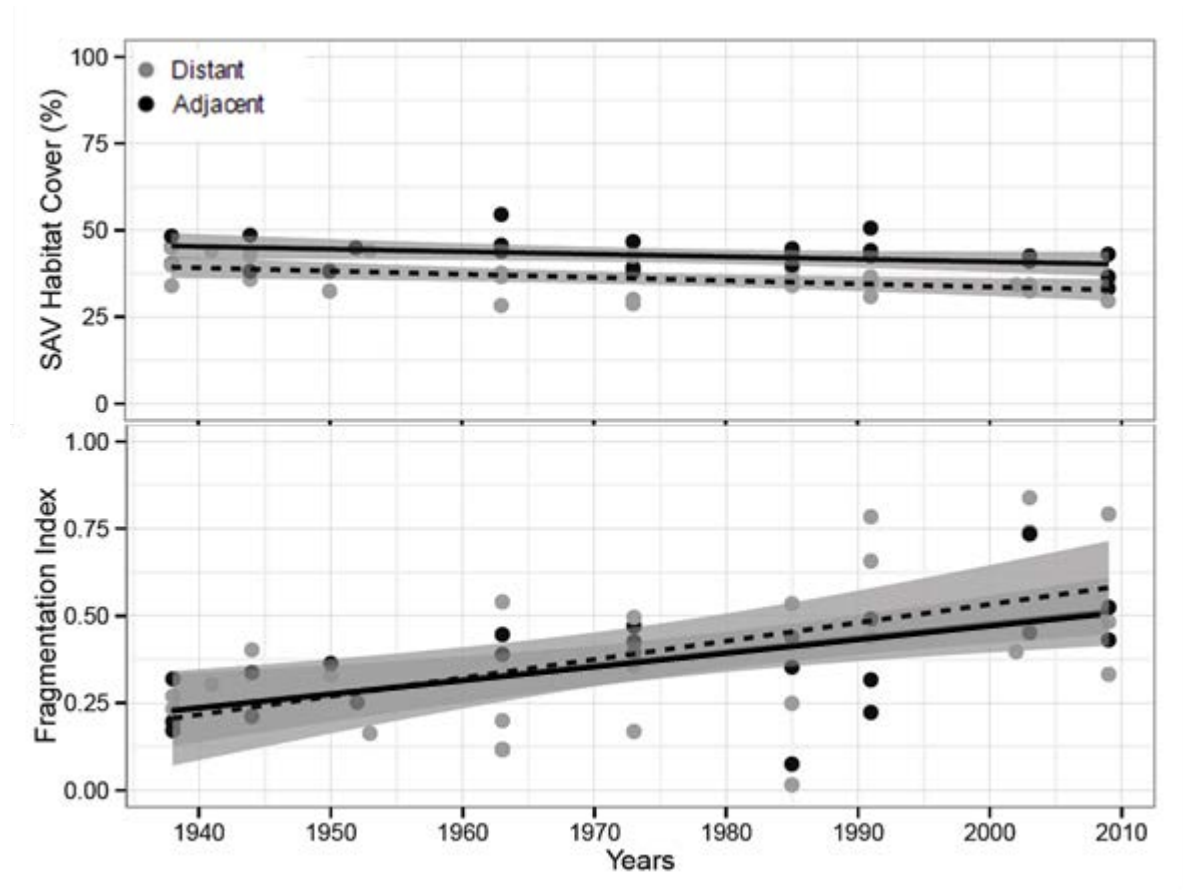


Figure 2.4. SAV cover and Fragmentation Index over time measured within the shoreline habitats (0-200m – left panel) and offshore habitats (200-500m – right panel). Solid and dashed lines (standard error = shaded area) represent temporal trend in habitat loss and fragmentation within areas adjacent and distant from a freshwater canal. Based on the ANCOVA results, the rate of habitat loss and fragmentation appears to be equal in both canal treatments but significant within the nearshore area; however, no significant trends were observed within the offshore areas

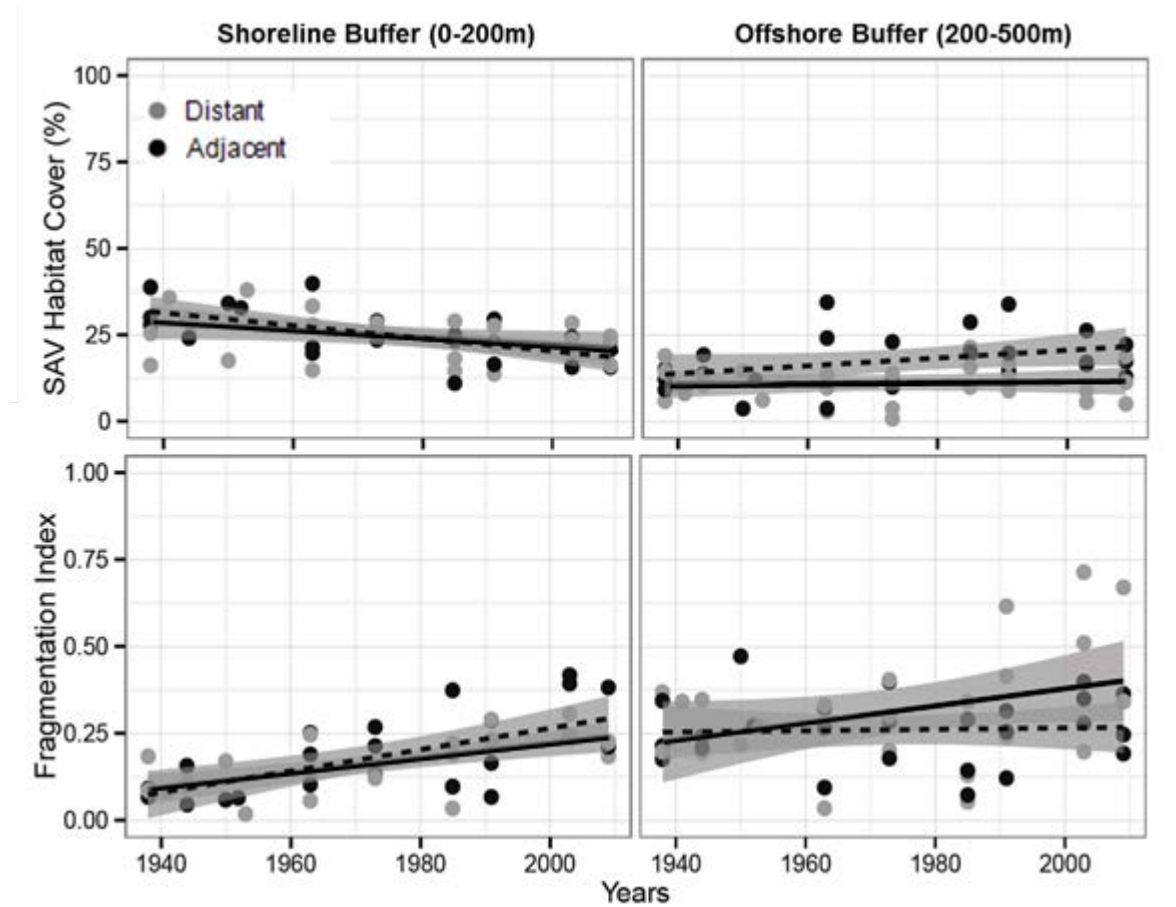


Figure 2.5. SAV seascape patterns calculated for the period 1938 to 2009. a) Index of area change; and b) proportion of SAV area gained and lost. Metrics were statistically different between canal treatments based on a one-way ANOVA ($p < 0.05$)

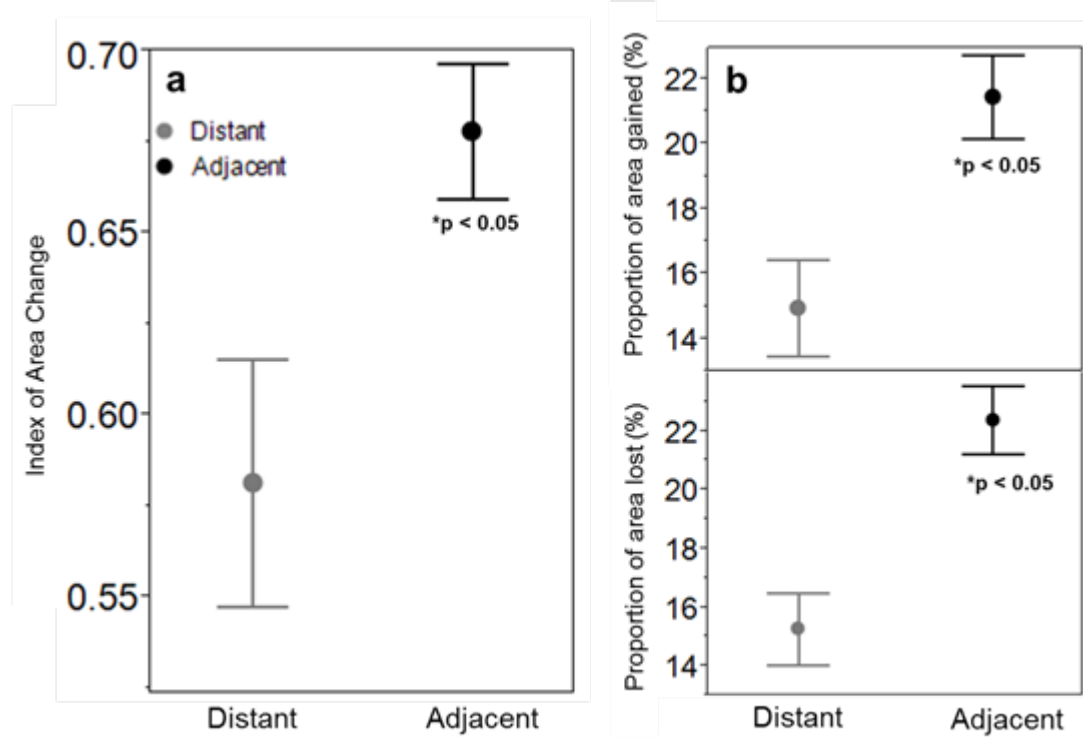


Figure 2.6. Vector lengths calculated from the coordinates of PCA biplot quantifying the magnitude of fragmentation (black) and defragmentation (grey) by canal treatment. Dots represent the mean values and bars/whiskers the standard error. No significant differences in vector length were found between fragmentation/defragmentation, but significant differences between canal treatments were observed (2-way ANOVA, $p < 0.05$)

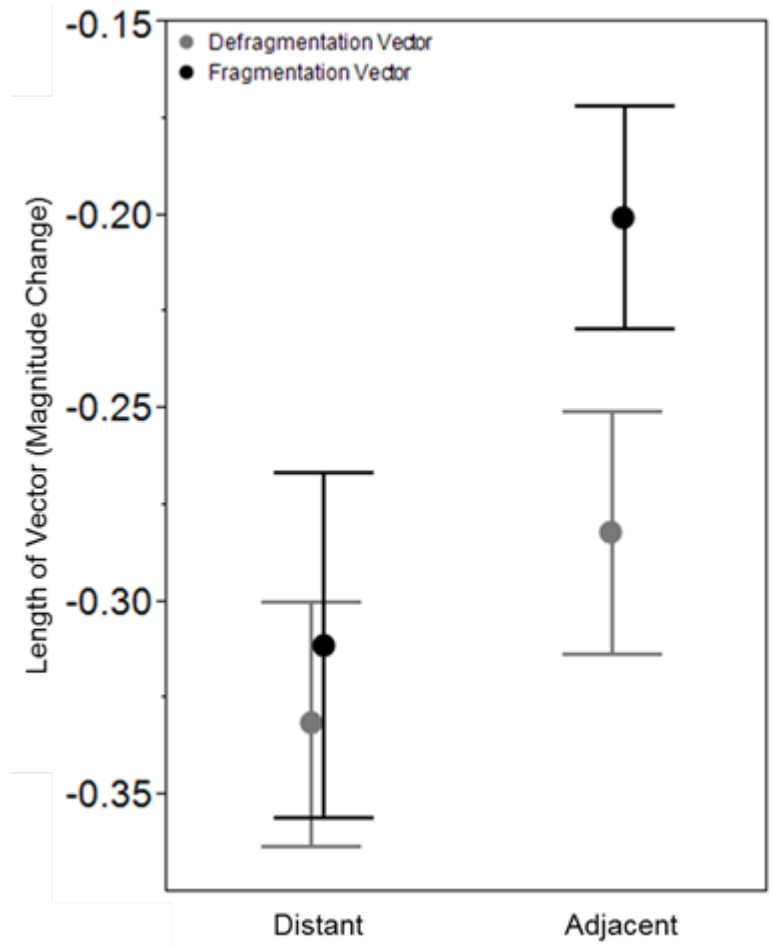
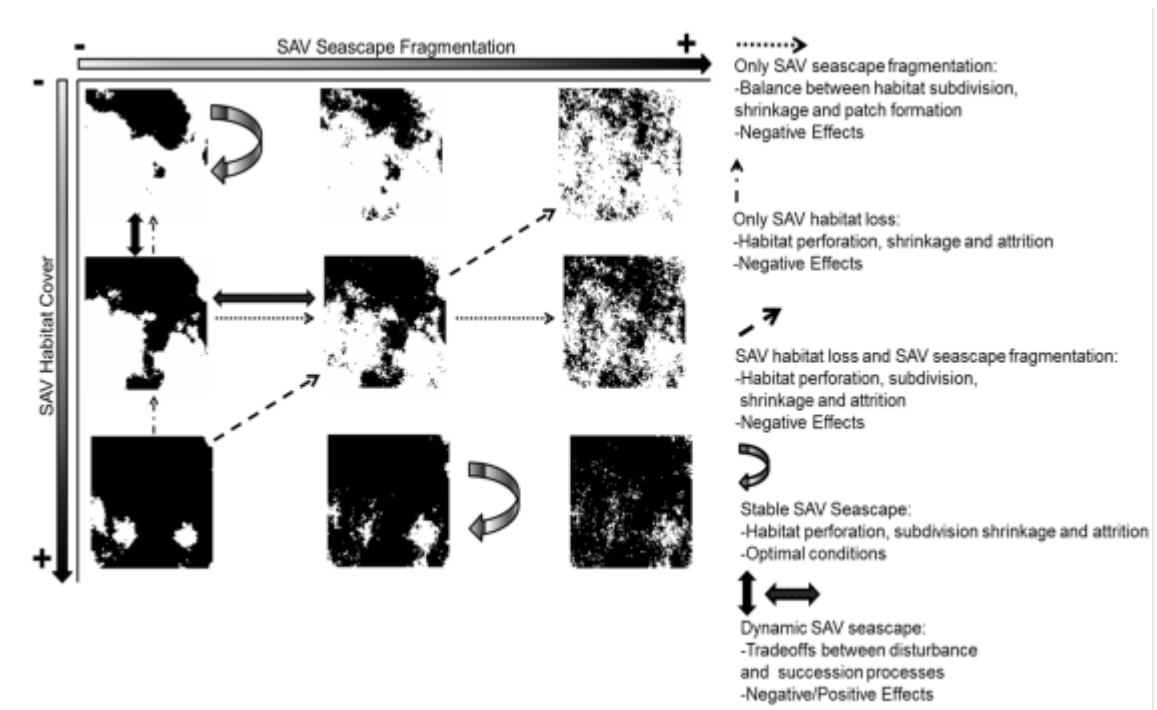


Figure 2.7. Conceptual SAV seascape transformation illustrating habitat loss/gain (vertical axis) and fragmentation (horizontal axis). SAV patches illustrated in black. Different arrows depict the most common process of SAV seascape transformation across time in Biscayne Bay



Chapter 3. Influence of fragmented versus continuously vegetated seascapes on marine faunal assemblages in a subtropical bay

Summary

Human modifications to coastal and marine ecosystems have resulted in changes to the spatial configuration of vegetated seascapes, yet little is known about the consequences of seascape fragmentation on associated marine organisms. Fragmentation and loss of benthic habitat are generally thought to impact negatively the distribution, community composition and behavior of marine fauna. In Biscayne Bay, Florida, freshwater discharge into nearshore areas has resulted in fragmentation of submerged aquatic vegetation (SAV) seascapes. To understand the influence of seascape fragmentation on fish and crustaceans, faunal communities associated with SAV within continuous (CS) and fragmented (FS) seascapes were sampled using seine nets. Non-parametric multivariate statistics were applied to describe differences between assemblages and functional groups associated with CS and FS. FS supported significantly higher species richness of fish and crustaceans and higher biomass of carnivorous fishes than did continuous seascapes. FS also had higher abundance of the pink shrimp *Farfantepenaeus duorarum* and the goby *Gobiosoma robustum*. In contrast, CS supported higher abundance of the pinfish *Lagodon rhomboides*. The community patterns were also influenced by salinity, indicating that both water quality and spatial properties of SAV seascapes play an important role in structuring faunal communities. These findings have relevance to understanding the role of spatial patterning in the evaluation of essential fish habitat and for freshwater management practices in Florida.

Background

The spatial structure and heterogeneity of habitats at a range of spatial scales influences the distribution and abundance of marine and terrestrial species (MacArthur & Pianka 1966, Wiens 1976, Robbins & Bell 1994a, Fahrig 2003). Research in terrestrial landscape ecology has focused on the process and consequences of habitat fragmentation, the process by which habitat loss results in the division of large, continuous habitats into smaller, more isolated patches (Fahrig 2003, Lindenmayer & Fischer 2007, Didham et al. 2012). Fragmentation changes the amount and ratios of edge and interior habitats, patch size, and connectivity. Species may respond to habitat fragmentation in different ways and at different scales depending on their specific ecological needs (Villard & Metzger 2014, Betts et al. 2014). Here, we evaluate the role of submerged aquatic vegetation (SAV) seascape composition and configuration on the abundance, distribution, and community structure of fish and crustaceans associated with seagrass beds in Biscayne Bay, Florida, U.S.A.

Seascape ecology (the marine counterpart of landscape ecology) studies have focused predominantly on SAV communities and mosaics of seagrass/algae patches within a sediment matrix, providing important insights into how spatial patterns in benthic structure influence faunal assemblages (Boström et al. 2011, Hensgen et al. 2014). Field studies and simulation modeling indicate that both the composition and spatial configuration of seascapes influence key ecological processes such as faunal recruitment, dispersal, survivorship, and habitat connectivity (Pittman et al. 2004, Hovel & Regan 2008, Mellin et al. 2009). SAV seascapes are spatially dynamic environments typically exhibiting complex patterns of change over time (Greening et al. 2011). SAV

patches can become fragmented by wave action and other hydrodynamic forces (Robbins & Bell 1994a, Fonseca & Bell 1998b), sedimentation events (Frederiksen et al. 2004a), diseases (Ralph & Short 2002), and herbivory (Bell et al. 2007). Habitat loss and fragmentation of SAV seascapes have also been driven by anthropogenic disturbances, such as declining water quality, nutrient loading, sediment runoff, and changes in salinity (Fourqurean & Robblee 1999b, Waycott et al. 2009, Santos et al. 2011), and direct physical removal by dredging, vessel groundings and propeller scarring (Orth et al. 2006).

While habitat fragmentation and habitat loss are typically reported as undesirable processes, some degree of habitat fragmentation can, in fact, increase species diversity and the abundance and growth of certain species through edge and spatial heterogeneity effects (Ries et al. 2004). Intermediate levels of fragmentation increase the proportion of edge-to-interior habitat, which may influence prey-predator interactions, the accumulation of food resources, and the proportion of specialist and generalist species (Bell et al. 2001, Ries & Sisk 2004). Also, habitat fragmentation can increase the amount and diversity of microhabitats (Pearson et al. 1996, Horinouchi et al. 2009). Several manipulative studies in seagrass beds have observed an increase in the diversity and abundance of epifaunal species after experimental seagrass fragmentation and patch size reduction (RW.ERROR - Unable to find reference:286, TANNER 2005, Macreadie et al. 2010b, Arponen & Boström 2012, Pierri-Daunt & Tanaka 2014). Furthermore, fragmented SAV seascapes can influence prey accessibility and predation success, which affects assemblage structure and function of the nektonic community. For example, studies have reported increased abundance of large predators and increased predation risk

for crustaceans (Hovel & Lipcius 2002), bivalves (Irlandi et al. 1995) and small fishes (Gorman et al. 2009) in patches with a higher proportion of edge habitat.

In this study, we evaluate the role of SAV seascape structural characteristics on the abundance and community structure of faunal assemblages associated with shallow-water seagrass beds of Biscayne Bay, Florida, U.S.A. This coastal lagoon is adjacent to the city of Miami and is heavily influenced by changes in water management practices that have resulted in the fragmentation of SAV communities in the vicinity of freshwater canals (Santos et al. 2011). The fragmentation of SAV seascapes in Biscayne Bay has been associated with salinity patterns created by the release of fresh water from canals (Santos et al. 2011). A greater understanding of linkages among water management practices, seascape fragmentation, and cascading effects on marine fauna is required to support science-based decisions within the adaptive management framework proposed for the restoration of the Florida Everglades.

To determine the effects of SAV seascape fragmentation on marine fishes and crustaceans, we combined concepts and analytical tools from landscape ecology, remote sensing and conventional marine ecology. Three hypotheses were tested: (H¹) Occurrence, abundance, and biomass of fauna are significantly different in fragmented seascapes compared to continuous seascapes; (H²) Abundance and biomass of predators is significantly higher in fragmented seascapes than in continuous seascapes; and (H³) Species richness is significantly higher in fragmented seascapes compared with continuous seascapes.

Materials and Methods

Study site

Biscayne Bay is a shallow-water subtropical lagoon located adjacent to the city of Miami and downstream of the Florida Everglades system (**Fig. 1a**). Sampling of marine fishes and crustaceans focused on nearshore benthic habitats (< 500 m from shore) in western Biscayne Bay, which are dominated by SAV composed of seagrasses and macroalgae (Lirman et al. 2008b, 2014). These vegetated communities, as well as the fringing mangrove shorelines, provide habitat for a large number of commercially and recreationally valuable species, including pink shrimp (Diaz et al. 2001), gray snapper, hogfish, and spotted seatrout (Serafy et al. 1997, 2003, Faunce & Serafy 2008).

Seascape mapping

The horizontal spatial patterning of seascapes in the study area was mapped using statistical classification techniques (K Nearest Neighbor supervised classification) applied to spectral information in high resolution (2.4-meter pixel size) satellite images (Quickbird-2 multispectral data using blue, green, red, and near-infrared wavebands) acquired in November 2009. To define the strata for sampling of fishes and crustaceans, seascapes were classified into two categories: 1) continuous (CS) and 2) fragmented (FS) seascapes.

Mapping patch types using broad cover classes for submerged vegetation based on estimates of horizontal foliage cover (i.e., low: 0-40% cover, moderate: 40-70% cover, and high: 70-100% cover) can produce maps with acceptable levels of accuracy (Phinn et al. 2008, Roelfsema et al. 2009). In this study, the seascape mapping focused on seagrass

patches with moderate to high macrophyte cover (> 40 %). Using the ENVI v4.5 Feature Extraction module (ITT Visual Information Solutions 2008), an object-based approach was used to identify and delineate this patch class. The object-based image classification optimized the delineation of exterior and internal patch boundaries and provided better discrimination between highly vegetated and sparse-barren patch classes under varying water depth and image quality than per-pixel based image classification methods (Santos et al. 2011). Because objects (i.e., image segments with distinct homogenous spatial, textural, and spectral characteristics) are used instead of individual pixels, results do not have “salt-and-pepper” effects or erroneously classified pixels across the image (Kelly & Tuxen 2009). Also, the segmentation of the images into objects with distinct properties (e.g., tone, color contrast, texture, shape) helped distinguish the borders between different benthic classes.

The data used for the training of the object-based classification procedure and the validation (i.e., ground-truthing) of the seascape map were obtained from geo-tagged images of the seafloor collected from a glass-bottom skiff in June-November 2009 (Lirman et al. 2014). The high-resolution (10 megapixel) images of the benthos were analyzed on a computer screen to determine the percent cover of SAV. Percent cover was defined as the fraction of the total quadrat or frame that was obscured by each taxon when viewed directly from above. The average percent cover of SAV from each site (n = 153 sites) was used to train the statistical classification of the patches. The delineation of the vegetated patches resulted in a user accuracy of 69%. As the user accuracy is a measure of the reliability of class in a thematic map, and because the patches of vegetation with higher cover have distinct boundaries and provide higher level of habitat

complexity, maps were accepted as accurate representation of the seagrass seascape in Biscayne Bay.

Quantifying the spatial structure of seascapes

In landscape ecology, horizontal spatial patterning is evaluated to quantify two broad groupings of structural attributes that were integrated in this study: 1) composition, defined as the abundance and variety of patch types in the landscape; and 2) spatial configuration, defined as the spatial arrangement or geometry of the landscape (Wedding et al. 2011). Differences in the areal habitat amount and the diversity of habitat patch types can be quantified with composition metrics and fragmentation can be quantified with configuration metrics.

Using a Geographical Information System (GIS), a grid with 500 x 500 m cells was superimposed over the seascape maps (Fig. 1b,c). The seascape characteristics within each grid cell were quantified using six spatial-pattern metrics that quantify different structural attributes of seascape composition (variety and amount of patch types) and spatial configuration (spatial arrangement of patches) (Table 1). The metrics selected were percentage of the seascape occupied by a given habitat type (PLAND), mean patch size (MPS), patch size coefficient of variation (PSCV), total edge (TE), area-weighted mean patch fractal dimension (AWMPFD), and patch density (PDENS). These metrics quantify habitat extent, subdivision, and geometric complexity and have been widely used in landscape ecology studies to investigate faunal-landscape associations in terrestrial and marine environments (Turner et al. 2001, McGarigal et al. 2005, Mellin et al. 2009, Boström et al. 2011). Principal component analysis (PCA) and hierarchical

cluster analysis were applied to standardized, log-transformed spatial-pattern metrics to classify survey sites (grid cells) as either a fragmented (FS) or continuous (CS) seascapes following Santos et al. (2011) (Fig. 1c).

Fish and crustacean sampling design

Six habitat grid cells were randomly selected from each of the seascape types (CS and FS) for sampling marine fauna using seine nets. Sampling was divided into two major salinity zones (Zone 1 = high and stable salinity; Zone 2 = low and variable salinity), with three replicates of each seascape type (CS and FS) within each salinity zone (**Fig 1c,d**). Zone 1 extended from Matheson Hammock to north of Black Point, and Zone 2 extended from south of Black Point to Turkey Point. These zones were delineated based on distinct salinity regimes described by Caccia & Boyer (2005) and Lirman et al. (2008a). Zone 1, an area with limited input of freshwater from canal structures, is characterized by higher and more stable salinity. In contrast, Zone 2 is significantly influenced by pulsed freshwater flows from canals that create a nearshore environment with low and variable salinity.

One plot (100 x 500 m) was randomly positioned perpendicular to shore within each cell (**Fig. 1d**). The plot was further divided into five distance-to-shore areas to integrate cross shelf patterns within cells. The location of each seine net deployment (n = 3 per cross-shelf section) was determined at random (n = 15 points per cell). At each of the randomly selected points, nocturnal nekton sampling was performed during the months of July-October 2012 (wet season). Sampling was conducted at night during the wet season, when many faunal species are actively foraging over seagrasses to maximize

the probability of capture (Luo et al. 2009, Hammerschlag et al. 2010a). Organisms were collected with a center-bag seine net (21.3 m long, 1.8 m deep, 3 mm mesh) following the Florida Marine Institute Fisheries Independent Monitoring Program Procedure Manual (SEFSC 2010). The seine was deployed and retrieved by motorboat, and each seine haul swept an area on the bottom of approximately 210 m². This type of net has been successfully used to monitor fishes in both vegetated and unvegetated substrate (SEFSC 2010).

Sample and data processing

Faunal samples were immediately stored on ice and returned to the laboratory for identification and body length measurements (total lengths, mm). Several metrics were calculated to quantify assemblage and species variables, including diversity indices, occurrence (presence/absence), and abundance (count of individuals per seine). Biomass (grams per seine) was estimated using published length-weight relationships for each of the species. Peer-reviewed scientific publications and reports were used to obtain allometric relationships to estimate biomass (See Supplementary Material A1 for a list of publications used). To account for zero-inflation (i.e., positively skewed data) the delta approach described by Serafy et al. (2007) was followed, where the data were separated into a binary occurrence matrix of the species (i.e., present = 1, absent = 0), and a matrix of the product of the mean abundance and biomass with the occurrence matrix.

Calculated diversity indices included Number of Species per sample (species richness), Shannon-Weiner Index, Simpson Diversity, and variation in Taxonomic Distinctness.

Different diversity indices were considered to minimize bias associated with any one diversity index. Variation in taxonomic distinctness is a measure of 'biological diversity'

that accounts for the taxonomic differences among the species rather than abundance (Clarke & Warwick 1998, Izsák & Papp 2000). FishBase (Froese & Pauly 2014) and Harborne et al. (2008) were used to classify species into seven functional categories: invertivore/piscivore, piscivore, invertivore of sessile prey, invertivore of small, mobile prey, planktivore, and grazer of turf algae.

Statistical analyses

Two-way analysis of similarities (ANOSIM, PRIMER v6 software) was used to test for differences in faunal assemblage composition within and among seascape types (CS versus FS) and salinity zones (Zone 1 & 2). ANOSIM was applied to the Bray-Curtis dissimilarity matrix of the presence/absence and log-transformed abundance and biomass data. ANOSIM tests for differences among groups of samples while allowing for treatment (seascape) and block (zone) effects, using a global R statistic that compares the average rank similarities within and among groups (Clarke & Warwick 2001). The null hypothesis of no difference between treatments and/or block effects can be accepted when R values are close to zero, and the significance of the observed value of R to its permutation distribution is $p > 0.05$ (Clarke & Warwick 2001). Following Clarke & Gorley (2001) when significant ($p < 0.05$), R-values were interpreted as > 0.75 (assemblages well separated); $0.3 < R < 0.5$ (assemblages different but overlapping); and $R < 0.25$ (assemblages barely separable).

Similarity percentages (SIMPER) (Clarke & Warwick 2001) was used to identify the species that contributed most to the dissimilarity between groups. In addition, the mean abundance and biomass of the functional groups, and the diversity indices were

compared among the seascapes types using a nonparametric Kruskal-Wallis analysis of variance. The clustering of the sites among the seascapes was visually examined with a hierarchical cluster analysis superimposed upon a non-metric multidimensional scaling (nMDS) plot.

Faunal assemblages were also assessed with a modified abundance/biomass comparison (ABC) method (Warwick 1986). This method considers that the distribution of the numbers of individuals among species should differ from the distribution of biomass among species when influenced by disturbances (Meire & Dereu 1990). This method can show a shift in the proportions of different taxa present in communities (e.g., taxon-specific large- and small-body changes), and intra- and interspecific shifts in the relative distributions of abundance and biomass (Warwick & Clarke 1994, Clarke & Warwick 2001). The ABC is performed by comparing the abundance and biomass curve in K-dominance plots, where curves rank species in order of importance on the x-axis versus the percentage of each species on the total abundance or biomass on a cumulative scale. An abundance curve below the biomass curve indicates a habitat is dominated by one or a few large species; whereas the reverse indicates the habitat is dominated by one or few very small species. A Kruskal-Wallis test comparing the Warwick-statistics (W statistic – Warwick 1986) was used to differentiate the ABC between vegetated seascapes, where the W statistic is expressed as:

$$W = \sum_{i=1}^S \frac{B_i - A_i}{[50(S - 1)]};$$

B and A are the biomass and abundance cumulative percent dominance value, respectively, of the ranks i , standardized with the total number of species (S). W-values approach 1 when there is an even abundance across species but the biomass is dominated by few species, and W approaches -1 when the biomass is even across species but the abundance is dominated by few species.

Results

A total of 62 species were identified, including 44 and 53 species from the CS and FS, respectively (**Fig. 2a**). A total of 45 and 43 species were identified in Zone 1 and Zone 2, respectively, with 12 unique species to Zone 1 and 10 to Zone 2 (**Fig. 2b**). *Eucinostomus* spp. (mojarra), *Atherinomorus stipes* (hardead silverside), and *Lucania parva* (rainwater killifish) were the most abundant, being distributed equally between the salinity zones, but with mojarra significantly more abundant in FS (Kruskal-Wallis ANOVA, $p < 0.05$). These species were removed from subsequent analyses because they masked more subtle differences in the faunal assemblage (i.e., their removal increased dissimilarity between seascape types by 11%).

Do fragmented and continuous seascapes differ in faunal occurrence, abundance and biomass?

The assemblage composition, based on occurrence and abundance of the species, differed significantly between the CS and FS (ANOSIM test, $R_{\text{occurrence}} = 0.33$ and $R_{\text{abundance}} = 0.5$, $p < 0.05$, **Fig. 3a,b**) and between salinity zones (ANOSIM test, $R_{\text{occurrence}} = 0.45$ and $R_{\text{abundance}} = 0.63$, $p < 0.05$, **Fig. 3a,b**). Even though the community structure based on occurrence was significantly different between seascape types and zones, there

was overlap between the communities (ANOSIM global $R < 0.5$) (**Fig. 3a,b**). In contrast, assemblage structure based on the biomass of the species was barely separable between seascape types and zones (ANOSIM test, $R = 0.05 < p < 0.10$) (**Fig.3c**).

Based on the occurrence and abundance matrix, there was an average dissimilarity of 44.18% and 52.50 %, respectively, among all pairwise comparisons of the replicates within the seascape types (**Table 2**). The dissimilarity based on occurrence was mainly driven by the higher probability of occurrence of small demersal fish and crustaceans in the FS (**Table 2a**). Caridean shrimp, *Lagodon rhomboides*, *Farfantepenaeus duorarum*, *Gobiosoma robustum*, and *Callinectes* spp. contributed approximately 50% of the average assemblage dissimilarity between seascape types (**Table 2b**). All of these species were dominant in the FS, except for *Lagodon rhomboides*, which was more abundant in CS (43 in FS versus 68 in CS). The average dissimilarity in biomass (31 %, **Table 2c**) was mainly attributed to the biomass of larger generalist carnivores such as *Haemulon sciurus*, *Lutjanus griseus*, *Callinectes* spp., *Harengula humeralis*, *Opsanus beta*, and *Strongylura notata*.

Are there more predators' abundance and biomass in fragmented versus continuous seascapes?

The species grouped into four functional categories: invertivores of small prey (IvSm), piscivores (Pi), invertivores/piscivores (Iv/Pi), and invertivores of sessile prey (IvS). Of the four groups, three varied significantly between seascape types (**Fig 4**). The abundance of IvS, Pi, and Iv/Pi, and the biomass of Iv/Pi and IvS were significantly higher in FS (Kruskal-Wallis ANOVA, $p < 0.05$). However, differences in abundance and

biomass between the seascape types were also influenced by salinity zone (**Fig. 4a,b**). The abundance and biomass of the IvS was consistently higher in the FS within both zones, but the abundance and biomass of Iv/Pi was higher in the FS located in Zone 1, and the abundance of Pi within FS was only significantly higher in Zone 2 (**Fig. 4a,b**).

The analysis of the ABC plots and the W-statistics indicate differences in abundance-biomass patterns between seascape types and zones. Therefore, intra- and interspecific species shifts occurred in the relative distributions of the abundance and biomass of individuals in response to spatial patterning of SAV and salinity zones. Assemblages were dominated by few small taxa/individuals, rather than large-bodied taxa/individuals (mean W-statistic = -0.049 ± 0.08 SD (-0.06 ± 0.06 in CS and -0.04 ± 0.09 in FS)). However, when separating the ABC plots and the W-statistics by zones (**Fig. 5**), there was a significantly higher positive W-statistic in the FS (0.089 ± 0.098) than in CS (-0.017 ± 0.098) present only in Zone 2 (Kruskal-Wallis ANOVA, $p < 0.05$). Also, Zone 2 has significantly higher W-statistics than in Zone 1 (Kruskal-Wallis ANOVA, $p < 0.05$). Therefore the faunal assemblages in Zone 2, especially within FS, tended to have more even abundance across species, but biomass dominated by fewer larger species.

Is species (taxonomic) richness higher in fragmented seascapes versus continuous seascapes?

Faunal assemblages in FS were significantly more diverse than in CS, according to all of the diversity indices, except for the Simpson diversity index ($1-\lambda$) (Kruskal-Wallis ANOVA, $p < 0.05$) (**Fig 6**). In addition, 8 species were only found in CS and 15 species only found in FS (**Fig. 2**).

Discussion

Applications of a landscape ecology approach to the marine environment are still relatively rare in marine ecology. This study integrated conventional faunal sampling techniques within a landscape ecology conceptual and analytical framework to quantify spatial patterning of SAV seascapes and to link these patterns to the structure of fish and crustacean assemblages. The faunal assemblage in fragmented seascapes (FS) (i.e., seascapes with high density of smaller vegetated patches with complex shapes) supported a more diverse faunal assemblage than continuous seascapes (CS) (i.e., seascapes with a higher proportion of vegetated patches including larger patches with simpler geometry), with higher occurrence of Gobiidae species, and higher abundance and biomass of caridean and paeneid shrimps, and larger generalist/omnivore individuals compared to continuous seascapes. In addition, the proportion of the abundance and biomass between different species, and between functional groups varied between salinity zones. This suggests that assemblage response patterns were also modulated by the salinity patterns and highlighting the importance of considering both seascape structure and physical-chemical properties of the environment.

Assemblage composition in continuous vs fragmented seascapes

As expected, there were differences in assemblage composition between seascape types, driven by higher abundance of small mobile species such as the caridean and paeneid shrimps in FS. Higher abundances of caridean and paeneid shrimps, among other crustacean species, have been positively related to: 1) the formation of distal isolated patches and seascapes with small patches and higher edge density (Bologna & Heck Jr.

1999, Bologna & Heck 2002, Healey & Hovel 2004), 2) patterns attributed to crowding effects (RW.ERROR - Unable to find reference:286, Macreadie et al. 2010a), and 3) the mobility along edges and increased connectivity between patches (Eggleston et al. 1998). For example, Browder et al. (1989) found a statistically significant positive linear relationship between brown shrimp catch and total patch edge in eroding salt marshes.

The community differences between seascapes were also influenced by higher abundance of *Lagodon rhomboides* (pinfish) and biomass of *Haemulon sciurus* in CS. *L. rhomboides* is an estuarine fish considered to be seagrass dependent and to have high site fidelity (Levin et al. 1997, Potthoff & Allen 2003). Pinfish use CS to avoid predation (Jordan et al. 1997, Froeschke & Stunz 2012) and enhance the tradeoff between growth and foraging efficiency (Levin et al. 1997). Irlandi & Crawford (1997) found that movement, growth, and abundance of pinfish was greater in areas of continuous vegetation (saltmarshes and seagrasses) than in areas with saltmarshes and adjacent unvegetated sand.

Seagrass beds are also an important nursery habitat for juvenile *H. sciurus* and other grunts, and play an important role in the cross-habitat utilization of grunts (Nagelkerken et al. 2000a, Nagelkerken et al. 2000b, Nagelkerken & van der Velde 2004, Grober-Dunsmore et al. 2007). For example, Yeager et al. (2012) observed that white grunt abundance and secondary production in the Bahamas were positively associated to high mean percent cover of seagrass, suggesting that CS could offer conditions that favor higher fitness for grunt species.

Patterns of functional groups and biomass

In this study, the abundance and biomass of invertivores and piscivores was significantly higher in FS. In addition, the nektonic community in FS (in Zone 2) was dominated by larger individuals, illustrating the permeability of this seascape type to predators and the potential effects of habitat patchiness on predation dynamics. For example, larger *Lutjanus griseus* (gray snapper), a generalist benthivore that forages at night (Layman et al. 2007), were observed more frequently in FS, suggesting that larger individuals of this species prefer patchy seascapes for foraging activities. Gaps, unvegetated patches, and macrophyte patches of low complexity within FS may serve as corridors facilitating the movement of large predatory species (Irlandi et al. 1995, Heck Jr & Orth 2006). In Australia King George whiting (*Silliginodes punctatus*) consumed higher quantities of prey in unvegetated areas within mosaics of seagrass and unvegetated patches (Jenkins et al. 2011), indicating increased foraging efficiency within patchy environments.

Food availability can play a significant role in describing the increased abundance of predator taxa in SAV habitats (Jenkins et al. 1996, Connolly & Hindell 2006).

Amphipods and isopods, important food items for the pink shrimp *F. duorarum* (Leber 1985, Corona et al. 2000, Schwamborn & Criales 2000), tend to accumulate at habitat edges and smaller patches (Eggleston et al. 1999, Bologna & Heck Jr. 1999, Bologna & Heck 2002, Healey & Hovel 2004), which may explain the higher abundance of pink shrimp in FS. Similarly, (Macreadie et al. 2010b) observed higher abundance of pipefish (Sygnathidae) at edges of experimental plots where their planktonic prey accumulates. Also, high densities of the brown shrimp (*Farfantepenaeus aztecus*) in marshes were

associated with seascapes with a high proportion of edges that provided positive tradeoffs between food availability and predation risk (Browder et al. 1989, Zimmerman et al. 2000, Haas et al. 2004).

Faunal diversity patterns associated with SAV seascapes

Habitat fragmentation has been shown to decrease the density and diversity of species in terrestrial systems (Debinski & Holt 2000). The opposite, however, is often observed for mobile marine fauna such as fishes, where habitat fragmentation and edge effects can have a positive influence (Bologna & Heck 2002, Pierri-Daunt & Tanaka 2014, Hensgen et al. 2014). As hypothesized, faunal species diversity was significantly higher in FS than in CS. This pattern observed in Biscayne Bay agrees with other studies that described higher species diversity in fragmented versus continuous marine habitats (Healey & Hovel 2004, Vega Fernández et al. 2005, Horinouchi et al. 2009). The positive effects of fragmentation on species diversity could be attributed to an increased co-existence of early and late-successional stages, generalist and specialist species, and high abundance of transient species (Debinski & Holt 2000, Fahrig 2003). The coexistence of two competing species has been shown to be promoted when the habitat is fragmented (Simon A. Levin 1974, Atkinson & Shorrocks 1981). This type of competition relaxation was probably reflected by the higher occurrence and abundance of *Gobiosoma robustum* and *Microgobius gulosus* in FS. These two species prefer seagrass habitats over bare sand, but, when competing directly for the same patch, *G. robustum* can displace *M. gulosus* onto patches of bare sand (Schofield 2003). In addition, in the presence of *Opsanus beta*, a predator observed in the bay, both species selected bare substrate over seagrass patches (Schofield 2003).

Moreover, fragmented seascapes may provide more niche space due to juxtaposed microhabitat patches that generalist and transient predator could exploit (Ryall & Fahrig 2006). For example, higher occurrence and abundance (biomass) of omnivore and generalist predators such as *Floridichthys carpio*, *Farfantepenaeus duorarum*, *Lutjanus griseus*, *Callinectes sapidus*, *Gobiosoma robustum*, and *Microgobius gulosus* were observed in fragmented versus continuous vegetated seascapes. Several studies have demonstrated how gaps within seagrass meadows and edges of fragmented patches can have species diversities and abundances that are similar to or even greater than seagrass core habitats (Horinouchi 2009, Horinouchi et al. 2009), which may also explain the enhanced diversity in fragmented seascapes.

Geographical influence on seascape faunal patterns

Variability in the effects of seascape spatial structure on nektonic abundance and diversity may be linked to interactions with other environmental processes. For example the variability of ecological responses to seascape spatial structure has been associated with proximity to oceanic inlets (Bell et al. 1988, Hovel et al. 2002), depth (Heithaus et al. 2009, Smith et al. 2011), and seasonal changes in populations size structures and life histories (Healey & Hovel 2004, Hensgen et al. 2014).

Our study included salinity regimes as a factor as salinity is known to influence the spatial attributes of biogenic habitats and nektonic ecological responses in the bay (Serafy et al. 2003, Browder et al. 2012). To control for confounding salinity effects, this study replicated samples and seascape treatments within two zones with distinct salinity regimes (See Lirman et al. 2008 and Santos et al. 2011 for details). The dissimilarities

between salinity zones were driven by higher abundance of *F. duorarum* in Zone 1 (higher, constant salinity) and of *L. rhomboides* in Zone 2 (lower, more variable salinity). The community metrics of the functional groups also varied between salinity zones. For example, significance differences in invertivores/piscivores abundance and biomass between seascapes were only observed in Zone 1. Both *Haemulon spp* and *Lutjanus griseus* were classified as invertivores/piscivores, species that have been observed in higher densities in Zone 1 and south of Zone 2 where salinities are higher and more stable, and closer to oceanic inlets (Faunce & Serafy 2007, Serafy et al. 2007). *L. griseus* preferred intermediate salinity levels both in the field and lab experiments, and swimming activity, may interfere with foraging efficiency, was also highest at intermediate salinity levels (Serrano et al. 2010). In contrast, the abundance of piscivores and ranked biomass cumulative dominance was different between seascapes within Zone 2. This zone is characterized by low, variable salinities and patches with lower seagrass cover (Lirman et al. 2008b, Lirman et al. 2014). The foraging efficiency of transient piscivores, such as *Sphyrnaena barracuda* and *Strongylura notata* may benefit from fragmented habitats and patches of low structural complexity by allowing access to different prey species (Heck Jr. & Orth 1980, Connolly & Hindell 2006, Horinouchi 2007).

Management relevance of a seascape approach

SAV habitats and nektonic communities have been monitored in Biscayne Bay for over a decade (Browder et al. 2012, Lirman et al. 2014); however, this study demonstrated for the first time how spatial differences in faunal abundance, community structure, and species diversity are correlated with SAV seascape spatial properties.

Understanding the influence of SAV fragmentation on associated fauna is of growing importance since SAV seascapes play important ecological roles (i.e. critical refuge and foraging habitat for a diverse number of species) but at the same time are continuously disturbed in coastal embayments and continue to decline worldwide (Orth et al. 2006). While this study observed higher diversity and abundance of dominant species in fragmented SAV seascapes, it is important to note that fragmentation is a continuous habitat transformation process and possible ecological thresholds may exist with respect to fragmentation gradients. Under continuous disturbance events SAV fragments may keep fragmenting or reduce in size, which may get to a point where most seagrass associated fishes disappear and the nektonic assemblage becomes similar to that on bare sand (Horinouchi 2007, Boström et al. 2011).

The Comprehensive Everglades Restoration Plan (CERP) is currently underway in Florida with a goal of capturing fresh water that currently flows to the ocean and redirecting it to inland areas to restore the Everglades and provide water for urban areas and agriculture. Future changes in freshwater flow are likely to further influence the spatial composition and configuration of vegetated seascapes in Biscayne Bay. Restoring a more natural pattern of freshwater inflows is a major focus of CERP with the spatial distribution of seagrasses potentially providing an effective indicator of ecosystem response to CERP activities. Thus, the interaction between the salinity zones and the seascape properties observed in this study heightens the importance of describing seascape level faunal relationships to identify linkages between CERP restoration scenarios, seascape fragmentation, and cascading effects on fauna.

Clearly, the ecological responses to changes in the structure of SAV seascapes should be incorporated into future studies on species persistence and community assemblage stability under anthropogenic disturbances. Using a seascape approach that combines statistical models, simulation, small-scale manipulations and broad-scale inter-annual surveys may provide the necessary information to identify critical thresholds that signal major ecosystem shifts, and help conceptualize the potential future effects of water management practices on the spatial composition and configuration of seagrass habitats and their associated nektonic communities.

Table 3.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne. Metrics were used in multivariate analysis to identified continuous and fragmented SAV seascapes

Metric	Acronym	Category	Aspect	Description	Formula
Percentage of Landscape	PLAND	Composition	Area/Density	<ul style="list-style-type: none"> Percentage of the total landscape made up of the corresponding class 	$PLAND = \frac{\sum_{j=1}^n a_{ij}}{A} (100)$
Mean Patch Size	MPS	Composition/ Configuration	Area/Density	<ul style="list-style-type: none"> Average size of a particular class Units in ha 	$MPS = \frac{\sum_{j=1}^n a_{ij}}{n_i}$
Patch Size Coefficient of Variation	PSCV	Configuration	Area/Density	<ul style="list-style-type: none"> Variability in patch measures Units in ha 	$PSCV = \sqrt{\frac{\sum_{j=1}^n [a_{ij} - MPS]^2}{n_i}} \frac{1}{MPS}$
Patch Density	PDENS	Configuration	Area/Density	<ul style="list-style-type: none"> Number of patches of a certain class divided by the total landscape area Units n of patches/ha 	$LD = \left[1 - \sum_{l=0}^n \left(\frac{a_l}{A} \right)^2 \right]$
Total Edge	TE	Configuration	Edge	<ul style="list-style-type: none"> Sum of the lengths of all edges Units in m 	$TE = \sum_{k=1}^m e_{ik}$
Area-Weighted Mean Patch Fractal Dimension	AWMPFD	Configuration	Shape	<ul style="list-style-type: none"> Measure of patch shape complexity 	$= \sum_{j=1}^n \left[\frac{2 \ln(.25 p_{ij})}{\ln a_{ij}} \left(\frac{a_{ij}}{\sum_{j=1}^n a_{ij}} \right) \right]$

Table 3.2. Results from the similarity percentages (SIMPER) analysis for the a) occurrence, b) abundance and c) biomass data. The first two columns present the average probability occurrence, abundance and biomass within each seascape type. Mean dissimilarity is the average species contribution to the separation, estimated from a Bray-Curtis dissimilarity matrix, between the seascape types. Last two columns expressed the percentage dissimilarity contributing to the global dissimilarity between treatments

a) Occurrence					
Species	Probability of occurrence in FSS	Probability of occurrence in CSS	Mean Dissimilarity	Contrib%	Cum.%
<i>Floridichtys carpio</i>	0.77	0.27	2.83	6.41	6.41
<i>Microgobius gulosus</i>	0.7	0.23	2.72	6.17	12.58
<i>Gobiosoma robustum</i>	0.8	0.37	2.61	5.9	18.48
<i>Strongylura notata</i>	0.77	0.47	2.32	5.26	23.74
<i>Callinectes</i> spp.	0.93	0.5	2.32	5.26	29
Syngnathidae	0.73	0.5	2.28	5.16	34.17
<i>Sphyraena barracuda</i>	0.63	0.57	2.19	4.96	39.13
<i>Opsanus beta</i>	0.67	0.57	2.18	4.93	44.06
<i>Harengula humeralis</i>	0.6	0.6	2.17	4.92	48.98
Caridean shrimps	0.77	0.63	2	4.54	53.51
b) Abundance					
Species	Mean Abundance (#) in FSS	Mean Abundance (#) in CSS	Mean Dissimilarity	Contrib%	Cum.%
Caridean shrimps	4.16	0.88	6.63	12.62	12.62
<i>Lagodon rhomboides</i>	4.26	5.23	5.35	10.19	22.81
<i>Farfantepenaeus duorarum</i>	28.96	15.61	5.14	9.79	32.6
<i>Gobiosoma robustum</i>	1.77	0.13	4.12	7.85	40.45
<i>Floridichtys carpio</i>	1.18	0.43	3.91	7.45	47.9
<i>Microgobius gulosus</i>	1.39	0.07	3.65	6.95	54.85
c) Biomass					
Species	Mean Biomass (g) in FSS	Mean Biomass (g) in CSS	Mean Dissimilarity	Contrib%	Cum.%
<i>Haemulon sciurus</i>	7.25	8.68	2.8	9.02	9.02
<i>Lutjanus griseus</i>	19.91	7.17	2.68	8.65	17.67
<i>Callinectes</i> spp.	10.59	2.67	2.44	7.87	25.54
<i>Harengula humeralis</i>	1.25	2.97	2.18	7.02	32.56
<i>Lagodon rhomboides</i>	80.45	80.45	1.89	6.1	38.66
<i>Opsanus beta</i>	3.22	4.05	1.55	4.98	43.64
<i>Strongylura notata</i>	2.32	1.56	1.36	4.37	48.01
<i>Floridichtys carpio</i>	1.25	0.58	1.3	4.19	52.2

Figure 3.1. a) Study area, b) seascape map, c) superimposed 500 x 500 m grid and areas classified and selected as continuous (light green) and fragmented (red) SAV seascapes. d) Within each selected grid cell three sampling replicates (yellow points) were randomly placed within 5 distance (to shore) strata/zones

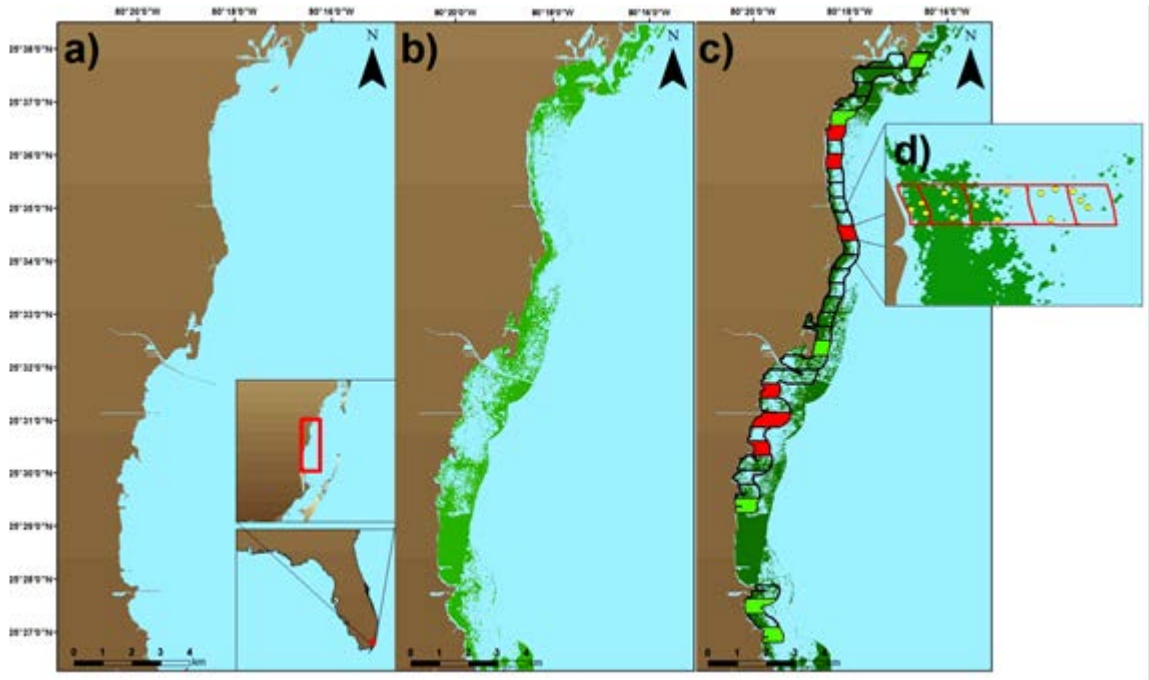


Figure 3.2. Relative abundance of faunal species within assemblages sampled from the nearshore area of Biscayne Bay by: a) seascape and b) zone. Bars illustrate the proportion of the abundance for each species observed within the CS (grey) and FS (black) SAV seascapes, and within Zone 1 (black) and Zone 2 (grey)

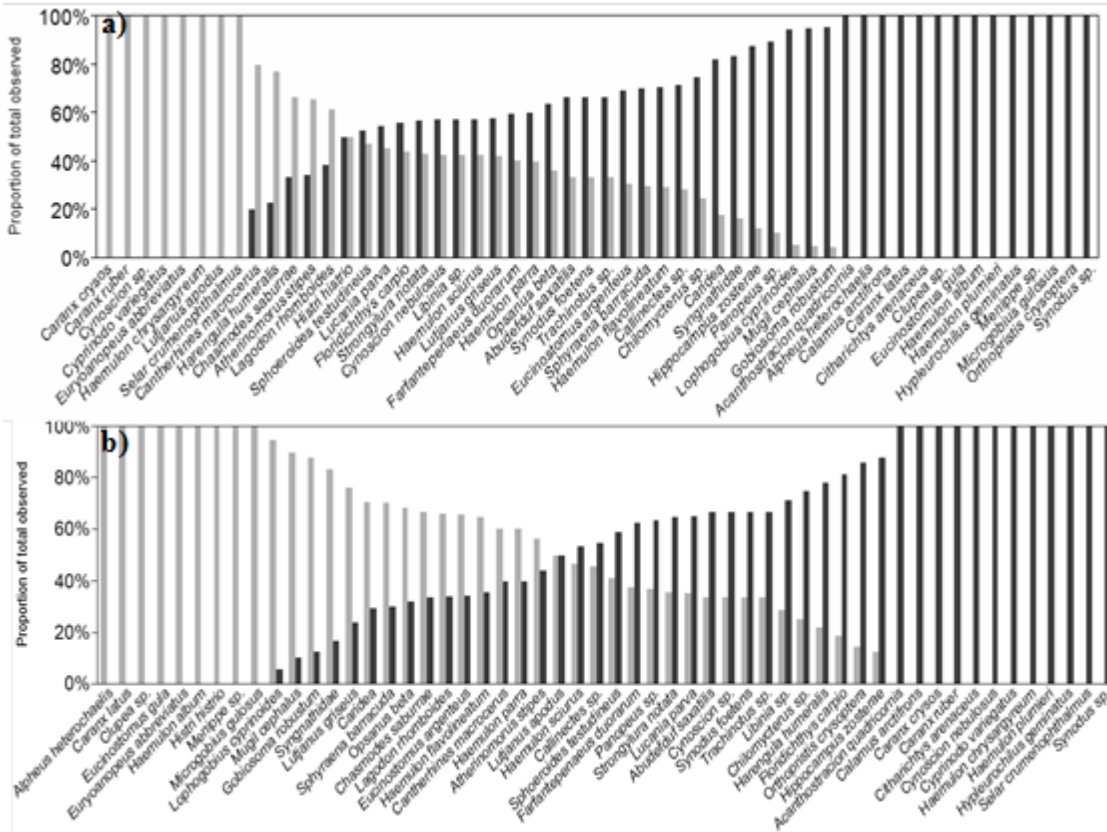


Figure 3.3. Multi-dimensional scaling (MDS) plots of the a) occurrence, b) abundance and c) biomass community data. Grey and black triangles illustrate the ordination space of continuous and fragmented SAV seascapes. The space between triangles is proportional to the level of dissimilarity. Blue lines represent the 75% similarity contour

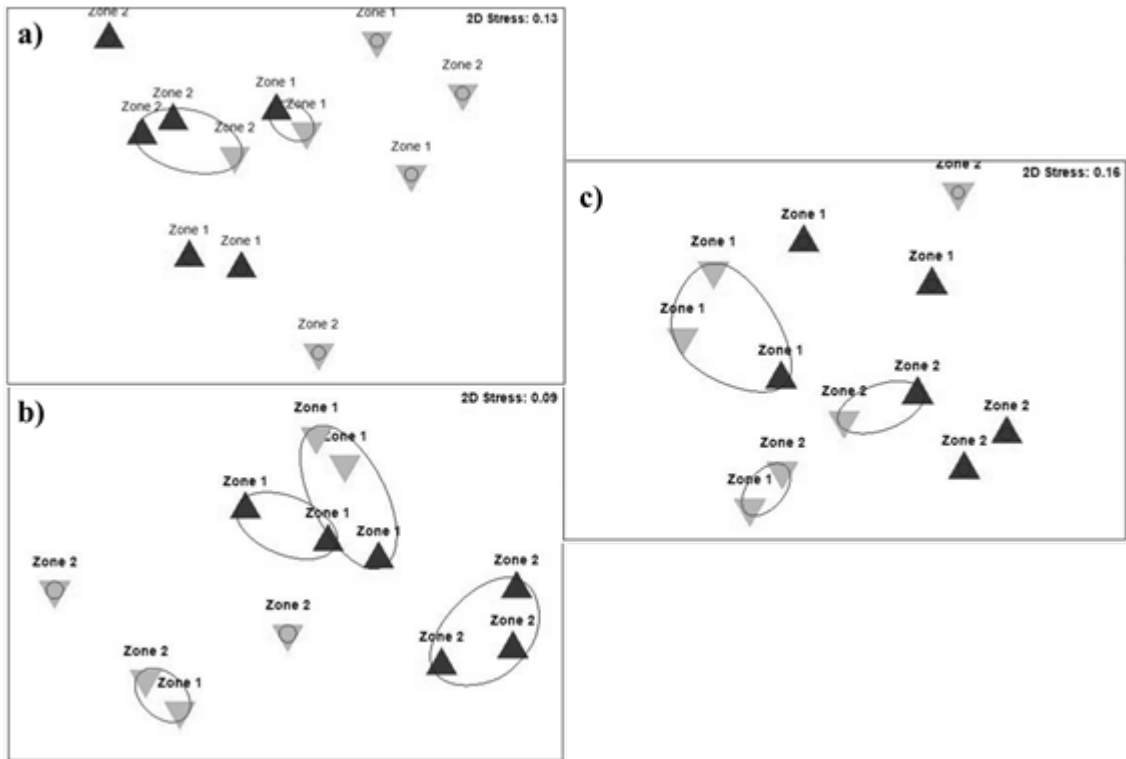


Figure 3.4. a) Abundance and b) biomass for functional groups (error bars: standard deviation): invertivores of sessile prey (IvS), invertivore of small mobile prey (IvSm), invertivore and piscivore (Iv/Pi) and piscivores (Pi). Asterisks (*) mark the functional groups which abundance and/biomass significantly differed between seascape types (Kruskal-Wallis analysis of variance, $p < 0.05$). Continuous and fragmented SAV seascape in light and black, respectively.

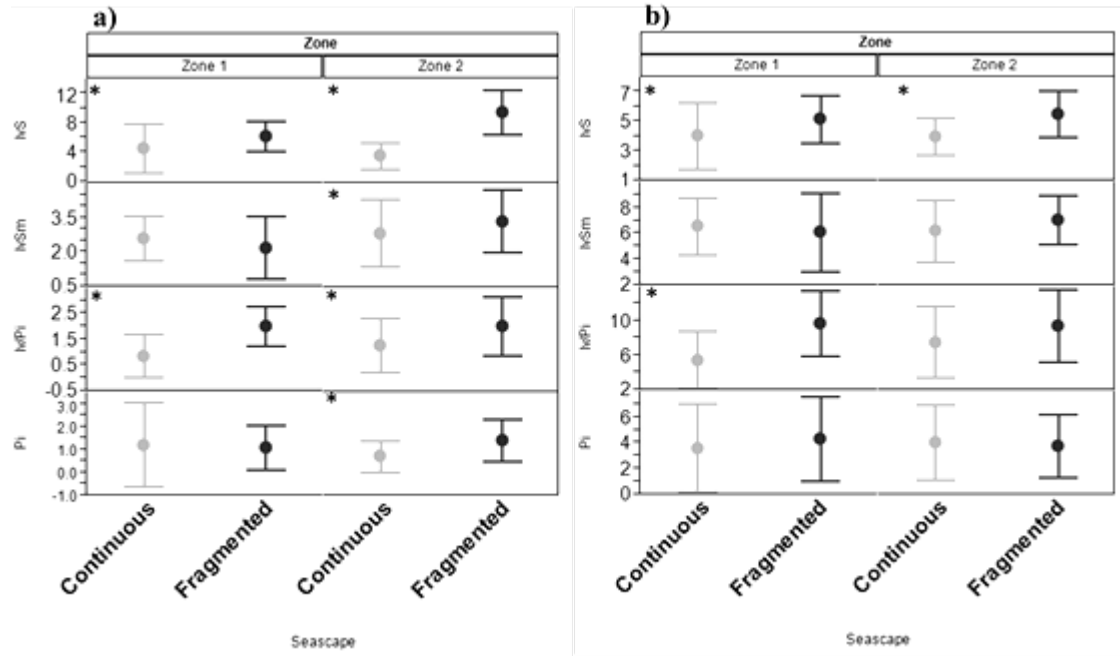


Figure 3.5. W-statistic compared between continuous (light gray) and fragmented (black) SAV seascapes. W statistics quantified the accumulative difference between the biomass and abundance cumulative dominance curves. Asterisks (*) mark where the W-statistic significantly differed between seascape types (Kruskal-Wallis analysis of variance, $p < 0.05$)

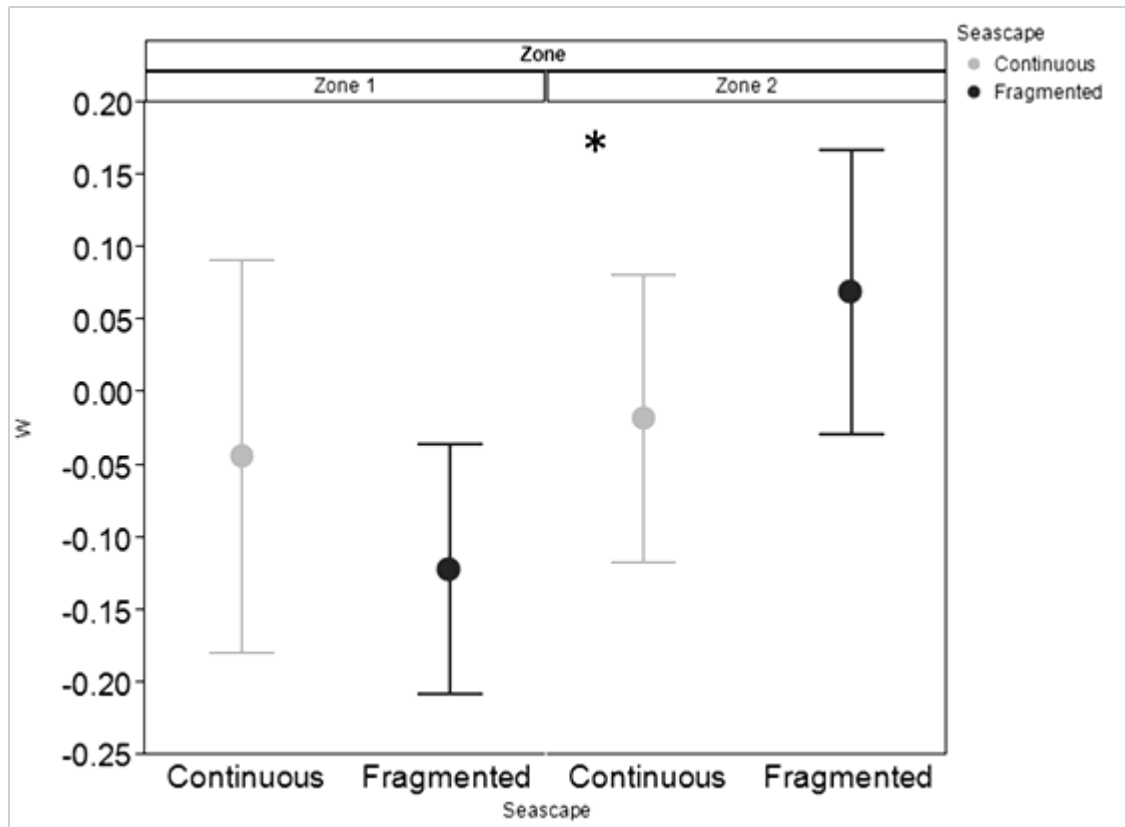
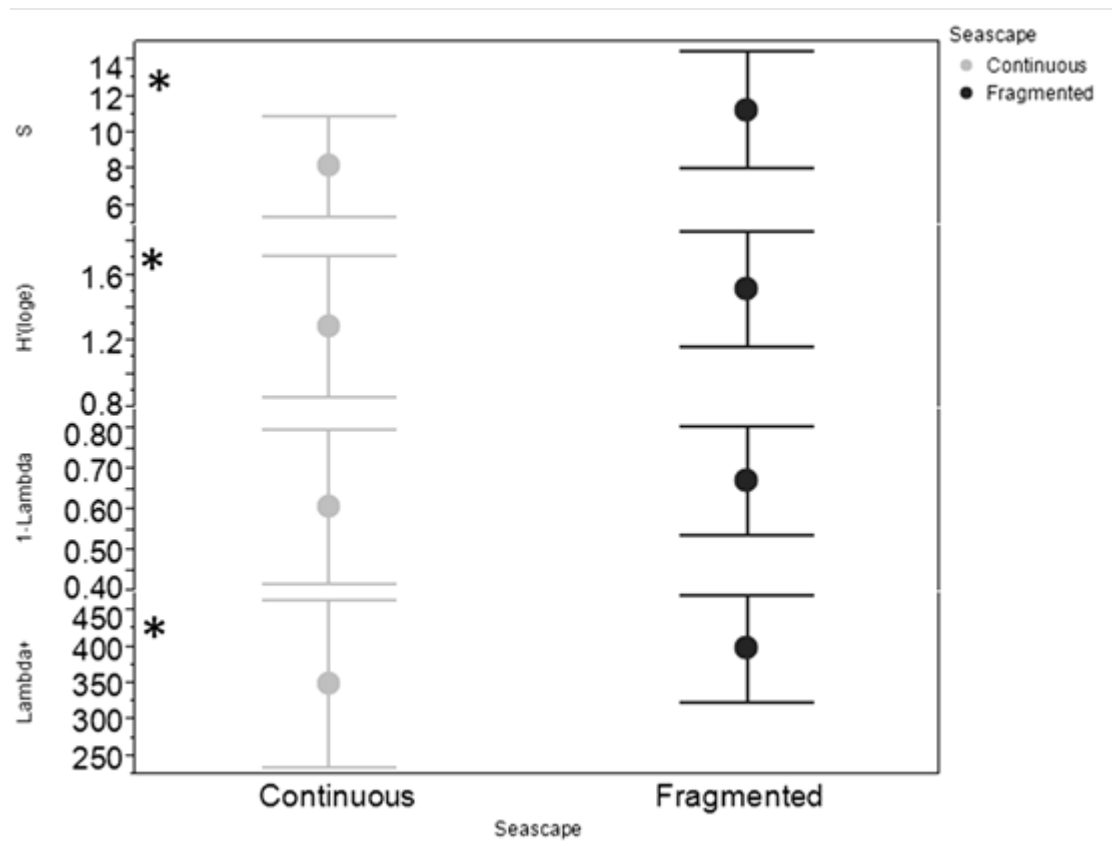


Figure 3.6. Species diversity indices (error bars: standard deviation): species richness (s), Shannon-Weiner ($H'(\log_e)$), Simpson diversity ($1-\text{Lambda}$), and variation in taxonomic distinctness ($\text{Lambda}+$) compared between continuous (light gray) and fragmented (black) SAV seascapes. Asterisks (*) mark the species diversity indices that significantly differed between seascape types (Kruskal-Wallis analysis of variance, $p < 0.05$)



Chapter 4. Ecological responses of three marine organisms to the spatial structure of seagrass habitat: habitat loss and fragmentation thresholds

Summary

Habitat destruction can have detrimental effects on the resilience and persistence of ecologically important marine species. To efficiently manage marine resources, it is important to assess how key populations respond to habitat amount and spatial configuration. This study was designed to determine the importance of seagrass patch complexity, and habitat spatial composition and configuration to the abundance of *Farfantepenaeus duorarum*, *Lagodon rhomboides* and *Lucania parva*. This study concentrated in Biscayne Bay, Florida, U.S.A where seagrass habitat loss and fragmentation have been linked directly to man-made changes to salinity patterns.

Seascapes were mapped using satellite images, and the nektonic species were sampled at night using seine nets. Generalized additive models (GAMs) were employed to explore non-linear faunal responses and detect abundance thresholds in relation to seascape properties. GAMs explained > 70% of the abundance patterns. The amount of seagrass habitat and its patch configuration (and their interactions), were the most influential predictors of faunal abundance. Abundance thresholds were identified for all species in response to patch complexity and habitat composition and configuration. Pink shrimp abundance (*Farfantepenaeus duorarum*) was highest in mesohaline conditions and intermediate levels of fragmentation. *L. rhomboides* abundance peaked at low and high values of fragmentation. Lastly, the abundance of *L. parva* was significantly related to the amount of habitat. This study demonstrated how the abundance of important nektonic species in Biscayne Bay could be susceptible to habitat loss and fragmentation.

Background

The spatial transformation of habitats is one of the main drivers of biodiversity loss in marine (Kennish 2002, Jackson 2008) and terrestrial ecosystems (Tilman et al. 2001, Balmford et al. 2003). The urgency in understanding the ecological consequences of spatial transformation is heightened by the rapid global decline in the area and quality of coastal habitats such as coral reefs, mangroves, and salt marshes (Pittman et al. 2011). Habitat transformation involves two components that often occur in concert: habitat loss and habitat fragmentation. The former is the reduction in the amount or the proportion of habitat space occupied by foundation species like seagrasses or mangroves, while the latter refers to the division of large, continuous habitat patches into smaller units, which influences mean patch size, patch isolation, and edge effects (Andren 1994, Fahrig 2003, McGarigal et al. 2005).

Habitat loss and fragmentation commonly occur simultaneously (Haila 2002) and their effects are often confounded (Didham et al. 2012). Robust ecological assessments and effective management practices require an understanding of both the independent and interactive effects of each of these two processes because restoration strategies may differ depending on the primary cause of habitat degradation (Lindenmayer & Fischer 2007). While habitat loss has been the historical focus of both observational (McGarigal & McComb 1995, Smith et al. 2011b, Villard & Metzger 2014) and experimental (Caley et al. 2001, Hovel & Lipcius 2001) studies of habitat degradation, the effects of fragmentation on associated fauna can also be significant (Andren 1994, Turner et al. 2001). In this study, I quantify the independent and interacting effects of submerged aquatic vegetation (SAV) habitat amount, spatial configuration, and within-patch

structural complexity on the occurrence and abundance of selected fish and shrimp species that inhabit seagrass and macroalgae habitats in Biscayne Bay, a subtropical coastal lagoon adjacent to the city of Miami, USA. By incorporating habitat structure, spatial seascape metrics, and generalized additive models (GAMs), we assessed the occurrence and abundance of pink shrimp (*Farfantepenaeus duorarum*), pinfish (*Lagodon rhomboides*), and rainwater killifish (*Lucania parva*) in relation to different SAV seascape characteristics and identified thresholds in the response of organisms to within-patch structure and SAV habitat composition and fragmentation.

A large number of studies have documented negative impacts of habitat loss on species richness and abundance (Schmiegelow & Mönkkönen 2002, Fahrig 2003, Smith et al. 2011a), but the effects of fragmentation on associated species are more variable and, in some cases, even positive (Debinski & Holt 2000, Fahrig 2003). Habitat loss causes negative impacts by eliminating key resources that influence, directly, reproduction, recruitment and survival (Fahrig 2003). While habitat losses are a required first step of habitat fragmentation (Didham et al. 2012), changes in the spatial configuration of habitat patches may have a positive outcome through the expansion and diversification of microhabitat types (Horinouchi et al. 2009, Horinouchi 2009), improved animal movement and patch interception (Connolly & Hindell 2006), reduced competition for resources, and modified dynamics of predator-prey systems (Hovel & Lipcius 2001, Fahrig 2003). Nevertheless, studies that have explored impacts of seagrass habitat fragmentation on associated fauna have reported mixed findings. For example, Healey and Hovel (2004) found that epifaunal density and diversity correlated with increasing patchiness, but responses were highly variable among taxa and in time.

Several studies have revealed how seagrass patchiness can increase predation risk from fish on crustaceans and bivalves (Irlandi et al. 1995, Hovel & Lipcius 2001). Using artificial seagrass patches Macreadie et al. (2010a, 2010b) observed higher fish densities in fragmented patches. Finally, edge effects in seagrass habitats, which tend to increase with fragmentation (Arponen & Boström 2012, Pierri-Daunt & Tanaka 2014), can have both negative (Hovel & Lipcius 2002, Bologna & Heck 2002) and positive (Bologna & Heck 2002; Arponen & Bostrom 2012) influences on the abundance of associated fauna. However, positive responses to increased availability of edge habitats were found more often than negative ones, especially for fish (Boström et al. 2011).

Both the composition and configuration of SAV seascapes influence key ecological processes such as faunal recruitment, dispersal, survivorship, and connectivity (Pittman et al. 2004, Pittman et al. 2007, Hovel & Regan 2008, Mellin et al. 2009, Boström et al. 2011). The majority of the studies that have evaluated ecological responses of marine species to habitat spatial properties, especially on seagrass and macroalgae habitats, have focused on the relationships between nektonic organisms and the within-patch structural complexity of their habitats (e.g., rugosity, benthic cover and composition) (Connolly & Hindell 2006, Horinouchi 2007, Pittman et al. 2011). Few studies have separated the effects of habitat loss and fragmentation on ecological responses (Caley et al. 2001, Healey & Hovel 2004, Bonin et al. 2011), and even fewer studies have identified critical thresholds where small changes in habitat spatial properties may lead to large changes in faunal responses (Salita et al. 2003, Pittman et al. 2004, Thistle et al. 2010). Seagrass and macroalgae (SAV) habitats are ideal for the study of habitat-faunal responses to seascape structure due to their propensity to form variable-

sized patches (Robbins & Bell 1994, Bell et al. 2007). Habitat loss and fragmentation are of great concern in seagrass ecosystems since seagrass habitats have declined significantly around the world in the last few decades due to anthropogenic disturbances such as declining water quality caused by freshwater discharges from canals, nutrient loading, sediment runoff, changes in salinity patterns, and direct physical removal by dredging, vessel groundings, and propeller scarring (Orth et al. 2006).

In this study, I combine the detailed mapping of SAV patch-mosaics and collections of fish and shrimp species within continuous and fragmented habitats (Chapter 2 and 3) to document species-specific responses to SAV seascape characteristics and to determine whether abundance thresholds with respect to seascape fragmentation and composition exist for key epibenthic species associated with seagrass habitats of Biscayne Bay, a coastal lagoon heavily influenced by water management practices that have resulted in the fragmentation of seagrass communities (Santos et al. 2011; Santos et al. accepted). I also combine field data and statistical models to develop spatial simulation scenarios to evaluate the response of pink shrimp to changes in SAV habitat configuration and composition under different salinity environments expected to be influenced by water management actions in South Florida as part of the Comprehensive Everglades Restoration Plan (Lirman et al. 2014).

Materials and Methods

Study site

The present study was conducted in western Biscayne Bay, Florida, USA (**Figure 4.1a**). Biscayne Bay is a shallow subtropical lagoon located adjacent to the city of Miami and downstream of the Florida Everglades system. Sampling of the selected species focused on nearshore submerged aquatic vegetation (SAV) habitats (< 500 m from shore), which are dominated by seagrasses and macroalgae species (Lirman et al. 2008b, 2014). Nearshore SAV habitats in the bay form distinct mosaics of patches with different spatial configuration that are influenced by freshwater pulses from canals (Santos et al. 2011, Santos et al. accepted).

Sampling design

Fishes and crustaceans species were collected at night seines in July-October 2012. One plot (100 x 500 m) was randomly positioned perpendicular to shore within locations previously selected to evaluate SAV seascape patterns by Santos (Chapter 2) (**Figure 4.1b**). Each location was further divided into 5 distance-to-shore areas to evaluate cross shelf patterns (**Figure 4.1b,c**). The location of each net deployment ($n = 3$ per cross-shelf section) was determined at random ($n = 15$ seine hauls per cell/location). Marine fish and crustaceans were collected with a center-bag seine net (21.3 m long, 1.8 m deep, 3 mm mesh) following the Florida Marine Institute, Fisheries Independent Monitoring Program Procedure Manual (FMRI 2010). The seine was deployed and retrieved by boat, and each seine haul swept approximately 210 m². For this study, I calculated the abundance (total number of individuals) of *Farfantepenaeus duorarum*

(pink shrimp), *Lagodon rhomboides* (pinfish), and *Lucania parva* (rainwater killifish).

These are the among most abundant species in the mainland nearshore of Biscayne Bay (Serafy et al. 1997, Browder et al. 2012) and were selected because they have a high economic value (Tilmant 1989, Nelson 2002, FWCC 2010) and play an important role in nearshore food webs (Schmidt 1989, Corona et al. 2000, Bruno & O'Connor 2005).

Seascape mapping

The spatial patterns of SAV seascapes in the study area were mapped using statistical classification techniques applied to spectral information on high resolution (1.6-meter pixel size) GeoEye multispectral (four spectral bands: blue, green, red, near-infrared) satellite images. Satellite image processing for the seascape mapping is described in detail in Chapter 2. A supervised object-based image classification was performed using the ENVI v4.5 Feature Extraction module (ITT Visual Information Solutions 2008) to delineate subtidal vegetated patches with medium to high horizontal foliage cover (i.e., 40-100%). Seascape maps with an overall 72% accuracy were created using the benthic information collected by Lirman et al. (2014) for training and validation (Chapter 2).

Seascapes spatial structure

Measures of SAV seascape composition and configuration, and within-patch structural metrics were used to characterize the response of the selected species. SAV seascape habitat composition and configuration were characterized based on spatial pattern metrics calculated with the FRAGSTATS software (McGarigal et al. 2012). Spatial pattern metrics quantified the proportional area or cover (i.e., composition -

habitat amount), and spatial configuration of patches in the seascapes (i.e., configuration - patchiness or fragmentation of seascapes) (**Table 4.1**). The proportional cover (PLAND) was used to quantify the amount of focal habitat, and was calculated as the percentage of the total seascape made up of SAV patches (termed “habitat cover” hereafter). The spatial configuration of SAV seascape was quantified with the patch density (PD), mean radius of gyration (GYRATE_MN) and mean patch fractal dimension (FRAC_AM) metrics. These metrics quantify respectively three distinct characteristics of spatial pattern affected by fragmentation: habitat subdivision, extensiveness, and geometry. These metrics were selected because they tend to be robust across spatial scales (i.e., grain and/or extent size) (Wu et al. 2002, Wu 2004), total areal coverage and aggregation of the target habitat (Neel et al. 2004; Sleeman et al. 2005; Cushman et al. 2008), and have been utilized previously to assess the effects of SAV seascape fragmentation on fish and invertebrate species (Hovel & Lapicus 2001, Salita et al. 2003, Boström et al. 2011).

Since the three spatial-pattern metrics used quantify different aspects of spatial properties (habitat size, compactness, habitat subdivision, and habitat geometry), these metrics were integrated into a single fragmentation index following a similar approach described in Chapter 2. Similar approaches have been used previously to assess the effects of fragmentation or habitat spatial configuration on ecological patterns (e.g., species diversity, probability of occurrence and abundance of terrestrial and marine species) independent of habitat loss or habitat amount (McGarigal & McComb 1995; Trzcinski et al. 1999; Kaufman 2011). The metrics used here were combined into the following composite fragmentation index (FragIndex):

$$\text{FragIndex} = \sqrt[3]{(\text{PD} * \text{FRAC_AM} * 1 / \text{Gyrate_MN})}$$

All metrics were standardized to produce a FragIndex ranging from 0 (low fragmentation) to 1 (high fragmentation).

Three circular seascape sample units (SSU) were created around the sampling points (N = 113), such that each point served as the center of 50 m, 100 m, and 150 m-radius plots (**Figure 4.1c**). Habitat cover and fragmentation metrics were then calculated for each circular plot, thereby allowing examination of epibenthic abundance patterns at these three spatial scales. The distance-to-shore was estimated for each point using ArcMap (ESRI).

Within-patch structure

Measurements of structural complexity within patches consisted of estimates of *Thalassia testudinum*, *Halodule wrightii*, and macroalgae percent cover, and measurements of canopy height collected from within the footprint of each seine (210 m²). Macroalgae were further divided into drift (algae not attached to the bottom and free to move around with the currents) and rhizophytic (algae with a firm attachment to the bottom through a holdfast) as described by Lirman et al. (2008a, 2008b). Percent cover values were obtained by estimating the proportion of the bottom occupied by each SAV taxon within digital images taken in situ by a diver. A total of ten random images (covering approximately 0.25 m² each) were scored to calculate averages for each taxon (Lirman et al. 2008a). In addition, 10 random measurements of canopy height were taken at each site as an estimate of within-patch topographical complexity.

Statistical analyses

Model fitting

Generalized additive models (GAMs) were used to assess the occurrence and abundance response of pink shrimp, pinfish, and rainwater killifish to SAV seascape characteristics. A GAM is a semi-parametric extension of the generalized linear model (GLM) that includes a linear predictor involving the sum of smooth functions of covariates (Guisan et al. 2002, Sagarese 2013). GAMs are especially useful to explore relationships that exhibit complex forms such as hump-shape curves (Crawley 2012) and can be used to identify ecological thresholds (Francesco Ficetola & Denoël 2009).

GAMs were applied in R (R Core Development 2010) with the package ‘mgcv’ (Wood 2006). Cubic regression splines were used as the penalized smoothing basis (R code: `bs = “cr”`), and a tensor product interaction was used to assess the contribution of two-way interaction effects of different covariates (R code = `ti`). A maximum of 5 dimensions of the bases (R code: `k = 5`) were used to represent the smooth term value that was justified with results from diagnostic tests within the mgcv package (`gam.check`) which assess whether the basis dimension choices are adequate or too small. A gamma value of 1.4 ($\gamma = 1.4$) was included to control for the overfitting of the smoothing estimated by the unbiased risk estimator (UBRE) criterion.

Occurrence (present = 1, absent = 0) and abundance (total number per seine) models were assessed separately to account for zero-inflation (i.e., positively skewed data) and overdispersion (Potts & Elith 2006). The occurrence GAMs (O_{gam}) were fitted

using a log link function and a binomial error distribution, and the abundance GAMs (A_{gam}) were fitted using a log link function and negative binomial error distribution.

Model selection

Patterns of habitat utilization by associated fauna may be scale-dependent (Pittman et al. 2004, Purkis et al. 2008). Therefore, the occurrence and abundance responses of each species to the seascape (e.g., cover and fragmentation indices) were calculated within SSU of increasing diameter (e.g., 50m, 100m, 150m— **Figure 4.1c**) to identify the optimum spatial scale to quantify these relationships. The optimum spatial pattern metric sub-model was selected based on the lowest Akaike's information criterion (AIC), and highest r^2 and deviance explained. These sub-models included the interactions between percent cover and the fragmentation index, and the interaction between these metrics and distance-to-shore. After the optimum spatial scale of the sub-model was selected, these models were combined with the measurements of within-patch structural complexity (SAV cover and canopy height) to form a single full model. To reduce model complexity and overfitting of the full model, an extra penalty was given to each smooth function, penalizing its 'fixed effect' component (Wood 2011). This was done with an automatic term selection in R, where the smoothing parameters for a term tending to infinity were zeroed out and selected out of the model (Wood 2011).

Model evaluation

The O_{gam} accuracy was evaluated using the receiver operating characteristic (ROC) and the associated area under the curve (AUC) calculated with the 'PresenceAbsence' package in R. The AUC is a test statistic that uses presence and

absence records to assess model predictive performance across a range of thresholds (Leathwick et al. 2006, Pittman & Brown 2011). AUC values between 0.7-0.8 reflect an acceptable prediction, and values >0.9 good as the true positive rate was high relative to the false positive rate (Pearce & Ferrier 2000, Pittman & Brown 2011, Sagarese 2013). Observed versus predicted values from simple linear regressions were created to measure model calibration, where the intercept and slope were interpreted as measures of bias and consistency respectively (Potts & Elith 2006).

The validation of the A_{gam} was performed using performance estimators such as calibration plots, correlation, and mean error (Potts & Ellith 2006). The calibration was conducted as described above, using the bias and consistency proxies from the observed-predicted linear regression coefficient, with perfect calibration indicated by slope of 1 and an intercept of 0. The Pearson's correlation coefficient provided an indication of how closely the observed and predicted values agree in relative terms, and the Spearman's rank correlation used as indication of similarity between ranks (Potts & Elith 2006). The root mean square error and average error were also used to assess discrepancy between the observed and predicted values. Spatial autocorrelation of the response variable was tested using a Mantel test on the model residuals.

Seascape simulations under different salinity environments

F. duorarum (pink shrimp) is a specific target species of the Comprehensive Everglades Restoration Plan (CERP) and of great economic value to South Florida (Browder & Robblee 2009). Previous studies have shown a clear relationship between salinity patterns significantly influenced by fresh water delivery into coastal bays from

the Everglades (Chapter 1) and shrimp abundance and distribution (Ault et al. 1999). Similarly, salinity patterns influence the abundance and distribution of seagrasses and macroalgae that provide habitat to shrimp (Lirman et al. 2014). Here, our *F. duorarum* abundance GAM model was applied to predict pink shrimp abundance for a series of simulated seascapes to quantify and illustrate the importance of habitat amount and configuration interrelationships to this species, and contrast their effects under different within-patch structural complexity scenarios influenced by salinity. Nine seascapes were created, three seascapes with 25%, 50% and 80% of habitat cover; each with three levels of fragmentation: high, medium, and low. Each seascape was simulated with the mean vegetation cover commonly found in 3 halohabitats previously identified in Biscayne Bay by Lirman et al. (2014): mesohaline (5-18 ppt), polyhaline (18-30 ppt), and euhaline (30-40 ppt).

The seascapes were created with Qrule, a program for the analysis of landscape patterns and generation of neutral models, using fractal random maps (Gardner & Urban 2007). The simulated seascape characteristics were control with the parameter of spatial autocorrelation (H) and the proportion of the landscape occupied by habitat patches (P). ArcGIS 9.3 was used to extract the habitat information from the overlapped simulated seascapes and the maps of the halohabitat scenarios, and applied the GAM models to produce different abundance maps using an inverse distance weighting interpolation procedure. Zonal statistics were used in ArcMap to summarize the abundance into number of individuals*hectare⁻¹ and performed an analysis of variance to depict abundance patterns between the simulated seascapes.

Results

Based on the lowest Akaike's information criterion (AIC) and highest deviance explained, the abundance sub-models presented a better fit within the 100m seascape sample unit (SSU) for all species (**Table 4.2a**). The optimum spatial scales were 50m, 100m, and 150m for the occurrence of *L. rhomboides*, *F. duorarum* and *L. parva*, respectively (**Table 4.2b**). The full abundance, A_{gam} and occurrence, O_{gam} models included only the spatial pattern metrics calculated within these optimum spatial scales.

Influential variables varied among species and between the abundance and occurrence GAMs (**Table 4.3, Fig. 4.2, 4.3**). Habitat amount and fragmentation (and their interactions) were the most influential predictors of faunal abundance for all three species (**Figure 4.2a**) and in the occurrence of *L. rhomboides* (**Figure 4.2b**). The deviance explained by the *F. duorarum*, *L. rhomboides* and *L. parva* abundance models was 75%, 74%, and 85% respectively. Only the O_{gam} results for the *L. rhomboides* showed was significant (**Table 4.3**). Even though the *F. duorarum* and *L. parva* O_{gam} showed a high explained deviance, these models were not considered for further analysis. After inspecting residual and response plots, and due to the lack of significant smooth parameters of these two models (**Table 4.3**), it was evident that the high percentage of explained deviance was a product of overfitting.

Seascape spatial pattern trends

Based on the proportions of deviance explained, fragmentation level and the interaction between fragmentation and the proportion of the seascape occupied by SAV (habitat amount) were the best predictors of species occurrence and abundance (**Figure**

4.2). By itself, the proportion of the seascape occupied by SAV explained only a limited portion of deviance observed (< 5%) (**Figure 4.2**). An abundance maximum for *L. parva* was evident when the habitat amount was 50 to 60% (**Figure 4.3c – PLAND_100**). *F. duorarum* abundance presented a weak negative response to fragmentation (**Figure 4.3a – FragIndex_101**), and *L. rhomboides* abundance had a U-shaped response, with abundance increasing at low and high levels of fragmentation (**Figure 4.3b – FragIndex_101**). *F. duorarum* and *L. rhomboides* abundance declined significantly after 300 m from the mangrove shoreline (**Figure 4.3a,b – Dist_Shore**). In contrast, *L. parva* abundance showed a significant negative linear relationship with distance-to-shore (**Figure 4.3c – Dist_Shore**). The effects of distance to shore on *L. rhomboides* probability of occurrence also peaked at 200m to 300m from shore.

Within-patch structure

The most influential within-patch predictors of the abundance of epibenthic species were the percent cover of *Thalassia testudinum* (Tt), followed by the cover of drift and rhizophytic algae (**Figure 4.2**). Low to intermediate levels of Tt percent cover had weak positive effects on *F. duorarum* and *L. parva* abundance (**Figure 4.3a, c – Tt**). However, Tt percent cover presented strong positive effects on *L. rhomboides* abundance and occurrence (**Figure 4.3b – Tt, Figure 4.4 – Tt**), with an abundance peak at mid-range values (**Figure 4.3b – Tt**). Drift algae percent cover had a significant positive effect on the abundance of *F. duorarum* and *L. rhomboides* (**Figure 4.3a,b – Drift**). Lowest levels of rhizophytic algae abundance were evident at 10% cover of rhizophytic algae, increasing with lower and higher cover values (**Figure 4.3a,b**). The probability of occurrence of *L. rhomboides* decreased linearly with rhizophytic algae cover (**Figure 4.4**

– **Rhizo**). The abundance of *F. duorarum* was highest at 20% cover of *H. wrightii*, while the abundance of *L. parva* increased with increasing *Halodule* cover (**Figure 4.3a-c – Hw**). Canopy height effect on the three species abundance was low overall.

Model validation

Modeled relationships exhibited a strong agreement between the predictions and observations (**Table 4.4a** - both Pearson's and Spearman's correlation coefficients >0.7). Based on the model calibration, the models indicated a relatively small but consistent bias (**Table 4.4a** – intercept: $-3 < b < 0.1$; slope: $1.01 < m < 1.15$). *L. parva* abundance model showed the largest amount of error around the predictions as indicated by the high RMSE and MAE values (**Table 4.4a**). Spatial autocorrelation was not evident in the A_{gam} residuals (Mantel test, $p > 0.05$).

Seascape simulation: *F. duorarum* abundance

The mean abundance of *F. duorarum* under mesohaline conditions was significantly higher compared to other halohabitats (post-hoc Tukey test, $p < 0.05$) (**Figure 4.5**). Shrimp abundance increased generally with increasing vegetated habitat cover in all halohabitat scenarios (**Figure 4.5**). Peaks of shrimp abundance were observed at intermediate levels of fragmentation when the habitat amount was either low or high. Shrimp abundance was lowest within seascapes with 25 % vegetated habitat cover and high fragmentation. However, medium fragmentation levels in these low habitat amount seascapes resulted in shrimp abundance levels similar to those observed in habitats with higher (50%) cover highlighting the positive effects of intermediate fragmentation levels for this species (**Figure 4.5**).

Discussion

This study incorporated remote sensing, GIS analyses, field collections and statistical models to evaluate the relationships between SAV seascape patterns and within-patch structure and associated fauna within seagrass habitats of a subtropical coastal lagoon. I showed that SAV seascape spatial patterns and the relative location of habitats across the seascape (i.e., distance-to-shore) outweigh fine-scale, within-patch properties, and interacted to influence abundance of important fish and invertebrate species in Biscayne Bay. Non-linear responses of fish and shrimp species were observed with respect to seascape composition and configuration (i.e., habitat cover and fragmentation), and, more importantly, threshold effects were documented for these relationships for the first time. I also documented the positive effects of fragmentation on fish and shrimp abundance under certain scenarios. Specifically, medium levels of fragmentation result in higher abundance of pink shrimp when SAV is abundant (80% of the bottom covered by submerged vegetation patches) or sparse (25%).

Two-stage models (e.g., hurdle or delta models) have been successfully applied to assess how environmental and ecological drivers influence species' occurrence and abundance (Maunder & Punt 2004, Potts & Elith 2006, Sagarese 2013). However, in our study abundance models outperformed occurrence models. Due to the low variability within the presence and absence data, the occurrence models were subject to overfitting, except for the pinfish occurrence model. Therefore, only the results of the abundance models are discussed hereafter.

Spatial scale of abundance responses

Species respond to their environments at different spatial scales; therefore, considerations of seascape spatial patterns and their effects should be scaled to the organisms and ecological processes being investigated (Addicott et al. 1987, Wiens 1989). The abundance of the three species examined here, *Farfantepenaeus duorarum* (pink shrimp), *Lagodon rhomboides* (pinfish), and *Lucania parva* (rainwater killifish), was best predicted by the seascape spatial patterns recorded within a circle of 100 m in radius around each sampling point. Since home range is a function of the interaction between foraging and sheltering strategies, and mobility abilities and habitat specializations (Addicott et al. 1987, Ewers & Didham 2006, Caldwell & Gergel 2013), this area could be considered as the seascape ecological domain of the species examined. *L. rhomboides* is an estuarine fish considered to be dependent on seagrasses and with high site fidelity, and based on mark-recapture studies, the home range of this species was shown to vary between 20-40 m (Irlandi & Crawford 1997, Potthoff & Allen 2003); however, depending on the proximity of safe grounds and tides, its home range can extend to approximately 100 m (Potthof & Allen 2003). Currently, there are not studies of home range or seascape scale movements for *F. duorarum* and *L. parva*. Although, these species actively move and select vegetated seascapes to forage and avoid predator encounters (Corona et al. 2000, Jordan 2002, Camp et al. 2012). The results suggest that these two species have similar home ranges, or, area least, significantly influenced by seascape structure metrics recorded within the 100-m range.

Importance of seascape spatial properties

While the optimum spatial scale was similar for all three species, differences in the relationships between abundance and broad- and fine-scale habitat properties were evident among species. For all species, vegetated habitat amount strongly predicted the abundance of *L. parva*, where abundance was higher at intermediate cover levels. This species is strongly associated with seagrass seascapes (Jordan 2002, Armindo-Tomoleoni 2007, Rozas et al. 2012) and avoids barren patches (Jordan 2002, Camp et al. 2012), which can explain the lower abundance at low habitat amount. The abundance of species with high specialization and affinity to suitable habitats, such as *L. parva*, tend to decline below 50-60% of habitat cover, which according to the percolation theory and random sample hypothesis is the critical expected amount of habitat where the largest patch spans the whole seascape and where species will reflect a random distribution across the seascape (Andren 1994, With et al. 1997). Below this habitat amount, population abundance could diminish due to constraints on dispersion patterns (With & Crist 1995).

In this study, habitat fragmentation had non-linear effects on *L. rhomboides* abundance. This species showed a positive parabolic response, with highest abundance at intermediate levels of fragmentation. *L. rhomboides* can utilize both unvegetated/sand and seagrass patches (Jordan et al. 1997, Levin et al. 1997, Stunz & Minello 2001). Jordan et al. (1996) found that *L. rhomboides* used both seagrass and sand patches in the absence of predators, but avoided sand patches when predators were present, and Stunz & Minello (2001) suggested that this species is more efficient in capturing fish prey in open water and gaps. Also, studies have revealed that shrimp productivity and survival are positively influenced by a patchy seascape configuration and saltmarsh seascapes with a

high density of habitat edges (Browder et al. 1989, Haas et al. 2004). Thus, seascapes with intermediate levels of habitat fragmentation may optimize the tradeoff between foraging and refuge from predation, with edges or gaps in patchy vegetated seascapes offering a higher foraging efficiency.

In addition to large-scale habitat metrics (i.e., composition and configuration), *F. duorarum*, *L. rhomboides*, and *L. parva* abundances were also related to the percent cover of different SAV species. *Thalassia* cover significantly explained the abundance of all species. The cover of this seagrass species have positive effects on *F. duorarum* and *L. rhomboides* abundance at low to intermediate cover; however, *Thalassia* had a weak parabolic effect on *L. parva* abundance. These species also had a positive response at intermediate values of *Halodule* cover. Many studies have shown how structural components of SAV habitat patches occurring at fine-scales (e.g., shoot density, canopy height, percent cover) may influence abundance, growth, and survival of associated fauna (Heck Jr. & Orth 1980, Attrill et al. 2000, Horinouchi 2007). Access to epibenthic prey, such as amphipods and isopods, by pink shrimp and pinfish tend to be limited by high within-patch structural complexity (Corona et al. 2000, Horinouchi 2007), which may explain the non-linear responses of fish and shrimp to *Halodule* and *Thalassia* cover. Also, this fish and shrimp species positively responded with drift macroalgae cover, a complex of rhodophytes that have been associated with high prey abundance and advantageous tradeoff between foraging and protection for the species examined here (Holmquist 1997, Brooks & Bell 2001, Adams et al. 2004). For example, Adams et al. (2004) observed lower predation on pinfish in patches with drift algae and seagrass, and Gore et al. (1981) observed high association of penaeid shrimp abundance with drift

algae in Indian River Lagoon, Florida. The cover of seagrass, especially *Halodule*, had a positive effect on *L. parva* abundance. This fish species relies on filamentous macroalgae and fine-bladed macrophytes to lay eggs (Foster 1967) and increase predator avoidance (Camp et al. 2012) which may explain the affinity of this fish species to *Halodule*, a fine-bladed seagrass species.

Tradeoffs and interactions

The interaction between seascape habitat amount (proportion of the seascape occupied by SAV) and configuration (fragmentation index) had one of the largest influences on the predicted abundances of the two fishes and one shrimp. The effects of habitat amount and configuration are often confounded (Smith et al. 2009, Didham et al. 2012, Villard & Metzger 2014); however, few studies have examined the interaction between these variables (Smith et al. 2009, Bonin et al. 2011, Villard & Metzger 2014). In Biscayne Bay, habitat configuration had a positive effect on abundance when the habitat amount was > 50 % (*F. duorarum*, *L. parva*) or < 20-30 % (*F. duorarum*, *L. rhomboides*). This seascape pattern supports suggestions by Didham et al. (2012) and Villard et al. (2014) that the effects of habitat amount and spatial arrangement are interdependent, and that the effects of landscape variables operate through a range of hierarchical mechanisms. Here, I show that habitat configuration has the potential to reduce or buffer the effects of habitat loss. Similar patterns have been observed in several marine field and modeling experiments. For example, using a manipulative field experiment, Bonin et al. (2011) documented positive effects of fragmentation and negative effects of habitat loss on the abundance of the damselfish *Crysiptera parasema* and fish species richness. The positive effect of fragmentation on *C. parasema* abundance

was more significant after 75% of the habitat was removed. Other experiments have demonstrated how the abundance of prey items such as amphipods and isopods increased in fragmented treatments (Healey & Hovel 2004, Macreadie et al. 2010b, Arponen & Bostrom 2011). Based on seascape simulations, Caldwell and Gergel (2013) found that the functional connectivity thresholds for less mobile fish were reached at lower habitat amount when habitats were fragmented. Also, different field and modeling experiments have demonstrated how patchy seagrass seascapes can benefit blue crab (*Callinectes sapidus*) populations and influence predator-prey interactions (Hovel 2003, Hovel & Regan 2008).

In addition to large- and small-scale effects, cross-shelf location of survey sites relative to the mangrove shoreline had significant effects on species' abundance. Abundance of *F. duorarum* and *L. rhomboides* presented a threshold response to distance-to-shore where the abundance abruptly declined after 300 m from shore. Also the abundance of *L. parva* declined with increasing distance-to-shore. Geographical threshold patterns suggest variability in the habitat suitability across the seascape, and are indicative of the existence of ecologically meaningful zonation across the SAV seascape likely mediated by ontogenic shifts and the spatial variance of resource availability, predation, and competition (Pittman & Brown 2011). For example in Biscayne Bay gray snapper and seabream avoided foraging close to shore, where their food was abundant, but predation risk was the highest (Hammerschlag et al. 2010a,b). Nevertheless, the food-risk patterns within the mangrove-seagrass ecotone described by Hammerschlag et al. (2010a,b) may vary as function of seagrass seascape properties since habitat amount and configuration are known to influence prey-predator interactions (Ryall & Fahrig 2006,

Hovel & Regan 2008, Hendrichsen et al. 2009), and how individuals maximize growth and minimize predation risk (Irlandi et al. 1995, Irlandi & Crawford 1997, Haas et al. 2004). For example, juvenile *L. rhomboides* are voracious (Stoner 1982, Adams et al. 2004), and patchy seascapes (seascapes with high fragmentation index) closer to the mangrove shore may confer higher fitness by minimizing the ratio of predation risk to foraging rate. In contrast, the fitness of juvenile pink shrimp individuals may be maximized in seascapes with higher habitat amount since seascapes above the percolation threshold (i.e., level of habitat amount at which the seascape transition from a connected to a disconnected system) may benefit their longshore and inter-habitat movements and density dependent processes.

Seascape scenarios and management implications

The effectiveness of management strategies designed to counter the negative effects of disturbances, such as reserve implementation and active restoration, may differ depending on the relative influence of habitat amount, configuration, and quality (Lindenmayer & Fischer 2007, Bonin et al. 2011, Mizerek et al. 2011). For example, it was evident here that *F. duorarum* would benefit from management and restoration strategies that increase the amount of vegetated habitats, minimize habitat loss, and/or actively protect larger areas. One of the goals of the Comprehensive Everglades Restoration Plan for Biscayne Bay is to increase the flow of freshwater into littoral habitats, thereby expanding the duration and spatial extent of mesohaline environments (Lirman et al. 2014). The expected outcome of these changes is the increase in seagrass cover and the abundance of associated fauna like pink shrimp (Browder & Ogden 1999, Lirman et al. 2008a,b). Based on the simulation exercise conducted here, the SAV

mesohaline conditions had the highest abundance of pink shrimp under all cover and fragmentation scenarios. This was especially evident in habitats with low SAV cover (25%) and high levels of fragmentation. Thus, mesohaline conditions could buffer the effect of both habitat loss and fragmentation. Also it was evident how intermediate levels of fragmentation overall benefited the abundance of *F. duorarum*, which suggests that positive effects of habitat configuration may buffer, to some degree the negative effects of habitat loss. In addition, by incorporating other spatial variables with seascape habitat metrics this study demonstrated that management strategies should be concentrated within 300 m from shore where the species-habitat relationship were the strongest and most dynamic.

In summary, abundance patterns showed several non-linear responses to seascape properties, and abundance changes at critical habitat thresholds. The identification of critical habitat thresholds can inform management strategies on the minimum amount and configuration of habitat necessary for the persistence of ecological functional species, and allow an objective definition of conservation targets. Managing habitat quality, habitat configuration and matrix properties may offer valuable alternatives to conserve species persistence and abundance in seascapes where a significant increase in seagrass habitat cover is impossible over the short term (Ewers & Didham 2006, Villard & Metzger 2014). In addition, incorporating a seascape approach with a patch-mosaic perspective could benefit delineations and productivity estimates of nursery habitats since habitat configuration and matrix connectivity can facilitate inter- and inner-patch movements of organisms through different ecological ontogenetic processes (Olds et al. 2012, Nagelkerken et al. 2013).

Table 4.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne. The configuration metrics were used to create a fragmentation index

Metric	Acronym	Category	Aspect	Description	Formula
Percentage of Landscape	PLAND	Composition	Area/Density	Percentage of the total landscape made up of the corresponding class	$PLAND = \frac{\sum_{j=1}^n \alpha_{ij}}{A} (100)$
Patch Density*	PDENS	Configuration	Area/Density	Number of patches of a certain class divided by the total landscape area N patches/ha	$PD = \frac{n_i}{A}$
Mean Radius of Gyration*	GYRATE_MN	Configuration	Area/Density	Measure of patch extensiveness Larger patches will have higher GYRATE values	$GYRATE_MN = \frac{\sum_{j=1}^n \left[\sum_{i=1}^n \left(\frac{n_{ij}^2}{2} \right) \right]}{n_i}$
Mean Patch Fractal Dimension*	FRAC_AM	Configuration	Shape	Measure of patch-shape complexity	$FRAC_AM = \sum_{j=1}^n \left[\frac{2 \ln(25 p_{ij})}{\ln \alpha_{ij}} \left(\frac{\alpha_{ij}}{\sum_{j=1}^n \alpha_{ij}} \right) \right]$

* Configuration metrics included in the fragmentation index - $FragIndex = \sqrt[3]{(PD * FRAC_AM * 1/Gyrate_MN)}$

Table 4.2. Measures of the **a)** abundance (A_{gam}) and **b)** occurrence (O_{gam}) generalized additive model performance based on the spatial pattern sub-models (i.e., abundance and occurrence response to habitat amount and configuration within each seascape sample unit). For a given species, light gray highlight marks the sub-model optimum scale that was selected based on the lowest Akaike's information criterion (AIC), and dark gray highlight mark the sub-model optimum scale selected based on the diagnostic plots and second lowest AIC. The selected sub-models were used in the final generalized additive models

a) A_{gam}					
Spatial Scale (m)	Species	Rsq	Deviance Explained	UBRE	AIC
50	<i>Farfantepenaeus duorarum</i>	0.10	15.82	0.16	1328.34
100	<i>Farfantepenaeus duorarum</i>	0.13	36.48	0.47	1316.48
150	<i>Farfantepenaeus duorarum</i>	0.21	45.82	0.62	1326.75
50	<i>Lagodon rhomboides</i>	0.19	26.53	0.20	847.80
100	<i>Lagodon rhomboides</i>	0.37	48.00	0.53	827.76
150	<i>Lagodon rhomboides</i>	0.27	36.46	0.34	847.89
50	<i>Lucania parva</i>	0.23	64.38	0.73	893.41
100	<i>Lucania parva</i>	0.31	74.84	1.03	868.85
150	<i>Lucania parva</i>	0.35	69.25	0.79	875.59
b) O_{gam}					
Spatial scale (m)	Species	Rsq	Deviance	UBRE	AIC
50	<i>Farfantepenaeus duorarum</i>	0.78	84.90	-0.57	37.01
100	<i>Farfantepenaeus duorarum</i>	0.67	76.30	-0.73	34.40
150	<i>Farfantepenaeus duorarum</i>	1.00	100.00	-0.69	15.93
50	<i>Lagodon rhomboides</i>	0.22	21.60	0.26	137.84
100	<i>Lagodon rhomboides</i>	0.19	17.48	0.24	136.44
150	<i>Lagodon rhomboides</i>	0.14	12.95	0.28	141.31
50	<i>Lucania parva</i>	0.39	35.80	0.06	113.62
100	<i>Lucania parva</i>	1.00	100.00	-0.24	61.72
150	<i>Lucania parva</i>	0.40	35.30	0.00	109.37

Table 4.3. Results of the **a)** abundance (A_{gam}) and **b)** occurrence (O_{gam}) generalized additive models for each species (columns). The first two rows show predictive performance measures: adjusted r^2 and percent deviance explained. The p-values (Chi-squared test) approximated for the habitat amount and configuration variables (light gray) and within-patch structure (dark gray) smooth terms. Values exhibiting significant trends ($p < 0.05$) are shown in bold

		a) A_{gam}		
		<i>Farfantepenaeus duorarum</i>	<i>Lagodon rhomboides</i>	<i>Lucania parva</i>
Adjusted r^2		0.62	0.49	0.66
Deviance Explained		75.20%	73.70%	85.30%
Approximate significance of smooth terms		p-value (Chi squared test)		
Habitat Amount & Configuration	Proportion of covered seascape(PLAND)	0.35	0.09	<0.00001
	Fragmentation Index (FragIndex)	0.3	<0.00001	0.9
	PLAND x FragIndex	0.00003	<0.00001	<0.00001
	Distance to shore (DistShore)	0.12	0.0005	<0.00001
	PLAND x DistShore	<0.00001	<0.00001	0.009
	FragIndex x DistShore	<0.00001	<0.00001	<0.00001
Within-patch Structure	<i>Thalassia testudinum</i> cover	0.0002	<0.00001	0.0002
	<i>Halodule wrightii</i> cover	0.0001	0.65	<0.00001
	Drift cover	0.003	0.007	0.09
	Rhizophytic algae cover	0.0004	0.028	0.25
	Canopy height	0.02	0.36	0.09
		b) O_{gam}		
		<i>Farfantepenaeus duorarum</i>	<i>Lagodon rhomboides</i>	<i>Lucania parva</i>
Adjusted r^2		1	0.31	1
Deviance Explained		100	30.8	100
Approximate significance of smooth terms		p-value (Chi squared test)		
Habitat Amount & Configuration	Proportion of covered seascape(PLAND)	0.54	0.96	1.00
	Fragmentation Index (FragIndex)	0.78	0.36	1.00
	PLAND x FragIndex	0.87	0.0231	0.95
	Distance to shore (DistShore)	0.61	0.0892	1.00
	PLAND x DistShore	0.91	0.0376	1.00
	FragIndex x DistShore	0.69	0.33	1.00
Within-patch Structure	<i>Thalassia testudinum</i> cover	0.71	0.001	1.00
	<i>Halodule wrightii</i> cover	0.98	0.49	1.00
	Drift cover	0.70	0.0217	1.00
	Rhizophytic algae cover	0.61	0.005	1.00
	Canopy height	0.92	0.4995	0.96

Table 4.4. Validation measures for the full abundance (A_{gam}) and occurrence (O_{gam}) generalized additive models for each species. Slope and intercept values are from the calibration line: observed = m(predicted) + intercept. Pearson's correlation and Spearman's rank correlation estimated from the calibration line. Root mean square error (RMSE) and mean average error (MAE) are other measures of error around the line. Area under the receiver operating characteristic curve (AUC) estimated for the occurrence models. For the O_{gam} only the results for *Lagodon rhomboides* were reported as the models for the other 2 species were not significant

a) A_{gam}			
	<i>Farfantepenaeus duorarum</i>	<i>Lagodon rhomboides</i>	<i>Lucania parva</i>
Pearson's correlation coefficient	0.87	0.84	0.89
Spearman's rank correlation coefficient	0.88	0.84	0.89
Intercept	0.1	-1.14	-2.63
Slope	1.01	1.15	1.11
RMSE	11.15	5.38	58.13
MAE	8.28	3.22	28.06
b) O_{gam}			
	<i>Farfantepenaeus duorarum</i>	<i>Lagodon rhomboides</i>	<i>Lucania parva</i>
Intercept	N.A.	-0.001	N.A.
Slope	N.A.	1.04	N.A.
AUC	N.A.	0.86	N.A.

Figure 4.1. Illustration of the a) study area within Biscayne Bay, b) SAV seascape map with the 100 x 500 m plots randomly located along the shoreline, and c) the locations of the three replicate seines that were randomly placed within distance-to-shore zones. The locations of each seine (yellow dots) were as the centroid for each seascape sample unit (black circles) for the calculation of the seascape metrics. The within-patch structural attributes (cover of each SAV taxon and canopy height) were calculated from the footprint of each seine deployment

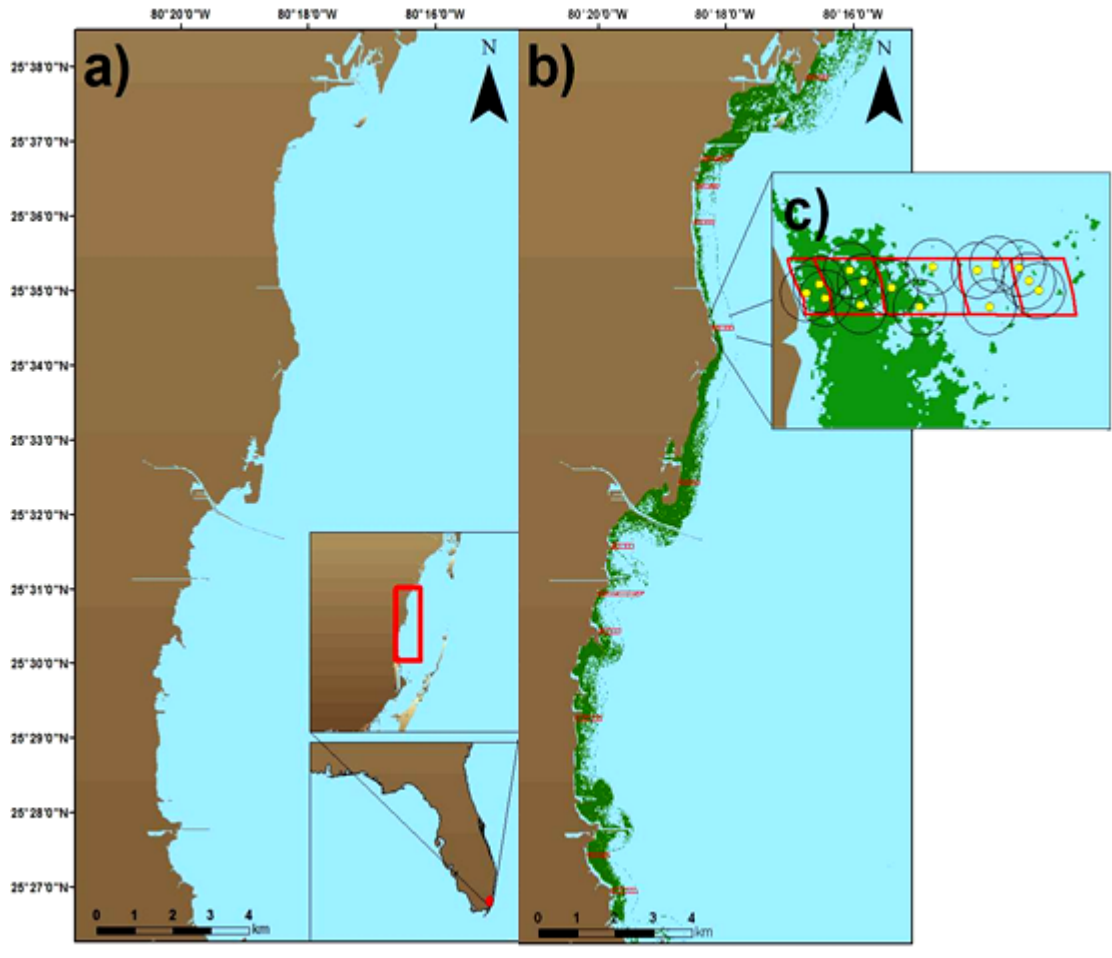


Figure 4.2. Bar graphs illustrating the percentage contribution of each predictor variable to the total deviance explained in the **a)** abundance (A_{gam}) and **b)** occurrence (O_{gam}) generalized additive models. For A_{gam} bar color index the predictor contribution for the *Farfantepenaeus duorarum* (FarDuo - black), *Lagodon rhomboides* (LagRho - dark gray) and *Lucania parva* (LucPar - light gray) abundance models. For the O_{gam} only the results for LagRho (dark gray) were reported. Deviance explained by: devPLAND = SAV habitat amount, devFrag = Fragmentation Index, devFPti = SAV habitat amount and fragmentation index interaction, devDist = Distance-to-shore, devDistti = interaction of SAV habitat cover, fragmentation and Distance-to-shore, devTT = *Thalassia testudinum* devHw = *Halodule wrightii*

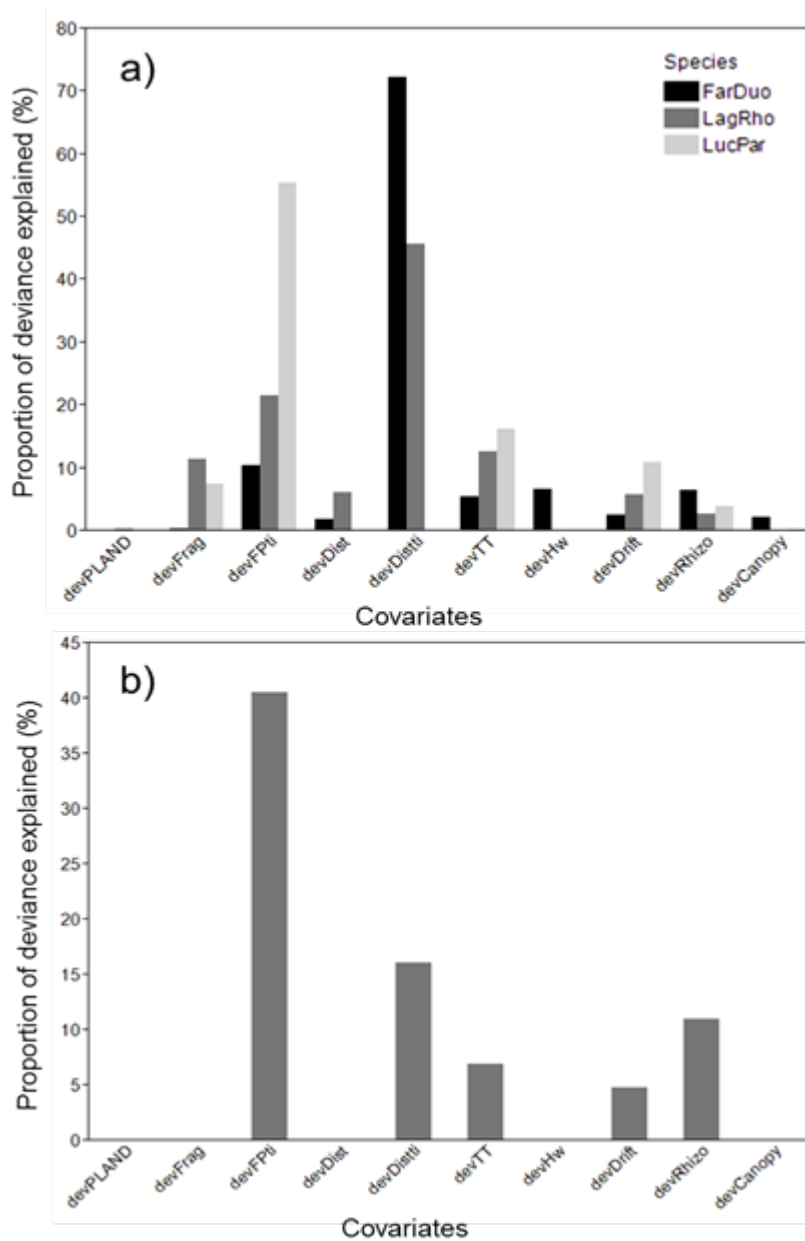


Figure 4.3. Additive effect smooth terms (y axis) of each covariate on a) *Farfantepenaeus duorarum*, b) *Lagodon rhomboides* and c) *Lucania parva* abundance model. Only significant variables (Chi-squared test, $p < 0.05$) are illustrated. PLAND = SAV habitat amount, FragIndex = Fragmentation Index, Dist_Shore = Distance-to-shore, Tt = *Thalassia testudinum*, Hw = *Halodule wrightii*, Drift = Drift algae, Rhizo = Rhizotypic algae

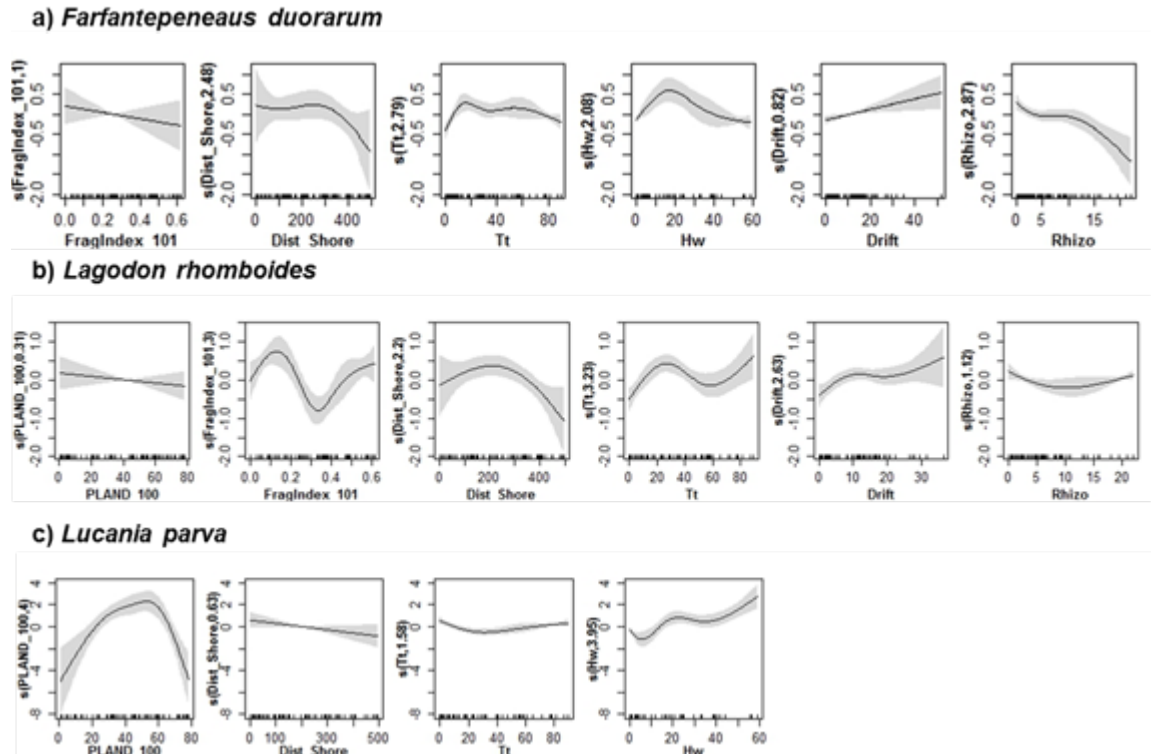


Figure 4.4. Additive effect smooth terms of each variable on *Lagodon rhomboides* (pinfish) probability of occurrence. Only significant variables (Chi-squared test, $p < 0.05$) are illustrated. Dist_Shore = Distance-to-shore, Drift = Drift algae, Rhizo = Rhizophytic algae

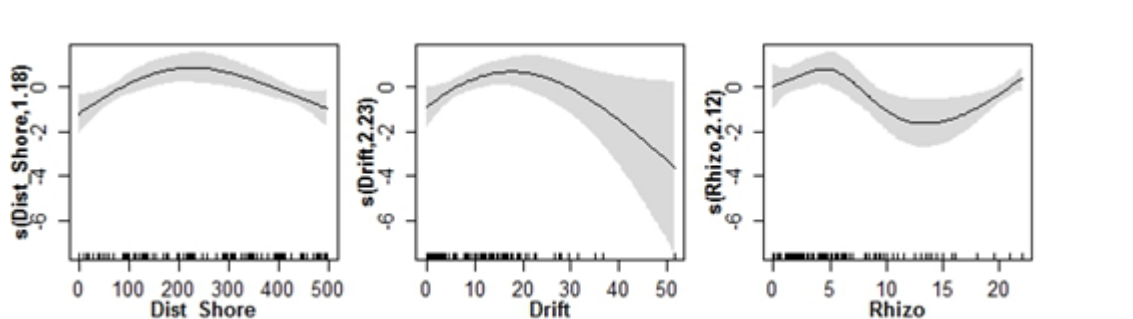
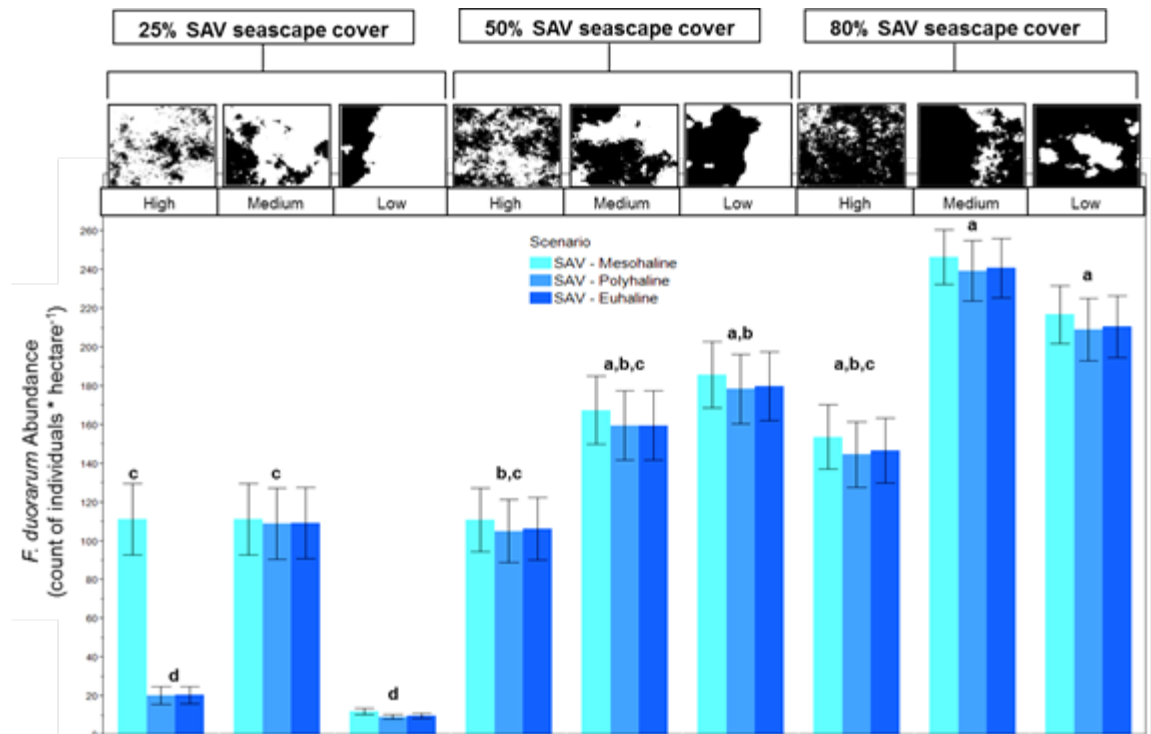


Figure 4.5. Predicted *Farfantepaneaus duorarum* abundance (# of individuals * hectare) within the 9 simulated seascapes. Three fragmentation levels: High, Medium and Low, were created within seascapes with 25%, 50% and 80% of habitat cover (amount). Illustration of the seascape type is included where the color black depicts vegetated habitat patches. The GAMs were calculated using the seascape information within the simulated seascape and the SAV data (within-patch characteristics) from three halohabitat scenarios: mesohaline, polyhaline, and euhaline. The abundance within the simulated seascapes and halohabitats were significantly different (two-way ANOVA, $p < 0.05$). Bars illustrate the standard error, and groups not connected by same letter are significantly different (post-hoc Tukey HSD test – $p < 0.05$)



Chapter 5. Predation risks in fragmented SAV seascapes

Summary

Changes in water quality, especially salinity patterns, caused by the management of the Everglades watershed have influenced the seascape structure of nearshore submerged aquatic vegetation (SAV) habitats of Biscayne Bay, a shallow lagoon adjacent to Miami, Florida, U.S.A. SAV seascape spatial changes have, in turn, influenced the community structure and abundance of associated fish and crustacean species. This study proposes predation risk effects (PRE) as a mechanism to describe faunal responses to changes in SAV seascape structure. Predation risks often result in changes in foraging and reproductive behaviors, and the spatial distribution of prey organisms. Such effects can cascade through the community by influencing trophic interactions and population dynamics. Based on predation and landscape effects models, prey species are expected to encounter higher predation risk in fragmented vegetated seascapes with high edge densities. The PRE across a range of seascapes with different habitat amount and configuration was assessed using baited remote underwater video surveys (BRUVS) and tethering experiments with *Farfantepenaeus duorarum* (pink shrimp) as prey. Both BRUVS and tether experiments identified higher predation risk at boundaries of the seagrass meadows (at mangrove-seagrass edges, and seagrass seaward edges). Based on allocation time and pecking rate recorded by the BRUVs, it was evident that habitat shifts occur in response to seascape spatial properties and risk of predation. However, patterns of habitat use with respect to PRE were specific to trophic groups. The food-risk tradeoffs observed across the seascape suggest that localized trophic cascades could occur in response to habitat loss and fragmentation. These results demonstrate how the

spatial structuring of benthic habitats can influence important ecological interactions known to affect the structure and resilience of economically and ecologically important fisheries species.

Background

Spatial properties of marine habitats are constantly changing mostly due to anthropogenic disturbances that modify the abundance and distribution of marine habitats (Bell et al. 2007). Habitat loss and fragmentation significantly transform the spatial structuring of the marine habitats or patch-mosaics (referred to as “seascape” hereafter) by reducing the amount of habitat, dividing continuous habitat patches into smaller units, reducing mean patch size, and increasing patch isolation and the amount of habitat edges (Turner et al. 2001, Fahrig 2003). Habitat loss and fragmentation of seascapes, especially through edge effects (i.e., accentuated negative or positive ecological response moving from patch boundaries to patch interiors – (Ewers & Didham 2006a), can influence the persistence, abundance, and diversity of associated mobile marine species (Connolly & Hindell 2006, Boström et al. 2011). For example habitat edges, which increase with fragmentation, are known to alter recruitment rates, inter-habitat connectivity, food supply, and predator-prey interactions (Ries et al. 2004, Ewers & Didham 2006b). Predation has been commonly cited to explain patterns of species abundance and diversity across fragmented habitats and edges (Ries & Sisk 2004, Connolly & Hindell 2006). Predation affects species’ distributions and persistence through both direct consumption and risk effects (i.e., non-consumptive effects) (Lima & Dill 1990, Brown et al. 1999). The majority of edge effect and fragmentation studies on predator-prey dynamics have concentrated mostly on direct predation effects (Creel & Christianson

2008). However, empirical studies have recently shown that risk effects can be significant, and sometimes substantially larger than direct effects. Therefore, studies that focus on patterns of prey consumption and ignore the effects of fear (risk) may underestimate the overall impact predators have on SAV seascape communities (Wirsing et al. 2008). In this study, we evaluate the influence of fear on the distribution and habitat use of fish and crustaceans (i.e., predation risk effects) associated with SAV habitats in nearshore environments of Biscayne Bay, a subtropical lagoon adjacent to the city of Miami, Florida, U.S.A., using baited remote underwater video surveys (BRUVS) and tethering experiments with *Farfantepenaeus duorarum* (pink shrimp) as prey.

Marine organisms generally experience a positive relationship between feeding opportunities and predation risk (Brown & Kotler 2004). Thus, habitats that contain abundant or diverse food resources are often the most risky. As a result, foragers and prey species face a trade-off between food and safety (Lima & Dill 1990, Hammerschlag et al. 2010b). The minimization between risk and foraging reward could be attained by behavioral modifications of time allocated to foraging, tenacity, and the use of apprehension or vigilance (Brown & Kotler 2004). Further, several studies have shown how these behaviors can be influenced by the spatial characteristics of the foraging habitat (Lima & Dill 1990, Schmitz 2007, Heithaus et al. 2009). Thus, the assessment of spatial patterns of predation risk or the "seascape of fear" could be used to identify seascape properties that are perceived to be relatively safer by prey as well as a proxy for the amount of food being relinquished by foragers avoiding dangerous seascapes (Wirsing et al. 2008).

Foraging efficiency and mobility may differ between seascapes according to habitat patch and edge density, mean patch size, and fractal dimensions (Irlandi et al. 1995, Hovel 2003, Macreadie et al. 2010b, Caldwell & Gergel 2013). Intermediate levels of fragmentation, especially in SAV seascapes, can provide edges and microhabitats with higher concentration of food and higher efficiency of prey evasion (Ries & Sisk 2004, Smith et al. 2008a). Several studies have indeed observed higher concentrations of fish and crustacean species at the seagrass-sand edge or in sand in proximity to seagrass patches (Smith et al. 2008b, Horinouchi 2009). Both manipulative experiments and field observations have observed accumulation of amphipods, copepods, and isopods, which are considered the primary consumers in seagrass habitats and important food source, at seagrass edges (Bologna & Heck 2002, Healey & Hovel 2004, Arponen & Boström 2012). Some studies have found also higher survival rates of blue crabs at edges or seascapes with high edge density (Hovel & Fonseca 2005). The fragmentation of benthic habitat coupled with predation risk also influence the movement of crustaceans (Hovel & Regan 2008) and fish (Turgeon et al. 2010) across the seascape. Therefore, the level of complexity of food-safety trade-offs may increase in a nonlinear fashion with fragmentation.

SAV seascapes in nearshore areas of Biscayne Bay have been fragmented over time during the last 70 years, mostly due to salinity patterns created by the release of fresh water from canals (Santos et al. 2011, Chapter 1). Moreover, SAV seascape changes have cascading effects on the assemblage composition of fish and crustaceans (Chapter 2), and influence the abundance of ecologically and economically important fish and shrimp species (Chapter 3). Several seascape ecology studies have investigated how

predation-risk effects influence species abundance along habitat gradients (e.g., patch center vs patch edge, vegetated vs un-vegetated) (Heithaus et al. 2009, Hammerschlag et al. 2010a, Smith et al. 2011). However, these studies have not directly assessed how predation-risk effects are influenced by the amount and spatial configuration of SAV habitats, even though seascape fragmentation is known to influence species interactions (Hovel et al. 2002, Hovel 2003, Carroll et al. 2012). The magnitude of predation-risk effects depends on both physical features of the habitats and predator-prey interactions (Lima & Dill 1990, Schmitz 2007, Heithaus et al. 2009). Therefore, the seascape of fear or the distribution of predation and predation-risk effects with respect to habitat spatial characteristics could be a key mechanism influencing patterns in fish and crustacean abundances. This study used two concurrent underwater field techniques, baited remote underwater video surveys (BRUVs) and tethering, to: 1) assess relative predation rate of an abundant crustacean prey with respect to the SAV seascape spatial properties, 2) evaluate probability of occurrence of predators across the SAV seascape, and 3) how predation risks influence food harvesting and predator avoidance and how these interact with seascape features.

Materials and Methods

Study site

Biscayne Bay is a shallow subtropical lagoon located adjacent to the city of Miami, Florida, U.S.A., and downstream of the Florida Everglades system (**Figure 5.1a**). Sampling of marine fish and crustaceans focused on nearshore seascapes (≤ 400 m from shore) in western Biscayne Bay, which are dominated by submerged aquatic vegetation

(SAV) composed of seagrasses and macroalgae (Lirman et al. 2008b, 2014). The spatial properties and fragmentation processes in the bay's SAV seascapes has been associated with salinity patterns created by the release of fresh water from canals (Santos et al. 2011). In turn, spatial properties have played an important role structuring the assemblage and distribution of fish and crustacean species in the bay (Chapter 2, 3). Biscayne Bay SAV seascapes provide key habitat for a large number of commercially and recreationally valuable species, including pink shrimp (Diaz et al. 2001), gray snapper, hogfish, and spotted seatrout (Serafy et al. 1997, 2003, Faunce & Serafy 2008).

Sampling design

Baited remote underwater video surveys (BRUVs) have been used effectively to assess faunal species diversity and abundance in coral reefs, seagrasses and pelagic habitats (Heagney et al. 2007, Harvey et al. 2012, Bond et al. 2012). This sampling technique can quantify the presence of predators, and visually document foraging behavior such as time allocated to foraging, tenacity, and vigilance (Smith et al. 2011). Tethering experiments can complement data collected with BRUVs by providing information on relative predation rates on different species and trophic interactions. Tethering has been used effectively to research relative predation on different taxa in several marine habitats (Bologna & Heck Jr. 1999, Hovel & Lipcius 2001, Chittaro et al. 2005, Hammerschlag et al. 2010a). Here, indirect and direct predation risk effects were quantified using BRUVs and a tethering experiment performed concurrently in July to September 2013, at night when many fauna are actively foraging over seagrasses (Luo et al. 2009, Hammerschlag et al. 2010a).

Tethering experiment

Tethering has been used to estimate prey mortality within and among habitat and between seascape types (Linehan et al. 2001, Hovel & Lipcius 2001, Hammerschlag et al. 2010a, Hammerschlag et al. 2010b). While tethering cannot be used to quantify absolute mortality due to predation, it can be used to compare rates of predation under the assumption that artifacts of the technique do not covary with habitat treatments or the properties being tested (Gorman et al. 2009). Pilot studies in the laboratory and field were used to minimize prey loss and mortality due to tethering and maximize prey movement. The tethering experiment was employed to quantify the relative predation of juvenile pink shrimp (10-20 mm carapace length) between seascapes, and in relationship to distance to the mangrove shoreline.

Design: The tethering deployments were conducted at a distance of approximately 50 m from the locations where the BRUVs were deployed (**Figure 5.1c**). Juvenile pink shrimp were attached to a 0.3 m monofilament tether line (0.3 mm, 4.5 kg test) using a jam knot around the body between the carapace and first abdominal segment. Five shrimp were attached every 2 meters on a weighted 10-m polypropylene line (**Figure 5.1d**). Three lines were randomly placed 10-20m apart within each distance-to-shore class (i.e., 4 distance-to-shore areas – **Figure 5.1b, c**). The replicates were retrieved after 2, 3, and 4 hrs to account for the effects of soak time.

BRUVs

BRUVs were deployed within 10 locations (100 x 400 m) that were randomly positioned perpendicular to shore at habitats previously described by Santos (Chapter 2,

3) (**Figure 5.1b**). Each plot was further divided into 4 distance-to-shore areas where the BRUV were deployed randomly (**Figure 5.1c**). Within each distance-to-shore class, two BRUVs were randomly allocated to two of four positions. After 1.5 hr, the BRUVs were retrieved and moved to the remaining two deployment points ($n = 4$ distance-to-shore classes \times 4 BRUVs = 16 BRUVs per location) (**Figure 5.1c**). The replicate deployments were placed no closer than 25 m from each other. The bait for the BRUVs was replaced between deployments and all plots were sampled within a three-hour interval during high tide.

Design: Each BRUV contained a GoPro HD video camera with a wide-angle lens (**Figure 5.2**). The cameras were mounted on a PVC frame, with a horizontal view of a baited plastic mesh container (25 x 15 cm, 1 cm mesh size) placed 0.8 m from the camera. Each unit was baited with 450 g of chum consisting of silversides, crabs, shrimp, oats, and fish oil, bait components that are commonly used by sport and recreational fishers locally. The BRUVs were weighted with lead sinkers and were built with 0.5 m and 0.25 m stabilizer arms in the center and ends respectively to provide stability and avoid overturning during deployment (**Figure 5.2**). Artificial lighting was provided by two Intova Mini Wide Angle 200 lumen underwater flashlights, covered with a Bright Red 026 filter to transmit red light in the wavelengths above the sensitivity of many marine fish (Cappo et al. 2004). After experiments in the field and laboratory, a 960 x 30 frame per seconds was selected as the optimal video frame size/memory/battery life combination. The sampling view was calculated to cover 0.75 m³.

Video Analysis: Fish and crustaceans observed in the video were identified to species and first time of sighting was recorded. Three metrics were recorded for each species from

the video: species abundance (MaxN), the amount of time fish spend in each habitat or allocation time (Time in View – TiV), and a proxy of vigilance behavior (Pecking rate – PRate). MaxN or the maximum number of fish from each species seen in a single frame in the video footage (Cappo et al. 2004) is considered a conservative estimate of the total number of fish present within the bait plume footprint (Heagney et al. 2007), and has been shown to accurately reflect species densities by eliminating multiple counts of the same individual (Cappo et al. 2004, Smith et al. 2011). TiV measurements were adapted from Smith et al. (2011) to provide an estimate of habitat usability (how long the habitat is been used) by recording the maximum time that individuals were within view. The time was stopped after individual/s abandoned the sampling view > 30 s to differentiate between returning individuals and newcomers. After accounting for retreat-return behaviors, the maximum TiV value was recorded for each species observed. PRate consisted of the total number of bites on the bait recorded during each deployment. PRate is considered inversely proportional to vigilance since vigilance behavior tends to occur when organisms switch from feeding to predator alertness (Brown & Kotler 2004). According to Brown et al. (1999), vigilance should decline with the quality or susceptibility of the animal's feeding opportunity, which makes this metric a viable behavioral indicator of predation risk. In combination with TiV, PRate can be used also as a tenacity measurement, or the ability of the forager to maintain a harvest rate in the face of predation risk (Brown & Kotler 2004). BRUVs sampling designs, especially small-scale studies, can be subject to overestimations and autocorrelation artifacts since foragers may be attracted from locations within the range of the plume. Therefore, the video footage within each replicate was divided into four time periods of equal duration

where the predation risk metrics (MaxN, TiV, PRate) were recorded and averaged to account for overestimations due to scaling and autocorrelation artifacts. In addition, the metrics were standardized by the time block to provide a value per minute of video.

Seascape metrics

The composition and configuration of the seagrass habitats where the BRUVs and tether lines were deployed were assessed using spatial seascape metrics described in detail in Chapters 1-3. The seascape within 100 m radius from each BRUVs and tethering trial was extracted using ArcGIS 9.3 Analysis Tools, and measures of habitat spatial composition and configuration were characterized based on spatial pattern metrics calculated with Fragstats v4 (McGarigal et al. 2012). Spatial pattern metrics quantified the proportional area or cover (i.e., composition: SAV habitat cover), and spatial configuration of patches in the seascapes (i.e., configuration: patchiness or fragmentation of seascapes) (**Table 5.1**). Habitat cover was measured as the percentage of the total seascape made up of SAV patches (PLAND), and habitat configuration was estimated with a fragmentation index which was the composite of three measures of configuration: patch density (PD – habitat subdivision), mean radius of gyration (GYRATE_MN – habitat extension) and mean patch fractal dimension (FRAC_AM – patch geometry) metrics (refer to Chapter 3 for details). All metrics were standardized to produce a FragIndex ranging from 0 (low fragmentation) to 1 (high fragmentation).

Distance-to-shore (and the mangrove shoreline) was included here (and in the tethering experiments) as another seascape covariate by calculating the distance of the sampling points to the mangrove shoreline, since edges, ecotones or ecological

boundaries, have profound effects on the dynamics of species and communities (Ewers & Didham 2006). For instance, in Biscayne Bay it has been recognized that the relative high predation risk within the mangrove-seagrass ecotone plays an important role structuring the abundance and distribution of small fish predators in nearshore habitats (Hammerschlag et al. 2010a, Hammerschlag et al. 2010b).

Statistical analyses

The species observed in the video were assigned to trophic groups, based on their feeding habitats and functional morphology based on FishBase (Froese & Pauly 2014) and Harborne et al. (2008) classifications. The groups were: 1) mesopredator (MesoP), 2) invertivore of small prey (IvSm), and 3) invertivore and piscivore generalists (IvPi). Generalized linear models (GLMs) were used to assess the trophic groups' predation risk response to SAV seascape spatial properties (habitat amount and configuration) and distance-to-shore (relative position to ecological boundaries – e.g., seagrass-mangrove edge vs seagrass-seaward edge). All GLMs were performed using R (R Core Development 2013) using the 'stats' package, and included a full factorial second-order polynomial structure, including all 1st-order interactions. MaxN was transformed to a binomial variable (presence-absence) and a GLM with a binomial distribution with a logit link function was applied to assess and compare probability of occurrence patterns. Also, a GLM with a Gamma distribution and log link function was used to characterize the TiV and PRate response of the functional groups. The probability of shrimp predation was estimated with a logistic GLM using the proportion of tethered shrimp removed from the tether line (i.e., proportion of shrimp consumed) as the response variable. A step-wise backward selection procedure (R – stepAIC function) was used to reduce the number of

explanatory variables and obtain the most parsimonious model using the minimum AIC as selection criterion. The percentage of deviance explained by a GLM model was calculated and its significance was tested using a Chi-square test. Only GLMs with significant deviance explained were evaluated.

Results

A total of 26 species were observed with the BRUVs. *Lagodon rhomboides*, *Callinectes sapidus*, *Farfantepenaeus duorarum*, and *Lutjanus griseus* were the most common species seen in the videos (**Appendix C1**). Mesopredators such as *Ginglymostoma cirratum*, *Negaprion brevirostris*, and *Sphyraena barracuda* were also observed (**Appendix C1**). Mean abundance, which consisted on the maximum number of individuals observed per minute (MaxN), of IvSm and IvPi ($1.9 \times 10^{-3} \pm 5.0 \times 10^{-3}$ and $8.0 \times 10^{-3} \pm 7.0 \times 10^{-3}$, respectively) were higher than the MesoP abundance ($3.0 \times 10^{-4} \pm 9.0 \times 10^{-4}$) (**Figure 5.3**). The observations of MesoP abundance was consistently low across the sites (**Figure 5.3**). The highest abundance for IvSm and IvPi were observed in site 12 ($1.45 \times 10^{-2} \pm 1.16 \times 10^{-2}$) and site 64 ($6 \times 10^{-3} \pm 9 \times 10^{-3}$), respectively (**Figure 5.3**). The abundance patterns between the functional groups observed across the sites suggest unique responses to SAV seascape structural properties.

Tethering experiments

Fragmentation and distance-to-shore explained 22.8 % of the deviance in shrimp relative predation (**Table 5.2**). The probability of predation increased with distance-to-shore and fragmentation level (**Table 5.3, Figure 5.4**). The lowest probability of predation was seen in the habitats with low fragmentation in vicinity of the mangrove

shoreline, where fragmentation was low (**Figure 5.3**). This pattern weakened significantly with soak time (**Table 5.3, Figure 5.4**), especially from the “two” to “three” hours submersion treatment; however, the interactive effects of distance to shore and fragmentation remained across the soak time treatments.

BRUVs

Seascape properties and distance-to-shore significantly explain the probability of occurrence of the three functional groups, with 11%, 22% and 13% of the deviance explained for MesoP, IvSm and IvPi respectively (**Table 5.2**). Distance-to-shore was a significant explanatory variable in all of these models (**Table 5.3**). MesoP occurrence showed a significant U-shape response (**Figure 5.4a**), with: (1) highest occurrence in close-to-shore habitats with low-intermediate cover as well as further from shore in habitats with high cover, and (2) lowest occurrence between 100 and 400 m from shore (**Table 5.3, Figure 5.5a**). IvSm and IvPi occurrence were related to the fragmentation level of the seascape and distance-to-shore, with probability of occurrence increasing with increasing distance-to-shore for IvSM (for low fragmentation levels) and IvPi (for all fragmentation levels). Interestingly, individuals within these functional groups (especially IvSm) significantly avoided nearshore hotspots with high MesoP occurrence (**Figure 5.5**).

TiV and PRate of generalist predators (IvSm and IvPi) was significantly related to habitat (SAV) cover and fragmentation, and significant interaction effects were observed between these variables and distance-to-shore (**Table 3**). IvSm responses were best explained by the SAV seascape variables (**Table 3**). At seascapes with 25 % SAV cover,

TiV was higher further away from the mangrove shoreline independent of fragmentation level; however, the PRate was higher closer to shore in seascapes with low fragmentation (**Figure 5.6a,d**). In contrast, when the seascape had medium-high SAV cover, cross-shelf location and fragmentation level had stronger interaction effects, and a TiV hotspot was present at 300 to 400 m from shore when fragmentation was high (**Figure 5.6 b - f**).

The TiV response of IvPi was also significantly associated with SAV seascape properties and varied based on SAV cover. At 25% SAV cover, TiV significantly increased with lower fragmentation values and increasing distance-to-shore (**Figure 5.7a**). At intermediate SAV cover, the highest TiV was seen at high fragmentation levels far from shore, while at high SAV cover, TiV of IvPi was highest at high fragmentation levels but closest to shore (**Figure 5.7b -c**). In contrast, PRate for IvPi was less influenced by distance-to-shore and exhibited a generally flat response to this variable in all cover scenarios (**Figure 5.7 d-f**). However, PRate was influenced significantly by fragmentation level and showed a distinct response based on SAV cover. PRate decreased with increasing fragmentation in seascapes with 25% SAV cover, but increased with increasing fragmentation within seascapes with 50%-80% SAV cover.

Discussion

The abundance and distribution of nektonic organisms associated with seagrass habitats in Biscayne Bay are significantly influenced by seascape properties (Chapters 1, 2). Here, I also show, for the first time, that SAV seascape properties such as habitat amount and configuration, and distance to the mangrove shoreline influence both predation rates and anti-predator behavior. The tethering experiments showed that

predation on juvenile pink shrimp is significantly influenced by habitat fragmentation and proximity to the mangrove-seagrass ecotone, consistent with the high abundance of this species near the mangrove-seagrass edge observed in Chapter 3. Using baited remote underwater video surveys (BRUVs), predation risks were also related to the spatial layout of SAV habitats. Foragers' occurrence, habitat time allocation and vigilance were associated with the presence of mesopredators, but also influenced by SAV seascape composition and configuration, and their interactive effects with distance to the mangrove shoreline. These results show that trophic cascades are possible due to predation risk effects, but that these interactions are also modulated by SAV seascape patterns and predator-prey interactions.

Shrimp predation and SAV seascape fragmentation

Habitat fragmentation has been associated with higher predation at habitat edges (Ries & Sisk 2004, Connolly & Hindell 2006). In this study, predation on juvenile pink shrimp was significantly higher in fragmented SAV seascapes, providing support for previous studies that have shown higher predation risks along habitat edges (Ries & Sisk 2004, Connolly & Hindell 2006). Edges often function as a microhabitat between structurally complex areas, which allows for greater visibility and mobility necessary for prey searching (Gorman et al. 2009), facilitating higher prey encounter rates (Ries et al. 2004). Using a series of tethering experiment and video sampling, Smith et al. (2011) observed higher occurrence of salmon along the sand-seagrass edges which they linked to lower abundance and changes in the distribution of prey fish species. Other tethering experiments using bivalves and crustaceans have also observed higher predation rates in

seagrass seascapes with higher proportion of edges (Bologna & Heck Jr. 1999, Hovel 2003, Carroll et al. 2012).

Even though predation on juvenile pink shrimp was higher in fragmented seascapes, the abundance of this species and other penaeid shrimps is greater within seascapes with high habitat edges (Browder et al. 1989, Haas et al. 2004, Chapter 2), suggesting that shrimp balance higher predation pressure with other ecological or nutritional benefits that maximize fitness at habitat edges. Similar to our findings, Macreadie (2010) and Smith et al. (2011) & 2009) found higher abundance of pipefish in fragmented seagrass habitat where predation was the highest. Pink shrimp is a major food source of commercially important fishes in Biscayne Bay (Browder & Robblee 2009) and further fragmentation of the SAV seascape due to human or natural stressors can have cascading trophic effects on this productive system.

Predation risks indirect effects

Predators affect their prey through both direct predation and non-consumptive or risk effects that modify the prey's habitat use and foraging behavior that may cascade through communities (Creel & Christianson 2008, Heithaus et al. 2009). Responses to predation risk can include changes in allocation time, vigilance, foraging, aggregation, movement patterns and sensitivity to environmental conditions (Creel & Christianson 2008). In this study, it was evident that foragers avoided areas of high predator occurrence. Higher probability of mesopredators such as juvenile lemon shark (*Negaprion brevirostris*) and nurse shark (*Ginglymostoma cirratum*) were observed closer to shore, as found in a similar study in the bay (Hammerschlag et al. 2010a). In

contrast, higher probability of occurrence of foragers such as pinfish and grey snapper were higher away from the mangrove-seagrass ecotone and closer to the seagrass seaward edge; thus, the distribution of forager species were consistent with predictions of a food risk tradeoff, where the ratio of predation risk to foraging rate was minimized in the safest habitat furthest from the mangrove (Hammerschlag et al. 2010b). Also, habitat shifts (i.e., shift in habitat use and distribution) were evident here by the changes in the TiV and PRate of invertivores of small prey based on the proximity to habitat boundaries and SAV cover. The indirect effects of predators on prey distribution and trophic cascades are common in terrestrial, freshwater, and marine ecosystems (Schmitz et al. 2004). Habitat shifts due to predation risk effects can cause changes in prey-predator interactions and may play a significant role in local trophic systems. Here, shrimp relative predation rate increased with distance from shore, in accordance with the extent within the SAV seascape that shrimp predators selected as result of the habitat shifts described above. In a conceptual predation risk model described by Heithaus et al. (2009), a positive indirect effect of tiger shark presence on the predator avoidance behavior of their prey, cormorant, resulted in the reduction in foraging by cormorants in prey-abundant areas. Similar indirect effects induced by predation risk and shifts of the habitat use by fish have been also observed in other aquatic systems (Werner et al. 1983, Power 1987). Using mesocosm experiments, Bruno and O'Connor (2005) found that predator identity and diversity had striking effects on the strength of epifaunal trophic interactions, and that the presence of omnivorous pinfish added a level of complexity to the pathways of the trophic cascades present in submerged aquatic vegetation habitats. Nevertheless, predation risk experiments in the field like this study should be complemented with diet

and prey-distribution assessment and fitness analyses (e.g., growth, fecundity, reproductive output) to confirm the potential indirect effects and trophic cascade shifts due to predator-induced habitat shifts.

Gradient in the “Seascape of Fear”

Seascape attributes can affect specific anti-predator behaviors and thereby induce habitat shifts (Brown & Kotler 2004, Heithaus et al. 2009). Foragers' time allocation (TiV – Habitat usability) and pecking rate (PRate – Vigilance), were significantly related to habitat amount and configuration and to the proximity to the mangrove-seagrass edge. In seagrass seascapes, the relative survival of epifaunal and infaunal organisms varies with seagrass patch size (Irlandi & Crawford 1997, Hovel & Lipcius 2001), proportional cover (Hovel 2003) and patch isolation (Micheli & Peterson 1999). When SAV habitat amount was scarce (25% habitat cover), invertivore and piscivore generalists concentrated their habitat use and harvesting rate toward the seaward edge of the seagrass seascape. In seascapes with scarce SAV cover, patches become smaller and more isolated with fragmentation (Fahrig 2003, Chapter 1). Predation rates on juvenile fish, bivalve and crustaceans have been reported as higher in smaller patches, presumably due to increased predation efficiency (Irlandi et al. 1995, Hovel et al. 2002, Laurel et al. 2003). When seascapes are composed of small patches, prey individuals may avoid long-distant movements to minimize predator encounters in open habitats without available refuge. In contrast, in seascapes with larger patches and higher patch connectivity, mobility may increase and prey may be more efficient at avoiding predators (Hovel & Regan 2008). This was evident in fragmented seascapes of scarce SAV cover where high tenacity (low vigilance) was observed (i.e., where both TiV and PRate were high), which indicates

reduced movement and less vigilance associated with long bouts of efficient feeding. Also, there were areas within the SAV seascape with low TiV but high PRate, indicating foraging areas with high predation risk and harvesting marginal rewards. According to foraging theory, the harvesting rate, in this case PRate, is expected to increase with risk and the quality and abundance of food resources (Brown & Kotler 2004). This was evident when the habitat was scarce and not fragmented, where invertivores of small prey (IvSm) showed high PRate and low TiV in areas closer to the mangrove defined as 'risky' habitats due the high occurrence of mesopredators. In addition, this PRate and TiV pattern may have been sustained in large seagrass patches adjacent to the mangrove edge which enhance the connectivity between both habitats (Nagelkerken et al. 2001, Pittman et al. 2004), and provide access to mangrove prop-roots used as refuge (Laegdsgaard & Johnson 2001).

At seascapes with intermediate-high SAV cover, both TiV and PRate were positively related to fragmentation. This shift in fragmentation preference was more prevalent with invertivore and piscivore generalists (IvPi). Seascape fragmentation characteristics such as total edge and patch density are higher between intermediate and high values of habitat amount (Pardini et al. 2010, Villard & Metzger 2014). Habitat edges of fragmented seascapes may provide a complementary habitat where food abundance and foraging cost of predation trade-offs are beneficial (Ries & Sisk 2004), and high edge densities within continuous SAV seascapes have higher probabilities of strengthening interactions (i.e., magnitude of edge effects increases with the abundance and adjacency of other edges –Porensky and Young 2012). The high allocation time and harvesting rate in fragmented seascapes may be associated with the characteristic of

patchy habitats that accumulate or increase epifaunal abundance and diversity along edges (Macreadie et al. 2010). In addition, fragmented SAV seascapes (when SAV cover > 50%) could benefit the trade-off between food and safety by providing gaps and microhabitats associated with a lower perceived risk of predation and lower cost of foraging (i.e., high marginal value of energy) (Lima & Dill 1990, Brown & Kotler 2004). Sand patches along the seagrass edges may provide a place for fish to forage in close proximity to shelter within seagrass patches (Anderson 2003, Smith et al. 2008). Using individual-based models (IBM), studies have predicted higher fitness of crustacean species in fragmented seascapes that benefited their ability to avoid mesopredators and access food without additional movement. This minimized fear (higher TiV and PRate) by invertivores and piscivores generalists in highly fragmented seascapes with intermediate amounts of SAV cover may support the high nektonic abundance observed in this type of seascape (Chapter 2 and 3).

Predation risk could vary by taxon due to species-specific anti-predator tactics (e.g., avoidance, detection, escape) (Lima & Dill 1990, Schmitz 2007, Heithaus et al. 2009). Here, the TiV and PRate of invertivores of small prey (IvSm) was influenced by distance-to-shore; while the foraging behavior of IvPi was more influenced by the degree of fragmentation of the seascape. Pinfish (*Lagodon rhomboides*) a dominant species in the IvSm group, have a small home range, and are considered a major prey item of mesopredators and larger piscivores (Jordan et al. 1997), making them highly susceptible to mesopredators near the mangrove shoreline where these predators patrol. Prey species with a narrow habitat domain (species microhabitat choices and the extent of spatial movement between chosen habitats) in the face of risk must tightly balance the costs of

continuous vigilance and movement against the likelihood of encountering the actively hunting predators (Preisser et al. 2007). Still, pinfish could also compete or become prey of sit-and-pursue (or wait) predator species abundant in continuous seascapes and highly complex patches (Horinouchi et al. 2013, Farina et al. 2014). Fragmented seascape may alleviate competition or predation risk by providing microhabitats and gaps that can broaden a forager diet. For example, pinfish's isotopic trophic niche width expansion has been observed in intermediated fragmented seascapes in Biscayne Bay (Santos et al. in prep). In a similar study in a Caribbean coral reef, Catano et al. (2014) observed a larger extent of diet diversity of herbivorous fish species in patch reefs with higher predator abundance and structural complexity (rugosity).

In contrast, IvPi such as the gray snapper (*Lutjanus griseus*), tend to have a broad home range due to their nocturnal search patterns along sparse and dense seagrasses (Luo et al. 2009, Hitt et al. 2011). Active foragers with a broad-domain can range across various microhabitats, and are better able to pursue prey or escape predators (Preisser et al. 2007). These ecological traits may reflect the high PRate and TiV of IvPi within fragmented seascapes independent of the proximity to riskier habitat (i.e., close to shore). In addition, these species feed primarily on penaeid shrimp, Cancroid crabs, and small demersal fish that are linked to an algal/seagrass diet (Kieckbusch et al. 2004) making fragmented seascapes highly efficient foraging grounds for IvPi.

In conclusion, this study demonstrated for the first time how predation risk of mobile, seagrass-associated fauna is related to the amount and configuration of SAV habitat in nearshore areas of Biscayne Bay. These results provide a mechanistic context behind the differences in community assemblages observed between fragmented and

continuous SAV seascapes, and changes in the nektonic abundance with respect to the spatial arrangement of marine habitats documented as part of this dissertation (Chapters 2 and 3). Seagrass management strategies and restoration projects, especially in coastal areas with high anthropogenic disturbance such as Biscayne Bay, should consider predator biomass and predation risk effects since these ecological components of the community play an important role in population and ecosystem resilience (Creel & Christianson 2008). Such information will provide valuable insights on the nursery value of seascapes (Grol et al. 2011). Lastly, improving our understanding of seascape-mediated species interactions should be a priority for ecosystem based management as this knowledge relates (both directly and indirectly) habitat structure to the dynamics of both commercially and recreationally important fisheries species. This is especially relevant for the economy of South Florida that is heavily dependent on its fisheries resources and where our research has shown direct links between water management practices, the structure of nearshore SAV seascapes, and associated fauna.

Table 5.1. Spatial pattern metrics used to quantify composition and configuration of SAV seascape patterns in Biscayne Bay. The configuration metrics were used to create a fragmentation index

Metric	Acronym	Category	Aspect	Description	Formula
Percentage of Landscape	PLAND	Composition	Area/Density	Percentage of the total landscape made up of the corresponding class	$PLAND = \frac{\sum_{j=1}^n a_{ij}^{(j)}}{A} (100)$
Patch Density*	PDENS	Configuration	Area/Density	Number of patches of a certain class divided by the total landscape area N patches/ha	$PD = \frac{n_i}{A}$
Mean Radius of Gyration*	GYRATE_MN	Configuration	Area/Density	Measure of patch extensiveness Larger patches will have higher GYRATE values	$GYRATE_MN = \frac{\sum_{j=1}^n \left[\sum_{r=1}^z (n_{ijr}^2) \right]}{n_i}$
Mean Patch Fractal Dimension*	FRAC_AM	Configuration	Shape	Measure of patch-shape complexity	$FRAC_AM = \sum_{j=1}^n \left[\frac{2 \ln(25 p_{ij})}{\ln a_{ij}} \left(\frac{a_{ij}}{\sum_{j=1}^n a_{ij}} \right) \right]$

* Configuration metrics included in the fragmentation index - $FragIndex = \sqrt[3]{(PD * FRAC_AM * 1 / Gyrate_MN)}$

Table 5.2. Percentage of deviance explained by the generalized linear models (GLMs) and the significance of the models based on Chi-square tests. Shrimp predation GLM was used to estimate the probability of relative predation. GLMs were performed to assess the relationships of mesopredators (MesoP), invertivores of small prey (IvSm) and invertivore/piscivore (IvPi) generalists' occurrence (estimated from the abundance data), allocation time (TiV – Time in View), and tenacity and vigilance (PRate – Pecking Rate). The deviance of the null and full model are presented, with significant deviance explained depicted in bold

Group	Model	Null Deviance	Model Deviance	Deviance Explained
Shrimp	Predation	296.0	228.4	22.8%
MesoP	Occurrence	91.5	81.7	10.7%
IvSm	Occurrence	115.9	90.9	21.6%
IvPi	Occurrence	165.5	145.9	11.9%
MesoP	TiV	1.7	1.6	4.9%
IvSm	TiV	59.6	43.1	27.7%
IvPi	TiV	45.5	37.3	18.1%
MesoP	Prate	0.0	0.0	2.7%
IvSm	Prate	8.3	5.6	32.4%
IvPi	Prate	0.1	0.1	12.8%

Table 5.3. Generalized linear models (GLMs) regression coefficients. GLMs variables included: distance-to-shore (D), habitat cover (HC), fragmentation (F), interaction terms ($X_1 \times X_2$), and second order polynomial term (X^2). Only the coefficients of the reduced models using a stepwise backward selection were included. GLMs were performed to estimate probability of predation of shrimp using tethering, and assess the relationships of mesopredators (MesoP), invertivores of small prey (IvSm) and invertivore/piscivore generalists occurrence (estimated from the abundance data), allocation time (TiV – Time in View), and tenacity and vigilance (Prate – Pecking Rate) using BRUVs. Significant coefficients in bold (red = $p < 0.05$; black = $p < 0.10$)

Group	Model	Method	D	HC	F	D x HC	D x F	HC x F	D ²	HC ²	F ²	Hrs
Shrimp	Predation	Tethering	4.0E-03		5.0E+00		-1.2E-01					-6.4E-01
MesoP	Ocurrence	BRUVs	-3.1E-02	-8.4E-02		3.0E-04			4.0E-05			
IvSm	Ocurrence	BRUVs	-1.9E-02	-3.2E-01	-3.8E+01		6.1E-01		7.4E-05	3.1E-03	5.0E+01	
IvPi	Ocurrence	BRUVs	1.6E-02	-7.9E-03	-1.2E+01	-2.6E-04		2.4E-01				
MesoP	TiV	BRUVs										
IvSm	TiV	BRUVs	2.8E-03	6.2E-03	1.4E+00			-3.9E-02				
IvPi	TiV	BRUVs	4.1E-03	2.9E-03	-2.5E+00	-7.0E-05		5.6E-02				
MesoP	Prate	BRUVs										
IvSm	Prate	BRUVs	-3.6E-03	-5.2E-02	-2.7E+00	5.4E-05	7.2E-03	4.1E-02		4.3E-04		
IvPi	Prate	BRUVs	1.5E-05	-2.6E-03	-1.8E-01			4.0E-03		2.1E-05		

Figure 5.1. Illustration of the a) study area within Biscayne Bay, b) SAV seascapes map with the 100 x 500 m plots randomly located along the shoreline, and c) the locations of the four BRUVs (yellow dots) and tethering (yellow x) replicates that were randomly placed within distance-to-shore zones

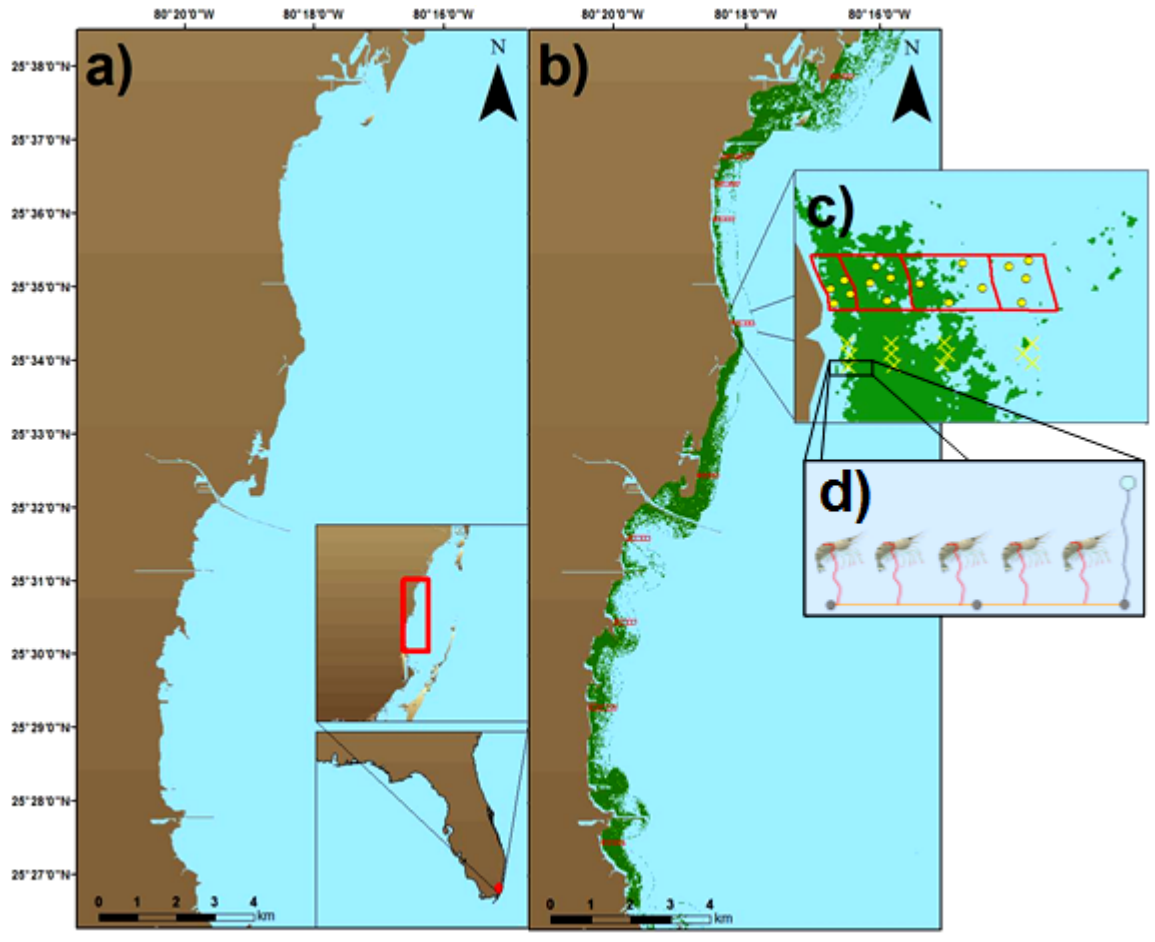
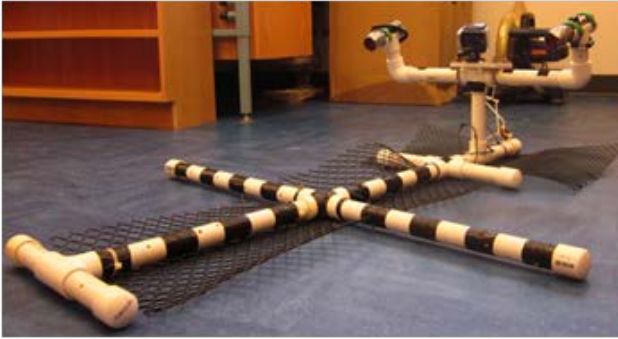


Figure 5.2. Illustration of the a) BRUVs design and b) sample video frames from one of the BRUVs. Video frames illustrate the presence of a pinfish (*Lagodon rhomboides*) and gray snapper (*Lutjanus griseus*), and lemon shark (*Negraprion brevirostris*). BRUV design consisted on a PVC frame holding a GoPro HD camera in one opposite of the frame, recording predator behaviors around a bait plastic bag. Horizontal arms were added for stabilization and size estimation. Each frame has two underwater flashlights with a red filter

a) BRUV frame design



b) BRUVs video sample

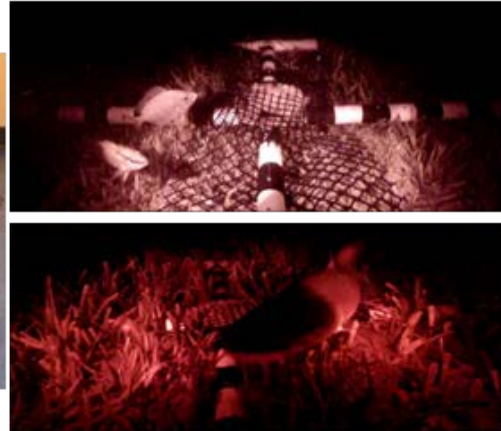


Figure 5.3. Mean (black dot) and standard error (bars) of the abundance (MaxN – max # of individuals*minutes⁻¹) per site and for each functional group: invertivore/piscivore generalists (IvPi), invertivores of small prey (IvSm), mesopredators (MesoP). Sites ordered left to right by increasing magnitude of fragmentation

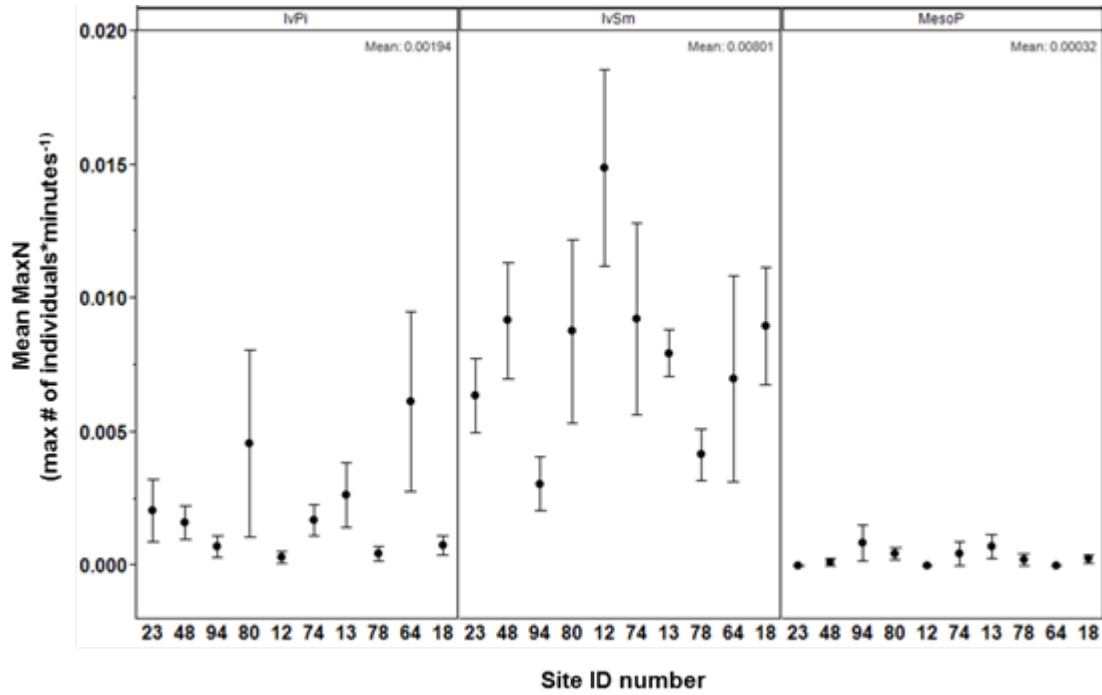


Figure 5.4. Probability of shrimp predation with respect to distance-to-shore, seascape fragmentation, and soaking time of the tethered lines. Blue and red areas illustrate low probability (predation $p < 0.5$) and high probability (predation $p > 0.5$) of predation, respectively. Each panel illustrates the probability of predation based on the soaking time: 2, 3, and 4 hours

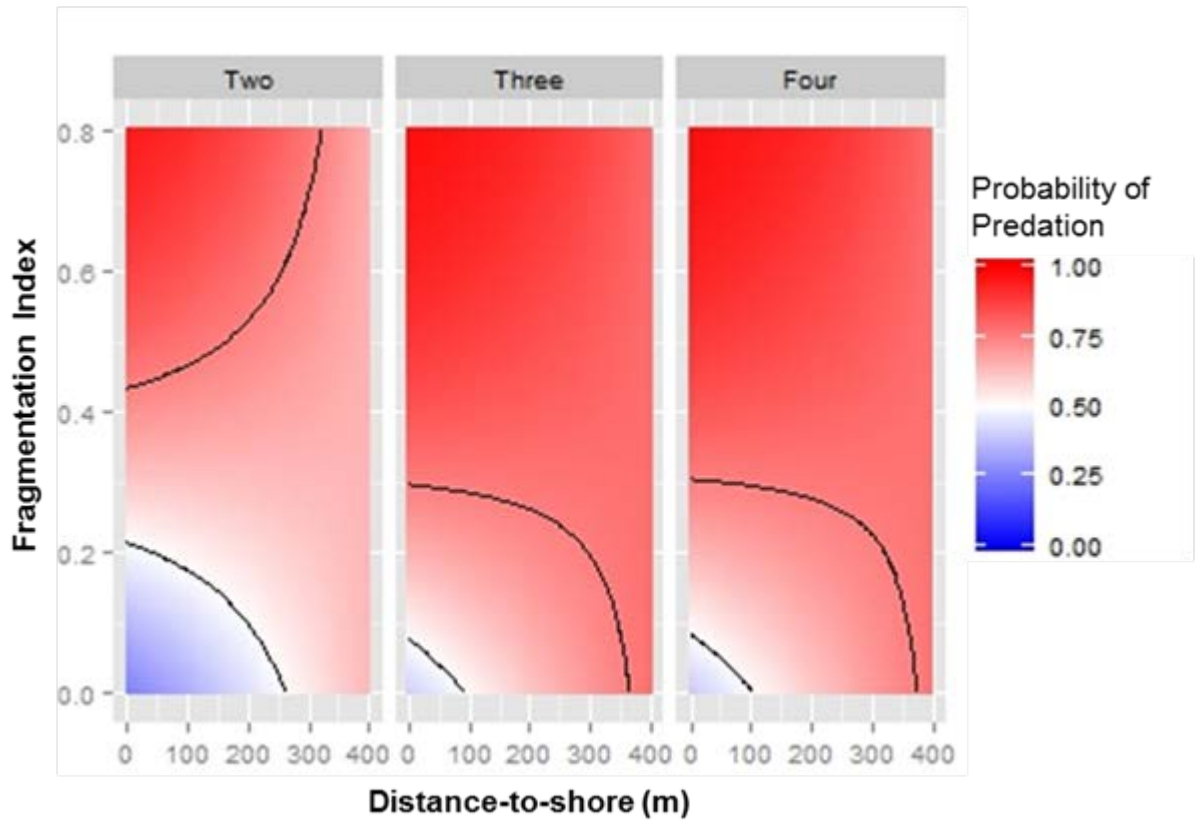


Figure 5.5. Probability of occurrence of a) mesopredators (MesopP), b) invertivores of small prey (IvSm), and b) invertivore/piscivore generalists. The probability is illustrated within the fragmentation (habitat cover for MesopP) and distance-to-shore. Blue and red areas illustrate low probability (predation $p < 0.5$) and high probability (predation $p > 0.5$) of occurrence, respectively. IvSm (b) and IvPi (b) were made using 50 % as habitat cover

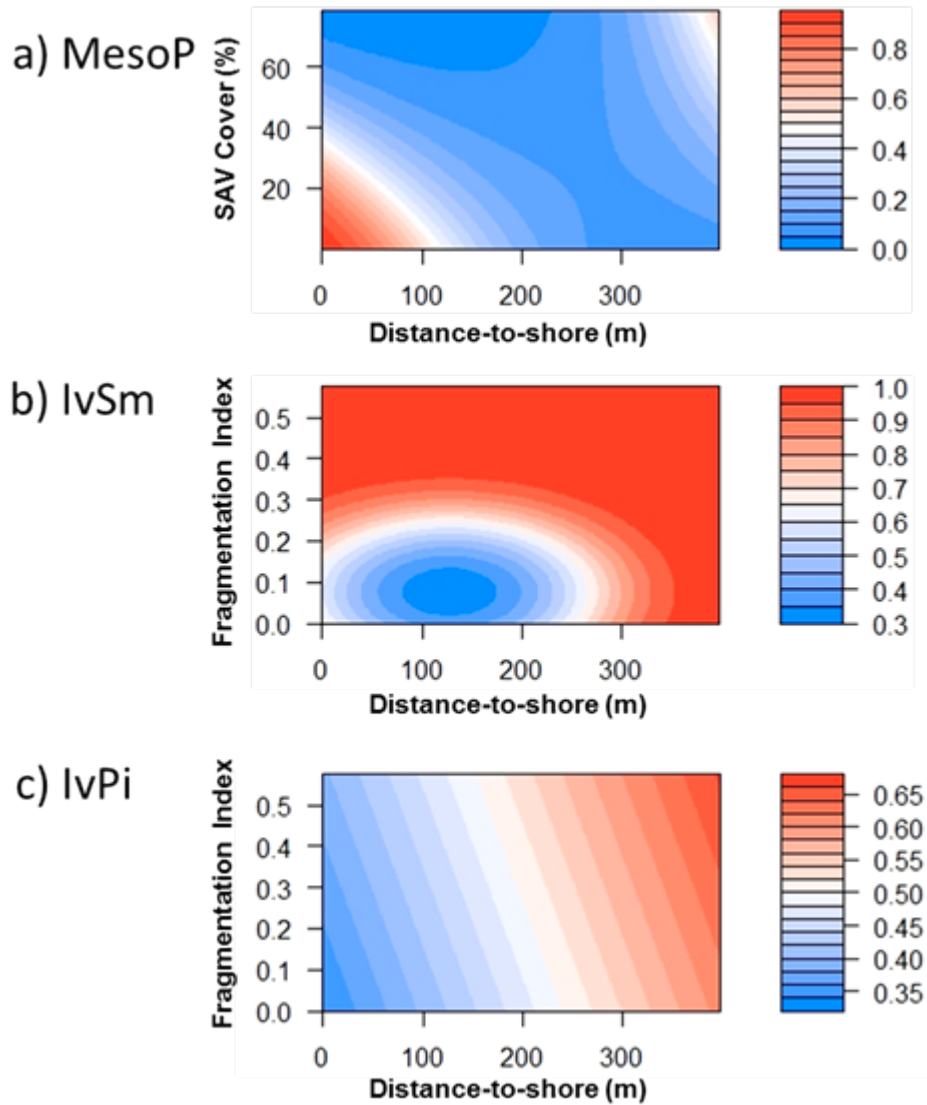


Figure 5.6. Time in view (TiV) and pecking rate (PRate) for Invertivores of small prey (IvSm) in relation to fragmentation levels and distance-to-shore for habitats with different SAV cover values. Each row represents the TiV and PRate patterns when SAV cover was scarce (25%, a and d), intermediate (50%, b and e), and abundant (80%, c and f). Blue and red areas illustrate low and high values, respectively. Bar is in a relative scale

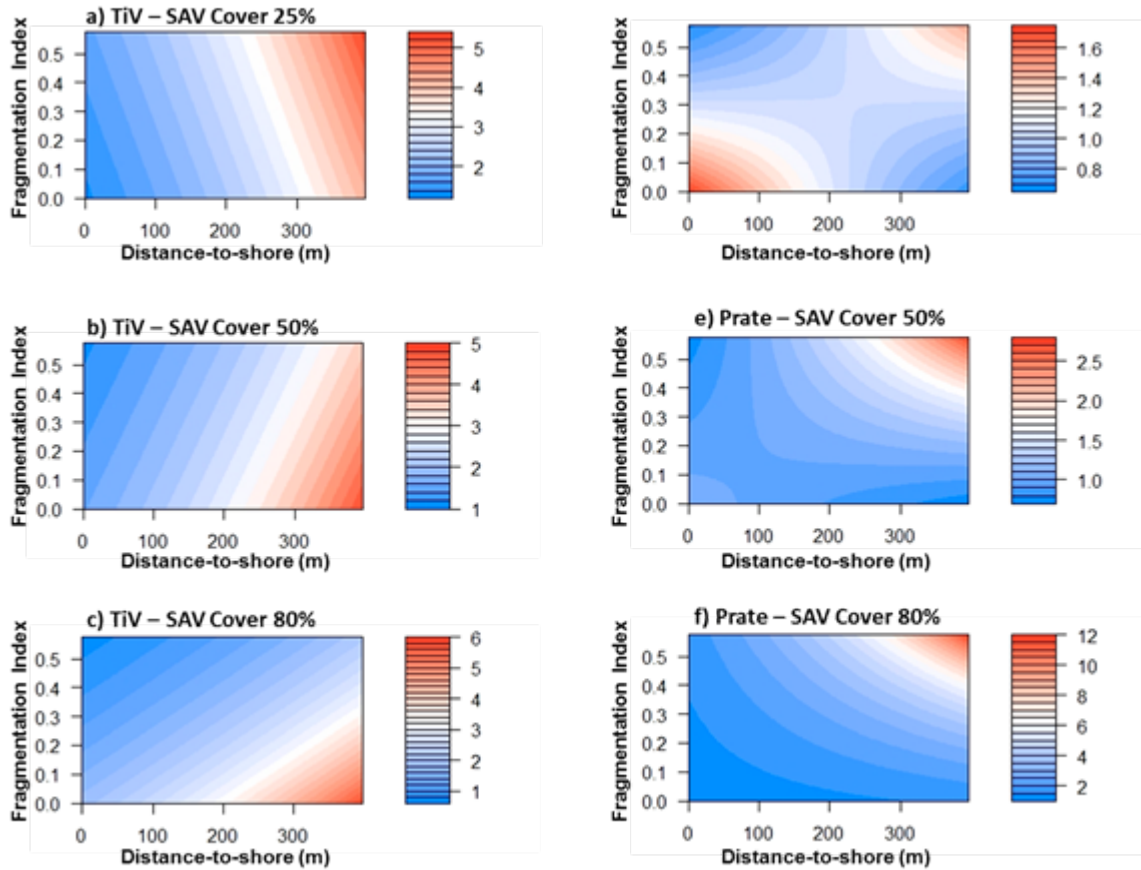
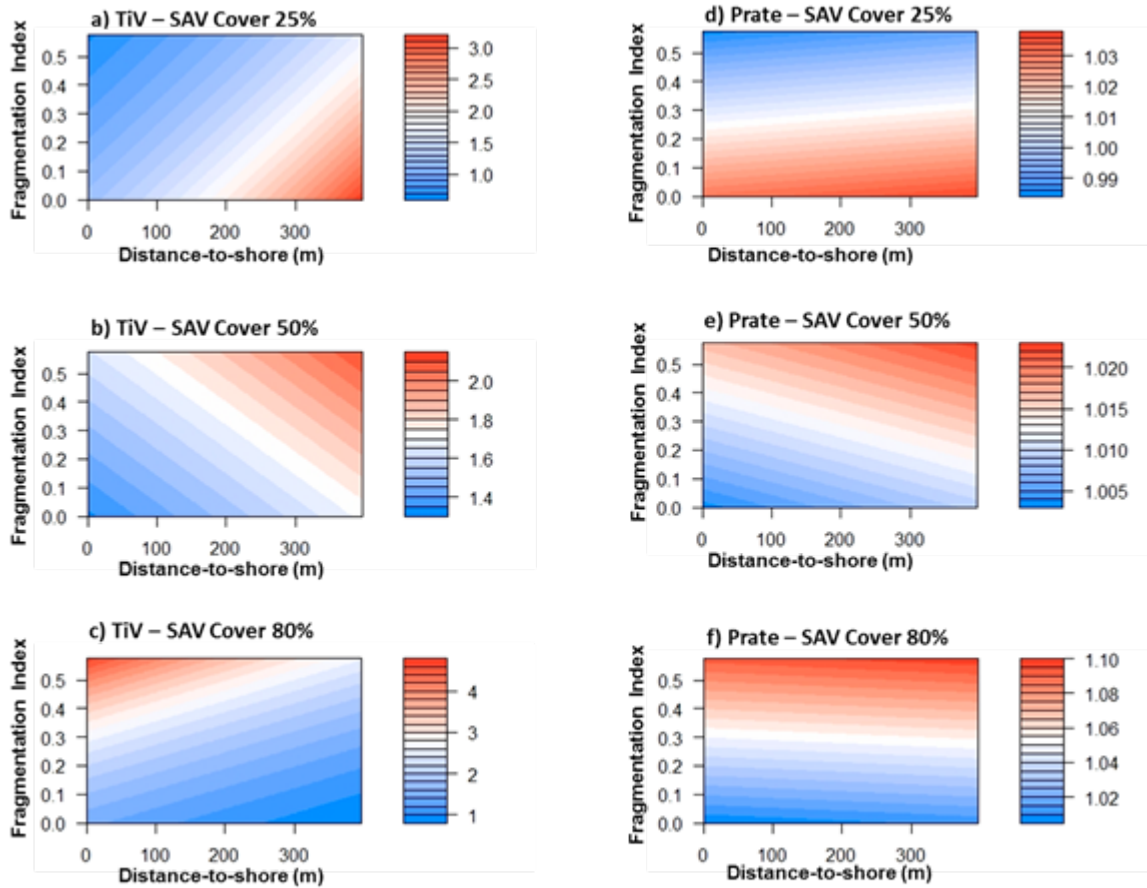


Figure 5.7. Time in view (TiV) and pecking rate (PRate) for Invertivore/Piscivore generalists (IvPi) in relation to fragmentation levels (F) and distance-to-shore (D) for habitats with different SAV cover values. Each row represents the TiV and PRate patterns when SAV cover was scarce (25%, a and d), intermediate (50%, b and e), and abundant (80%, c and f). Blue and red areas illustrate low and high values, respectively. Bar is in a relative scale



Chapter 6: Conclusions

Key Findings

The results of this dissertation showed the value of considering seascape-level habitat characteristics to evaluate the impacts of freshwater management decisions on the spatial patterning of SAV seascapes and potential cascading effects on associated fauna.

Specifically, my research has shown that:

- 1) the SAV seascape patterns in Biscayne Bay have been significantly influenced by changes in salinity caused by water management practices, resulting in more fragmented habitats over the past 70 years;
- 2) spatial SAV seascape patterns are related to the abundance, diversity, and distribution of key associated faunal taxa;
- 3) most faunal species studied have a non-linear response to habitat fragmentation, and intermediate levels of fragmentation under conditions of high SAV habitat amount can actually enhance the abundance of fish and crustaceans; and
- 4) SAV seascape structure influences both direct predation and predation risk, thus highlighting a mechanism that can explain, at least in part, the influence of seascape structure on the dynamics of SAV-associated faunal assemblages.

Spatio-temporal Dynamics of SAV Seascapes

The spatio-temporal dynamics of the amount (cover) and pattern (fragmentation) of submerged aquatic vegetation (SAV) seascapes in Biscayne Bay were assessed with a unique data-set of archived aerial images (1938-2009) to quantify changes in SAV seascapes in relation to the inflow of fresh water from water management canals. By using spatially explicit approaches to measure change in the amount and configuration of seascapes, including the development of an innovative fragmentation index, I showed significant variability in SAV cover (habitat amount) and spatial configuration (fragmentation) over a 71-year time period. Spatial variability (i.e., dynamics gains and losses in SAV amount) of SAV seascapes concentrated mostly in areas disturbed by freshwater pulses (close to man-made freshwater canals and close to shore). Even though the net loss in SAV cover was relatively low, the spatial configuration of the SAV seascapes shifted significantly from continuous (i.e., seascape dominated by few large patches) to fragmented seascapes (i.e., many small patches, perforated SAV meadows). These conflicting patterns (i.e., small change in SAV cover but significant fragmentation) highlighted the importance of incorporating both metrics of habitat amount and configuration in assessments of SAV habitats. This work showed, for the first time, that changes in watershed hydrology and freshwater deliveries into coastal bays can have significant influences on the spatial patterning of vegetated seascapes. This is important because these seascapes are associated with provisioning of a number of key ecological services to South Florida, including nutrient and C sequestration, sediment stabilization, and serve as essential habitat to important fisheries species.

Limitation and future work

Even though direct associations between the temporal instability of SAV seascapes and freshwater canals were established, it is still necessary to identify and understand possible mechanisms behind these SAV seascape spatial transformations. Recent assessments of seagrass and macroalgae composition and abundance, water quality and quantification of daily discharges from canals could be combined with a SAV seascape approach to understand how changes in macrophyte composition and water quality (e.g., nutrients, phytoplankton blooms) and physical properties (e.g., salinity, temperature, turbidity) translate into distinct spatial properties of SAV seascapes. In addition, this approach could help in the developing of species size-structured models to predict the persistence of SAV seascapes under different restoration, disturbance, or climate-change scenarios.

Faunal Responses to SAV Seascape Patterns

By quantifying spatial patterning of the seascape using remote sensing and GIS, and then sampling marine fauna using nocturnal seine sampling conducted within fragmented and continuous seascape habitats, I showed that faunal assemblages in fragmented seascapes differed significantly from those in continuous seascapes. Fragmented seascapes supported: 1) a more diverse community, 2) higher probability of occurrence and abundance of Gobiidae species and crustaceans, and 3) larger generalist/omnivore individuals. These results demonstrated clearly that seascape fragmentation can influence marine faunal communities through species-specific and functional-group responses to the structure of SAV seascapes. Because the response of

organisms to the spatial structure of the habitats they occupy may be complex and non-linear, the data were further explored using a combination of non-linear models (GAMs), GIS, and spatial simulation modeling to identify habitat-response thresholds to habitat loss and fragmentation. The amount of SAV habitat and its configuration, as well as the interaction of these two seascape attributes with the relative location of sites across the seascape (i.e., distance-to-shore/mangroves) were the most influential predictors of faunal abundance. The majority of the examined species showed abundance hot spots (peak in abundance) at intermediate levels of fragmentation when the SAV habitat was abundant.

Both organism-habitat relationship studies performed in my dissertation showed how the fragmentation of seascapes can actually increase fish and shrimp abundance, depending on the amount of habitat available. The positive effects of fragmentation on species diversity was attributed to: 1) increases in the co-existence of early and late-successional stages; 2) increases in the co-existence of generalist and specialist species; 3) high abundance of transient species; and 4) expansion of niche space due to the increase in variety and availability of microhabitat patches. The higher abundance of foragers associated with fragmented seascapes, especially in seascapes with intermediate levels of fragmentation and abundant habitat, was interpreted to be associated to: 1) higher food availability at habitat edges; 2) increased foraging efficiency within patchy environments; 3) higher mobility along edges; and 4) increased connectivity between patches. Moreover, the information provided in these studies (Chapter 3 and 4) suggests that the effectiveness of management and restoration strategies of essential fish habitats would depend on the SAV habitat amount within the seascape. For example, management strategies for pink shrimp should prioritize the creation or maintenance of a SAV species

composition under mesohaline conditions when habitat amount is low but highly fragmented.

Limitations and future work

It is important to mention that the organism-habitat studies in this dissertation were performed only during one (wet) season. The faunal relationships with seascape level habitat properties could vary due to yearly and seasonal ontogenetic and recruitment cycles influenced by factors beyond the seascape spatial scale (Hovel et al. 2002, Healey & Hovel 2004, Hensgen et al. 2014). Therefore, the significance, direction, and magnitude of the fauna-seascape relationships observed in this dissertation should also be explored across time to assess the cyclical nature of organism-habitat relationships which may further influence the recruitment, abundance, and persistence of marine populations. Incorporating such spatiotemporal fauna-seascape relationships with models that predict SAV seascape transformation based on different environmental drivers may provide: 1) the information needed to support ecosystem-based management strategies; and 2) a more accurate quantification or prediction of ecosystem phase shifts that could either be caused by water management practices (e.g., CERP) or factors attributed to climate change (e.g., hurricane frequency and strength, increase in wet-wet or dry-dry years).

Ecological Mechanisms Behind Responses

While the bulk of this dissertation focused on examining organism-habitat relationships within the context of seascape structure, I also explored the potential role of predation as one of the mechanisms/processes that may mediate the fundamental response of SAV-associated fauna to seascape structure. Using baited remote underwater

video surveys (BRUVS) and tethering experiments, I showed that the distribution and foraging activity of selected fish and crustacean species were influenced by predation risk effects that were, in turn, influenced by seascape properties. This suggests that predation could be one of the main mechanisms behind the faunal responses to seascape patterns observed in Biscayne Bay.

Species distribution and habitat preferences in nearshore areas of Biscayne Bay are significantly influenced by predation risk effects that covaried with seascape properties. Habitat shifts (i.e., changes in how and which habitats are used) of foragers were associated with higher occurrence of larger predators such as juvenile lemon and nurse sharks and barracuda. In turn, these habitat shifts overlapped with the seascapes that encountered a relative higher predation rate on small prey, suggesting that indirect effects and trophic cascades are possible due to predation risk effects, but that these interactions are also modulated by SAV seascape patterns and predator-prey interactions. In addition, these patterns were also supported by changes in anti-predator behavior and food-safety tradeoffs, where peaks of time allocation and vigilance of foragers depended on the amount of SAV habitat and the location relative to the distribution of mesopredators.

Based on my results, future research should be conducted to fully document seascape-mediated, indirect consumer effects since these are the primary drivers of coastal benthic ecosystem structure and function (Valentine et al. 2007). My predation risk study (Chapter 5) suggested that indirect effects on species interactions could be modulated by the spatial patterning of seagrass habitats within the seascape. Therefore, this shows the relevance of understanding seascape-mediated consumer and producer

effects. Moreover, disturbances associated with climate change and anthropogenic drivers that cause significant habitat loss and fragmentation have the potential to affect species interactions, which could yield undesired impacts on the resilience of coastal ecosystems (Connell et al. 2011).

Limitations and future work

The BRUVs and tethering experiments quantified changes in foraging behaviour based on seascape characteristics and predation risk; however, my study did not consider the ecological and biological implications of such behavioral changes. Mesocosm and field manipulative experiments could be combined with organism tracking analyses to assess predator-induced changes in fitness (e.g., growth, fecundity, reproductive output), and confirm the existence of indirect effects and trophic cascades caused by seascape-mediated predation risk effects. Very few studies have used tracking of organisms to link ecological activities with respect to seascape spatial properties. Acoustic tracking and mark-and-recapture techniques could be employed to assess changes in fitness due to home range expansion or shrinkage, and habitat shifts of marine species in response to habitat loss and fragmentation. Their integration with other analysis such as stable isotope and gut-content, and prey distribution analysis could also provide the necessary information needed to understand how larger predators relate to the spatial patterning of marine habitats and their role in the resilience of marine communities in seascapes facing habitat loss and fragmentation.

Emerging Priorities and Research Questions

Seascape ecology is a relatively recent and growing discipline adapted from landscape ecology. As an emerging field, there are still knowledge gaps that need to be explored further. Based on my dissertation experience, I strongly believe that the development of seascape ecology concepts such as the relative and interrelated ecological effects of habitat loss and fragmentation, and mechanistic and predictive ecological models will go in hand with the advances in remote sensing and other mapping techniques. The application of new hyperspectral and drone (i.e., unmanned aerial vehicle) technologies could improve the quantification of seascape dynamics of habitat patches using fine-resolution class descriptors. By improving the mapping precision of habitat-forming species, we can expect to advance our understanding in the following emergent research areas:

- a) stable and unstable states of SAV seascapes based on specific habitat classes (i.e., *Thalassia* patches vs *Halodule* patches);
- b) relative and interrelated ecological effects of the spatial properties of optimal, suboptimal, and matrix habitats; and
- c) edge effects based on supplementary, complementary, and interactive processes between different habitat patches.

In addition, as suggested by Wedding et al. (2011) there remains a need to develop robust spatial pattern metrics that consider the physical properties of marine environments. For example, in my dissertation I developed a fragmentation index based on metrics that have been tested on seagrass habitats. However, it is necessary to create fragmentation metrics that could be used across different seascapes, locations, and habitat

types to provide standardization when comparing the effects of habitat loss and fragmentation occurring in different ecosystems. One way to address this is to use seascape maps from archived aerial and satellite imagery in combination with neutral and fractal maps. This could provide the information necessary to develop a fragmentation index based on theoretical maxima and minima values tested with empirical data.

The functions of nursery habitat, habitat selection, and faunal recruitment are other research areas that could be explored within a seascape approach. Many marine species undergo ontogenic habitat shifts where different life history stages depend on specific type of habitats. Even though there is abundant empirical data illustrating the habitat preferences at different life stages, there still a lack of knowledge about how the spatial arrangement of habitats influence the functional connectivity among habitats that are part of specific ontogenic migrations. Using a seascape approach, we can determine whether the recruitment of target species is dependent on the amount and/or spatial configuration of benthic habitats. Conversely, this approach could inform whether recruitment is influenced by drivers operating below (e.g., within-patch characteristics) or above (e.g., geographical attributes) the seascape level. For example, the simulation exercise that I performed for juvenile pink shrimp here showed that the abundance of this species at this particular life stage benefited more from seascape-level characteristics rather than fine-scale habitat characteristics. This type of work could be expanded with laboratory and field experiments to determine the mechanisms behind the habitat selection processes operating at different spatial scales and ontogenic stages.

Agent-based models (ABM) could be developed as a tool to test and develop hypothesis about mechanisms that drive faunal responses to seascape characteristics.

Empirical data from laboratory and field experiments could be used to define agent rules that take into consideration faunal responses such as predator avoidance, foraging and movement. Seascape agent-based models have been applied only to crustacean in seagrass and salt-marsh habitats (Haas et al. 2004, Hovel & Reagan 2008) with satisfactory results. Therefore, ABM could be employed to formulate questions that consider the interrelation of habitat amount and configuration, and edge-effects using a patch-mosaic perspective. For instance, under different trophic system scenarios, ABMs could help explore questions such as:

- a) What is the habitat amount that supports the largest population of a target species?
- b) How species persistence is influenced by habitat amount and configuration?
- c) When are edge effects positive, negative, or neutral?
- d) Which seascape characteristics provide the most efficient connectivity between habitats?

Seascape ecology concepts can also be employed to project and understand ecosystem phase shifts and ecological effects associated with climate change disturbances. The effects of climate-change associated disturbances such as the increase in storm frequency and strength, and precipitation extremes will likely manifest themselves at broad-spatial scales; therefore, making the study of seascape dynamics and fauna-seascape relationships critical for the assessment and mitigation of climate-change effects. In addition, increasing the accuracy of SAV seascape maps and the robustness of fauna-seascape relationships and their associated mechanisms could provide for the quantification of carbon sequestration rates under different seascape scenarios, and

productivity estimates of ecosystems under different forecasted climate scenarios. Therefore, progress in these emergent research areas in seascape ecology will be indispensable for the development of robust ecosystem-based management fishery strategies, and the projection and mitigation of climate change effects on the many services provided by SAV ecosystems.

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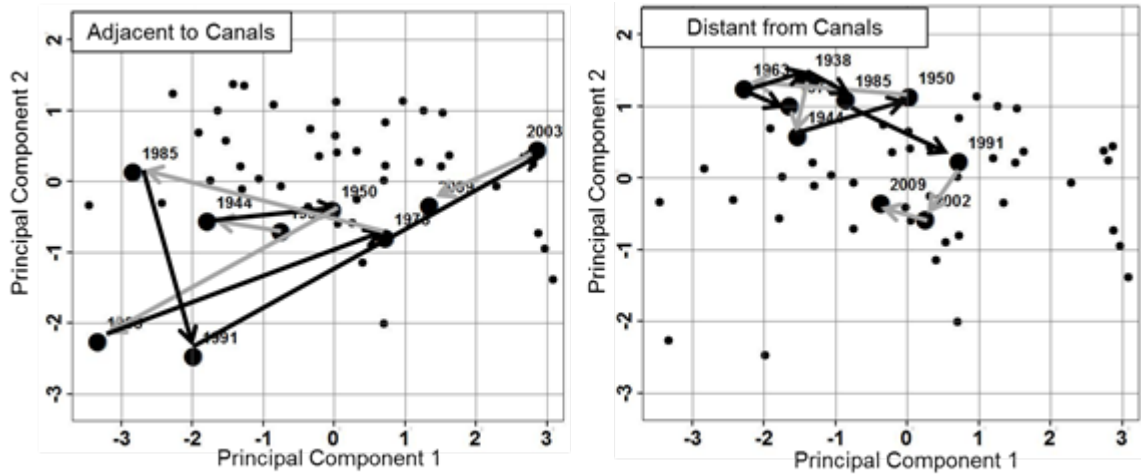
APPENDICES

Appendix A – Chapter 2 Supplementary Material

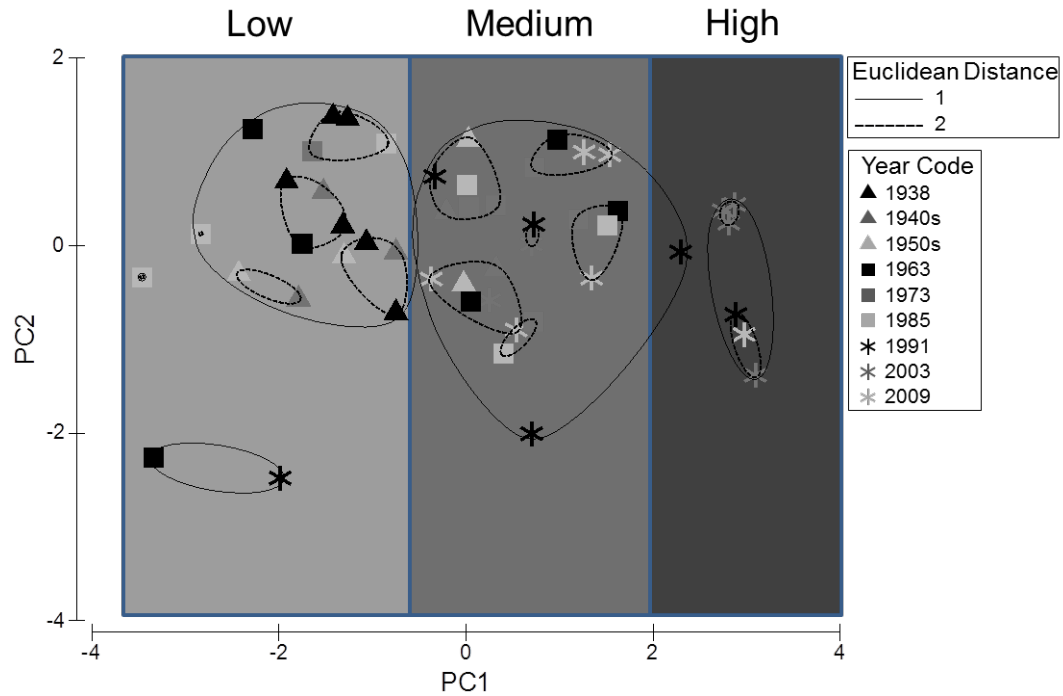
Appendix A1 Description of the aerial photographs obtained for each year. All aerial photographs were obtained during the dry season of Biscayne Bay (December to May). SC – Snapper Creek, CK – Chicken Key, BL – Black Point Lagoon, BP – Black Point, CP – Convoy Point, TP – Turkey Point. The scale and pixel size are described under photo resolution. B/W – Black and White, Color – RGB). FDOT – Florida Department of Transportation, UF – University of Florida, FIU – Florida International University

Year	Date/Season	Site Availability	Photo Resolution	Format Color	Source
1938	12/20 Dry Season	SC, CK, BL, BP, CP, TP	1:44,150 1m pixel	B/W	FDOT, FIU GIS Center(Peter Harlem)
1944	3/27 Dry Season	CK, BL, BP, CP, TP	1:44,100 1m pixel	B/W	UF Map & Digital Imagery Library
1952	3/16 Dry Season	SC, BP, CP	1:27,000 1m pixel	B/W	UF Map & Digital Imagery Library
1953	3/27 Dry Season	CK, BL	1:27,000 1m pixel	B/W	UF Map & Digital Imagery Library
1963	12/27 Dry Season	SC, CK, BL, BP, CP, TP	1:20,000 1m pixel	B/W	UF Map & Digital Imagery Library
1973	12/11 Dry Season	SC, CK, BL, BP, CP, TP	1:24,000 1m pixel	B/W	FDOT Surveying & Mapping Office
1985	02 to 04 Dry Season	SC, CK, BL, BP, CP, TP	1:24,000 1m pixel	B/W	FDOT Surveying & Mapping Office
1991	03/11 Dry Season	SC, CK, BL, BP, CP, TP	1:25,000 0.35m pixel	B/W	FDOT Surveying & Mapping Office
2003	Dry Season	SC, CK, BL, BP, CP, TP	1:32,400 0.35m pixel	B/W	FDOT Surveying & Mapping Office
2009	01/09 Dry Season	SC, CK, BL, BP, CP, TP	1:24,000 0.30m pixel	Orthophoto color	FDOT Surveying & Mapping Office

Appendix A2 Principal component analysis (PCA) plot overlaid with a vector analysis. The black and grey arrows indicate respectively the direction of SAV seascapes fragmentation and defragmentation, and the length represents the strength of these changes relative to years between each point



Appendix A3 Principal component analysis sites classified based on the seascape spatial metrics. Colors and shapes are used to identify the sites based on decade of survey. The black and dotted lines encircle the sites grouped together by a cluster analysis based on the Euclidean dissimilarity matrix. Based on this cluster analysis, the PCA biplot was divided in three zones indicating low (grey), medium (dark grey), and high (black) fragmentation levels



Appendix B – Chapter 3 Supplementary Material

Appendix B1. Peer-reviewed scientific publications and reports used to obtain allometric relationship to estimate biomass.

Species	Reference	Note
<i>Abudefduf saxatilis</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-215	
<i>Cantherhines macrocerus</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-216	
<i>Caranx ruber</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-217	
<i>Haemulon parra</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-218	
<i>Haemulon plumieri</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-219	
<i>Lagodon rhomboides</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-220	
<i>Lutjanus griseus</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-221	
<i>Sphyraena barracuda</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS SEFC-222	
<i>Euryoanopeus abbreviatus</i>	McKinney RA, Glatt SM, McWilliams SR (2004) Allometric length-weight relationship for benthic prey of aquatic wildlife in coastal marine habitats	
<i>Panopeus sp.</i>	McKinney RA, Glatt SM, McWilliams SR (2004) Allometric length-weight relationship for benthic prey of aquatic wildlife in coastal marine habitats	
<i>Farfantepenaeus duorarum</i>	Hutchins DL, Chamberlain GW, Parker JC (1979) Length-Weight relations for several species of Panaeid shrimp cultured in Ponds near Corpus Christi, Texas. Proceedings World Mariculture Society	
<i>Cyprinodon variegatus</i>	Liehr GA, Browder JA, Jackson TL, Petteway LH (in Review) Exploring conditions of epifaunal fish species along Biscayne Bay shoreline in relation to salinity using length-weight relationship (LWR) and the relative condition factor Kn.	
<i>Lucania parva</i>	Liehr GA, Browder JA, Jackson TL, Petteway LH (in Review) Exploring conditions of epifaunal fish species along Biscayne Bay shoreline in relation to salinity using length-weight relationship (LWR) and the relative condition factor Kn.	
<i>Microgobius gulosus</i>	Liehr GA, Browder JA, Jackson TL, Petteway LH (in Review) Exploring conditions of epifaunal fish species along Biscayne Bay shoreline in relation to salinity using length-weight relationship (LWR) and the relative condition factor Kn.	
<i>Opsanus beta</i>	Fine ML (1975) Sexual dimorphism of the growth rate of the swimbladder of the toadfish <i>Opsanus tau</i>	Values based on <i>Opsanus tau</i>
<i>Eucinostomus argenteus</i>	Vega-Cendejas ME, de Santillana MH, Arceo D (2012) Length-weight for selected fish species from a coastal lagoon influenced by freshwater seeps: Yucatan peninsula, Mexico	
<i>Eucinostomus gula</i>	Vega-Cendejas ME, de Santillana MH, Arceo D (2012) Length-weight for selected fish species from a coastal lagoon influenced by freshwater seeps: Yucatan peninsula, Mexico	
<i>Floridichthys carpio</i>	Liehr GA, Browder JA, Jackson TL, Petteway LH (in Review) Exploring conditions of epifaunal fish species along Biscayne Bay shoreline in relation to salinity using length-weight relationship (LWR) and the relative condition factor Kn.	

Species	Reference	Note
<i>Syngnathidae</i>	Liehr GA, Browder JA, Jackson TL, Petteway LH (in Review) Exploring conditions of epifaunal fish species along Biscayne Bay shoreline in relation to salinity using length-weight relationship (LWR) and the relative condition factor Kn.	Values based on <i>Syngnathus scovelli</i>
<i>Calamus arctifrons</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Caranx crysos</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Chilomycterus sp.</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Cynoscion nebulosus</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Cynoscion sp.</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Haemulon album</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Haemulon chrysargyreum</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Haemulon flavolineatum</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Haemulon melanurum</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Harengula humeralis</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Lutjanus apodus</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Mugil cephalus</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Orthopristis crysoptera</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Selar crumenophthalmus</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Atherinomorus stipes</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
SIT_ARE	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Sphaeroides testudineus</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Strongylura notata</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Synodus foetens</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Synodus sp.</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Trachinotus sp.</i>	Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication. www.Fishbase.org	Values based on publications on FishBase.org
<i>Callinectes sp.</i>	Atar HH, Secer S (2003) Width/Length relationship of the blue crab (<i>Callinectes sapidus</i> Rathbun 1896) population living in Beymelek Lagoon Lake. Turk J Vet Anim Sci 27	
Caridea	Anger K, Moreira GS (1998) Morphometric and reproductive traits of tropical Caridean shrimps. J Crust Bio 18	

Species	Reference	Note
<i>Haemulon sciurus</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC-215	Value from averaged family values in publication
<i>Hypleurochilus geminatus</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC-216	Value from averaged family values in publication
<i>Lophogobius cyprinoides</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC-217	Value from averaged family values in publication
<i>Gobiosoma robustum</i>	Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC-218	Value from averaged family values in publication

Appendix C – Chapter 5 Supplementary Material

Appendix C1 Percentage of the total the abundance (MaxN), pecking rate (PRate) and time in view (TiV) observed by species. A total of 26 species were identified. The species name are sort in decreasing order of percentage abundance observed.

Species	% of MaxN Total	% of Prate Total	% of TiV Total
<i>Lagodon rhomboides</i>	75.21%	96.57%	79.24%
<i>Callinectes sapidus</i>	6.72%	2.41%	9.08%
<i>Lucania parva</i>	5.18%	0.01%	1.27%
<i>Farfantepenaeus duorarum</i>	4.22%	0.00%	1.16%
<i>Eucinostomus argenteus</i>	1.77%	0.04%	2.64%
<i>Lutjanus griseus</i>	1.38%	0.20%	1.10%
<i>Opsanus beta</i>	1.33%	0.24%	3.04%
<i>Sphyraena barracuda</i>	1.01%	0.00%	0.37%
<i>Unkown spp</i>	0.69%	0.00%	0.49%
<i>Nudibranchia</i>	0.40%	0.00%	0.04%
<i>Negaprion brevirostris</i>	0.38%	0.00%	0.04%
<i>Orthopristis crysoptera</i>	0.23%	0.50%	1.37%
<i>Elops saura</i>	0.20%	0.00%	0.01%
<i>Ginglymostoma cirratum</i>	0.20%	0.01%	0.01%
<i>Strongylura notata</i>	0.18%	0.00%	0.01%
<i>Atherinomorus stipes</i>	0.13%	0.00%	0.01%
<i>Rachycentron canadum</i>	0.13%	0.00%	0.01%
<i>Floridichthys carpio</i>	0.08%	0.00%	0.01%
<i>Gobiosoma robustum</i>	0.08%	0.00%	0.00%
<i>Libinia sp.</i>	0.07%	0.01%	0.00%
<i>Albula vulpes</i>	0.07%	0.00%	0.01%
<i>Calamus arctifrons</i>	0.07%	0.00%	0.00%
<i>Anthozoa</i>	0.07%	0.00%	0.03%
<i>Syngnathidae</i>	0.07%	0.01%	0.03%
<i>Pogonias cromis</i>	0.06%	0.00%	0.00%
<i>Caranx latus</i>	0.06%	0.00%	0.00%